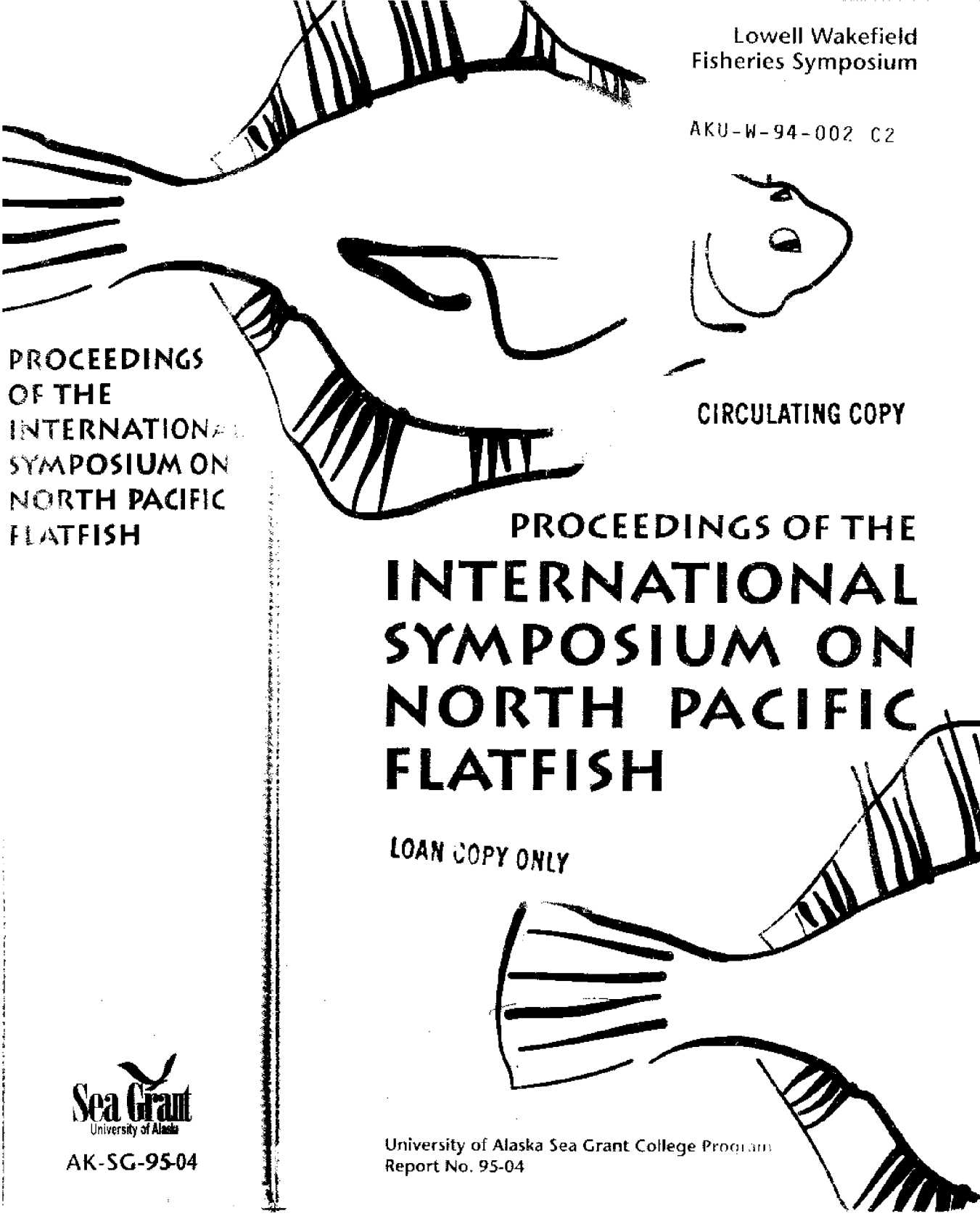


Lowell Wakefield
Fisheries Symposium

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PROCEEDINGS
OF THE
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SYMPOSIUM ON
NORTH PACIFIC
FLATFISH

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PROCEEDINGS OF THE
**INTERNATIONAL
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**Sea Grant**
University of Alaska

AK-SG-95-04

University of Alaska Sea Grant College Program
Report No. 95-04

Lowell Wakefield Fisheries Symposium

PROCEEDINGS OF THE
**INTERNATIONAL
SYMPOSIUM ON
NORTH PACIFIC
FLATFISH**



October 26-28, 1994
Anchorage, Alaska



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About the Symposium

The International Symposium on North Pacific Flatfish is the twelfth Lowell Wakefield symposium held since 1982. The program concept was submitted by A.J. Paul in early 1991, and the meeting was held October 26-28, 1994, in Anchorage, Alaska. The symposium was organized and coordinated by Brenda Baxter, Alaska Sea Grant College Program, with the assistance of the program committee. Committee members are: Barry Bracken, Alaska Department of Fish and Game; Robert McConnaughey, National Marine Fisheries Service; A.J. Paul, Institute of Marine Science, University of Alaska Fairbanks; Hank Pennington, University of Alaska Marine Advisory Program; Robert Trumble, International Pacific Halibut Commission; and David B. Witherell, North Pacific Fishery Management Council.

Symposium sponsors are: Alaska Department of Fish and Game; International Pacific Halibut Commission; National Marine Fisheries Service; North Pacific Fishery Management Council; and Alaska Sea Grant College Program, University of Alaska Fairbanks.

Executive Summary

R.L. Smith

Institute of Marine Science and Department of Biology and Wildlife
University of Alaska Fairbanks, Fairbanks, Alaska, USA

The International Symposium on North Pacific Flatfish was held in Anchorage, Alaska, October 26-28, 1994. Forty-nine papers were presented during the symposium, and 35 of those are included in this proceedings book.

Dr. Donald McCaughran, executive director of the International Pacific Halibut Commission, gave the keynote speech in which he addressed some of the research needed to better understand and manage Pacific halibut. He suggested that more survey data was needed to correlate with commercial catch data. Also, a spatial analysis of CPUE data is needed. Dr. McCaughran indicated that we need to examine harvest strategies for halibut. Halibut bycatch and the issue of regulatory and economic discards of halibut were also discussed.

The first session, reproduction, consisted of four papers. We heard of the influence of hydrometeorological events on the reproduction of five species from the West Kamchatkan shelf (Dyakov) and of the latitudinal patterns in life history traits of northeast Pacific flatfishes (Castillo). The batch spawning behavior of yellowfin sole in the Bering Sea was described (Nichol) as were the interrelationships of condition, gonad development, and the possibility of skip spawning in winter flounder (Burton).

Eleven papers were presented in the early life history session. They included an analysis of early life history patterns (Chambers), and a major focus on nursery habitats of flatfish (Norcross, Donohoe, Minami, Holladay, and Toole). In addition, there were papers on the variation in distribution and abundance of flatfish eggs and larvae (Grigorev), on larval types (Mulligan), and the copepod prey of flatfish larvae were documented (Paul). The hormonal, morphological, and

physiological changes associated with Japanese flounder metamorphosis were documented (Tanaka).

A general biology session included two papers. The Bechtol paper addressed biological characteristics of three abundant flatfish species in Kachemak Bay, Alaska. The Meyer paper discussed characteristics of the southcentral Alaska sport halibut fishery and alluded to potential conflicts between commercial and sport fisheries.

Nine papers addressed feeding and growth of flatfishes in session four. Four papers (Yang, Lang, Chilton, and Yokoyama) dealt with food habits and diet overlap. The Chilton and Yokoyama papers reported on single-species feeding habits, while the Yang and Lang papers examined diet similarity and diet overlap among several species. Otoliths were the focus of two papers: Blood compared age reading techniques on Pacific halibut otoliths, and Hagen examined microstructures and their deposition patterns in halibut. The three remaining papers addressed different aspects of food and energy requirements in three different flatfish species: brown sole (Tominaga), yellowfin sole (Smith), and flathead sole (Paul).

Session five was on abundance, biomass and distribution and consisted of 10 papers, 8 of which were single species studies. Those species were: English sole (Shi and Sampson), Greenland turbot (Ianelli, Kodolov, and Varulina), Pacific halibut (Kodolov and Hooge) and petrale sole (Castillo). Papers by McConnaughy and Ivankova dealt with multispecies populations.

A session on pollution, parasites, and disease included four papers. Avoidance of hydrocarbons in sediments was discussed by Moles and contaminant effects on reproductive output was reported by Sol. Lesions and parasites were discussed by Smith while the utility of parasites as indicators of flatfish biological characteristics was described by Moles.

Management and economics was the subject of the final session of contributed papers. Problems confronting the arrowtooth flounder commercial fishery were described by Cullenberg. Mortality of Pacific halibut caught incidental to other fisheries was described and analyzed by Trumble and Williams. The Witherall paper addressed management of flatfish in U.S. waters.

The last session was a discussion of future research needs. Participants identified a list of topics that require further research activity. The areas identified could serve as a guide for further cooperation between the agencies and institutions represented at this symposium. Further, it could serve as a reference for future research funding priorities.

Flatfish Management in the Eastern Pacific Ocean with Special Reference to Pacific Halibut

Donald A. McCaughran

International Pacific Halibut Commission
Seattle, Washington USA

Abstract

Commercial flatfish harvesting began in the eastern Pacific in the late 1800s. Several vessels began fishing for Pacific halibut on the coast of Washington and British Columbia in 1883. The fishery quickly expanded to British Columbia and Alaska, and by 1920 harvesting of Bering Sea stocks had begun. Harvesting of other species of flatfish began later than halibut mainly due to the ease of fishing halibut with longline fishing techniques. Most species of flatfish are too small to be caught with longline gear. It was not until the arrival of the modern "trawler" that fishing for the other species of flatfish began. Early in the 1900s several steam-driven "otter" trawlers were brought from New England and tried unsuccessfully to trawl for halibut. These vessels did not develop fisheries for other species of flatfish but instead turned to longlining halibut. Later, diesel powered trawlers were built, and sporadic trawling began for species such as English and petrale sole, but it was not until after the Second World War that intensive fishing for other flatfish species developed.

A brief discussion of the various flatfish fisheries is given, and since Pacific halibut have been harvested for a much longer time, and have received a higher level of research and management, a more thorough discussion will be presented for that species.

Table 1. Exploited flatfish species of the northeast Pacific and eastern Bering Sea.

Common name	Scientific name
Alaska plaice	<i>Pleuronectes quadrituberculatus</i>
Arrowtooth flounder	<i>Atheresthes stomias</i>
Butter sole	<i>Pleuronectes isolepis</i>
Dover sole	<i>Microstomus pacificus</i>
English sole	<i>Inopsetta ischyra</i>
Flathead sole	<i>Hippoglossoides elassodon</i>
Greenland turbot	<i>Reinhardtius hippoglossoides</i>
Longhead dab	<i>Pleuronectes proboscidea</i>
Pacific sanddab	<i>Citharichthys sordidus</i>
Pacific halibut	<i>Hippoglossus stenolepis</i>
Petrale sole	<i>Eopsetta jordani</i>
Rex sole	<i>Errex zachirus</i>
Rock sole	<i>Pleuronectes bilineatus</i>
Starry flounder	<i>Platichthys stellatus</i>
Yellowfin sole	<i>Pleuronectes asper</i>

The Flatfish Resource

The flatfish species that are currently being harvested in the eastern Pacific are given in Table 1. The estimated present (1993) biomass and yield of each species is given for the eastern Bering Sea, Gulf of Alaska, British Columbia, and the Washington-Oregon coasts (Table 2) (Fargo 1994, NPFMC 1994, PFMC 1994). The yields of flatfish amount to 12% of the total Bering Sea groundfish yield, 27% of the Gulf of Alaska, 9% of British Columbia and 9% of the Washington-Oregon groundfish yield. This amounts to a significant impact on the total economy of our North American fisheries. The ex-vessel value of Pacific halibut alone is approximately 130 million dollars annually. Only Alaska pollock exceeds flatfishes in economic value.

The importance of flatfish will continue to grow since many species are not exploited at their full potential, we have barely begun to exploit arrowtooth flounder for example. The only species fully exploited are Pacific halibut and yellowfin sole in the Bering Sea, and petrale sole, Dover sole, and English sole off the Pacific Coast. All other species are under-utilized, particularly in the Gulf of Alaska.

Table 2. Biomass and removals/landings (t) of flatfish coastwide (1993 values).

Species	Region									
	Eastern Bering Sea		Gulf of Alaska		Canada		Pacific Coast		All areas	
	Biomass	Removals	Biomass	Removals	Biomass	Landings	Biomass	Landings	Biomass	Landings/ removals
Yellowfin sole	1,880,000	106,000								
Rock sole	1,790,000	64,300			—	2,080	—	3,600		
Arrowtooth flounder	519,000	9,300	1,889,900	19,200						
Greenland turbot	165,000	8,500								
Pacific halibut	17,400	3,900	132,500	28,900	29,700	6,900 ^a	1,600	422 ^a		
Dover sole, rex sole, & Greenland turbot		227,600		6,700						
Rock sole, yellowfin sole, starry flounder, & butter sole			261,700	9,100						
Flathead sole			247,300	2,600						
Petrale sole					—	733	10,300 ^b	1,000		
Dover sole					—	3,660	83,000 ^c	16,000		
English sole					—	1,421	133,300 ^b	1,600		
Other flatfish	1,240,000	28,900					—	2,000		
Total	5,611,400	220,900	2,759,000	66,800	(29,700)	14,794	228,200	24,622	8,628,300	327,100

^a Removals

^b Vanc+Col

^c Eur+Col

Strange as it might seem, to those not familiar with these fisheries, it is often the bycatch of Pacific halibut that controls the yields of many of the other species.

Stock assessment and management

Table 3 summarizes the methods used for stock assessment and harvesting strategy for most of the exploited flatfish species. Pacific halibut will be discussed in detail later because of its long history of exploitation and management. Trawl surveys and catch at age analyses are the most common stock assessment methods. Trawl surveys alone often give extremely variable results, however when combined with age structure analysis satisfactory results can be obtained.

The most common exploitation strategy used is the so-called $F_{35\%}$ method developed by Dr. William Clark of the International Pacific Halibut Commission (Clark 1991). Strangely enough, as we will see later, this method is not used for Pacific halibut. In addition, the older $F_{0.1}$ method is used with considerable success in British Columbia. Both the $F_{35\%}$ and the $F_{0.1}$ methods are largely empirical methods but seem to work quite well for many species. The test of any method is the "test of time." If "good" yields can be taken from a species over a long period of time and thereby creating stability in the supply side of the industry, then the method is deemed a "good strategy." The $F_{35\%}$ is relatively new in its deployment; only time will tell if this strategy combined with the current stock assessment methods produces a satisfactory management and harvesting strategy.

Pacific Halibut

Pacific halibut (*Hippoglossus stenolepis*) is the largest of the Pacific Ocean flatfishes. It occurs from northern California throughout the Gulf of Alaska and Bering Sea across to the coast of Russia and south to northern Japan. In the eastern Bering Sea and the eastern Pacific it has the longest history of exploitation and management of any of the flatfishes. Its exploitation and management structure therefore are worthy of a detailed description.

Historic catches

Historically, the annual domestic yield of halibut has varied between 13,000 and 45,000 tons. The catches began with less than 100 tons in the 1880s and rose quickly to 40,000 tons by 1915 and dropped to 21,000 by 1918 (Figure 1). This drop in catches was a major concern

Table 3. Stock assessment and management strategies coastwide.

Species	Region							
	Eastern Bering Sea		Gulf of Alaska		Canada		Pacific Coast	
	Assessment method	Exploitation strategy	Assessment method	Exploitation strategy	Assessment method	Exploitation strategy	Assessment method	Exploitation strategy
Yellowfin sole	Trawl survey	$F_{35\%}$						
Rock sole	Trawl survey	$F_{35\%}$		Catch-age analysis	$F_{0.1}$		Trawl surveys	$F_{35\%}$
Arrowtooth flounder	Trawl survey	$F_{35\%}$	Trawl survey	$F_{35\%}$				
Greenland turbot	Trawl survey	$F_{35\%}$						
Pacific halibut	Catch-age analysis	CEY	Catch-age analysis	CEY	Catch-age analysis	CEY	Catch-age analysis	CEY
Dover sole, rex sole, & Greenland turbot			Trawl survey	$F_{35\%}$				
Rock sole, yellowfin sole, starry flounder, & butter sole			Trawl survey	$F_{35\%}$				
Flathead sole			Trawl survey	$F_{35\%}$				
Petrale sole					CPUE trends	Limited incidental removals	Catch-age, trawl surveys	$F_{35\%}$
Dover sole					Surplus production	$F_{0.1}$	Catch-age, trawl surveys	$F_{35\%}$
English sole					Catch-age analysis	$F_{0.1}$	Catch-age, trawl surveys	$F_{35\%}, F_{0.1}$
Other flatfish	Trawl survey	$F_{35\%}$					Historical catch	—

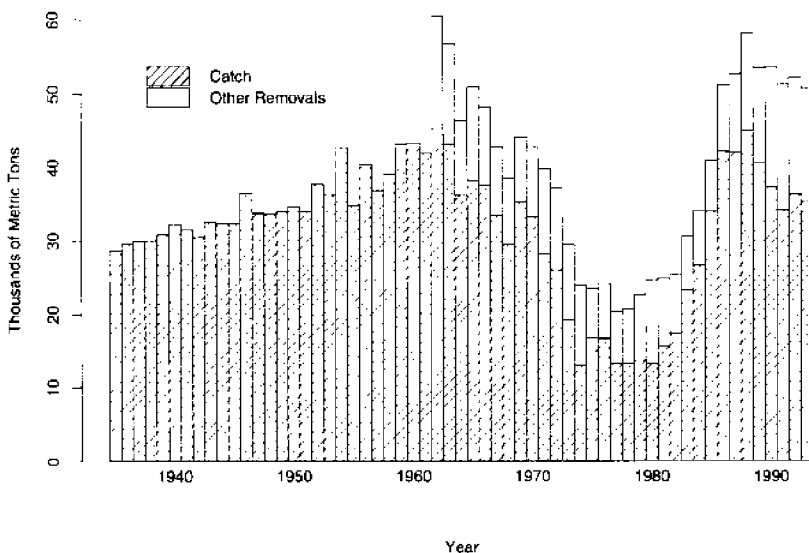


Figure 1. Historic halibut commercial catches.

for fishermen and created the demand for management. The International Fisheries Commission was formed by the United States and Canada in 1923. With the onset of management and winter fishing closures the stock began to grow until a yield of 42,000 tons was reached in 1961. At that time groundfish fishing began by non-domestic vessels and within several years these vessels had an annual bycatch of halibut in the 15,000 ton range. The large bycatch combined with high domestic catches at that time resulted in a precipitous decline in halibut stocks. The commission quickly reduced domestic catches and by the mid-1970s were the lowest in the modern history of the fishery (13,300 mt). With the imposition of the U.S. and Canada 200 mile zones bycatch was finally controlled and by 1985 the total bycatch was 3,200 mt. Combined with reduced domestic removals and a favorable environment (increased survival), in the 1980s, the stocks grew to a level that allowed a harvest of 45,000 tons in 1988. This has been followed by a natural downturn in recruitment and the stocks have decreased to a level that now produce a yield of 34,500 tons.

History of management

Thirty years after the fishery began the decline in catches mentioned earlier prompted fishermen and processors to lobby their governments for some type of research and management program. The governments of Canada and the United States negotiated a treaty (signed in 1923) to jointly investigate the causes for the apparent decline in the stocks. The International Fisheries Commission was created and a staff of seven undertook a series of research projects to study halibut life history and to investigate the necessity of imposing catch restrictions on the fishery. In 1930 the treaty was revised to allow the commission to restrict catches by area and time and to provide a forum with industry to annually promulgate fishing regulations. Further amendments to the treaty have been made from time to time increasing the commission's role in the conservation of the stocks. The commission was renamed the International Pacific Halibut Commission (IPHC) in 1953. The last amendment to the treaty was made in 1979 in response to the creation of the national 200 mile zones. The amendments continued the commission's conservation role and allowed the two national governments to allocate among domestic user groups providing the national regulations do not conflict with those of the commission.

Stock assessment

Prior to 1960 no scientifically based estimates of halibut biomass were attempted. Fortunately, the commission had set up a data collection system in the 1930s to sample otoliths and logbooks from various ports over the range of the fishery. The logbook program was initiated to obtain estimates of effort and catch-per-effort. As stock assessment methods developed, these long-term data sets became very useful. In the 1970s as population assessment methods developed the commission began to use age structure data to estimate biomass. Cohort analysis was the first method used to provide the commission with estimates of biomass. The commission staff developed a computer program called "CAGEN" to implement catch at age data in its annual stock assessment. We use a modification of this method at present. The method produces annual estimates of exploitable biomass (8-20 years old) by region and re-estimates the past 13 years annual estimates as well.

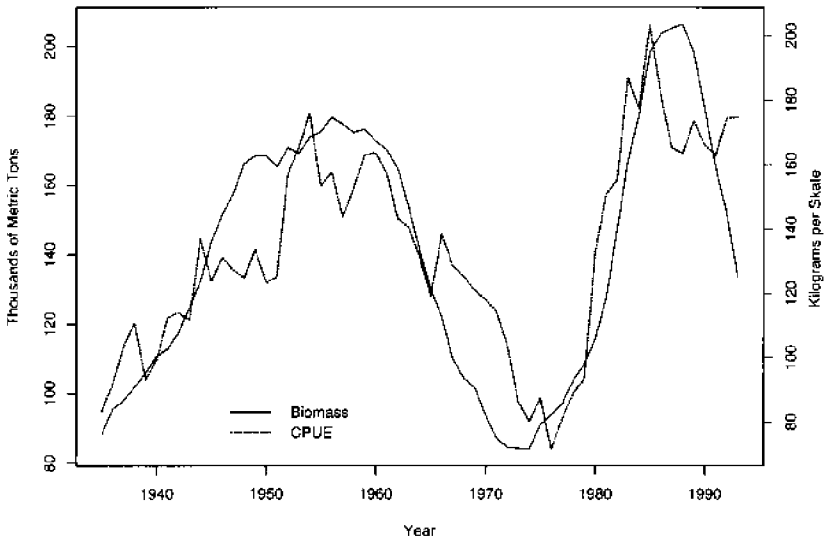


Figure 2. Historic halibut CPUE and biomass.

Harvesting strategies

Prior to 1975 the commission had no real scientifically based harvesting strategy. The commission had long data records of catch and effort. Yield recommendations were arrived at by trial and error. Yields were increased when catch per effort increased and were reduced when CPUE dropped. In retrospect this was not too bad an approach, since CPUE follows the stock biomass very well (Figure 2). The method was conservative and achieved a great deal of success as measured by a re-analysis of the older data to produce historic biomass estimates. In the 1960s the commission used yield-per-recruit analysis and stock production methods to attempt to arrive at an estimate of maximum sustainable yield. The commission abandoned the strategy of managing the stocks to produce maximum sustainable yield 25 years ago and has investigated and employed a variety of different harvesting strategies since that time. In the 1970s, after the rapid decline in the stocks, an emphasis was placed on rebuilding the depressed biomass. With biomass estimates available from cohort analysis, a temporary strategy of setting yields at 75% of the annual surplus production was used with success until 1984 when a more

scientific long term fishing strategy called constant exploitation yield was initiated.

This method began by setting yields at 35% of the exploitable biomass (ages 8-20). The 35% was initially arrived at by looking at the exploitable stock size that produced the calculated maximum sustained yield and recognizing that MSY was 35% of that value. This strategy has the desirable feature of having yields follow the natural cycles in stock abundance caused by a somewhat cyclic recruitment pattern. The constant exploitation rate strategy was then subjected to a great deal of analysis by computer simulation and was found to produce large long term yields while offering little risk of over-fishing. The commission felt this strategy would serve the halibut industry best by insuring a considerable measure of stability.

In 1991 further research on the exploitation rate was conducted. It was found that 0.30 resulted in a small reduction in long term yield but gave a very high assurance that the spawning biomass would not drop below the lowest recorded level. This additional measure while more conservative was considered to be desirable and the commission adopted it in 1992. We are at present computing yields at 0.30 of the exploitable biomass.

Bycatch

Prior to 1960 there was little bycatch of halibut in the fisheries for other species. Figure 3 shows the tremendous increase in bycatch since that time, and documents the events which caused the increase.

Non-domestic trawlers were mainly responsible for the rapid increase in bycatch. The large and poorly documented bycatch began at a time when the commission was attempting to maximize catches from a stock in excellent condition (high level of abundance). The high bycatch and high catches coincided with the natural downturn in the recruitment cycle. The combined result of these factors caused the stocks to drop to very low levels in a very short period of time. The official documented maximum bycatch by the non-domestic trawl fleet was 15,000 tons. IPHC believes the maximum bycatch occurred in the late 1960s and was probably in the 20,000 ton range. With the creation of the 200 mile zones in the United States and Canada bycatch controls were placed on the foreign fleets and bycatch declined to 3,200 tons by the mid-1980s. As the foreign fleets were replaced by a domestic fleet bycatch again increased until protests from the halibut industry and IPHC caused bycatch caps to be imposed. At present the bycatch is capped in the Bering Sea and Gulf of

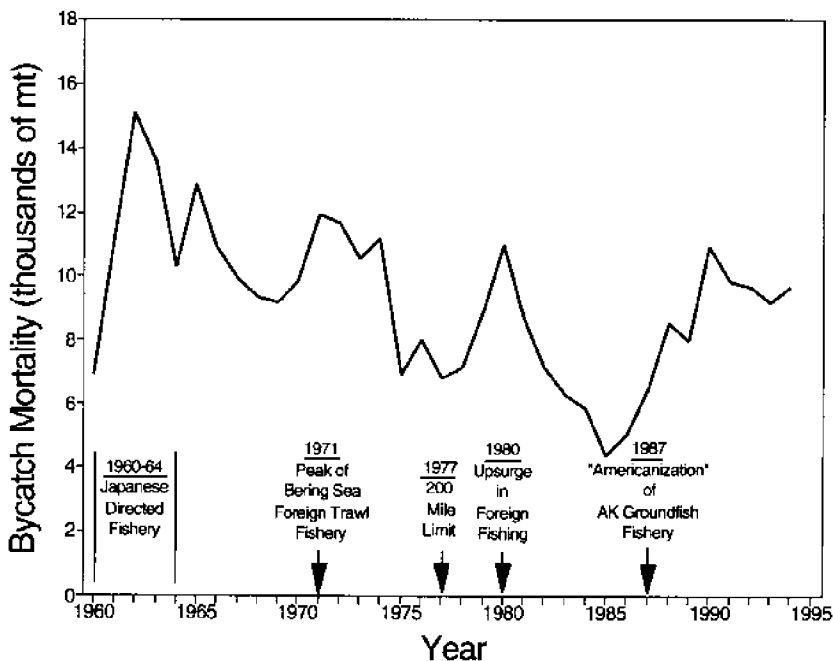


Figure 3. Historic bycatch mortality.

Alaska, but not in British Columbia and the Washington-Oregon fisheries. The present total bycatch is approximately 10,000 tons.

The IPHC compensates the halibut stocks for the reproductive loss from bycatch by reducing the domestic commercial catch by the total amount of bycatch and allocates the reductions on a regional basis proportional to the biomass of halibut in each region.

The IPHC believes that the bycatch is higher than necessary to prosecute the groundfish fisheries in both the United States and Canada. The high bycatch is caused by too many fishing vessels fishing for groundfish which in turn causes a "race" for fish and a disregard for selective fishing practices. Reductions in bycatch will only be brought about by an incentive program such as an individual vessel bycatch quota system.

The fishery

The first 75 years of the north American halibut fishery was very stable. In total there was less than 1,500 vessels participating in the

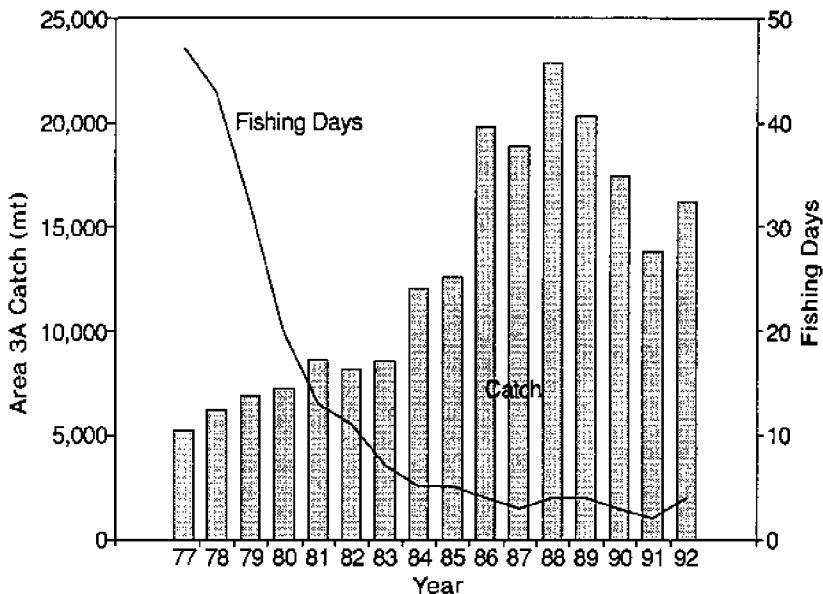


Figure 4. Number of fishing days and catch in Area 3A (central Alaska).

fishery. Beginning in the mid-1970s and continuing into the 1990s a large increase in the number of vessels occurred. This increase occurred mainly in Alaska. The result was fewer and fewer fishing days. Figure 4 shows the number of fishing days in Area 3 (central Alaska) and the catch from 1977 to 1992. The fishery is now completed in two 24-hour fishing periods. The total yield is 35,000 tons. This is spread over the various management areas proportional to the biomass in each area. The commission has adopted the strategy of subdividing areas whenever it is determined that unequal exploitation rates are occurring in a large area.

Over the past 15 years a sizable sport fishery for Pacific halibut has developed, partially in response, in some areas, to reduction in salmon stocks. The sports fishery has grown into a profitable business in many areas of the coast and the 1993 removal by sport fishermen was approximately 4,000 tons.

As previously mentioned, the total allowable catch by area is computed as $0.3 \times$ exploitable biomass in each area. Once these estimates are obtained bycatch, sports catch, wastage caused from lost gear, and juvenile handling mortality are subtracted and the

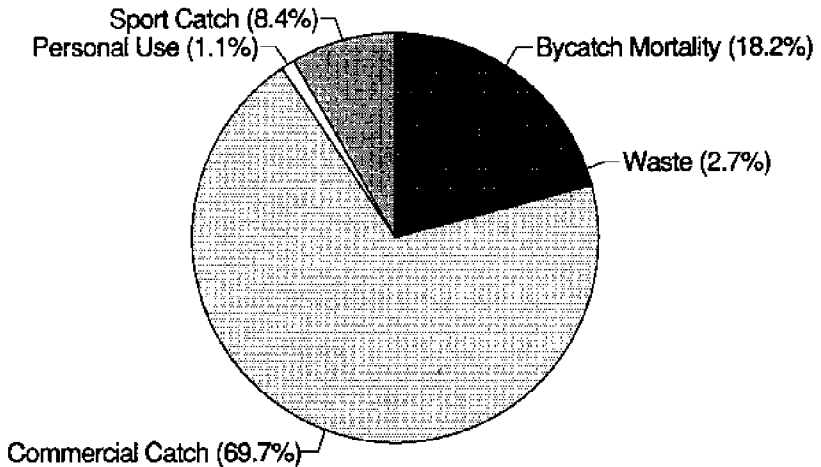


Figure 5. Halibut removals from various sources in 1993.

remainder allocated to commercial halibut fishermen. Seasons are computed which do not allow overages in catch to occur and, if necessary, trip limits by vessel size are imposed. Figure 5 shows the removals from the various sources. In Area 2A (Washington, Oregon) further allocation is done by the U.S. government to sports, commercial, and native Indian treaty tribes.

In Area 2B (British Columbia) the Canadian government further allocates to each vessel in an individual fishing quota system. The Canadian fishery is open from March 1 to October 31 and quota holders fish any time during that period. The Canadian catch mainly goes to the domestic (United States and Canada) fresh market and brings the highest price (\$2.50-2.80 per pound U.S.).

In 1995 the United States hopes to implement an individual vessel quota system as well. Their vessels will also fish from spring to fall. This system will bring order, safety, and consolidation to the U.S. fishery, and make the management of the fishery easier.

These changes create a more professional and responsible fleet with a stronger interest in conservation. Since the U.S. system also applies to sablefish there should be a reduction in the halibut bycatch in the sablefish fishery. These savings will then be passed onto the halibut/sablefish fleet directly.

The future

As previously indicated, the fishery will change dramatically with the advent of individual vessel quota systems. These changes will improve the prosecution and management of the fishery considerably. The economic value of the fishery will increase with a larger proportion of the catch being sold fresh. With a more complete log book system, and with better navigation (GPS) we hope to be able to refine the level of management. We anticipate using spatial statistical methods to get more precise estimates of CPUE by area. This will improve the biomass estimates as well as improving allocation by area. Continual analysis of different harvesting strategies may find better methods of computing harvest levels.

If the U.S. government can create a system of individual bycatch quotas for its groundfish fleet we expect to see reductions in bycatch in the future, allowing more harvesting by the domestic halibut fleets.

The IPHC has enjoyed considerable success in the past in managing this valuable resource. We feel the future may prove to be even more successful.

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Reproduction of Some Flounder Species from the West Kamchatkan Shelf

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Abstract

Reproductive aspects of five species of commercially important flounders inhabiting the shelf off Kamchatka were studied as part of a long-term research project (1963-1990). They are: yellowfin sole (*Pleuronectes asper* Pallas), Alaska plaice (*Pleuronectes quadrituberculatus* Pallas) Sakhalin flounder (*Limanda sakhalinensis* Hubbs), longhead dab (*Limanda proboscidea* Gilbert) and flathead flounder (*Hippoglossoides elassodon* Jordan et Gilbert).

Experiments were carried out to ascertain the influence of abundance, biological structure of the parental stock, and hydrometeorological conditions on brood formation. The analyses were used to judge the optimum number of spawners necessary to maintain the population in a stable state and to obtain high catches. The analyses were also used to forecast year-class abundance entering the commercial stock. The dependence of brood abundance on parental stock abundance and biological structure was examined. The dependence of brood abundance on the commercial stock biomass of the species and of the total for all flounders was studied.

The species were determined and the coefficients of reproduction models were calculated describing brood abundance dependence on corresponding indicators common to the species. It appears that brood abundance is dependent on the parental stock and can be described as a certainty by nonlinear equation.

Hydrometeorological conditions during spawning influenced the formation of year-class abundance. Year-class abundance decreased

for some species of flounders during years of high storm activity. This is probably caused by an increase in fish mortality during early life. The forecast equations of year-class harvest dependence on storm activity were calculated for three flounder species.

Introduction

When investigating the reproductive cycle of any animal species, especially fish, factors influencing their dynamics are considered. Main factors include the status of the reproductive segment of the population and the environment of the offspring. Year-class abundance in the offspring can be quite dependent on the quantity and biological state of the spawners, and on the population as a whole. In addition, formation of year-class abundance is determined by their survival, which is influenced by environmental factors during early life.

This article is devoted to the influence of population dynamics, biological structure, and hydrometeorological factors (storm activity) on the formation of brood abundance for five species of flounders of Kamchatka's western shelf: yellowfin sole (*Pleuronectes asper* Pallas), Alaska plaice (*Pleuronectes quadrituberculatus* Pallas), Sakhalin flounder (*Limanda sakhalinensis* Hubbs), longhead dab (*Limanda proboscidea* Gilbert) and flathead flounder (*Hippoglossoides elassodon* Jordan et Gilbert). Analyses showed the optimum level of spawners needed to maintain a stable population and obtain rather high catches. Analyses were also used to forecast year-class abundance entering the commercial stock.

No early investigations of the flounders off western Kamchatka were conducted. The only known attempt recognizes the influence of the abundance of the parental stock on brood harvest for yellowfin sole (Tikhonov, unpublished data). The results, however, were not published and no definite conclusions were found.

Materials and Methods

Samples were collected by trawl survey in the waters off western Kamchatka by scientists from the Kamchatka and central departments of the Pacific Scientific Research Institute of Fisheries and Oceanography during flounder spawning in spring and summer of 1963-1989. The dynamics and biomass of the flounder reserves were determined by squares (Aksyutina et al. 1965). Calculation of spawners and fish population fertility is based on sex, sexual maturity rate, individual

fertility, and the age structure of the population. Calculation of the individual fish fertility of various age groups was carried out by Tikhonov (1977, 1982).

Regressive analysis was performed to show how parental stock traits influence reproductive efficiency. The analysis demonstrated the possibilities of forecasting year-class abundance by size and biological status of the population. The analysis contained some mathematical models describing identical reproductive processes. Harvest stock formation is probably not influenced solely by parental stock abundance, but also by its biological structure: sex, age, and total fish in the population. The dependence of absolute year-class abundance on the brood (million fish: Y) was analyzed by 12 indicators characterizing the state of the population. The indicators include the following:

1. Number of males in the parental stock (million fish): X_1
2. Number of females in the parental stock (million fish): X_2
3. Number of parents in stock (million fish): X_3
4. Absolute population fertility (million eggs): X_4
5. Relative population fertility (thousand eggs), for one female in accordance with the abundance and age structure of the population: X_5
6. The number of fish of a commercial stock of the investigated species (million fish): X_6
7. Biomass of a commercial stock of the investigated species (thousand ton): X_7
8. Biomass of a commercial stock of all the investigated flounders (thousand ton): X_8
9. Absolute number of fish spawning first (spawning replenishment) (million fish): X_9
10. Relative number (to the total number of spawning stock) of fish spawning first (spawning replenishment) of the investigated species (%): X_{10}
11. Median age of the spawning replenishment of the investigated species (years): X_{11}
12. Median age of the spawning stock (years): X_{12}

The reproduction models used for approximating corresponding connections were the Beverton-Holt model, the Ricker model, a model by Cushing, linear equation, parabola equation, and parabola equation modified.

Year-class abundance at 4+ was defined retrospectively based on the number of fish and age when recorded during the trawl survey. One calculation, assuming year-class abundance in the current year

will be the same as in a previous year, taking into account natural diminution and catch, is expressed as:

$$(N_{t-1} - n_{t-1})(1 - \varphi_{M_{t-1}}) = N_t;$$

where N_t = absolute year-class abundance (million fish) at the age t , starting from the year of recruitment into the fishery

N_{t-1} = absolute abundance (million fish) of the same brood in a previous year

$\varphi_{M_{t-1}}$ = natural diminution (portion of the unit) of brood in a previous year

n_{t-1} = the number of brood caught fish (million fish) in a previous year.

The natural reduction $\varphi_{M_{t-1}}$ at various ages was determined by the method developed by Zykov and Slepokurov (1982). The final formula for retrospective calculations was obtained by further transformations:

$$N_{t-1} = \frac{N_t + n_{t-1}(1 - \varphi_{M_{t-1}})}{1 - \varphi_{M_{t-1}}}$$

The calculation of first spawner abundance was made in accordance with the formula:

$$S = \sum_j \sum_i [N_{t_i+1} - (N_{t_i} - n_{t_i})(1 - \varphi_{M_{t_i}})]_{t_j}$$

where S = absolute first spawning fish abundance (million)

t_i = age of maturing fish of the same brood in different years

t_j = age of the maturing fish of different broods in a concrete year

N_{t_i}, N_{t_i+1} = absolute abundance of maturing fish (million) of brood at age t_i and t_i+1

n_{t_i} = the number of maturing fish at age t_i , caught in a period of fishing

$\varphi_{M_{t_i}}$ = the natural diminution in a portion of the unit at age t_i .

Investigating the connection between brood abundance and storm activity, we took into consideration the fact that the formation of year-class abundance at that time was influenced by hydrometeorological factors mainly during early ontogenesis. Thus, the number of days when storms passed through areas of flounder habitation during spawning, March-September, was used in corresponding calculations. Time gradation of the duration of storm activity was calculated taking into account the spawning period for each species. In other words, in

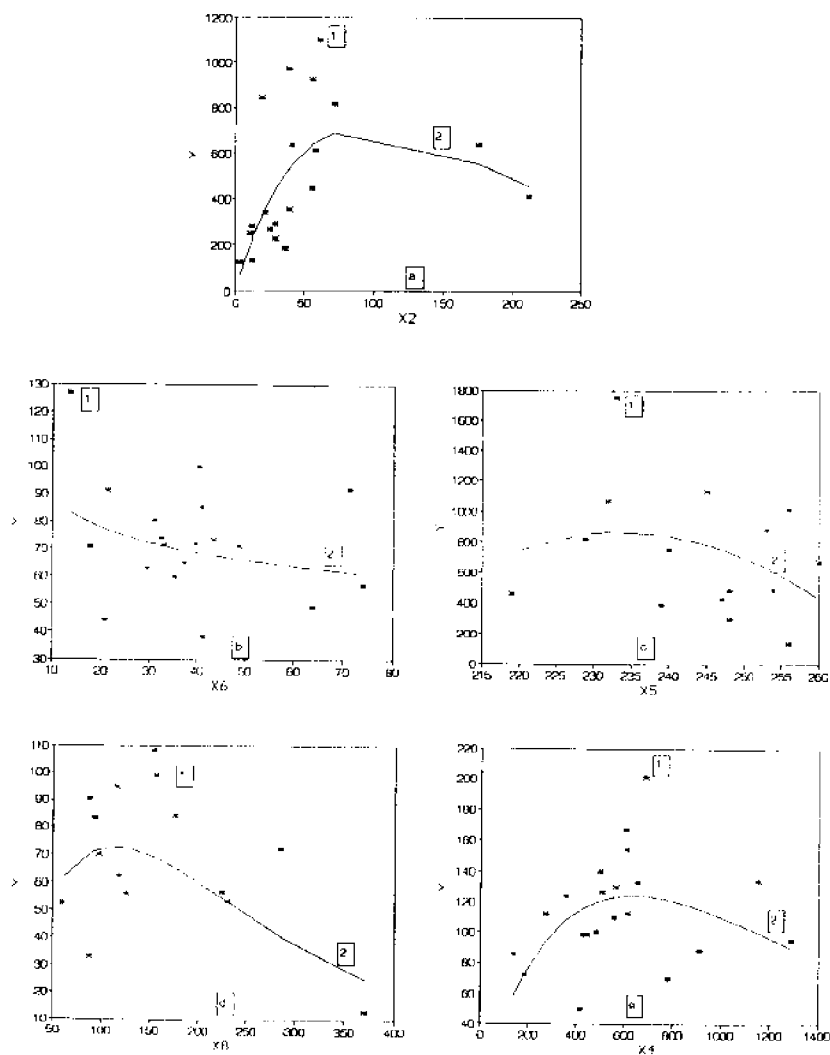


Figure 1. Dependence of year-class absolute abundance in brood on internal population factors for yellowfin sole (a), Alaska plaice (b), Sakhalin flounder (c), longhead dab (d), flathead flounder (e). Y = brood abundance, X = population factors (explanation is in the text); 1 = empirical data, 2 = curve, calculated by equation.

order to calculate correlated connections with year-class abundance indicators, the total days with storms for 1, 2, 3, and 4 closely connected months with a successive step into one month was used as a variable.

Results and Discussion

The dependence of brood abundance on internal population factors

Year-class abundance at 4+ for species under investigation varies. The abundance for yellowfin sole varies between 100 and 1,100 million fish, for Alaska plaice between 40 and 130 million fish, for Sakhalin flounder between 100 and 1,800 million fish, for longhead dab between 30 and 110 million fish, and for flathead flounder between 70 and 200 million fish (Figure 1). Thus, yellowfin sole and Sakhalin flounder can be classified as high abundance species, but the others are low abundance.

In order to calculate the influence of various internal factors on the formation of brood abundance, the nature of its dependence on the above indicators was examined using a regressive equation. Their significance in numbers is given in Tables 1-5. In selecting models and population factors, we chose those which showed minimum mean square deviation of empirical data of brood absolute abundance calculated by the models. The corresponding regressive equations are shown in Table 6. Mean deviation (percent) of empirical data calculated by equation (forecast error) and cases not increasing the indicated error (forecast supply) are also shown in Table 6.

The regressive analysis shows that the reproduction of yellowfin sole, longhead dab, and flathead flounder can be indicated by the Ricker equation more satisfactorily. Mainly, brood abundance is dependent on the following: yellowfin sole from number of females in the parental stock (X_2), longhead dab from biomass of a commercial stock for all the flounder species under investigation (X_6), and flathead flounder from absolute population fertility (X_4). For a mathematical description of Alaska plaice reproduction, the Cushing equation can be used; for Sakhalin flounder reproduction, the modified parabola equation is employed. Brood abundance of the first species is very dependent on the number of fish in its commercial stock (X_6), but for the second species, brood abundance depends on relative population fertility (X_4).

Table 1. Meanings of some population factors for yellowfin sole in figures (designation factors are given in Materials and Methods).

Factors	Year broods									
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
Y	125.2	131.8	183.1	227.2	290.8	280.5	351.4	251.5	268.4	339.8
X ₁	34.7	32	48.7	40	28.8	21.6	118.5	25.5	64.4	40.4
X ₂	3.5	12.9	36	29.2	28.2	12	39.4	10.7	25.3	21.2
X ₃	38.2	44.9	84.7	69.2	57	33.6	151.9	36.2	89.7	61.6
X ₄	2,805	9,464	24,144	23,247	21,533	8,334	27,141	7,421	13,128	12,220
X ₅	801	734	671	796	764	694	689	694	519	576
X ₆	85	76.2	128.3	100.4	76.1	44.1	217.9	49.1	142	82.5
X ₇	19.4	18.5	32.5	31.5	25.9	12	54.5	14.3	29.8	22.3
X ₈	-	-	-	-	-	-	230	59.5	115.3	86.2
X ₉	-	34.4	73.7	40.1	34	12.3	144.2	2.9	80	25.6
X ₁₀	-	76.6	87	57.9	59.6	36.6	91.3	8	89.2	41.6
X ₁₁	-	7.7	7.4	7.5	6.8	5.9	6.8	5	6.3	6.4
X ₁₂	6.7	7.7	7.6	7.9	7	7.3	6.9	7.2	6.5	7

Factors	Year broods									
	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
Y	634.7	845.1	971.9	923.8	1,101.3	816.8	612.1	444.6	415.1	640.2
X ₁	69.8	55.8	67	171.3	65.8	81.6	104.2	190.7	187.4	293.6
X ₂	41.2	18.9	38.6	55.9	61.2	71.9	58.3	56.2	211.6	175.1
X ₃	111	74.7	105.6	227.2	127	153.5	162.5	246.9	399	468.7
X ₄	23,285	10,542	24,915	25,958	35,871	40,758	26,974	33,912	106,721	127,959
X ₅	565	558	645	464	586	567	463	603	504	731
X ₆	132.8	96.4	141.6	306.6	146	178.5	233.2	339	540.2	639.4
X ₇	33.6	22.3	31.3	67.1	34.2	47.8	56	77	125.4	163.3
X ₈	92.2	87.3	96.5	176	124.9	117	155.6	153.4	224.8	370.3
X ₉	88.7	44.5	83.4	201	31.6	125.5	97.1	157.4	262.2	241
X ₁₀	79.9	59.6	79	88.5	24.9	81.8	59.8	63.8	65.7	51.4
X ₁₁	6.6	5.9	6.9	6.5	6.4	6.9	5.6	6.3	6.5	7.3
X ₁₂	6.9	6.7	7	6.7	7.3	7.1	6.4	6.7	6.9	7.7

Table 2. Meanings of some population factors for Alaska plaice in figures (designation factors are given in Materials and Methods).

Factors	Year broods									
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
Y	73.2	71.3	62.9	48.8	56.8	91.2	91.8	65.1	71.2	73.7
X ₁	5.6	4.1	4.5	8.5	10.8	1.9	8.4	3.5	3.4	3.2
X ₂	12.5	8.9	11.7	17.6	21.5	4	21.6	5.6	6.2	4.8
X ₃	18.1	13.0	16.2	26.1	32.3	5.9	30.0	9.1	10.3	8.0
X ₄	2,909	2,158	3,048	3,973	4,641	881	6,199	1,210	1,408	957
X ₅	233	242	261	226	216	220	287	216	227	199
X ₆	43.5	33	29.7	63.9	74.1	21.2	71.4	37.4	48.7	32.6
X ₇	24	17.9	21.1	35.2	42.2	8.8	40.2	12.1	15.7	15.1
X ₈	-	-	-	-	-	-	230	59.5	115.3	86.2
X ₉	-	7.8	12.6	20.2	23.4	0.8	24.8	2.1	6.9	4.8
X ₁₀	-	60	77.8	77.4	72.4	13.6	82.7	23.1	67	60
X ₁₁	-	10.8	11.6	10.8	10.8	8	11.6	8.2	10.8	9.1
X ₁₂	11.5	11.5	12	11.3	11.2	11	11.8	10.7	10.7	10.2

Factors	Year broods								
	1973	1974	1975	1976	1977	1978	1979	1980	1981
Y	38.2	70.7	99.8	127	85.1	59.6	71.8	44.1	80.3
X ₁	2.6	0.9	2	1.2	2.8	3.5	2.8	1.3	3
X ₂	3.8	1.3	2.9	2.3	3.2	6.1	5.3	2.5	4.5
X ₃	6.4	2.2	4.9	3.5	6.0	9.6	8.1	3.8	7.5
X ₄	518	179	485	439	439	1,133	1,159	486	743
X ₅	136	138	167	191	137	186	219	194	165
X ₆	41.2	17.7	40.4	13.6	40.8	35.3	39.8	20.7	30.9
X ₇	17.5	6	12.7	6.3	16.5	16.9	16.6	8.5	14.7
X ₈	92.2	87.3	96.5	176	124.9	117	155.6	153.4	224.8
X ₉	3.6	0.8	4.4	2.2	4.7	8.3	3.1	0.8	5.6
X ₁₀	56.2	36.4	89.8	62.9	78.3	86.5	38.3	21.1	74.7
X ₁₁	9.8	8.2	10	10.4	8.9	10.4	10.2	9.6	9.6
X ₁₂	10	9.4	10	10.5	9.5	10.4	10.9	9.7	10.1

Table 3. Meanings of some population factors for Sakhalin flounder in figures (designation factors are given in Materials and Methods).

Factors	Year broods							
	1969	1970	1971	1972	1973	1974	1975	1976
Y	885.1	1019.2	820.5	459.6	485.7	751.3	1,070.5	1,133.4
X ₁	146	78.3	75.6	81.7	44.3	72.2	71.1	215.6
X ₂	191.1	99.5	102.1	110.8	56.2	94.5	94.2	277.1
X ₃	337.1	177.8	177.7	192.5	100.5	166.7	165.3	492.7
X ₄	48,285	25,491	23,412	24,229	13,917	22,684	21,948	67,766
X ₅	253	256	229	219	248	240	233	245
X ₆	411.3	212.6	230.2	253.6	122.2	208.2	210.7	604.9
X ₇	53.5	19.6	21.2	21	16.9	30	28.9	73.8
X ₈	230	59.5	115.3	86.2	92.2	87.3	96.5	176
X ₉	-	91.4	147.1	144.9	50.8	156.6	144.2	466.4
X ₁₀	-	51.4	82.8	75.3	50.5	93.9	87.2	94.7
X ₁₁	-	5.7	5.4	5.2	5.6	5.8	5.6	5.9
X ₁₂	6	6.1	5.7	5.5	5.9	5.8	5.7	5.9

Factors	Year broods						
	1977	1978	1979	1980	1981	1982	1983
Y	491.5	432.6	391.5	295.5	135.9	670.5	1,753.5
X ₁	165.7	54.6	123.6	142	182.7	272.6	121.4
X ₂	211	71	161	180.2	231.6	348.8	158.2
X ₃	376.7	125.6	284.6	322.2	414.3	621.4	279.6
X ₄	53,499	17,523	38,425	44,761	59,257	90,809	36,863
X ₅	254	247	239	248	256	260	233
X ₆	452.6	154.6	355.3	391.2	495.7	740.6	353.2
X ₇	56.1	23.7	43.7	57.5	67.9	117.8	43.1
X ₈	124.9	117	155.6	153.4	224.8	370.3	285.3
X ₉	243.3	82.3	239.4	220.1	292.7	467.2	176.8
X ₁₀	64.6	65.5	84.1	68.3	70.6	75.2	62.2
X ₁₁	5.8	5.6	5.6	5.7	5.8	5.9	5.3
X ₁₂	6	5.9	5.8	5.9	6	6.1	5.7

Table 4. Meanings of some population factors for longhead dab in figures (designation factors are given in Materials and Methods).

Factors	Year broods										
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Y	149.7	84.2	76.5	46	48.1	52.6	53.1	52.6	64.8	90.3	83.5
X ₁	19.3	13.4	13.7	12	22.7	6.3	58.6	5.1	34	8.8	15.6
X ₂	13.3	8.9	7.2	9	15.7	3	41.1	4	20.2	5	8.8
X ₃	32.6	22.3	20.9	21	38.4	9.3	99.7	9.1	54.2	13.8	24.4
X ₄	6,035	3,991	3,078	4,136	7,161	1,278	18,784	1,836	8,921	2,191	3,854
X ₅	454	448	427	460	456	426	457	459	442	438	438
X ₆	38.2	26	24.9	24.4	45.2	11.4	116.3	10.5	64.6	16.4	29.1
X ₇	10.4	6.5	7.5	6.9	12.3	2.7	28.4	2.8	14.6	3.9	6.5
X ₈	—	—	—	—	—	—	230	59.5	115.3	86.2	92.2
X ₉	—	16	16.8	15.6	33.4	3.4	96.8	0.4	52.5	4.6	20.7
X ₁₀	—	71.7	80.4	74.3	87	36.6	97.1	4.4	95.6	33.3	84.8
X ₁₁	—	5.8	5.7	6.1	6.1	5.1	6.2	4.7	6	5.2	5.8
X ₁₂	6.2	6.1	6	6.3	6.2	5.9	6.2	6.4	6	6	6.5

Factors	Year broods									
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Y	33.1	70.1	84.2	55.8	62.3	98.9	108.4	56.4	12.9	72.2
X ₁	7.8	20.1	12.8	14.5	15.9	37.6	6	15.1	35.9	24.4
X ₂	4.5	9.7	6.6	8.2	7.7	20.8	2.5	7.1	19.4	13.6
X ₃	12.3	29.8	19.4	22.7	23.6	58.4	8.5	22.2	55.3	38
X ₄	1,958	4,080	2,809	3,551	3,259	8,950	1,023	2,887	8,367	5,942
X ₅	435	421	426	433	423	430	409	407	431	437
X ₆	14.7	36.4	23.4	27	28.8	69.6	10.8	30.8	66.1	45.7
X ₇	3.7	6.3	5	5	5.5	13.5	1.7	5	13.6	10
X ₈	87.3	96.5	176	124.9	117	155.6	153.4	224.8	370.3	285.3
X ₉	7.4	27.8	13.8	16.4	20	48	2.8	18.6	46	19
X ₁₀	60.2	93.3	71.1	72.2	84.7	82.2	32.9	83.8	83.2	50
X ₁₁	5.6	5.7	5.6	5.7	5.7	5.8	4.6	5.5	5.8	5.3
X ₁₂	6	5.8	5.9	6	5.8	6	5.6	5.7	6	6

Table 5. Meanings of some population factors for flathead flounder in figures (designation factors are given in Materials and Methods).

Factors	Year broods										
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Y	201.8	139.7	133.2	109.2	95.1	88.5	133.8	112.3	112.6	100.6	98.7
X ₁	13.9	10.5	14.4	10	23	19.3	27.3	5.7	17.9	9.9	9.2
X ₂	8.6	6.4	8.6	7	15.8	11.7	15.4	3.5	8.1	6.2	5.7
X ₃	22.5	16.9	23	17	38.8	31	42.7	9.2	26	16.1	14.9
X ₄	684	498	654	558	1289	908	1152	274	612	484	448
X ₅	79	78	76	80	82	78	75	78	76	78	79
X ₆	104.1	76.5	109.5	74	136.3	134.8	211.8	38.3	122	67	64.7
X ₇	24.5	20.3	31	22	46.9	34.9	53.4	10.7	34	23.9	17.7
X ₈	-	-	-	-	-	-	230	59.5	115.3	86.2	92.2
X ₉	-	11.7	19.3	9.9	34.4	18.2	32.1	1.4	23.6	8	9.9
X ₁₀	-	69.2	83.9	56.9	88.7	58.7	75.2	15.2	90.8	49.7	66.4
X ₁₁	-	6	6	6.2	6.5	5.8	5.9	5	6.2	5.8	5.9
X ₁₂	6.4	6.3	6.2	6.6	6.6	6.4	6.2	6.4	6.3	6.4	6.4

Factors	Year broods										
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	
Y	49.4	98.4	129.8	124	126.5	154.5	86	72.6	70.2	167.2	
X ₁	9.5	8.5	12.4	6.1	11.1	13.2	3.3	4.1	17.5	16.8	
X ₂	5.6	5.7	7.5	4.8	6.6	7.9	1.9	2.5	10.4	7	
X ₃	15.1	14.2	19.9	10.9	17.7	21.1	5.2	6.6	27.9	23.8	
X ₄	419	430	565	359	510	611	136	184	780	605	
X ₅	75	75	75	75	77	77	72	74	75	86	
X ₆	76.3	61.3	93.9	43.7	75.1	90.5	28.9	34.2	138.4	105.9	
X ₇	25.3	17.3	23.8	13.1	23.1	25.8	8.7	11.8	47.7	34.4	
X ₈	87.3	96.5	176	124.9	117	155.6	153.4	224.8	370.3	285.3	
X ₉	11.5	11	16.4	5.2	15.5	13.2	1.8	4	36.2	8.9	
X ₁₀	76.2	77.5	82.4	47.7	87.6	62.6	34.6	60.6	93.9	37.4	
X ₁₁	5.9	6	6	5.6	6.3	5.9	5	5.7	6.1	5.9	
X ₁₂	6.2	6.3	6.2	6.3	6.4	6.3	6	6.1	6.2	6.6	

Table 6. The equations of dependence of brood absolute abundance upon some population factors.

Species	Regressive equation	Forecast error	Forecast supply	Number of broods
Yellowfin sole	$Y = 20.7X_2e^{-1.07 \times 10^{-2}X_2}$	42.4	60	20
Alaska plaice	$Y = 132.997X_6^{-1.799 \times 10^{-1}}$	20.5	63.2	19
Sakhalin flounder	$Y = -32,240.8 \times 10^4 + 283.607X_5 - 0.6074X_5^2$	45.7	60	17
Longhead dab	$Y = 1.733X_8e^{-8.791 \times 10^{-3}X_8}$	28.3	60	20
Flathead flounder	$Y = 0.527X_4e^{-1.565 \times 10^{-3}X_4}$	22.3	66.7	20

Results show that brood abundance depends on internal factors for all flounder species investigated by us except longhead dab. The reproduction efficiency of yellowfin sole, Sakhalin flounder, and flathead flounder is mainly influenced by the number and the age structure of females. Apparently, the number of males in the populations during this study was such that it could greatly influence the formation of brood abundance.

In the case of Alaska plaice, the brood abundance decreased while the commercial stock of this species increased. This can be caused by reduced fish fertility resulting from decreased food supply. The food supply decrease may be due to the high numbers of commercial stock, and food competition with the more numerous yellowfin sole which shares both habitat and food preferences with the Alaska plaice.

In the case of the less numerous longhead dab, the brood abundance is greatly influenced by the total size of the commercial stock of all studied species. Longhead dab probably holds a subordinate position, compared to other species, during formation of year-class abundance. This explains the low level of its biomass.

Forecasting year-class harvest by calculated equations can be more precise for low abundance species: Alaska plaice, longhead dab, and flathead flounder. Forecasting brood number by the status of parental stock is less accurate for yellowfin sole and Sakhalin flounder.

Table 7. Correlation coefficients between flounder year-class abundance and the duration of storm processes in a period of spawning and early life period. (In parentheses: critical correlation coefficients at a 5% level of significance.)

Species	Number of days with storm correlation		Number of broods
	April-June	April-July	
Yellowfin sole	-0.45 (0.44)	-0.46 (0.44)	20
Alaska plaice	-0.60 (0.46)	-0.56 (0.46)	19
Sakhalin flounder	-0.45 (0.55)	-0.56 (0.55)	13
Longhead dab	0.28 (0.44)	0.19 (0.44)	20
Flathead flounder	0.14 (0.44)	0.22 (0.44)	20

Forecasting is related to the extent of brood abundance pressure. It varies 10-18 times for high abundance species, and 3-4 times for low abundance species (Figure 1).

Thus, for the first time, data on population factors have been obtained for forecasting brood abundance for flounders of the western Kamchatka Shelf and also to identify the optimum level of spawners necessary for reproduction.

Influence of storm activity on formation of flounder year-class abundance

Variations in year-class abundance, and the degree and character of its relation to the atmospheric processes of storm activity in areas of flounder habitat have been examined. The negative correlation has been ascertained between the number of fish in broods and the duration of storm activity in a year broods were born for yellowfin sole, Alaska plaice, and Sakhalin flounder. Connections like these have not been observed for longhead dab and flathead flounder (Table 7).

The specific connections made it possible to calculate equations describing the abundance variation for each species in correlation with the change in number of days with storm activity. The equations have been chosen for approximations that represent the minimum mean square deviations of the estimated data to the empirical data.

The variation of the yellowfin sole year-class abundance is inversely proportional to the number of days with storms, and is more satisfactorily described by the linear equation:

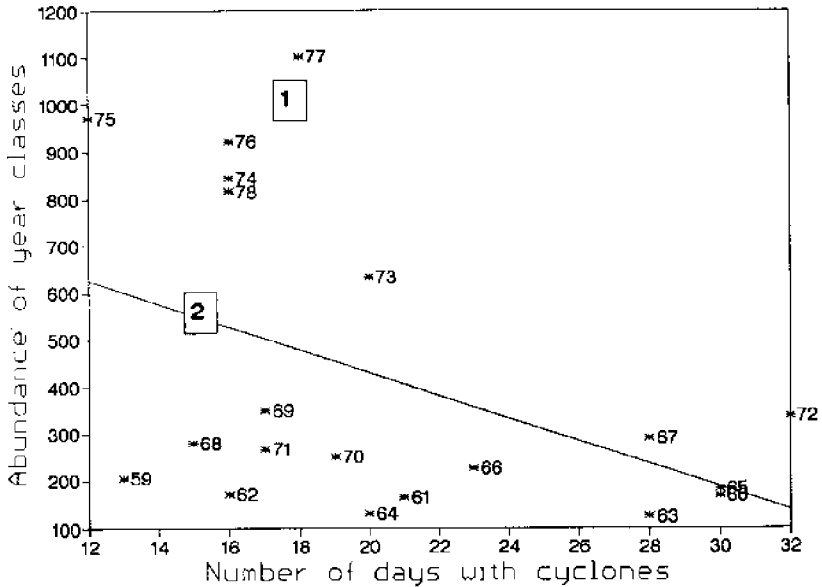


Figure 2. Connection of year-class abundance for yellowfin sole with the number of days with storm activity in April-July. Brood birth years are indicated by figures. 1 = empirical data; 2 = curve, calculated by equation.

$$Y = 918.20 - 24.34X \text{ (limits } X : 12 - 32)(1);$$

where Y = year-class abundance (million fish) at the age 4+
 X = the number of days with storms.

It should be noted that the brood abundance for yellowfin sole that began life before 1973 was relatively low, varied little, and was not dependent upon storm activity. Starting with 1973, brood abundance has greatly increased and is influenced by hydrometeorological conditions (Figure 2). This is probably the main reason for a reduction in the increasing year-class harvest of flounders, mainly yellowfin sole, during the Alaska pollock fishery. Beginning with 1973, the flounder catch by the Alaska pollock fishery decreased dramatically compared to previous years. Consequently, before 1973 there was larger commercial pressure on the yellowfin sole segment of the maturing population. It should be noted that in the late 1950s and early 1960s the commercial influence on flounder populations was especially great in conjunction with an intensive specialized harvest (Shuntov

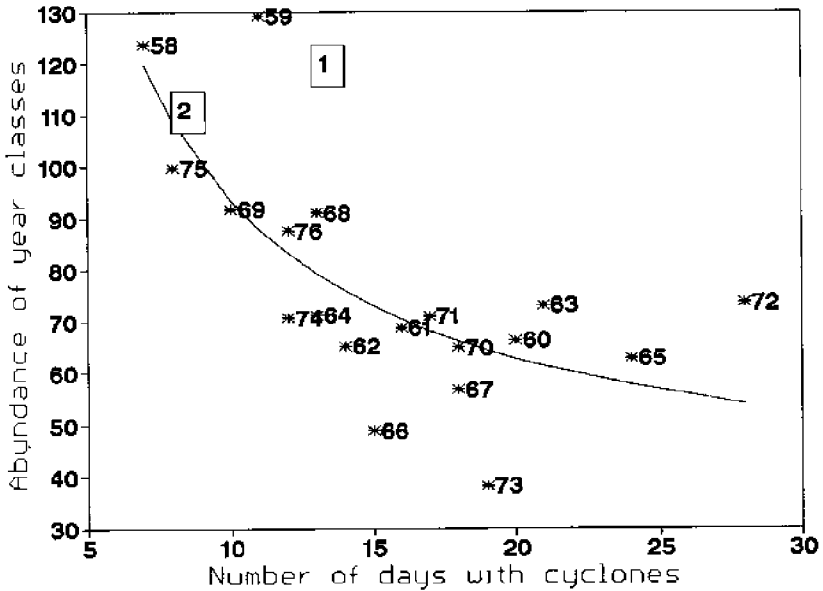


Figure 3. Connection of year-class abundance for Alaska plaice with the number of days with storm activity in April-June (the same signs as in Figure 2).

1985). This could be the cause for yellowfin sole abundance decreasing to a level lower than optimum for reproduction. Brood abundance at a given period was low even under favorable hydrometeorological conditions, and was mainly dependent on the status of the parental stock.

We examined the correlation between year-class harvest and storm activity in the spring-summer months for Alaska plaice and Sakhalin flounder. There is an abundance level for both species after which it stops decreasing while the number of days with storm activity is increasing (Figures 3-4). The abundance level for Alaska plaice is about 70 million fish, and for Sakhalin flounder about 500 million. The dependence investigated for both species is shown by a hyperbolic curve and the equation is as follows:

Alaska plaice: $Y = 612.77 / X + 32.2$ (limits $X : 7 - 28$)

Sakhalin flounder: $Y = 13374.98 / X - 76.02$ (limits $X : 12 - 32$)

Notations are the same as for equation 1.

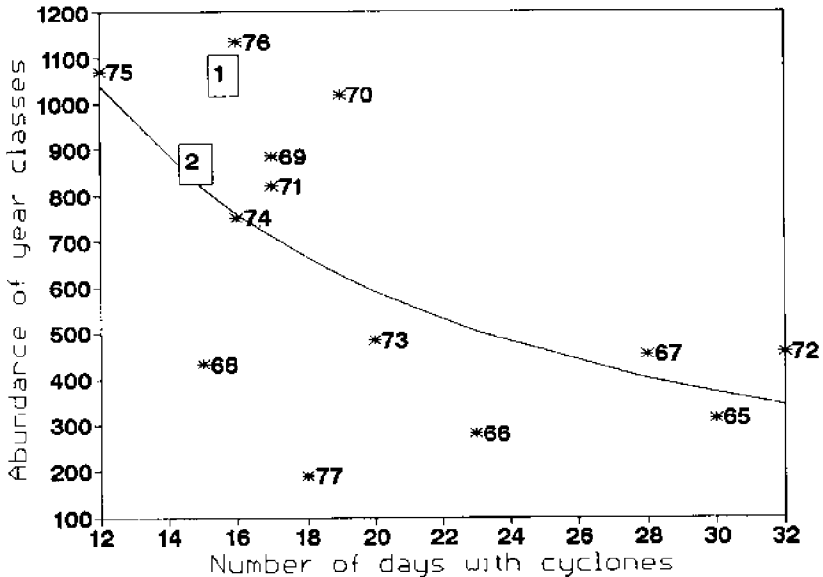


Figure 4. Connection of year-class abundance for Sakhalin flounder with the number of days with storm activity in April-July (the same signs as in Figure 2).

Results of calculated equations using corresponding data for year-to-year deviations of year-class abundance indicators for these species equal 15.1% for Alaska plaice and 30.7% for Sakhalin flounder.

We need to consider why flounder year-class abundance depends less on the duration of storm processes in fish spawning areas. Pertseva-Ostroumova (1961) addressed storm influence on the increase in egg mortality and the growth in number of deformed embryos. Tikhonov (1968) showed that when environmental factors in experimental conditions were unfavorable (changes in temperature, shaking), specific gravity of the eggs increased and they fell down to the vessel's bottom, thus escaping mechanical influence. Consequently, the growth of storm activity increases egg mortality on the surface and causes the eggs to go deeper. Eggs are kept at depth for a certain period of time, where they are not influenced by storms as on the surface. Habitat conditions for the embryos and larvae of these species are probably worse at depth than on the surface. This is one more factor for decreased brood abundance for those born in years with a greater number of storms.

The reason for decreasing flounder year-class abundance is a decrease in water temperature as storm activity increases. Tikhonov (1968) proved by experiment that an increase in water temperature within certain limits reduced the incubatory period for eggs. There is well expressed hyperbolic dependence between these variables. Consequently, flounder eggs develop more slowly in colder water during long storm periods, which can increase mortality.

Last, deteriorating food supplies for flounder larvae at depths also may be responsible for the decrease in year-class abundance.

Thus, we have described mathematically the influence of hydro-meteorological conditions during flounder spawning on year-class abundance, achieving conformity for three of the five species investigated. Strong storm activity unfavorably influences fish survival during early ontogenesis. This is the factor responsible for the decrease in commercial fish stocks. The importance of these results will be obvious when problems connected with long term abundance forecasts for commercial species of flounder are solved.

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Spawning and Maturation of Female Yellowfin Sole in the Eastern Bering Sea

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Abstract

Yellowfin sole (*Pleuronectes asper*) females from the eastern Bering Sea were examined to determine timing and location of spawning, and length and age at maturity. A total of 768 ovary pairs were collected in June during the 1993 eastern Bering Sea crab-groundfish bottom trawl survey conducted by the Alaska Fisheries Science Center. Approximately 10 ovary pairs were collected at each of 83 stations spaced 20 miles apart, from Bristol Bay northwest to Nunivak Island. Sampling was concentrated at stations with bottom depths ≤ 50 m.

Survey samples suggest that yellowfin sole are determinate batch spawners. Spawning and near spawning females were predominately found at bottom depths < 30 m where the yellowfin sole density was also highest. The presence of pre-spawning, spawning, and post-spawning females in samples indicated a protracted spawning season that began as early as May and extended into July or August. Based on 1992 and 1993 eastern Bering Sea survey collections, lengths at which 50% of the females were mature were 30.7 and 29.3 cm total length, respectively. Ages at 50% maturity during 1992 and 1993 were 10.5 and 10.6 years, respectively.

Introduction

Adult yellowfin sole, *Pleuronectes asper* (formerly *Limanda aspera*), in the eastern Bering Sea undergo annual migrations from wintering

areas near the continental shelf-slope break (approximately 200 m bottom depth) off Unimak Island and the Pribilof islands to nearshore areas of Bristol Bay and east of Nunivak Island in summer (Fadeev 1970, Wakabayashi 1989). Ichthyoplankton surveys (Musienko 1963, Kashkina 1965) have shown that yellowfin sole spawn in these nearshore areas during summer months. Investigations have also examined size and age at maturation for yellowfin sole during the late 1950s to early 1960s (Fadeev 1963, Fadeev 1970), 1970s (Wakabayashi 1989), and more recently in 1990 (Wilderbuer et al. 1992).

Preliminary observations of yellowfin sole ovaries during 1990 and 1991 Alaska Fisheries Science Center (AFSC) eastern Bering Sea crab-groundfish trawl surveys indicated that spawning may occur in batches. More comprehensive data collections in 1992 and 1993, with results presented here, provide details on yellowfin sole spawning activity and size and age at maturity during June and July of 1992 and 1993.

Methods

Female yellowfin sole were examined for maturity condition in June-July during the 1992 and 1993 eastern Bering Sea crab-groundfish trawl surveys conducted by the AFSC. The survey area included the Bering Sea continental shelf, from nearshore bottom depths of 16 m to the slope edge (200 m), and from the Alaska Peninsula north to approximately latitude 62°N. One bottom trawl tow, usually 30 minutes in duration, was completed during daylight hours at each of 336 and 355 standard stations in 1992 and 1993, respectively. Stations were spaced 20 nautical miles apart except in areas surrounding St. Matthew Island and the Pribilof Islands where higher intensity sampling occurred (Figure 1). The survey began in inner Bristol Bay and followed south-north directed transects, proceeding westward with each finished transect. Each survey used two chartered fishing vessels that sampled alternate transects. Yellowfin sole were captured at 231 and 243 stations during the 1992 and 1993 surveys, respectively.

Maturity tables specific to yellowfin sole females were constructed based on macroscopic observations made during 1990 and 1991 AFSC eastern Bering sea trawl surveys (Table 1). General maturity code tables previously used by the AFSC for a variety of fish species were deemed inappropriate due to the possibility that yellowfin sole were batch spawners.

In 1992, maturity codes (Table 1) were assigned to female yellowfin sole at sea in conjunction with two separate collections: total

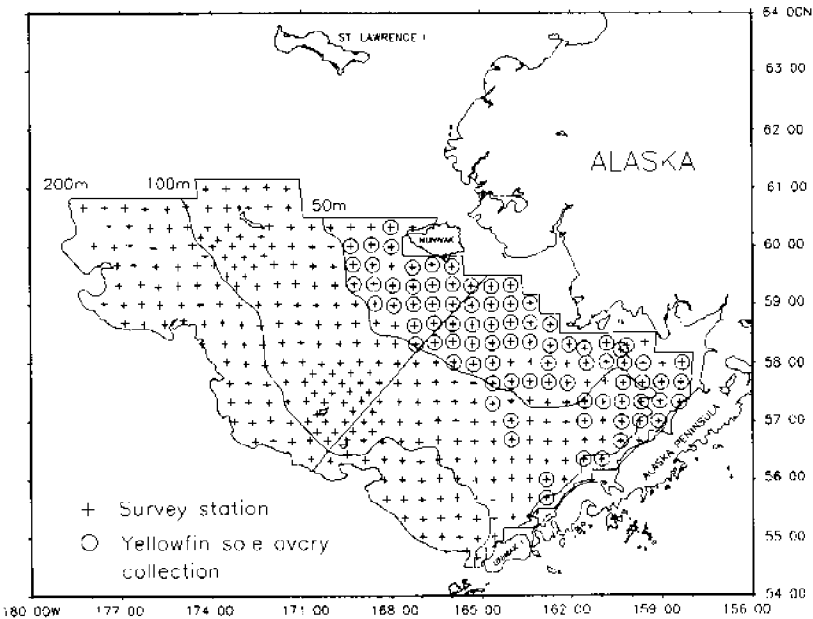


Figure 1. Alaska Fisheries Science Center crab-groundfish bottom trawl survey stations. Stations where yellowfin sole ovaries were collected during 1993 are circled.

length (TL) measurements from randomly selected females and sagittal otolith collections by cm-TL intervals (Table 2). Random length-maturity observations and otolith-maturity collections were not systematic by area and did not emphasize yellowfin sole spawning areas. Therefore 1992 maturity data is used here only to describe female yellowfin sole size and age at maturity.

Systematic maturity collections which emphasized yellowfin spawning areas were made in 1993. Seven hundred sixty-eight ovary pairs were collected from females captured among 83 stations (Figure 1) during June of the 1993 survey. Most of these stations were located within the 50 m bottom depth contour line. Based on the minimum size of mature females observed in 1992 (26 cm TL), 1993 collections emphasized mature females by collecting only females ≥ 25 cm TL. An attempt was made to collect ovary pairs from 10 females per station, 2 females 25-30 cm TL, 4 females 31-35 cm TL, and 4 females > 35 cm TL. This sampling scheme emphasized the collection of mature ovaries needed to examine evidence of spawning activity, but still

Table 1. Macroscopic maturity code designation for female yellowfin sole ovaries.

Code	Condition	Description
1	Immature	Ovary clear to slightly pink or grey-pink. No distinct oocytes. Ovarian wall thin and taut around ovary interior.
2	Maturing	Ovary usually opaque colored with distinct (vitellogenic) opaque colored oocytes. A network of veins covers the ovary.
3	Hydrated	As above but some portion of oocytes are clear-translucent (hydrated-unovulated). Hydrated are larger than the opaque oocytes and are randomly scattered about the ovary.
4	Spawning	Hydrated (clear) oocytes in core of ovary (ovulated). A continuous band of hydrated oocytes may also be visible from the ovary sides. Eggs may run with slight pressure. If all oocytes are clear-translucent, this represents the last batch of eggs to be spawned in the season.
5	Spent	Deflated ovary, often with blood. Ovary wall thick and often flaccid around ovary interior.

Table 2. Summary of female yellowfin sole (*Pleuronectes aspera*) maturity collections. Numbers in parentheses indicate number of stations sampled.

Year	Number of Maturity Samples		
	Random length measurements	Otolith collections ^a	Ovary collections ^a
1992	1,260 (14)	326 (14)	—
1993	—	313 (17)	768 (83)

^a Includes sample length measurements in addition to random length measurements.

allowed for an adequate number of immature females needed to compute proportions of size at maturity. Maturity codes (Table 1) were assigned to females at sea. Ovaries were stored in 10% buffered formalin and were subsequently weighed (nearest 0.01 g) in the laboratory. Histological cross-sections through the middle portion of all collected ovaries were prepared for later microscopic analysis.

As in 1992, maturity codes (Table 1) were also assigned to female yellowfin sole in conjunction with sagittal otolith collections (by cm-TL interval) during June and July of 1993 (Table 2). Otoliths were stored in a 50% glycerol/water solution and were subsequently aged by the Age and Growth unit of the Resource Ecology and Fisheries Management Division at the AFSC.

A relative measure of ovary-size to body size, a gonadosomatic index (GSI), was calculated for each collected ovary pair as:

$$GSI = \frac{\text{Paired Ovary Weight (g)}}{\text{Total Length (cm)}} \times 100$$

Length and age at 50% maturity were calculated by fitting the logistic curve:

$$P_X = \frac{1}{1 + e^{AX+B}}$$

to the data where P_X = Proportion mature at length or age X . Constants A and B were estimated using non-linear least squares regression (SAS Institute 1987). Length and age at 50% maturity (L_{50} and A_{50}) were computed as:

$$X = \frac{-B}{A}$$

Catch per unit effort (CPUE) of yellowfin sole (sexes combined) was calculated for each tow in kilograms per hectare. Area swept (in hectares) was calculated as the distance towed multiplied by the average net width within each tow.

Results

How

Observations of partial ovary hydration, where only a portion of the oocytes within an ovary were hydrated (stages 3 and 4; Table 1), confirmed that individual yellowfin sole spawned eggs in batches. Initial hydration of oocytes (stage 3) occurred randomly within ovaries. After ovulation (stage 4), hydrated oocytes accumulated in the

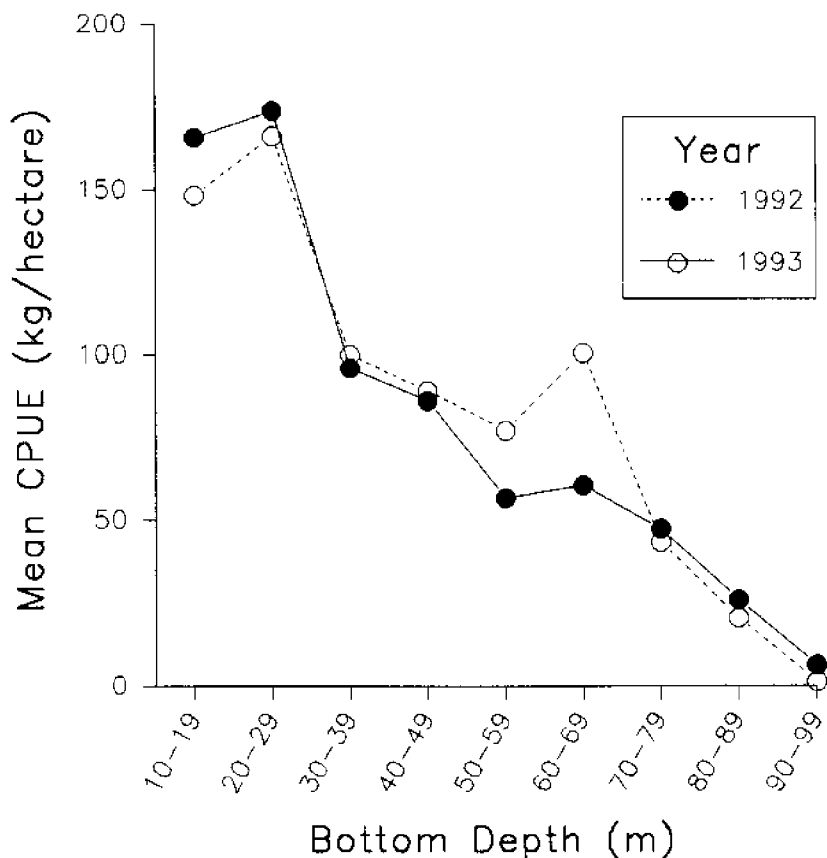


Figure 2. Mean catch per unit effort (CPUE) of yellowfin sole, by bottom depth, during 1992 and 1993 AFSC crab-groundfish bottom trawl surveys.

center of the ovary (Table 1). Preliminary histological examination of collected ovaries indicated the occurrence of only one mode of advanced yolked oocytes prior to oocyte hydration suggesting that yellowfin sole are determinate batch spawners.

Where

CPUE (kg/ha) data from both 1992 and 1993 indicated yellowfin sole (sexes combined) abundance was concentrated in areas < 30 m bottom depth (Figure 2). Spawning (stage 4) and near spawning (stage

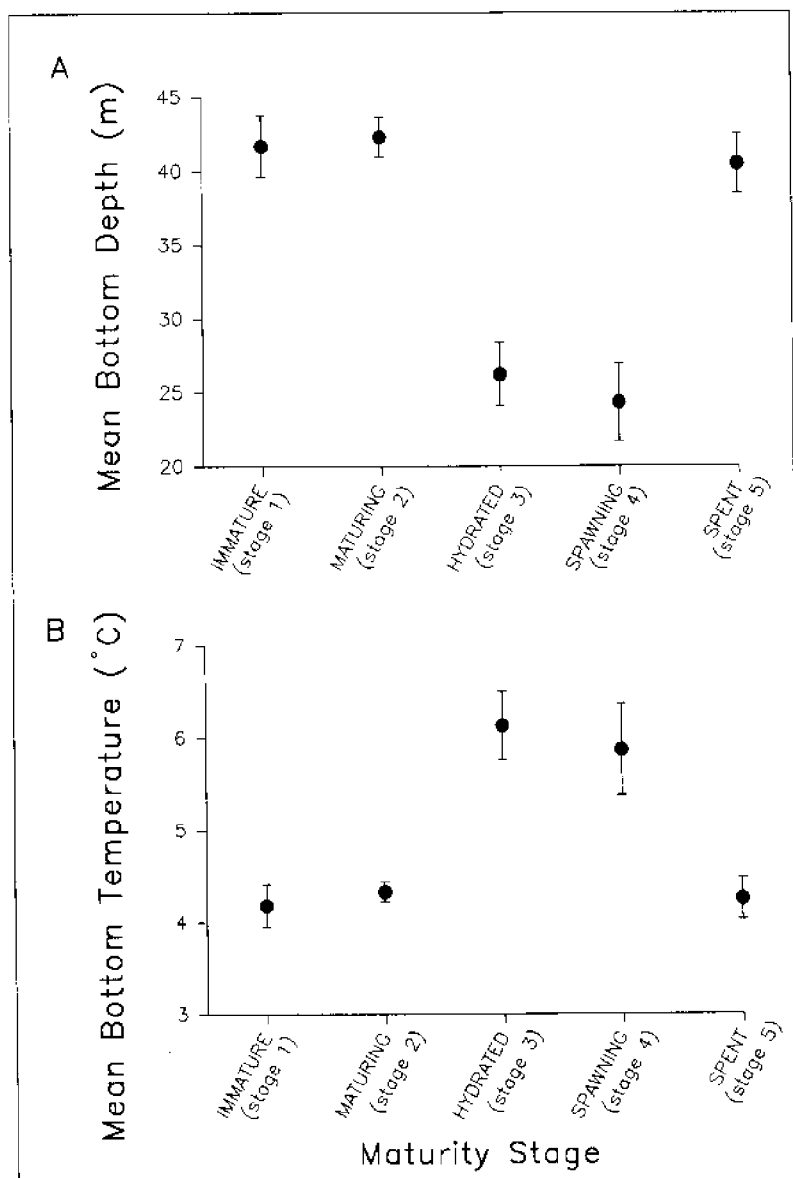


Figure 3. Average bottom depth (A) and bottom temperature (B) at which yellowfin sole females with ovaries in different maturity stages were observed in June 1993. Bars indicate 95% confidence intervals.

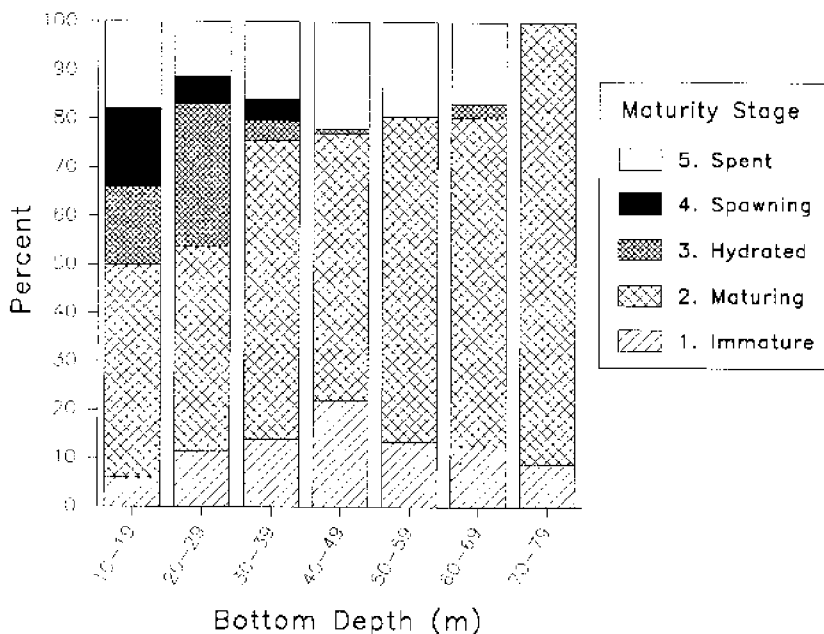


Figure 4. Percent frequency distribution of yellowfin sole females with different maturity stages by bottom depth, during June 1993. Note that immature females < 25 cm TL are excluded.

3) yellowfin sole were found primarily at bottom depths < 30 m (Figure 3A) and bottom temperatures between 5.5°C and 6.5°C (Figure 3B), from Bristol Bay north to Nunivak Island. Most mature females (66.1%) had maturing/vitellogenic (stage 2) ovaries. Females in this stage were common in all depth strata (Figure 4). Immature (stage 1) and spent (stage 5) females were also found at nearly all depths sampled, but were less common.

Maturing females in shallower nearshore waters had proportionately larger ovaries (stage 2) relative to their body length than did females further offshore. Gonadosomatic indices of stage-2 ovaries increased twofold from bottom depths of 70-79 m to bottom depths < 20 m (Figure 5).

When

The concurrence of pre-spawning, spawning, and post-spawned females suggested a protracted spawning season that began prior to

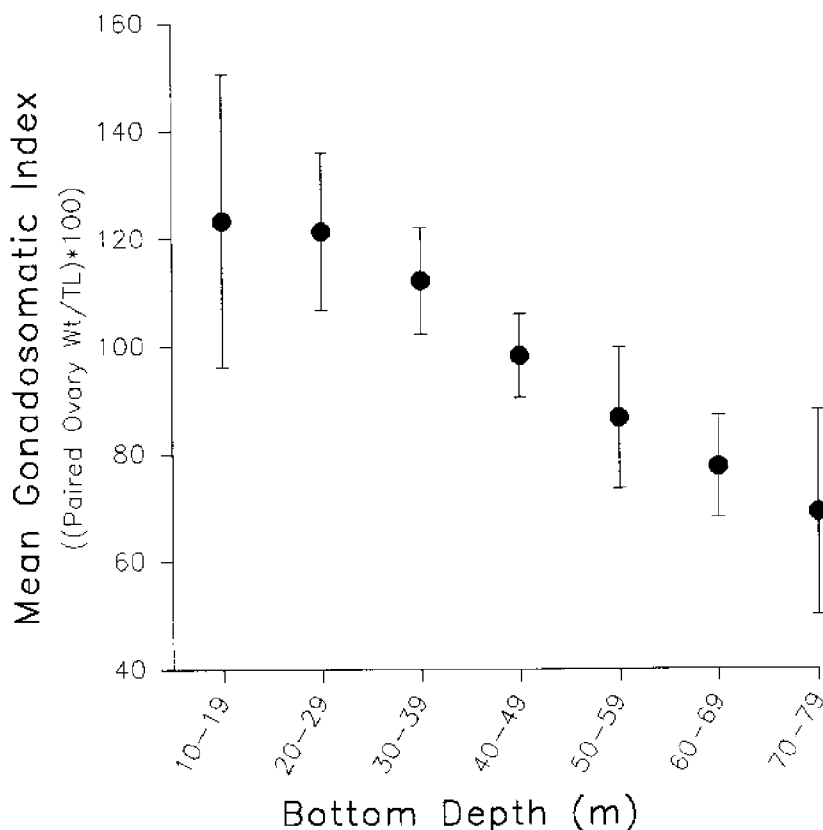


Figure 5. Average gonadosomatic index of maturing (stage 2) female yellowfin sole by bottom depth, during June 1993. Bars indicate 95% confidence intervals.

June and extended into July or August. The frequency of females with spent ovaries was low at the beginning of sampling (June 4), but increased considerably by the end of June (Figure 6). The percentage of females in near spawning to spawning conditions (stages 3 and 4) did not appear to change during this period.

Size and age at maturity

All yellowfin sole females < 26 cm TL and younger than age 5 were immature. Estimates of length at 50% maturity (L_{50}) were 30.7 cm TL in 1992 and 29.3 cm TL in 1993 (Figure 7A; Table 3). Age-maturation

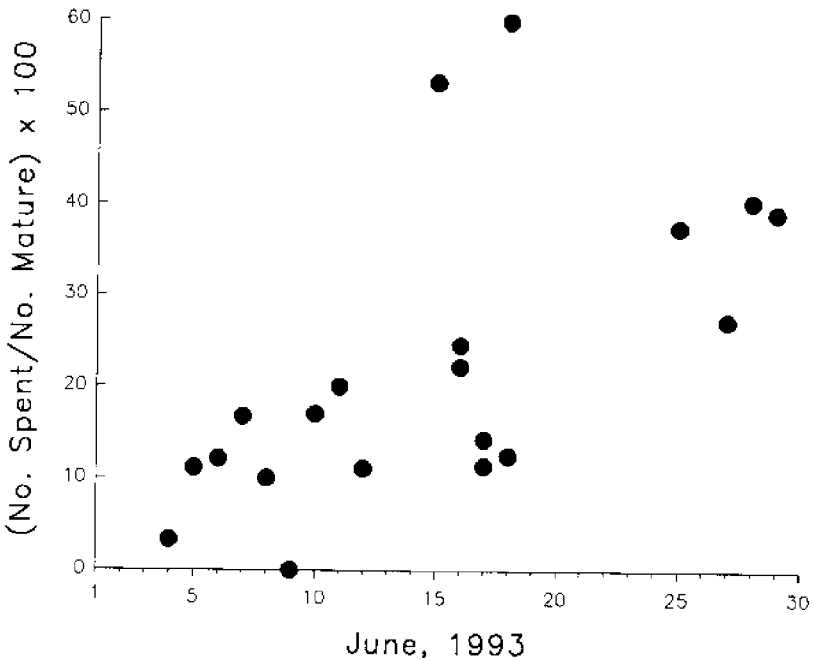


Figure 6. Percentage of spent female yellowfin sole among all mature females sampled, from 4 June through 29 June 1993.

relationships were nearly identical between 1992 and 1993 (Figure 7B; Table 3). Estimates of A_{50} were 10.5 years and 10.6 years in 1992 and 1993, respectively.

Discussion

How?

Yellowfin sole females in the eastern Bering Sea, like those in the northwestern Sea of Japan (Ivankov and Ivankova 1974) are batch spawners. Maturing oocytes develop synchronously to a fixed size through vitellogenesis, then a portion of this mature oocyte "stock" is hydrated. After this "batch" is spawned, another portion of the original stock is hydrated. In this manner ovaries progress from a maturing (stage-2) condition to unovulated hydrated (stage 3) and ovulated hydrated (stage 4) conditions, and then back to the stage-2 condition (Table 1). This loop is repeated until all eggs have been spawned

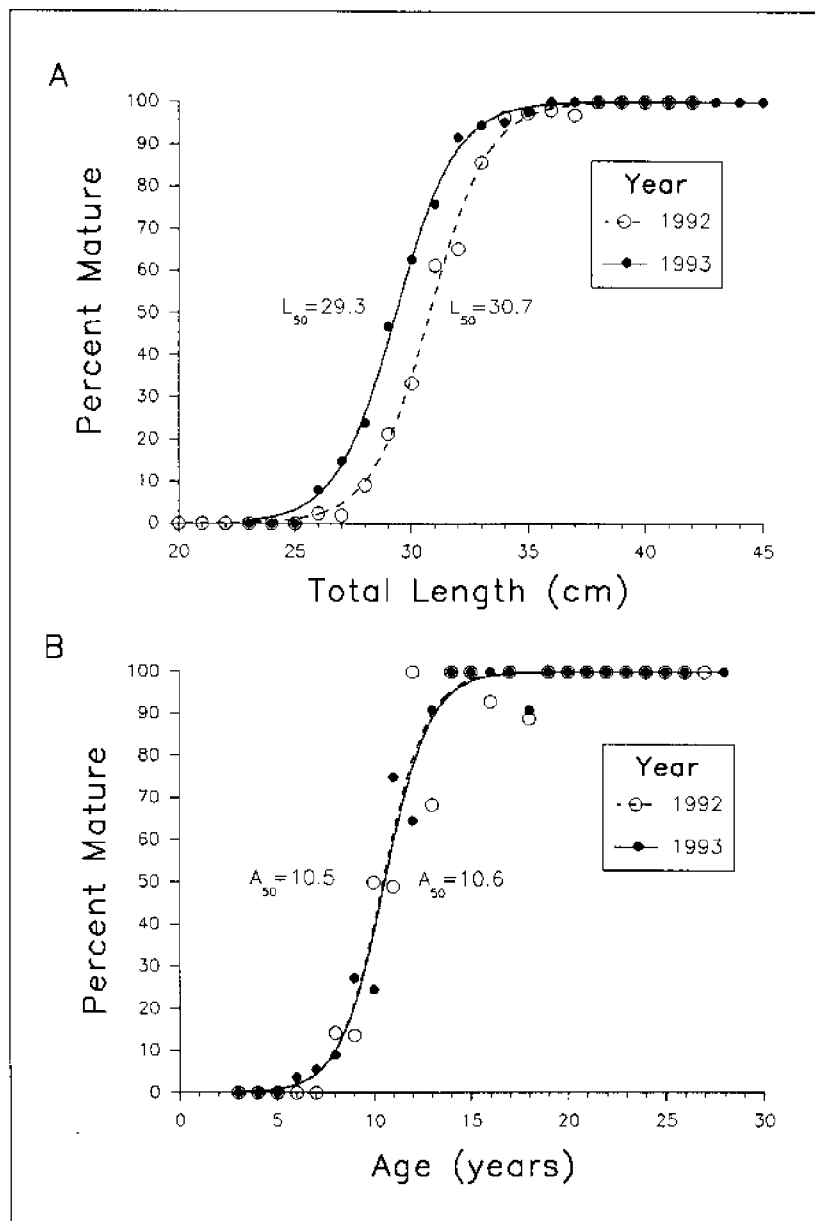


Figure 7. Observed (circles) and predicted (lines) percentages of mature female yellowfin sole at length (A) and age (B), during 1992 and 1993.

Table 3. Estimates of length and age at 50% maturity derived from the logistic equation $P_X = 1/(1+e^{-AX+B})$ fitted to proportions of mature female yellowfin sole at length (cm) and age (years). TL = total length; n = number of females used in proportions.

X	Year	Constants		r^2	n	50% maturity estimate
		A	B			
TL	1992	-0.79	24.45	>0.99	1,260	30.7
	1993	-0.78	22.94	>0.99	1,029	29.3
Age	1992	-0.88	9.18	0.98	326	10.5
	1993	-0.86	9.05	0.99	313	10.6

(stage 5). Assuming yellowfin sole in the eastern Bering Sea exhibit the same general spawning strategy as yellowfin sole in the northwestern Sea of Japan (Ivankov and Ivankova 1972), a female may spawn as many as five batches during the course of one reproductive season.

Given that yellowfin sole are batch spawners, the selection of females for fecundity estimation requires careful screening for partially spawned ovaries. Hunter et al. (1992) noted that the inclusion of fecundity data from partially spawned ovaries can significantly bias (underestimate) estimates of potential annual fecundity, the standing stock of advanced yolked oocytes prior to the onset of spawning. Unfortunately, pre-spawning stage-2 ovaries can be indistinguishable macroscopically from stage-2 ovaries that have already released one or more batches. For fecundity analyses, microscopic examinations are needed to determine previous spawnings (i.e., presence of postovulatory follicles within ovaries) and thereby eliminate potential bias.

Where?

Previous authors have shown from maturity studies (Fadeev 1963, Fadeev 1970, Wakabayashi 1989) and ichthyoplankton studies (Musienko 1963, Kashkina 1965) that, in general, yellowfin sole in the eastern Bering Sea spawn at bottom depths < 50 m. In this study we found that the majority of yellowfin sole females, at least in 1993, spawned at bottom depths < 30 m (Figure 3A).

Musienko (1963) and Kashkina (1965) observed recently spawned yellowfin sole eggs at bottom temperatures of 4.4°C to 11.4°C. These correspond roughly to the bottom temperatures where spawning females were captured during 1993 (Figure 3B).

In June-July of 1992 and 1993, the highest concentrations of yellowfin sole were found at bottom depths < 30 m where females spawn (Figures 2, 3). Because concentrations were highest at the shallowest stations sampled, the yellowfin sole spawning grounds presented here probably extend closer to shore.

Fadeev (1963) concluded that because spent females were observed in the central portion of the eastern Bering Sea shelf in July, they must have migrated from nearshore shelf areas when spawning was finished. In the present study, females with partially deflated stage-2 ovaries, presumably those that have spawned at least one batch but not all, were observed at bottom depths greater than 30 m. This suggests that females may not necessarily remain on the spawning grounds (< 30 m bottom depth) until all batches have been spawned. They may actually move offshore then back nearshore after each successive batch is spawned. Continuing research that includes histological examination of collected ovaries should verify this pattern of movement.

Females with maturing (stage 2) ovaries appeared to gain ovary weight from offshore (> 70 m) to nearshore (< 20 m) (Figure 6). This increase is likely due to an increase in oocyte size through yolk accumulation as females migrate inshore to spawn. Another possibility, however, is that a higher percentage of females offshore relative to those nearshore had already spawned at least one batch. Planned research which includes egg-size measurements and histological evaluation of ovaries should clarify this relationship.

When?

Previous investigations have indicated protracted spawning of yellowfin sole in the eastern Bering Sea, with spawning beginning in June or July and ending by August or September (Musienko 1963, Fadeev 1965, Fadeev 1970, Musienko 1970, Wakabayashi 1989). More recent studies (Wilderbuer et al. 1992), including this investigation, also indicate a protracted spawning season, but it may begin as early as May. Given that the spawning period for individual yellowfin sole females can be extended due to batch spawning, the presence of spent females in

Table 4. Estimates of female yellowfin sole length (L_{50}) and age (A_{50}) at 50% maturity, from various investigations.

Reference	Location ^a	Year of collection	L_{50} (cm)	A_{50} (years)
Present study	EBS	1992	30.7	10.5
		1993	29.3	10.6
Wilderbuer et al. (1992)	EBS	1990	28.8	9
Wakabayashi (1989)	EBS	1973	25.5-26.0	—
		1974	25.5-26.0	—
		1978	27.0-27.5	11
Fadeev (1970)	EBS	1959-64	30-32	9
Tikhonov (1978)	WKS	1961-63	29.9	8.5
		1964-66	28.0	8.0
		1967-69	27.2	7.2

^a EBS=eastern Bering Sea; WKS=western Kamchatka Shelf

early June (Figure 6) suggests some individuals began spawning well before June.

At what length and age?

Tikhonov (1977) noted a decrease in size and age at maturity (Table 4), along with an increase in fecundity in female yellowfin sole captured off the western Kamchatka shelf from 1961 to 1969. He attributed a decrease in L_{50} and A_{50} to a decrease in population abundance. Wakabayashi (1989) and Wilderbuer et al. (1992) suggested a similar trend for yellowfin sole in the eastern Bering Sea. Values of L_{50} and A_{50} derived from females examined in 1959-64 (Fadeev 1970) when the fishery was productive (Wilderbuer et al. 1992), were high relative to 1973-78 estimates (Wakabayashi 1989), when stock size was presumably much lower. Relatively high yellowfin sole biomass estimates, 2.2 million metric tons (mt) in 1990 to 2.5 million mt in 1993 (Wilderbuer 1993), coincide with high values of L_{50} and A_{50} (Table 3).

Further research

Ongoing research includes the estimation of total and batch fecundity of yellowfin sole following methods of Hunter et al. (1992). Histologi-

cal preparation of ovary cross-sections from the 1993 ovary collections ($n = 768$) has been completed. Maturing (stage 2) ovaries that show no evidence of previous batches spawned will be selected for total fecundity estimation. Batch fecundity will be estimated from ovaries with unovulated hydrated oocytes (stage 3).

Additional research also includes an examination of spatial factors (i.e., northwest vs. southeast and nearshore vs. offshore), that may refine estimates of length and age at maturity.

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Latitudinal Patterns in Reproductive Life History Traits of Northeast Pacific Flatfish

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Abstract

Information on spawning period and age-length at maturity are critical to determine the reproductive capacity of fish populations. The timing and duration of spawning and age-length at maturity were examined in six species of Northeast Pacific flatfish to infer potential latitudinal variations (Pacific halibut, petrale sole, English sole, starry flounder, Dover sole and rex sole). Throughout the species' geographical range, spawning occurred mainly during winter (Pacific halibut, petrale sole and English sole), from winter to spring (Dover sole and starry flounder), and from winter to summer (rex sole). With the exception of Pacific halibut and English sole, all species tended to spawn in later months toward their northern habitats. Spawning period of starry flounder, petrale sole, Dover sole and rex sole seemed to be shorter in the northern range of the species' distribution. Yet, spawning period for English sole appeared to be longer in its central geographical range. A clear trend for earlier age at first maturity toward lower latitudes was only suggested for Pacific halibut. However, the reported age or length at 50% (or 100%) maturity for females appeared to increase toward the northern range of the species' distribution for Pacific halibut, petrale sole, English sole, starry flounder and rex sole. Thus, spawning period and age or length at 50% (or 100%) of maturity could be more environmentally influenced than age or length at first maturity. With the exception of rex sole, long-term averages of sea temperature (at 0, 30 and 122 m of depth) did not support the hypothesis that fish populations from high latitudes tend

to spawn during the warmer months of the year. The tendency for later spawning period of flatfish at high latitudes could be an adaptation to match a subsequent onset of food production for fish larvae.

Introduction

The lifetime reproductive output and the reproductive strategy of a species is determined by several life-history characteristics such as the spawning period, the age at first maturity, fecundity and other reproductive traits (Wootton 1982). Moreover, the variation in spawning strategies of marine fishes from high and low latitudes may have evolved as a result of different limitations on growth and survival of larvae (Houde 1989). Latitudinal variations in the production cycle are characterized by a later spring bloom at high latitudes. Such time lag is ascribed both to a subsequent increase in light intensity, and to a later shallowing of the mixed layer, relative to areas away from the poles (Valiela 1984). However, temperature could control the poleward propagation of the spring bloom (Mann and Lazier 1991) as well as the spawning timing of fish populations in different latitudes (Bagenal 1971, Thorpe 1977).

Life history theory predicts that toward higher latitudes fish will maximize fitness in a variable environment by increasing both age at maturity and life span and decreasing brood size (Dillinger et al. 1987). On the other hand, some studies suggest that the spawning season of fish start earlier at low latitudes of the species' range and continue poleward following the production cycle (Bagenal 1971, Theilacker and Dorsey 1980). Although this later hypothesis is consistent with an adaptation to enhance the feeding of fish larvae (Nikolsky 1963), it has not been examined in recent reviews of environmental effects on fish reproduction (e.g., Munro et al. 1990, Wootton 1994).

With the exception of a study in Pacific halibut (St-Pierre 1984), information on the spawning period and age-length at maturity has not been summarized for widely distributed species of flatfish in the Northeast Pacific Ocean. The objectives of this study were to examine if six species of Northeast Pacific flatfish of the family Pleuronectidae exhibit latitudinal trends in: (1) the onset and duration of the spawning period and (2) the age-length at first maturity and/or age-length at 50% (or 100%) maturity. A complementary objective was to investigate if fish populations from high latitudes ($>45^{\circ}\text{N}$) tend to spawn during the warmer months of the year.

Table 1. Latitudinal range, bathymetric distribution and estimated age at metamorphosis for the six species of flatfish considered in this study. About 50% of the species' occurrences are included between the lower depth and the mid depth. Latitude ranges were based on Miller and Lea (1972) and Allen and Smith (1988).

Species	Latitude range (degrees N)	Depth (m)			Age at metamorphosis (months)
		Lower	Mid	Maximum	
Pacific halibut <i>Hypoglossus stenolepis</i>	34-66	6	150	1097	6.0 ^a
Petrale sole <i>Eopsetta jordani</i>	32-60	0	150	550	6.0 ^b
English sole <i>Pleuronectes vetulus</i> ^c	27-61	0	150	550	2.2 ^d
Dover sole <i>Microstomus pacificus</i>	27-61	10	200	1189	9.0 ^e
Starry flounder <i>Platichthys stellatus</i>	34-67	0	50	375	1.5 ^f
Rex sole <i>Errex zachirus</i> ^g	28-61	0	150	800	12.0 ^h

^a IPHC (1978)

^b Castillo et al. (1994, their figure 2)

^c *Parophrys vetulus*

^d Laroche et al. (1982)

^e Markle et al. (1992)

^f Orcutt (1950)

^g *Glyptocephalus zachirus*

^h Pearcy et al. (1977).

The six species of flatfish selected for this study were: Pacific halibut, petrale sole, English sole, Dover sole, starry flounder and rex sole. These species were chosen for this study because of their wide latitudinal range (Table 1), and because they have more complete information on spawning period and age/length at maturity than other species of flatfish in the Northeast Pacific Ocean and/or the Bering Sea. On the other hand, estimated age at metamorphosis and bathymetric ranges of species's occurrences indicate large variations between some of the species considered (Table 1).

Methods

This study was based on a literature review on spawning period and age-length at maturity (first maturity and 50% or 100% maturity). Although 50% maturity and 100% maturity are defined as the age or size in which the cumulative percent of mature individuals is 50% and 100% respectively, no operational definition was found for age or length at first maturity. Therefore, the age or length at first maturity was defined here as the age or size in which the cumulative percent of mature individuals is 1%. Although the later definition is a rough approximation to the data on first maturity cited in this review, it reduces the possibility of considering rare cases of earlier maturity. Despite that the spawning periods were stated in most of the studies considered, spawning was also inferred from the presence of fish eggs in the plankton (Van Cleve and Seymour 1953, Kendall and Dunn 1985). Average monthly sea temperatures for the Northeast Pacific and the Gulf of Alaska at the surface and 122 m of depth were obtained between 30°N and 60°N from Robinson (1976). The previous reference was also used to obtain temperature averages at the sea surface and at 30 m of depth in the Eastern Bering Sea (nearly at 60°N). Sea tempera-

PACIFIC HALIBUT SPAWNING PERIOD

SPAWNING AREAS		OC	NO	DE	JA	FE	MR	AP	MY	JN	JL	AU	SE
SOURCE													
BERING SEA	1	■	■	■	■	■	■						
	2	■	■	■	■	■							
	3			■	■	■							
GULF OF ALASKA	4		■	■	■	■							
GULF OF ALASKA TO BRITISH COLUMBIA	5			■	■	■	■	■	■				
	6		■	■	■	■	■						
BRITISH COLUMBIA	7			■	■	■	■						

Figure 1. Monthly variation in the spawning period of Pacific halibut in the Northeast Pacific Ocean and the Bering Sea. Spawning areas are ordered from north to south. Reported spawning peaks are represented by larger black bars. Sources: 1-(Novikov 1968); 2-(Pertseva-Ostroumova 1961); 3-(Best 1981); 4-(Dunlop et al. 1964); 5-(Thompson 1914); 6-(IPHC 1978); 7-(Van Cleve and Seymour 1953).

Table 2. Age and length at first maturity of Pacific halibut in the Northeast Pacific Ocean and the Eastern Bering Sea. Spawning areas are ordered from north to south.

Spawning area	Age at first maturity (years)		Length at first maturity (cm)		Source
	females	males	females	males	
Eastern Bering Sea	9	7	90	70	Novikov (1968)
	10	7	-	-	St-Pierre (1984, his table 2)
Northeast Pacific	8	5	-	-	Dunlop 1957, cited by Novikov (1968)
	7	5	-	-	St-Pierre (1984, his table 2)

tures at 30 m of depth (rather than at 122 m) were used because of the shallower waters of the Eastern Bering Sea.

Since many studies only reported the general location of spawning, the spawning areas were ordered by broad regions and approximate latitude ranges, these areas are: California (32-42°N); Oregon (42-46°N); Washington (46-48°N); British Columbia (48-54°N); Gulf of Alaska (54-60°N); and Bering Sea (52-66°N). Although the latitude ranges of the Gulf of Alaska and the Bering Sea overlap partially, the long-term monthly average temperatures shown by Robinson (1976) are lower for the Eastern Bering Sea than for the Gulf of Alaska during most of the year.

Results

Pacific halibut

No latitudinal trends were detected in the timing of spawning for this species (Figure 1). First maturity for both sexes seems to occur 2 or 3 years earlier in the Northeast Pacific than in the Eastern Bering Sea (Table 2). However, Novikov (1968) reported that in isolated cases males may mature at age 4 (55 cm) and females at age 6 (60 cm) in the Bering Sea. Yet, he also suggested an earlier age of maturation for Pacific halibut in the Northeast Pacific than in the Bering Sea.

PETRALE SOLE SPAWNING PERIOD

SPAWNING AREA	SOURCE	OC	NO	DE	JA	FE	MR	AP	MY	JN	JL	AU	SE
OFF BRITISH COLUMBIA	1				■	■	■	■					
	2				■	■	■	■					
OFF BRIT. COLUM. AND WASHINGTON	3				■	■	■	■					
OFF WASHINGTON	4			■	■	■	■	■					
OFF OREGON	5		■	■	■	■	■	■	■				
OFF CALIFORNIA	6			■	■	■							
	7		■	■	■	■	■	■					
	8		■	■	■	■	■	■					

Figure 2. Monthly variation in the spawning period of petrale sole in the Northeast Pacific Ocean. Spawning areas are ordered from north to south. Reported spawning peaks are represented by larger black bars. Sources are: 1-(Forrester 1969); 2-(Barraclough 1954); 3-(Alverson and Chatwin 1957); 4-(Pedersen 1975); 5-(Harry 1956); 6-(Best 1963); 7-(Porter 1964); 8-(Gregory and Jow 1976).

St-Pierre (1984) reported 50% maturity in the Northeast Pacific coast at about age 8 in males and at age 12 in females. Females also reach 50% of maturity at age 12 in the Yakutat region, Alaska (Schmitt and Skud 1978). For the Eastern Bering Sea, age at 50% of maturity is about 14 years for females and 12 years for males (St-Pierre 1984, his table 2). On the other hand, Best (1981) reported ages at 50% maturity in the Bering Sea of about 14 years for females and 7.5 years for males. Thus, only female Pacific halibut seem to have earlier age at 50% of maturity in low latitudes.

Petrale sole

The spawning seems to begin at least one month later off British Columbia than off Oregon and California (Figure 2). With the exception of the December-February spawning reported for the California Coast, spawning period appears more protracted toward lower latitudes by at least 1 month. Although the size or age at first maturity for males and females did not show a clear latitudinal trend (Table 3),

Table 3. Age and length at first maturity of petrale sole in the Northeast Pacific Ocean. Spawning areas are ordered from north to south.

Spawning area	Age at first maturity (years)		Length at first maturity (cm)		Source
	females	males	females	males	
Off British Columbia	5	4	35	32	Forrester (1969)
	—	—	35	32	Ketchen and Forrester (1966)
	4	2	37	30	Cleaver (1949, his table 6)
	—	—	37	31	Pedersen (1975, his table 16)
Off Washington to Northern Oregon	—	—	34	32	Pedersen (1975, his table 16)
Off Oregon	—	—	31	29	Harry (1956)
Off California	5	—	32	—	Porter (1964)

Table 4. Age and length at first maturity of English sole in the Northeast Pacific Ocean. Spawning areas are ordered from north to south.

Spawning area	Age at first maturity (years)		Length at first maturity (cm)		Source
	females	males	females	males	
Off British Columbia	3	2	—	—	Ketchen (1956)
	—	—	25	—	Tyler et al. (1987)
	—	—	29	—	Foucher et al. 1989, their table 4)
	3	—	30	25	Forrester (1969)
Washington (Puget Sound)	3	2	—	—	Smith (1936)
Off Oregon	4	—	26	19	Harry (1956 and 1959)

ENGLISH SOLE SPAWNING PERIOD

SPAWNING AREA	SOURCE	SE	OC	NO	DE	JA	FE	MR	AP	MY	JN	JL	AU
GULF OF ALASKA	1	■											
OFF BRITISH COLUMBIA	2				■	■	■	■	■				
	3				■	■	■	■	■				
	4		■	■	■	■	■	■	■				
	5		■	■	■	■	■	■	■				
PUGET SOUND	6				■	■	■	■	■				
	7				■	■	■	■	■				
OFF OREGON	8			■	■	■	■	■	■	■			
	9	■	■	■	■	■	■	■	■	■			
OFF CALIFORNIA	10		■	■	■	■	■	■	■	■			
	11			■	■	■	■	■	■	■			
	12			■	■	■	■	■	■	■			
	13				■	■	■	■	■	■	■		
	14				■	■	■	■	■	■	■		

Figure 3. Monthly variation in the spawning period of English sole in the Northeast Pacific Ocean. Spawning areas are ordered from north to south. Reported spawning peaks are represented by larger black bars. A left (or right) half black bar represents spawning in the early (or late) part of the month. Sources are: 1-(Kendall and Dunn 1985); 2-(Ketchen 1956); 3-(Forrester 1969); 4-(Clemens and Wilby 1961); 5-(Fargo and Tyler 1994); 6-(Smith 1936); 7-(Johnson et al. 1991); 8-(Harry 1956 and 1959); 9-(Kruse and Tyler 1983); 10-(Jow 1969); 11-(Villadolid 1927); 12-(Jow 1969); 13-(Budd 1940); 14-(Jow 1969).

Ketchen and Forrester (1966) suggested earlier maturation and/or smaller size at maturity off the Columbia River than in the Hecate Strait. Pedersen (1975, his Table 17) showed that lengths at 50% of maturity for males and females were larger in the Hecate Strait (females 44 cm and males 38 cm) than off the Columbia River (females nearly 40 cm and males nearly 35 cm). Pedersen (1975) also indicated a declining trend for female sizes at 50% maturity along 6 areas from the Hecate Strait to off California. In the later area, Best (1961) reported that female petrale sole reach 50% maturity at about 36 cm. Thus, increasing size at 50% of maturity from south to north is suggested for both sexes, but particularly for females.

DOVER SOLE SPAWNING PERIOD

SPAWNING AREA SOURCE	OC	NO	DE	JA	FE	MR	AP	MY	JN	JL	AU	SE
BERING SEA 1						■	■	■	■			
GULF OF ALASKA 2							■	■	■			
OFF BRITISH COLUMBIA 3			■	■								
OFF OREGON 4		■	■	■	■	■	■					
5			■	■								
6					■	■	■	■	■	■		
OFF CALIFORNIA 7		■	■	■	■	■						
8			■	■	■	■	■	■				

Figure 4. Monthly variation in the spawning period of Dover sole in the Northeast Pacific Ocean. Spawning areas are ordered from north to south. Reported spawning peaks are represented by larger black bars. Sources are: 1-(Hirschberger and Smith 1983); 2-(Kendall and Dunn 1985); 3-(Clemens and Wilby 1961); 4-(Demory 1975); 5-(Yoklavich and Pikitch 1989); 6-(Hosie cited by Markle et al. 1992); 7-(Hagerman 1952); 8-(Hunter et al. 1990).

English sole

No latitudinal trends in the onset of the spawning period or the spawning peak were detected for this species (Figure 3). However, the spawning period may be more protracted off Northern California-Oregon than at higher or lower latitudes (Figure 3, sources 9 and 10). On the other hand, age or length at first maturity for both sexes did not suggest differences in age at first maturity off Oregon and off British Columbia (Table 4). Moreover, lengths of female English sole at first maturity in the Hecate Strait did not show a relationship between size at first maturity and latitude (Foucher et al. 1989, their figures 17 to 20).

The size at 50% maturity of female English sole in the Hecate Strait increased from south to north from about 33 cm to 35 cm (Foucher et al. 1989). Off northern Oregon, the estimated size at 50% maturity for female English sole was nearly 31 cm (Harry 1959). Thus,

Table 5. Age and length at first maturity of Dover sole in the Northeast Pacific Ocean. Spawning areas are ordered from north to south.

Spawning area	Age at first maturity (years)		Length at first maturity (cm)		Source
	females	males	females	males	
Off Oregon	—	—	33	—	Harry (1956)
	6	6	30	30	Demory (1975)
	—	—	24	—	Yoklavich and Pikitch (1989)
Off California	5	4	35	32	Hagerman (1952)
	6	—	29	—	Hunter (1990)

a consistent northward increase in the size at 50% of maturity was evident for female English sole.

Dover sole

The spawning peak in this species tends to start earlier off Oregon and California than off the Bering Sea. Moreover, the spawning period seems to be shorter off British Columbia and the Gulf of Alaska than in lower latitudes. The only exception to this pattern was reported for the southern Oregon coast (Figure 4, source 6). However, Markle et al. (1992) suggested that the information for the southern Oregon coast may be biased toward later-spawning fish. Moreover, smaller Dover sole may have an earlier and/or shorter spawning season than larger fish (Yoklavich and Pikitch 1989), and small fish are discarded prior to sampling from commercial catches (TenEyck and Demory 1975). Although Hunter et al. (1992) stated that the spawning season off central California begins in December, they considered November as the earliest month of spawning. They also reported that the percent of spawning females during November-December was higher off California (2.9% of females) than off Oregon (1% of females). Hence, the previous study supports an earlier onset of the spawning period for Dover sole off California than off Oregon.

Data on age or length at first maturity did not show a consistent latitudinal trend for Dover sole (Table 5). Potential sampling bias do not allow reliable comparison of age or length at 50% maturity in Dover sole (Yoklavich and Pikitch 1989, Hunter et al. 1992). On the

STARRY FLOUNDER SPAWNING PERIOD

SPAWNING AREA	SOURCE	OC	NO	DE	JA	FE	MR	AP	MY	JN	JL	AU	SE
BERING SEA	1								■	■			
	2								■	■			
GULF OF ALASKA	3							■	■	■	■		
	4					■	■	■					
PUGET SOUND	5					■	■	■					
	6		■	■	■	■							
OFF CALIFORNIA	6		■	■	■	■							

Figure 5. Monthly variation in the spawning period of starry flounder in the Northeast Pacific Ocean and the Bering Sea. Spawning areas are ordered from north to south. Reported spawning peaks are represented by larger black bars. A left (or right) half bar indicates spawning in the early (or late) part of the month. Sources are: 1-(Musienko 1972); 2-(Fadeev 1968); 3-(Kendall and Dunn 1985); 4-(Smith 1936); 5-(Hart 1973); 6-(Orcutt 1950).

other hand, estimated sizes at 100% maturity for female Dover sole in Northern Oregon were nearly 46 cm (Harry 1959) and 32 cm (Yoklavich and Pikitch 1989). Such large variation of size for the same area did not allow reliable comparison with lengths at 100% maturity off California (nearly 45 cm, Hagerman 1952, his table 3) or with combined estimates for California and Oregon (nearly 42 cm, Hunter et al. 1992, their Figure 11).

Starry flounder

The spawning period seems to be less protracted northward, and appears to occur progressively later toward the northern range of the species' distribution (Figure 5). Hart (1973) indicated that starry flounder spawns off British Columbia in about the same period than in Puget Sound, but no months were stated.

Ages at first maturity for females did not indicate a latitudinal trend between California and Puget Sound (Table 6). On the other hand, ages at 50% of maturity for starry flounder off Monterey Bay, California, are about 3 years for males and 4 years for females (Orcutt 1950, his table 11). The corresponding ages at 50% of maturity off Oregon for both sexes (Beardsley 1969, his figure 11), were nearly one

Table 6. Age and length at first maturity of starry flounder in the Northeast Pacific Ocean. Spawning areas are ordered from north to south.

Spawning area	Age at first maturity (years)		Length at first maturity (cm)		Source
	females	males	females	males	
Washington (Puget Sound)	3	2	—	—	Smith (1936)
Oregon (Yaquina Bay)	4	3	30	22	Beardsley (1969, his figure 11)
California (Monterey Bay)	3	2	24	22	Orcutt (1950)

more year than those estimated for starry flounder off California. Thus, older ages at first maturity and 50% maturity are suggested for starry flounder from Oregon than from California.

Rex sole

The spawning period in this species tends to start earlier off California-Oregon than off British Columbia and the Bering Sea (Figure 6). The spawning also seems considerably less protracted in the Eastern Bering Sea when compared to lower latitudes.

For rex sole off Northern Oregon, Hosie (1975) reported that ages and sizes at first maturity were 4 years and about 19 cm for females, and 3 to 4 years and about 13 cm for males. Off California, females seem to reach first maturity in their third year of life (Frey 1971). Hence, limited data for female rex sole suggest earlier age at first maturity in its southern range.

Hosie and Horton (1977) also suggested that rex sole may mature at earlier age in the southern part of their range. Both male and female rex sole have been found fully mature at age 4 off California (Villadolid 1927), while 100% mature fish off Oregon have been found at older ages (age 5 in males and age 9 in females, Hosie and Horton 1977).

Latitudinal variation in sea temperatures

Only the spawning period for rex sole coincided with the months of peak average surface and subsurface sea temperatures at high latitudes (Figures 7 and 8). On the other hand, no time-lags of warmer

REX SOLE SPAWNING PERIOD

SPAWNING AREA	SOURCE	OC	NO	DE	JA	FE	MR	AP	MY	JN	JL	AU	SE
EASTERN BERING SEA	1												
	2											■	■
GULF OF ALASKA	3							■	■	■	■	■	■
BRITISH COLUMBIA	4						■	■	■				
OFF WASHINGTON	5								■				
OFF OREGON	6				■	■	■	■	■	■			
OFF CALIFORNIA	7				■	■	■	■	■	■	■	■	
	8				■	■	■	■	■	■	■	■	

Figure 6. Monthly variations in the spawning period of rex sole in the Northeast Pacific Ocean and the Bering Sea. Spawning areas are ordered from north to south. Reported spawning peaks are represented by larger black bars. A left (or right) half black bar indicates spawning in the early (or late) part the month. Sources are: 1-(Mineva 1968); 2-(Musienko 1963, cited by Musienko 1972); 3-(Kendall and Dunn (1985); 4-(Forrester, cited by Hart 1973); 5-(Smith 1936); 6-(Hosie 1975); 7-(Reed, cited by Hosie 1975); 8-(Villadolid 1927).

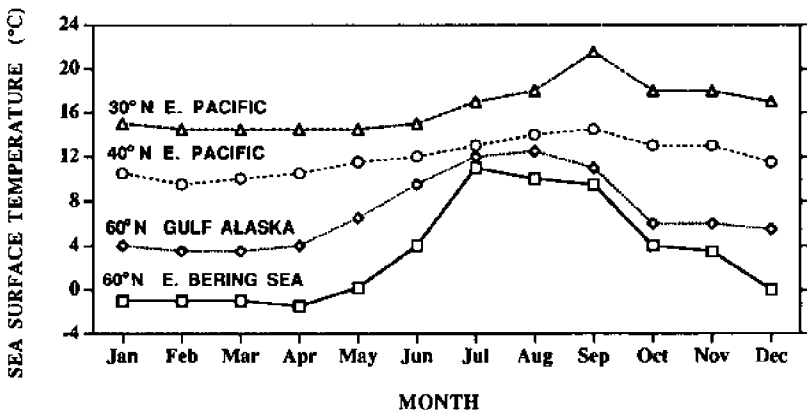


Figure 7. Long-term (1942-1969) average monthly sea surface temperatures at different latitudes along the continental shelf of the Northeast Pacific Ocean and the Eastern Bering Sea (Based on Robinson 1976).

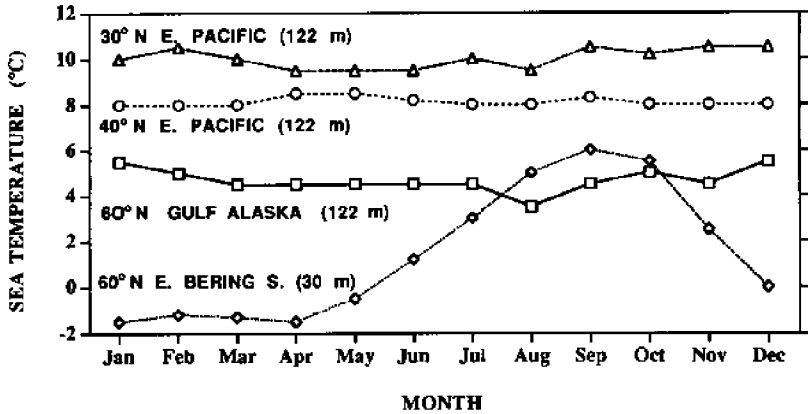


Figure 8. Long-term (1942-1969) average monthly sea temperatures (at 30 m or 122 m of depth) at different latitudes along the continental shelf of the Northeast Pacific Ocean and the Eastern Bering Sea (Based on Robinson 1976).

monthly surface, and subsurface, sea temperatures between 30°N and 60°N were evident throughout the year. Hence, the apparent delay of the spawning period toward high latitudes observed for starry flounder, Dover sole and petrale soles seems unrelated to average monthly fluctuations in sea temperature.

Discussion

The tendency for both brief and later spawning periods at high latitudes for most of the fishes considered in the present study is consistent with the hypothesis that the simultaneous delay of the spawning period and the production cycle toward high latitudes may have resulted from an adaptation to favor the feeding of fish larvae. Further evidence in support of such hypothesis include:

1. The spring phytoplankton peak seems to occur earlier (March-April) off the Washington-Oregon coast (Landry et al. 1989), than in the eastern Bering Sea (May-June, Meshcheryakova 1972). Therefore, food production for fish larvae could be available later at high latitudes than at lower latitudes.
2. The six species of fish analyzed in this study have pelagic larvae (Matarese et al. 1989). Thus, the larval stages of these species may rely on production of planktonic food.

3. The duration of annual production cycles in the ocean decrease from tropical regions to Arctic regions (Cushing 1959). Moreover, Nikolsky (1963) implied that the longer the period in which exogenous food is available to first feeding larvae, the more protracted is the spawning period. Thus, adequate food items for fish larvae may tend to be available for shorter periods in high latitudes.

With the exception of rex sole, in which no studies on oocyte development were available, all the species in the present study fit into Hempel's (1979) definition of discontinuous spawning strategy, that is, non-serial spawning (e.g., Orcutt 1950, Porter 1964, St-Pierre 1984, Yoklavich and Pikitch 1989, Fargo and Tyler 1994). However, the temporal differences in the occurrence of larval stages of rex sole in the plankton (Pearcy et al. 1977) and the duration of the spawning period suggest that rex sole also has a discontinuous spawning strategy.

Although the spawning of rex sole in the Eastern Bering Sea occurs after the spring phytoplankton bloom, the spawning tends to coincide with the warmest sea surface and subsurface temperatures of the year. Hence, the hypothesis that fish populations in their poleward limit of the species' range breed during the warmer months of the year (Qasim 1956), is only supported by rex sole in the present study. On the other hand, Meshcheryakova (1972) reported a fall phytoplankton peak during September-October in the Eastern Bering Sea. Thus, spawning of rex sole in the Eastern Bering Sea could be an adaptation to both higher temperatures and to the provision of food for fish larvae.

The duration of the larval stages for the species considered in this study and their maximum depths of reported species' occurrences suggests a tendency for later age at metamorphosis for species found in deeper waters (Table 1). Although English sole and Pacific halibut are within the ranges of age at metamorphosis and bathymetric species' distribution of the other four species (Table 1), no latitudinal trends in the spawning periods of Pacific halibut and English sole were evident. Therefore, the spawning of English sole and Pacific halibut may be synchronized to other factors besides the subsequent food production for fish larvae. The protracted spawning of English sole seems to be due to spawning of different individuals at different times (Hewitt, cited by Kruse and Tyler 1983). Moreover, some spawning activity could be present throughout the year (Kruse and Tyler 1983). In the case of Pacific halibut, Novikov (1968) indicated that while some individuals start spawning as early as October in the

Eastern Bering Sea, others are still in a state of development until March.

Petrale sole seems to be the only species considered in this study in which an earlier spawning period was previously suggested for a southern location of the species' range (Taylor 1957). However such pattern was only based on fish collected in two locations off British Columbia and California. A later spawning period at high latitudes relative to low latitudes has been reported for few species of flatfish elsewhere (e.g., American plaice, Pitt 1966; winter flounder, Kennedy and Steele 1971; North Sea plaice, Bagenal 1971). Yet, this spawning pattern could be common in species having a broad latitudinal distribution. In Northwestern Pacific flatfish of the family Pleuronectidae, spawning occurs in winter-spring in temperate waters, but shifts to summer at high latitudes (Minami and Tanaka 1992). However, the previous study did not mention potential latitudinal variations in the timing of spawning for individual species.

Although minimum age of first reproduction is genetically set (Wootton 1982), food availability or predation of larvae on juvenile stages may control the age at first maturity in some species of fish (Nikolsky 1963, Reznick and Endler 1982, Roff 1982). In addition, commercial exploitation may increase the proportion of genotypes that mature at younger ages (Beacham 1983).

With the exception of Pacific halibut, the lack of a clear latitudinal trend for the age or length at first maturity in the present study suggests that first maturity may be less influenced by latitudinal gradients in the environment than 50% (or 100%) maturity.

Hunter et al. (1992) stated that differences in criteria for determining maturity in Dover sole or timing of sampling can result in variations in length at 50% of maturity as large as those previously reported in this species. However, the size of fish at first maturity should be relatively independent of season because it is unlikely that identification of maturity stage would be inaccurate for all small fish (Yoklavich and Pikitch 1989). Thus, the age-length at first maturity may be more reliable than age-length at 50% (or 100%) maturity. Although no reliable data on age-length at 50% (or at 100%) maturity of Dover sole were available for latitudinal comparisons, the age or size at 50% (or 100%) of maturity showed a poleward increase in all other species considered in the present study. Thus, the generalization that maturity usually sets in earlier in regions of higher water temperature or lower latitudes (Gunter 1950, Nikolsky 1963, Dillinger et al. 1987), seems to apply more to the age at 50% of maturity than to the

age at first maturity in the present study. In warmer waters of the Atlantic Ocean however, witch flounder has shown earlier ages both at first maturity and 50% maturity than in colder waters (Beacham 1983).

Considering that natural mortality of fish tend to be positively correlated with temperature (Pauly 1980), and that age at 50% maturity tends to be correlated with the reproductive life span of fish (Roff 1981, Gunderson 1988), it is conceivable that the reproductive life span of fish may also tend to increase poleward. This later hypothesis is consistent with the occurrence of smaller final sizes of fish in warmer waters than the same species in colder waters and with the longer life of animals in colder seas (Gunter 1950). The previous hypothesis is also supported by bet-hedging predictions of life history traits in variable environments (Stearns 1976). Thus, despite the tendency for a more protracted spawning season for fish populations in lower latitudes, the reproductive effort of a year-class may be distributed over a greater number years for populations found in higher latitudes than for populations of the same species present in lower latitudes.

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Reproduction, Muscle Hydration, and Condition Cycle Variation _____ in Northern Pleuronectids

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Abstract

Jellied (soft) muscle and irregular or regular non-annual spawning indicate that some northern pleuronectids may be reacting to nutritional constraints in different ways. We have studied inshore winter flounder (*Pleuronectes americanus*) and American plaice (*Hippoglossoides platessoides*) from deeper water. Winter flounder do not feed during the winter off Newfoundland and show considerable annual and interannual variations in their condition cycles. In addition adults may not spawn every year, a state which is related to poor somatic condition the previous year. In females, and possibly also in males, the critical period, determining whether spawning will occur the next year, occurs early in the feeding season, close to the normal spawning period. Therefore it is possible to designate some fish as at risk of spawning omission in the following year, based on either pre- or postspawning condition factors. Laboratory held winter flounder, with satiation feeding during the normal feeding season, have less variation in condition cycle and show a regular annual spawning pattern.

American plaice, which live further offshore and are reported to have reduced winter feeding, have been stated to sacrifice soma to maintain gonads. Very high muscle hydrations were reported in the 1950s, notably from large females. We have not been recording such high values, although we have found increased hydrations during the spawning season. It is also possible that within a fish (flounder or

plaice) there are regional variations in the hydration, with some areas more readily utilized. Muscle from fish with high hydrations merits careful analysis; shrinkage, changes in myofibril organization (both species) and holes (flounder) are found in sections of white muscle from fish with high hydration but it is not yet known whether locomotion is compromised.

Introduction

North Atlantic flatfish such as American plaice or long rough dab (*Hippoglossoides platessoides*) and winter flounder (*Pleuronectes americanus*, formerly *Pseudopleuronectes americanus*) have highly variable life cycles. The American plaice is found as two distinct populations on each side of the Atlantic and does not attain large size off Scotland (Bagenal 1957). Bagenal used field derived measurements to show a condition cycle for a 20 cm length hypothetical fish. In this case the condition cycle was shown to swing up during the summer and decline during the winter. This kind of condition cycle is expected if feeding is best during the summer and spawning occurs in the spring. Off Newfoundland American plaice attains larger size but has been reported to have high incidence of jellied muscle, particularly associated with large fish (Templeman and Andrew 1956). Jellied or soft muscle has also been reported from other flatfish, e.g. *Liopsetta putnami*, now *Pleuronectes putnami* (McKenzie 1956) and *Microstomus pacificus* (Fisher et al. 1987). Such muscle is obviously a concern in commercial fisheries; the highly hydrated muscle is not acceptable in the market as reported by Templeman and Andrews (1956), and it is recognized as a quite different condition to that known as chalky or milky muscle, which is due to a parasite (Patashnik and Groninger 1964).

Reports of non-annual spawning in flatfish have also been widespread although few details are usually given. Fedorov (1971) recorded mass resorption of gametes in *Reinhardtius hippoglossoides* in the Barents Sea with subsequent disruption of the next spawning cycle. Bell (1981) did not accept Novikov's (1964) view that halibut, *Hippoglossus hippoglossus*, might not spawn annually. Nikol'skii (1961) reports that *Pleuronectes glacialis* (formerly *Liopsetta glacialis*), the Arctic flounder, spawns every other year. American plaice may not spawn every year according to brief statements by Templeman and Andrews (1956), Bagenal (1957) and Pitt (1966). These reports give no details and it is difficult to evaluate them. However it is now certain that at least one northern pleuronectid does not always spawn every

year (Burton and Idler 1984, 1987a, 1987b). Winter flounder off Newfoundland have a prolonged winter fast (Kennedy and Steele 1971, Fletcher and King 1978) and some years it is particularly noticeable that a proportion of the adult fish are thin and will not spawn. Such non-reproductive adults lack advanced stages of gametes in their gonads at the time when reproductive adults have sperm or vitellogenic (yolky) oocytes. The non-reproductive adults can be differentiated from immature or juvenile fish by overall size, the non-reproductive fish are of adult length, and often are quite large fish (Burton and Idler 1984, 1987a). Moreover histologically the gonads of nonreproductive adults are very distinctive; whereas juvenile or immature fish that have never spawned have thin gonad walls, the gonads of non-reproductive fish have very thick walls (Burton and Idler 1987a). This non-reproductive state occurs with both males and females (Burton and Idler 1984, 1987a, 1987b) and it is reversible (Burton and Idler 1987b, Burton 1991a). Irregular non-annual spawning is more opportunistic than the two year cycle reported for *Pleuronectes glacialis* (Nikol'skii 1961) and may be a response to varying feeding success (Burton 1991b) reflected in condition cycle variation.

In this study we have looked at both winter flounder and American plaice. We report seasonal condition cycles and muscle hydration data as well as preliminary information on determining fish at risk of omitting reproduction.

Materials and Methods

Fish were obtained either by divers from the Field Services Unit of the Ocean Sciences Centre (OSC) or with the cooperation of the Department of Fisheries and Oceans (DFO). Flounder were normally held in 270 L tanks under seasonal conditions of temperature and photoperiod. Plaice were held in 900 L tanks where seasonal temperatures were mitigated with either heated (in winter) or chilled (in summer) seawater, the aim being to restrict the temperature variations to levels more akin to the deeper water from which they were taken. This last summer (1994) however we were not able to hold the water temperatures down because the incoming water was around 15°C which is higher than we usually record.

Fed fish were given chopped capelin (*Mallotus villosus*) which is a natural food for wild flounder off Newfoundland (Kennedy and Steele 1971). Fish were fed two or three times a week to satiation (optimal feeding); with amounts given recorded, and excess removed after 24 hours. Amounts given were continually adjusted to maintain satiation.

Laboratory held fish were tagged with numbered fingerling tags through the operculum. When fish were killed samples of gonads and muscle were taken for histology, after determining body weight and length as well as gonad, gut and liver weights. For histology samples were fixed in Bouin's, dehydrated in an ethanol series, cleaned and embedded in wax with sections taken at around 7-8 μm . Sections were stained with Ehrlich's haematoxylin and eosin. Muscle samples were always taken from beneath the reference points (Maddock and Burton 1994) straddling the lateral line approximately halfway down the body, with skin attached to give orientation. Muscle samples were also taken from other regions for comparison.

Condition factors were determined using the equation:

$$CF = \frac{\text{Body weight} \times 100}{\text{Length}^3}$$

Gonadosomatic index was calculated using the equation:

$$GSI = \frac{\text{Gonad weight} \times 100}{\text{Body weight}}$$

Condition factors were plotted against time to show condition cycles, using means. To show individual variation CF values were grouped for both males and females and plotted. Conditions factors close to spawning were used to estimate risk of spawning omission the following year for flounder because there is an association between poor condition (low CF) early in the feeding cycle and spawning omission the following year (Burton 1994). Risk factors were allocated based on previous work (Burton 1991b, 1994). Prespawning condition factors < 1.00 were regarded as high risk for both males and females. Condition factors < 1.10 for males and < 1.20 for females were regarded as risky; the actual risk would depend on current fecundity and early feeding success.

As for histology, muscle samples for determining hydration were taken from the mid-region of the upper surface (Maddock and Burton 1994) close to the lateral line. Additional samples were also taken from specific regions of the upper surface for some of the fish. Hydration was determined by drying to constant weight (Maddock and Burton 1994). Hydrations were compared seasonally and with condition factors, and also compared with the histological samples.

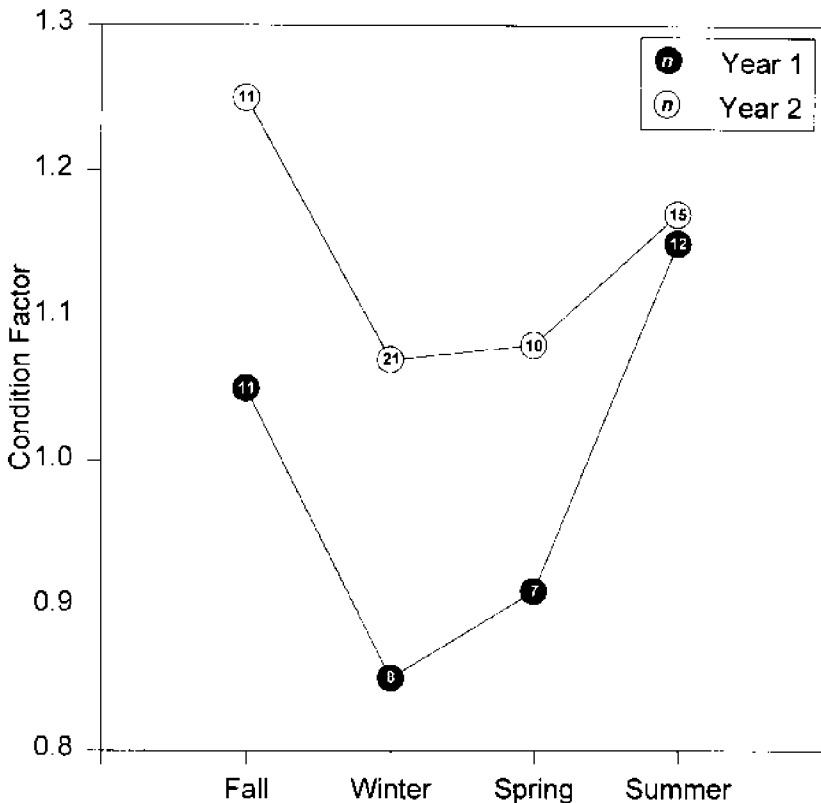


Figure 1. Condition factors of recently caught male winter flounder from Conception Bay, for two years. Condition factors represented as means.

Results

Condition cycles

Freshly caught winter flounder showed considerable interannual and annual variation in condition, as means (Fig. 1, 2). Two adjacent years plotted for males (Fig. 1) from Conception Bay show that in the fall, after the summer feeding season, there was a mean of about 1.05 for one year as opposed to the much higher mean of 1.25 for the other year. Loss of condition over the non-feeding winter for both years, was followed by recovery in the spring and summer, during the feeding

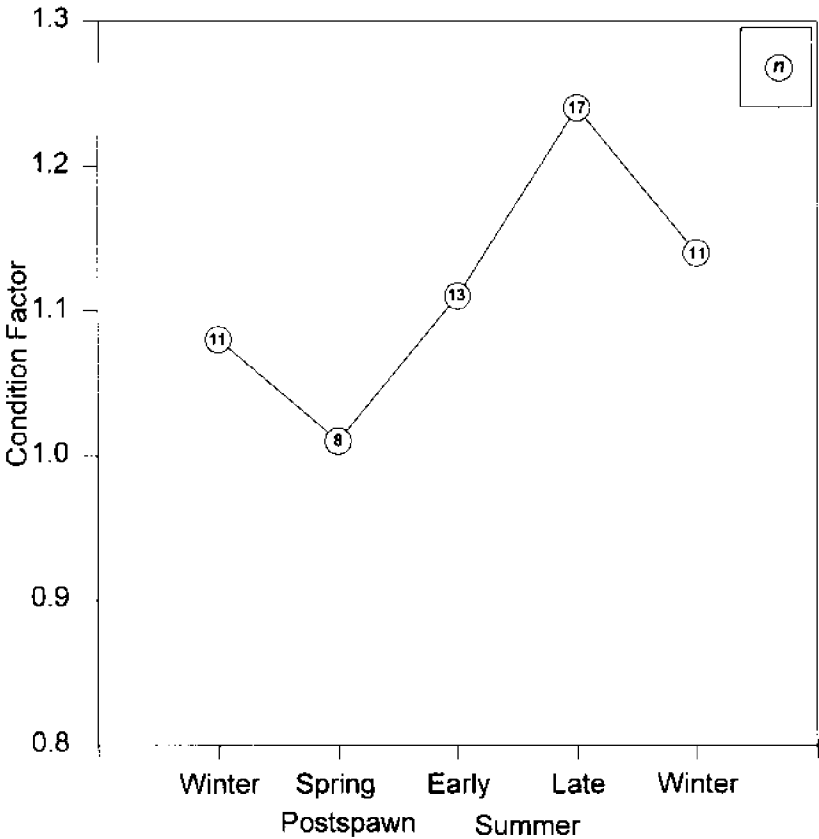


Figure 2. Condition factors of recently caught female winter flounder from Conception Bay. Condition factors represented as means.

season. A similar pattern occurred for wild females from the same locality (Fig. 2), with loss of condition over the winter followed by a recovery during the summer. However, variation also occurs so that with two successive winters there is a mean CF of about 1.08 succeeded by a better CF the following winter, sampled fish attaining a mean of 1.14. These winter means for females were much better than the low value attained by the males, with a mean CF of 0.83. Fig. 3 shows condition factors reached under optimal feeding in the laboratory, measuring the same fish over a year. The females maintained a value close to 1.40, with some loss over the winter, while the males showed a

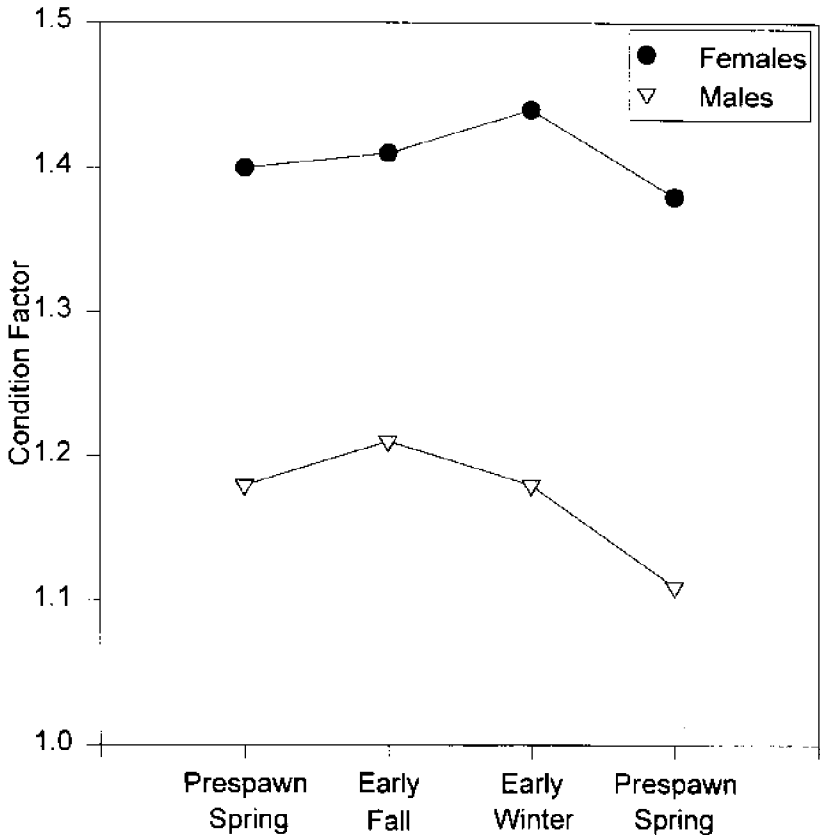


Figure 3. Condition factors of laboratory held, satiation fed fish. Condition factors as means, using the same fish throughout, males n = 6, females n = 8.

maximum around 1.20, with an overwinter loss diminishing the CF to about 1.10. These optimally fed fish showed regular repeat spawning. As yet we do not have a complete annual cycle for American plaice, but overall their CF are much lower than those for flounder (Fig. 4).

Within sample variation for wild winter flounder is shown in Fig. 5, with about 100 fish grouped by condition factor; the range of condition can be seen for prespawning adults from the same locality (Conception Bay). Risk of becoming non-reproductive in the next year is also shown, with 9% of males and 2% of females at high risk, while 25% of males and 51% of females were at risk by the criteria used.

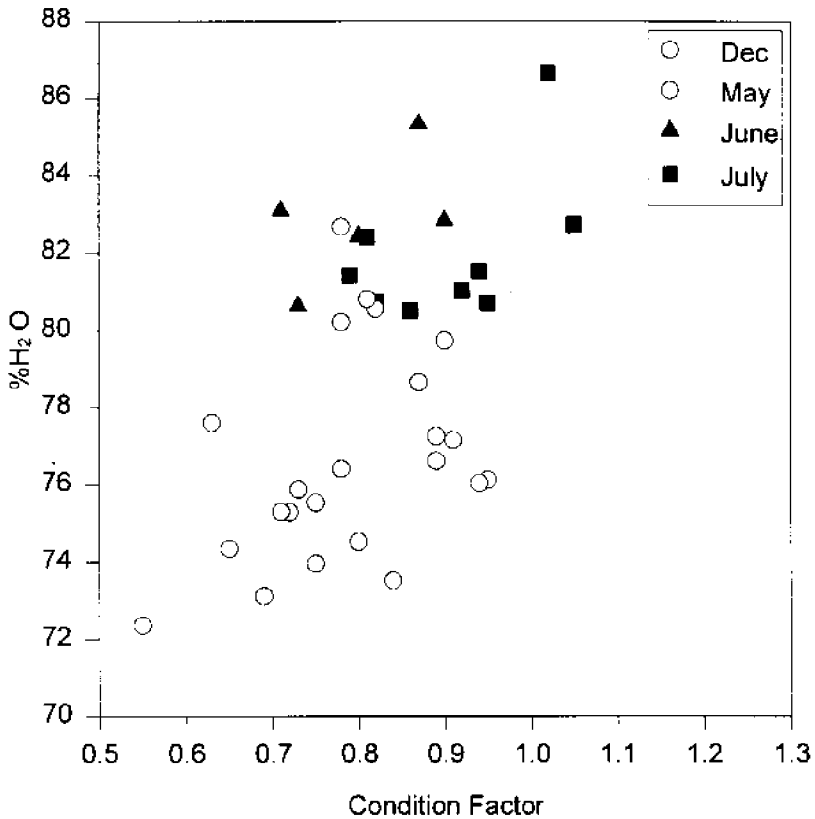


Figure 4. Condition factors and muscle hydration for recently caught individual American plaice. Muscle sample taken from standard upper mid-region.

Muscle

Hydration for freshly caught wild winter flounder reached as high as 86% close to spawning although wild winter flounder from the fall had lower values (Maddock and Burton 1994). Similarly wild plaice had increased values in the early summer (Fig. 4), but for the mid-region sampled routinely there were no values in the 90s. However other regions of the wild fish (July) could show higher values, and the muscle in such regions was different from that in the less hydrated positions (Fig. 6). Some regions showed myofibril disorganization but no well-defined holes like those we have reported (Maddock and

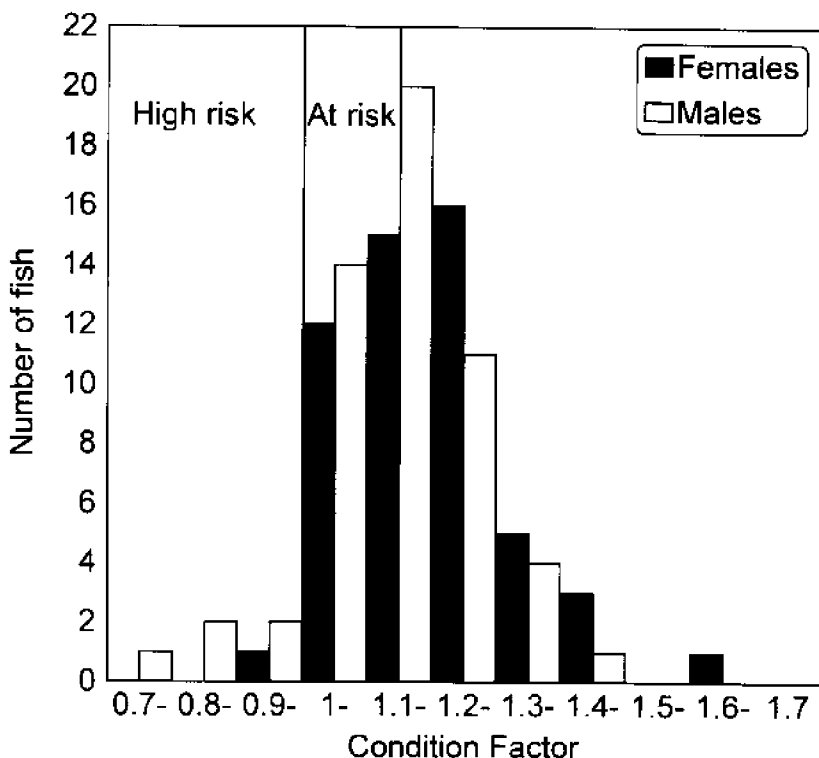


Figure 5. Range of individual condition factors from prespawning recently caught winter flounder, with males and females shown separately. Risk and high risk shown, indicating that these fish had low enough condition factors prespawning to put them into categories where they might not be reproductive the following year.

Burton 1994) for jellied muscle experimentally produced in winter flounder.

American plaice reproduction

American plaice off Newfoundland show gametogenesis well-established by the early winter. In a December sample of 19 fish (Table 1) five males had sperm and one had spermatids but the largest male only had secondary spermatogonia, and was classified as a non-reproductive adult. Among the larger females obtained there were some which were not showing vitellogenesis and had low GSI in

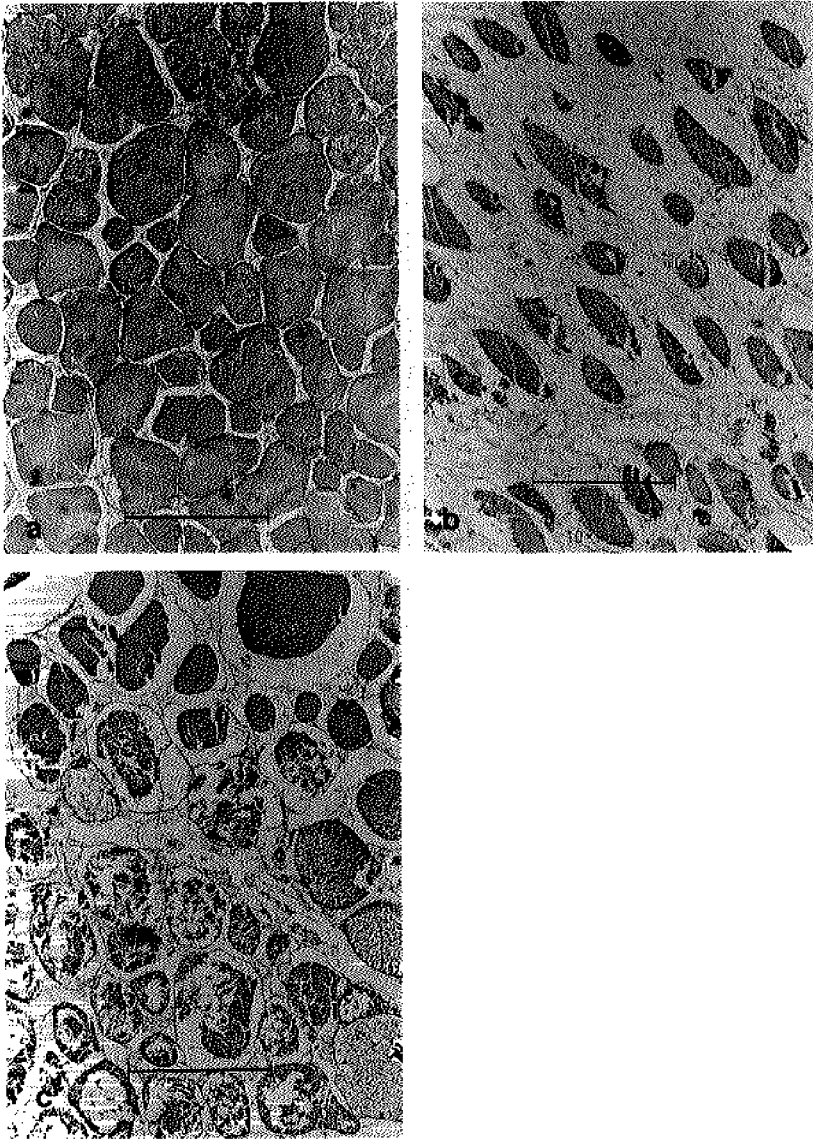


Figure 6. White muscle samples from the same fish showing regional differences in hydration and cytology. a. From mid-region, upper surface; hydration 87%. b. From anterior abdominal side, upper surface; hydration 92%; cytology showing apparent loss of protein. c. From anterior region, superior to lateral line, upper surface; hydration 87%. Some myofibrillar disorganization.

Table 1. Lengths and gonadosomatic indices for American plaice sampled in December.

Females			Males		
GSI	Length (cm)	Reproductive status	GSI	Length (cm)	Reproductive status
0.66	26.0	I	1.52	20.6	R
0.74	28.0	I	1.18	22.9	R
0.85	28.5	I	1.70	22.9	R
4.20	30.0	R	1.75	26.7	R
0.89	31.5	I?	1.80	27.8	R
5.35	32.2	R	1.57	28.3	R
1.30	32.6	I	0.74	38.5	NR
3.83	33.9	R			
0.70	35.7	I?			
0.76	36.6	NR?			
5.30	38.6	R			
4.36	40.2	R			

R = reproductive, NR = non-reproductive, I = immature (juvenile).

contrast with the reproductive females. The values of December GSI for the American plaice are low for both males and females. May, June and July samples did not show high GSI values either; the highest value recorded for a reproductive male was 1.80 (December) while a spermiating male in May had a GSI of 1.23. The highest value for a reproductive female was 5.35 (December). In July some females had residual eggs showing that spawning had occurred by this time.

Discussion

We did not find very highly hydrated muscle in wild American plaice, contrary to the reports on wild American plaice from the 1950s (Templeman and Andrews 1956). However, the fish we analyzed were generally quite small whereas Templeman and Andrews specifically state that high hydration was associated with large size. The few large fish we did access did not show any higher hydrations than the smaller fish, i.e., there was no obvious trend with size in our samples. The trend that was noticeable, however, was an increased hydration in the spring as compared to early winter. December plaice had low

hydrations as compared to any fish reported by Templeman and Andrews (1956) and also low hydrations as compared to winter flounder samples at the same season (Maddock and Burton 1994). It is too early yet to make generalized statements about regional differences in hydration within fish, although we found that it can occur in individuals. The possibility remains that once a fish is severely compromised nutritionally it will withdraw protein from one region of white muscle preferentially, with a tendency to conserve white muscle in one region just as red muscle is conserved in winter flounder (Maddock and Burton 1994). Reports on American plaice from the Gulf of St. Lawrence show that they have very reduced winter feeding and have moved offshore (Powles 1965). Effectively most of these fish seem to have a winter fast but this may only be because of low food availability in the deeper water; we do not know for sure whether they will feed in the minimum winter temperatures, although Morgan (1993) has reported American plaice feeding at 1°C, and the deeper water fish studied by Powles were at 3-6°C. Winter flounder will not feed in the winter, if given the opportunity, so long as the tank temperatures reflect the ambient inshore (their normal habitat) winter values of around 0°C. However, they will take food if the temperatures are raised to around 4°C (Burton, unpublished data). Given that American plaice off Newfoundland tend to live in deeper waters (warmer in winter) than the flounder it seems possible that they might continue to feed if food is available at their depth, and not have an absolute winter fast. They could thus have reduced winter feeding similar to that found for cod (Burton et al. 1994).

With samples so far available to us we have not yet clearly established whether female American plaice are batch-spawners like *Hippoglossus hippoglossus* (Daniel et al. 1993) and *Pleuronectes platessa* (Horwood et al. 1989) or single-event spawners like winter flounder (Burton and Idler 1984). If the American plaice are batch-spawners the relationship between successive batches and protein depletion may be quite complex. It might be acceptable to have a short period of compromised muscle phased with batch maturation when fish might not be actively feeding. Although Pearcey (1961) reported wild winter flounder from Mystic (U.S.A.) with jellied muscle we have not yet found wild winter flounder off Newfoundland with such muscle. It is interesting, though, that the highest hydration values we have recorded in wild fish have been close to spawning and subsequent to the winter fast.

In calculating risk factors for winter flounder we used two sets of cut-off points for condition factors, saying that condition factors less than 1.00 for a prespawning adult constituted high risk. Given that a fecund female can lose 20% of her pre-oocyte hydration body weight at spawning and that males lose about 6% (based on pre- and post-spawn GSIs, Burton and Idler 1984) this represents a very conservative estimate of risk of becoming non-reproductive for the following season. By adding the two risk zones, high risk and risk, the rather high figures of 35% for males and 53% for females are obtained. Because actual fecundity varies considerably as well as food intake the real risk, which depends on nutritional condition in the critical period close to spawning, is not very accessible at present. However, samples of wild populations show that about 35% of wild males and 30% of wild females can be non-reproductive in the winter following a poor feeding season (Burton 1991a, and unpublished data for males). Allowing for the fact that some low condition fish will have died following spawning these figures seem to correlate quite well with the values of the predictions from CF variation prespawning.

Although Templeman and Andrews (1956), Bagenal (1957) and Pitt (1966) all mention non-reproductive plaice no detailed information is given, either as to prevalence or how such classification was obtained. We did find a large male that was classified as non-reproductive because it only had spermatogonia at a time when the other males in the sample had reached at least the spermatid stage of spermatogenesis. We also found a few moderately large females that were not reproductive but they could have been large immature fish. The situation, particularly with females, requires further study. The gonadosomatic indices for the plaice we have examined were low, as compared with those of winter flounder. Males from the general spawning period May/June did not show any GSI values above 2, in contrast with the usual range of around 7 to 8 achieved by winter flounder (Burton and Idler 1984). This indicates that American plaice expend less on their reproduction than winter flounder and thus have less demand on their energy reserves, lipids and proteins, and should not therefore show highly hydrated muscle. However we do not know whether the American plaice, as individuals, have a protracted spawning season, with recruitment and active gametogenesis close to the spawning season, which would be a marked difference from winter flounder which form their gametes early and hold them in advanced stages over the winter, with no signs whatsoever of any later augmen-

tation. If American plaice do have an extended spawning season, with active recruitment, and are unable to feed very actively at the same time, then a period of protein loss from the muscles is not a surprising result, especially if the fish had a winter fast or reduced winter feeding, and little opportunity to feed before the spawning season.

Acknowledgments

This work was supported by the Natural Sciences and Engineering Research Council. We wish to thank personnel at the Department of Fisheries and Oceans for help in obtaining American plaice; thanks are especially due to Joanne Morgan who donated live plaice. Roy Ficken helped with photography and we are grateful to Peter Earle for his advice on computers.

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Distribution of Alaska Plaice, Flathead Sole, and Bering Flounder Eggs in the Eastern Bering Sea During April-July, 1988-1990

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Abstract

In the spring ichthyoplankton of the eastern Bering Sea, the abundance and frequency of eggs of three flatfish species (Alaska plaice, flathead sole, and Bering flounder) are exceeded only by walleye pollock eggs. From late April to early July, eggs of Alaska plaice were found in the vast shelf area from Unimak Island to St. Matthew Island, including Bristol Bay. During the spring of 1988-1990, areas with eggs present ranged from 14,400 to 17,200 km² and eggs were captured from 35.8 to 53.4% of the stations. Egg distribution was stable. Maximum concentrations of eggs were found in coastal waters to 50 m in the northern part of the study area from Kuskokwim Bay to Nunivak Island. Egg abundance by year varied insignificantly from 9.7 to 11.7 billion eggs.

Frequency of stations with aggregated flathead sole and Bering flounder eggs was similar to that of Alaska plaice, but egg distribution differed. Two main regions of egg concentration were: a northwestern region near Nunivak, Pribilof, and St. Matthew islands, and a more significant southeastern region north of Unimak Island and the Alaska Peninsula. In 1988 the areas with eggs present were close to each other, but the following two years they were farther apart. We assumed

that flathead sole eggs are distributed mainly in the southeastern region, and that Bering flounder eggs are found in the northwestern region. The total area with eggs of these two species ranged from 9,700 to 11,500 km², and abundance varied from 1.5 to 1.73 billion eggs.

Insignificant fluctuation of egg abundance of Alaska plaice and aggregated flathead sole and Bering flounder indicated comparatively stable stocks of their spawners. The change in egg abundance of these species doesn't correspond to the trawl survey stock assessments. Despite the evidence for increasing adult biomass during these three years (maximum in 1990), the egg abundance of these species was at maximum in 1988 or 1989, and at minimum in 1990. Perhaps it is due to the changing ratio of mature to immature specimens in populations.

Introduction

Flatfishes of the eastern Bering Sea contribute to important fisheries (Fadeev 1965). Information on their biology has been published by Mineva (1964) and Fadeev (1971, 1987). Data on egg and larva distribution in the eastern Bering Sea has been published by Musienko (1970), Bulatov (1982, 1983), Waldron and Vinter (1978), and Waldron (1981). Trawl surveys have been used in this region to determine flatfish abundance (Bakkala and Sample 1983, Halliday and Sassano 1979), though attempts to calculate abundance of bigmouth flatfish were implemented in 1976-1981 (Bulatov 1983).

In the eastern Bering Sea Alaska plaice, flathead sole, and Bering flounder spawn during spring, while other flatfish spawn at other times. Abundant eggs were observed during the annual ichthyoplankton surveys conducted under the international walleye pollock abundance assessment program. The objective of this study was to characterize egg distribution and abundance estimation for the three flatfish species in the eastern Bering Sea. Combining egg data with trawl surveys provides a more exact adult biomass assessment and additional information for flatfish abundance forecasts.

Methods

In this study results of ichthyoplankton surveys in the eastern Bering Sea during April-July 1988, 1989, and 1990 were used. In 1988 and 1989 the study region expanded from Unimak Island to 62°N latitude. In 1990 the survey area was expanded to St. Lawrence Island. The number of stations sampled during these years was: 174 (1988), 163 (1989), 461 (1990). Ichthyoplankton was sampled by conical net IKS-80

with 80 cm mouth diameter. Vertical tows from bottom to surface at 17-150 meters depth were implemented. Ichthyoplankton samples were analyzed on the vessels. Water temperatures were measured in centigrade.

Egg density distribution was counted per 1 m² of sea surface. Egg abundance was obtained by calculation of areas where egg density differed. This abundance was compared with bottom trawl survey results. During the survey period recorded egg totals were 10,279 eggs of Alaska plaice, and 2,440 eggs of aggregated flathead sole and Bering flounder.

Results and Discussion

Alaska plaice (*Pleuronectes quadrituberculatus*)

In the eastern Bering Sea the distribution of Alaska plaice extends into Bristol Bay and other coastal bays. Spawning appeared just after ice melt and continued to mid-June. Spawning grounds were located over shelf regions close to the 100 m isobath. Eggs were carried mainly by local currents (Pertseva-Ostroumova 1961, Bulatov 1982).

During the 1988-1990 spring ichthyoplankton surveys in the eastern Bering Sea, eggs of Alaska plaice were observed from late April to early July. Eggs were 1.6-2.1 mm (average 1.8-1.9 mm) in diameter. The eggs were observed all through the survey region from Unimak Island north to an area near St. Matthew Island (excluding a few stations west of Unimak Island and north toward St. Matthew Island). The largest egg concentrations occurred from late May to early June in Bristol Bay and south from Nunivak Island.

In 1988 eggs were taken at surface water temperature of 0.3-3.5°C. The largest catch (228 eggs) was south from Nunivak Island at 30 m depth with surface water temperature 1.6°C.

In 1989 egg concentrations of this species occupied a smaller area than in 1988, although their density was greater. Eggs were observed where surface water temperature was 0.4 to 5.9°C. The largest catch (809 eggs) occurred in Kuskokwim Bay at 19 m bottom depth with surface water temperature of 1.5°C.

In 1990 Alaska plaice egg distribution was similar to that in 1988, but more patchy. Surface water temperature where collections were made varied from -0.3 to 7.0°C. The largest catches occurred southward from Nunivak Island (maximum catch was 201 eggs at 34 m depth with surface water temperature of 2.6°C). Alaska plaice egg distribution is shown in Figure 1.

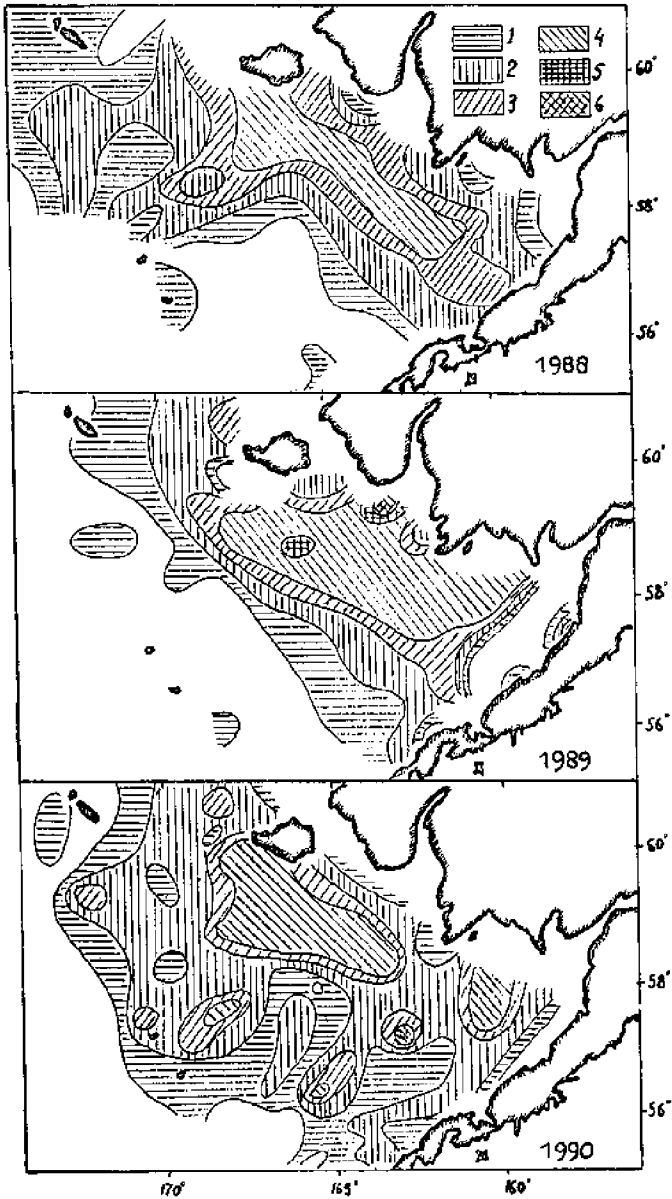


Figure 1. Alaska plaice egg distribution in the eastern Bering Sea during April-July 1988, 1989, and 1990. Legend (eggs/ m^2): 1. 1-10, 2. 11-50, 3. 51-100, 4. 101-500, 5. 501-1,000, 6. more than 1,000.

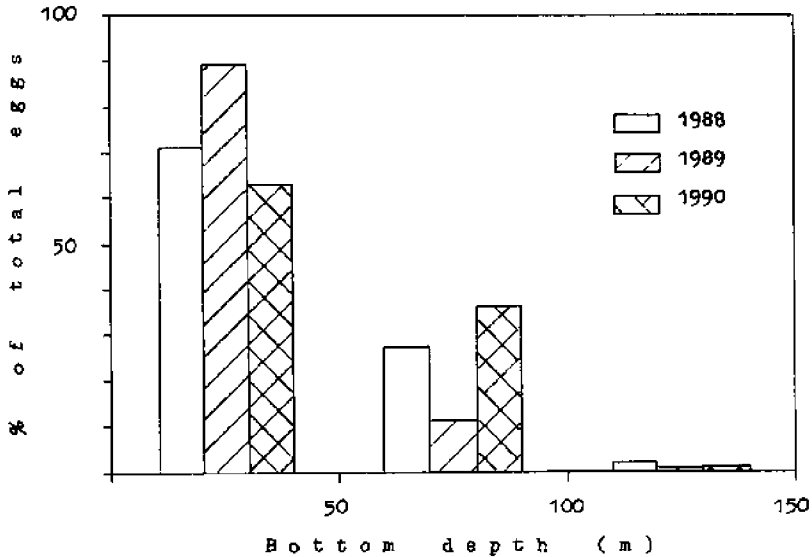


Figure 2. Alaska plaice total egg catch distribution and bottom depths, eastern Bering Sea, April-July 1988, 1989, and 1990.

The majority of the Alaska plaice eggs (60-90%) were collected near shore at less than 50 m bottom depth. Egg abundance in the samples decreased with increasing bottom depth (Figure 2).

The eggs were collected at low water temperatures. In 1988 and 1989 the greatest egg abundance was observed at a surface water temperature 1 to 2°C, and in 1990 at 2 to 3°C. Egg abundance decreased with increasing surface temperature (Figure 3).

Egg distribution during the period of highest abundance in 1990 (from late May to early June) showed a predominance of eggs at mid-stage of development. Based on the egg development chronology (Pertseva-Ostroumova 1961), it appears spawning of this flatfish peaks in early May.

In the eastern Bering Sea during 1988-1990, areas with Alaska plaice eggs ranged from 14,400 to 17,200 km². Abundance estimates ranged from 9.7 billion eggs in 1990 with high surface water temperature (average 4°C) to 11.7 billion eggs in 1989 with low surface water temperature (average 2.4°C) (Table 1).

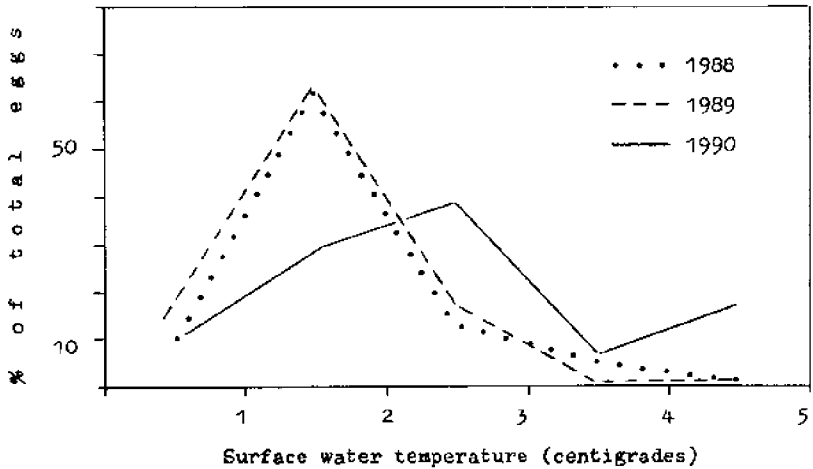


Figure 3. Alaska plaice total egg catch distribution and surface water temperatures, eastern Bering Sea, April-July 1988, 1989, and 1990.

Bigmouth flatfishes of the genus *Hippoglossoides*

Two abundant species of bigmouth flatfishes in the eastern Bering Sea are: flathead sole *Hippoglossoides elassodon* and Bering flounder *H. robustus* (Fadeev 1978, Bogdanov et al. 1979). Pertseva-Ostroumova (1961) and Bulatov (1983) found the egg size for these two species distinctive from other flatfish. Despite the overlap in habitat areas of these species in the eastern Bering Sea, flathead sole is distributed in more southern areas than Bering flounder. Based on the data of Pertseva-Ostroumova (1961) and Bulatov (1983), the majority of flathead sole spawn over the continental shelf at 50-150 m depth and bottom water temperature of -0.4 to 2°C . The eggs developed near the surface at water temperature of -1.2 to 5.4°C . Bering flounder spawn mainly in the northern Bering Sea. Spawning occurred during early spring in inshore zones at 25-130 m depth in colder water (Musienko 1970). The region near St. Lawrence Island is also an important spawning area (Bulatov 1983).

There are difficulties in separating the eggs of these two species because of similar egg diameter (2-3.5 mm), similar spawning periods, and areas of distribution overlap. Therefore, the eggs were investigated for this research without differentiating between species.

Table 1. Flatfish egg assessment results compared with trawl assessment in the eastern Bering Sea in 1988-1990.

	1988	1989	1990
Alaska plaice			
Stations with egg catches, %	53.4	43.1	35.8
Ave. bottom depth, m	65	56	66
Ave. surf. water temperature, °C	2.1	2.4	4
Total catch, eggs	2,928	4,133	3,218
Ave. catch, eggs per station	32	57	19
Area with eggs, 1,000 km ²	17.2	14.4	16.8
Total abundance, billion eggs	10.2	11.7	9.7
Trawl assessment, 1,000 t (Rus)	481	452	674.5
(USA)	-	287-451	652.5
Flathead sole and Bering flounder			
Stations with egg catches, %	61.5	41.3	26.5
Ave. bottom depth, m	73	81	78
Ave. surf. water temperature, °C	2.9	3.5	4.3
Total catch, eggs	1,698	518	624
Ave. catch, eggs per station	10	8	5
Area with eggs, 1,000 km ²	11.4	9.7	11.5
Egg total abundance, billion eggs	1.73	1.59	1.5
Trawl assessment, 1,000 t (Rus)	279	280	329
(USA)	-	201-322	652.5

During ichthyoplankton surveys in the eastern Bering Sea in 1988-1990, eggs of these two species occurred from late April to mid-July together with eggs of Alaska plaice, although in a smaller area. We found two main concentrations of eggs of these species: northwest (near St. Matthew Island) and southeast (northward from Unimak Island and in Bristol Bay). This separation is probably caused by the difference in habitat of these two flatfish species. Bulatov (1983) found eggs of these species similarly distributed.

In 1988 egg concentrations of flathead sole and Bering flounder were observed at surface water temperatures of 0.7 to 5°C. The largest catches in the southeastern region (more than 50 eggs per sample) were northward from Unimak Island in nearshore waters at 60-90 m

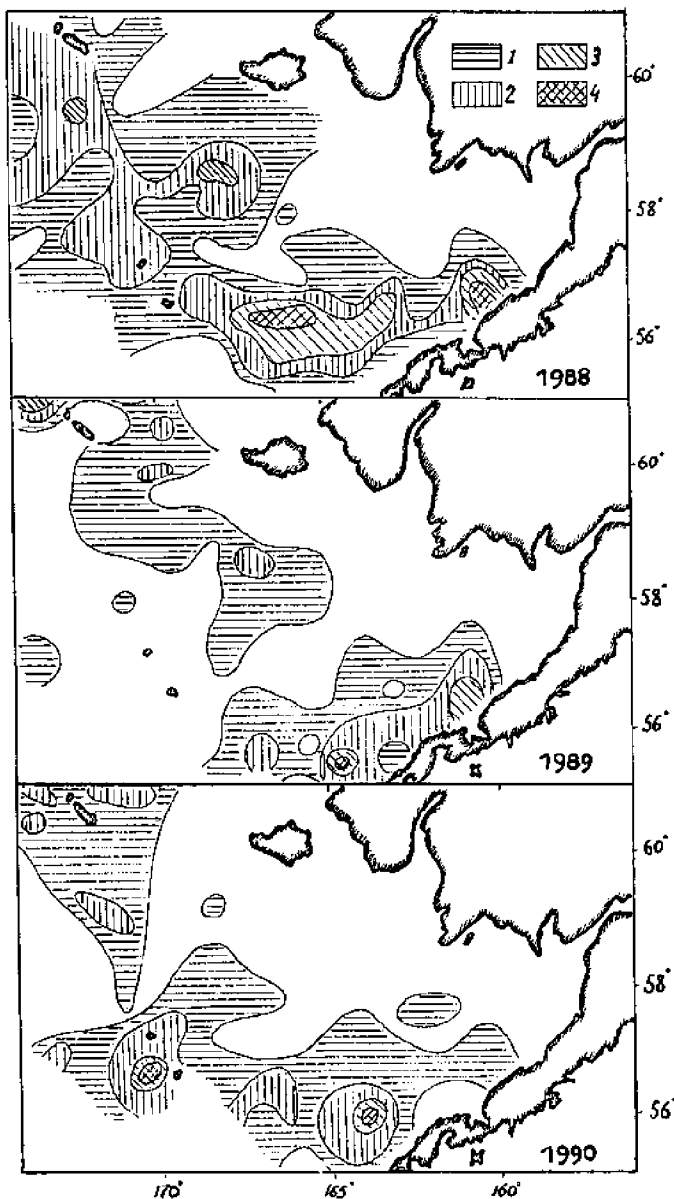


Figure 4. Flathead sole and Bering flounder egg distribution in the eastern Bering Sea during April-July 1988, 1989, and 1990. Legend (eggs/m²): 1. 1-10, 2. 11-50, 3. 51-100, 4. more than 100.

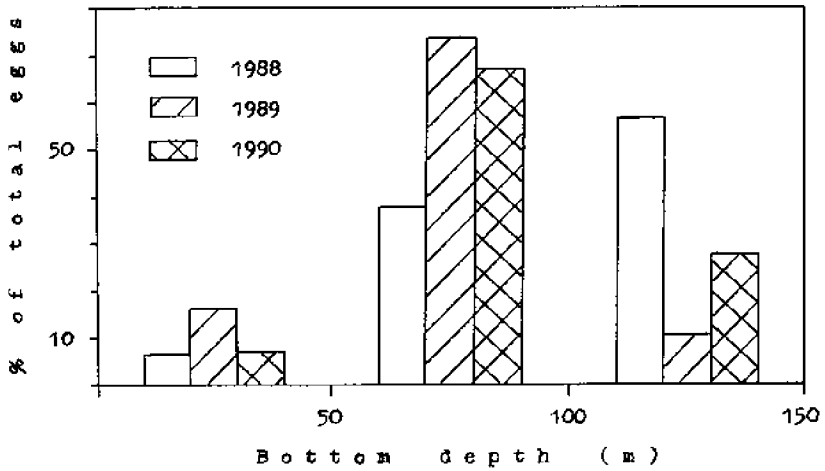


Figure 5. Flathead sole and Bering flounder total egg catch distribution and bottom depths, eastern Bering Sea, April-July 1988, 1989, and 1990.

depth with surface water temperatures of 2.2 to 4.7°C. The largest catches in the other region were observed southward from St. Matthew and Nunivak islands at about 80 m depth with surface water temperature of 1.5°C.

In 1989 egg concentrations of these two species occupied a smaller area than in 1988. Eggs were observed at surface water temperatures of 0.5 to 7.4°C. Egg distribution in the southern concentration located northward from Unimak Island was similar to that in 1988 and largest catches were close to those occurring northward from the Alaska Peninsula. The northern concentration in 1989 was found even farther north than in 1988. The largest catches in the northwest region (36 and 37 eggs per sample) occurred northward from St. Matthew Island at 65-94 m depth, when surface water temperature was 1.5 to 1.9°C.

In 1990 egg concentrations occupied comparatively greater areas and were distributed slightly farther north than in 1988 and 1989, but were less dense (particularly the patch near St. Matthew Island, where the largest catch was 22 eggs per sample). The southern egg concentration spread to the west; and catches of more than 50 eggs per sample were made both north of Unimak Island and in the region of the Pribilof Islands. That year eggs were collected in surface water temperatures of -0.8 to 7.6°C. Egg distribution of flathead sole and Bering flounder together is shown in Figure 4.

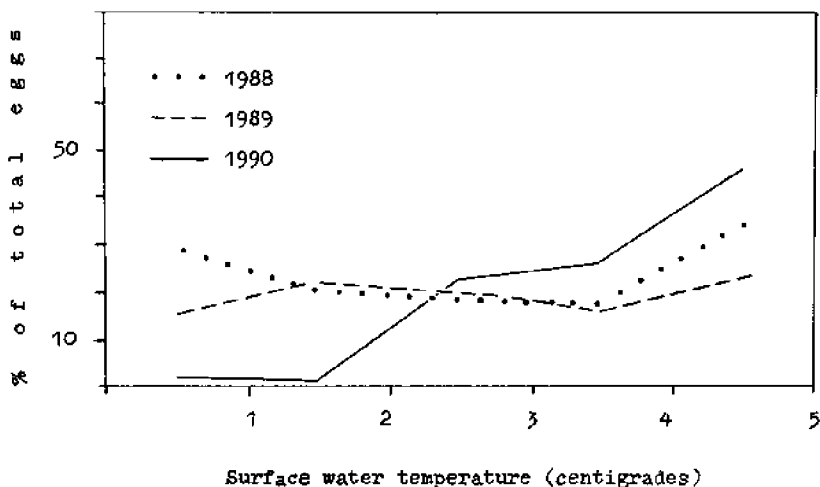


Figure 6. Flathead sole and Bering flounder total egg catch distribution and surface water temperatures, eastern Bering Sea, April-July 1988, 1989, and 1990.

Eggs of the two bigmouth flatfish were distributed over deeper water than eggs of Alaska plaice. The largest catches of these eggs in 1989-1990 occurred at 50-100 m depth. In 1988 principal egg catches were made at depths of more than 100 m (Figure 5). This relationship was confirmed by the significant egg distribution at warmer surface water (Figure 6), despite the largest egg catches occurring in comparatively cold surface waters. Surface water temperature increased as bottom depth increased.

During 1988-1990 areas occupied by eggs of aggregated flathead sole and Bering flounder were similar in size to those occupied by eggs of Alaska plaice, but total abundance of flathead sole and Bering flounder was considerably less than the plaice abundance. The year with the largest total abundance of flathead sole and Bering flounder (1988) was also the year with the smallest averages for both surface water temperature and bottom depth (Table 1).

Conclusion

In the eastern Bering Sea during spring, eggs of Alaska plaice, flathead sole, and Bering flounder occupied a vast area. The major concentrations of Alaska plaice eggs occurred southeast of Nunivak Island in inshore regions at 50-100 m bottom depth. Eggs of flathead sole and

Bering flounder were distributed farther offshore and split into two main regions: near St. Matthew Island, and northward from Unimak Island. It is assumed that flathead sole eggs were distributed mainly in the south region, and Bering flounder eggs were to the north.

The estimated total abundance of flatfish eggs has no direct relation to their total adult biomass. Comparison of total adult biomass estimated by trawl surveys shows similar numbers of Alaska plaice and both bigmouth flatfish species, whereas total egg abundance of Alaska plaice is much higher than both other species. This irregularity could depend on fecundity which is essentially unknown. Available data on individual fecundity of flathead sole (Matarese et al. 1989) show a substantial variation (from 70,000 to 600,000 eggs). Long-term observations of spawning peculiarities, egg and larva distribution, and the environment during spawning and early development is probably needed to further define this relationship. The insignificant fluctuation in egg abundance of Alaska plaice and aggregated flathead sole and Bering flounder explain the comparatively stable stocks of their spawners. The change in egg abundance of these species doesn't correspond to the stock assessments made by trawl surveys. Despite the evidence of increasing adult biomass during these three years (highest in 1990), the egg abundance of these species was highest in 1988 or 1989, and lower in 1990. Perhaps this is because of changes in the ratio of mature to immature specimens in the populations.

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Characteristics of Flatfish Eggs and Larva Samples near Eastern Kamchatka and in the Western Bering Sea During June-July 1991

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Abstract

Flatfish eggs and larvae have not been recorded during annual ichthyoplankton surveys for pollock assessment in the northwestern Pacific, resulting in a lack of data on flatfish early life history.

During our investigations flatfish eggs and larvae were important ichthyoplankton components, although the contents of the samples were insignificant. More abundant were the eggs of *Acanthopsetta nadeshnyi*. Also found were eggs and larvae of *Hippoglossoides elassodon* and *Pleuronectes quadrituberculatus*, and larvae of *Hippoglossoides robustus*, *Platichthys stellatus*, and *Limanda proboscidea*. *H. elassodon* eggs occurred between eastern shores of the North Kuril Islands and Anadyrski Bay at 39-132 m bottom depth. Catches were generally one or two eggs per station. Egg diameters varied from 2.68 to 3.7 mm. Almost all eggs collected were close to hatching. Eggs of *A. nadeshnyi* were collected from southeast Kamchatka to Olyutorski Cape at 23-214 m bottom depth. The greatest egg concentration (14 eggs per 1 m²) was observed in Osernoi Bay. Egg diameter varied from 0.8 to 1.2 mm. More than 50% of the eggs were at an early stage. Larvae of *P. quadrituberculatus* were observed along the shore of southeast Kamchatka.

Assessment results showed the existence of a few ecological groups of this species near eastern Kamchatka and in the western Bering Sea. The resource in these areas differ in time of spawning and rate of early development. The pattern of flatfish spawning and development in the northwest Pacific is not clear at present because of flatfish attachment to certain biotopes, distinction in spawning periods, and the rate of individual development.

Introduction

Flatfishes are important North Pacific resources. Their biology is comparatively well studied. However, there is imbalance between ichthyofauna studies in the western and eastern waters of the northern Pacific. Better exploration of the northeastern Pacific was conducted by the United States with greater industrial and scientific potential, while the northwestern Pacific waters were mainly under Russian jurisdiction. Till recently the biology of the northeastern Pacific was also studied extensively by Soviet scientists because of the Soviet fishery near Alaskan waters prior to the establishment of the 200-mile zone. A similar situation occurred in studying flatfish early life history.

Distribution of flatfish eggs and larvae in the northeastern Pacific was described by Bulatov (1983), Fadeev (1971), Kashkina (1965), Waldron and Vinter (1978), and Waldron (1981). These data were obtained mainly during spring. Data on flatfish eggs and larvae from the northwestern Pacific during summer were discussed by Musienko (1961) and Khrapkova (1961a, 1961b). Some data on flatfish eggs and larvae from the Sea of Okhotsk were cited by Rass and Zheltenkova (1948). The most detailed data on flatfish early life history was collected by Pertseva-Ostroumova (1961). Summary data on spawning and early life history of flatfishes in the Bering Sea was cited by Musienko (1970). Many of the flatfish eggs and larvae that can be found in the waters off Kamchatka were described in the atlas edited by Okiyama (1988).

Undoubtedly the most complete data on the early life history of North Pacific flatfish were contained in the guide by Matarese et al. (1989). Significant data on the distribution of flatfish eggs and larvae in the northwest Pacific were obtained by the Japanese research vessel *Oshoro Maru*, but these surveys included no shelf regions. In spite of the ichthyoplankton surveys implemented by Russian vessels during the last few decades in the northwestern Pacific, the main goal of the surveys was to record walleye pollock egg and larvae; other taxa were

generally not recorded. Moreover, these surveys were generally implemented during the spring. Thus, there was a lack of data on flatfish early life history and their egg and larva distribution in the northwestern Pacific shelf. Therefore, the main goal of this study was to determine characteristics of flatfish early development during summer.

Methods

In this research we used results of ichthyoplankton surveys performed with the author's participation from the shelf regions of eastern Kamchatka and the western Bering Sea at bottom depths of 20-200 meters from June 11 to July 10, 1991. Vertical tows from bottom to surface were made using ichthyoplankton conical nets with a mouth diameter of 80 cm (IKS-80). Fish eggs and larvae were examined and stored in a formalin solution. Generally, the length of larvae from the beginning of the rostrum to the end of the notochord (NL) was used. Larvae with yolk are referred to as prelarvae. Water temperature was measured in degrees centigrade. Special attention was directed toward thoroughly categorizing flatfish eggs and larvae, since there was much confusion about their identification in ichthyoplankton studies. The main reference for flatfish egg and larvae identification during this work was the monograph by Pertseva-Ostroumova (1961).

Results and Discussion

During these investigations flatfish eggs and larvae were numerous among ichthyoplankton components, although less abundant than walleye pollock eggs and larvae. During the survey 201 ichthyoplankton stations were implemented. Flatfish eggs and larvae were only observed at 43 stations; eggs of *Acanthopsetta nadeshnyi* were more abundant. In addition, eggs and larvae of *Hippoglossoides elassodon* and *Pleuronectes quadrituberculatus*, larvae of *Hippoglossoides robustus*, *Platichthys stellatus*, and *Limanda proboscidea* were found. Places where flounder eggs and larvae were caught are shown on Figures 1 and 2.

Eggs and larvae of the genus *Hippoglossoides*

Along eastern Kamchatka and in the western Bering Sea there are two species of bigmouth flatfishes of the genus *Hippoglossoides*: *H. elassodon* and *H. robustus*. The first species is more abundant, and the second occupies comparatively northern areas. *Hippoglossoides*

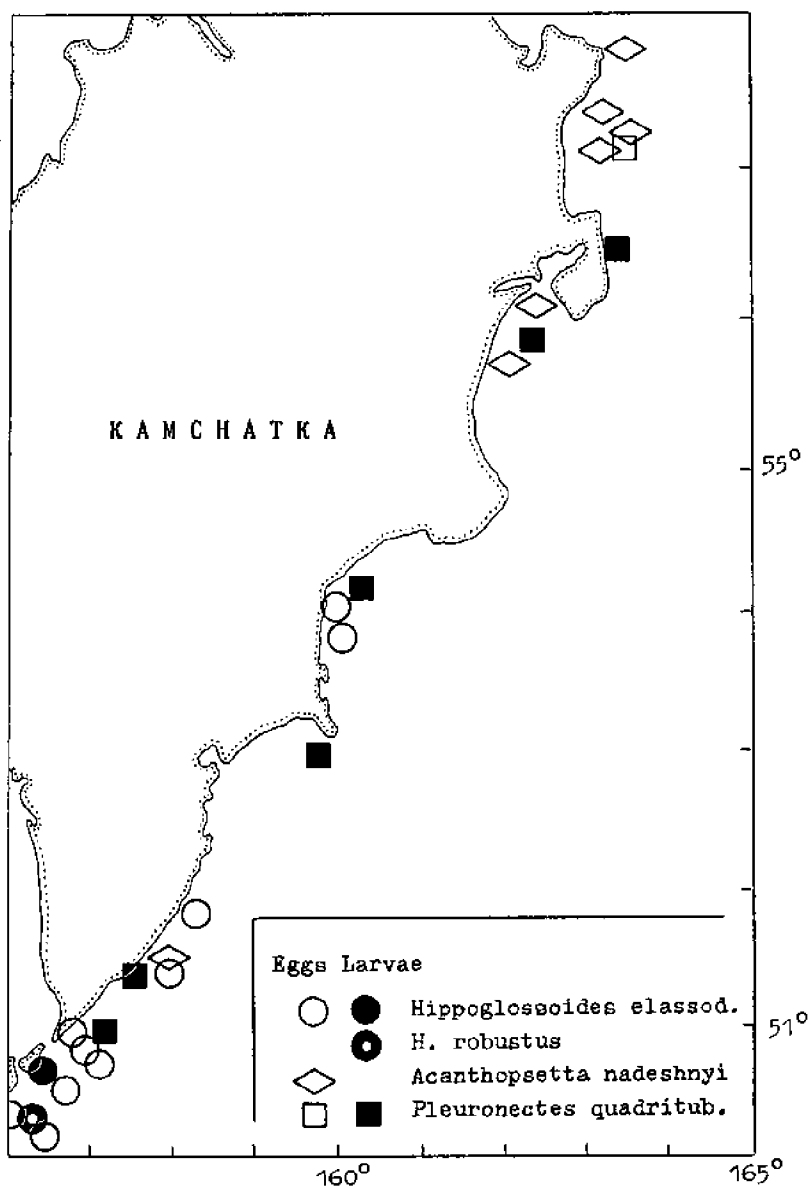


Figure 1. Location of flatfish eggs and larvae finds near east Kamchatka.

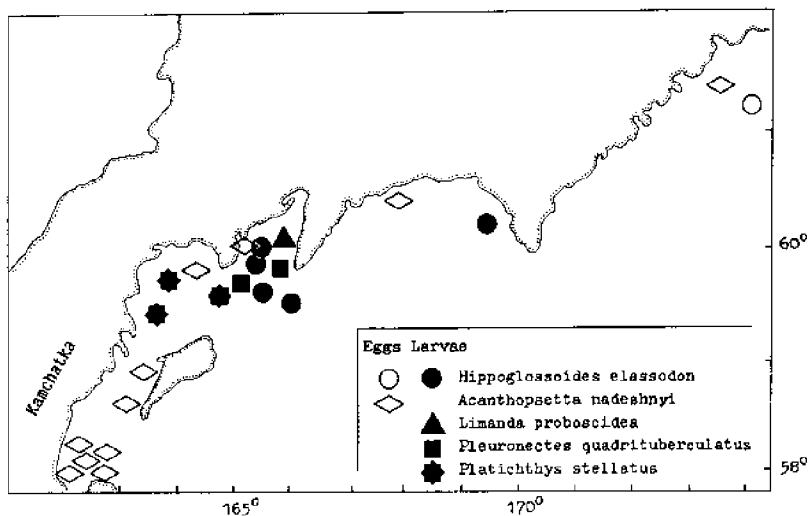


Figure 2. Location of flatfish eggs and larvae finds in the western Bering Sea.

dubius can be found in the northwestern Pacific also, but it is distributed in more southern areas. Eggs of *Hippoglossoides* sp. are easy to identify because of their large size and wide perivitelline space, though it is difficult to separate eggs of these species. In the north-eastern Pacific Bulatov (1983) attempted to separate species of *H. elassodon* and *H. robustus* by egg diameters.

According to Pertseva-Ostroumova (1961), *H. elassodon* spawns off southeast Kamchatka from April to June, and in the northwestern Bering Sea it spawns later finishing in July. The spawning occurs in the shelf regions. The length of larvae found ranged from 5.4 mm in May to 17.2 mm in August. The main density of larvae occurred near spawning regions, and during ontogenesis they moved closer to shore. The data on spawning of *H. robustus* were not numerous. Its eggs were found near east Kamchatka in April-May and in the western Bering Sea in May-June. The eggs of *H. robustus* were separated from those of *H. elassodon* by smaller overall diameter (*H. robustus* egg diameter was 2.4-2.69 mm whereas *H. elassodon* eggs had a diameter of 2.45-3.67 mm). A sample of *H. robustus* larvae 10.5 mm long from Avachinski Bay and two juveniles of 27.7 and 30.9 mm long were observed.

Eggs of *H. elassodon* occurred from June 11 through July 9 between the eastern shores of the northern Kuril Islands and Cape Navarin, in the northern Bering Sea, at 39-132 m bottom depth, but catches were insignificant (generally one or two eggs per station). Egg diameters varied from 2.68 to 3.7 mm. At the most southern station, near the eastern shore of Paramushir Island, we found three small eggs ranging from 2.68 to 2.82 mm, while the rest of the eggs of this species were more than 3 mm in diameter. Almost all the eggs collected were close to hatching, except one early-stage egg was found northeast of Olyutorski Cape at 90 m bottom depth.

The eggs were identified by their large diameter and wide perivitelline space. Eggs of *Hippoglossoides robustus* found at that time have a smaller egg diameter. The unusually small eggs were close in diameter to *H. robustus* and *H. dubius* and had features of *H. elassodon* (one of the three eggs had pigment on the surrounding tail finfold), and features of *H. robustus* (all eggs had melanophores passed to the yolk). If we take into account that pigmented yolks were also observed in larger eggs, whose embryos had specific features of *H. elassodon*, as well as the presence of one *H. elassodon* prelarva in the sample, we can probably correctly identify these distinctive eggs as *H. elassodon*. Small diameter eggs of *H. robustus* have been observed from Avachinski Bay (Pertseva-Ostroumova 1961). This phenomenon can result from a period of swelling caused by recent spawning. However, in this case the eggs of *H. elassodon* were near hatching, which could explain the differences in overall egg size among the groups.

All eggs of *H. elassodon* had ellipsoidal yolks with a diameter of 0.5-1.65 mm. The majority of the eggs had melanophores passed to the front and lower parts of the yolks which was not previously observed for this species. The last stage embryos had the pigmentation characteristic of four bands on the tail.

As indicated above, prelarvae of 4.3 mm NL in poor condition with characteristics of *H. elassodon* (four pigmented bands on the tails and pigment on the finfold surrounding the urostyle) were found from Paramushir Island eastward together with the small eggs of the species. The remainder of the *H. elassodon* larvae were caught in the Bering Sea. Among these was one prelarva of 4.6 mm NL caught on July 6 in Olyutorski Bay at 44 m depth, and water temperature of 4.6°C at the surface and 4.3°C at the bottom. Six larvae were caught on July 1 in Korf Bay at 57-132 m depth in water 7.4 to 9.5°C at the surface and -0.15 to 0.7°C at the bottom. All *H. elassodon* larvae including

Table 1. Body ratio of *Hippoglossoides* larvae (* = data from Pertseva-Ostroumova 1961; NL = notochord length, AL = anteanal length, BD = greatest body depth, HL = head length, ED = eye diameter, sL = snout length).

Species	Region	NL, mm	% of body length (NL)			% of head length	
			AL	BD	HL	ED	sL
<i>H. elassodon</i>	S-E Kamchatka	4.3	40.0	7.0	10.0	-	-
	Olyutorski Bay	4.6	41.5	6.5	17.2	38.0	17.7
	Korf Bay	5.3	41.5	5.7	15.1	37.5	20.0
		6.0	45.0	9.5	20.2	33.1	17.4
		8.0	36.3	5.0	15.8	29.4	20.6
		8.7	38.5	5.9	14.8	31.8	15.5
		8.7	36.8	6.2	17.2	27.3	20.7
		9.1	33.9	5.1	13.6	31.5	21.8
	West Bering Sea*	5.4-10.3	28.9-35.5	3.6-5.6	10.7-14.6	25.3-41.1	13.3-21.8
<i>H. robustus</i>	S-E Kamchatka	5.1	34.3	4.8	13.2	40.5	29.1
	Avachinski Bay*	10.5	35.9	7.8	18.9	22.7	17.2

prelarvae had open mouths, heavily pigmented eyes (except the smallest prelarva lacking eyes), clear pigment bands on the tails, and melanophores on the finfold around the urostyle.

We observed no eggs of *H. robustus* during the survey. A single *H. robustus* prelarva of 5.1 mm NL was caught on June 13 eastward of Shumshu Island at 65 m depth, water temperature 3.8°C at the surface and 2°C at the bottom. The prelarva tail turned up toward the head, an indication that it had recently hatched. The prelarva had an ellipsoidal yolk of 1.1 mm length and 0.65 mm in diameter, closed mouth, and unpigmented eyes. There was a small amount of pigment only on the eye pupil perimeter. Body pigmentation was moderate and consisted of small, dispersed melanophores. There were no pigment bands on the tail. Note that eye pigmentation and pigment bands on the tail of *H. elassodon* appear during the egg stage before hatching. The prelarva of *H. robustus* had melanophores on the front and bottom parts of the yolk, and on the dorsal and anal finfolds, although there was no pigment on the finfold near the urostyle.

Measurements of *Hippoglossoides* larvae showed their body proportions broader than cited by Pertseva-Ostroumova (1961). Therefore, it is too difficult to separate larvae of *H. elassodon* and *H. robustus* by their measurements (Table 1). Table 1 also shows that the

antennal length of the larvae decreased during ontogenesis. The other changes in age noted by Pertseva-Ostroumova for *H. elassodon* larvae as increased body depth, decreased eye diameter, and increased head and snout lengths do not appear on this table, probably due to the small amount of change in these values.

Thus *H. elassodon* and *H. robustus* eggs at hatching, and the early larval stages of these species, can be separated by intensity of general body pigmentation, eye pigmentation, and presence or absence of pigment bands on larvae (or embryo) tails. However, features such as egg diameter, presence or absence of pigmentation on the yolk and the finfold around the urostyle, the measurements, and body length at hatching seem less reliable for identification.

Eggs of *Acanthopsetta nadeshnyi*

Acanthopsetta nadeshnyi is a small, comparatively deep water flatfish for which no directed fisheries have been implemented. However, in some areas of its distribution it was caught in great abundance. There are spawning data on this flatfish in Peter the Great Bay and in open parts of the Sea of Japan in July-August, and near the western shore of Sakhalin in September. Concentrations of males and females were observed just before spawning and single eggs of this fish were collected at 50-70 m depth. Larvae of *A. nadeshnyi* were found on the western shore of Sakhalin in late August. These data were cited by Pertseva-Ostroumova (1961), who also described eggs of this fish from Tatarski Strait and from Peter the Great Bay, and the Sea of Japan in comparatively deep water (53-295 m). The egg diameter varied from 0.86 to 1.03 mm (average 0.92 mm); the perivitelline space formed 6.9-16.8% of the egg diameter.

During the survey discussed here, eggs of *A. nadeshnyi* were caught from June 14 to July 8 along the shore between 51°N latitude at southeast Kamchatka and 61°N northeast from Olyutorski Cape at 23-214 m (average 64.4 m) depth with surface water temperature of 3.4-11.9°C (average 7.0) and bottom water temperature of -0.9 to -2.3°C (average 0.5). The greatest egg concentration (14 eggs per m²) was observed in Osernoi Bay at 47 m depth. Egg diameter varied from 0.8 to 1.2 mm (average 0.95 mm) and perivitelline space formed 5-10% of the egg diameter. Total catch was 53 eggs of *A. nadeshnyi*. Among them more than 50% of the eggs were in early stages. A few eggs near hatching were caught southward from the Bering Sea.

The main characteristic of these flatfish eggs was their small size. Aside from *A. nadeshnyi*, other species with small egg size found in

this region are *Limanda aspera*, *L. proboscidea*, *Lepidopsetta bilineata*, and *Platichthys stellatus*. Eggs of *Limanda* spp. differ in smaller average egg diameter and in embryo pigmentation; *Lepidopsetta bilineata* has demersal eggs, and its embryogenesis occurs earlier. For precise identification eggs of *A. nadeshnyi* were compared with available eggs of *P. stellatus* from the Bering Sea and from the Sea of Okhotsk. Eggs of *P. stellatus* differ in having pink and striated egg envelopes, and in brighter yellow yolks and embryos, although the melanin pigmentation characteristic of the eggs of the two species was similar. In addition, spawning of *P. stellatus* occurs earlier and in shallower waters.

Embryo pigmentation of *A. nadeshnyi* was similar to the description given by Pertseva-Ostroumova (1961) for Peter the Great Bay. Embryos showed pointed melanophore pigmentation on the head in a dorsal row and pigmentation around the end of the urostyle. The eggs of *A. nadeshnyi* caught near east Kamchatka and in the western Bering Sea differ from eggs of this species from Peter the Great Bay in greater average egg diameter and comparatively greater yolk.

Larvae of *Limanda proboscidea*

In spite of the wide distribution of *Limanda proboscidea* in the Bering Sea and the fact that catch percentages are sometimes significant (Pertseva-Ostroumova 1961), there is little data about the early life history of this species. Andriyashev (1954) pointed out that this flatfish approached the shore for spawning earlier than other flatfishes, and left the inshore after spawning later. Spawning occurred at shallow depths where fishing vessels seldom operated. This partly explains the scarce data on spawning and early life history of *L. proboscidea*.

Spawning of *L. proboscidea* is known to occur in nearshore waters, shallower than other flatfishes, in all areas of its distribution. In the Sea of Okhotsk the spawning lasted from June through September. In the Bering Sea spawning was observed in June, and determined to continue during July and August (Pertseva-Ostroumova 1961). Pertseva-Ostroumova described eggs and larvae of *L. proboscidea*, distinguishing the eggs of this species from those of *L. aspera* which are very similar. She also described *L. proboscidea* larvae with a length of 3.3 mm (with resolved yolk sac) to 4.6 mm, which were caught in late June in Olyutorski Bay. Prelarvae and late larvae of *L. proboscidea* were not described.

Only a single larva of *L. proboscidea* with notochord length of 5.1 mm was caught during the 1991 summer ichthyoplankton survey. It

Table 2. Body ratio of *Limanda proboscidea* larvae from the western Bering Sea (* = data from Pertseva-Ostroumova 1961; + = measured on figures; NL, AL, BD, HL, ED, and sL = as on Table 1; HD = head depth after eye, EI = eye interval).

Catch date	NL, mm	% of NL			HD	% of HL		
		AL	BD	HL		ED	sL	EI
June 26*	3.3-3.5	34.1-40.8	4.5-5.8	15.8-16.8	12.6+	35.7-45.5	17.9-20.0	34.6-37.5
	4.5-4.6	33.3-36.7	5.5-5.9	15.6-16.3	12.2+	33.8-39.4	16.3-18.3	29.6-29.7
July 1	5.1	46.6	8.4	19.9	21.0	36.4	16.6	25.0

was caught July 1 in Korf Bay at a bottom depth of 55 m with a surface water temperature of 11.9°C and bottom temperature of -0.3°C. The larva was generally similar to those descriptions by Pertseva-Ostroumova (1961) of smaller larvae of *L. punctatissima* and *L. proboscidea*: straight urostyle, almost vertical mouth, extensive and curved gut tube but without a loop. The larva had no fin rudiments; only mesenchyme thickening was apparent instead of caudal fin rays. The larva had 41 myomeres (22 preanal and 19 caudal); its pigmentation corresponded to the available description. Melanophores stretched mainly on the lower side of the body. There were melanophore patches on the upper side of the midtail that formed a likeness to a band of all bottom edge melanophores. A band like this is a peculiar feature of *L. punctatissima* and *L. proboscidea* larvae which distinguishes them from *L. aspera* larvae. Distinct from available descriptions, the larva of *L. proboscidea* had melanophores on the lower edge of the tail under the end of the urostyle, which was identified by Pertseva-Ostroumova (1961) for larvae of *L. punctatissima* but was not identified for *L. aspera* or *L. proboscidea*. Moreover, the larva had a lightly pigmented row on the lower edge of the anal finfold and pigment on the lower edge of the base lobe of the pectoral fins, which were identified by Pertseva-Ostroumova for larvae of *L. aspera*, but were not identified for *L. punctatissima* or *L. proboscidea*.

Thus through some morphological features, the larva fits all three taxa of *Limanda*. Presumably pigmentation on the lower edge of the finfold and on the lower edge of the pectoral fin lobe (which can disappear after fixation) was not as significant an identifying feature as the tail pigment band. Absence of *L. punctatissima* in the Bering Sea and near east Kamchatka precluded collection of its larvae there.

Therefore, the larva analyzed can in all probability be attributed to *L. proboscidea*.

Details of the larva measurements provide additional data about changing body proportions during early life history (Table 2). The table shows that during early ontogenesis *L. proboscidea* body depth and head length increased in relation to other measurements, but snout length and eye interval decreased.

Eggs and larvae of *Pleuronectes quadrituberculatus*

This species is widely distributed in the North Pacific and is significant in fisheries. The most complete data about its spawning and its distribution during early development in the western Bering Sea and near east Kamchatka were cited by Pertseva-Ostroumova (1961). According to these data, spawning occurred over the shelf regions from early spring to late June, and periods of spawning depended on geographic position. The greatest egg concentrations were observed in late April near east Kamchatka, and in May in the western Bering Sea. Egg diameter of this species in Olyutorski and Anadyrski bays varied from 1.67 to 2.21 mm. Character traits of the eggs distinguishing them from the eggs of walleye pollock were the reddish color of the envelope after fixation and the pigmented yolk. Larvae of this flatfish were also described.

During the survey, *Pleuronectes quadrituberculatus* eggs were caught on June 25 at only one station in Osernoi Bay. Four eggs 1.78 to 2 mm in diameter and close to hatching (embryo tail approaching the head) were caught at a bottom depth of 47 m where surface water temperature was 6.0°C and bottom water temperature was -0.17°C. Because no eggs of this fish were observed in more northern regions of the western Bering Sea, the spawning period of this species is probably more extensive than observed and is not dependent only on the geographical location of the spawning areas.

Larvae of *P. quadrituberculatus* were observed from June 13 to July 1 along the shore from southeast Kamchatka to Korf Bay at 40-200 m bottom depth with surface water temperature of 4.7 to 7.7°C, and at bottom water temperature of -0.17 to 2.3°C. The total sample collected at 8 stations was 10 larvae at 5.3-10 mm NL. Larvae collected between southeast Kamchatka and Kronotski Bay had body lengths of 7.5-8.9 mm (except for a single larva 5.3 mm long in poor condition from Avachinski Bay). Two of the smallest larvae with body lengths of 6.1 and 6.3 mm were caught in Kamchatkski Bay, and the two most mature larvae with body lengths of 8 and 10 mm were caught in Korf

Table 3. Comparative body ratio of *Pleuronectes quadrituberculatus* larvae caught in June-July 1991 near east Kamchatka and in the western Bering Sea (designations as on Table 1).

Region	NL, mm	% of NL			% of HL	
		AL	BD	HL	ED	sL
Southeast Kamchatka	7.5	—	8.3	16.1	35.5	—
	7.5	37.3	8.1	16.1	24.8	8.3
	8.0	40.6	10.6	12.4	35.5	23.6
	8.5	44.1	8.4	15.2	—	—
Avachinski Bay	5.3	44.5	13.4	20.2	38.3	26.7
Kronotski Bay	8.9	38.8	6.7	16.9	32.7	10.1
Kamchatski Bay	6.1	41.0	7.7	16.7	37.1	15.8
	6.3	38.6	8.4	18.1	35.1	10.5
Korf Bay	8.0	46.9	19.6	20.0	26.9	22.0
	10.0	41.0	13.7	16.4	31.1	17.2

Bay. A larva from Korf Bay 8 mm long was more mature than larvae 8-8.9 mm long caught south of the Bering Sea. It was characterized by a thicker body (Table 3), bent urostyle, the appearance of ray rudiments in caudal and anal fin bases, and the appearance of pectoral fin rudiments in both larvae from Korf Bay; whereas the bodies of the larvae from Kronotski Bay were still rounded, with finfold, without pectoral fin rudiments, and without ray rudiments. Among the larvae caught south of the Bering Sea, only one 8.5 mm long was close to flexion and had the appearance of caudal fin ray rudiments.

Based on this data, it's possible to consider the existence of several ecological groups of *Pleuronectes quadrituberculatus* near east Kamchatka and in the western Bering Sea that differ in spawning periods and in rate of early ontogenesis. The irregular early life history of this species was observed by Pertseva-Ostroumova (1961), but she didn't address the traits of the larvae in these regions.

We counted 42 myomeres on the larvae (13-14 preanal and 28-29 caudal). All larvae (except for a 10 mm NL larva) apparently had the remainder of the yolk. Larva pigmentation was mainly on the lower part of the body and on the lower finfold, and was similar to the description by Pertseva-Ostroumova (1961). There was an apparent row of pigment over the tail notochord and pigment at the base of the

caudal fin rays in larvae with ray rudiments of caudal and anal fins. The sequence of fin ray formation was next: caudal, anal, dorsal, pectorals, and pelvics.

Larvae of *P. quadrituberculatus* can be found together with larvae of *Platichthys stellatus* and *Limanda* spp., and are similar to them in pigmentation, but can be distinguished mainly by their greater body length at similar stages.

Eggs and larvae of *Platichthys stellatus*

This is one of the most extensively distributed flatfish in the northern Pacific. It generally exists in shallow waters, and sometimes enters freshwater. Significant concentrations of this fish were observed near east Kamchatka. It spawned in shallow nearshore waters during June-July at east Kamchatka. In the western Bering Sea, eggs of this fish were observed during late May and early June, and its larvae were observed in June (Pertseva-Ostroumova 1961). The early life history of *P. stellatus* was well studied by Pertseva-Ostroumova who also used descriptions by Orcutt (1950) and Yusa (1957). Based on those data, egg diameter in the Bering Sea and near east Kamchatka was 0.92-1.24 mm, and prelarva body length at hatching was 2.25-2.35 mm. Also, larvae 3.5-6.6 mm in body length were collected June 26, 1952 at three stations in Olyutorsky Bay at 35-96 m bottom depth.

During the survey discussed here three larvae of *P. stellatus*, 4.0, 5.0, and 5.5 mm in body length, were caught June 29 and 30 at three stations in northern Karaginski Bay at 23-67 m bottom depth, with surface water temperature of 7.5-9.3°C and bottom temperature of 0.3-2.8°C.

A total of 35-38 myomeres were counted on the larvae (8-11 preanal and 27-30 caudal). The larva pigmentation was close to the available description by Pertseva-Ostroumova (1961). Pigment existed mainly on the lower part of the body and on the anal finfold. There was apparent pigmentation in front of the pectoral fin base. Melanophores on the body sides near the midtail resembled a band. The urostyle of larvae 5 mm body length was close to flexion. Results of larva measurement show unequal body proportion changes during early life history (Table 4). These few data also show that body length of larvae increased in proportion to bottom depth, and confirmed the inshore spawning characteristic of the fish after which the eggs and larvae can be carried to deeper waters by the currents.

Larvae of *P. stellatus* can be caught with *Limanda* spp. which are similar in size and body pigmentation. However, upon careful exami-

Table 4. Body ratio of *Platichthys stellatus* larvae from the western Bering Sea (* = data from Pertseva-Ostroumova 1961, measured on figures; AL, BD, HL, ED, and sL as on Table 1).

NL, mm	Bottom depth, m	% of NL			% of HL	
		AL	BD	HL	ED	sL
4.0	23	35.0	11.3	21.4	38.2	21.6
4.6*	46	41.6	6.6	16.9	38.5	15.4
5.0	34	29.1	13.0	18.6	35.5	26.1
5.5	67	43.6	13.6	20.8	26.3	22.6
5.9*	96	39.6	9.4	17.8	29.7	13.2
6.6*	96	41.7	16.0	18.7	28.6	11.9

nation the *P. stellatus* larvae can be isolated by the following features: closed mouth, smaller head depth, thicker body, lack of melanophores on lower edge of pectoral fin base lobe, melanophores forming a band on the tail do not cross dorsally, lack of pigmentation around the urostyle, and fewer myomeres.

Eggs of *P. stellatus* were not caught during the survey. However, a single egg of this species 1.06 mm in diameter was caught with a Juday net during a herring survey on May 18 of the same year in Korf Bay, western Bering Sea, at a bottom depth of 18 m. The egg had a characteristic red-pink and striated envelope, and the yolk diameter was 0.91 mm. The embryo made up three-fourths of the yolk perimeter; its tail was not separated from the yolk. The embryo had characteristic pigmentation with a row of melanophores on the lower part of the tail. The eyes were unpigmented.

Conclusion

The survey was implemented following the primary spawning period of flatfishes (*Pleuronectes quadrituberculatus*, *Hippoglossoides* spp., *Platichthys stellatus*, and probably *Limanda* spp.) in the northwestern Pacific. Therefore, very few eggs and larvae of the flatfishes were collected during the survey. Among the northwestern Pacific flatfish, *Acanthopsetta nadeshnyi* eggs were the most abundant. The eggs were mainly at early stages; no larvae were observed.

Distribution of flatfishes in the region of the North Pacific discussed here is very limited. In the region 12 species of flatfish occur

(Schmidt 1950, Andriyashev 1954, Pertseva-Ostroumova 1961): *Atheresthes evermanni*, *Reinhardtius hippoglossoides*, *Hippoglossus stenolepis*, *Hippoglossoides elassodon*, *H. robustus*, *Acanthopsetta nadeshnyi*, *Lepidopsetta bilineata*, *Limanda aspera*, *L. proboscidea*, *Pleuronectes quadrituberculatus*, *Liopsetta glacialis*, and *Platichthys stellatus*. Eggs and/or larvae of only six species were observed during the survey. Bigmouth flatfishes such as *Atheresthes evermanni*, *Reinhardtius hippoglossoides*, and *Hippoglossus stenolepis* spawn during winter; their eggs and larvae appear during the winter-spring period, principally in deep water. Therefore, neither eggs nor larvae of these species were found. *Lepidopsetta bilineata* is abundant in the region, has demersal eggs, and spawns in early spring. Therefore, this species was also not present in the samples. Eggs and larvae of *Liopsetta glacialis* occur near Kamchatka and probably can be caught earlier and in shallower waters where the survey was not implemented. Eggs of *L. glacialis* were previously observed in the Chukchi Sea during winter (Andriyashev 1954). At present the question of occurrence of *Limanda aspera* eggs and larvae is not clear, although egg concentrations of *L. aspera* in the western Bering Sea through August-September was noted by Khrapkova (1961 a). Matarese et al. (1989) recorded spawning of this fish in summer.

The entire pattern of flatfish spawning and development in the northwestern Pacific is not clear at present. Because of their attachment to certain biotopes and species, spawning period and development rate studies are needed on the separate ecological and early developmental traits of flatfish by local region. Since flatfish have prolonged spawning periods which are not coincident among species, longer surveys are required to record flatfish eggs and larvae than are required for walleye pollock abundance estimates.

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Mesoscale Variation in Spring Abundance of Copepod Nauplii Prey of Larval Flatfish in a Southeastern Alaskan Bay

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Abstract

This study examined the vertical and horizontal patchiness of copepod nauplii, which are prey of flatfish larvae, in an Alaskan bay and its major passage. Larvae of rock sole, *Pleuronectes bilineatus*, and flathead sole, *Hippoglossoides elassodon*, were the most common flatfish larvae in the study area. During the period when both species were present there were currents capable of transporting the larvae and their prey both into and out of the bay.

Total copepod nauplii concentration were seldom less than 10 L^{-1} , even in April before the phytoplankton bloom or pycnocline formation. From mid-May on, after pycnocline formation, total nauplii concentrations generally exceeded 30 L^{-1} somewhere in the upper 15 m of the water column. There were no consistent patterns of nauplii abundance, either in the horizontal or vertical plane, between sample sites in the bay and its outside passage. Copepod nauplii were distributed throughout the upper 15 m and typically did not show thin

vertical or horizontal "patchiness." Throughout the spring the depth of maximum nauplii abundance was not consistent from station to station. In terms of prey abundance both the inner bay and its outside channel, and any depth in the upper 15 m of the water column, appeared to be equally endowed with copepod nauplii prey for fish larvae.

Rock sole larvae hatched from April through mid-May, prior to the spring copepod bloom and formation of the pycnocline. Thus rock sole larvae did not have stable water column conditions that could have facilitated prey patch formation. When they were present, nauplii were generally 10-20 L⁻¹. The nauplii abundance profiles suggest that rock sole larvae have adapted to feeding at nauplii concentrations typical of pre-spring phytoplankton bloom conditions. By hatching early in the season they may minimize predator encounters but they must feed when prey concentrations are at their lowest.

Flathead sole larvae hatched after pycnocline formation, in mid-May through June, while the spring copepod bloom was occurring. When they started feeding, nauplii concentrations were frequently over 40 L⁻¹. Flathead sole, by hatching during the spring phytoplankton bloom, had a stable water column and much higher prey concentrations to feed on than did the rock sole larvae. There seemed to be adequate numbers of nauplii to support flathead sole larvae anywhere above the 15 m deep pycnocline during their planktonic period. The measurements of nauplii abundance indicated flathead sole larvae did not need to find isolated prey patches to feed successfully.

Introduction

In southern Alaska, a geographically complex mixture of shallow bays, fjords, islands and deep passages serve as important nursery grounds for many commercially important species. Inside the bays small copepods like *Pseudocalanus* spp. and *Acartia clausi* dominate (Coyle et al. 1990, Paul et al. 1990a) while outside in the major passages larger copepods like *Neocalanus* spp., *Calanus marshallae* and *Metridia ochotensis* are prevalent (Coyle et al. 1990). Since these species have different reproductive strategies, it seemed possible that the bays and their passages might have different copepod nauplii abundances, unless physical transport mechanisms mix the populations. Many of the fish larvae present in the area prey on copepod nauplii (Dagg et al. 1984, Purcell and Grover 1990, Monteleone and Peterson 1986, Haldorson et al. 1989, Grover and Olla 1990). Some larvae, like the rock sole, *Pleuronectes bilineatus* (Ayres 1855), hatch

prior to the spring phytoplankton bloom and others like flathead sole *Hippoglossoides elassodon* Jordan and Gilbert, 1880 hatch during the bloom (Haldorson et al. 1989, 1993). The larvae of both the above mentioned flatfishes are pelagic and are subjecte to physical transport.

Historically fish ecologists have assumed that variations in larval fish survival is one of the primary factors controlling year class strength. Three major hypotheses have been proposed to explain the relationship between feeding conditions and larval survival. The "Critical Period Hypothesis" (Hjort 1914) claims that larval fish are especially susceptible to low prey concentrations during the period when they first begin to feed. If they do not encounter prey at suitable concentrations during this critical period they rapidly decline in condition, pass a point-of-no-return and die. Two variations on the "Critical Period Hypothesis" are the "Stable Ocean" (Lasker 1975) and the "Match-Mismatch" hypotheses (Cushing 1975). The main theme of the Stable Ocean hypothesis assumes that fish larvae are dependent on the formation of prey aggregations or "patches" to feed successfully. Theoretically prey patches are dependent on stratification in the water column (for an example see Dagg et al. 1987). While there has been some previous reporting on the vertical distribution of copepod nauplii in the study area (Paul et al. 1991) data concerning their horizontal patchiness has not been previously presented. This report provides information on the early vs. late spring spatial variability of nauplii concentrations inside and outside the bay. The results are used to examine the applicability of the Stable Ocean hypothesis stated above to rock sole or flathead sole larvae in the inside passage of southeastern Alaska.

Methods

Study site

Samples were collected during the spring of 1988 in Auke Bay (58°22'N, 134°40'W), and Stephens Passage, southeast Alaska (Fig. 1), a glacially influenced region with high precipitation. Generalized physical oceanographic conditions for the bay are described in Coyle et al. (1990). The area is relatively protected from wind and the mixed layer depth was 5 to 10 m during the period examined. The bay is 50 m deep and the Stephens Passage station 64 m deep. There was an intense diatom bloom in April and May (Coyle et al. 1990; Paul et al. 1990a, 1990b; Ziemann et al. 1991; Fig. 2).

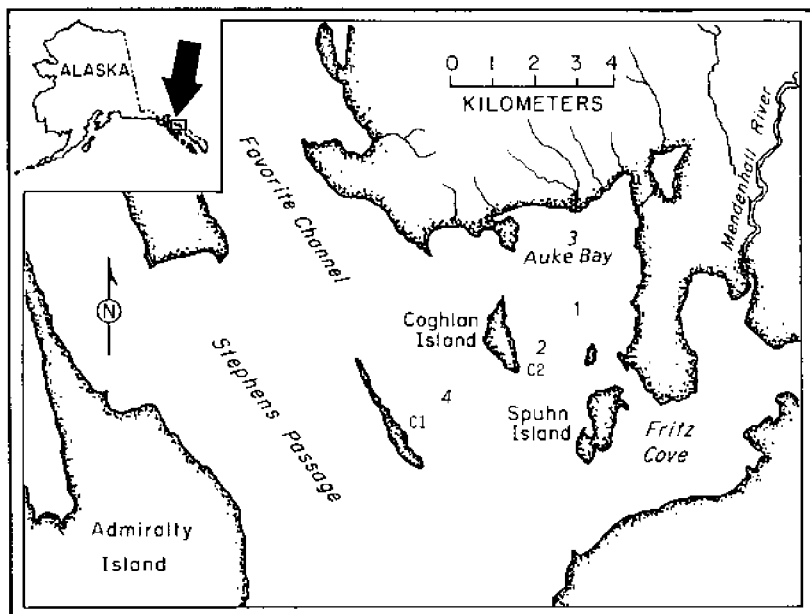


Figure 1. Map of the study area and sampling stations (1, 2, 3 and 4), where copepod nauplii were collected, and current meter stations (C1 and C2).

Physical oceanography

Salinity-temperature profiles were collected at least twice weekly using an Applied Microsystems CTD. The probe was lowered to 40 m depth, equilibrated for 1 min and retrieved at 5 m min⁻¹. Three Aanderaa RCM4 current meter moorings were installed at C1, and C2 (Fig. 1). The primary mooring with four current meters at C2 examined the major exchange between the bay and adjacent waters. The C1 mooring recorded water movement in the channel adjacent to the bay. Weather and wind speed data were collected at the nearby Juneau airport. A data report containing all the physical measurements is available (Nebert 1990).

Larval fish sampling

Fish larvae were collected in Auke Bay from mid-March through mid-June 1988. Weekly or biweekly samples, with five replicates, were collected with a NIO Tucker trawl (1 m² opening, 505 µm mesh) towed

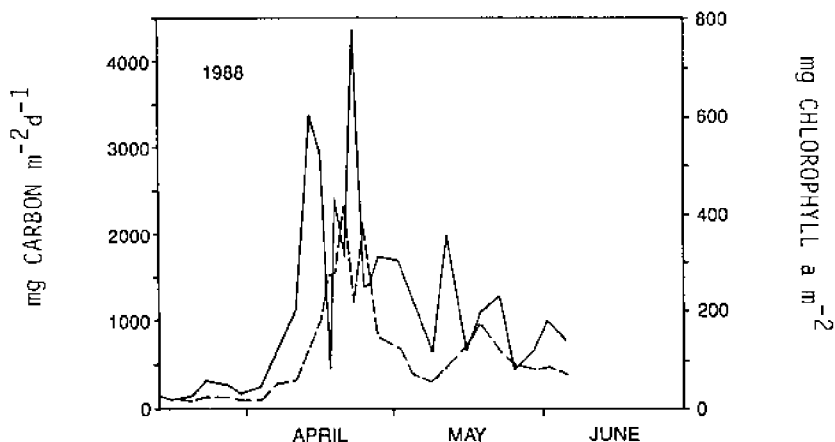


Figure 2. Primary production (solid line) and chlorophyll *a* (dotted line) concentrations in Auke Bay, Alaska, 1988. Data from Paul et al. 1990b.

in a double-oblique trajectory to a depth of 30-35 m. All collections were taken between 0800 and 1500 hrs at station 1. A digital flow meter in the net opening measured the volume filtered. These collections were fixed immediately in buffered 5% formalin. Mean densities were calculated as number per square meter of surface.

Nauplii sampling

Nauplii were collected at 0.5, 5, 10, and 15 m depths with a 30 L Niskin bottle from April into early June. Single bottle samples (one sample at each depth) were done at Stations 1, 2, 3 inside Auke Bay and Station 4 in Stephens Passage outside the bay (Fig. 1) during 1988. Water from the bottle was passed through a 64 μ m mesh bag net and the concentrated samples preserved for microscopic analyses. Nauplii were measured with an ocular micrometer and divided into three groups; small (< 150 μ m), intermediate (150-350 μ m,) and large (> 350 μ m) body length. Large nauplii often occurred at less than 1 L⁻¹ and their abundance is not presented. Size specific abundance is reported because some larval fish species are selective as to the size of nauplii they consume (Cohen and Lough 1983; Dagg et al. 1984; Munk et al. 1989). Copepod nauplii counts are plotted to provide information on time, area and depth variations in their abundance.

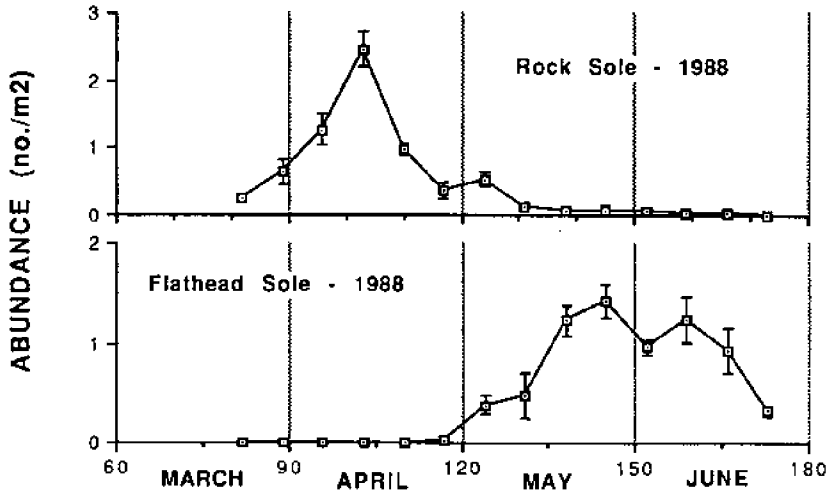


Figure 3. Mean densities of *Pleuronectes bilineatus* and *Hippoglossoides elassodon* vs. month or Julian day in Auke Bay, Alaska, during 1988.

Results

Fish larvae

Rock sole larvae first appeared in the samples in March and peaked in abundance with about 2.5 m^2 in early April (Fig. 3). By May rock sole larvae were rarely encountered in the samples. Thus, their planktonic period was completed before the spring phytoplankton bloom (Fig. 2). Flathead sole larvae first appeared in the samples in late April and were most numerous in late May and early June with 1.0 to 1.5 m^2 . By late June they were no longer common in the plankton (Fig. 3). Their planktonic period coincided with the spring phytoplankton bloom (Fig. 2).

Physical oceanography

During the period of 5-20 April 1988 when rock sole eggs were hatching, there were active exchanges of water between the bay and its passages (Figs. 4-6). During the first half of this period, there were strong local winds from the southeast causing downwelling events along the outer coast of southeastern Alaska. Following these winds there was an influx of more dense waters into Auke Bay. From the physical measurements and current meter record it appears that the

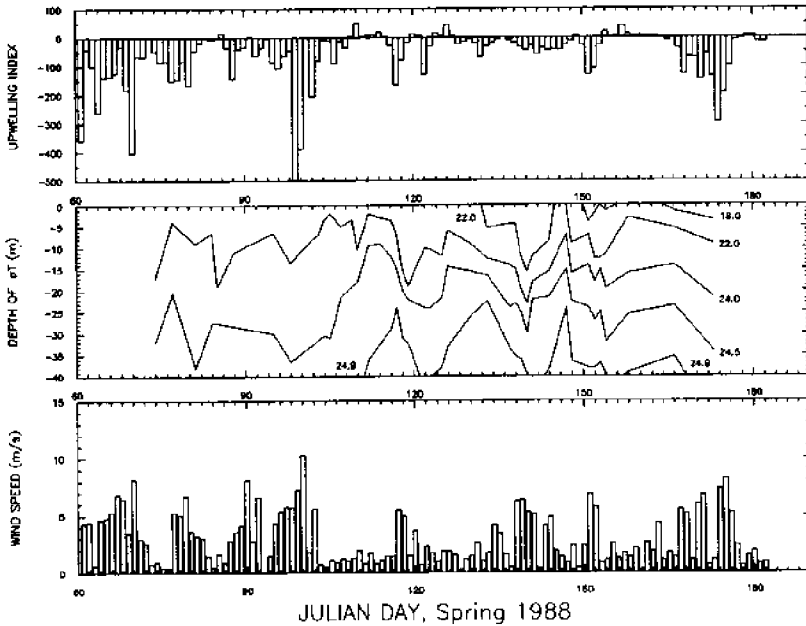


Figure 4. Time series of upwelling index near Sitka, Alaska (upper), density field (σ_t) for Auke Bay, Alaska (middle), and wind speed at the Juneau airport during spring and summer 1988.

waters at the lower depths were replaced by waters from the outside passage. During this exchange, upper water column waters were probably flushed from the bay. Flow at 12 m depth at mooring C1 during this period was primarily northward, corresponding to outflowing upper water column currents in the bay. Currents at C2 mooring show an outflow from Auke Bay at 12 meters from 6-16 April, while at 40 m currents were flowing into the bay. Throughout April the water column had a uniform density and there was no vertical stratification that could facilitate nauplii patch formation (Fig. 7).

During 10 May-10 June when flathead sole larvae were present, the physical measurements (Figs. 4-6) showed several exchange events. Starting on 12 May the density of bottom waters declined until about 19 May suggesting a loss of deep water, which was replaced by an influx of upper water column water. About 19 to 25 May, an intrusion occurred at the middle depths and the surface waters were flushed out. From 25 May through 1 June there was an influx at the surface and loss at the bottom. Between 1 and 10 June there was a

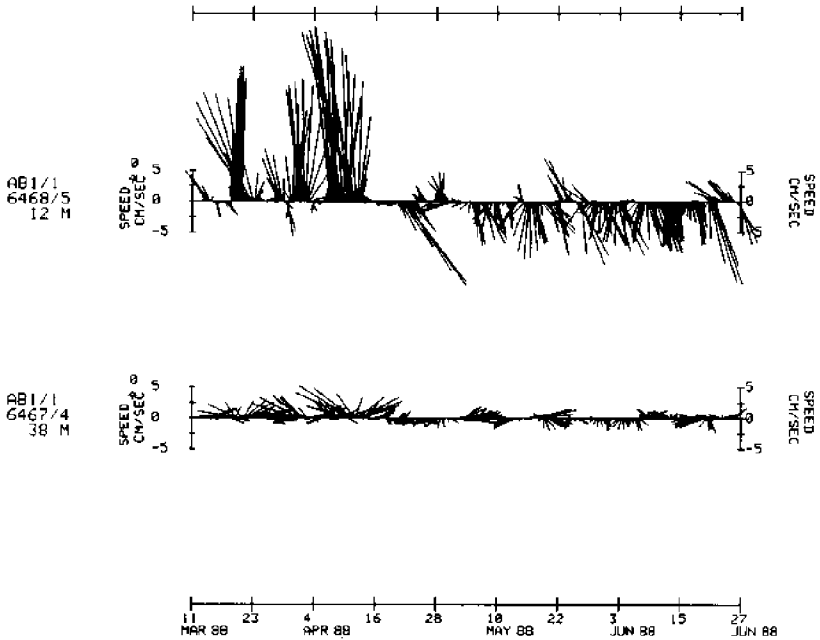


Figure 5. Stick plots of currents at mooring C1 in Auke Bay, Alaska, during spring and summer 1988.

strong intrusion at 15 meters. The C1 current meter showed that the upper 12 m water was generally moving southward and the C2 meter monitored inflows of upper water column water into the bay. The general trends during the time flathead sole were present was deep water entering the bay while the upper water was leaving it. By early May the water column began to exhibit vertical density stratification and by the month's end there was a mixed layer depth to about 5 m and a distinct pycnocline at about 15 m depth (Fig. 7). Thus flathead sole larvae coexisted with the type of environment consistent with the conditions needed to invoke the Stable Ocean hypothesis.

Copepod nauplii

Small copepod nauplii ($< 150 \mu\text{m}$) were typically $< 10 \text{ L}^{-1}$ during April (Fig. 8), while the larger nauplii ($150\text{-}350 \mu\text{m}$) ranged from < 1 to $\approx 25 \text{ L}^{-1}$ (Fig. 9). During the first two weeks of May numbers of both nauplii

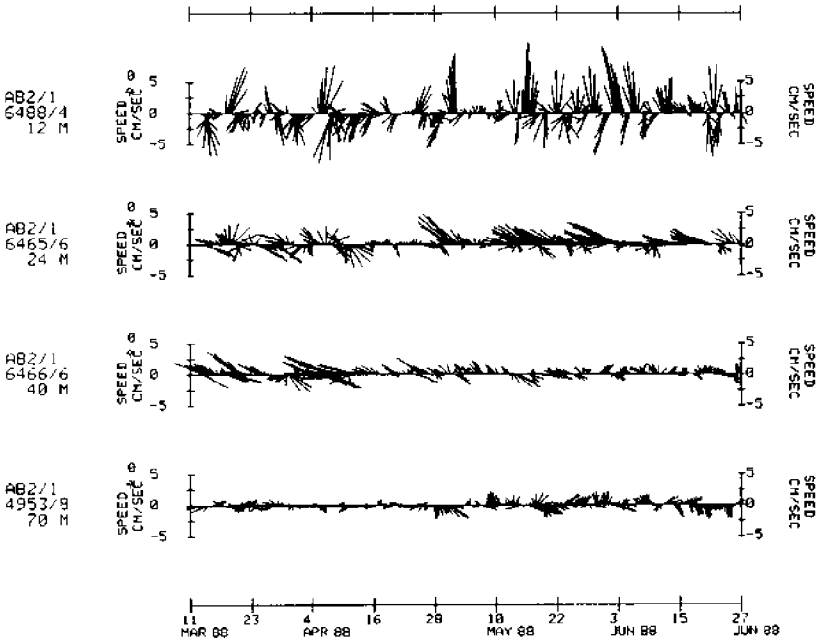


Figure 6. Stick plots of currents at mooring C2 in Auke Bay, Alaska, during spring and summer 1988.

size groups increased to $> 30 L^{-1}$ as copepod egg production increased during the spring phytoplankton bloom (Paul et al. 1990a). This seasonal increase in abundance was apparent at all stations and depths. The highest counts ($> 100 L^{-1}$) for both large and small copepod nauplii were from the 0.5 m depth samples.

Typically copepod nauplii were the most abundant at 0.5 m and least abundant at 15 m depth. In the samples collected on any given date at 0.5 m depth, there were some very large differences (factor of 8 times) in nauplii abundance between stations. At the other depths differences in nauplii abundance was frequently a factor of 2 or less (Figs. 8, 9). In April there were relatively small variations in nauplii abundance with depth. During May and June there were definite depths of maximum nauplii abundance but it was not consistent from station to station.

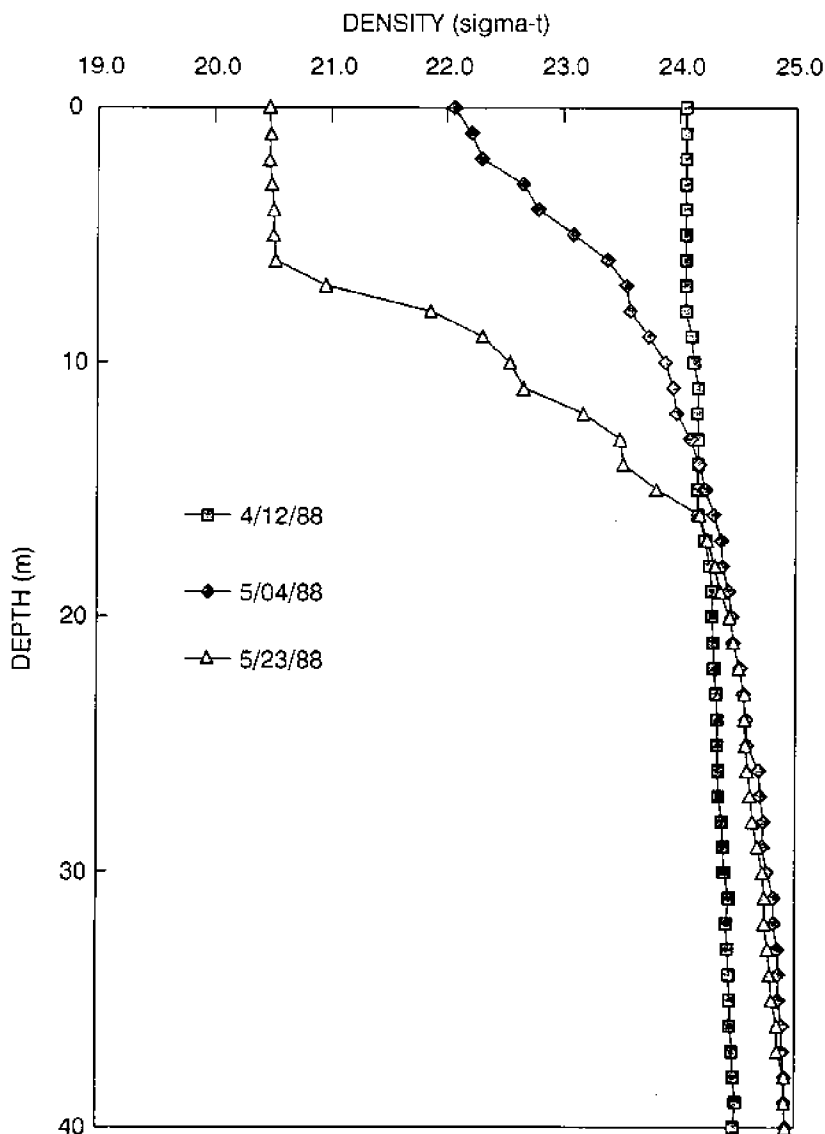


Figure 7. Profiles of sea water density for three days illustrating vertically uniform (4/12), mixed layer (5/04), and stable (5/23) conditions at Auke Bay Station 1 during spring 1988.

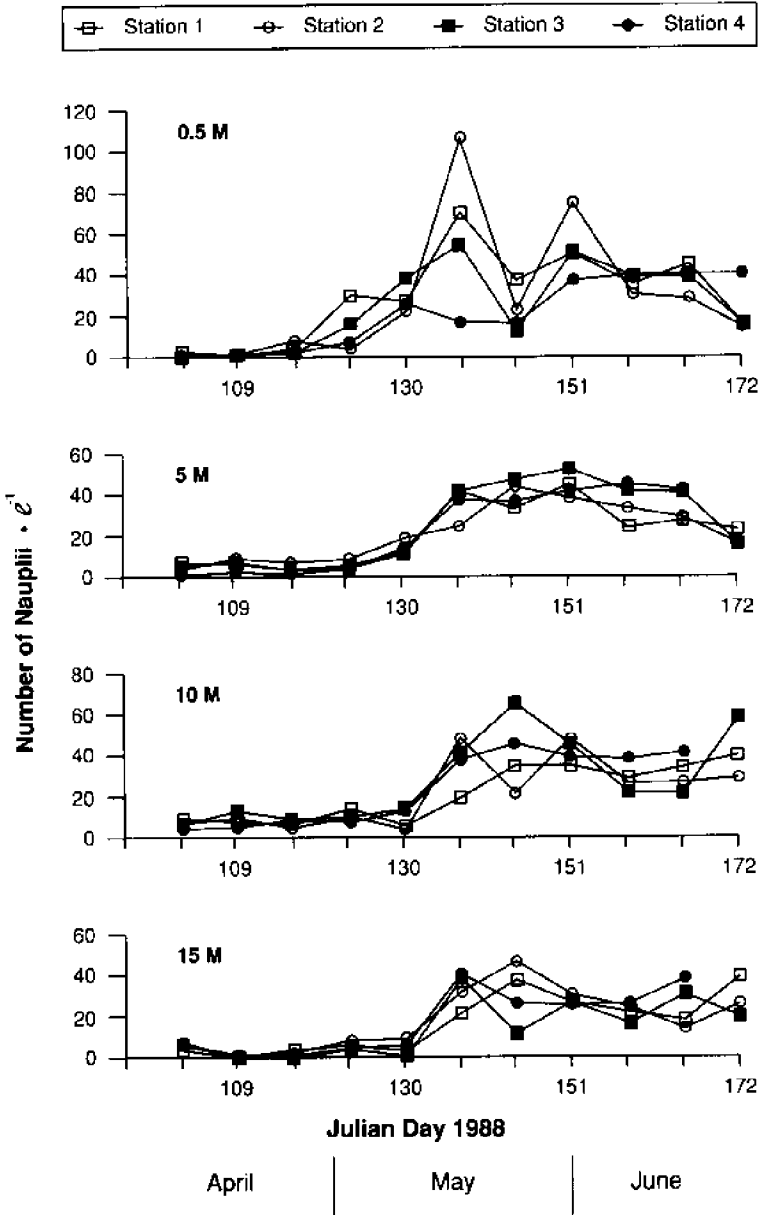


Figure 8. Station to station variation in copepod nauplii (< 150 μm length) in the area of Auke Bay, Alaska, between 12 April and 21 June 1988.

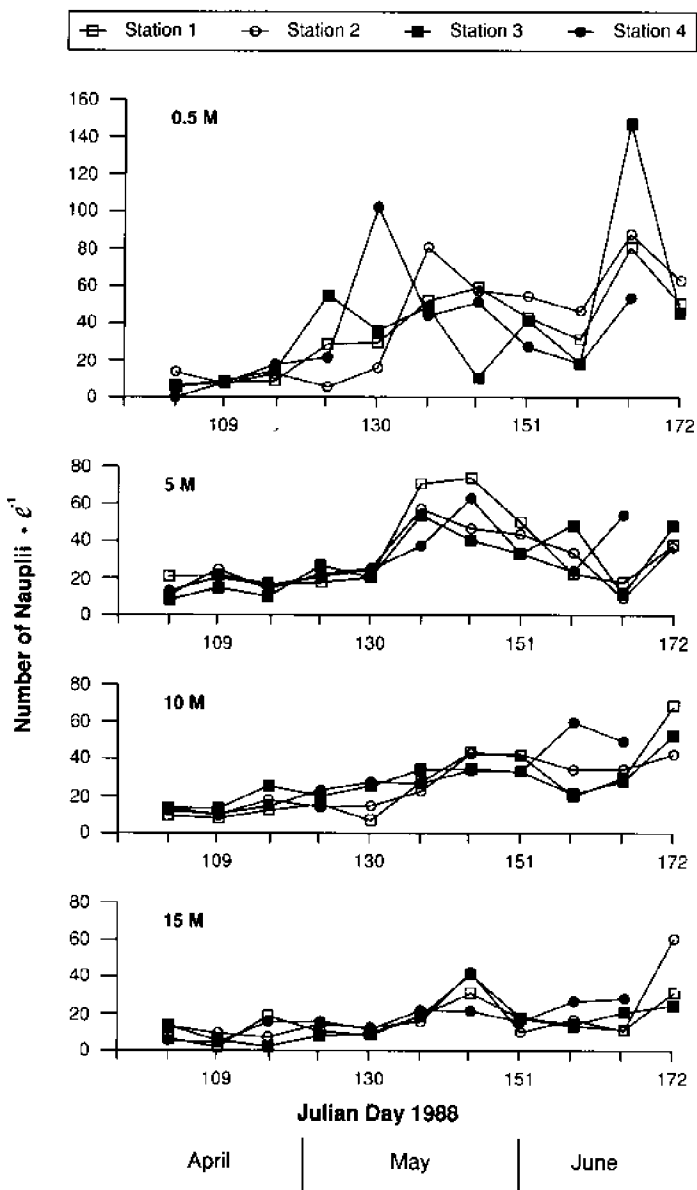


Figure 9. Station to station variation in copepod nauplii (150–350 μm length) in the area of Auke Bay, Alaska, between 12 April and 21 June 1988.

Discussion

Physical oceanography

The physical measurements show that the bay is a well ventilated estuary. In addition to major advective events which completely changed the upper water column containing the fish larvae and copepod nauplii, tides and minor events seen in the density series and current meters, but not noted in the text here because of uncertainties in interpretation, would contribute more flushing. Obviously the bay cannot be considered a static basin but rather one which frequently exchanges water with its adjacent passages. Planktonic copepod nauplii must be transported into and out of the bay with these advective events, as are adult copepods (Coyle et al. 1990).

Fish larvae

The larval fish samples shown in this report are part of a larger data set which includes four years of sampling in Auke Bay (Haldorson et al. 1993). In all four years rock sole larvae appeared before the spring phytoplankton bloom, and water column stratification, while flathead sole larvae appeared after the bloom in the stratified period. Clearly these different hatching strategies must be fixed in the evolutionary history of these species. By hatching early in the season rock sole may minimize predator encounters but they must feed when nauplii concentrations are at their lowest. Obviously they must be relatively competent at capturing prey in order to survive. In contrast flathead sole larvae co-exist with high prey concentrations since they hatch after the spring copepod bloom has started. However, they must also deal with more predators, such as euphausiids that swarm into the bay to feed during the spring phytoplankton bloom (Paul et al. 1990b).

There is growth rate data for selected cohorts of flathead sole larvae from 1986 and 1987 (Haldorson et al. 1989). That study suggested that flathead sole reach saturation feeding at nauplii concentrations below 15 L^{-1} . By mid-May there were more than $15 \text{ nauplii L}^{-1}$ at all depths and stations sampled. Thus, during 1988 there was never a period when their growth rate should have been severely limited by access to prey. A review of generalized copepod nauplii abundance for the study area showed that during 1986 to 1989 mass starvation of competent flathead sole larvae was unlikely (Paul et al. 1991).

Copepod nauplii

Two previous papers describe the temporal and interannual variation in nauplii abundance in Auke Bay (Haldorson et al. 1989, Paul et al. 1991). Those reports give mean abundance values for 150-350 μm length nauplii, but not the mesoscale variation (plots with actual nauplii counts) in copepod nauplii distribution for Auke Bay. Two other reports provide copepod nauplii abundances from other Alaskan areas (Dagg et al. 1984, Incze et al. 1990), and they show station to station variation in nauplii concentrations similar to those in this report. The references cited above show that there is usually a strong vertical patchiness for copepod nauplii. The latter two reports note that vertical mixing in the water column alters nauplii concentrations and depth distribution patterns. In Auke Bay the post-spring bloom mixed layer depth is generally restricted to the upper 5 m. This factor probably explains why the 0.5 m depth samples had the most site to site variation in nauplii abundance. The copepod nauplii concentrations in Auke Bay ($\approx 20\text{-}40\text{ L}^{-1}$) during the spring phytoplankton bloom period were very similar to the values reported for British Columbia, Canada (Purcell and Grover, 1990). But these values are higher than those in the southeastern Bering Sea where nauplii counts under 20 L^{-1} are common (Dagg et al. 1984).

In Auke Bay advective events which bring deep water copepod species into the bay (Coyle et al. 1990), water temperature (Coyle et al. 1990), and the number of female copepods present at the time of the spring phytoplankton bloom (Paul et al. 1990a) all modify nauplii springtime production. In 1988 copepod nauplii concentrations in the bay and its passage were similar so that even with a massive exchange of water, marked station to station changes in nauplii abundance were not apparent during this study. This study did not observe indications of prominent horizontal patchiness of copepod nauplii that persisted in any consistent manner, but we sampled a relatively small area. In the future there must be a larger scale examination along the coast of southeastern Alaska to determine how variable nauplii abundance is in the horizontal scale, and how representative Auke Bay is of the inside passage.

Hypothesis for larval fish feeding in Auke Bay

The common hypothesis proposed to explain year class success, Stable Ocean, Critical Period and Match-Mismatch all have a common core thought that the spatial and temporal variation in prey availability is critical to survival of larval fish. The Stable Ocean hypothesis

seems not to be particularly valid for rock sole larvae because their planktonic period is completed prior to water column stratification and the spring copepod bloom. Throughout the inside passage the surrounding mountains and islands preclude strong vertical mixing of waters like that which occurs in the open ocean. Thus, the Stable Ocean hypothesis is not very applicable for flathead sole in Auke Bay because they hatch after the stratification period when the mixed layer depth is less than 5 m. Copepod nauplii appear to be abundant enough throughout the upper water column of Auke Bay and its channel (Paul et al. 1991) that fish larvae do not have to rely on ephemerally formed thin or isolated patches of nauplii to find adequate prey concentrations. It would appear that in Auke Bay some other factor, such as loss to predators, is probably more important in determining survival rates of year classes of flathead and rock sole than feeding failure during the early larval stage.

Acknowledgments

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The Significance of Morphological Variation in Adults and Larvae of the Rock Sole, *Pleuronectes bilineatus*, from the Bering Sea and Northeastern Pacific Ocean

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Abstract

Larvae of the rock sole, *Pleuronectes bilineatus*, have been collected regularly in Alaska Fisheries Science Center ichthyoplankton cruises in the Bering Sea and Northeast Pacific. In recent years, a question arose as to whether a larval morphotype previously identified as a variant of the sand sole, *Psettichthys melanostictus*, was in fact a second morphotype of rock sole. A multi-faceted project was undertaken to clarify possible morphological variation in both larval and adult rock sole. Larvae reared by spawning known adults verified that the larval morphotype in question was rock sole. An analysis of meristic characters of adult rock sole from the Bering Sea, Gulf of Alaska, Washington Coast, and Puget Sound verified the presence of two morphologically distinct adult forms, distinguished primarily by gill raker counts. Canonical discriminant analysis, based on five meristic characters, showed Bering Sea adults to be different from Northeast Pacific adults. An independent electrophoretic analysis on the same adult samples showed genetic differentiation that parallels the meristic differences. Distributions of larval morphotypes were correlated with distributions of adult forms within the study area. This indicates a possible system-

atic basis for the different larval morphotypes; however, environmental determinants must also be considered.

Introduction

The rock sole, *Pleuronectes bilineatus*, is a morphologically diverse member of the family Pleuronectidae and is a species of moderate economic importance throughout its range (Forrester 1969, Horton and Morton 1989). The genus *Lepidopsetta* has recently been synonymized with *Pleuronectes* following a revision of the family Pleuronectidae (Sakamoto 1984, Robins et al. 1991). Forms of *Lepidopsetta* (= *Pleuronectes* in part) that have been given subspecific or specific status are peripherally distributed in shallow waters in the northern Pacific and across the Bering Sea (Wilimovsky et al. 1967, Nikiforov et al. 1983, Horton and Morton 1989).

Systematic relationships among pleuronectids previously allocated to *Lepidopsetta* have been unclear, with at least two and sometimes three species or subspecies being recognized (Norman 1934, Wilimovsky et al. 1967, Nikiforov et al. 1983). To date, the most thorough investigation of relationships is a study of meristic variation by Wilimovsky et al. (1967). They reviewed the synonymy of *Lepidopsetta* and, based on the results of their study, proposed the existence of one species with three subspecific designations. They proposed a western Pacific subspecies, *Pleuronectes bilineatus* (= *Lepidopsetta bilineata*) *mochigarei*, ranging northward from Korea to the southern Kurile Islands and southern Sea of Okhotsk where it intergrades with a northern form. Wilimovsky et al. (1967), for the first time, gave the northern form, *P. b. peracuata*, subspecific status. They suggested that *P. b. peracuata* is distributed across the Bering Sea and throughout the Aleutian Islands and southeastern Alaska. An eastern Pacific subspecies, *P. b. bilineatus*, ranges northward from Nicholas Island and Monterey, California, to the Gulf of Alaska where it intergrades with *P. b. peracuata* in the area of the Queen Charlotte Islands, Canada. They differentiated these forms primarily on the basis of gill raker number and, to a lesser degree, number of lateral line pores, with the northern subspecies having higher counts for both characters. More recently, Nikiforov et al. (1983), proposed species status for *P. b. mochigarei* based on an observed lack of intermediate forms in its area of contact with *P. b. peracuata*.

Pleuronectes bilineatus larvae have been collected regularly during Alaska Fisheries Science Center (AFSC) ichthyoplankton cruises in the northeastern Pacific and the Bering Sea. In recent years, a question

arose as to whether a larval morphotype which closely resembled larvae of the sand sole, *Psettichthys melanostictus*, was instead a second morphotype of *Pleuronectes bilineatus* (this second morph will be referred to hereafter as a Type II larva) (Matarese et al. 1989). Previously, these larvae had been tentatively identified as a morphological variant of sand sole.

Systematic clarification of the Type II larval morphotype is necessary: first, to verify that the larvae in question are rock sole and, second, given the taxonomic variation currently recognized within *P. bilineatus*, to determine if the differences in larval morphology have taxonomic significance.

This study was designed to address these questions by looking at both adult and larval rock sole in the Bering Sea and eastern North Pacific. Four approaches were used: (1) a meristic analysis of adult *P. bilineatus* patterned after that of Wilimovsky et al. (1967); (2) a protein electrophoretic analysis of the same adults to determine the degree of genetic differentiation associated with the meristic variation; (3) spawning of adult rock sole and rearing of larvae in order to verify that the morphotype in question is a rock sole; and (4) use of correlative methods to determine if larval distributions are associated with distributions of adult forms.

Methods

Adult analysis

Five collections of adults from four geographic areas were obtained: two from the Bering Sea (one AFSC trawl survey, one commercial catch); one from the Gulf of Alaska (AFSC trawl survey); one from Puget Sound, WA (Washington Department of Fisheries (WDF) trawl survey); and one from the Washington Coast (AFSC trawl survey) (Table 1). Individual hauls from different sites were combined for each collection. All specimens from the trawl surveys were frozen on dry ice at the time of collection; the Bering Sea commercial catch was flash-frozen upon catch. Samples of eye, heart, liver, and muscle tissue were removed from partially thawed adults and frozen at -80°C for electrophoretic analysis. The results of the electrophoretic analysis are discussed by Seeb (1991).

After removal of tissue samples for electrophoresis, these specimens were fixed in 10% formalin for later meristic analysis. Meristic characters chosen for analysis included upper gill rakers, lower gill rakers, total gill rakers, lateral line pores, dorsal fin rays, anal fin rays,

Table 1. Collections of adult rock sole, *P. bilineatus*, from the Bering Sea and northeastern Pacific Ocean used in meristic and electrophoretic analyses.

Collection	Latitude	Longitude	Month/year
Bering Sea/ AFSC Trawl Survey	59°40'	177°05'	Aug. 1989
	60°19'	177°20'	
	60°19'	176°42'	
	60°20'	176°00'	
	60°20'	175°24'	
	60°40'	175°27'	
Bering Sea	Commercial catch		Jan.-Feb. 1989
Gulf of Alaska/ AFSC Trawl Survey	59°35'	148°42'	Sept. 1989
	59°42'	148°06'	
Washington Coast/ AFSC Trawl Survey	45°33'	124°21'	Sept. 1989
	46°34'	124°28'	
	46°53'	124°28'	
	47°13'	124°38'	
	47°58'	124°50'	
	48°12'	125°22'	
	48°13'	124°53'	
Puget Sound/ WDF Trawl Survey	48°02'	122°52'	May-June 1989
	48°04'	122°46'	
	48°09'	123°38'	
	48°53'	123°05'	
Puget Sound	Hood Canal		Jan. 1989

and eyed-side pectoral rays. Methodology followed Hubbs and Lagler (1958). Meristic values were tabulated and subjected to simple univariate statistics for descriptive purposes. For discriminatory purposes, a suite of characters consisting of total gill rakers, lateral line pores, anal fin rays, dorsal fin rays, and pectoral fin rays were used in a canonical discriminant function analysis. All statistical analyses were carried out using SAS, Release 6.03 (SAS Institute 1988).

Larval analysis—spawning and rearing

Adult rock sole were collected during the natural spawning season from various sites throughout Puget Sound, WA. Captive adults were

Table 2. Collections of larval rock sole, *P. bilineatus*, and the Type II morph, from the Bering Sea and northeastern Pacific Ocean.

Location	Year	# of samples	Month
Bering Sea	1971	7	July
	1977	36	April-May
	1979	50	May-June
	1980	3	Jan.-Feb.
Gulf of Alaska	1985	120	March-June
	1986	92	April-May
	1987	37	April-May
	1988	181	March-June
	1989	244	April-June
Strait of Georgia	1983-1988	25	March-June
Puget Sound	1985-1988	7	April-Sept.

maintained in outdoor, flow-through, 1,500 L circular tanks at the Seattle, WA Public Aquarium. Spawning was carried out during March and April 1989. Attempts to naturally spawn captive fish were unsuccessful. Therefore, spawning was induced by injecting female rock sole with human chorionic gonadotropin using methods modified from those outlined by Smigielski (1975) for winter flounder. All males were spawned without the use of hormones. Single females were crossed with from one to three males. Newly hatched larvae were reared until the time of yolk absorption in 1 L glass containers, using Puget Sound water at 6 to 9°C. A minimum of 25 larvae from each viable cross was examined. Viable crosses were defined as those in which the spawned eggs appeared normal, fertilization and hatch rates were high, larvae appeared normal, and few mortalities were observed. The larvae were categorized as *P. bilineatus* or Type II larvae based on pigment pattern, the primary criterion used for identification at this stage (Matarese et al. 1989).

Larval analysis—field collections

Larval samples from the Bering Sea (AFSC ichthyoplankton cruises), the Gulf of Alaska (AFSC ichthyoplankton cruises), Puget Sound, WA, (AFSC collections), and the Strait of Georgia, B.C., (Vancouver Public Aquarium collections) were used in determining the distributions of *P.*

Table 3. Summary statistics for seven meristic characters for adult rock sole, *P. bilineatus*, from the Bering Sea and northeastern Pacific Ocean.

	N	Range	Mean	Stderr
Upper gill rakers				
Bering Sea 1	51	2-6	4.16	0.126
Bering Sea 2	51	2-6	4.16	0.126
Gulf of Alaska	37	2-4	2.68	0.117
Washington Coast	46	2-4	2.63	0.090
Puget Sound	61	2-4	2.38	0.071
Lower gill rakers				
Bering Sea 1	52	6-8	7.17	0.081
Bering Sea 2	51	6-8	7.25	0.096
Gulf of Alaska	37	4-7	5.19	0.094
Washington Coast	46	4-7	5.32	0.083
Puget Sound	61	4-7	5.21	0.067
Total gill rakers				
Bering Sea 1	51	9-13	11.33	0.162
Bering Sea 2	51	8-14	11.41	0.192
Gulf of Alaska	37	6-11	7.86	0.182
Washington Coast	46	6-10	7.96	0.142
Puget Sound	61	6-11	7.59	0.115
Lateral line pores				
Bering Sea 1	51	82-94	87.71	0.328
Bering Sea 2	50	82-93	87.22	0.350
Gulf of Alaska	36	78-87	83.17	0.379
Washington Coast	45	76-86	82.16	0.312
Puget Sound	58	74-84	79.62	0.322
Dorsal fin rays				
Bering Sea 1	52	71-81	76.69	0.305
Bering Sea 2	51	71-81	75.80	0.322
Gulf of Alaska	37	75-83	79.08	0.334
Washington Coast	46	71-85	77.89	0.377
Puget Sound	60	68-80	75.65	0.287

Table 3. (continued.)

	N	Range	Mean	Stderr
Anal fin rays				
Bering Sea 1	52	55-64	59.25	0.253
Bering Sea 2	51	55-63	58.84	0.260
Gulf of Alaska	37	57-64	61.05	0.279
Washington Coast	46	56-63	59.98	0.246
Puget Sound	61	54-62	58.74	0.217
Pectoral fin rays				
Bering Sea 1	52	10-12	11.17	0.076
Bering Sea 2	50	10-13	11.24	0.097
Gulf of Alaska	36	11-13	11.81	0.087
Washington Coast	46	11-13	11.78	0.069
Puget Sound	61	9-12	11.24	0.080

bilineatus and Type II larvae (Table 2). Criteria for discrimination of the two forms were those outlined by Matarese et al. (1989).

Results

Adult analysis

The meristic data differentiate two distinct regional groupings of adult rock sole. The two Bering Sea samples show essentially no between-site differences, while being clearly distinct from the Gulf of Alaska, Washington Coast, and Puget Sound samples. Bering Sea adults have higher upper, lower, and total gill raker counts than specimens from the Gulf of Alaska, Washington Coast, and Puget Sound (Table 3). Although some overlap exists for marginal values, the overall patterns show a clear break between the Bering Sea and the more southerly locations. Bering Sea fish have a mean total gill raker count of 11.37 (range 8-14) while the other three groups yield a mean of 7.80 (range 6-11).

In comparison to gill raker counts, lateral line pore counts show greater variability within each region, but among sampling locales they show a pattern similar to that of gill raker counts (Table 3). Bering Sea samples again show minimal between-site variation and

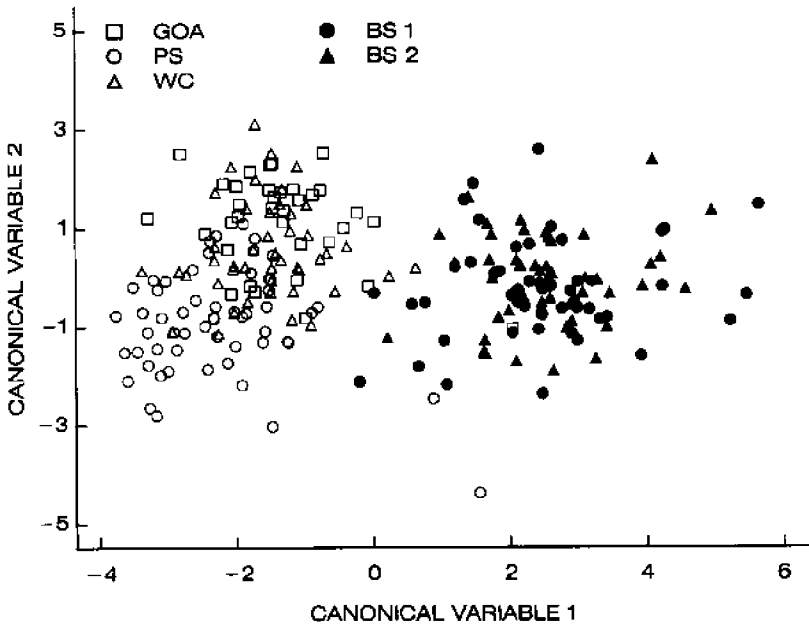


Figure 1. Discrimination of five groups of adult rock sole, *P. bilineatus*, from the Bering Sea and northeastern Pacific Ocean based on a canonical discriminant function analysis utilizing five meristic variables.

have a higher mean pore count, 87.46 (range 82-94), than do the other three locations (mean 81.65, range 74-87). There is more among-site heterogeneity for lateral line pore counts at the three southern locales than is seen in gill raker counts, with Puget Sound fish having the lowest mean count, 79.62, versus 83.17 and 82.16 for Gulf of Alaska and Washington Coast specimens, respectively.

The magnitude of between-site variation of dorsal, anal, and pectoral fin ray counts is less than that seen in gill raker and lateral line pore counts. No distinct, among-site pattern of variation such as that seen in gill rakers and lateral line pores is distinguishable. Gulf of Alaska and Washington Coast fish tend to have slightly higher fin ray counts than do the Puget Sound and Bering Sea samples (Table 3).

Canonical discriminant function analysis of the combined meristic characters shows the same pattern of discrimination as was seen in individual meristic characters. Based on the five meristic characters included in the analysis (dorsal, anal, and pectoral fin rays; total gill

Table 4. Results of canonical discriminant function analysis based on five meristic variables for adult rock sole, *P. bilineatus*, from the Bering Sea and northeastern Pacific Ocean.

Character	Standardized coefficients	
	Canonical Variable 1	Canonical Variable 2
Total gill rakers	1.381	-0.263
Lateral line pores	1.176	0.545
Dorsal rays	0.048	0.627
Anal rays	-0.148	0.268
Pectoral rays	-0.190	0.506
Class means on canonical variables		
Collection	Canonical Variable 1	Canonical Variable 2
Bering Sea 1	2.454	-0.245
Bering Sea 2	2.546	0.002
Gulf of Alaska	-1.330	1.140
Washington Coast	-1.532	0.555
Puget Sound	-2.277	-0.913

rakers; and lateral line pores), the two Bering Sea samples are clearly differentiated from the Gulf of Alaska, Washington Coast, and Puget Sound specimens ($P < 0.0001$) (R^2 for Canonical Variable 1 = 0.82; R^2 for Canonical Variable 2 = 0.32) (Figure 1, Table 4). Discrimination between the Bering Sea and the more southern sites is greatest along the first canonical variable. Differences in class (collection site) means are greater between the two Bering Sea sites and Puget Sound (mean difference = 4.78), than between the Bering Sea and Washington Coast sites (mean difference = 4.03) or between the Bering Sea and Gulf of Alaska sites (mean difference = 3.83). The magnitude of differentiation between the Gulf of Alaska, Washington Coast, and Puget Sound is much less and is greatest on the second canonical variable. On both canonical variables, the differences between class means among the three southern sites is greatest between the Gulf of Alaska and Puget Sound (Can2 = 2.05; Can1 = 0.95), next greatest between Washington Coast and Puget Sound (Can2 = 1.47; Can1 = 0.75), and least between the Gulf of Alaska and Washington Coast (Can2 = 0.58; Can1 = 0.20). The latter difference is only slightly greater than the differences

between the two Bering Sea samples, which are virtually indistinguishable.

The results of the electrophoretic analysis, detailed in Seeb (1991), show the same pattern of differentiation. The Bering Sea collections are clearly genetically distinct from the Gulf of Alaska, Washington Coast, and Puget Sound groups which are more closely related to each other. Among the three southern locations, the Gulf of Alaska and Washington Coast fish show the least genetic differentiation.

Larval analysis—spawning and rearing

Viable crosses were obtained from a total of 11 different matings of Puget Sound fish that utilized 6 different females and 13 different males. Twenty-five larvae from each of the eleven viable crosses were examined and scored for morphological type at the end of yolk sac absorption. Pigment pattern was the primary criterion used for distinguishing between *P. bilineatus* and Type II larvae. Pigmentation of all larvae corresponded with that outlined by Matarese et al. (1989) for Type II larvae. Among hundreds of additional reared larvae that were examined in a more cursory fashion, no *P. bilineatus* larvae were seen.

Larval analysis—field collections

Specimens were collected from Puget Sound between 1985 and 1988 in the locale of the AFSC Field Laboratory at Manchester, WA (Table 2). Of 20 larvae identified as rock sole, all were of the Type II morph. No *P. bilineatus* larvae were identified from Puget Sound collections.

From ichthyoplankton collections made between 1983 and 1988 in the Strait of Georgia, B.C. area, 52 larvae were identified as Type II larvae (Table 2). Initially, these larvae had been tentatively identified as *Psettichthys melanostictus*. Although adult rock sole are common in the locale of the larval collections, *P. bilineatus* larvae are not collected in this area (Pers. comm. J.B. Marliave, Vancouver Public Aquarium, Vancouver, B.C. V6B 3X8, Canada, May 1993).

A total of 96 samples containing 255 larvae were collected in the Bering Sea from 1971 to 1980 (Table 2). All larvae collected in the Bering Sea were of the *P. bilineatus* type. A mean abundance calculated for 27 samples containing *P. bilineatus* larvae was 12.1 larvae/1,000 m³ (range 2.5-40.2 larvae/1,000 m³).

The largest collections of larvae were obtained during AFSC ichthyoplankton cruises in the Gulf of Alaska from 1985 to 1989 (Table

Table 5. Time of collections of larval rock sole, *P. bilineatus*, and the Type II morph, from the Gulf of Alaska, 1985-1989. Mean abundance is mean abundance of larvae in samples in which a given morph was present.

Larval type	Month collected				Overall mean
	March	April	May	June	
<i>P. bilineatus</i>					
Mean abundance (#/1,000 m ³)	5.75	25.93	28.03	19.76	25.5
No. samples	12	223	284	100	
Type II					
Mean abundance (#/1,000 m ³)	0.00	3.90	14.98	7.60	11.34
No. samples	0	2	54	49	

2). This was the only area sampled where the two types of larvae were found to co-occur. A total of 674 individual samples containing either *P. bilineatus* larvae, Type II larvae, or both larval types were collected during 18 cruises. *P. bilineatus* larvae were present in the greatest number of samples and were generally more abundant when found (Table 5). For 619 samples that contained *P. bilineatus* larvae, the mean abundance was 25.5 larvae/1,000 m³ (range 2.1 to 650.1) with 186 samples having ≥ 20 larvae/1,000 m³ and 35 samples having ≥ 100 larvae/1,000 m³. Type II larvae occurred in 105 samples with a mean abundance when collected of 11.3/1,000 m³ (range 2.7 to 179.2) with only 11 samples having ≥ 20 larvae/1,000 m³.

The two larval morphs were collected together over only a portion of the area of the Gulf of Alaska in which rock sole larvae were found (Figure 2). *P. bilineatus* larvae were collected from 53°34'N to 59°20'N latitude and 148°20'W to 166°12'W longitude. Type II larvae were collected from 52°42'N to 56°46'N latitude and 149°37'W to 167°23'W longitude. *P. bilineatus* larvae were abundant over a wider area, being found in appreciable numbers along the Alaskan Peninsula and Aleutian Island chain. Type II larvae exhibited a relatively patchy distribution, being found predominantly in the vicinity of Kodiak Island and at the more southern sampling sites. They were present in greater numbers than *P. bilineatus* larvae in only two areas: (1) south

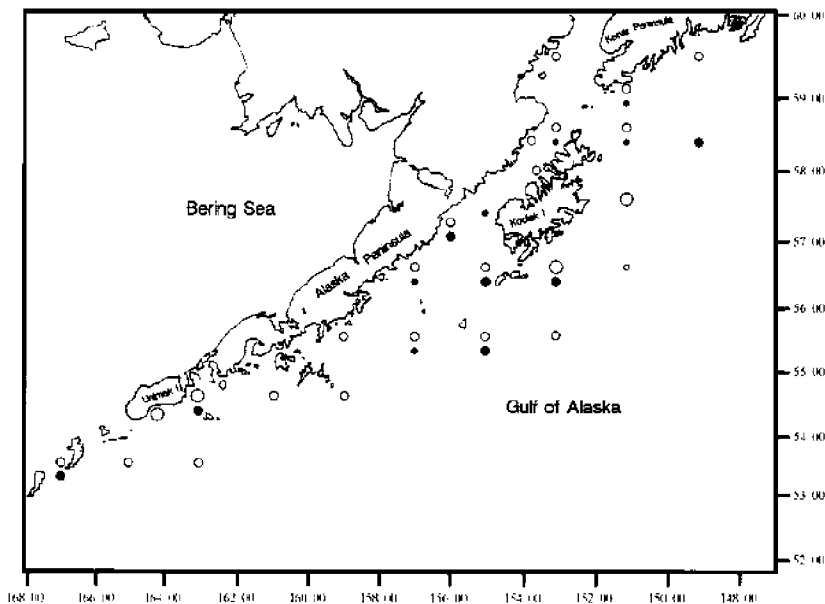


Figure 2. Relative abundance of larval rock sole, *P. bilineatus* and the Type II morph, in the northwestern Gulf of Alaska. Open circles represent *P. bilineatus* larvae; closed circles represent the Type II morph larvae. Symbols represent mean number of larvae/1,000m³ for all collections containing that form. Small circles—mean < 10 larvae/1,000m³; medium circles—10 larvae/1,000³ ≤ mean < 50 larvae/1,000m³; large circles—mean > 50 larvae/1,000m³.

of Unalaska (lat. 53°12'N, long. 167°23'W) and (2) at the most southern location that either morph was taken (lat. 52°43'N, long. 156°38'W). *P. bilineatus* larvae were not collected in either of these two areas.

There was some evidence for further localization of the two types of larvae. Water column depth at site of collection did not differ significantly. However, ANOVA showed larval depth at capture to be significantly greater for *P. bilineatus* larvae (mean depth 148.8 m, range 0 to 311 m) than for Type II larvae (mean depth 108.9 m, range 0 to 275 m) ($P < 0.0001$).

There was also a temporal difference in larval abundance (Table 5). *P. bilineatus* larvae appeared earlier (March) and were found in relatively high abundance by April. Type II larvae first were collected in April and were at peak abundance in May.

Discussion

Differences in the meristic characters of adult rock sole from the Bering Sea, Gulf of Alaska, Washington Coast, and Puget Sound serve to differentiate two morphological forms that are clearly the same as those recognized by Wilimovsky et al. (1967). In the current study, discriminant function analysis, using five meristic characters, separated the five collections into two distinct groups, a Bering Sea group versus a more southern group composed of the Gulf of Alaska, Puget Sound, and Washington Coast sites. The Bering Sea form identified in this study is characterized by total gill raker counts clustered from 10 to 12 (range 8-14) (Table 3) and is clearly the northern "high gill-rakered" form of Wilimovsky et al. (1967). The thirteen collections of this type, that were made by Wilimovsky et al. (1967), had mean total gill raker counts of approximately 10 to 12 (range 9-13). Similarly, in the present study, the Gulf of Alaska, Washington Coast, and Puget Sound collections are clearly equivalent to the "low gill-rakered" form of Wilimovsky et al. (1967). In the current collections, most individuals from these three sites have 7-9 total gill rakers (range 6 to 11). In Wilimovsky et al.'s (1967) seven collections of the "low gill-rakered form," mean total gill raker counts ranged from 7.2 to 8.3 (range 6 to 9).

In both this study and that of Wilimovsky et al. (1967), lateral line pore counts are more variable than the gill raker counts but show a similar pattern, with the northern form having higher values. The 1967 study had a range of sample means of 84.00 to 90.73 lateral line pores for the "high gill-rakered" form and 78.61 to 83.50 for the "low gill-rakered" form. The present study had mean lateral line pore counts of 87.22 to 87.71 for the Bering Sea samples and 79.62 to 83.17 for the southern sites (Table 3). In both studies, the other meristic characters examined had no clear discriminatory power.

Electrophoretic analysis of the same specimens used for the meristic study showed a pattern of discrimination similar to that of the meristic data. The greatest genetic differentiation was observed in rock sole from the Bering Sea versus the three northeastern Pacific sites (Seeb 1991). Nei's genetic distances between the Bering Sea samples and the three northeastern Pacific locations ranged from 0.029 and 0.037, while the genetic distance between the two Bering Sea samples was 0.002. The correlation between the meristic and genetic data is also apparent when comparing the three northeastern Pacific locations. Based on canonical discriminant function analysis of meristic characters, the Gulf of Alaska and Washington Coast collec-

tions were more similar to each other than to the Puget Sound samples. Similarly, genetic distances among the three northeastern Pacific locations were 0.002 (Gulf of Alaska and Washington Coast), 0.006 (Puget Sound and Gulf of Alaska), and 0.011 (Puget Sound and Washington Coast).

The correlation between the patterns of meristic and genetic differentiation seen in the present study suggest that there is a genetic basis for the meristic differences that were observed in adult rock sole. This tends to support Wilimovsky et al.'s (1967) proposed subspecific designation of *P. bilineatus bilineatus* for a southern "low gill-rakered" form and *P. bilineatus peracuata* for a northern "high gill-rakered" form. However, there are differences in the distributions of the two adult forms between the present study and the 1967 study.

In the present study the intergradation between the two adult forms, as evidenced by a discontinuity in both the genetic and meristic data, occurs between the Bering Sea and the Gulf of Alaska. However, Wilimovsky et al. (1967) found the break in meristic values that differentiates the two forms to occur further south in the area of the Queen Charlotte Islands, B.C. Both studies obviously identified the same two forms of adult rock sole based on meristic characters. A probable explanation for the differences in distribution patterns would be a shift in the relative distributions of the two forms in the intervening years. A recent, prolonged warming trend in the northeastern Pacific and eastern Bering Sea, presumably associated with El Niño-Southern Oscillation events, has been observed since the mid-to-late 1970s (Pearcy and Schoener 1987, Niebauer 1988, Trenberth 1990). Northward shifts in the occurrences of numerous marine biota, including several species of fishes, have been recorded in the northeastern Pacific, including the Gulf of Alaska, during this time (Karinen et al. 1985, Pearcy and Schoener 1987) and are presumably associated with increased ocean temperatures associated with the climatic anomalies. Because the area in question is at the contact zone between the two adult forms, a slight northward migration could account for the presence of the southern form in the Prince William Sound-Kodiak Island area. It is possible that both forms may be co-occurring in the northern gulf at the present time. Our sample from this site was the most spatially restricted of all of the adult collections (Table 1) and could well misrepresent a patchy or overlapping distribution of both forms in the northern gulf. Given the distribution of the meristic forms identified in the present study and in the 1967 study, it appears likely that both morphs occur in the northern Gulf of

Alaska. More extensive sampling might determine if, at the present time, the area of intergradation extends somewhat further north in the Gulf of Alaska than was proposed by Wilimovsky et al. (1967).

The distribution of the two larval morphotypes corresponds closely to patterns of adult distributions throughout much of the study area. In the Bering Sea, the present study documented only *P. bilineatus* larvae. In that area we identified only the genetically distinct, "high gill-rakered" adults (Table 3). In Puget Sound, only Type II larvae were collected or spawned and the adult collections from that site were of the "low gill-rakered" type. The collections from the Strait of Georgia area consisted solely of Type II larvae and *P. bilineatus* larvae are not normally collected there. Although the present study does not include adults collected from that area, Wilimovsky et al. (1967) document the "low gill-rakered form" from the Strait of Georgia.

The Gulf of Alaska was the only site in this study where *P. bilineatus* larvae and Type II larvae were found to co-occur. *P. bilineatus* larvae were collected more often, were generally present in greater abundance when collected, and were relatively more evenly distributed over a wider area. The distribution of the Type II larvae in the Gulf of Alaska was more disjunct and somewhat more southerly than that of the *P. bilineatus* larvae, and only the Type II morph was collected at the most southern sampling locations. Correlation of the distributions of the two larval morphs with the adult distributions within the Gulf of Alaska is somewhat more difficult than was the case with the Bering Sea, Strait of Georgia, and Puget Sound. However, both forms of adults have been shown to occur, at least historically, in the northern Gulf of Alaska. Presumably, if a northward migration of the southern form has occurred in recent years in response to climatic changes, we can propose that the area of intergradation of the two adult forms extends somewhat farther north than was suggested in the 1967 study. This could result in the predominant adult form along the Alaskan Peninsula and Aleutian Island Chain being the Bering Sea "high gill-rakered" form as reported by Wilimovsky et al. (1967), with the proportion of "low gill-rakered" forms increasing southward. If this pattern of adult distributions is accepted, the larval distributions are easily explained. The primary site of production of Type II larvae (from low gill-rakered adults) would be more southerly, predominating from the Queen Charlotte Islands along the British Columbia Coast, with relatively limited numbers farther north, off the coast of Alaska. The predominant form of larvae along the Alaskan Peninsula and the

Aleutian Islands would be *P. bilineatus* (from high gill-rakered adults) larvae. The resulting larval distributions would resemble those observed for *P. bilineatus* and Type II larvae in this study.

The temporal difference in abundances of the two larval morphs in the Gulf of Alaska, with *P. bilineatus* larvae reaching their peak abundance earlier in the spawning season, and the significant difference in depth of capture of the two morphs may also be indicative of a taxonomic difference between the two types of larvae.

Although the presumption that there is a taxonomic basis for the difference in larval morphotypes is well supported, other explanations are possible. Geographic variation in larval morphology, including pigmentation pattern, has been suggested as a possible problem in larval identification (Powles and Markle 1984, Marliave 1988). Marliave (1988) showed significant differences in pigment patterns between tidepool sculpin, *Oligocottus maculosus*, larvae from inland and coastal waters in the Vancouver Island-Howe Sound area of British Columbia. Inland waters yielded more densely pigmented larvae while coastal forms were less densely pigmented. He suggests that increased pigmentation of tidepool sculpin larvae and larvae of other taxa in the Strait of Georgia may be due to environmental conditions. Rock sole Type II larvae, the morph found in the Strait of Georgia and Puget Sound, are more heavily pigmented than *P. bilineatus* larvae, a difference potentially attributable to environmental influences. However, Kendall et al. (1984) state that while differences in melanophore contraction may have a physiological basis (implying environmental determination), melanophore placement is thought to be genetically based and therefore of systematic significance. The differences in pigment pattern between the two morphotypes in question appear to be differences in melanophore placement rather than state of contraction. In addition, the consistency of the differences over a wide geographical range and the fact that the two types of larvae co-occur in the Gulf of Alaska argue against environmental determination.

To summarize the four points that were addressed in this study:

- (1) The meristic analysis of adult specimens identified the same morphological forms as identified by Wilimovsky et al. (1967);
- (2) Based on the present electrophoretic analysis (Seeb 1991), there is a genetic basis underlying this morphological differentiation;
- (3) Based on spawning of adult rock sole and examination of the resulting larvae, Type II larvae are definitely a second morphotype of *Pleuronectes bilineatus*;
- (4) The analysis of the geographical distributions of the larval and adult forms provide strong correlative evidence

supporting a taxonomic basis for the observed differences in larval morphology.

A further study that is focused in the northern Gulf of Alaska, that demonstrates co-occurrence of both adult and larval morphs, and that includes a genetic analysis of both life stages, could provide definitive evidence.

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Habitat Models for Juvenile Pleuronectids Around Kodiak Island, Alaska, USA

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Abstract

Juveniles of four species of pleuronectid flatfishes were abundant in bays and nearshore areas around Kodiak Island, Alaska, during August 1991 and August 1992. The four most abundant species of juvenile (age-0 or age-1) pleuronectids, rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), Pacific halibut (*Hippoglossus stenolepis*), and yellowfin sole (*Pleuronectes asper*) appeared to share nursery areas. However, examination of associated distribution, depth and substrate patterns revealed characteristics that limited the amount of nursery area overlap. Linear discriminant analysis was used to identify physical characteristics that were most important in determining the presence or absence of juveniles for each species in 1991. The resulting discriminant functions were tested successfully on 1992 data.

The following conceptual habitat models were based originally on the linear discriminant function analyses of 1991 data, single factor correlations with fish abundance and visual display of distribution data. These models remain unchanged after the addition of 1992 data.

Model #1: Age-0 rock sole are found predominantly in water depths less than 50 m on sand or mixed sand substrate within 10 km of bay mouths.

Model #2: Age-0 flathead sole are found predominantly in water depths greater than 40 m on mud or mixed mud substrate throughout bays.

Model #3: Age-0 Pacific halibut are found predominantly in water depths less than 40 m on mixed sand substrate near or outside mouths of bays.

Model #4: Age-1 yellowfin sole are found predominantly in water depths less than 40 m on mixed substrate at upper reaches of bays.

Introduction

In general, recently metamorphosed flatfishes are thought to recruit to shallow, nearshore nursery areas with fine-grained sediments (Edwards and Steele 1968, Gibson 1973, Toole 1980, Hogue and Carey 1982, de Ben et al. 1990). Intertidal zones, estuaries and shallow protected bays are nursery areas for flatfishes in the continental United States (Krygiel and Pearcy 1986, Allen 1988, Rogers et al. 1988, Wyanski 1990), Canada (Tyler 1971), Europe (McIntyre and Eleftheriou 1968, Gibson 1973, Lockwood 1974, Poxton et al. 1982, Poxton and Nasir 1985, van der Veer and Bergman 1986), and Japan (Tanaka et al. 1989). Abundance and size distributions have been related to water depth (Edwards and Steele 1968, McIntyre and Eleftheriou 1968, Lockwood 1974, Riley et al. 1981, Poxton et al. 1982, Wyanski 1990), sediment size (Poxton et al. 1982, Poxton and Nasir 1985, Wyanski 1990, Jager et al. 1993, Keefe and Able 1994, Moles and Norcross 1995) and food availability (McIntyre and Eleftheriou 1968, Allen 1988, Jager et al. 1993). The generally accepted rationale for juvenile recruitment to shallow, fine-grained nursery areas includes escape from predation, increased cover and food availability, and decreased intraspecific food competition (Toole 1980, de Ben et al. 1990, Minami and Tanaka 1992).

The coastline of Kodiak Island, Alaska, encompasses a variety of habitats from shallow, fine-grained tidal flats to deep and rocky areas. Kodiak Island is mountainous, cut by many fjords and open bays, with shallow waters (< 10 m) usually limited to within 0.5 km of the beach and a tidal range of 3 to 4 m. The region is characterized by deep bays, rough bottom topography, strong currents, and bottom characteristics that change rapidly over relatively short distances. Around Kodiak Island, juvenile flatfishes occupy fine-grained sediments in bays and nearshore waters as flatfishes do in other locations, yet waters less than 10 m in depth are only a minor component of the area utilized (Norcross et al. 1995).

A nursery may be partitioned into areas dominated by individual species or intraspecific age groups (Edwards and Steele 1968, Harris and Hartt 1977, Smith et al. 1976, Zhang 1988). Habitats occupied by juvenile rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), Pacific halibut (*Hippoglossus stenolepis*) and yellowfin sole (*Pleuronectes asper*) collected on the east and south sides of Kodiak Island in August 1991 can be differentiated based on associated depth, substrate and within-bay distribution (Norcross et al. 1995). Conceptual models suggest that age-0 rock sole are found predominantly in water depths less than 50 m, on sand or mixed sand substrate outside of or less than 10 km within bays. Age-0 flathead are found predominantly in water depths greater than 40 m, on mud or mixed mud substrate throughout bays. Age-0 Pacific halibut are found predominantly in water depths less than 40 m, on mixed sand substrate near or outside mouths of bays. Age-1 yellowfin sole are found predominantly in water depths less than 40 m, on mixed substrates at upper reaches of bays.

Linear discriminant functions, used to identify physical characteristics important in determining presence or absence of juveniles for each species in August 1991 (Norcross et al. 1995), are tested here for collections made around the entire island of Kodiak in August 1992.

Methods

Sample collections

Two cruises were conducted in the nearshore waters of Kodiak Island, Alaska (Figure 1), during August 1992. These cruises were similar to, but covered more area than, two cruises conducted in August 1991 (Norcross et al. 1993, 1995). Cruise K19201 consisted of land-based collections conducted in Kalsin, Middle and Womens Bays near the town of Kodiak from a 7.3 m skiff from 9 to 14 August 1992. Because these bays were sampled with a skiff, extremely shallow collections could be made. Collections ranged in depth from 1 to 60 m. Ten stations were occupied in Kalsin Bay, six stations in Middle Bay and five stations were occupied within Womens Bay. Kalsin and Middle Bays had been sampled in 1991.

A 14-day cruise (K19202) from 16 to 29 August 1992 aboard a 24.7 m chartered trawling vessel followed the land-based sampling. Collections ranged in depth from 5 to 180 m during K19202. Cruise K19202 followed a counterclockwise circuit around Kodiak Island. Areas sampled in 1992, but not sampled in 1991, included bays on the

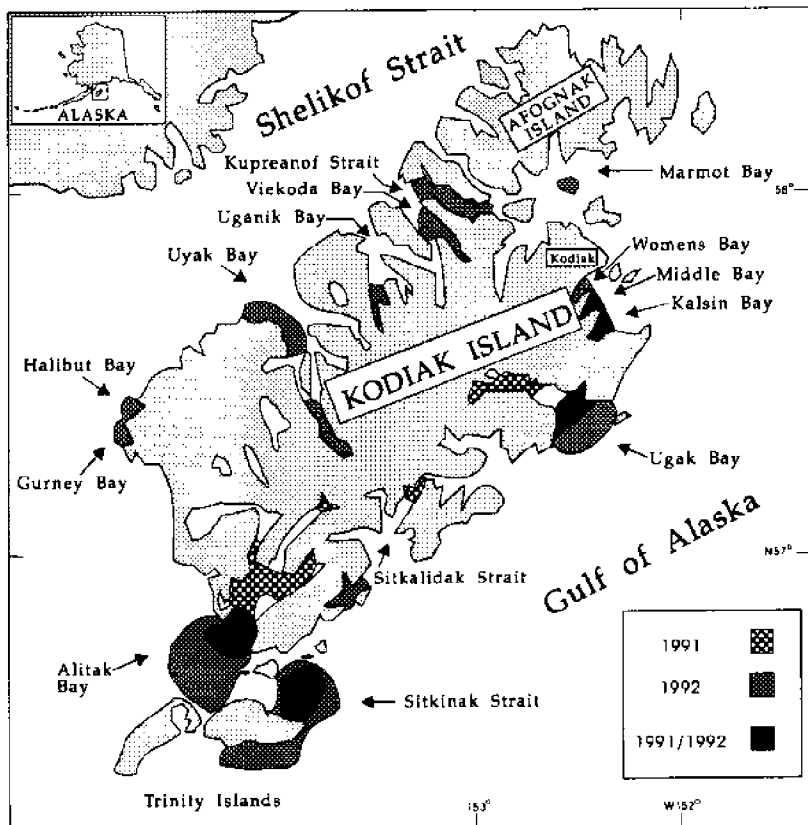


Figure 1. Areas sampled around Kodiak Island, Alaska, in 1991 and 1992.

north and west sides of the island. Two stations were occupied in outer Womens and Middle Bays. Data were collected at eight stations in northwestern and southcentral Marmot Bay. Seven stations were sampled within Kupreanof Strait. Collections were made at six stations in Viekoda Bay, seven stations in Uganik Bay, and twelve stations from the mouth to the head of Uyak Bay. On the southwest side of Kodiak island, four stations within Halibut Bay and six in adjacent Gurney Bay were occupied.

South Kodiak, Sitkalidak Strait and Ugak Bay, which were sampled in 1991, were sampled again in 1992. Ten stations were sampled near the mouth of Alitak Bay, the southernmost bay on Kodiak Island. Eleven stations to the south and west of the mouth of Alitak Bay and

nine stations in east Sitkinak Strait were sampled. In addition, five stations were occupied in the nearshore region south of Sitkinak Island. In 1991, we had sampled throughout and outside the mouth of Alitak Bay but only on the eastern side of Sitkinak Strait. In 1992 samples were collected at six stations in Kaguyak Bay, an area not sampled in 1991. In 1991 samples from Sitkalidak Strait were collected at the narrow part of the strait, near the town of Old Harbor, an area not sampled in 1992. Samples were collected during 1992 only around the mouth of Ugak Bay, but samples were collected from both outer and inner Ugak Bay in 1991.

For consistency in sampling strategy, collection gear, sampling vessels and vessel operators were the same as employed in August 1991 (Norcross et al. 1993, 1994, 1995). At each station one sediment sample was collected with a 0.06 m³ Ponar grab for analysis of grain size, and a portable conductivity, temperature and depth (CTD) profiler was deployed to measure bottom temperature and salinity. Fishes were collected on rising tides during daylight hours using a modified 3.7 m plumb staff beam trawl with a double tickler chain (Gunderson and Ellis 1986). Tows from both the skiff and the trawler were of 10 min duration.

Sample processing

Substrate type, water depth, bottom temperature, bottom salinity and distance from the mouth of the nearest bay were evaluated for each station. Sediment samples were analyzed using the same procedures as in 1991, in which a simplified sieve/pipette procedure was used to obtain the percents of gravel, sand, and mud (Norcross et al. 1995).

Distance from each station to the nearest position at the mouth of a bay was calculated after drawing a line across the mouth of each bay on a chart. The shortest distance from the station to this line was measured. Stations inside the mouth were designated as positive distances, and stations outside of bays were assigned negative distances.

Flatfishes were identified and total length (mm) was measured in the field using a Limnoterra digital fish measuring board. Ages of flatfishes captured in August 1992 were estimated using (1) total length/frequency plots of fishes collected August 1992 (Norcross et al. 1994), (2) total length/frequency plots (Norcross et al. 1993) and analysis of regional differences in total lengths (Norcross et al. 1995) of fish caught in August 1991 and (3) available literature (Southward 1967; Best 1974, 1977; Harris and Hartt 1977; Blackburn and Jackson

1982; Walters et al. 1985). Catch-per-unit-effort (CPUE) was calculated for each species at a station based on a 10 min tow time.

Statistical analyses

Linear discriminant functions derived for 1991 data were used to predict the presence or absence of each species at each station sampled in 1992. Two discriminant functions were used for each species, based on the three and two parameters that had the highest predictive power in 1991 (Norcross et al. 1995). The performance of each linear discriminant function was evaluated for the 1992 test data using misclassification (error) rates.

We repeated the linear discriminant function analysis using combined 1991 and 1992 data since a wider range of depths and substrate types was sampled in 1992 compared to 1991. Misclassification rates based on cross validation were evaluated as outlined in Norcross et al. (1995) to test whether the same parameters were selected as best discriminators as were selected based solely on 1991 data (Norcross et al. 1995).

Data from 1991 and 1992 were combined to calculate Spearman's rank correlation (ρ) between the abundance of each fish species and each physical parameter. The significance of rank correlations was evaluated at the 5% level. To maintain an overall confidence level of 5%, a Bonferroni adjusted critical level was calculated as

$$\alpha = 0.025 / 28 = 0.001$$

for the two-tailed test and for 28 comparisons (4 species \times 7 variables). The nonparametric test using Spearman's ρ was chosen because of non-normality of the data (even after transformation) and because of the high sensitivity of the parametric correlation coefficient (Pearson's r) to outliers.

Results

Rock sole was the most abundant flatfish captured in our 1992 sampling (67% of flatfish) as it was in 1991 (51% of flatfish). In 1992, a total of 4,625 age-0 rock sole (17-60 mm) were collected across almost all locations though the highest CPUE was in the Sitkinak Strait region (Figure 2). Age-0 rock sole were mainly found near the mouths of the bays \pm 8-10 km, except for a single large collection at the head of Uyak Bay. Age-0 rock sole were somewhat more abundant with increasing depth between 0 and 30 m, and were collected in high numbers to 70 m, though they were also found deeper. Age-0 rock sole were

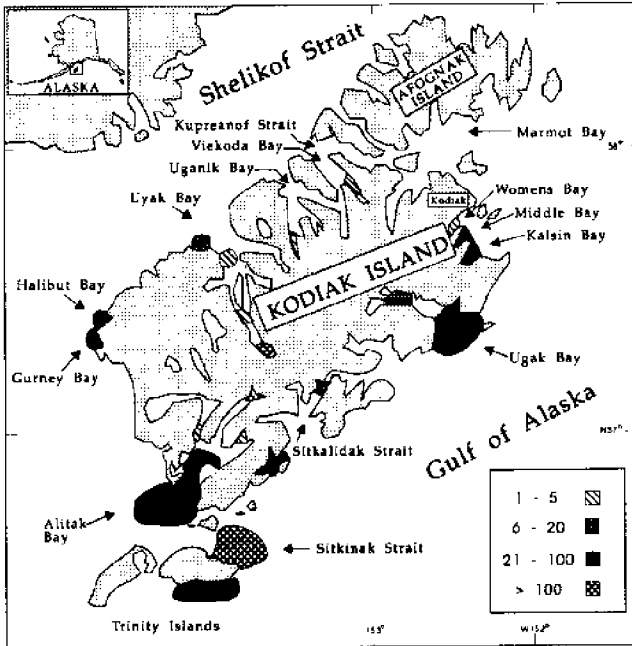


Figure 2. Juvenile rock sole captured August 1991 and August 1992.

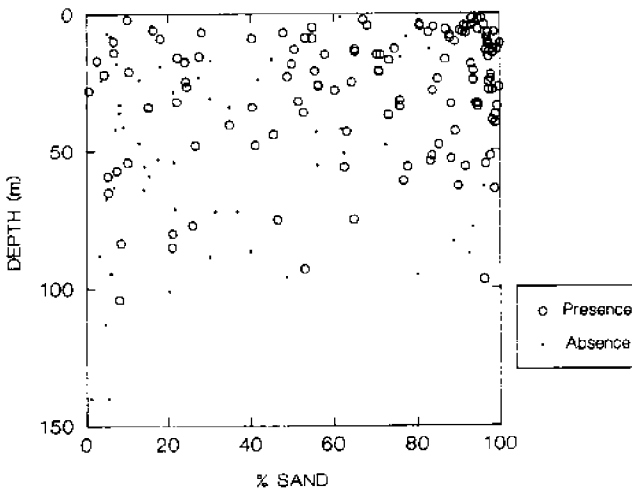


Figure 3. Distribution of age-0 rock sole by depth and percent sand.

Table 1. Spearman's rank correlation coefficients between CPUE of four flatfish species and environmental parameters using 1991 and 1992 data combined. * = significant at 0.05.

Parameter	Rock sole	Flathead sole	Pacific halibut	Yellowfin sole
Depth	-0.258*	0.644*	-0.284*	-0.369*
Distance	-0.308*	-0.074	-0.314*	0.204
Temperature	0.193	-0.467*	0.346*	0.212
Salinity	-0.083	0.246*	-0.163	-0.192
Gravel	-0.240*	-0.219	-0.078	-0.168
Sand	0.583*	-0.219	0.449*	0.113
Mud	-0.310*	0.540*	-0.417*	0.188

collected in large numbers between 7.5 and 9.5°C. This species was most often found at salinities of 32.5-33.0‰. Rock sole were predominantly on sand and mixed sand substrates. While found in almost all combinations of depth and sand, rock sole were somewhat more concentrated in shallow, sandy locations (Figure 3). Spearman's rank correlation coefficients (Table 1) indicated that rock sole abundances were positively correlated with percent sand in the substrate, and negatively correlated with depth, distance from mouth of bay, gravel and mud. The rank correlation was highest with percent sand in the substrate.

Flathead sole increased from 12% of 1991's catch to 18% of 1992's catch. We captured 1,079 age-0 flathead sole 23-52 mm during 1992. The distribution pattern of flathead sole was more restrictive than it was for rock sole. Age-0 flathead sole were found almost everywhere around the island, but were in reduced numbers in Southeast Kodiak (Figure 4). They were concentrated mainly in central, deep areas of bays. They were mainly in waters 80-120 m, 6.0-9.0°C, 31.5-33.5‰, on mud or mixed mud substrates throughout bays.

High abundances of flathead sole were associated with deep stations, low temperatures, high salinities, low sand content, and high mud content. The highest rank correlations for flathead sole were obtained for depth and mud (Table 1). They were consistently collected in depths > 40 m, except when no mud was present (Figure 5).

Pacific halibut composed 5% of the samples in 1991 and 7% in 1992. During 1992, 627 age-0 halibut 22-84 mm were found in all locations on the east and south sides of Kodiak Island in exposed sites

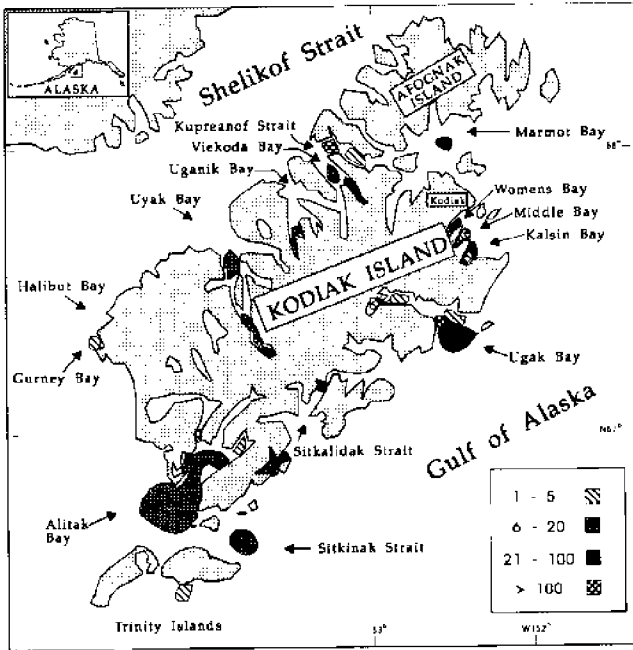


Figure 4. Juvenile flathead sole captured August 1991 and August 1992.

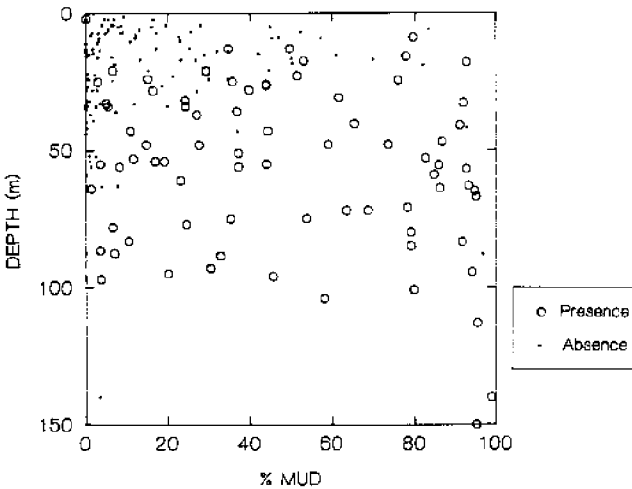


Figure 5. Distribution of age-0 flathead sole by depth and percent mud.

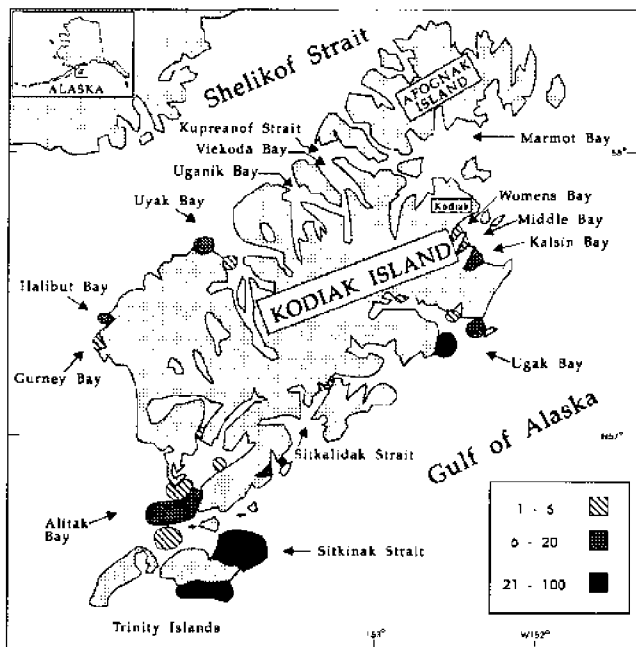


Figure 6. Juvenile Pacific halibut captured August 1991 and August 1992.

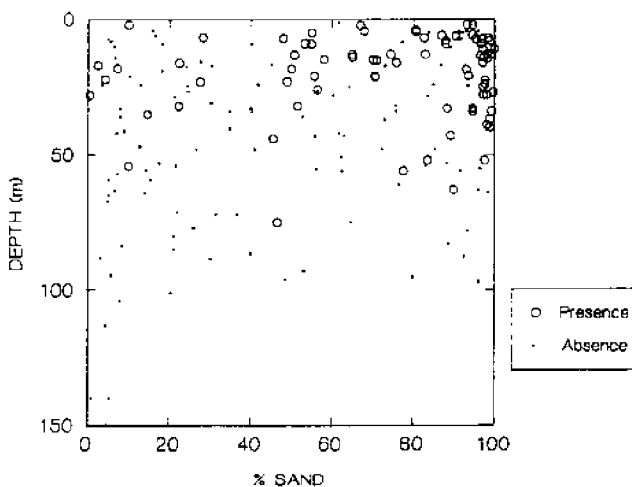


Figure 7. Distribution of age-0 Pacific halibut by depth and percent sand.

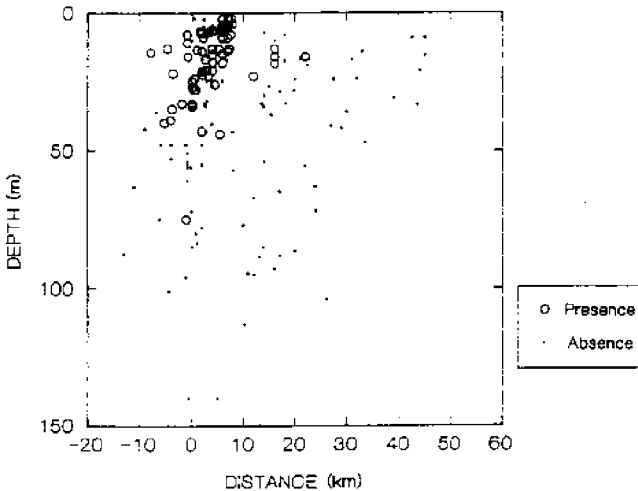


Figure 8. Distribution of age-0 Pacific halibut by depth and distance (negative values represent locations outside of the bay).

(Figure 6). In northwestern Kodiak, halibut were only collected at the mouth of Uyak Bay. Age-0 halibut were found mainly in 10-70 m depth, 7.0-10.5°C, 32.0-33.0‰, on mixed sand substrates, outside of or within 7 km of bay mouths. Pacific halibut abundances were positively correlated with temperature and sand content, and negatively correlated with depth, distance from mouth of bay and mud content in the substrate. The highest rank correlations were with sand and mud (Table 1). Unlike rock sole they were seldom found in water deeper than 50 m. Halibut juveniles, like rock sole, were concentrated most often in shallow waters with sandy substrate (Figure 7) near or outside of mouths of bays (Figure 8) where their presence could be predicted.

Yellowfin sole was very abundant in 1991, accounting for 28% of captured flatfishes, but only represented 4% of the total in 1992. Yellowfin sole do not settle until August or September, therefore few ($N = 4$) age-0 fish 15-20 mm were collected. Because of the small number and size of age-0 yellowfin sole taken, age-1 yellowfin sole (41 to 105 mm) were analyzed in both 1991 and 1992. During 1992, 268 age-1 yellowfin sole were collected at depths less than 40 m, mainly between 5 and 30 m. Age-1 yellowfin sole were found near the heads

of bays, in warm (9.0–11.5°C) saline (31.0–33.5‰) water. They were on sandy mud and gravelly muddy sand and muddy sand. Unlike rock sole and halibut, yellowfin sole were collected in the inner reaches of bays around Kodiak Island (Figure 9). The only significant correlation between yellowfin sole abundance and an environmental variable was a negative rank correlation with depth (Table 1). They were never found deeper than 50 m and were always on mixed substrate, i.e. not predominantly one grain size (Figure 10).

Linear discriminant functions derived for 1991 data were used to predict presence or absence of each of the four flatfish species at each station sampled in 1992. The linear discriminant analysis as used in this study assumes a multivariate normal distribution and equal covariance matrices. These assumptions do not hold for our data set, since most of the variables have a highly skewed distribution. We attempted to transform the nonnormal data to data more nearly normal through use of logarithmic, root-root, and power transformations. Neither the normality nor the homoscedasticity assumption was met under any of the transformations.

In addition to the parametric approach, we explored the use of non-parametric discriminant models based on the kernel method or the k -nearest-neighbor method. Neither method resulted in a good classification of the observed data (unpubl. data). Thus, as suggested by Johnson and Wichern (1992), the linear discrimination was used without worrying about the form of the underlying distribution, because it worked reasonably well and resulted in lower error rates than other discrimination methods.

Using linear discriminant functions, misclassification rates were higher for all four species for the 1992 test data compared to cross validation error rates from the 1991 training data (Table 2). Overall error rates, based on the two "best" predictors for classifying 1991 stations, were substantially higher in the 1992 test data, ranging from 19% in yellowfin sole to 39% in rock sole (Table 2). Error rates differed little whether the discrimination was based on three or two parameters. Thus, including temperature as a predictor for halibut, yellowfin sole, or flathead sole added little or no predictive power (Table 2). For halibut, rock sole, and yellowfin sole, the 1991 error rates for predicting presence were much lower than error rates for predicting absence, suggesting that these species were mostly restricted to relatively well-defined depth/substrate combinations. However, error rates from the 1992 test data were higher for predicting presence, except for yellowfin sole. This probably reflects the expansion of sampling effort to new

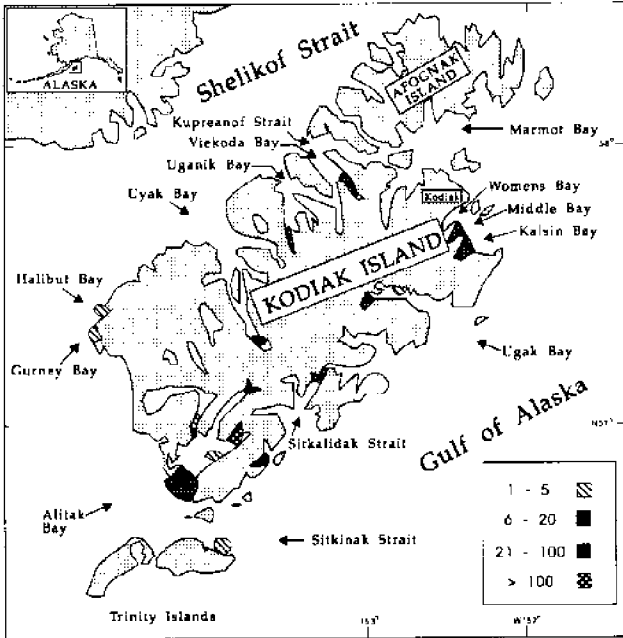


Figure 9. Juvenile yellowfin sole captured August 1991 and August 1992.

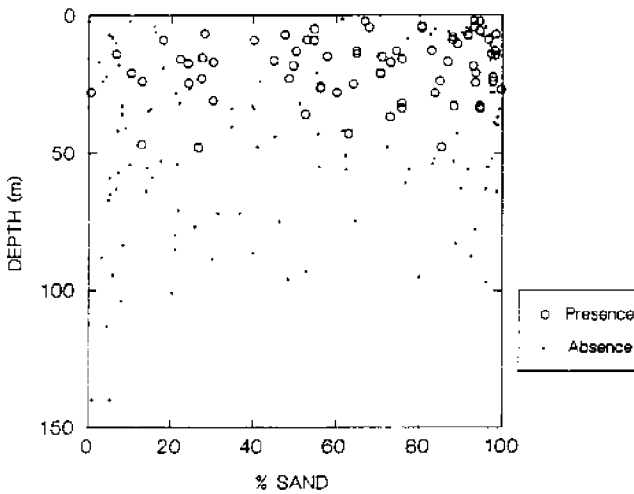


Figure 10. Distribution of age-1 yellowfin sole by depth and percent sand.

Table 2. Linear discrimination between stations with and without four flatfish species, based on physical parameters.

Species	Parameters	1991 training data error rates*	1992 test data error rates*
Rock sole	Depth, sand, gravel	25 (20)	30 (34)
	Depth, gravel	26 (21)	32 (39)
Flathead sole	Depth, temp, mud	16 (27)	24 (29)
	Depth, mud	16 (27)	21 (26)
Pacific halibut	Depth, temp, sand	24 (17)	27 (34)
	Depth, sand	21 (17)	26 (34)
Yellowfin sole	Depth, temp, gravel	21 (13)	25 (19)
	Depth, gravel	20 (13)	23 (19)

*Overall error rate (error rate for Presence only)

stations with depth and substrate characteristics not sampled in 1991. Alternatively, the distribution of these species with respect to the measured parameters may have differed between years due to other unobserved factors. For flathead sole, presence was not as easy to predict as absence for both the 1991 and 1992 data, because they were generally absent from shallow areas without mud in both years. Rock sole had the highest error rates of all species, which is consistent with their ubiquitous distribution.

Linear discriminant function analysis for combined 1991/1992 data resulted in depth having the highest canonical loading for flathead sole and yellowfin sole, the second highest loading for rock sole and the third highest loading for Pacific halibut (Table 3). The three highest loadings for all species except flathead sole were associated with depth, temperature, and sand. The first three parameters most closely associated with flathead sole included mud instead of sand.

Total misclassification rates for predicting the presence or absence of four flatfish species at 195 stations combined from sampling in 1991 and 1992 ranged from 17% for flathead sole to 27% for yellowfin sole when all parameters were used (Tables 4-7). When four or fewer parameters were used, error rates remained the same or even decreased slightly. In most cases, little or no predictive power was lost

Table 3. Canonical loadings from linear discriminant function analysis for combined 1991 and 1992 flatfish data.

Parameter	Rock sole	Flathead sole	Pacific halibut	Yellowfin sole
Depth	-0.557	-0.776	-0.620	-0.696
Distance	-0.379	-0.011	-0.501	0.234
Temperature	0.474	-0.597	0.647	0.545
Salinity	0.180	-0.225	-0.026	-0.005
Gravel	-0.453	0.321	-0.249	-0.377
Sand	0.783	0.220	0.655	0.406
Mud	-0.391	-0.624	-0.473	-0.099

Table 4. Linear discrimination between stations with and without rock sole, based on physical parameters. (Cross validation error rates.)

Absence	Presence	Total	Parameters
30	21	25	All
25	25	25	Depth, temperature, gravel, sand
27	25	26	Depth, temperature, sand
27	26	26	Depth, gravel, sand
34	28	31	Depth, temperature, gravel
29	23	26	Temperature, gravel, sand
29	23	26	Temperature, sand
27	26	26	Depth, sand
25	27	26	Gravel, sand
33	29	31	Depth, gravel
49	25	37	Depth, temperature
39	30	34	Temperature, gravel

Table 5. Linear discrimination between stations with and without flathead sole, based on physical parameters. (Cross validation error rates.)

Absence	Presence	Total	Parameters
9	25	17	All
8	21	15	Depth, temperature, gravel, mud
8	31	19	Depth, temperature, mud
8	23	15	Depth, gravel, mud
11	32	21	Depth, temperature, gravel
15	27	21	Temperature, gravel, mud
8	30	19	Depth, mud
13	28	20	Depth, gravel
11	34	23	Depth, temperature
15	31	23	Temperature, mud
16	38	27	Gravel, mud
31	28	29	Temperature, gravel

Table 6. Linear discrimination between stations with and without Pacific halibut, based on physical parameters. (Cross validation error rates.)

Absence	Presence	Total	Parameters
33	13	23	All
36	13	24	Depth, temperature, distance, sand
29	26	28	Depth, temperature, sand
35	13	24	Depth, distance, sand
39	12	26	Depth, temperature, distance
35	14	24	Temperature, distance, sand
35	15	25	Temperature, distance
29	20	25	Depth, sand
36	12	24	Depth, distance
39	14	26	Depth, temperature
30	29	29	Temperature, sand
40	27	33	Distance, sand

Table 7. Linear discrimination between stations with and without yellowfin sole, based on physical parameters. (Cross validation error rates.)

Absence	Presence	Total	Parameters
37	18	27	All
34	15	24	Depth, temperature, gravel, sand
37	15	26	Depth, temperature, sand
30	14	22	Depth, gravel, sand
30	15	23	Depth, temperature, gravel
40	25	32	Temperature, gravel, sand
30	14	22	Depth, gravel
37	14	25	Depth, sand
41	16	28	Depth, temperature
40	23	32	Temperature, gravel
38	34	36	Temperature, sand
48	23	36	Gravel, sand

by basing the discrimination on only two parameters instead of all measured parameters.

For rock sole, several combinations of three predictor variables resulted in identical cross validation error rates (Table 4). The error rate increased substantially only if sand was omitted as a predictor variable. Thus, all combinations of two variables from depth, temperature, gravel, and sand were tested to determine the two best predictor variables. The combinations temperature/sand, depth/sand and gravel/sand resulted in the lowest total error rates for rock sole (26%). For most combinations of variables, error rates were higher for stations where rock sole were absent. Thus, for the combined 1991 and 1992 data, the presence of rock sole could be more accurately predicted than their absence.

Sand is clearly a good predictor for rock sole presence and should be included in a habitat model for rock sole. Depth and temperature perform equally well in the discrimination due to their high (negative) correlation. Since rock sole abundance was significantly rank correlated with depth but not with temperature, sand and depth seemed to be the most important variables determining rock sole distribution.

The three best predictor variables for flathead sole were depth, gravel and mud. Of these, depth and mud resulted in the lowest total error rates (Table 5). Since these variables also had the largest rank

correlations with abundance (Table 1), they are likely to be the most important parameters for flathead sole distribution. For flathead sole the error rates for stations where flathead sole was absent were consistently much lower than for stations where they were present.

Pacific halibut presence or absence could be most accurately predicted using either depth or temperature with distance or sand (Table 6). The best two predictor variables, based on error rates from all combinations of two variables, were depth and distance (24% error rate), but a similar error rate (25%) was achieved using sand with depth or temperature. The error rate for any combination of two variables was highest when neither depth nor temperature were included. The rank correlation of halibut abundance was higher with temperature than with depth and was lower for distance than for sand. It is difficult to evaluate the relative importance of depth and temperature and of sand and distance due to high correlations among these variables. Therefore, all four variables will be retained in building a habitat model. The exclusion of either one or two variables does not significantly change error rates for predicting presence or absence, except if both depth and temperature are excluded. Thus the depth-temperature factor probably explains most of the observed distribution. Error rates for stations where Pacific halibut were present were consistently much lower than for stations where no halibut were found, indicating that this species was strongly associated with specific habitat characteristics.

The three best predictors for yellowfin sole were depth and gravel combined with either sand or temperature (22% and 23% error rate respectively). Of these, depth and gravel resulted in the lowest total error rates (Table 7). Only depth was significantly rank correlated with yellowfin sole abundance (Table 1) and at this time stage yellowfin distribution can only be explained in terms of depth. Any other parameter that we measured adds very little information, since yellowfin sole occur over a wide range of substrate types. As for halibut, the error rates for stations where yellowfin sole were present were much lower than for stations where no yellowfin sole were present, reflecting the restricted depth range within which yellowfin sole were encountered.

Discussion

A test of linear discriminant function models developed from 1991 data successfully showed that relationships among fish distributions and

habitats within the geographically restricted areas of the eastern side of Kodiak Island apply to the general Kodiak area sampled in 1992. Of the variables examined in this study, two groups of variables seem to explain much of the observed distribution. These were a depth/temperature factor and substrate composition. The relative importance of temperature and depth or of gravel, sand and mud is difficult to assess since temperature and depth as well as gravel, sand, and mud are highly correlated (Norcross et al. 1995).

These parameters have been linked to the habitat quality of juvenile flatfishes in many locations (Gibson 1994). Larvae of flatfishes are known to settle in shallow water (Edwards and Steele 1968, Lockwood 1974) or settle offshore and move into shallow water (Gibson 1973, Lockwood 1974, Tanaka et al. 1989). As noted in our results, depth and its effect on water temperature may play an important part in determining distribution of juveniles (Gibson 1994). Water temperature affects growth and feeding rates, and shallow, warm waters promote faster growth (Malloy and Target 1991, van der Veer et al. 1994).

Distribution of juvenile flatfishes has been linked to substrate type available (Tanda 1990, Kramer 1991, Gibson and Robb 1992). Juvenile flatfish species appear to avoid coarse sediments (Moles and Norcross 1995) and choose fine grained sediments (Rogers 1992, Keefe and Able 1994) which vary in size from mud (Wyanski 1990, Veer et al. 1991) to sand (Jager et al. 1993). Choice of settlement location is affected by the ability of juvenile flatfishes to bury in the sediment (Gibson and Robb 1992) as well as the prey available in the substratum (Burke et al. 1991). Growth and survival are related to these choices (Gibson 1994).

A discriminant analysis was employed in this study to test whether stations could be accurately classified into groups defined by the presence or absence of a given species. The classification based on the observed parameters resulted in relatively high error rates for all species. Between one-sixth and one-third of the stations were not classified correctly. Obviously, no discrimination method will be able to correctly distinguish between populations (of stations with or without a flatfish species) that have an overlapping distribution. Stations with the same or very similar physical characteristics may or may not have a flatfish species and can therefore not be separated by any discrimination method based on the observed parameters. There are several possible reasons for the observed high error rates. For halibut, rock sole, and yellowfin sole, error rates for predicting presence were generally much lower than error rates for predicting

absence. This may indicate that these species were mostly confined to relatively well-defined depth/substrate characteristics. The high misclassification rate for absence suggests that there are many stations that may offer suitable depth, temperature and substrate conditions for a species, but the species is not found there for other reasons. These could be related to another unobserved variable, it could be a chance event, or it may simply indicate that the species was not caught in the beam trawl, although it may have been present in the area. We are likely to miss species, since no replicate tows were taken at most stations. At stations where replicate tows were taken the number of species captured generally increased with the number of tows (unpubl. data).

For flathead sole the situation was different since their presence was not as easy to predict as their absence. Stations where they were absent are generally in shallow areas with little mud, whereas they are usually present in, but are not restricted to, deep, muddy places.

The classification results suggest that the seven environmental variables used in our discriminant analysis alone cannot account for the observed flatfish distributions, but they are a first cut at defining them. Thus although our location variable as measured was not statistically significant, we incorporated a parameter which qualitatively describes distribution with respect to position with bays into the conceptual models along with depth and substrate parameters. These conceptual models developed from 1991 data (Norcross et al. 1995) are still applicable after incorporating 1992 data.

Clearly, additional factors influence the presence or absence of these flatfish species at any given station. Possible factors that were not included in this study are a location parameter, prey and predator abundance, and a substrate or habitat parameter to account for microhabitat features that are not reflected in the sediment composition. A location parameter may be a categorical variable assigning each station to a well-defined geographical area. For example, we observed large differences in the abundance of halibut and rock sole between the east and west side of Kodiak Island and among different bays (unpubl. data). These differences possibly reflect oceanographic conditions that lead to recruitment of juvenile flatfishes into near-shore areas around Kodiak Island. The oceanographic conditions underlying recruitment cannot be parameterized until the recruitment mechanisms are better understood, but habitat models incorporating geographical and oceanographic information may help to reveal these mechanisms.

The abundance of prey (McIntyre and Eleftheriou 1968, Minami 1986, Allen 1988) and predators (van der Veer et al. 1991, Seikai 1993) are likely to influence the distribution and abundance of flatfish species, but cannot be quantified without extensive surveys. Incorporating prey or predator abundance in a general habitat model is therefore not practical and is of little use in applying the model to other areas.

Additional substrate information is desirable to more adequately describe the microhabitat at each station. During our sampling we obtained qualitative descriptions of the benthic flora and fauna that were collected at each station and a very rough quantification of the dominant invertebrates that were caught together with the fishes. In the future, we will attempt to consolidate this information into a categorical "community descriptor" for each station. This "community descriptor" can then be used as an additional explanatory variable in future models.

Rather than a simple discrimination into stations where a flatfish species is present or absent, for future analysis it is desirable to obtain an estimate of the probability of a species being present at a given station and/or an estimate of its predicted abundance. The probability of a species being present can be estimated by logistic regression analysis, using the parameters that were used in this study and additional parameters as discussed above. Logistic regression is an alternative method of classification when the multivariate normal model is not justified and is applicable for any combination of discrete and continuous variables (Afifi and Clark 1990). Prediction of expected abundance may be obtained using multiple regression models, but this method critically depends on the normality assumption and is very sensitive to outliers (Pers. comm. Ron Barry, Univ. of Alaska Fairbanks, Sept. 1994).

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Diet Diversity as a Mechanism for Partitioning Nursery Grounds of Pleuronectids

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Abstract

Because competitive feeding relationships are potentially important to nursery habitat quality, diets were investigated for the four most abundant juvenile flatfishes around Kodiak Island, Alaska. The diets of ages-0 and -1 rock sole (*Pleuronectes bilineatus*), yellowfin sole (*Pleuronectes asper*), flathead sole (*Hippoglossoides elassodon*) and Pacific halibut (*Hippoglossus stenolepis*) were examined in relation to location, depth and substrate of capture. Crustacean taxa comprised most of the diet of all eight predator groups. Diets appeared to be related to the physical parameters of capture, including location, depth and substrate type. In particular, mysids, cumaceans and gammarid amphipods were sometimes consumed by multiple predator groups within a location, depth increment or substrate type. Within the physical parameters examined, predators generally consumed different prey taxa or a variety of prey. When predator groups overlapped in spatial distribution, generally the dietary overlap at sites of co-occurrence was reduced from or similar to the overall dietary overlap for those predator groups. When the most abundant predator groups (age-0 rock sole and age-1 yellowfin sole) co-existed, one or both predator groups altered their feeding and thereby diminished the amount of interspecific dietary overlap. Flathead sole and halibut decreased intraspecific diet overlap by age-class segregation of diet.

Introduction

Juvenile fishes congregating in nursery areas potentially can diminish habitat quality through competition for prey, yet different patterns of food resource use may limit intraspecific and interspecific competition. Diet diversity is a possible mechanism for reducing competition of co-occurring juvenile flatfishes. Many studies have documented the localized partitioning of food resources among co-occurring species of adult (Kravitz et al. 1977, Stickney et al. 1974, Pearcy and Hancock 1978, Livingston 1987) and juvenile flatfishes (Edwards and Steele 1968, Gibson 1973, Hogue and Carey 1982, Sturdevant 1987). In these studies, co-occurring species or intraspecific age groups are found to partition food resources by restricting feeding locale, by feeding from a diverse assemblage of prey taxa, or by consuming different species within a prey type favored by one or more flatfishes. It is important to understand the trophic roles of abundant flatfishes in order to determine their relationships with similar species and other commercial and noncommercial species within the ecosystem.

Nursery areas along the northern Pacific coast are usually shallow (< 100 m) estuaries, bays and nearshore coastal areas (Krygier and Pearcy 1986, Gunderson et al. 1990, Kramer 1991). Estuaries and protected bays may provide better nursery habitat than other coastal areas in part because of improved feeding. Feeding strategy may be a primary reason juvenile flatfishes enter shallow waters (Tyler 1971). Nutrients from land runoff permit high productivity in estuarine areas. Thus, distribution of juvenile fishes in estuaries may result in improved growth conditions (Kuipers 1977, Kramer 1991). Toole (1980) hypothesized that newly settled juveniles in estuaries experienced less feeding competition from larger flatfishes. Substrate type, depth and food availability are among the many factors that may guide initial settlement as well as the distribution of older flatfishes. Abundance and size distributions of juvenile flatfishes has been related to food availability (McIntyre and Eleftheriou 1968, Allen 1988) as well as substrate and depth (e.g., Norcross et al. 1995).

Relationships among juvenile flatfishes in Alaskan waters are poorly understood, despite the strong economic value of these fishes in commercial and sport fisheries. Inshore waters near Kodiak Island, Alaska serve as nursery grounds for many species of flatfish (Harris and Hart 1977, Blackburn and Jackson 1982, Norcross et al. in press), the co-occurrence of which may result in competitive interactions.

The objective of this study is to compare and contrast diets of abundant juvenile flatfishes in a region of geomorphologic diversity. We will pursue this objective through investigation of summer diets of ages-0 and -1 of the four most abundant flatfishes around Kodiak Island, Alaska. We will relate the prey of each of these eight predator groups to the location, depth and substrate of the collection site, and we will evaluate diet overlap between predator species and age groups.

Summary of species distribution around Kodiak

Norcross et al. (in press) related the distribution of juvenile flatfishes captured along Kodiak Island's east and south coasts to the physical characteristics of their capture sites, including location, depth, substrate, distance from the mouth of a bay, bottom temperature and salinity. Concentrations of the most abundant flatfishes, ages -0 and -1 rock sole (*Pleuronectes bilineatus*), yellowfin sole (*P. asper*), Pacific halibut (*Hippoglossus stenolepis*), and flathead sole (*Hippoglossoides elassodon*) can usually be grouped based on the first three physical parameters, thus providing our rationale for examining diet based on these same parameters. However, at many sites these species are found concurrently. When juveniles of one or more age classes of these four pleuronectids coexist, the extent to which they compete for habitat is unknown.

Rock sole, yellowfin sole, Pacific halibut and flathead sole are collected in bays and straits along the east and south coasts of Kodiak Island in each location sampled by Norcross et al. (1993, in press) (Figure 1). Rock sole of both age groups and age-0 halibut are captured primarily in water depths less than 40 m. Age-1 halibut are found in water depths less than 50 m. Age-0 yellowfin sole are scattered within the depth range of 10-90 m, but age-1 yellowfin sole are found most often in depths less than 40 m. Ages-0 and -1 flathead sole are found in greater abundances with increasing depth, and are mainly captured deeper than 40 m (Norcross et al. 1995). Usually age-0 and age-1 of a species are found on similar substrates. Rock sole are captured mainly on sand or mixed sand substrate. Flathead sole are found predominantly on mud or mud mixed with sand or gravel. Pacific halibut are mainly found on sand mixed with some gravel and mud. Age-0 yellowfin sole do not demonstrate a clear substrate preference, but age-1 yellowfin are captured most often on mixed substrates containing mud as well as gravel or sand.

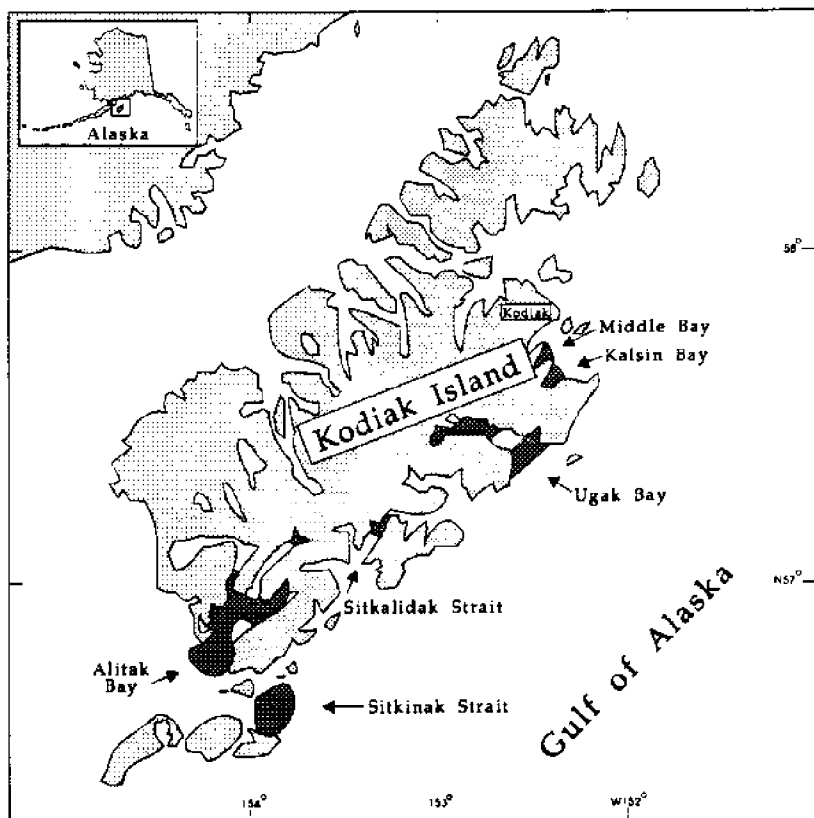


Figure 1. Locations around Kodiak Island, Alaska, where fishes were collected for stomach content analyses.

Methods

Collections

Feeding analyses were in conjunction with an exploratory study on the distribution of juvenile flatfishes (Norcross et al. 1993, 1995, in press). From 11 through 25 August 1991, collections of fishes and sediment were made in six bays and straits along the east and south coasts of Kodiak Island, Alaska (Figure 1). Kodiak Island is a large island in the Gulf of Alaska with a geomorphologically diverse coastline. Sample sites in Middle, Kalsin, Ugak and Alitak Bays and

Sitkalidak and Sitkinak Straits encompassed a wide range of depths and sediment strata. A detailed description of these localities is given by Norcross et al. (in press).

Collections were stratified in 10 m depth increments to 100 m, with the exception of the separation of the 0-10 m strata into 5 m increments. Station locations were randomly selected within depth strata within the constraints of suitable bottom type for trawling. The substrates over which we trawled ranged from fine silt to gravel. Sediment was collected with a 0.06 m³ Ponar grab for laboratory grain size analysis (Folk 1980). The primary sediment type, i.e., gravel, sand or mud, was used in the analysis of feeding in relation to substrate. Because some juvenile flatfishes feed more during flood tides (Edwards and Steel 1968, DeGroot 1971, Tyler 1971, Kuipers 1975) and daylight (DeGroot 1971, Gibson 1973, Oñate 1991), fish were collected only during these periods. Fishing gear was a 3.7 m plumb staff beam trawl of 7 mm stretch mesh with a 4 mm bar mesh codend liner. Abundance (catch-per-unit-effort) of each species was calculated based on a 10 min tow time. Rock sole, yellowfin sole, Pacific halibut and flathead sole were captured in numbers sufficient to examine dietary trends versus the physical parameters of capture.

Sample processing

Following field identification, fishes were frozen and returned whole to the laboratory for analyses. In the laboratory, total length (TL) of thawed fishes was measured (mm). Age groups were estimated as summarized by Norcross et al. (1993) through the use of literature references and plots of length frequency. Ages used in dietary analyses correspond to fish length as follows: age-0 (12-49 mm) and age-1 (50-148 mm) rock sole, age-0 (12-23 mm) and age-1 (30-84 mm) yellowfin sole, age-0 (31-75 mm) and age-1 (94-169 mm) halibut, age-0 (22-54 mm) and age-1 (61-112 mm) flathead sole.

Stomachs were excised at the esophagus and pyloric caecae, blotted dry and weighed (mg). Contents were removed and the empty stomach was weighed to determine total weight of stomach contents. Prey were identified to lowest taxon practical, usually species or family level, based on a variety of references (e.g. Banse and Hobson 1974, Butler 1980, Hart 1982, Kozloff 1987). For each prey taxon, individuals were counted and then combined to attain a cumulative wet weight for the prey taxon. Whole animals and heads were counted as individuals; all fragments from an identifiable taxon received a count of one individual regardless of the number of fragments.

Time constraints required that we subsample the catch for stomach contents. Subsampling of the catch for diet analysis was done in two ways. Rock sole, yellowfin sole, Pacific halibut and flathead sole were each present at some stations in large quantities. When many representatives of a single year-class of a species were found at a station, we randomly selected and examined 20%, but not less than 25 individuals. In addition, we subsampled stations by omitting stomach content analysis of rock sole, yellowfin sole and/or flathead sole when the parameters (i.e., depth and substrate combinations) of the omitted station were repeated in stations for which we made thorough examination.

Prey were pooled into taxonomic groups (usually the family level) for calculation of an index of relative importance (IRI). $IRI = (N + W) \times F$, where N = percent number of prey, W = percent weight of prey and F = percent frequency of fish consuming the prey (Pinkas et al. 1971). This index was chosen because it considers the number of fish consuming the prey taxa as well as the quantity and biomass of prey. Prey taxa with IRI values of ≥ 0.5 were considered important.

Diet was analyzed by age class for age-0 and age-1 rock sole, yellowfin sole, flathead sole and Pacific halibut. The IRI contributed by a prey taxon to the overall diet of age-0 and age-1 groups of each predator was calculated, and the IRI contributed to the diet by important prey taxa was determined for predators captured in each location, depth and substrate type.

Dietary overlap between species and between age groups of a single species were examined using Schoener's (1970) index. This index is calculated as follows:

$$C_{xy} = 100 \times \left(1.0 - 0.5 \sum_{i=1}^N |P_{xi} - P_{yi}| \right)$$

where P_{xi} and P_{yi} are the proportional weights of prey i in the diets of species x and y , respectively. The prey of age-0 yellowfin sole were insufficiently heavy to weigh, therefore for this species, we used proportional IRI values of prey in place of proportional weights. Schoener's index can range in value from 0 to 1. A value of 0 indicates no dietary similarity, and a value of 1 represents complete dietary overlap in which all prey are found in equal proportions for both predators. Schoener's index was used to calculate overall diet overlap between predator groups. A separate index value was calculated for localized diet overlap between pairs of predators at the station where both groups were concentrated, and the less abundant fish was at its greatest abundance.

Results

Overall diets

Benthic and epibenthic invertebrates, consumed whole, formed the majority of the prey eaten by juvenile flatfishes. The overall diet of both ages of each of the four species examined relied more on crustaceans than other phyla (Table 1). Several crustacean taxa were of great importance (> 10% of overall IRI) in the diets of more than one predator group. Harpacticoid copepods comprised an important portion of the diet of age-0 rock sole (35.8%), age-0 yellowfin sole (89.9%) and age-1 yellowfin sole (20.5%). Mysids were very important to age-0 rock sole (25.1%), age-0 halibut (52.7%) and age-1 flathead sole (61.2%). As a group, gammarid amphipods accounted for 12.0-53.4% of the diets of ages 0 and -1 rock sole, age-1 yellowfin sole, age-0 halibut and both ages of flathead sole. However, these predator groups usually consumed amphipods from different taxonomic families. Unidentified Gammaridea juveniles accounted for a large proportion of the diet of age-0 rock sole (19.8%) and age-1 yellowfin sole (16.2%). Gammaridae was consumed by age-1 rock sole (16.6%), age-1 yellowfin sole (4.8%), age-0 (7.8%) and age-1 (3.7%) halibut. Isaeidae was important in the diet of age-1 rock sole (7.4%) and age-1 yellowfin sole (6.0%). Oedicerotidae was consumed by age-1 yellowfin sole (17.7%), age-0 (49.5%) and age-1 (11.0%) flathead sole.

Polychaete worms followed crustaceans in dietary importance for age-0 (12.8%) and age-1 (30.0%) rock sole and for age-1 yellowfin sole (13.0%). Only crustaceans were important in the diets of age-0 groups of yellowfin sole and halibut. The second most important food eaten by age-1 halibut was teleost fishes (12.9%). Bivalves were of secondary importance in the diet of age-0 (23.6%) and age-1 (2.6%) flathead sole. Molluscs were the third most important food of age-1 rock sole, amounting to 12.5% of the diet; no other predator group had important prey in three taxonomic phyla.

Diet of rock sole

Rock sole was the most abundant flatfish (age-0, N = 2286; age-1, N = 397) captured (Norcross et al. in press) and it consumed the greatest diversity of prey taxa. Age-0 rock sole consumed species from 46 different families or classes, and age-1 fish consumed taxa from 57 groups (Table 1). Ages-0 and -1 rock sole shared 29 prey taxa. Overall, the most important prey of age-0 rock sole included harpacticoid copepods, mysids, gammarid amphipods and polychaetes. The overall

diet of age-1 rock sole relied on polychaetes, gammarid amphipods, bivalves, cumaceans and mysids. The apparent importance of polychaetes in the diet of age-1 rock sole may be an artifact of the taxonomist's inability to identify to family due to the generally poor condition of consumed polychaetes. It was quite rare for the stomachs of age-0 rock sole to be empty (2% of the fish examined) although age-1 fish were empty with relative frequency (24%).

When relative importance of prey taxa in the diets of ages-0 and -1 rock sole were examined by location, depth or sediment type, the most important prey items were sometimes different from the overall diet. The predominant prey taxa of rock sole was related to location of capture (Table 2). Age-0 fish consumed harpacticoid copepods and gammarid amphipods in all regions, and consumed primarily mysids in Middle Bay, polychaetes in Kalsin Bay and Sitkalidak Strait, gammarid amphipods in Ugak Bay, cumaceans in Sitkinak Strait and harpacticoid copepods in Alitak Bay. Harpacticoid copepods were not important prey in any location for age-1 rock sole, although they were important in all locations for age-0 fish. Gammarid amphipods were the primary food source of age-1 rock sole in Middle, Kalsin and Ugak Bays. Age-1 rock sole fed largely on two prey groups in Sitkinak Strait (bivalves and cumaceans) and Alitak Bay (polychaete worms and gammarid amphipods). The single most important prey of age-0 rock sole was different from that eaten by age-1 rock sole in all locations, except in Ugak Bay, where both ages consumed primarily gammarid amphipods.

Diets of rock sole were related to depth of capture (Table 3). In each of two depth increments, age-0 rock sole consumed primarily Cumacea (0-5 m and 60-70 m) or gammarid amphipods (5-10 m and 80-90 m). Polychaetes were the most important prey of age-0 rock sole by a small margin in 10-20 m. In the 20-30 m depth increment, harpacticoids and mysids shared the role of primary prey for age-0 rock sole, and from 30 to 60 m depth, harpacticoid copepods were the predominant food source. Age-1 rock sole mainly consumed gammarid amphipods from 0 to 30 m depth, although in the 20-30 m depth range, mysids were of similar dietary importance. Polychaete worms were eaten by age-1 rock sole most often in 30-40 m, brachyuran crabs were consumed in 40-50 m, and cumaceans were the predominant food source at 60-70 m depth. When a single prey taxa was consumed most often, the diets of age-0 and age-1 rock sole coincided only in 5-10 m (Gammaridea) and in 60-70 m (Cumacea). In 20-30 m, the most important prey of rock sole of both ages included mysids and either harpacticoids (age-0) or amphipods (age-1).

Feeding of age-0 rock sole was also related to the three primary substrates surveyed (Table 4). Although more age-0 rock sole were examined from sand substrates ($N = 478$), feeding was more diverse on gravel, where only 55 predators were examined. Harpacticoids were eaten by age-0 rock sole on all substrates, but were the most important prey only on gravel. On sand, age-0 rock sole fed mainly on gammarid amphipods, and polychaete worms were the predominant prey on mud. Gammarid amphipods were eaten by age-1 rock sole widely on all substrates, but were the dominant food source only on sand. Polychaeta was the principal prey of age-1 rock sole on gravel as well as on mud. Gammaridea was the most important prey for both ages of rock sole on sandy substrate, and Polychaeta was the most important food of both ages of rock sole on mud. On mud, rock sole age-1 had high IRI values for bivalves, cumaceans and gammarid amphipods as well as its primary food source, Polychaeta.

Diet of yellowfin sole

The diet of yellowfin sole, the second most abundant flatfish captured (age-0, $N = 16$; age-1, $N = 1103$), was less diverse than the diet of rock sole. Age-0 yellowfin consumed prey from only two taxa (Ostracoda and Harpacticoida), and age-1 yellowfin consumed 36 taxa; ages-0 and -1 yellowfin sole shared only one prey taxon, Ostracoda (Table 1). Age-1 yellowfin sole fed on Gammaridea, Harpacticoida, Polychaeta, Calanoida, and Cumacea in order of decreasing dietary importance. Ten percent of age-0 fish and 19% of age-1 fish were empty.

Age-0 yellowfin sole fed primarily on harpacticoid copepods in Kalsin and Alitak Bays and divided its diet between ostracods and harpacticoid copepods in Sitkinak Strait. Few age-0 yellowfin sole were examined from any location ($N \leq 4$). Age-1 yellowfin sole consumed primarily gammarid amphipods in Middle, Kalsin and Ugak Bays (Table 2). Age-1 yellowfin sole fed primarily on cumaceans in Sitkalidak Strait and on veneroid bivalves in Sitkinak Strait. In Alitak Bay, age-1 yellowfin sole fed primarily on copepods (both Calanoida and Harpacticoida). Ages-0 and -1 yellowfin sole fed on the same prey only in Alitak Bay, where harpacticoid copepods were the most important prey of age-0 fish and were of secondary importance to age-1 fish.

Age-0 yellowfin sole fed only on harpacticoids in depths of 0-20 m, and divided its diet between harpacticoids and ostracods in deeper areas (Table 3). Few age-0 yellowfin sole were examined ($N \leq 3$) in any depth increment. Age-1 yellowfin sole consumed primarily Gammaridea across depths of 0-5 and 10-30 m; in the 5-10 m depth

Table 1. Indices of relative importance $\times 1,000$ of all prey taxa consumed by the four most abundant juvenile flatfishes captured near Kodiak Island during August 1991. IRI values are multiplied by 1,000 to allow items of lesser importance to be included. N = total number of stomachs examined (number of stomachs that were empty).

Prey taxa	Rock sole		Yellowfin sole		Pacific halibut		Flathead sole	
	age-0 N=575(10)	age-1 N=94(23)	age-0 N=10(1)	age-1 N=254(48)	age-0 N=171(2)	age-1 N=28(4)	age-0 N=226(64)	age-1 N=101(16)
Animalia ^a	1,901.4	3,283.6	5,547.4	2,632.1	4,451.5	3,805.3	1,750.4	4,413.5
Foraminiferida	b							
Actiniaria						7.7		
Kinorhyncha	b							
Polychaeta ^a	243.8	999.4		367.3	9.1	10.7	15.6	21.9
Polynoidae	1.0			b	0.4			
Phyllodoctidae	b							
Goniadidae		10.9						
Lambrineridae	b	27.2		1.2	0.1	4.2		0.6
Spionidae		6.6						
Opheliidae	14.5	3.4		32.4				
Pectinariidae	b							
Ampharetidae		0.6						
Terebellidae	1.1	0.2		2.2			0.2	
Oligochaeta		b						
Mollusca ^a	14.4	409.7		23.4	0.5		413.4	116.9
Gastropoda ^a		4.7		0.9	0.4			
Retusidae		0.7						
Nudibranchia		3.6						
Bivalvia ^a	14.4	405.0		22.5	0.1		413.4	116.9
Nuculanidae	b			0.6				
Thyasiridae		1.0						
Cardiidae		0.7						
Tellinidae		0.8						
Lyonsiidae		0.9						
Ophiuroidea		1.1						
Chaetognatha		155.8						
Crustacea ^a	1,643.2	1,714.8	5,547.4	2,441.4	4,439.7	3,297.2	1,321.0	4,272.3
Cladocera				0.2	b			
Ostracoda	18.3	2.8	559.6	53.3	0.1		0.8	
Calanoida ^a	1.1	0.4		309.4	0.2		1.2	
Calanidae	b							
Pseudocalanidae	0.9			0.1			0.2	
Aetideidae				b			0.4	
Centropagidae	0.1	0.1		308.9	0.2			
Acartiidae		0.3						
Harpacticoida	655.3	10.6	4,987.8	581.5	14.1	3.4	42.8	0.2
Cyclopoida	b							
Caligoida	b					4.0		
Cirripedia	b							
Balanomorpha		3.7						

Table 1. (continued.)

Prey taxa	Rock sole		Yellowfin sole		Pacific halibut		Flathead sole	
	age-0 N=575(10)	age-1 N=94(23)	age-0 N=10(1)	age-1 N=254(48)	age-0 N=171(2)	age-1 N=28(4)	age-0 N=226(64)	age-1 N=101(16)
<i>Crustacea (continued)</i>								
Mysidae	440.2	203.2		4.5	2,346.4	54.2	161.5	2,794.0
Cumacea ^a	113.3	394.1		190.3	1280.2	3.7	36.6	13.8
Lamproidae	37.8	333.7		163.7	130.6		29.1	7.0
Diastylidae	0.1	52.6		0.1	1,135.6	3.7	1.4	
Nannostaciidae				0.1	0.1			1.1
Tanaidacea		0.1						
Isopoda ^a	1.0			2.5			13.8	0.4
Flabellifera	^b			1.6			13.7	0.4
Sphaeromatidae	0.1							
Gammaridea ^a	410.9	993.6		1,278.0	533.5	187.6	933.6	566.2
Ampeliscidae	^b	0.6			2.3	23.0		
Ampithoidae	^b	33.6						
Argissidae	^b							
Arylidae		1.9			17.8	22.6		
Corophiidae		0.1			0.1			
Dexaminidae		^b						
Eusiridae	2.0							
Gammaridae	10.8	545.1		137.1	347.3	142.0	21.7	46.1
Haustoriidae	8.9	3.7		1.1	0.1			
Isaeidae	10.5	244.5		169.8	29.5		0.3	0.4
Lafystiidae				0.1				
Lysianassidae		35.2		8.5	0.6			
Oedicerotidae	3.0	90.9		502.5	93.8		866.0	486.6
Phoxocephalidae	^b	4.1		0.3	0.9			
Pleustidae	^b			0.3	2.1			
Podoceridae		^b						
Stenothoidae		^b						
Caprellidae		4.8		5.3	0.2			0.2
Euphausiidae	0.7			0.3	0.7			3.0
Dendrobranchiata ^a	0.5	13.3		6.5	164.5	514.2	128.0	860.1
Hippolytidae	0.3	3.8			13.5	241.7	90.0	269.4
Pandalidae	0.1				5.4	45.0		22.8
Crangonidae	0.1	5.7		6.5	137.3	222.2	0.4	526.8
Paguridae	0.2	36.0		6.0	44.8	834.5		22.6
Brachyura ^a	0.2	19.1		1.9	0.5	1,485.1		
Majidae		6.0				1,419.0		
Cancriidae		5.3						
Chironomidae		^b						
Teleostei ^a		0.8				489.7		1.3
Cottidae						215.9		0.8
Pleuronectidae		0.2				208.8		

^aReports the cumulative importance of the taxa included within this category, including the importance of unidentified prey.

^bSignifies the adjusted IRI for that prey species was < 0.1.

Table 2. Relative importance (IRI) of major prey taxa to the diets of juvenile flatfish in each location sampled. N = number of fish examined (number of empty stomachs).

	Middle Bay	Kalsin Bay	Ugak Bay	Sitkalidak Strait	Sitkinak Strait	Alitak Bay
Rock sole age-0	N = 96(4)	133(3)	106(1)	23(0)	131(2)	86(0)
Polychaeta		2.2		9.7		1.0
All molluscs ^a						0.9
Bivalvia						0.9
All crustaceans ^a	9.3	5.2	5.6	1.8	5.5	7.0
Harpacticoida	1.9	1.7	1.9	0.5	1.1	6.1
Mysida	5.8	0.6		0.8		
Cumacea		1.3			2.7	
Gammaridea	1.3	1.5	3.0	0.5	1.6	0.5
Rock sole age-1	N = 32(5)	16(0)	7(1)	0	30(13)	9(4)
Polychaeta	1.9	2.4	1.2			1.6
All molluscs ^a			1.3		0.9	
Bivalvia			1.2		0.9	
All crustaceans ^a	5.4	8.7	7.0		1.1	1.8
Mysida	1.3					
Cumacea	0.5	1.8	1.9		0.8	
Gammaridea	3.3	6.5	4.7			1.3
Yellowfin sole age-0	N = 0	4(0)	1(1)	0	3(0)	2(0)
All crustaceans ^a		9.0			6.0	7.9
Ostracoda					3.1	1.1
Harpacticoida		9.0			2.9	6.8
Yellowfin sole age-1	N = 35(2)	129(30)	14(4)	2(1)	3(1)	71(10)
Polychaeta	0.7	0.6				0.7
All molluscs ^a			1.0		2.0	
Bivalvia			1.0			
Veneroida					2.0	
All crustaceans ^a	10.1	6.1	6.1	4.9	2.0	8.4
Ostracoda						0.5
Calanoida						4.0
Harpacticoida				0.7		3.3
Cumacea		0.7		2.6	1.0	
Gammaridea	9.5	5.3	4.8	1.6		0.6
Brachyura					1.0	

Table 2. (continued.)

	Middle Bay	Kalsin Bay	Ugak Bay	Sitkalidak Strait	Sitkinak Strait	Alitak Bay
Pacific halibut age-0	N = 45(0)	30(0)	5(0)	3(0)	52(0)	36(2)
All crustaceans ^a	15.2	12.3	13.2	8.0	13.2	4.0
Mysida	13.3	1.2	5.4	2.0		1.5
Cumacea		2.5		0.9	12.6	
Gammaridea	1.7	6.8	6.3	1.2	0.5	1.3
Caridea		1.5	1.1	0.7		
Anomura				2.7		0.5
Pacific halibut age-1	N = 0	0	0	0	12(0)	16(4)
All crustaceans ^a					6.4	3.6
Gammaridea					0.5	
Caridea					0.7	1.8
Anomura					1.2	0.7
Oxychyncha					3.9	
All fishes ^a					2.3	
Cottoidei					1.2	
Pleuronectoidei					1.1	
Flathead sole age-0	N = 42(10)	73(17)	36(8)	27(7)	15(12) ^b	33(10)
All molluscs ^a			9.1	0.9		
Bivalvia			9.1	0.9		
All crustaceans ^a	3.7	4.1		4.1		3.2
Mysida	1.6					
Flabellifera						0.6
Gammaridea		3.5		3.7		1.9
Caridea	1.5					
Flathead sole age-1	N = 16(0)	23(2)	23(5)	18(0)	0	21(9)
Chaetognatha				4.9		
All molluscs ^a			0.7			
Bivalvia			0.7			
All crustaceans ^a	12.9	6.9	4.9	8.7		2.3
Mysida	7.8	4.8		5.1		1.0
Gammaridea	0.5	0.6	2.0	0.7		1.2
Caridea	4.6	1.3	2.1	2.6		

^aReports the cumulative importance of the taxa within this category.

^bSignifies there are no important prey for this location.

Table 3. Relative importance (IRI) of major prey taxa to the diets of juvenile flatfish in each depth increment sampled.
N = number of fish examined (number of empty stomachs).

	Depth (m) increment										
	0-5	5-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Rock sole age-0	N = 32(2)	53(4)	170(3)	90(1)	113(0)	4(0)	28(0)	55(0)	0	30(0)	0
Polychaeta		1.0	2.6		0.5	0.8	0.6				
All molluscs ^a					1.1						
Bivalvia					1.1						
All crustaceans ^a	7.1	7.6	4.6	6.2	6.5	9.1	11.0	11.0		11.8	
Harpacticoida		2.0	1.9	2.7	4.8	6.3	7.3				
Mysida		0.5	0.5	2.5	0.7	2.5					
Cumacea	5.0						1.6	10.8			
Gammaridea	1.8	4.4	1.8	0.7	0.7		1.4			11.8	
Rock sole age-1	N=5(0)	5(2)	44(13)	15(1)	20(7)	4(0)	0	1(0)	0	0	0
Polychaeta		1.1	1.4	1.2	1.3	1.9					
All molluscs ^a	1.3	0.6	0.5		0.9						
Nudibranchia	1.3										
Bivalvia		0.6	0.5		0.9						
All crustaceans ^a	14.2	3.8	3.3	7.4	1.6	5.0		18.0			
Mysida				3.2							
Cumacea	0.9	1.1	1.2		0.6			18.0			
Gammaridea	13.1	2.3	2.0	3.7	0.5	1.4					
Brachyura						2.7					
Yellowfin sole age-0	N=3(0)	1(0)	1(0)	1(0)	1(0)	0	0	2(0)	0	1(0)	0
All crustaceans ^a	9.0	9.0	9.0	9.0	9.0			4.6			
Ostracoda				4.5	5.2			2.3			
Harpacticoida	9.0	9.0	9.0	4.5	3.8			2.3			

Table 3. (continued.)

	Depth (m) increment										
	0-5	5-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Yellowfin sole age-1	N=9(2)	57(14)	115(19)	57(7)	7(4) ^b	1(1)	0	0	0	0	0
Polychaeta		0.8	0.7								
All crustaceans ^a	10.3	4.7	5.4	7.4							
Calanoida		1.9		0.5							
Harpacticoida		0.7	0.6	0.8							
Cumacea				1.6							
Gammaridea	10.2	1.8	4.5	4.5							
Pacific halibut age-0	N=33(0)	28(0)	36(2)	11(0)	38(0)	0	0	25(0)	0	0	0
All crustaceans ^a	13.9	11.8	5.6	8.8	6.4			17.2			
Harpacticoida				1.7							
Mysida	10.2	8.0	0.8	0.8	1.2			17.1			
Cumacea		0.6	0.8		3.6						
Gammaridea	3.2	2.8	2.8	5.1	0.9						
Caridea			0.9								
Anomura				0.8							
Pacific halibut age-1	N=0	1(0)	8(3)	6(1)	13(0)	0	0	0	0	0	0
All crustaceans ^a		20.8	2.5	6.1	6.9						
Mysida			0.7								
Gammaridea		6.4		0.5							
Caridea		6.3	0.9	2.3	0.8						
Anomura			3.1	3.1	0.9						
Oxyrhyncha			0.6		4.3						
All fishes ^a					2.3						
Cottoidei					1.0						
Pleuronectoidei					1.0						

Table 3. (continued.)

	Depth (m) increment										
	0-5	5-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Flathead sole age-0	N=0	0	2(1)	52(12)	21(3)	7(6) ^b	40(7)	13(9) ^b	6(2)	83(22)	2(2)
All molluscs ^a											
Bivalvia										2.3	
All crustaceans ^a			4.5	5.5	6.3		3.9		2.5	1.3	
Mysida					1.0		1.2		0.5		
Cumacea				0.5							
Flabellifera					0.9						
Gammaridea		4.5	4.8		3.7		1.0		2.0	0.9	
Caridea							1.6				
Flathead sole age-1	N=0	0	3(1)	16(3)	10(4)	7(1)	19(0)	7(2)	5(1)	34(4)	0
Chaetognatha										1.4	
All crustaceans ^a		4.0	8.8		4.0	9.7	12.1	3.1	0.7	5.1	
Mysida		2.0	7.1		2.8	2.0	6.2			1.6	
Gammaridea			0.8		0.9	1.0	0.7	2.4		1.3	
Caridea		1.7	0.8			6.7	5.1		0.7	1.7	

^aReports the cumulative importance of the taxa within this category.^bSignifies there are no important prey in this depth range.

Table 4. Relative importance (IRI) of major prey taxa to the diets of juvenile flatfish, in each substrate sampled. N = number of fish examined (number of empty stomachs).

	Gravel	Sand	Mud
Rock sole age-0	N = 55(0)	478(10)	42(0)
Nematoda	0.5		
Polychaeta			4.7
All molluscs ^a	0.6		
Bivalvia	0.6		
All crustaceans ^a	7.3	3.0	2.9
Harpacticoida	4.4	0.7	1.6
Mysida	1.9		
Cumacea	0.2	0.5	
Gammaridea	0.7	1.3	
Rock sole age-1	N = 19(4)	71(19)	4(0)
Polychaeta	1.9	0.9	5.8
All molluscs ^a	0.6		4.3
Bivalvia	0.6		3.7
Veneroida			0.6
All crustaceans ^a	2.4	3.3	6.3
Cumacea	0.7	0.7	2.0
Gammaridea	1.1	2.3	3.9
Yellowfin sole age-0	N = 1(0)	7(0)	2(1)
All crustaceans ^a	9.0	6.7	2.3
Ostracoda	5.2	0.6	
Harpacticoida	3.8	6.1	2.3
Yellowfin sole age-1	N = 40(4)	172(39)	42(5)
Polychaeta		0.5	1.5
All crustaceans ^a	7.8	6.0	7.8
Ostracoda	0.9		
Calanoida	2.4		3.8
Harpacticoida	3.7		1.8
Cumacea		0.5	
Gammaridea		5.4	2.1

Table 4. (continued.)

	Gravel	Sand	Mud
Pacific halibut age-0	N = 32(0)	129(2)	10(0)
All crustaceans ^a	7.4	7.2	9.5
Mysida		3.0	5.6
Cumacea	5.4	1.9	
Gammaridea	1.5	1.8	2.8
Pacific halibut age-1	N = 16(1)	11(3)	1(0)
All crustaceans ^a	5.6	3.3	18.0
Mysida			13.3
Gammaridea		0.7	
Caridea	1.4	1.3	
Anomura	1.4		4.7
Oxyrhyncha	2.2	0.8	
All fishes ^a	1.5		
Cottoidei	0.7		
Pleuronectoidei	0.6		
Flathead sole age-0	N = 28(8)	119(34)	79(22)
All molluscs ^a	0.8		2.0
Bivalvia	0.8		2.0
All crustaceans ^a	3.8	3.2	0.8
Gammaridea	3.5	2.2	0.6
Flathead sole age-1	N = 23(5)	35(2)	43(9)
Chaetognatha	3.0		
All crustaceans ^a	5.3	11.1	3.3
Mysida	3.2	7.4	0.6
Gammaridea		0.9	1.4
Caridea	1.6	2.8	1.0

^aReports the cumulative importance of the taxa within this category.

increment, its diet was divided nearly equally between calanoid copepods and gammarid amphipods. Ages-0 and -1 yellowfin sole did not consume the same primary prey in any depth increment.

Age-0 yellowfin sole consumed mainly ostracods on gravel and harpacticoid copepods on both sandy and muddy substrates (Table 4). Few age-0 yellowfin sole were examined on gravel (N = 1) or mud (N = 2). Age-1 yellowfin sole consumed mainly harpacticoid copepods on gravel, gammarid amphipods on sand and calanoid copepods on mud. Ages-0 and -1 yellowfin sole did not feed on the same primary prey taxa on any substrate.

Diet of Pacific halibut

Pacific halibut was the least abundant of the four flatfishes examined (age-0, N = 217; age-1, N = 28). Halibut consumed prey from 35 (age-0) or 20 (age-1) taxonomic groups; they shared 15 prey taxa (Table 1). Mysids, cumaceans and amphipods were the most important prey of age-0 halibut, while age-1 halibut consumed mainly brachyuran and anomuran crabs, shrimps, fishes and amphipods. Stomachs of age-0 and age-1 halibut were seldom empty (1% and 14% of fish, respectively).

Age-0 halibut ate mysids in most locations and amphipods in all locations (Table 2). Age-0 halibut consumed primarily mysids in Middle Bay, gammarid amphipods in Kalsin Bay, and cumaceans in Sitkinak Strait. In Ugak and Alitak Bays and Sitkalidak Strait, the primary prey of age-0 halibut was mysids and either gammarid amphipods (Ugak and Alitak Bays) or anomuran crabs (Sitkalidak Strait). Age-1 halibut captured in Sitkinak Strait ate brachyuran crabs, and in Alitak Bay fed primarily on caridean shrimps. Ages-0 and -1 halibut did not share the same primary prey in any area.

The predominant prey of age-0 halibut was mysids in depths less than 10 m, gammarid amphipods in 10-30 m, and cumaceans in deeper sites (Table 3). Age-1 halibut caught in depths from 5 to 20 m divided their diet among multiple crustacean taxa. In deeper water, age-1 halibut consumed mainly anomuran (20-30 m) or brachyuran (30-40 m) crabs. Ages-0 and -1 halibut did not consume the same primary prey in any depth increment.

Age-0 halibut consumed primarily cumaceans on gravel and mysids on substrates of sand and mud (Table 4). Age-1 halibut consumed primarily crabs (Brachyura and Anomura) on gravel, shrimps (Caridea) on sand and mysids on mud. Halibut of both ages

ate mysids on mud, although it should be noted that only one age-1 halibut was examined on this substrate.

Diet of flathead sole

Flathead sole was the third most abundant flatfish captured along the east and south coasts of Kodiak (age-0, $N = 320$; age-1, $N = 187$). Age-0 flathead sole preyed on 23 families, and age-1 flathead sole consumed species from 24 families of prey (Table 1). Ages-0 and -1 flathead sole shared prey from 16 taxonomic families, and fed primarily on the same four prey groups. In order of importance, age-0 flathead sole preyed on amphipods, bivalves, mysids and shrimps, while age-1 flathead sole consumed mysids, shrimps, amphipods and bivalves. Of the four fishes examined, the stomachs of flathead sole were empty most often (28% of age-0 fish and 16% of age-1 fish, Table 1). Flathead sole was the only species in which the percentage of empty stomachs decreased with increasing age.

Gammarid amphipods were the primary food of age-0 flathead sole in Kalsin and Alitak Bays and in Sitkalidak Strait (Table 2). In Ugak Bay, age-0 flathead fed primarily on bivalves, and in Middle Bay, the diet was divided fairly equally between mysids and caridean shrimps. Age-1 flathead sole fed primarily on mysids in Middle and Kalsin Bays. In other locations, age-1 flathead sole fed primarily on two prey taxa. Age-1 flathead sole consumed Gammaridea and either Caridea (Ugak Bay) or Mysida (Alitak Bay). In Sitkalidak Strait, age-1 flathead sole consumed Mysida and Chaetognatha. When ages-0 and -1 flathead sole shared a predominant prey (mysids in Middle Bay or gammarid amphipods in Alitak Bay) one of the predator groups had a second prey taxa which was of similar importance to the predominant prey type.

Few age-0 ($N = 2$) or age-1 ($N = 3$) flathead sole were examined in the 10-20 m depth increment. Age-0 flathead sole in depths 10-40 and 70-80 m consumed mainly gammarid amphipods (Table 3). Age-0 flathead split their diet among Caridea, Mysida and Gammaridea in 50-60 m depth, and in 80-90 m age-0 flathead sole ate mainly Bivalvia. Age-1 flathead sole primarily consumed mysids at depth increments of 20-40 and 50-60 m. In depths from 10 to 20 and 40 to 50 m, age-1 flathead sole consumed nearly equal amounts of mysids and caridean shrimps. In 80-90 m depth, mysids, amphipods, shrimps and chaetognaths were of similar importance in the diet of age-1 flathead sole. In depths where ages-0 and -1 flathead sole utilized the same primary

prey (50-60 and 80-90 m), one or both ages consumed multiple prey in similar quantities.

On gravel and sand, the diet of age-0 flathead sole primarily consisted of gammarid amphipods, while on mud this predator mainly consumed bivalves (Table 4). Age-1 flathead sole primarily consumed mysids on sand, but mysids and chaetognaths were of similar importance on gravel and gammarid amphipods and caridean shrimps were of similar importance on mud. Ages 0 and -1 flathead sole did not primarily consume the same prey over any substrate.

Through examination of diet versus location, depth increment or substrate type, it was apparent that predators do not consistently take the majority of their diet from a single prey taxon. Multiple predator groups may rely primarily on a single prey taxon within some physical parameters of capture. In particular, mysids, cumaceans and gammarid amphipods were utilized as the primary food source by more than one predator group in many locations, depths or substrates. When a prey taxon was the primary food of more than one predator group, often one or more of the predators relied to a similar extent on additional prey.

Dietary overlap between predator groups

Dietary overlap between the entire diets of most juvenile flatfishes was fairly high (Table 5). In general, dietary overlap between predator groups ranged from 30 to 50%. Age-0 yellowfin sole had the least amount of dietary overlap with other predator groups (0.0-3.0%). The diet of age-1 halibut also overlapped little with other predator groups (0.0-32.3%). The greatest similarity in overall diets was between age-0 Pacific halibut and age-1 flathead sole (56.9%).

The overall diets of age-0 and age-1 rock sole were similar to each other and to the diets of other flatfishes (Table 5). When rock sole co-existed with other predator groups, dietary overlap at a specific site was usually reduced or did not change appreciably from overall dietary overlap. For example, at the site where the most age-0 rock sole and age-1 yellowfin sole were assembled together, diet overlap was much less (22.2%) than when considering the entire diets of these predator groups (50.4%). An exception to this situation occurred at one station in 60-70 m depth, on a sand substrate where age-0 rock sole (N = 264) and age-0 halibut (N = 71) were captured. Dietary overlap at this station (65.9%) was greater than overall diet overlap (43.9%) for these two predators.

Table 5. Percent of dietary overlap between the overall diets of predator groups (between pairs of predators at the station where these fishes were most abundant).

	Rock sole		Yellowfin sole		Pacific halibut		Flathead sole
	age-0	age-1	age-0	age-1	age-0	age-1	age-0
Rock sole age-1	51.3 (15.4)						
Yellowfin sole age-0	1.0 a	1.0 a					
Yellowfin sole age-1	50.4 (22.2)	51.3 (50.8)	3.0 a				
Pacific halibut age-0	43.9 (65.9)	45.2 (40.3)	0.0 u	30.6 (31.2)			
Pacific halibut age-1	11.6 a	21.1 a	0.0 a	11.5 a	28.9 (11.9)		
Flathead sole age-0	36.4 a	40.4 a	0.0 a	38.7 (67.0)	35.1 a	17.0 a	
Flathead sole age-1	41.4 a	33.6 a	0.0 a	25.6 a	56.9 a	32.3 a	47.9 (13.4)

^aSignifies predator pairs which were rarely or never captured at the same site.

Yellowfin sole of age-0 were not abundant and had little dietary overlap with other predator groups (Table 5), but age-1 yellowfin sole usually overlap spatially with concentrations of ages-0 and -1 rock sole and age-0 halibut (Norcross et al. 1993, 1994). When age-1 yellowfin were captured concurrently with these groups, dietary overlap between predator groups at that site was usually reduced from or similar to overall dietary overlap. Age-1 yellowfin sole and age-0 flathead sole usually did not co-occur, but at one site (20-30 m, on sand) both groups were abundant ($N = 11$ and 44 , respectively). At this station, the dietary overlap between age-1 yellowfin and age-0 flathead (67.0%) was greater than overall (38.7%) dietary overlap.

Although the overall diets of age-0 and age-1 halibut were most similar to age-1 flathead sole, these predator groups rarely co-exist (Norcross et al. 1993, 1994). When age-0 halibut occupied a site concurrently with another predator group, dietary overlap was usually

similar to or less than the overall dietary overlap between the two predators. An exception to this is the previously mentioned co-occurrence of age-0 halibut and age-0 rock sole in one site where dietary overlap between halibut and rock sole was greater (65.9%) than overall dietary overlap (43.9%).

Discussion

Ages-0 and -1 rock sole, yellowfin sole, Pacific halibut and flathead sole primarily feed on crustaceans in all areas of capture, including those sites where predator groups are found concurrently. The overlap between the entire diets of these predator groups can be high, although differences in geographic centers of distribution (Norcross et al. 1993, 1994) minimize dietary competition between flathead sole and other predator groups and between age-1 halibut and other predator groups. When two predator groups are sampled concurrently, the similarity of their diets is often reduced. Thus, direct competition for food among these eight predator groups may be less than is suggested by the high similarities between entire diets. Results of investigations into the diet and distribution of adult rock sole, yellowfin sole and Alaska plaice (*Pleuronectes quadrituberculatus*) in the Bering Sea (Lang 1992) are similar to this study. These three congeners occupy separate centers of distribution and their diets are dissimilar in an area of known distribution overlap.

Other studies also document the use of diet to reduce competition for nursery habitat. Localized feeding strategy in age-0 North Sea plaice (*Pleuronectes platessa*) and common dabs (*Limanda limanda*) may lead to food partitioning on nursery grounds and reduced spatial overlap of these fishes (Edwards and Steele 1968). Size differences within the age-0 group of Pacific halibut correspond to dietary differences (Holladay and Norcross in press). The diet of older juvenile halibut continues to shift toward larger crustaceans and fishes as predator size increases (Best and Hardman 1982, Best and St-Pierre 1986).

Depth can strongly influence the feeding habits of juvenile and adult flatfishes. In a study similar to this one, Percy and Hancock (1978) related the feeding habits of juvenile and adult Dover sole (*Microstomus pacificus*) captured over a range of depths (74-195 m) and substrates (0-100% sand) along the continental shelf of the central Oregon coast with depth, substrate and prey availability. In their study, depth-related factors exerted more influence on the composition of benthic fishes and their prey than did sediment type. Diet

composition in age-1 and age-2 yellowtail flounder (*Pleuronectes ferrugineus*) collected from 0-220 m depth varied more strongly with depth than with temperature (Langton 1979). The present study is not sufficiently in-depth to evaluate the relative influence of physical parameters or species interactions on the diets of juvenile flatfishes, but previous examination of these data have related the diet of age-0 halibut more strongly to fish size and location than to depth or substrate (Holladay and Norcross in press).

The baseline data presented here on the diets of juvenile flatfishes suggest a need for further research on feeding competition and diet selectivity. This research has established a large potential for interspecific and intraspecific dietary overlap between juvenile flatfishes in Alaskan waters. The present study suggests that prey consumption is related to fish abundance and age as well as to the physical parameters of the capture location. Our results may indicate feeding preference, dietary competition or fluctuations in prey availability. A concurrent examination of the density and distribution of the established prey taxa is needed to determine whether these juvenile flatfishes preferentially select among prey taxa or certain size ranges of available prey. Clarification of the interrelationships of abundant juvenile flatfishes may lend guidance to future management policies.

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Food Habits and Diet Overlap of Arrowtooth Flounder (*Atheresthes stomias*) and Pacific Halibut (*Hippoglossus stenolepis*) in the Gulf of Alaska

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Abstract

The food habits of two flatfish, arrowtooth flounder (*Atheresthes stomias*), and Pacific halibut (*Hippoglossus stenolepis*), in the Gulf of Alaska groundfish ecosystem are presented.

A total of 1,144 arrowtooth flounder stomachs and 467 Pacific halibut stomachs collected in Gulf of Alaska in summer 1990 were analyzed. Walleye pollock (*Theragra chalcogramma*) were the most important prey of both arrowtooth flounder and Pacific halibut; they comprised 66% and 57% by weight of the total stomach contents, respectively. Arrowtooth flounder fed mainly in the water column. Shrimp was the predominant food of arrowtooth flounder < 20 cm fork length while capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*) were the main prey for arrowtooth flounder 20-39 cm long. Walleye pollock dominated the diet of arrowtooth flounder \geq 40 cm. Pacific halibut had benthic feeding habits; their diets varied greatly by predator size. Hermit crabs comprised the highest percentage (28% in depth < 100 m, and 41% in depth 100-200 m, respectively) by weight of the stomach contents of fish < 50 cm. Crabs (including *Chionoecetes* sp., *Oregonia* sp., *Hyas* sp., and *Cancer* sp.) were the main food of Pacific halibut 50-79 cm long while the main food of the largest size group (\geq 80 cm) of this species was pollock.

High dietary overlaps (expressed as Schoener's indices) were found for the same size groups of the same species in different depths. Between different species, high dietary overlap occurred between arrowtooth flounder ≥ 40 cm and Pacific halibut ≥ 80 cm. These high dietary overlaps were mainly attributed to the high percentage of walleye pollock in the diet of these fish.

Introduction

Arrowtooth flounder (*Atheresthes stomias*) and Pacific halibut (*Hippoglossus stenolepis*) are important groundfish species in the Gulf of Alaska. During 1990, Pacific halibut had an exploitable biomass of 216,888 metric tons (t) (3A, 3B, and 4A International Pacific Halibut Commission Regulatory Areas) (Pers. commun., P. J. Sullivan, International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98145-2009, September 1993) and a commercial catch of 23,836 t (data compiled from International Pacific Halibut Commission). Even though the commercial catch (17,641 t in 1990) of arrowtooth flounder was low, the exploitable biomass (1,144,242 t in 1990) was the highest in the groundfish complex in the Gulf of Alaska. Since both arrowtooth flounder and Pacific halibut feed on commercially important fish like walleye pollock (*Theragra chalcogramma*), it is important to study the food habits of these two flatfish species, their impact on commercially important prey, and the diet overlap between them.

Materials and Methods

Study area

In summer 1990, the Resource Assessment and Conservation Engineering (RACE) Division at the Alaska Fisheries Science Center (AFSC) conducted its third comprehensive triennial survey of groundfish resources in the western and central Gulf of Alaska (North Pacific Fishery Management Regulatory areas). This survey covered the area from the Islands of Four Mountains (170°W longitude) to Cape St. Elias (144°30'W longitude). The Food Habits Program at the Resource Ecology and Fishery Management (REFM) Division of the AFSC collected fish stomach samples during this survey. The sampling stations (Fig. 1) covered the area from 161°35'W longitude to 144°30'W longitude.

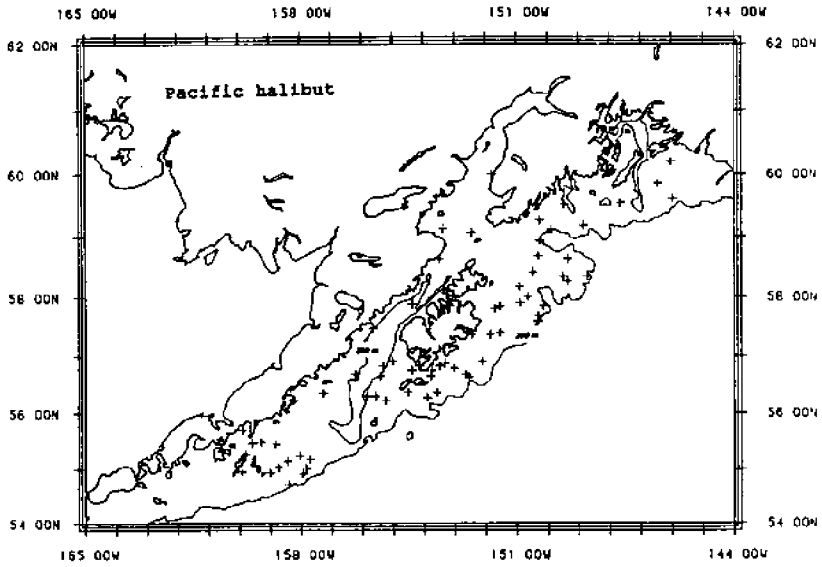
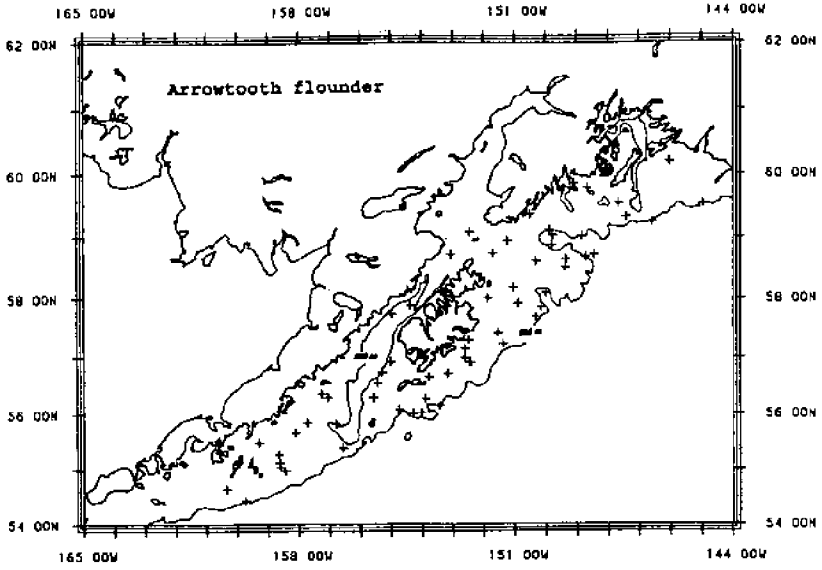


Figure 1. Haul locations (+) for arrowtooth flounder and Pacific halibut stomachs collected in the Gulf of Alaska in summer 1990.

Sample collection

Stomach samples were collected by scientists on board the chartered vessels *Pat San Marie* and *Green Hope* during the AFSC bottom trawl survey from late June to early September in 1990. Both vessels used standard RACE poly-Nor'eastern high-opening bottom trawls rigged with roller gear. Trawls were constructed of 5 inch (12.7 cm) stretched-mesh polyethylene web with a 1.25 inch (3.2 cm) mesh nylon liner in the codend (Stark and Clausen, in prep.).

Before excising the stomach, fish were checked for evidence of regurgitation or net feeding. If a fish had food in its mouth or around the gills, or if the stomach was inverted or flaccid, it was categorized as a "regurgitated" fish, and the specimen was discarded. If a predator had fresh food (usually fish) sticking out of the mouth or the throat, it was categorized as a "net-feeding" fish and was also discarded. When a qualified stomach was excised from a fish, it was put in a cloth bag. A field tag with the species name, fork length (FL) of the fish, and haul data (vessel, cruise, haul number, specimen number) was also put in the bag. All of the samples collected were then preserved in 5 gallon buckets containing a 10% Formalin solution. When the samples arrived at the laboratory, they were transferred to a 70% ethanol solution before a stomach contents analysis was performed.

Stomach contents analysis

In the laboratory, the stomach contents were first blotted with a paper towel and the wet weight was then recorded to the nearest one tenth of a gram. After obtaining the total stomach contents' weight, the contents were placed on a petri-dish and examined using a microscope. Each prey item was classified to the lowest practical taxonomic level. The prey items of Pacific halibut were weighed and enumerated; however, counts of non-commercially important prey were not recorded for arrowtooth flounder and the percent volume of these prey items was visually estimated. Prey weights and numbers of commercially important crabs and fish were recorded. Standard lengths of prey fish, carapace widths (CW) of Tanner crabs and snow crabs, and carapace lengths (CL) of king crabs were also recorded. During this study, discarded fish parts from commercial fish processing operations were also found in the stomachs of Pacific halibut. Prey items were identified as a fishery discard (processing offal) if the parts (usually heads or tails) had a clean cut.

Data analysis

For each predator, the general diet of each species was described. The diet was compared among three depth groups (Depth 1, < 100 m; Depth 2, 100-200 m; Depth 3, ≥ 200 m) and three predator size groups for each species, in terms of the frequency of occurrence and the percent weight of the main prey items. Stomach content data were first analyzed for every 10 cm (FL) predator size groups. Based on the similarity of the main prey of these size groups, arrowtooth flounder were categorized into < 20 cm, 20-39 cm, and ≥ 40 cm (FL) size groups and Pacific halibut were categorized into < 50 cm, 50-79 cm, and ≥ 80 cm (FL) size groups. The prey size data of the commercially important fish and crabs were also summarized by predator size groups. Schoener's (1970) index was calculated to show the diet overlap among the different groups within and between these two species in the Gulf of Alaska. Schoener's index (C_{xy}) is calculated as

$$C_{xy} = 1 - 0.5 \left(\sum |P_{x,i} - P_{y,i}| \right)$$

where $P_{x,i}$ and $P_{y,i}$ are the proportions by weight of prey i in the diets of species x and y , respectively.

Results

Arrowtooth flounder

General diet

A total of 1,144 arrowtooth flounder stomachs were analyzed. Of this total, 489 were empty and 655 (57%) contained food. Arrowtooth flounder sizes ranged from 12 to 80 cm FL with a mean and standard deviation (SD) of 42.1 and ± 10.1 cm, respectively. The average depth of the 62 hauls where stomachs were collected was 164 ± 69 m with a range from 66 to 432 m.

Even though many invertebrate species like euphausiids, pandalid shrimp, squid, mysids, and amphipods were found in the diet of arrowtooth flounder, they comprised only 10% by weight of the total stomach contents. The remaining 90% of stomach content weight was made up of fish. Walleye pollock was the most important prey of arrowtooth flounder; they comprised 66% by weight of the total stomach contents. Pacific herring (*Clupea pallasii*) and capelin (*Mallotus villosus*) comprised 9% and 8% of the total stomach con-

Table 1. The percent weight of the main prey items of different size groups of arrowtooth flounder collected in Depth 1 (< 100 m), Depth 2 (100-200 m), and Depth 3 (≥ 200 m) in the Gulf of Alaska in summer 1990.

Prey item	< 100 m			100-200m			≥ 200 m		
	< 20 cm	20-39 cm	≥ 40 cm	< 20 cm	20-39 cm	≥ 40 cm	< 20 cm	20-39 cm	≥ 40 cm
Cephalopod	ND	0	0	0	0	< 1	0	1	6
Euphausiid	9	10	17	12	3	2	< 1	< 1	
Caridea	7	< 1	66	8	3	98	21	2	
<i>Clupea pallasii</i>	63	28	0	12	6	0	34	8	
<i>Mallotus villosus</i>	3	4	16	42	6	0	8	1	
<i>Theragra chalcogramma</i>	2	50	0	4	80	0	36	82	
Zoarcidae	0	0	0	1	1	0	0	0	
Stichaeidae	0	<1	0	2	<1	0	0	0	
<i>Ammodytes hexapterus</i>	0	0	0	0	<1	0	0	0	
<i>Thaleichthys pacificus</i>	0	0	0	8	0	0	0	0	
Salmonidae	0	2	0	0	0	0	0	0	
Scorpaenidae	0	0	0	0	1	0	0	0	
Pleuronectidae	13	5	0	0	<1	0	0	0	
<i>Pleurogrammus monoptyerygius</i>	0	0	0	8	0	0	0	0	
Fishery discard	0	0	0	0	1	0	0	<1	
Sample size	0	24	67	8	147	178	2	20	71

ND indicates no data.

tents by weight, respectively. Arrowtooth flounder also consumed some eulachon (*Thaleichthys pacificus*), Atka mackerel (*Pleurogrammus monoptyerygius*), Pacific sand lance (*Ammodytes hexapterus*), arrowtooth flounder, flathead sole (*Hippoglossoides elassodon*), fishery discard, and some non-commercially important species (zoarcids and stichaeids).

Spatial and size differences

Few differences were found in the food of arrowtooth flounder < 20 cm (FL) in Depth 2 (100-200 m) and Depth 3 (≥ 200 m). Fish in both areas consumed large amounts of shrimp (≥ 66% by weight) (Table 1).

Arrowtooth flounder 20-39 cm (FL) consumed a higher percent (63%) by weight of Pacific herring in Depth 1 (< 100 m) than in Depth 2 and Depth 3 (12% and 34%, respectively); however, the percent

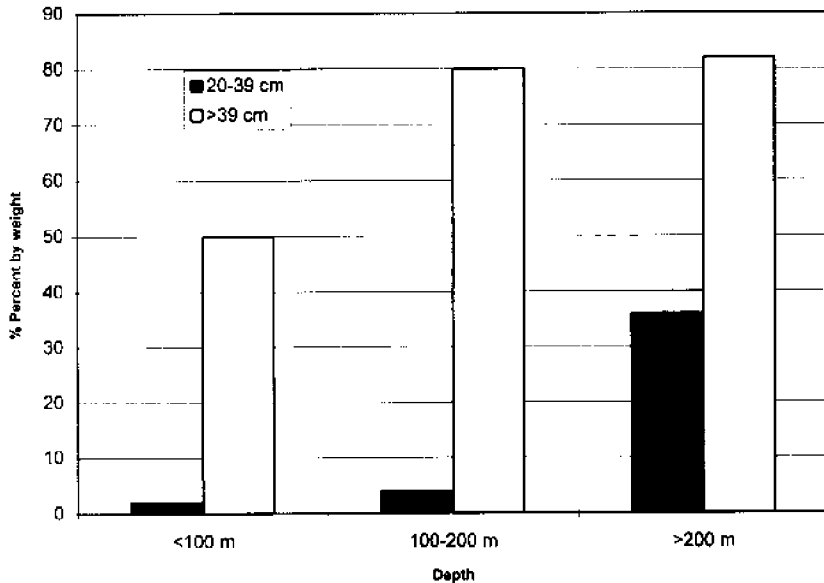


Figure 2. Percent weight of walleye pollock consumed by different size-groups of arrowtooth flounder collected in different depths in the Gulf of Alaska in summer 1990.

frequency of occurrence ($\leq 5\%$) of Pacific herring were low at all three depths. This size group of arrowtooth flounder consumed more capelin (42% by weight) in Depth 2 than in the other two depths. The percent of frequency of occurrence of capelin ($\geq 15\%$) in the three depths was higher than those of Pacific herring. The consumption of walleye pollock by this size group of arrowtooth flounder was highest in Depth 3 (Fig. 2). Euphausiids were found mainly in Depth 1 and Depth 2. Although euphausiids were about 10% by weight of the stomach contents, they occurred in about 60% of the stomachs analyzed. The consumption of shrimp (mainly pandalids) by this size group of arrowtooth flounder decreased as the depth increased. The percent frequency of occurrence of shrimp in the stomachs collected in Depth 3 was high (55%).

Large arrowtooth flounder (≥ 40 cm FL) consumed high percentages ($\geq 50\%$ by weight) of walleye pollock in all three depths (Fig. 2). The percent by weight of pollock in the diet increased with depth (50%, 80%, and 82%, for Depths 1, 2, and 3, respectively). The frequency of occurrence of capelin consumed by large arrowtooth

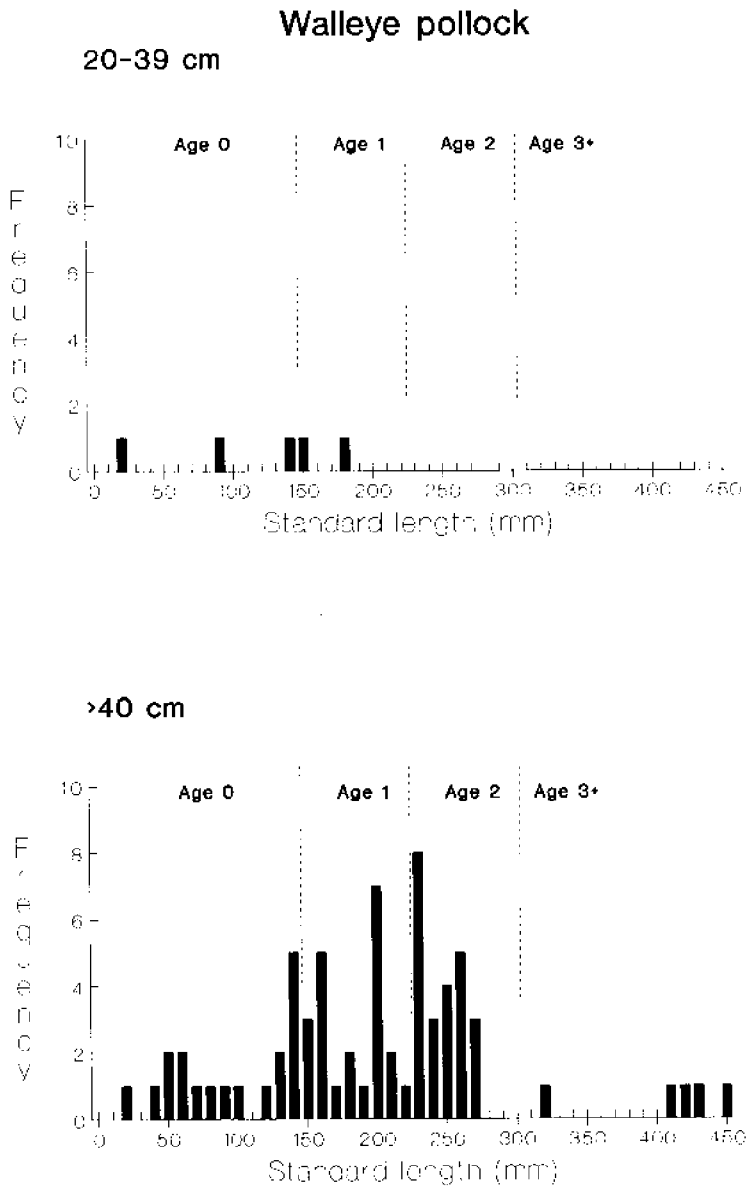


Figure 3. Size frequency distribution of walleye pollock consumed by two size groups of arrowtooth flounder in the Gulf of Alaska in summer 1990.

Table 2. Mean standard length (X), standard deviation (SD), and size range (R) of the prey fish consumed by arrowtooth flounder (ATF) and Pacific halibut (PH) in the Gulf of Alaska in summer 1990.

Prey fish	ATF		PH	
	X + SD (mm)	R (mm)	X + SD (mm)	R (mm)
Pacific herring	160 ± 23	127-195	*	*
Capelin	85 ± 18	43-130	79 ± 15	46-108
Flathead sole	130 ± 0	130-130	146 ± 96	58-280
Atka mackerel	128 ± 0	128-128	*	*
Eulachon	142 ± 17	130-154	120 ± 0	120-120
P. sand lance	70 ± 0	70- 70	137 ± 27	55-187
Walleye pollock	196 ± 89	21-450	316 ± 155	34-670
Coho salmon	*	*	475 ± 35	450-500
Pacific cod	*	*	380 ± 0	380-380
Pacific ocean perch	*	*	208 ± 0	208-208
Pacific halibut	*	*	26 ± 6	21- 36

* Indicates no measurement.

flounder in Depths 1 and 2 was higher than that in Depth 3, even though the percentage by weight of capelin consumed was low ($\leq 6\%$) at all depths. Large arrowtooth flounder also consumed a higher percentage (28%) by weight of Pacific herring in Depth 1 than in Depths 2 and 3 (6% and 8% by weight, respectively). Similar to the 20-39 cm size group, euphausiids occurred most frequently in large size arrowtooth flounder in Depths 1 and 2 (58% and 42%, respectively). They occurred in only 1% of the stomach collected in Depth 3. In contrast, shrimp were found most frequently (24%) in Depth 3.

Prey size trend

Arrowtooth flounder less than 20 cm FL did not consume walleye pollock. The medium-sized arrowtooth flounder (20-39 cm FL) contained some age-0 (< 140 mm SL) and age-1 (140-220 mm SL) pollock. The larger sized (≥ 40 cm FL) arrowtooth flounder had age-0 to age-3 (> 300 mm SL) pollock (Fig. 3). Pacific herring were found in medium-sized and larger sized arrowtooth flounder. Capelin were consumed only by arrowtooth flounder longer than 20 cm FL. Table 2 lists the average, standard deviation, and range of the prey fish standard lengths.

Pacific halibut

General diet

A total of 467 Pacific halibut stomachs were analyzed, of which 79 were empty and 388 (83%) contained food. The size range of the Pacific halibut was between 11 to 151 cm FL with a mean and SD of 71.5 ± 25.9 cm FL. The average depth of the 71 haul locations was 109 ± 48 m with a range from 20 to 234 m.

Nearly 80% of the total stomach contents weight was fish while invertebrates comprised only 20% by weight. Walleye pollock was the most important prey of Pacific halibut. They were the most frequently occurring prey in the stomachs (28%). In terms of weight, they comprised 57% of the total stomach contents. Coho salmon (*Oncorhynchus kisutch*) made up 5% of the total stomach contents by weight, but they did not often occur in the Pacific halibut sampled. Capelin were consumed quite frequently (14%) but they comprised less than 1% of the total stomach contents weight. Other commercially important fish consumed by Pacific halibut include Pacific cod, Pacific sand lance, Pacific ocean perch (*Sebastes alutus*), flathead sole, rock sole (*Pleuronectes bilineatus*), yellowfin sole (*Pleuronectes asper*), Dover sole (*Microstomus pacificus*), and young Pacific halibut. Pacific halibut also consumed 7% by weight of fishery discards (processed fish carcasses). Many non-commercially important fish (eulachon, Pacific sand lance, arrowtooth flounder, cottids, agonids, cyclopterids, bathymasterids, and stichaeids) were also consumed by Pacific halibut; however, they played a minor role as food. Tanner crabs (*Chionoecetes bairdi*) were the most important invertebrate prey of Pacific halibut; they comprised about 6% of the total stomach content's weight. Less important invertebrate prey included octopus (4.8%), lyre crab (*Hyas lyratus*) (2.7%), cancer crab (*Cancer oregonensis*) (2%), hermit crab (1.3%), and decorator crab (*Oregonia gracilis*) (1%). All of the other invertebrates consumed (polychaetes, gastropods, clams, squid, shrimp, and other crustaceans) were found less frequently and were considered to be relatively less important as food of Pacific halibut.

Spatial and size differences

Pacific halibut < 50 cm fork length. Pacific halibut < 50 cm FL long ate more hermit crab in Depth 2 (41% by weight) than in Depth 1 (28% by weight). However, the frequency of occurrence of hermit crab in the diet was higher in Depth 1 (59%) than in Depth 2. This size group of

Table 3. The percent weight of the main prey items of different size groups of Pacific halibut collected in Depth 1 (< 100 m), Depth 2 (100-200 m), and Depth 3 (≥ 200 m) in the Gulf of Alaska in summer 1990.

Prey item	< 100 m			100-200m			≥ 200 m		
	< 20 cm	20-39 cm	≥ 40 cm	< 20 cm	20-39 cm	≥ 40 cm	< 20 cm	20-39 cm	≥ 40 cm
Cephalopod	3	3	13	0	3	4	ND	ND	0
Caridea	4	< 1	< 1	19	1	< 1			0
Pagurid	28	9	< 1	41	9	< 1			0
<i>Chionoecetes bairdi</i>	4	3	28	4	11	1			76
Majidae	10	26	3	1	17	1			0
Other crab	5	23	2	0	17	< 1			0
Echinodermata	0	0	0	13	0	0			0
Salmonidae	0	0	0	0	0	7			0
<i>Mallotus villosus</i>	6	8	< 1	0	4	< 1			0
<i>Theragra chalcogramma</i>	< 1	6	35	0	18	72			24
<i>Gadus macrocephalus</i>	0	0	6	0	3	0			0
Zoarcidae	5	4	1	0	1	0			0
Scorpaenidae	0	5	0	0	0	0			0
Cottidae	5	1	3	0	0	0			0
Bathylagidae	2	1	0	0	0	0			0
Stichaeidae	2	1	0	0	0	0			0
<i>Ammodytes hexapterus</i>	13	1	3	0	0	0			0
Pleuronectidae	7	6	1	22	14	6			0
Fishery discard	< 1	0	3	0	1	9			0
Sample size	86	109	34	5	47	105	0	0	2

ND indicates no data.

Pacific halibut contained a higher percentage by weight of Tanner crab and other majid crabs in Depth 1 (14%) than in Depth 2 (5%). Another phenomenon was that Pacific halibut in the Depth 1 ate more miscellaneous fish than in Depth 2, although this is probably caused by the small sample size in Depth 2. Details of the prey items consumed by Pacific halibut were listed in Table 3.

Pacific halibut 50-79 cm fork length. Hermit crabs and Tanner crabs were not the dominant prey of Pacific halibut 50-79 cm FL in any of the depth groups (Table 3). Instead, other majid crabs (26% by weight)

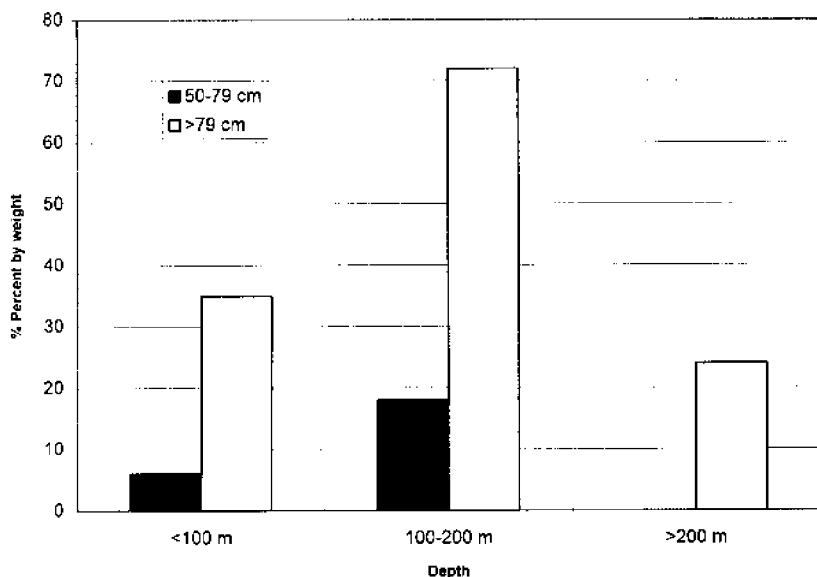


Figure 4. Percent weight of walleye pollock consumed by different size-groups of Pacific halibut collected in different depths in the Gulf of Alaska in summer 1990.

and pygmy cancer crab (*Cancer oregonensis*) (23% by weight) were more important in Depth 1. The percent weight of these two prey in the diet was less in Depth 2 (17% each). The percentage of walleye pollock consumed by this size group of Pacific halibut was higher in Depth 2 than in Depth 1 by weight (Fig. 4). Also, there were more miscellaneous fish consumed in Depth 1 than in Depth 2 (Table 3).

Pacific halibut ≥ 80 cm fork length. Like the 50-79 cm FL size group, Pacific halibut ≥ 80 cm FL ate a higher percentage (72%) by weight of walleye pollock in Depth 2 than in Depth 1 (Fig. 4). Conversely, Tanner crab, miscellaneous fish and cephalopods comprised a higher percentage of the stomach contents in Depth 1 than in Depth 2.

The sample size of the stomachs collected in Depth 3 was small. Only two Pacific halibut larger than 80 cm FL were collected in this area. The stomach contents were comprised of 76% Tanner crab and 24% walleye pollock by weight.

Prey size trend

Pacific halibut < 50 cm FL consumed very few walleye pollock, whereas the walleye pollock consumed by the medium-sized Pacific halibut (50-79 cm FL) were mainly age-0 fish plus a few age-1 to age-3 fish. The larger-sized Pacific halibut (≥ 80 cm FL) contained many different sizes of walleye pollock including both pre-recruits (< 300 mm SL) and recruits (≥ 300 mm SL) (Fig. 5). The average (mean \pm SD) standard length of pollock consumed by Pacific halibut was 315.9 ± 155.0 mm SL with a range from 34 to 670 mm long (Table 2). The size of Tanner crabs consumed by the two smaller sized groups of Pacific halibut were mainly age-0 (< 9 mm CW) and age-1 (9-34 mm CW) crabs, whereas large Pacific halibut (≥ 80 cm FL) consumed mainly age-1 *C. bairdi* and some age-2 and older crabs (> 34 mm CW) (Fig. 5). The mean CW of the *C. bairdi* consumed were 24.7 ± 18.0 mm with a range from 3 to 97 mm. For Pacific halibut, capelin occurred mainly in the 50-79 cm FL size-group, and only a few were measurable for the smallest (< 50 cm FL) and the largest (≥ 80 cm FL) size groups. The Pacific sand lance consumed by Pacific halibut were mainly between 100 and 150 mm SL. The average, standard deviation, and range of prey fish standard lengths are shown in Table 2.

Diet overlap

The diet composition data from Tables 1 and 3 were used to calculate values of Schoener's index of diet overlap (Fig. 6). Diet overlaps within arrowtooth flounder (A), between arrowtooth flounder and Pacific halibut (B), and within Pacific halibut (C) are shown. For each section, actual values of Schoener's Indices (percentage) between different categories are shown and categorized into low (< 30%), medium (30-55%), and high (> 55%) values. Arrowtooth flounder less than 20 cm FL were not included in the diet overlap analysis because of the small sample size (Table 1). For the same reason, stomach content data of Pacific halibut collected from Depth 3 were not included in the diet overlap analysis either. Overall, Figure 6 shows that the highest diet overlap category within arrowtooth flounder occurred mainly in the larger size groups (≥ 40 cm FL) in the two deeper areas. Large Pacific halibut from Depth 2 had high diet overlap with large arrowtooth flounder from all depth zones. Within Pacific halibut, there was one high diet overlap value. It was between the same 50-79 cm FL size groups collected in Depth 1 and Depth 2. Intermediate (30-55%) diet overlaps were common in within-species and across-species tables.

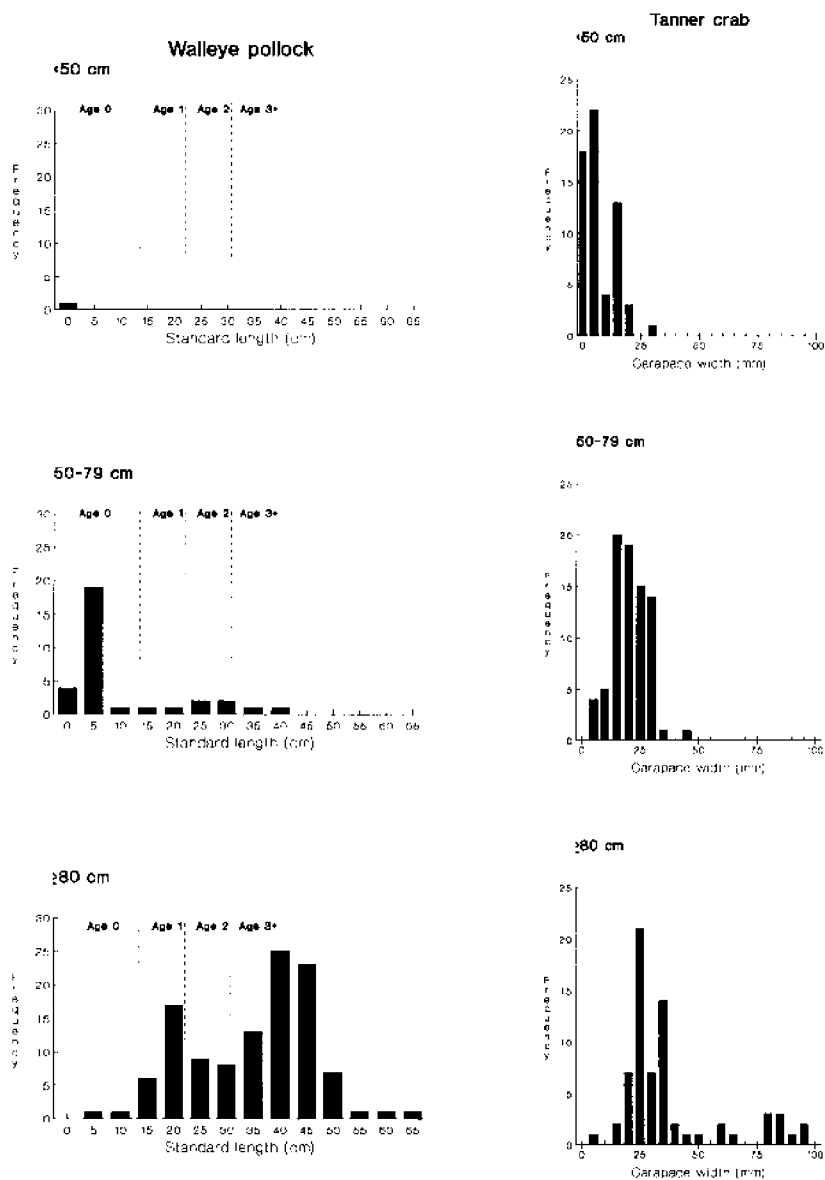


Figure 5. Size frequency distribution of walleye pollock consumed by three size groups of Pacific halibut in the Gulf of Alaska in summer 1990.

A. Arrowtooth flounder vs. Arrowtooth flounder							
Depth		<100 m	<100 m	100-200 m	100-200 m	≥200 m	>200 m
	Length	20-39 cm	≥40 cm	20-39 cm	≥40 cm	20-39 cm	≥40 cm
<100 m	20-39 cm						
<100 m	≥40 cm	49					
100-200 m	20-39 cm	33	30				
100-200 m	≥40 cm	17	63	23			
>200 m	20-39 cm	46	68	32	51		
>200 m	≥40 cm	13	59	15	89	48	
B. Arrowtooth flounder (horizontal) vs. Pacific halibut (vertical)							
Depth		<100 m	<100 m	100-200 m	100-200 m	≥200 m	>200 m
	Length	20-39 cm	≥40 cm	20-39 cm	≥40 cm	20-39 cm	≥40 cm
<100 m	<50 cm	14	9	13	10	13	6
<100 m	50-79 cm	11	15	14	14	15	10
<100 m	≥80 cm	3	36	5	36	36	41
100-200 m	<50 cm	20	5	8	3	19	2
100-200 m	50-79 cm	19	27	10	24	24	23
100-200 m	≥80 cm	8	57	4	72	37	76
C. Pacific halibut vs. Pacific halibut							
Depth		<100 m	<100 m	<100 m	100-200 m	100-200 m	100-200 m
	Length	<50 cm	50-79 cm	≥80 cm	<50 cm	50-79 cm	≥80 cm
<100 m	<50 cm						
<100 m	50-79 cm	41					
<100 m	≥80 cm	20	21				
100-200 m	<50 cm	44	19	6			
100-200 m	50-79 cm	44	66	42	29		
100-200 m	≥80 cm	11	17	42	8	29	
Diet Overlap		<30%		30-55%		>55%	
		Low		Medium		High	

Figure 6. Diet overlap (expressed as Schoener's index, %) of arrowtooth flounder and Pacific halibut in Gulf of Alaska in summer 1990. A. within arrowtooth flounder; B. between arrowtooth flounder and Pacific halibut; C. within Pacific halibut.

Discussion

General diet

Both arrowtooth flounder and Pacific halibut feed largely on fish. Walleye pollock contributed the largest percentage by weight to the diets of these two species, followed by Pacific herring and capelin for arrowtooth flounder, and miscellaneous fish and crabs for Pacific halibut. Smith et al. (1978) found that similar prey items (walleye pollock, euphausiids, shrimp, and miscellaneous fish) were consumed by arrowtooth flounder in the Gulf of Alaska area. In the Bering Sea area, arrowtooth flounder also consumed a high percentage (56% by weight) of pollock (Yang 1991). Earlier food habits studies of Pacific halibut also showed that the diet was primarily composed of walleye pollock, Tanner crab, and miscellaneous fish (Novikov 1968, Hunter 1979, Best and St.-Pierre 1986, and Livingston et al. 1993). Best and St.-Pierre (1986) showed that, in the Gulf of Alaska, Pacific halibut also consumed a relatively large number of octopus. Octopus was found in the Pacific halibut stomachs in this study; however, they comprised only about 5% by weight of the total stomach contents weight.

Spatial and size difference

The main prey items of the arrowtooth flounder and the Pacific halibut (Tables 1 and 3) show that arrowtooth flounder feed mainly in the water column and Pacific halibut feed mainly on benthic prey. Smaller sized arrowtooth flounder feed on euphausiids and shrimp; when they grow larger, they feed mainly on pelagic fish such as Pacific herring, capelin, and smaller sized walleye pollock (usually in the upper water column). On the other hand, Pacific halibut feed mainly on crabs (hermit crabs, Tanner crabs, and other crabs), miscellaneous fish (mainly bottom fish like cottids, zoarcids, stichaeids, and flatfish), and larger sized walleye pollock (which usually stay in the lower water column or near bottom). Table 2 lists the mean standard length and size range of the prey fish consumed by these two species. It indicates that, in general, Pacific halibut consumed larger sized prey fish because they are bigger. This can also be observed by comparing the size of walleye pollock consumed in Figures 2 and 3. Pacific halibut also consumed more fishery discard than arrowtooth flounder did.

Diet overlap

The type of prey eaten by a fish corresponds with the morphology of the alimentary tract of the fish (De Groot 1971, Ebeling and Cailliet

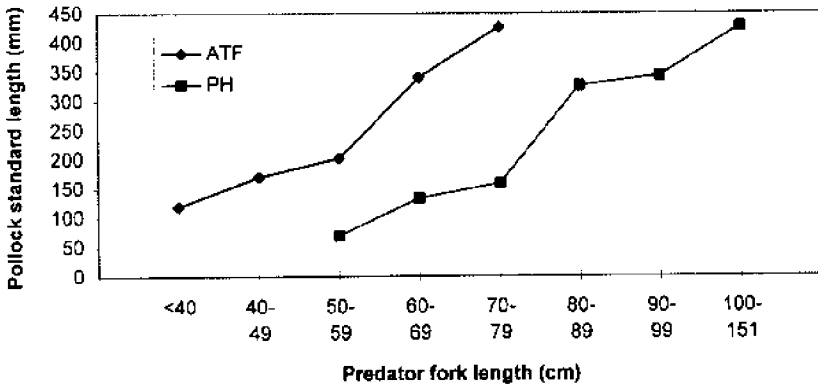


Figure 7. Mean standard length of prey walleye pollock consumed by arrowtooth flounder and Pacific halibut in the Gulf of Alaska in summer 1990.

1974, and Allen 1982). The structure of the mouth of arrowtooth flounder and Pacific halibut is similar in some aspects but with apparent differences that contribute to the similarity or dissimilarity of their diets. Both arrowtooth flounder and Pacific halibut have a very large terminal mouth that is nearly symmetrical with a wide gape. However, the upper jaw of the arrowtooth flounder extends beyond the posterior margin of the lower eye whereas the upper jaw of the Pacific halibut extends only to the mid-orbit of the lower jaw. Thus, arrowtooth flounder should have a larger mouth gape than a similar-sized Pacific halibut and should be able to consume larger prey. This is supported by comparing the average size of pollock consumed by arrowtooth flounder and Pacific halibut (Fig. 7). At all sizes, arrowtooth flounder were able to consume larger pollock than a similar size of Pacific halibut.

Figure 6 shows that only the diets of the largest size groups (arrowtooth flounder ≥ 40 cm FL and Pacific halibut ≥ 80 cm FL) of these two species had high diet overlap. According to the Alaska Fisheries Science Center 1990 Gulf of Alaska Survey (Stark and Clausen, in prep.), 16% of the biomass of arrowtooth flounder were found at depths ≥ 200 m and they were mainly the larger sized (≥ 40 cm FL) fish, whereas only 5% of the biomass of Pacific halibut was found in the same area. Thus, little spatial overlap and competition occurred in this area.

Smaller arrowtooth flounder (< 40 cm FL) had a higher percentage of shrimp, euphausiids, and pelagic fish (e.g., capelin) in their diet.

Their slender gill rakers (with teeth) might play a role in preventing zooplankton from escaping through the mouth. When arrowtooth flounder grow larger (≥ 40 cm FL), the wide mouth gape and the sharp teeth enable them to catch larger fish like walleye pollock. On the other hand, smaller Pacific halibut (< 50 cm FL) consumed less shrimp but more crabs (hermit crabs, Tanner crabs, lyre crabs). The fewer blunt gill rakers of halibut may not prevent smaller prey like euphausiids and other zooplankton from escaping from the mouth, but probably contribute to holding of the prey (for example, crabs).

There are many factors that affect the diet composition of a fish. The environmental factors include availability of food, water temperature, salinity, habitat, bottom depth, etc. The biotic factors include the morphological characteristics (especially the alimentary tracts) of the fish, feeding behavior, predator size, and the physiological factors such as the spawning conditions. This study focused on the diet variations of different predator size groups by depth in one particular year. Future study should include the evaluation of seasonal and interannual diet changes and the possible role of environmental factors in influencing diet.

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Food Habits of Three Congeneric Flatfishes: Yellowfin Sole (*Pleuronectes asper*), Rock Sole (*P. bilineatus*), and Alaska Plaice (*P. quadrituberculatus*) in the Eastern Bering Sea

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Abstract

The stomach contents were identified from a total of 9,096 yellowfin sole (*Pleuronectes asper*), 586 rock sole (*P. bilineatus*), and 513 Alaska plaice (*P. quadrituberculatus*) collected from the eastern Bering Sea from 1984 to 1988. In terms of percent by weight, yellowfin sole had the broadest diet of the three species, consuming similar amounts of benthopelagic prey such as clams, other marine worms (sipunculans, echiurids, and priapulids), and polychaetes. Rock sole preyed primarily on polychaetes, other marine worms, and fish in smaller amounts. Alaska plaice exhibited the narrowest diet selection, consisting of polychaetes and other marine worms nearly exclusively. Slight dietary variation was seen with respect to predator size and depth strata for each of the species.

The diets of Alaska plaice and rock sole were similar due to their reliance upon polychaetes, while yellowfin sole differed from these two because of the variety of prey items in its diet. In addition, the

Table 1. Habitat characteristics of yellowfin sole, *Pleuronectes asper*, rock sole, *P. bilineatus*, and Alaska plaice, *P. quadrituberculatus*, in the eastern Bering Sea (from Allen 1984 and Allen and Smith 1988).

	Yellowfin sole	Rock sole	Alaska plaice
Bottom type	Sand (soft)	Gravel (coarse)	Sand (soft)
Depth range (m)	10-600	0-575	6-475
Depth optimum (m)	50-100	50-100	50-100
Geographic range	Korea-B.C., Canada	Korea- California	Peter the Great Bay-Gulf of Alaska
Life zone	Inner-outer shelf	Inner-outer shelf	Inner-outer shelf
Zoogeography	Arctic-NW boreal Pacific	NE boreal Pacific	Arctic-N boreal Pacific
Refuge	Bury	Bury	Bury

areas of highest abundance of each of these fish were somewhat geographically separate. It appears that competition for similar prey items between species was low. Despite slight differences in their gross feeding morphology, these three fish were all well-suited for benthic-oriented invertebrate predation.

Introduction

Yellowfin sole (*Pleuronectes asper*), rock sole (*P. bilineatus*), and Alaska plaice (*P. quadrituberculatus*) are small-mouthed flatfish abundant in the eastern Bering Sea. The three species are similar in their general habitat characteristics (Table 1) and in their distribution throughout the eastern Bering Sea (Fig. 1), although their individual areas of highest abundance are slightly separate. Both yellowfin sole and rock sole support commercial fisheries, with catches of 149,569 metric tons (t) (Wilderbuer 1993) and 56,998 t (Wilderbuer and Walters 1993) in 1992, respectively. Additionally, 18,985 t of Alaska plaice were caught in 1992 (Walters and Wilderbuer 1993).

The diet of yellowfin sole consists of clams, crustaceans, polychaetes, and other benthic invertebrates (Haflinger and McRoy 1983, Wakabayashi 1986, 1989, Allen 1984, Livingston et al. 1986). Food habits investigations have shown that rock sole consume polychaetes, echiurids, and gammarid amphipods (Brodeur and Livingston 1988,

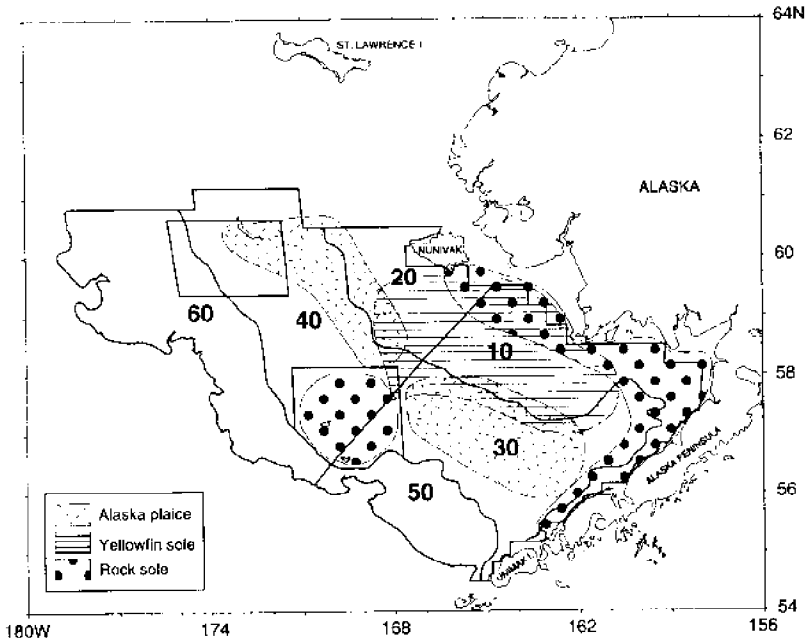


Figure 1. Areas of highest density of yellowfin sole, rock sole, and Alaska plaice in the eastern Bering Sea.

Corcobado-Onate 1991). Previous studies on Alaska plaice have shown that polychaetes make up the majority of their diet, although mollusks, echinoderms, and benthic crustaceans are also consumed (Moiseev 1953, Skalkin 1963, Mineva 1964, Zhang 1988, Allen 1984). These studies had small sizes and limited spatial and/or temporal coverage.

Comparative food habit studies of these species were performed by Allen (1984) and Zhang (1988). Allen (1984) found that even though yellowfin sole, rock sole, and Alaska plaice had similar feeding morphologies and co-occurred in 65% of the samples from the middle shelf of the eastern Bering Sea, they had dissimilar diets. Zhang (1988) found as much as 80% diet overlap between Alaska plaice and rock sole when prey were classified to the phylum level; yellowfin sole did not show as much overlap with either species. These studies present some insight into the trophic relationships of these three species. However, they were limited to very small (11-12 fish per species)

sample sizes and did not account for variation in the diet due to size of fish or location.

Since these fish constitute one-quarter of the exploitable ground-fish biomass in the eastern Bering Sea (North Pacific Fishery Management Council (NPFMC) 1993) and are important to the commercial trawl fishery, it is essential to study their life history characteristics and, in particular, their trophic dynamics. Knowledge of their individual food habits, as well as their interaction with each other and the ecosystem, becomes a critical element as fisheries management takes a multi-species approach. In addition, there exists a need to understand how three congeners with similar morphology, distributions, and trophic characteristics utilize the same basic resource. Therefore, a comprehensive, detailed investigation of the food habits of these three fish and of their dietary relationships is needed. The purpose of this study is to (1) present, compare, and contrast the diets of these three flatfish; (2) determine which factors are important in depicting each diet; and (3) discuss the trophic and ecological status of each species.

Methods and Materials

Stomach samples were collected from 9,096 yellowfin sole in the eastern Bering Sea from May 1984 through September 1988; 513 Alaska plaice and 586 rock sole stomach samples were also collected between June and August of 1984, 1987, and 1988 (Table 2). Additional samples collected during the 1989-1991 eastern Bering Sea resource assessment surveys were used for canonical correspondence analysis (CCA) (Table 2). Samples were collected aboard National Marine Fisheries Service (NMFS), Resource Assessment and Conservation Engineering (RACE) Division research cruises and by biological observers from the Research Ecology and Fisheries Management (REFM) Division Fisheries Observer Program on commercial fishing vessels.

Fish were randomly selected from a subsample of the catch for stomach sampling. Stomachs were collected from fish that showed no signs of either net feeding (e.g. presence of fresh prey in the mouth, esophagus, or gill chamber) or regurgitation (e.g. presence of digested prey in the mouth or gill chamber, or a flaccid or water-filled stomach). Acceptable stomachs were excised at sea and preserved in 10% buffered formalin. Predator length, sex, spawning condition, haul location, date, and time were recorded for each specimen collected.

Table 2. Number of yellowfin sole, rock sole, and Alaska plaice stomach samples analyzed from the eastern Bering Sea for the periods 1984-1988 and 1989-1991.

Predator species and sample period	Number of samples		
	With food	Empty	Total
Yellowfin sole			
1984-1988	6,133	2,963	9,096
1989-1991	2,444	682	3,126
Total	8,577	3,645	12,222
Rock sole			
1984-1988	470	113	568
1989-1991	1,095	147	1,257
Total	1,565	260	1,825
Alaska plaice			
1984-1988	449	64	513
1989-1991	818	61	879
Total	1,267	125	1,392

Samples were transported to the laboratory and stored in a 70% ethanol solution.

In the laboratory, contents of individual stomachs were analyzed. Prey items were sorted and identified to the lowest practical taxon, counted, and weighed to the nearest milligram.

To examine and compare the diets of these three species, it was necessary to consolidate the diet into a small number of common prey categories. The following eight prey types were chosen because they represented the seven most common prey plus a catch-all miscellaneous category. This combination of eight categories also resulted in the lowest percentage of miscellaneous prey of the combinations that were tried. The eight prey categories were:

- Polychaetes—polychaete annelid worms
- Clams—bivalve mollusks
- Gammarids—gammarid amphipods
- Decapods—decapods crustaceans, shrimp, and crab
- Marine worm—echiurids, priapulids, sipunculans
- Echinoderms—sand dollars, brittle stars, sea cucumbers, sea stars

Fish—teleost fish

Miscellaneous—all other prey types, including unidentified prey.

Size categories, by fork length, for yellowfin sole (≤ 20 cm, 20-30 cm, ≥ 30 cm), rock sole (≤ 20 cm, 20-35 cm, ≥ 35 cm), Alaska plaice (≤ 20 cm, 20-40 cm, ≥ 40 cm) were determined based upon the most obvious ontogenetic changes seen in the diet.

Three depth zones, < 50 m, 50-100 m and 100-200 m, were used for dietary analysis. These depth zones were chosen due to the distinct oceanographic and hydrographic characteristics that separate the three areas (Favorite et al. 1976, Kinder and Shumacher 1981). These depth zones were further subdivided into six strata by dividing the area into northwest and southeast sections. Strata 10 and 20 represent the southeast and northwest sections of the < 50 m depth zone, respectively, strata 30 and 40 the 50-100 m depth zone, and strata 50 and 60 the 100-200 m depth zone.

Schoener's index (Schoener 1970) was used to calculate the percentage of dietary overlap between the sizes and years (1984-1988) for the three species in each of three depth zones. Schoener's index (C_{xy}) was expressed as

$$C_{xy} = (1 - 0.5 \sum_{j=1}^n |P_{xj} - P_{yj}|) \times 100,$$

where

C_{xy} = percentage of dietary overlap for predators x and y ,

n = number of prey categories,

P_{xj} = proportion by weight of prey j in the diet of predator x ,
and

P_{yj} = proportion by weight of prey j in the diet of predator y .

Schoener's index has a range of values from zero, representing no dietary similarity, to 100, representing complete dietary similarity where all prey were found in equal proportions in each predator.

Canonical correspondence analysis using Canoco (ter Braak 1987-1992), a FORTRAN computer program for canonical community ordination, was performed for stomach samples that contained food. For our analysis, samples were grouped across all years (May-September, 1984-1991) by sampling station for each species size group. Canonical correspondence analysis is used to explain relationships between species distribution and environmental parameters. The eight prey groups were entered as the prey species; predator size group (size 1, size 2, size 3) and strata were entered as nominal

environmental variables. Samples from the deepest strata were not included in the analysis due to inadequate sample sizes.

Results

The primary prey of Alaska plaice were polychaetes and marine worms (86% of the total diet) by weight (Fig. 2). Polychaetes and marine worms accounted for more than 60% of the rock sole diet; fish prey were also prevalent (>16%). Yellowfin sole exhibited the broadest diet of the three; no single category of prey accounted for more than 25% of their diet. Yellowfin sole fed primarily on polychaetes and marine worms, and clams. The diets of all three fish were much more similar by frequency of occurrence (Fig. 2). Gammarids, polychaetes and marine worms occurred more frequently in the diets of rock sole and Alaska plaice than in yellowfin sole. Frequencies for other prey categories were relatively similar in all three species.

The diet of Alaska plaice did not change appreciably by percent weight over the three depth zones; polychaetes and marine worms were the most prevalent prey (Fig. 3) always accounting for at least 80% of the diet of Alaska plaice. Rock sole consumed the same basic prey at the two deeper zones (polychaetes and marine worms). Fish prey, primarily Pacific sand lance (*Ammodytes hexapterus*), replaced marine worms as the second most dominant prey by weight in the diet of rock sole in the < 50 m depth zone. The diet composition of yellowfin sole collected in the two shallower depth zones (< 50 m and 50-100 m) were very similar; only slight fluctuations in clam consumption were seen. In the deepest zone, the diet of yellowfin sole consisted primarily of polychaete and echinoderm prey. Echinoderms were not important in the diet of either rock sole or Alaska plaice. All three species relied almost exclusively on only two prey categories in the 100-200 m depth zone.

Ontogenetic shifts were seen in the diets of all three predators by percent weight (Fig. 4). With increasing size yellowfin sole consumed more marine worms, echinoderms, fish and clams, while polychaetes and gammarids were less important. Smaller rock sole consumed more gammarids and fewer polychaetes and fish than the larger fish. Smaller Alaska plaice consumed more clams and gammarids and fewer polychaetes by weight than the larger fish.

The area of greatest diet similarity between species and size groups based upon Schoener's index was in the shallowest depth zone (Fig. 5). All species/size pairs exhibited at least 30% diet similarity;

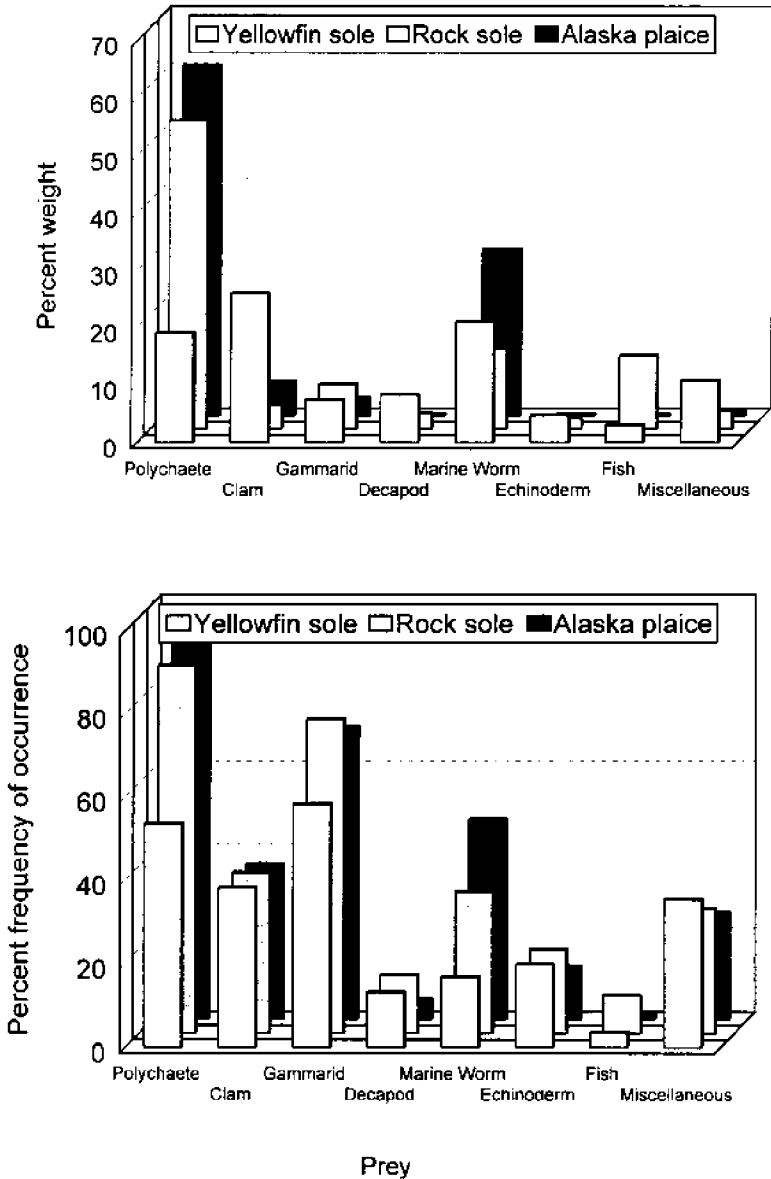


Figure 2. Diet of yellowfin sole, rock sole, and Alaska plaice in the eastern Bering Sea, 1984-1988, by percent weight and percent frequency of occurrence.

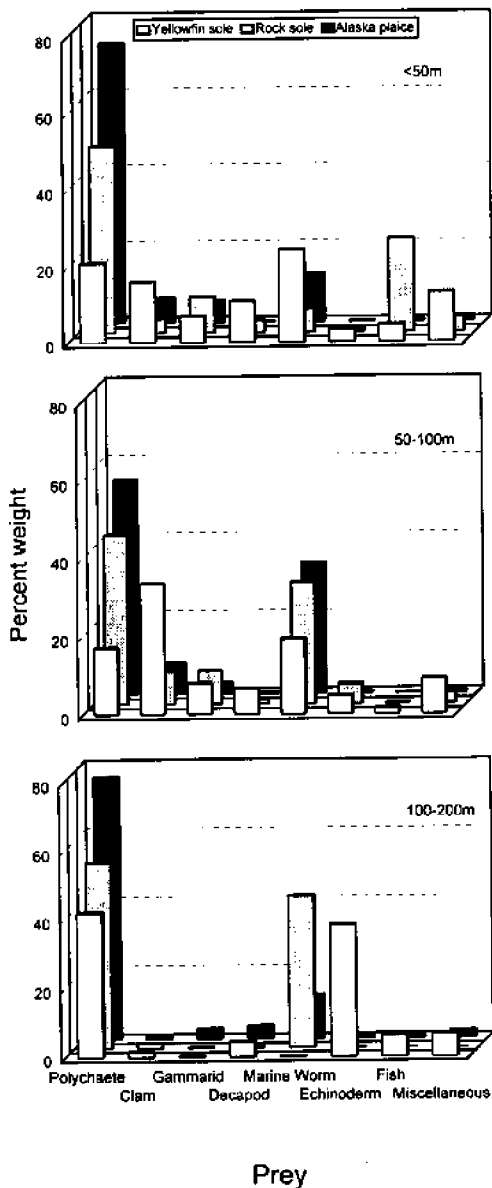


Figure 3. Diet of yellowfin sole, rock sole, and Alaska plaice in the eastern Bering Sea, 1984-1988, by percent weight by depth zone.

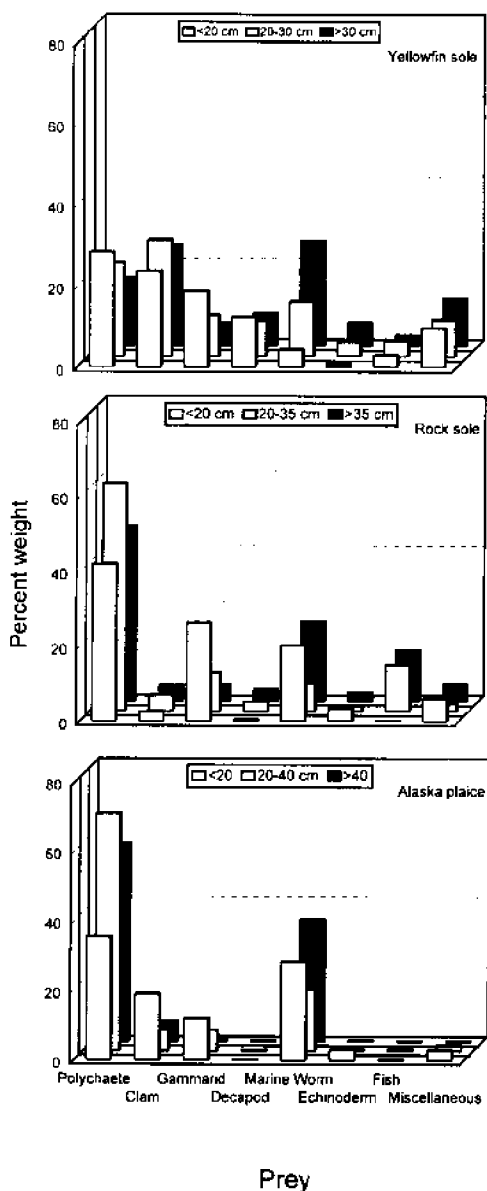


Figure 4. Diet of yellowfin sole, rock sole, and Alaska plaice in the eastern Bering Sea, 1984-1988, by percent weight and predator size group.

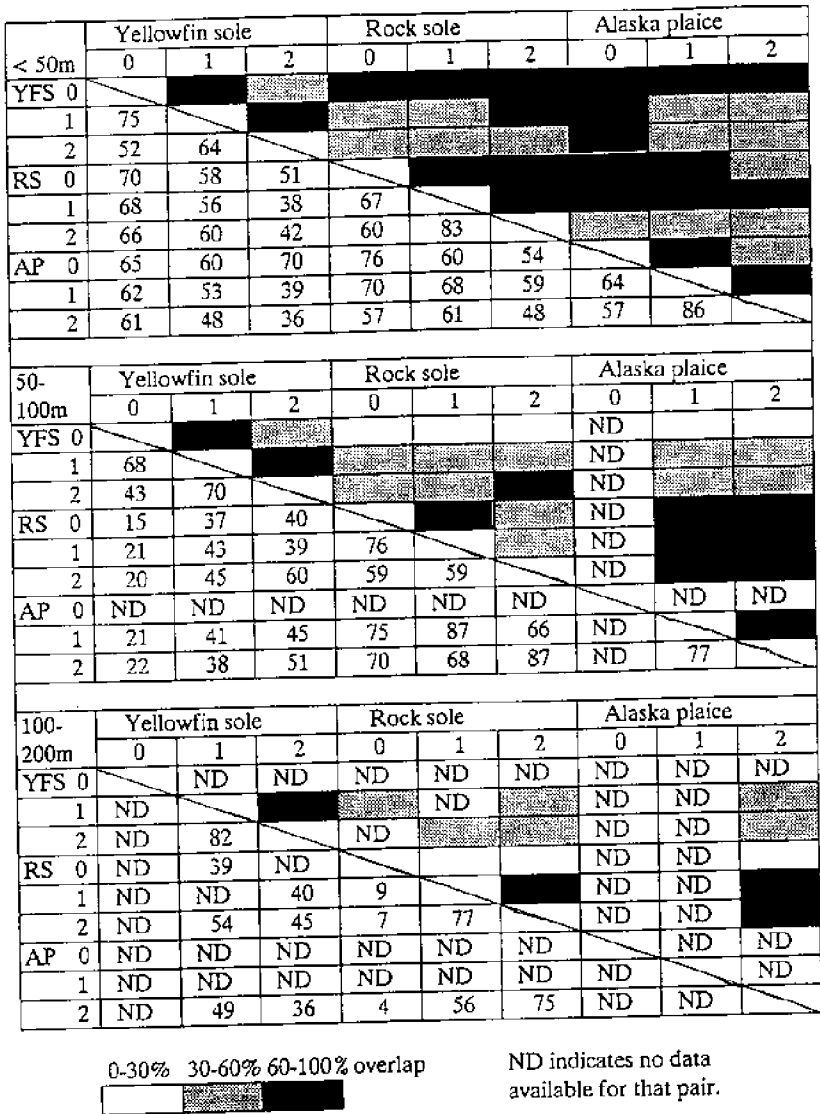


Figure 5. Schoener's index of dietary overlap of yellowfin sole (YFS), rock sole (RS), and Alaska plaice (AKP) in the eastern Bering Sea, 1984-1988, May-September. 0, 1, and 2 indicate predator size category.

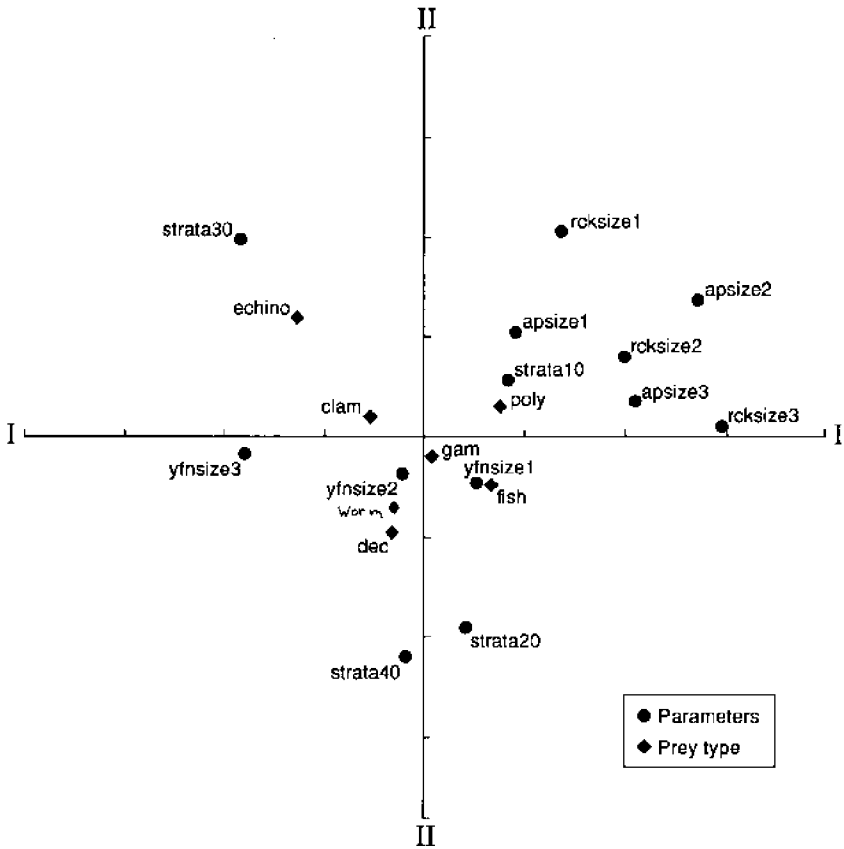


Figure 6. Canonical correspondence analysis species-environment biplot of yellowfin sole, rock sole, and Alaska plaice diet data from the eastern Bering Sea, 1984-1988, by predator size group and strata.

Poly = polychaetes, clam = bivalves, gam = gammarid amphipod, dec = decapod, worm = marine worm, echino = echinoderm, fish = teleost fish.

greatest overlap was seen in the smaller sized fish. At the intermediate depth, most species/size pairs had at least 30% diet similarity; highest similarity was seen in the larger fish. Too few samples were collected from the deepest zone to allow a thorough comparison; most species/size pairs that were sampled did show at least 30% diet similarity.

The first ordination axis of the CCA biplot separates the three predators (Fig. 6); yellowfin sole is found to the left, rock sole and Alaska plaice to the right. The second axis represents the northwest (strata 20 and 40) Bering Sea toward the bottom of the diagram and the southeast (strata 10 and 30) Bering Sea toward the top of the diagram. Polychaetes and clams were more closely associated with the first axis and, marine worms, decapods, and gammarids were associated with the second. Echinoderms and fish were not strongly associated with either axis. Eigenvalues for the two axes were 0.126 and 0.093, respectively. The cumulative percentage variation of the species-environment relation explained by these axes was 36.5 and 63.2, respectively.

Discussion

Allen (1984) characterized yellowfin sole in the eastern Bering Sea as a benthopelagivore exhibiting a searcher/ambusher predatory behavior. The prey consumed by yellowfin sole in this study, although somewhat different and from a broader taxonomic range, support this classification of feeding strategy. Sessile benthic prey (clams, polychaetes), mobile benthic prey (crabs, fish), and more pelagic prey (shrimp, fish, and euphausiids and mysids that were lumped into the miscellaneous category) were common in the diet of yellowfin sole. Tokoranov (1990) described the diet of yellowfin sole from the southwestern Bering Sea as consisting primarily of polychaetes, clams, echinurids, decapods, and amphipods. Wakabayashi (1989) described the diet of yellowfin sole in the eastern Bering Sea as composed of bivalves, echinurids, polychaetes, and amphipods. The results of our study are consistent with these studies.

Rock sole exhibited a more benthic-oriented diet that consisted primarily of polychaetes and marine worms. Fish, primarily Pacific sand lance, were more important in the diet of rock sole than the other species. However their importance may not be as great as the percent weight figure indicates since large, soft-bodied, high calorie prey such as fish digest more slowly and remain in the stomach longer than do smaller prey with exoskeletons such as amphipods (Huebner and Langton 1982). Corcobado-Onate (1991) found that polychaetes,

amphipods, and echiurids were the primary prey of rock sole in the eastern Bering Sea based upon a limited spatial and temporal sampling scheme; fish were not found as a significant dietary component. Skalkin (1963) did find Pacific sand lance, occasionally in high numbers, in the diet of rock sole in the eastern Bering Sea; polychaetes and mollusks were found to be the primary prey. Allen (1984) characterized rock sole in the eastern Bering Sea as a searcher/stalker predator upon sedentary and infaunal prey, as was seen in the current study.

Pelagic prey were essentially nonexistent in the diet of Alaska plaice; polychaetes and marine worms dominated the diet. Skalkin (1963) found polychaetes, mollusks, and crustaceans to be of equal importance in the diet of Alaska plaice in the eastern Bering Sea. Zhang (1988) described polychaetes, sipunculans, and amphipods as the main prey; fish and other pelagic prey were shown to play a limited role in the diet of Alaska plaice. Allen (1984) characterized Alaska plaice as a stalking predator upon sedentary and infaunal prey, particularly infaunal polychaetes. While our study did not distinguish between infaunal and epibenthic or pelagic polychaetes, polychaetes were the primary prey of Alaska plaice. Our study, with polychaetes as the main prey of Alaska plaice, showed similar results as the earlier studies.

Ontogenetic shifts in the diets of fish are well documented (Schmitt and Holbrook 1984, Ross 1978, Keast 1985, Werner 1974, Grossman 1980). As a predator grows, a greater variety of prey become available due to larger mouths which allow larger prey to be consumed and greater mobility which allows more mobile prey species to be consumed. Therefore, it is not surprising to see a shift toward larger, more mobile prey as predator size increased. Gammarid amphipods are relatively small, benthic-oriented prey that were common in the diets of all of the smallest size groups of the three predators, but less important in the medium and large size groups. Marine worms (echiurids, sipunculans, and priapulids) are much larger in diameter when compared with a polychaete worm of similar length or weight; these prey were most common in the diets of the largest predators. The importance of polychaetes and marine worms showed opposite trends in the yellowfin sole diet by size, perhaps indicating a selective preference for marine worm prey and their inability to prey upon marine worms at smaller sizes.

The diets of yellowfin sole and rock sole became more restricted with increasing bottom depth while the diet of Alaska plaice did not

change due to its narrow diet of polychaetes. Polychaetes were the dominant prey item in the diets of each of the predators at the greatest depth zone. Echinoderms accounted for 35% of the diet of yellowfin sole in the 100-200 m depth interval. Skalkin (1963) reported that ophiuroids (Echinodermata) became the primary component of the diet of yellowfin sole in water depths greater than 75 m. Pacunski (1990) found that ophiuroids (Echinodermata) dominated the diet of flathead sole (*Hippoglossoides elassodon*) in deeper waters of the eastern Bering Sea. Ivanov (1964) reported that the most dominant brittle star (*Ophiura sarsi*) in the eastern Bering Sea was found most abundantly at two stations with water depths of 92 and 97 m, and that most echinoderms were found in the middle shelf (50-100 m) and northwest region based upon benthic samples. Our study did not look specifically at echinoderm species or the location where they were consumed; however, we did find increased consumption of echinoderms with depth for yellowfin sole. Pacific sand lance are found most commonly in water less than 50 m deep in the eastern Bering Sea (Allen and Smith 1988), the same depth zone at which most of the Pacific sand lance predation by rock sole occurred. Some species of clams, gammarids, and polychaetes had ubiquitous distributions throughout the eastern Bering Sea shelf (Stoker 1981). Therefore, it is likely that most of the changes in the diet with respect to depth are related to differences in prey assemblages.

Based upon similarity of the percent frequency of occurrence of the eight prey in the diet of each of these predators, it appears that they are exposed to the same basic prey assemblage in the eastern Bering Sea. Such similarity was not seen in the percent weight figures which suggests that they are utilizing the prey resources in a different manner, and that their diet is primarily one of choice rather than of opportunity. Alaska plaice and rock sole exhibited more specialized diets, yellowfin sole were more generalized. All three of these species have a feeding morphology that is well-suited for benthic predation (Table 3). Relatively few, small gill rakers allow sediment and other debris incidentally consumed with the prey to be easily expelled through the gill opening. Each of the predator's field of vision is well-suited for benthic prey, allowing them to see the substrate directly in front of their mouths. Yellowfin sole had the broadest field of vision, which likely allows them to see a wider range of prey at any given time. Rock sole and especially Alaska plaice have a slightly more specialized feeding morphology than yellowfin sole. Pharyngeal teeth, as seen in Alaska plaice, are adaptations that allow prey to be held and

Table 3. Selected morphological characteristics of yellowfin sole, rock sole, and Alaska plaice (from Allen 1984, Baxter 1990, Hart 1972, and Yang 1991).

	Yellowfin sole	Rock sole	Alaska plaice
Gape direction	Forward and upward	Downward, forward, dorsal	Straight forward
Gape	Widest of the three	Most extendable	Scarcely projects
Teeth	Blunt, conical, single row	Obtusely conical	2 rows, with pharyngeal teeth
Gill rakers	5-8 + 7-10 = 13-18	3-4 + 6-8 = 10-12	1-3 + 0-1 + 6-8 = 8-10
Field of vision	Broadest	Narrowest	Intermediate
Maximum size	45 cm	60 cm	61 cm
Pyloric caeca	3	2-8	3

extracted from the substrate more efficiently; two rows of teeth, primarily on the blind side, also likely aid in capturing prey such as polychaetes and marine worms. The functional morphology of the gape, extendibility (most pronounced in rock sole), and direction are likely adaptations to capture and extract relatively sessile infaunal prey as well. Yellowfin sole does not have dentition or gape adaptations that are aimed strictly at the benthos; they appear to be able to take prey from all directions well. Their generalized morphology relative to the other two species likely allows them to consume many prey types efficiently.

Dietary overlap was greatest between the smallest fish at the shallower depth zone. Smaller predators have a more limited array of prey available to them and therefore dietary overlap should be greatest in this size group. Polychaetes, gammarids, and marine worms were common to the diets of all three species, causing the high degree of overlap. Smaller fish were also more common in the shallower depth strata, which may also lead to increased dietary competition. The presence of echinoderm prey in the diet of yellowfin sole at greater depths accounted for the decreased dietary similarity at that depth despite the more restricted diets of all three species. The greatest similarity at all depths was seen between rock sole and Alaska

plaice due to their consumption of similar large percentages of polychaetes and marine worms. Had there been adequate samples of rock sole and Alaska plaice from the deeper depth zone, there would have likely been a high degree of overlap between all sizes there as well. The greatest diversity of benthic infauna, in terms of number of species, is in the middle shelf area (Haflinger 1981), the area where dietary overlap was low. Therefore, it appears these three species were being selective in their choice of prey when prey diversity was high.

Canonical correspondence analysis also showed that Alaska plaice and rock sole of each size group had very similar diets, and that the yellowfin sole diet was less similar. The relative proximity of both rock sole and Alaska plaice to polychaetes in the CCA biplot indicate that they were closely associated in these samples. The association of clams and miscellaneous prey with the left side of the first axis indicate that they were most common in the diet of larger yellowfin sole. The greatest separation of predators in the diagram was between the larger size groups of yellowfin sole versus those of Alaska plaice and rock sole, which is consistent with the results obtained using Schoener's Index. The relative proximity of echinoderms to strata 30 (i.e., 50-100 m depth zone, southeastern shelf) indicates that they were seen most commonly in this area. Lack of adequate sample sizes from the deeper strata prevented their inclusion in the analysis; however, had they been available, echinoderm prey would have likely been closely associated with them as well. Yellowfin sole was not closely associated with any one prey, which supports their classification as a generalist relative to the other two species. The northwest/southeast gradient of the second axis indicates that spatial distribution was a factor in determining which prey were consumed, and that prey distribution differed between areas.

Up until 1993, yellowfin sole is the most abundant flatfish in the eastern Bering Sea (NPFMC 1993). Their success is likely due in part to their generalist feeding behavior (no single prey > 25% by weight, miscellaneous prey 11.6% by weight). Alaska plaice had the most specialized diet (polychaetes and marine worms accounted for > 80% of the diet by weight), smallest biomass (NPFMC 1993), and most limited distribution of the three species. Rock sole and Alaska plaice had similar diets, but different habitat preferences and somewhat separate areas of highest abundance which may minimize competition. The areas of highest abundance for each of these fish has been historically somewhat separated on the eastern Bering Sea shelf; rock sole exhibited a preference for a more coarse substrate, as is found

along the northern edge of the Alaska Peninsula (Feder et al. 1976); this may influence their distribution. In recent years, however, the distribution and abundance of rock sole has increased to a point where there is substantial overlap with the distribution of yellowfin sole (Bakkala 1993). It is not clear at present what effect this may have upon the diets of yellowfin sole. Increased rock sole biomass may increase competition between rock sole and Alaska plaice due to their similar diets. Alaska plaice and yellowfin sole exhibit preferences for the softer substrate which is found throughout most of the eastern Bering Sea shelf (Feder et al. 1976); however, Alaska plaice were most commonly found in the colder middle shelf waters, whereas yellowfin sole were found in the warmer, inner shelf waters (Bakkala 1993). Differences in the distribution of Alaska plaice and yellowfin sole, and differences between the diets of rock sole and yellowfin sole, should minimize competition for food resources. Despite the strong reliance on polychaetes in the diets of rock sole and Alaska plaice, it is possible that they consumed different species of polychaetes. However, it is difficult to substantiate this observation as prey abundance and distribution data for polychaete species is incomplete and detailed identification of polychaetes was not done in this study. Tokoranov (1990) compared the diets of rock sole, yellowfin sole, and Alaska plaice in the southwestern Bering Sea and concluded that the level of dietary similarity between these three species depended upon the taxonomic level to which the prey were identified. Zhang (1988) also concluded that the level of dietary similarity between rock sole and Alaska plaice depended upon the level of prey identification. More detailed study of the benthic infaunal species composition, distribution, and abundance would help further define prey availability and usage patterns of small-mouthed flounders included in this study and of other infaunal predators such as crab and predatory starfish. Further studies in this area should focus on the effect increased rock sole abundance, and distribution has had on the diets, abundance and distribution of yellowfin sole and Alaska plaice.

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Feeding Habits of Red Flounder *Hippoglossoides dubius* in Funka Bay and Its Offshore Waters, Hokkaido, Japan

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Abstract

In Funka Bay and its offshore waters, the red flounder *Hippoglossoides dubius* predominates throughout the year in demersal fish communities. From May to July, the feeding intensity of the red flounder is high. In this period an apparent interspecific competition for food is not found because red flounder can feed on various organisms. In the active feeding area adult fish feed mainly on ribbon prickleback *Lumpenus saggita* (Pisces: stichaeidae), while the small crustaceans (mostly gammarids and cumaceans) are the dominant prey of young red flounder. Such a difference of diet between adult and young fish reduces the intraspecific competition for food.

Introduction

Red flounder *Hippoglossoides dubius* is mainly distributed in 200-500 m depths of the Sea of Japan and the North Pacific Ocean around Hokkaido, Japan. This species supports otter trawl and bottom gillnet fisheries. Funka Bay is a unique and superior fishing ground for red flounder in Japan because the bay is an inland sea less than 100 m in depth and the catch is 1,000-3,000 metric tons each year. Red flounder predominates through the year in demersal fish communities in Funka Bay and its offshore waters at a depth of less than 200 m (Yokoyama et al. 1989). During the spawning period (January-April),

adult red flounder segregate in the shallower area of the bay. Most of the red flounder have empty stomachs and low feeding intensities are observed. From May to July, the feeding intensity of adult red flounder increased. In this period young and adult red flounder migrated to the southern middle part of the bay, which is their feeding ground (Yokoyama et al. 1990, 1991).

Yokoyama et al. (1994) predicted that red flounder might seldom compete with other demersal fish for prey because the diet composition of red flounder reflected an abundance of megalobenthic organisms. In this study, the interspecific feeding relationships between adult and young red flounder and other dominant demersal fish were investigated. Distributions of megalobenthic organisms and small demersal fish, which were the major diet for adult and young red flounder, were previously reported (Yokoyama et al. 1994). Macrobenthic organisms in the stomach contents of red flounder were not described in previous studies (Shintani 1948, Yamamoto 1949, Hayase and Hamai 1974). It was found that they were important in the diets of young fish, hence their distribution is also related.

Materials and Methods

In Funka Bay and its offshore waters at a depth of less than 200 m, demersal fish and macrobenthos were collected in July 1985, and May and July 1986, on cruises of the R/V *Ushio Maru* of Hokkaido University (Fig. 1). These months corresponded to the active feeding period of red flounder (Yokoyama et al. 1991). Demersal fish were caught by a 24 m otter trawl net (codend of 12 mm mesh). Otter trawl nets were usually towed for 15 minutes at speeds of about 3 knots on the bottom. Sampled fish were frozen and carried to the laboratory. Fish were measured to the nearest 1 mm in total length. The stomachs were removed from the fish, fixed immediately in 10% formalin solution and preserved for later examination. The stomach contents of each fish were sorted into major taxa, identified to species whenever possible, and damp weights were determined to an accuracy of 1 mg. To make comparisons for each diet composition similarity (the Pianka's α index) was calculated (cf. Kimoto and Takeda 1989). Relationship of these similarities was expressed in a dendrogram using cluster analysis with a group average method based on α (cf. Tanaka et al. 1984). Because red flounder were numerous in the sampled fish, they were distinguished between adult and young fish with the total length being the standard of classification (Yokoyama et al. 1991).

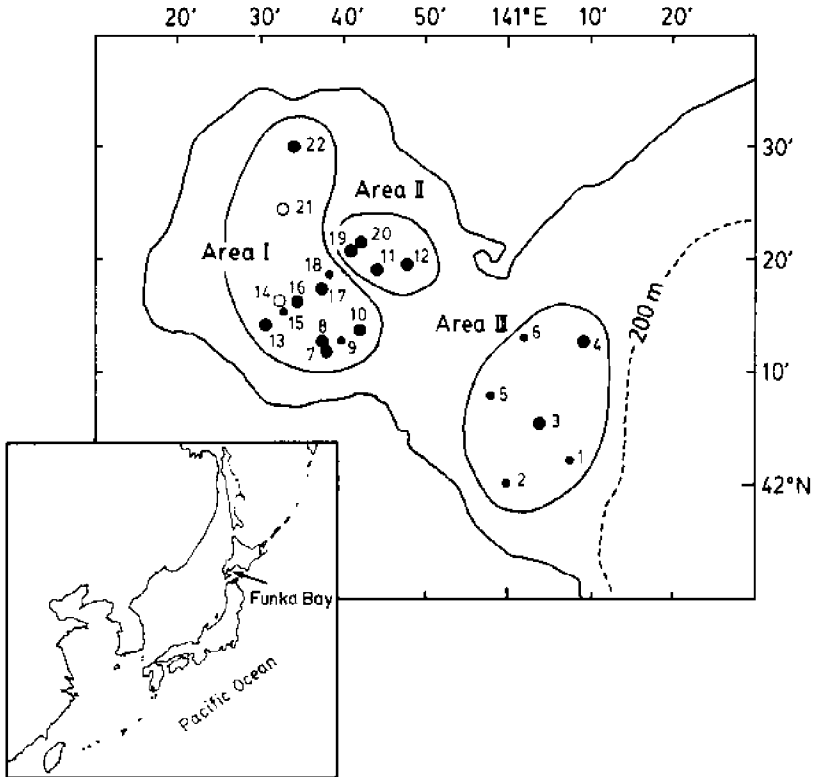


Figure 1. Map of the northwestern Pacific and Funka Bay showing sampling localities and their divisions based on Yokoyama et al. (1994). Circles and dots indicate otter trawl and grab stations.

Macrobenthic organisms were taken with a Smith-McIntyre grab (0.1m^2) at the median point of the tow lines after trawling (sampling times: three per point) in July 1985 and May 1986. Grab samples were washed onto a 1 mm aperture sieve screen and macrobenthic organisms were preserved in 10% formalin solution for later examination. In the laboratory each organism item was sorted and counted. To examine the vertical distribution of macrobenthic organisms in sediment, grab samples were collected at Stations 1 and 17 in May and July of 1986 (Fig. 1). The surplus water on sediment in a grab was gently exhausted with a tube. Then subsamples were scraped from the surface of a sampled sediment, and divided into three or four vertical

Table 1. Six leading species (in weight) in otter trawl catches in area I, II, and III shown in Fig. 1.

Rank	July 1985						May 1986			
	Area I		Area II		Area III		Area I		Area II	
	Species	%	Species	%	Species	%	Species	%	Species	%
1	Rfy	63.1	Kf	17.4	Wpy	36.5	Rfy	37.7	Wpy	83.8
2	Rfa	20.2	Rfa	13.8	Sr	19.1	Rfa	26.0	Pf	2.5
3	Sp	5.8	Sp	13.3	Rfy	16.1	Wpy	23.3	Ls	2.3
4	Ls	4.8	Rfy	13.2	Rfa	12.1	Ls	7.2	Sp	2.1
5	Kf	3.4	Ls	11.2	Kf	7.0	Sp	3.7	Rs	1.6
6	Sr	0.9	Es	7.3	Ss	1.8	Rp	3.7	Rfy	1.5

Rfy = young red flounder *Hippoglossoides dubius*, Rfa = adult red flounder, Sp = sailfish poacher *Podothecus sachi*, Ls = long shanny *Stichaeus grigorjewi*, Kf = korean flounder *Glyptocephalus stelleri*, Sr = sea raven *Hemirhamphus villosus*, Es = elkhorn sculpin *Alicichthys alcicornis*, Wpy = young walleye pollock *Theragra chalcogramma*, Ss = sakhalin sculpin *Triglops jordani*, Rp = ribbon prickleback *Lumpenus sagitta*, Pf = pointhead flounder *Hippoglossoides pinetorum*, and Rs = rainbow smelt *Osmerus mordax dentex*.

layers, that is, 0-5, 5-10, 10-15. The thickness of the lowest subsample differed with sediment type. The obtained subsamples were treated in the manner described above.

Yokoyama et al. (1994) defined that the megalobenthic organisms, such as Macrura, Ophiuroidea, and Mollusca, were collected by a sledge net with a codend of 3 mm mesh. Ophiuroidea and Mollusca, however, were collected by both a grab and a sledge net. In this paper they are not included as macrobenthic organisms because a grab could not obtain them better than a sledge net.

Results

Feeding relations among demersal fish

In Table 1 six leading species of demersal fish by weights are shown for each area that combined the stations following the demersal fish communities in July 1985 and May 1986 (Yokoyama et al. 1989). Only adult and young red flounder occurred within the 6 ranks in all areas, and in particular they occupied more than 60% in area I.

The weight composition of the stomach content of each fish in Table 1 (which had more than 5 stomachs examined except for the

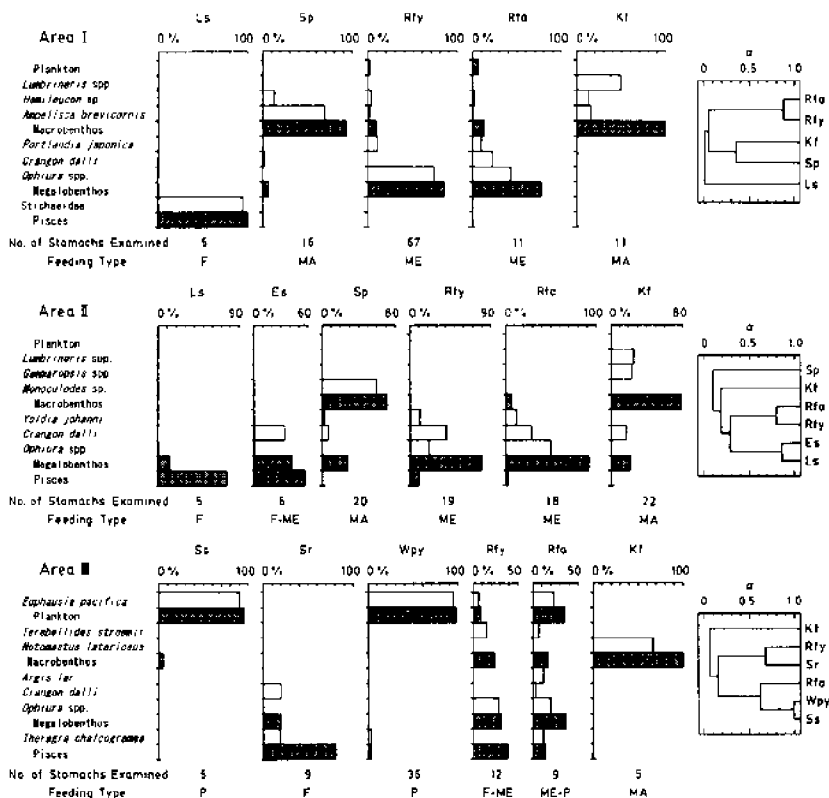


Figure 2. Weight compositions (%) and dendrograms showing similarity (α) of diets of dominant demersal fish in July 1985. Shaded rectangles show values combined with the same taxon. Acronyms of demersal fish are given in Table 1. (P = plankton feeder, MA = macrobenthos feeder, ME = megalobenthos feeder, and F = piscivorous).

empty stomachs) and their similarities are shown in Figs. 2 and 3. The feeding type was determined by the prey group occupying more than 70% of the stomach contents by weight (Kudo et al. 1969). If no prey group totaled 70%, the feeding type was determined by two dominating prey groups. The number of stomachs examined and the mean total length of the demersal fish in Table 1 are shown in Table 2.

In area I for July 1985 (Fig. 2), diet composition of long shanny *Stichaeus grigorjewi*, sailfish poacher *Podothecus sachi*, and Korean flounder *Glyptocephalus stelleri* had few similarities. The α value

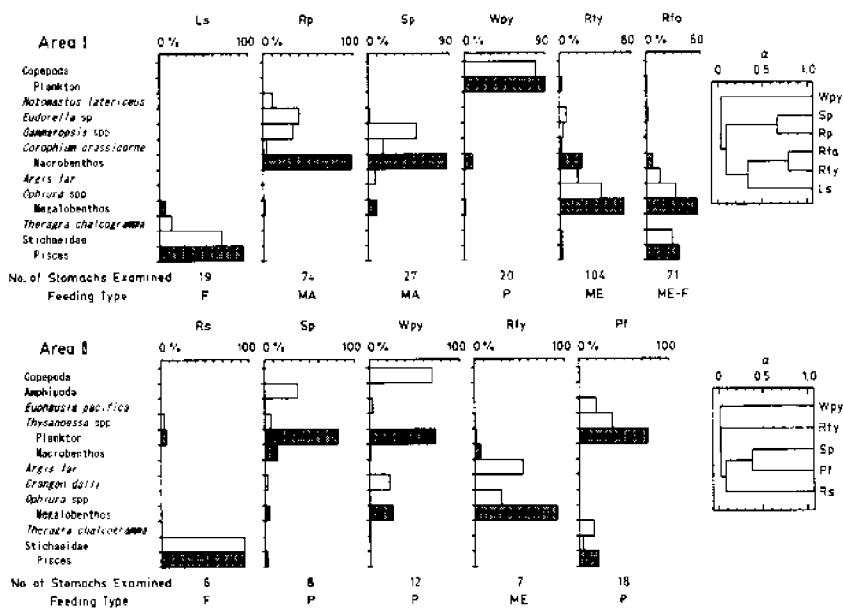


Figure 3. Weight compositions (%) and dendrograms showing similarity (α) of diets of dominant demersal fish in May 1986. Shaded rectangles show values combined with the same taxon. Abbreviations and acronyms are the same as in Fig. 2.

between sailfish poacher and Korean flounder of the macrobenthos feeder was low (0.35) because the former fed chiefly on the Gammaridea *Ampelisca brevicornis*, and the latter on the Polychaeta *Lumbrineris* spp. The dominant diet of adult and young red flounder was *Ophiura* spp., hence the α value among them was very high (0.87) and diet compositions of other demersal fish were not similar to them. In area II for July 1985 (Fig. 2), the α values between the piscivorous long shanny and elkhorn sculpin *Alicichthys alcicornis*, and the megalobenthos feeder adult and the young red flounder were high (0.86, 0.80). Diet composition of the sailfish poacher was not similar to that of the Korean flounder in the same as those in area I of July 1985. In area III for July 1985 (Fig. 2), diet compositions of adult and young red flounder had diversity in comparison with those in areas I and II, and a low value of α among them was found (0.15). The similarity between adult red flounder, which fed well on *Euphausia pacifica* (23.7%), and the plankton feeder sakhalin sculpin *Triglops jordani* and walleye pollock *Theragra chalcogramma* young was indicated (0.62).

Table 2. Mean and standard deviation of total length (mm) and stomach examined number of demersal fish in Table 1 (ND = no data).

Species	July 1985						May 1986			
	Area I		Area II		Area III		Area I		Area II	
	TL	N	TL	N	TL	N	TL	N	TL	N
Rainbow smelt	ND	0	ND	0	ND	0	ND	0	177±11.3	7
Walleye pollock young	ND	0	ND	0	174±26.4	36	138± 8.7	22	144± 5.9	12
Long shanny	383±41.1	8	387±61.3	7	ND	0	432±50.5	49	446±70.2	4
Ribbon prickleback	ND	0	ND	0	ND	0	313±59.1	74	ND	0
Sakhalin sculpin	ND	0	ND	0	139± 7.1	6	ND	0	ND	0
Sea raven	168±40.0	2	ND	0	189±50.4	12	ND	0	ND	0
Elkhorn sculpin	ND	0	228±71.7	7	ND	0	ND	0	ND	0
Sailfish poacher	271±34.1	17	283±58.9	21	ND	0	289±45.3	28	260±36.3	8
Red flounder adult	269±14.2	23	279±27.7	23	270±13.3	9	284±30.0	86	ND	0
Red flounder young	206±33.1	72	219±28.4	22	165±46.1	12	199±35.4	125	137± 8.4	8
Pointhead flounder	ND	0	ND	0	ND	0	ND	0	197±12.3	26
Korean flounder	241±31.2	12	226±26.2	24	267±37.4	5	ND	0	ND	0

As Pisces was important comparatively in the diets of young red flounder (37.3%), the α value between young red flounder and the piscivorous sea raven *Hemirhamphus villosus* was high (0.69).

In area I for May 1986 (Fig. 3), the dominant species in the diets of adult and young red flounder was the same, *Ophiura* spp., as those in area I for July 1985. The similarity between long shanny of the piscivorous and adult and young red flounder was slightly indicated (0.32), because adult red flounder consumed stichaeidae (mostly ribbon prickleback *Lumpenus sagitta*). Sailfish poacher mostly fed on Gammaridea *Gammaropsis* spp. and ribbon prickleback fed on Cumacea *Eudorella* sp. Common macrobenthic organisms also were eaten by both fish. The α value among them was high (0.66). In area II for May

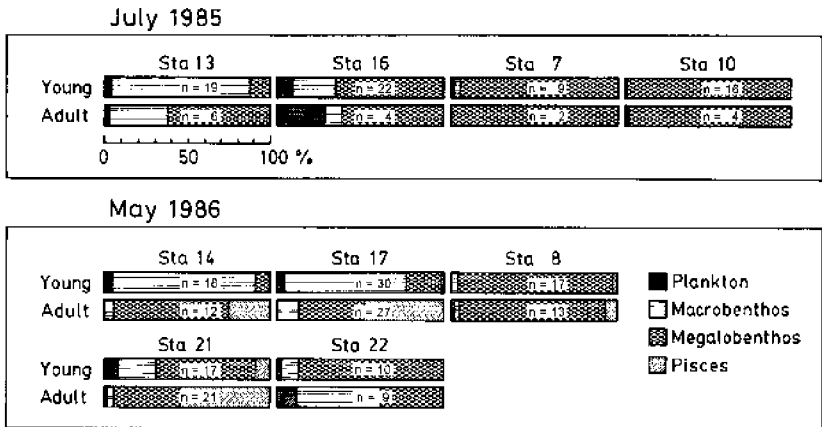


Figure 4. Diet compositions (%) of young and adult red flounder in each station of area I (n = number of stomachs examined).

1986 (Fig. 3), young red flounder preyed chiefly upon *Macrura Argis lar* and *Ophiura* spp. The diet composition for them was different from that of other demersal fish. The diet compositions of the plankton feeders, sailfish poacher, and pointhead flounder *Hippoglossoides pinetorum* resembled each other slightly (0.37).

In area I, where red flounder was concentrated, the diet composition of young and adult red flounder were compared by sampling stations (Fig. 4). There was no difference between diet composition of adult and young fish at Stations 7 and 10 (July 1985) and Station 8 (May 1986) near the bay mouth. At Stations 13 and 16 (July 1985) and Stations 14, 17, and 21 (May 1986) in the inner part of the bay the principal diets of the adult fish were different from those of the young fish. The former were plankton, megalobenthic organisms, and Pisces, and the latter were macrobenthic organisms, especially *Cumacea Eudorella* sp. Much of the diet of the adult fish at Station 22 in May 1986 was composed of macrobenthic organisms because part of them fed on large Sedentaria.

Distributions of macrobenthic organisms

The sampling efficiency of the Smith-McIntyre grab was examined in the muddy area of the inside bay and in the sandy area of the outside bay as ten successive collections per point (Fig. 1: Stations 1 and 17).

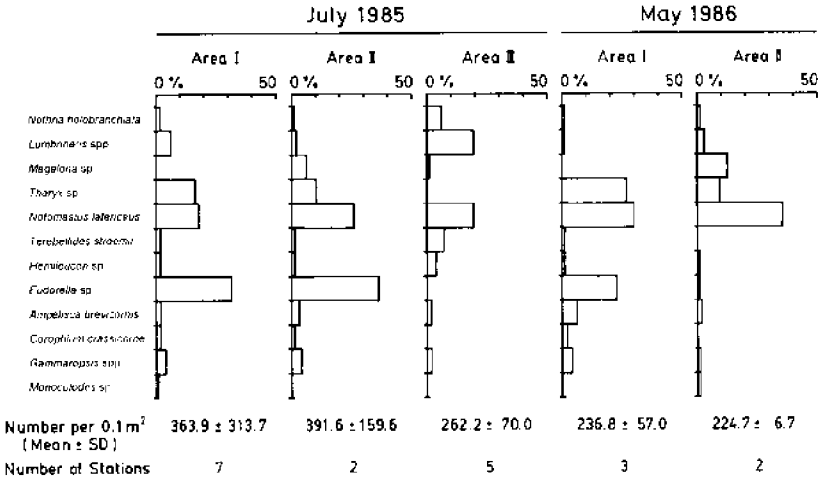


Figure 5. Occurrence of main macrobenthic organisms given as numerical abundance in each area, July 1985 and May 1986.

At both stations the number of individuals and species in the sum of the three collections was more than 80% of the total of all collections.

The frequency of occurrence of main macrobenthic species in each area for July 1985 and May 1986 is shown in Fig. 5. Cumacea *Eudorella* sp., Sedentaria *Tharyx* sp. and *Notomastus latericeus* predominated in area I for July 1985. In area II, besides these species, Sedentaria *Magelona* sp. also dominated. In area III the dominant species were Errantia such as *Nothria holobranchiata* and *Lumbrineris* spp. In area I for May 1986, species composition of macrobenthic organisms was almost similar to that in area I for July 1985. In area II for May 1986, however, Cumacea and Gammaridea had few occurrences in comparison with July 1985. It is assumed that small crustaceans, such as *Eudorella* sp., which was the predominant species in July 1985, decreased in May 1986 or they escaped due to the rolling of the ship while collecting macrobenthic organisms and shock waves when the grab reached the sea bottom.

In the muddy area (Station 17) and the sandy area (Station 1), the frequency of occurrence of macrobenthic organisms by 5 cm increment layers in the sediment is shown in Fig. 6. In the muddy area plenty of macrobenthic organisms were concentrated in the 0-5 cm layer. However, *Tharyx* sp. and *N. latericeus*, which were dominant in

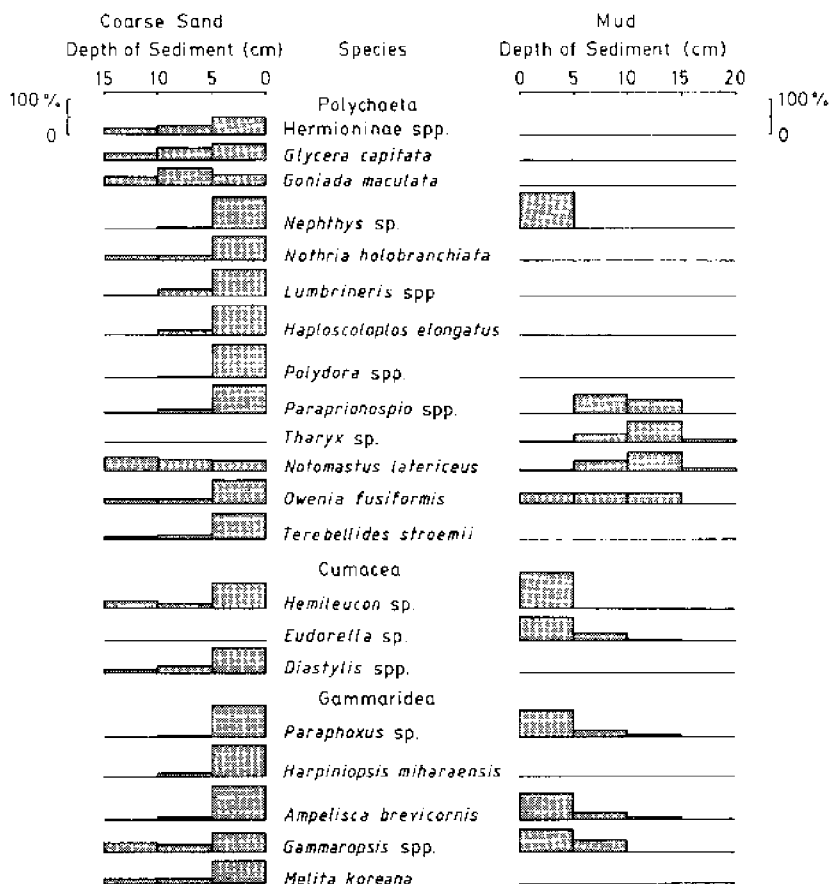


Figure 6. Occurrence of macrobenthic organisms in terms of numerical abundance at each sediment stratum of coarse sandy (Sta. 1) and muddy (Sta. 17) stations in May and July 1986.

this area, were distributed mostly in the 10-15 cm layer. The distribution of macrobenthic organisms in the sandy area was the same as that in the muddy area.

Discussion

In the study area the most important diet of adult and young red flounder was megalobenthos, followed by macrobenthos, plankton,

and Pisces (Figs. 2 and 3). This feeding habit coincided with that reported in previous studies from the Funka Bay (Shintani 1948, Hayase and Hamai 1974) and the southwestern part of the Sea of Japan (Yamamoto 1949). Diet composition of adult and young red flounder were seldom similar to that of other dominant demersal fish except those in area III for July 1985 (Figs. 2, 3). In area III for July 1985 the similarity index between adult red flounder and sakhalin sculpin (or young walleye pollock), and that between young red flounder and sea raven were slightly higher, while rates of common diets in the stomach contents of adult and young red flounder were low, 24% and 37% respectively (Fig. 2). These results suggest only a possibility of competition when the amount of important diet components of the red flounder is limited. The feeding relationships between red flounder and other dominant demersal fish were similar to those between yellowfin sole *Pleuronectes aspera* and other demersal fish in the eastern Bering Sea (Wakabayashi 1992). The feeding habit of yellowfin sole was the same polyphagous as the red flounder.

The available foods of red flounder are the abundant organisms among plankton, Bivalvia, Ophiuroidea, Macrura, and demersal and pelagic fish (Yokoyama et al. 1994). In addition, abundant macrobenthic organisms such as *Eudorella* sp. were also the main diet for young red flounder (Figs. 4, 5). *Tharyx* sp. and *N. laterieus*, which were the predominant species in areas I and II, were important diet components for the macrobenthos feeder, Korean flounder, and ribbon prickleback, whereas they were not available as food for young red flounder (Figs. 2, 3). It cannot be said that young red flounder were in competition with Korean flounder and ribbon prickleback for macrobenthic organisms, because ribbon prickleback were sometimes eaten by young red flounder (Fig. 3). *Tharyx* sp. and *N. laterieus* tended to gather into deeper layers in the sediment than other macrobenthic organisms (Fig. 6). Hayashi (1988) reported similar vertical distribution in the sediment for species of the same genera. Their vertical distribution is considered unsuitable for feeding of young red flounder.

The diet composition of adult red flounder differed conspicuously from that of young fish in the southern part of area I (Fig. 4). The feeding of adult red flounder was active in this area where they concentrated after spawning (Yokoyama et al. 1991). Their main diet was abundant, and consisted of large prey such as Macrura and Pisces. Spawning adult red flounder would require available foods for recovery. These facts suggest food segregation between adult and

young red flounder to avoid intraspecific competition. Young red flounder would chiefly feed on macrobenthic organisms to avoid competition with adult fish in spite of the fact that they could also feed on *Macrura* and *Pisces*.

Adult and young red flounder will seldom compete with other dominant demersal fish for prey because they can feed on various organisms such as pelagic, benthic, and planktonic organisms. The food segregation between adult and young fish in the active feeding area may be necessary to maintain the large stock in Funka Bay.

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Seasonal Change in Daily Ration of Brown Sole *Pleuronectes herzensteini* in the Coastal Waters of Northern Niigata Prefecture, Japan

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Abstract

Stomach contents of 2,407 brown sole *Pleuronectes herzensteini* collected from the Sea of Japan off northern Niigata Prefecture, Japan, during 1982-1985 were examined to estimate daily ration. Samples were collected throughout the 24-h day. Instantaneous evacuation rate (R) was estimated from the depletion of stomach contents (percent body weight) with time during the night for using Elliott and Persson's (1978) model. When the obvious feeding periodicity was not seen, R was estimated from the relationship between R and temperature (T) described by Durbin et al. (1983); $R = 0.043 e^{0.115T}$. Gastric evacuation rates were used in conjunction with the field data to estimate the daily ration. Brown sole fed mainly on polychaetes through the year except April 1984. *Bregmaceros japonicus* (Pisces; Bregmacerotidae) was an important component of the diet in April 1984. Daily ration was high during the post-spawning season and highest in May (4.75% of body weight). In autumn and winter, the daily ration was low and was

lowest in February/March, just before the spawning season (0.48% of body weight). The seasonal variation of the daily ration seems to be closely related to physiological conditions. It is estimated that the annual ration was about 831.5% of body weight and about 8,870 metric tons of food were consumed by brown sole per year in this study area.

Introduction

Brown sole *Pleuronectes herzensteini* is an important commercial flatfish and one of the target species of stock enhancement studies (Aritaki and Yoseda 1994) in the coastal waters of Niigata Prefecture which is located in the northern part of Honshu Island. Brown sole inhabit the continental shelf area throughout the year (Tominaga et al. 1991). Tominaga and Nashida (1991) showed that brown sole ranked second in terms of both relative abundance (number/haul) and relative biomass (kg/haul) in experimental bottom trawl catches in this area. These results suggest that brown sole is a key member of the demersal fish community on the continental shelf.

The study of interspecific relationships for food is important in order to understand the role of brown sole in the demersal fish community. Previous studies provided a general description of the diet (Tominaga and Nashida 1991) and seasonal changes in feeding intensity expressed as stomach content index (Tominaga et al. 1991). However, the amount of food consumption was not estimated in these papers.

For better understanding of the relationship between brown sole and other demersal fishes, quantitative determination of the food is required. The quantity of food consumed by fish is commonly estimated on a daily basis. The daily ration model of Elliott and Persson (1978), which assumes an exponential gastric evacuation, is widely accepted as the most theoretically rigorous (Cochran 1979; Eggers 1979; Elliott 1979). The objective of this paper is to evaluate seasonal change in the daily food consumption of brown sole in the northern coastal waters of Niigata Prefecture. In addition, we discuss the annual food consumption of the brown sole population in this study area.

Materials and Methods

Sample collection and stomach content analysis

Six cruises were carried out in the areas where brown sole were densely distributed from May 1982 to February/March 1985 (Fig. 1),

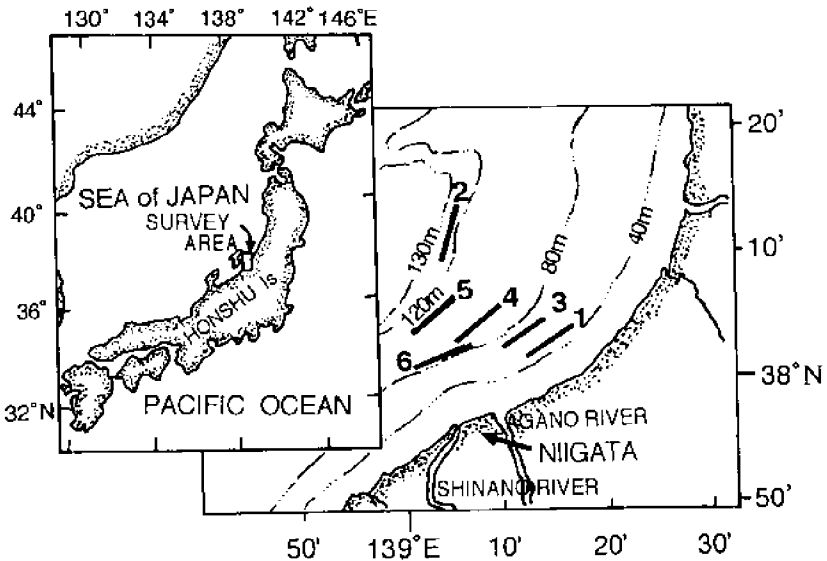


Figure 1. Map of the coastal waters of northern Niigata Prefecture showing locations of 24-hr. surveys in May 1982 (1), September 1983 (2), April 1984 (3), July 1984 (4), November 1984 (5), and February/March 1985 (6).

based on the results of the station surveys in this study area (Tominaga et al. 1991). Brown sole were caught by commercial fishing boats equipped with small otter trawls at 2-4 hour intervals over a 24-hr. period in each cruise (Table 1). Trawl nets were usually towed for an hour at speeds of about 3 knots on the bottom (Table 1). Fish were preserved in about 10% sea water formalin on board and carried to the laboratory.

Standard length of all captured brown sole were measured to the nearest millimeter and weights were taken to the nearest 0.1g. Stomachs were excised and preserved in 10% formalin for later analysis. The total stomach contents were weighed to the nearest milligram after blotting with filter paper and prey items were identified to the lowest possible taxonomic level and counted under the microscope. Wet weights of the prey items were recorded to the nearest milligram.

For diet analysis, percent frequency of occurrence (%F), percent of total number (%N), and percent of total weight (%W) of stomach contents were calculated for the entire data set for each cruise. Because of an insufficient number of specimens and similar diet

Table 1. Dates, time and number of *P. herzensteini* collected by whole-day and night surveys in the coastal waters of northern Niigata Prefecture from May 1982 to February 1985.

Date	Time of trawl tows		Number of individuals	Time interval of catches
	Start	Haul		
May 18 1982	06:04	07:02	01	2.00
May 18 1982	08:02	09:01	48	2.83
May 18 1982	10:55	11:44	49	3.17
May 18 1982	14:01	15:00	49	2.00
May 18 1982	16:02	17:00	50	1.83
May 18 1982	18:05	18:33	09	2.17
May 18 1982	20:07	21:02	31	4.00
May 19 1982	00:09	00:57	38	4.33
May 19 1982	04:23	05:11	44	1.67
May 19 1982	06:07	06:57	46	
Total			369	
Sep. 19 1983	04:02	05:02	57	1.92
Sep. 19 1983	05:59	06:50	59	1.92
Sep. 19 1983	08:03	08:42	52	2.00
Sep. 19 1983	09:59	10:42	55	2.00
Sep. 19 1983	12:03	12:45	54	2.00
Sep. 19 1983	13:59	14:43	59	4.00
Sep. 19 1983	17:59	18:43	99	2.00
Sep. 19 1983	20:00	20:41	60	2.00
Sep. 19 1983	22:00	22:42	60	2.00
Sep. 20 1983	00:00	00:43	59	2.00
Sep. 20 1983	02:00	02:43	60	
Total			674	
Apr. 7 1984	13:45	14:17	11	1.67
Apr. 7 1984	15:07	16:14	30	3.00
Apr. 7 1984	18:08	19:10	17	3.00
Apr. 7 1984	21:08	22:08	08	2.92
Apr. 8 1984	00:05	01:08	20	3.25
Apr. 8 1984	03:19	04:23	10	2.83
Apr. 8 1984	06:07	07:08	23	1.50
Total			119	

Table 1. (continued.)

Date	Time of trawl tows		Number of individuals	Time interval of catches
	Start	Haul		
Jul. 12 1984	04:05	05:05	19	2.93
Jul. 12 1984	07:00	08:03	17	3.13
Jul. 12 1984	10:08	11:11	14	2.93
Jul. 12 1984	13:05	14:05	09	1.95
Jul. 12 1984	15:12	15:52	28	2.07
Jul. 12 1984	17:06	18:07	06	2.42
Jul. 12 1984	19:30	20:33	37	2.53
Jul. 12 1984	22:01	23:06	59	3.25
Jul. 13 1984	01:05	02:22	51	2.73
Jul. 13 1984	04:01	05:04	41	
Total			281	
Nov. 29 1984	04:29	05:32	56	2.70
Nov. 29 1984	07:12	08:12	41	2.83
Nov. 29 1984	10:02	11:03	24	3.05
Nov. 29 1984	13:05	14:05	42	2.98
Nov. 29 1984	16:03	17:05	37	3.07
Nov. 29 1984	19:08	20:09	51	3.07
Nov. 29 1984	22:12	23:13	66	2.93
Nov. 30 1984	01:06	02:10	48	3.03
Nov. 30 1984	04:08	05:12	38	
Total			403	
Feb. 28 1985	04:06	05:07	81	3.03
Feb. 28 1985	07:03	08:05	79	2.95
Feb. 28 1985	10:10	10:52	94	2.87
Feb. 28 1985	13:03	13:43	31	3.07
Feb. 28 1985	16:06	16:48	38	3.02
Feb. 28 1985	19:07	19:48	59	3.07
Feb. 28 1985	22:10	22:54	60	2.90
Mar. 1 1985	01:02	01:50	60	3.25
Mar. 1 1985	04:17	05:05	62	
Total			564	

composition by fish size (Tominaga 1990), the data were not separated by predator size group for all analyses.

Daily ration

The daily ration of brown sole was estimated in terms of percent of body weight from the Elliott and Persson (1978) model:

$$C_t = (S_t - S_0 e^{-Rt}) Rt / (1 - Rt); \quad (1)$$

where the consumption of food (C_t) during the time interval t_0 to t_1 from the average food amount in the stomach expressed as stomach content index (stomach content weight \times 100/body weight) at time t_0 (S_0), the average stomach content index at time t_1 (S_t) and the instantaneous evacuation rate (R). The estimates of C_t calculated for each time interval are then summed to give the total daily ration. Feeding is assumed constant within each time interval.

In the laboratory experiments to examine the feeding periodicity, brown sole fed on live polychaeta during hours of light but didn't feed during hours of dark (Tominaga 1990). It suggests that brown sole are day feeders. Assuming no feeding between sunset and sunrise, R was estimated from the depletion of stomach content index during the nights (including empty stomachs). Evacuation rate is therefore given by

$$S_{sr} = S_{ss} e^{-Rt'} \quad (2)$$

which, in its logarithmic form, is

$$\ln(S_{sr}) = \ln(S_{ss}) - Rt' \quad (3)$$

therefore,

$$R = (1/t') \ln(S_{ss}/S_{sr}) \quad (4)$$

where the instantaneous evacuation rate (R) is calculated from the average SCI of the sample collected shortly before or after sunset t_{ss} (S_{ss}), the average SCI shortly before or after sunrise t_{sr} (S_{sr}) and the time interval between t_{ss} and t_{sr} (t').

The clear depletion of SCI during night was not found in September, November, and February/March. R of three cruises could not be calculated from equation (4). Fortunately, Elliott (1972) found the general relationship between R and temperature (T) was exponential:

$$R = ae^{bT}. \quad (5)$$

In addition, Durbin et al. (1983) concluded that the slope (b) may be fairly constant for different prey types and both freshwater and marine fishes within their preferred temperature range (mean = 0.115), while the intercept (a) changes with prey type and can be estimated from gastric evacuation experiments. In this study, intercept was obtained from the data of the July cruise because the diet composition of brown sole collected in September, November, and February/March were similar to that in July. Bottom temperatures in the survey area were based on Naganuma and Ichihashi (1985).

Results

The stomach contents data from the sample collected at each tow were combined by cruise. The brown sole ranged in length from 92 mm to 266 mm with the majority (about 87% of the total number of specimens) between 110 mm to 190 mm BL. Fish from the May cruise were the smallest on average (mean = 129.4 mm, 95% C.I. = 1.45) and fish from the November cruise were the largest (mean = 156.6mm, 95% C.I. = 3.03). A total of 2,407 stomachs were analyzed. Of these, 963 (40.0%) stomachs were empty. The percentage of empty stomachs of brown sole collected from September, November, and February/March cruise were higher than those collected from April, May and July.

At least 39 different prey taxa were identified in the stomachs examined. Polychaetes were the most important food prey item throughout the year. Euphausiids and *Bregmaceros japonicus* (Pisces: Bregmacerotidae) were temporarily dominant by number and by weight, respectively. Bivalves also were temporarily dominant numerically but considerably lower by weight.

Diet composition by season

Polychaetes were the most abundant taxa in all numeric indicators (%N, %W, %F) in July, September, November, and February/March (Table 2). Of all polychaetes, sigalionids were the most common important prey item (%N 1.8-17.5%, %W 39.4-69.0%, %F 26.4-37.2%). Sigalionids are big worms, so most of them found in the stomachs were the anterior part of body. Other important polychaetes were different by month. In July *Euchone* sp. was more abundant in terms of %N (80%) and %F (73.4%) than sigalionids. *Euchone* sp. was a small food organism (mostly 0.01 g/individual), and less by weight than sigalionids. *Nothria* sp. was the third-ranking taxon in terms of %W. In

Table 2. Prey item found in stomachs of *Pleuronectes herzensteini* collected in the northern coastal waters of Niigata Prefecture from May 1982 to February/March 1985. N% = percent by number, W% = percent by weight, F% = percent frequency of occurrence.

Prey item	February/March			April			May			July			September			November			
	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	
Polychaetes	78.6	90.0	92.3	39.6	10.7	77.2	80.7	42.7	83.1	91.5	93.7	93.7	51.5	97.8	69.1	79.9	72.2	93.9	
Euraetia total	39.3	72.9	64.4	5.2	7.5	53.5	8.2	19.6	41.1	8.4	57.1	73.8	19.5	76.9	49.5	26.3	58.1	48.6	
Aphroditidae	0.1	0.1	0.3	0.0	0.0	0.9	1.2	0.6	8.3	0.1	0.0	1.7	0.1	0.0	0.3				
Sigalionidae	17.5	56.8	37.2	0.6	3.5	14.0				1.8	39.4	30.9	9.8	69.0	29.6	13.2	48.9	26.4	
Euzatia sp.	1.5	4.4	3.7	0.0	0.0	0.9	0.5	0.5	3.5	0.1	0.0	1.7	0.6	0.1	2.3				
Syllidae							0.0	0.0	0.3				0.3	0.0	1.0	0.3		0.7	
Nereidae	0.3	0.1	0.6	0.0	0.1	0.0	0.0	0.0	0.3				0.1	0.0	0.3				
Nephtys sp.	9.7	0.1	19.5	1.5	0.0	24.6	1.0	0.2	9.3	1.4	0.3	25.3	3.4	0.1	11.4	0.9	0.0	2.0	
Glyceridae	0.3	0.0	0.6				0.5	0.1	3.5	0.0	0.6	1.3				1.3	0.0	2.7	
Gomelidae	5.3	5.4	14.2	0.1	0.4	3.5	0.8	0.1	6.1	0.6	4.2	11.8	1.5	0.7	7.5	1.6	0.2	3.4	
Eunicidae							0.0	0.0	0.3				1.1	5.7	3.9	0.9	0.8	2.0	
Nereis sp.	1.8	0.5	4.3	2.7	2.7	26.3	0.2	0.2	1.3	3.9	10.6	32.9	1.4	0.6	4.6	5.6	1.8	11.5	
Lumbrineridae	1.7	5.4	4.0	0.2	0.7	4.4	0.9	0.3	6.4	0.5	1.7	11.8	1.3	0.7	4.6	1.6	6.2	3.4	
Other Euraetia	0.1	0.0	0.3				2.9	17.7	20.1	0.0	0.3	1.3	0.1	0.0	0.3	0.9	0.2	2.0	
Sedentaria total	39.0	17.0	58.2	34.4	3.2	68.4	72.3	23.0	74.8	83.0	35.8	81.9	30.9	19.2	50.2	53.6	14.1	68.2	
Orbinidae	0.8	0.2	1.9	0.0	0.0	0.9	0.0	0.0	0.3	0.0	0.0	0.4				0.9	0.3	2.0	
Sponidae	10.2	0.2	22.6	0.3	0.0	4.4	2.4	0.1	11.5	0.2	0.0	4.2	3.8	0.1	11.1	2.5	0.1	4.7	
Megalona sp.							0.9	0.1	3.2										
Chironomidae	2.9	1.7	10.2	0.2	0.3	6.1				0.2	2.0	5.9	2.6	5.3	9.4	6.9	4.5	13.5	
Frabelligeridae	0.1	0.2	0.3	0.0	0.0	0.9	0.1	0.0	0.6	0.0	0.1	0.8	0.3	0.9	1.0	0.9	0.2	2.0	
Scalibregmidae				0.0	0.0	0.9	0.1	0.0	0.6							0.6	0.3	1.4	
Ophelidae	0.8	0.1	1.9				6.9	3.8	25.2	0.3	0.1	5.9	12.3	0.7	16.9	3.4	0.3	7.4	
Caprellidae	0.3	0.0	0.6				25.0	5.3	48.6	0.1	0.1	1.7	1.4	0.1	4.6	2.2	0.0	4.7	
Arenicolidae	0.4	0.1	0.9				0.0	0.3	0.3			0.2	0.3	0.7					
Maldanidae	4.3	0.2	10.5	0.3	0.1	7.9	1.4	0.3	10.2	0.6	0.3	14.8	5.5	7.6	16.9	6.0	4.9	12.8	

Table 2. (continued.)

Prey item	February/March			April			May			July			September			November		
	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%
Sedentaria (continued)																		
Pectinariidae																		
<i>Sternosys scutata</i>	2.4	0.1	4.3	0.0	2.6	1.6	0.2	0.1	1.6	0.2	0.1	4.6	0.2	0.1	4.9	0.3	0.0	0.7
Ampharetidae	1.7	0.1	3.7	0.1	8.8	23.6	9.8	1.1	23.6	1.0	1.6	16.9	1.9	0.2	4.9	20.7	1.7	24.3
Terebellidae	5.5	13.1	14.2	0.1	2.6	12.5	2.3	9.0	12.5	0.5	2.2	10.1	0.5	0.1	4.6	2.8	1.0	6.1
<i>Euchone</i> sp.	7.5	0.8	15.8	32.7	68.4	17.9	4.7	0.2	17.9	80.0	29.1	73.4	1.5	0.1	4.6	5.6	0.6	10.8
Unidentified polychaetes	0.4	0.1	0.9				0.2	0.1	1.6	0.1	0.9	2.1	1.0	1.7	3.6			
Crustacea																		
Gammaridea	9.2	2.2	16.7	50.0	78.1	22.7	4.1	2.8	22.7	6.7	1.7	54.4	17.5	0.8	25.7	6.9	0.4	12.2
Mysids	0.1		0.3	0.7	12.3	15.7	2.8	0.1	15.7	5.1	0.9	40.1	5.3	0.1	10.1	1.9	0.0	2.7
Mactra	1.4	1.9	3.4	0.2	5.3	5.8	0.8	2.5	5.8	0.0	0.3	0.4	0.5	0.0	2.0	0.6	0.0	1.4
Brachyura	1.7	0.2	3.4	0.3	5.3	1.0	0.1	0.1	1.0	0.4	0.5	9.7	0.6	0.1	2.3	1.6	0.2	3.4
Cumacea	0.4	0.0	0.9	0.1	0.9					1.2	0.2	21.9	8.7	0.2	10.1	1.9	0.0	4.1
<i>Euphausia pacifica</i>				48.6	72.8													
Other crustacea	0.1	0.0	0.3	0.1	2.6		0.3	0.1	1.9				0.1	0.0	0.3	0.6	0.0	1.4
Sipunculoidea																		
Mollusca	4.9	3.2	11.5	0.4	8.8	21.7	4.1	2.5	21.7	1.2	1.5	6.8	31.9	0.6	27.7	2.2	0.1	4.1
Bivalvia	1.3	0.3	3.1				0.4	0.1	1.6	0.9	0.1	3.0	31.2	0.6	26.1	1.9	0.0	3.4
Anaspidea	3.2	0.7	7.7	0.4	8.8	20.4	3.7	2.4	20.4	0.1	1.4	3.8				0.3	0.0	0.7
Other Mollusca	0.4	2.2	0.9							0.2	0.0	0.4	0.7	0.0	1.6			
Actinaria																		
Ophiuroidea	3.3	0.3	8.0	0.2	4.4	3.5	0.5	0.2	3.5	0.2	0.2	3.8	6.0	0.5	21.2	5.3	0.1	11.5

Table 2. (continued.) Prey item found in stomachs of *Pleuronectes herzensteini* collected in the northern coastal waters of Niigata Prefecture from May 1982 to February/March 1985. N% = percent by number, W% = percent by weight, F% = percent frequency of occurrence.

Prey item	February/March			April			May			July			September			November			
	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	N%	W%	F%	
<i>Telenostis</i>																			
<i>Bregmaceros japonicus</i>	0.6	2.2	1.5	8.8	61.0	75.4	0.5	2.9	3.5				0.1	0.5	0.3				
<i>Sardinops melanostictus</i>	0.1	0.3	0.3				4.2	47.2	30.4										
Other Pisces	0.5	1.3	1.2							0.0	0.0	0.4							
Other food organisms	2.4	0.1	1.9	1.0	0.1	7.9	3.8	4.3	21.1	0.2	2.8	5.5	1.2	2.4	3.6	5.6	27.2	12.2	
Total	782	101	323	2919	184	114	2242	94.5	314	6100	91.8	237	1100	86.9	307	319	73.5	148	
Total stomachs with food																			
No. of empties			241			5			55			44			367			255	
Percent of empties			42.7			4.2			14.9			15.7			51.5			63.3	

September sigalionids alone comprised 69% by weight of the prey in the stomach. Ophelids accounted for 12.3% of all individuals in the stomachs examined, but only 0.7% by weight. Eunicids, cirratulids, and maldanids were relatively abundant by weight. Bivalves indicated 31.9% and 27.7% in terms of %N and %E, respectively, but comprised only 0.6% of total weight. In November ampharetids were present in 24.3% of the stomachs and the percentage of unidentified food organisms was extraordinarily high by weight (27.2%). In February/March terebellids occupied a relatively large portion by weight (13.1%).

In April, frequency of occurrence of polychaetes was 77.2% but they contributed only 10.7% by weight (Table 2). *Bregmaceros japonicus* was the most abundant species by weight (61.0%), followed by *Euphausia pacifica* (27.6%). Frequency of occurrence of *B. japonicus* and *E. pacifica* were 75.4% and 72.8%, respectively. Since *B. japonicus* was collected by a standard-type Smith-McIntyre grab in our benthos research survey, it seems reasonable to suppose that they occur in or on the bottom sediment like a polychaete annelid. *E. pacifica* was also an important species and occurred in the stomachs only in April. A diurnal vertical migration of *E. pacifica* was reported by Terazaki (1981) and Ebisawa (1994). Ebisawa (1994) collected *E. pacifica* 60 cm above the bottom by sledge net during daytime. Thus, epibenthic animals were also available food organisms for brown sole.

In May polychaetes were the dominant prey taxa by percentage of total number (80.7%) and frequency of occurrence (83.1%). However, they were the second-ranking taxa by weight (42.7%). Sardine, *Sardinops melanostictus*, was the highest percentage by weight (47.2%). Sardine in the stomach was identified by the shape of the pyloric appendage. Brown sole did not feed on the whole body of the sardine but a part of the body, especially the gut. In 1981 and 1982, a large number of dead sardine were observed in the study area. If this had not occurred, polychaetes might have been the dominant prey taxa by weight.

Estimate of instantaneous evacuation rate (*R*)

The average SCIs of brown sole collected in April, May, and July were high during daytime (Fig. 2). They had a tendency to decline during the night, while the percentage of empty stomachs gradually increased after sunset (Fig. 3). The average SCI of the samples taken on the February/March, September, and November cruises were constantly low throughout the whole day and clear depletions of SCI were

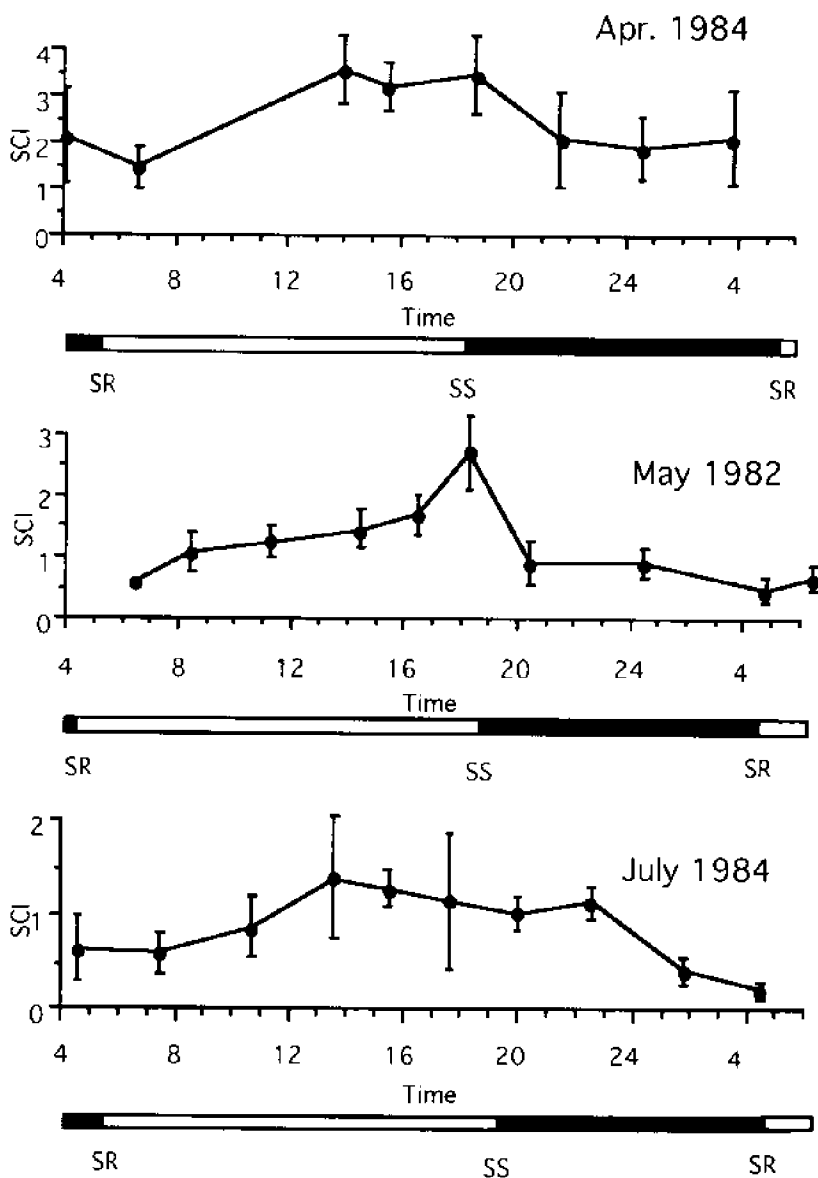


Figure 2. Diel changes in average stomach content index (SCI) of *P. herzensteini* in April 1984, May 1982, and July 1984. Vertical lines indicate 95% confidence interval. SR: sunrise. SS: sunset

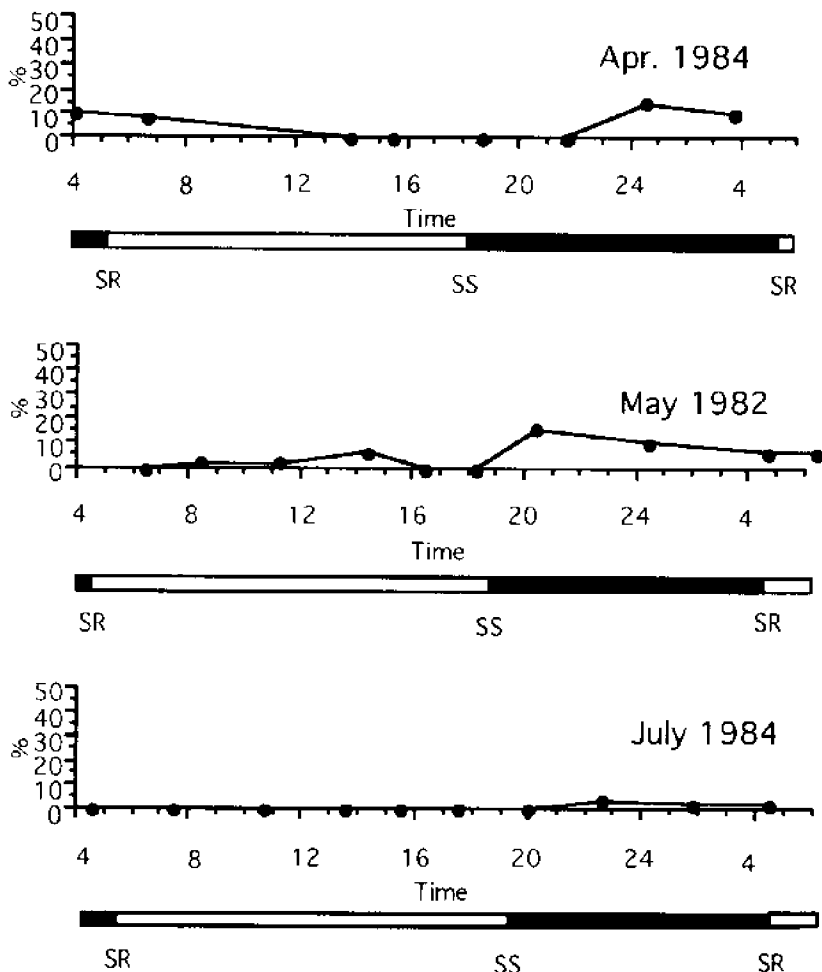


Figure 3. Diel changes in the percentage of empty stomachs of *P. herzensteini* in April 1984, May 1982, and July 1984. SR: sunrise, SS: sunset

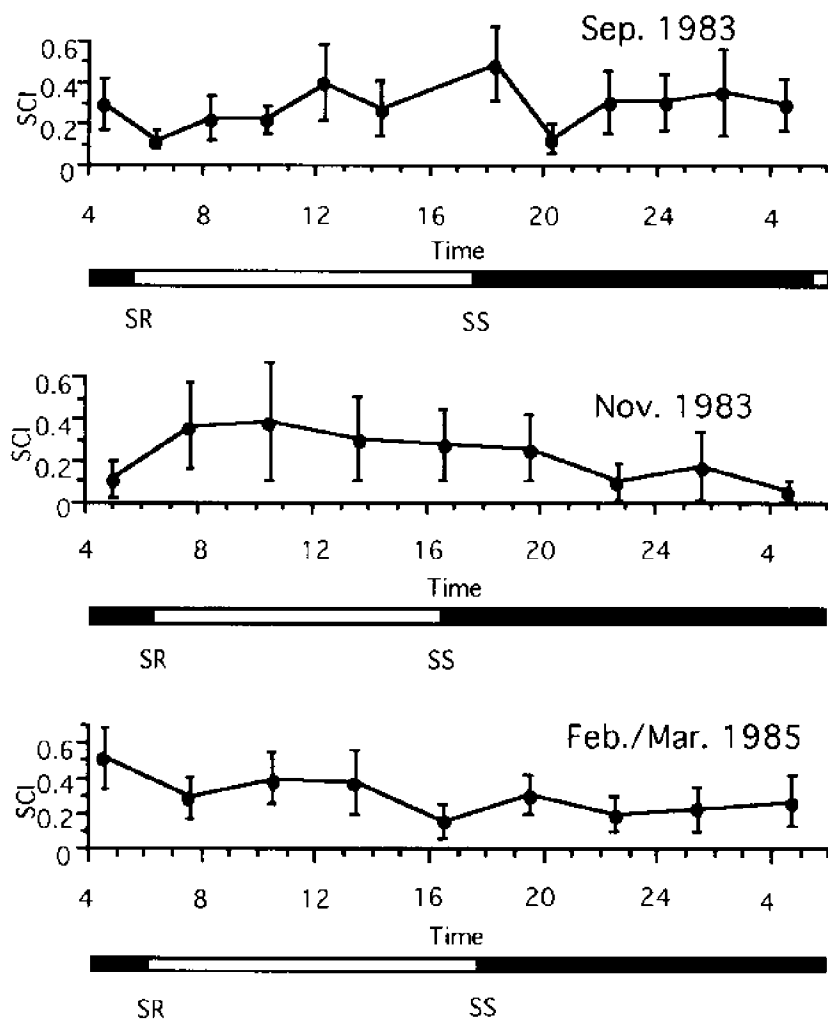


Figure 4. Diel changes in average stomach content index (SCI) of *P. herzensteini* in September 1983, November 1984, and February/March 1985. Vertical lines indicate 95% confidence interval. SR: sunrise, SS: sunset

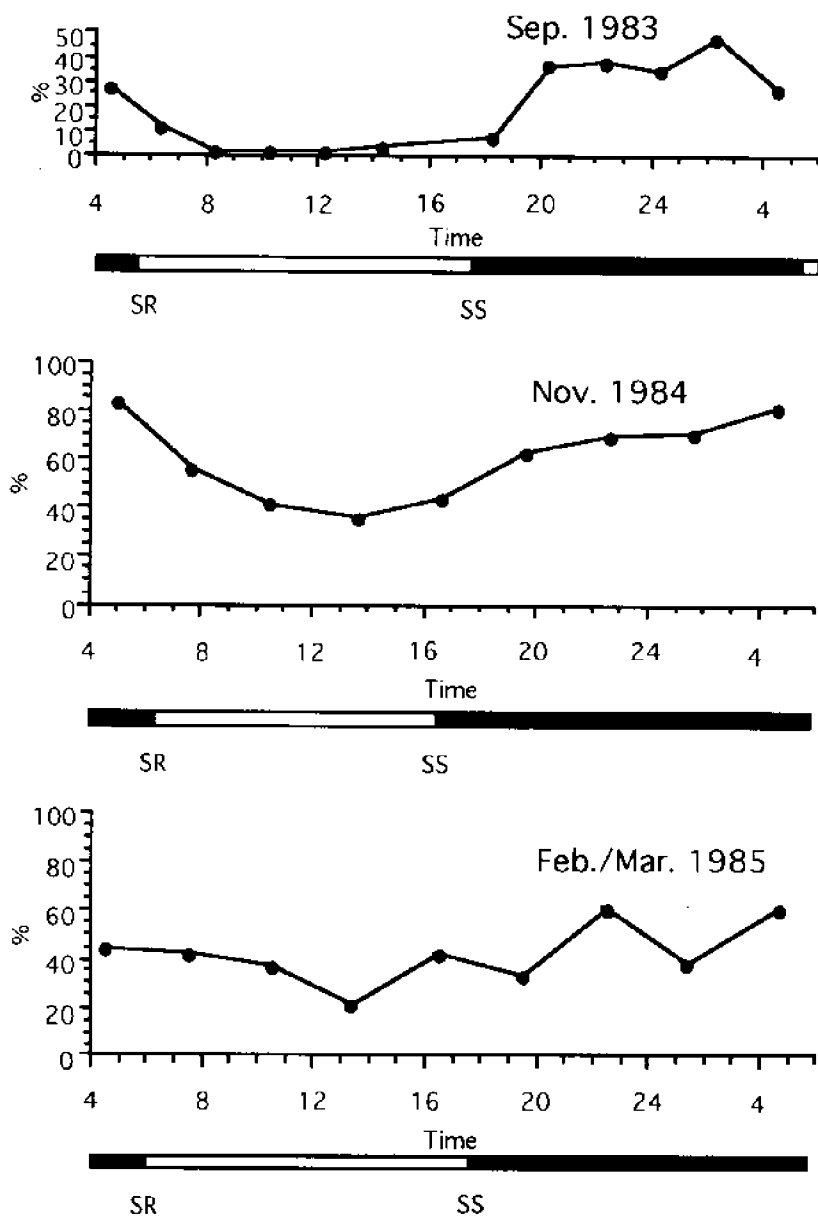


Figure 5. Diel changes in the percentage of empty stomachs of *P. herzensteini* in September 1983, November 1984, and February/March 1985. SR: sunrise, SS: sunset

Table 3. Instantaneous evacuation rate (R), stomach content index at shortly before or after sunset (S_{ss}), one at shortly before or after sunrise (S_{sf}) and time intervals between the two tows in April 1984, May 1982, and July 1984.

Month	R	S_{ss}	S_{sf}	T
April	0.073	3.49	1.45	12.0
May	0.166	2.73	0.48	10.5
July	0.192	1.04	0.22	8.5

Table 4. Instantaneous evacuation rate (R) calculated by $R = 0.043 e^{0.115T}$, and water temperature (T) of September 1984, November 1984, and February/March 1985.

Month	R	T
September	0.242	15
November	0.242	15
February/March	0.108	08

not seen during the night (Fig. 4), although the percentage of empty stomachs gradually increased during the night (Fig. 5).

Instantaneous evacuation rate (R) for the samples of April, May, and July (Table 3) was estimated by using equation (4). The evacuation rate estimate of July was the highest (0.192), followed by May (0.166) and April (0.073). R for the remaining three months (Table 4) was calculated by equation (5). In the equation, slope (b) was approximated by 0.115 (Durbin et al. 1983). As the diet composition of brown sole collected in September, November, and February/March were similar to that in July, intercept ($a = 0.043$) was calculated with R (0.192) and bottom temperatures (13°C) in the survey area (Naganuma and Ichihashi 1985) of July. The R -temperature (T) relationship was described as follows:

$$R = 0.043 e^{0.115T} \quad (6)$$

Instantaneous evacuation rates of September, November, and February/March calculated by substituting the bottom temperature at

each month into T in equation (6) were 0.242 ($T = 15^{\circ}\text{C}$), 0.242 ($T = 15^{\circ}\text{C}$), and 0.108 ($T = 8^{\circ}\text{C}$), respectively.

Daily ration

The average stomach content index, which included fish with empty stomachs, was used to estimate the average food consumption for each time interval (C_i) during the day with equation (1). The estimates of food consumption per unit time (hour) were sometimes negative as well as positive (Table 5). Daily rations were obtained by summing the amount of food consumption during each interval, including negative values.

In April, May, and July, food consumption per unit time was comparably high during daytime and fluctuated considerably with some negative values (Table 5). In the other three months, food consumption per unit time was low throughout 24 hours and clear feeding periodicity was not seen.

The daily ration began to increase in April (4.43% BW), and reached peak in May (4.75% BW) (Fig. 6). It was relatively high until July and then gradually decreased. The minimum value (0.48% BW) of the daily ration was found in February/March, at the mid-spawning season. The annual ration of brown sole obtained from the area surrounded by yearly change in daily ration in Fig. 6 was 831.5% BW.

Discussion

In the present study, the Elliott and Persson (1978) model was used to determine the daily food consumption of brown sole. This model requires two assumptions: (1) the rate of food consumption is constant within the time interval between samplings, and (2) the rate of gastric evacuation (R) is exponential.

Elliott and Persson (1978) showed that even if feeding is not constant, the first assumption is satisfied by collecting samples at intervals within 3 hours. In this study, although the sampling interval was sometimes over 3 hours, this assumption was almost satisfied.

By assuming that the stomach content index exponentially decreased during nighttime, R was obtained in this study. In the previous studies, some models assumed a linear gastric evacuation (Bajkov 1935; Hunt 1960; Seaburg and Moyle 1964; Kitchell and Windell 1968; Swenson and Smith 1973; Daan 1973; Brodeur 1984), others use a square root (Jobling 1981; Brodeur 1984; Tomiyama et al. 1985), or exponential model (Aoyama 1957; Mochizuki and Ishiwata

Table 5. Estimated average amount (C_t) of food ingested and that per hour during time intervals (t) of catch in April 1984, May 1982, July 1984, September 1983, November 1984, and February/March 1985.

Time	t	C_t	C_t/t	Time	t	C_t	C_t/t
April 1984				September 1983			
03:50-06:40	2.83	-0.301	-0.106	04:30-06:25	1.92	-0.086	-0.045
06:40-14:00	7.34	3.528	0.481	06:25-08:20	1.92	0.182	0.095
14:00-15:40	1.67	0.065	0.039	08:20-10:20	2.00	0.101	0.051
15:40-18:40	3.00	0.999	0.333	10:20-12:20	2.00	0.320	0.160
18:40-21:40	3.00	-0.806	-0.269	12:20-14:20	2.00	0.029	0.015
21:40-00:35	2.92	0.256	0.088	14:20-18:20	4.00	0.581	0.145
00:35-03:50	3.25	0.685	0.211	18:20-20:20	2.00	-0.217	-0.109
Total		4.425		20:20-22:20	2.00	0.281	0.140
				22:20-00:20	2.00	0.135	0.068
May 1982				00:20-02:20	2.00	0.202	0.101
06:30-08:30	2.00	0.787	0.393	02:20-04:30	2.17	0.105	0.049
08:30-11:20	2.83	0.717	0.253	Total		1.236	
11:20-14:30	3.17	0.920	0.290				
14:30-16:30	2.00	0.720	0.360	November 1984			
16:30-18:20	1.83	1.745	0.954	05:00-07:42	2.70	0.409	0.152
18:20-20:30	2.17	-1.160	-0.535	07:42-10:32	2.83	0.270	0.096
20:30-00:30	4.00	0.618	0.154	10:32-13:35	3.05	0.149	0.049
00:30-04:50	4.33	0.038	0.009	13:35-16:34	2.98	0.170	0.057
04:50-06:30	1.67	0.362	0.217	16:34-19:38	3.07	0.167	0.055
Total		4.746		19:38-22:42	3.07	-0.046	-0.015
				22:42-01:38	2.93	0.168	0.057
July 1984				01:38-04:40	3.03	-0.048	-0.016
04:35-07:31	2.93	0.286	0.098	Total		1.241	
07:31-10:39	3.13	0.696	0.222				
10:39-13:35	2.93	1.147	0.391	February/March 1985			
13:35-15:32	1.95	0.363	0.186	04:36-07:34	3.03	-0.096	-0.032
15:32-17:36	2.07	0.318	0.154	07:34-10:31	2.95	0.206	0.070
17:36-20:01	2.42	0.352	0.145	10:31-13:23	2.87	0.098	0.034
20:01-22:33	2.53	0.601	0.237	13:23-16:27	3.07	-0.138	-0.045
22:33-01:48	3.25	-0.289	-0.089	16:27-19:28	3.02	0.225	0.075
01:48-04:32	2.73	-0.040	-0.015	19:28-22:32	3.07	-0.034	-0.011
Total		3.434		22:32-01:26	2.90	0.089	0.031
				01:26-04:41	3.25	0.129	0.040
				Total		0.480	

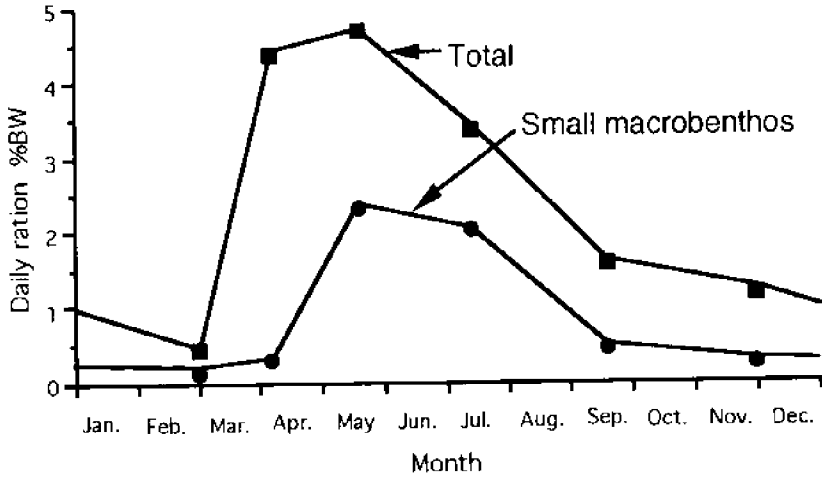


Figure 6. Seasonal change in daily ration (% of wet body weight) of *P. herzensteini* (solid square and solid line) and daily amount of small macrobenthos consumed by *P. herzensteini* (solid circle and solid line) in the coastal waters of northern Niigata Prefecture.

1970; Tyler 1970; Elliott 1972; Kiorboe 1978; Ishiwata 1978; Lane et al. 1979; Koshiishi 1980; Macdonald et al. 1982; Huebner and Langton 1982; Brodeur 1984; Tomiyama et al. 1985; Nashida and Tominaga 1987). Of these three models, when the gastric evacuation rate is small enough, a square root model and an exponential model closely resemble each other (Tomiyama et al. 1985). Therefore, gastric evacuation models were classified into two types of models except for fish with large R value, like larvae or juveniles.

Persson (1986) reanalyzed several studies on food evacuation of fishes in his review and concluded the exponential model is generally the most appropriate. Although Jobling (1981) concluded that the majority of gastric evacuation studies showed that the application of the square root model in general provided the better fit to the data, his later study (Jobling 1986) showed that the exponential evacuation model generally gave a better description of the rate of food evacuation, when fish were fed on relatively small and easily digestible low-energy prey. Exponential models have been applied to the gastric evacuation rate of pleuronectiformes fishes (Kiorboe 1978; Huebner and Langton 1982; Macdonald et al. 1982; Nashida and Tominaga 1985). In the present paper, although the instantaneous evacuation

rate was estimated by assuming that the stomach content index decreased exponentially, the prey items of brown sole were small and easily digestible and application of the exponential model was thought to be reasonable.

The instantaneous evacuation rate (R) is calculated by equation (4). When the exponential model is applied to the gastric evacuation rate, stomach content weight decreases rapidly during the first few hours and afterward it gradually diminished. Therefore, the stomach content index of brown sole collected during the first few hours after sunset varied widely. This variation of SCI decreased with time during the night. This is the reason why we used the S_{ss} and S_{sr} to estimate R .

The daily ration increased from mid-spawning season and peaked (4.75% BW) in May. Then it decreased gradually to the lowest value (0.48% BW) in February/March. Tominaga et al. (1991) showed the period May to July to be an active feeding season and that of August to December to be an inactive one. The present study supports the results of seasonal variation of feeding intensity by Tominaga et al. (1991).

In the laboratory study of the temperature-daily ration relationship of brown sole (Takahashi et al. 1987), at temperatures below 18–19°C, the daily ration (% wet body weight/day) increased with increasing temperature and began to decrease remarkably at about 19°C. The highest daily ration (6.8–11.4% BW) of brown sole was seen at temperatures of 17.8–19.0°C and the brown sole cease to feed at temperatures below 0.7°C. The daily rations in the laboratory were 6.0 to 7.2% BW at temperatures (10–13°C) of the active feeding season in the study area, and were relatively high compared with daily ration estimates in the field. The reason for this seemed to be due to more abundant and bigger food items in the laboratory.

The temperatures of the study area in the inactive feeding season were from 13–17.5°C. Even at 13°C, the daily ration in the laboratory was approximately over four times (7.2% BW) as much as that estimated in the field during this season. This suggests that physiological conditions affect the feeding intensity of brown sole as Takahashi et al. (1982) and Tominaga et al. (1991) stated.

The annual ration of brown sole was estimated to be 831.5% BW. For the brown sole in the coastal waters of Niigata Prefecture, a biomass of 1,482.5 metric tons and an abundance of 82,624,000 were calculated by cohort analysis (Niigata Prefectural Fisheries Experimental Station 1987). Estimated population biomass of brown sole in this study area was about 1,067 metric tons on the basis of the ratio of commercial catch amount in this study area to the total amount of

commercial catch in Niigata Prefecture. Therefore, it was estimated that brown sole consumed about 8,872 metric tons of animals distributed in this study area annually.

Brown sole fed exclusively on polychaetes except for spring. In spring, polychaetes were not the most dominant in their stomachs but still important food items. Hayashi (1988) showed that polychaetes were the most abundant and the largest biomass of the small macrobenthos community (less than 1 g in wet weight but larger than 1 mm in size) in this study area. Hayashi (1987) estimated that the annual production of small macrobenthos in this study area was about 40,000 metric tons. Judging from the observation that brown sole feed only during daylight in the laboratory (Tominaga 1990), they must use vision in their search for food. Brown sole easily search for and eat polychaetes which have head and/or feeding appendages, or they move on the bottom but can't feed on polychaetes inhabiting the deep layer of bottom sediment. Hayashi (1987) also estimated the production of small macrobenthos in 0-2 cm of bottom sediment to be about 15,000 metric tons. It seems reasonable to suppose that the amount of available small macrobenthos is about 15,000 metric tons.

The annual amount of small macrobenthos consumed by brown sole is estimated to be about 416% BW (Fig. 6) on the basis of wet weight percent in the stomachs, and it is calculated that brown sole consume about 4,440 metric tons of small macrobenthos. This value is equivalent to about 30% of the annual production of available small macrobenthos. In addition to small macrobenthos, brown sole cut and eat parts of Sigalionids which are larger than 1 g in wet weight. Moreover, they took euphausiids, small fish, *B. japonicus*, and/or dead sardine in their active feeding season. Therefore, food availability for brown sole is thought to be sufficiently high.

There is no abundant fish that feeds mainly on polychaetes in this study area, except for brown sole (Tominaga and Nashida 1991). This is advantageous to brown sole. Brown sole consumed about 80% of the annual ration from April to September. They feed on various food organisms besides polychaetes and were distributed widely during this period (Tominaga et al. 1991). This might reduce intraspecific competition for food.

In the present study, the annual ration was estimated from the daily rations of different years. Therefore, it was at best only an approximation. By conducting both field experiments throughout the year and laboratory experiments, we might get better estimates of the annual ration of brown sole.

Acknowledgments

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Minimal Food Requirements for Yellowfin Sole in Alaska: Estimates from Laboratory Bioenergetics

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Abstract

The boundaries of minimal food requirements in yellowfin sole in two separate geographical populations from Alaska were estimated based on energy-growth relationships derived in the laboratory combined with weight at age data derived from field measurements. In the eastern Bering Sea, yellowfin grow 0.50% BWd⁻¹ in their first year. To achieve that growth rate they require a ration of 1.65-6.2% BWd⁻¹ depending on prey energy content. By age 15 growth has declined to 0.026% BWd⁻¹ and minimal food required has declined to 0.43-1.6% BWd⁻¹.

In the Gulf of Alaska, fish in their first year grow 0.53% BWd⁻¹ and require a ration of 2.4-9.0% BWd⁻¹, depending on prey energy content. By year 13, growth declines to 0.20% BWd⁻¹ and food requirement declines to 0.53-2.0% BWd⁻¹.

Previous daily ration estimates for Bering Sea yellowfin sole were either based on stomach content and evacuation rate data (Elliott and Persson model) or on assumptions about food conversion efficiency. Those estimates, 0.12, 0.40 and 1.16% BWd⁻¹, are too low to account for the growth yellowfin sole actually exhibit in the field and none account for the effect of fish size on feeding. In terms of yellowfin sole

impact on prey stocks, the previous estimates predict that the Bering Sea yellowfin stock annually consumes the equivalent of 18%, 61% and 423% of its biomass in prey, respectively. Our data predict an annual prey consumption of from 2.4 to 9 times the biomass of the yellowfin stock, depending on prey energy content.

Introduction

The yellowfin sole, *Pleuronectes asper* (Pallas 1811), is the most abundant flatfish in Alaskan waters. Its standing stock in the Bering Sea is about 1.2 to 2 million t (Bakkala et al. 1982; Wakabayashi 1986), representing 64% of flatfish biomass and 23% of the total fish biomass (Bakkala 1981). Stock size in the Gulf of Alaska is much lower, placing yellowfin sole eighth in terms of flatfish abundance. It is a principal predator of other potentially valuable marine species including pandalid shrimps, king crab, tanner crab and gadid fishes (Livingston et al. 1986). It is also important prey for fishes like the Pacific halibut (Bakkala 1981). Previous efforts to estimate the ecological impact of yellowfin sole have included stomach content analyses (Wakabayashi 1986; Livingston et al. 1986, 1993), respiration rates (Paul et al. 1990a) and food intake and growth experiments (Smith et al. 1990).

This paper employs the relationship of food intake to growth in the laboratory to establish the probable boundaries for minimum food consumption by fish in their natural environment. Both growth and minimum food consumption by age class is modeled for two populations of yellowfin sole living in different temperature regimes. These estimates are relevant to assessments of the ecological impact of this abundant species on its prey stocks.

Materials and Methods

Information on weight at age in yellowfin sole from both the Bering Sea and the Gulf of Alaska (Niggol 1982) was used to calculate growth rates for these two populations. The instantaneous growth equation of Chapman (1978) yields a coefficient that is approximately equivalent to daily growth rate expressed in percent of body weight. The equation is:

$$G_x = [\log_e W_i - \log_e W_{i-1}] / 365$$

where W_i is the weight at age i and W_{i-1} is the weight the previous year.

The relationship of food intake to growth in the laboratory was elucidated by Smith et al. (1990) in 30 d feeding experiments at two

relevant temperatures, 3 and 6°C. A total of 36 groups of fish consisting of from one to four individuals provided information on growth and consumption. Fish were weighed on day 1 and day 31; growth was calculated using the formula:

$$G = [W_t - W_0] / W_0 \times 100 / t$$

where G is growth in percent body weight per day, W_0 is the initial weight, W_t is final weight and t is the duration of the experiment (always 30 days). Food consumption, in percent body weight per day, was calculated using the formula:

$$C = [C_t / 30n] / W$$

where C_t is total food ingested over the 30 d, n is number of fish in the group and W is the mean fish weight during the experiment. The weight consumed was converted to an energy value using caloric measurements performed on an adiabatic calorimeter: 8.36 KJg⁻¹ wet weight for herring (*Clupea harengus pallasii*) and 2.37 KJg⁻¹ wet weight for octopus (*Octopus dofleini*). In the 3°C experiments herring was used as food while at 6°C both octopus and herring were used.

The resulting growth-energy equations were used to predict the energy required to achieve the growth rates exhibited by the different age classes of yellowfin sole from the two populations. To estimate the likely limits on daily ration for the age classes of these populations we converted the energies required into equivalent rations (% BWD⁻¹) of bivalves, euphausiids and a fish, the walleye pollock (*Theragra chalcogramma*). These groups are all typical foods of yellowfin sole. Energy contents per g wet weight used in this exercise were: bivalves, 1,600 J (Thayer et al. 1973); euphausiids, 2,560 J (Paul et al. 1990b); walleye pollock, 6,020 J (Smith et al. 1986).

Results

Growth coefficients, expressed as growth in percent body weight per day, are plotted versus age for fish from the Bering Sea (Fig. 1a; $y = 0.577x^{1.14}$; $r^2 = 0.99$) and from the Gulf of Alaska (Fig. 1b; $y = 0.782x^{1.34}$; $r^2 = 0.97$).

The equation representing growth as a function of energy intake at 6°C in the laboratory (Smith et al. 1990b) was:

$$y = 0.0045x - 0.125 (r^2 = 0.77)$$

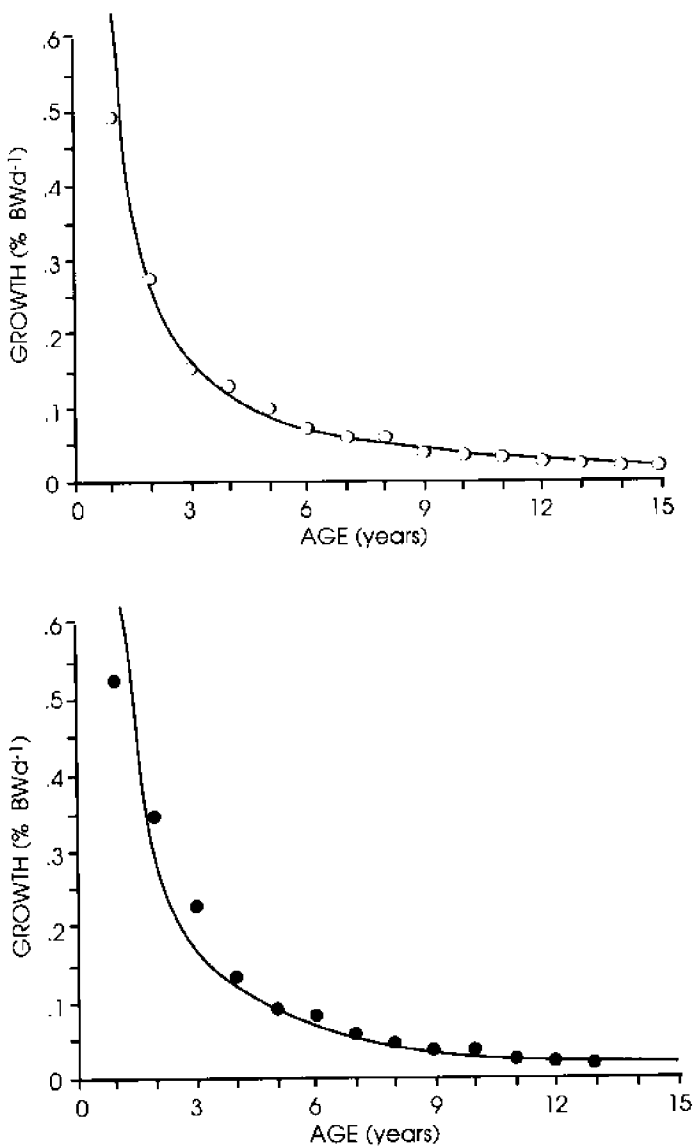


Figure 1. Growth, in % BWd⁻¹, as a function of age in yellowfin sole from (above) the Bering Sea, and (below) the Gulf of Alaska. Growth was estimated based on mean weight-at-age data (Niggol 1982) and an instantaneous growth rate equation (Chapman 1978).

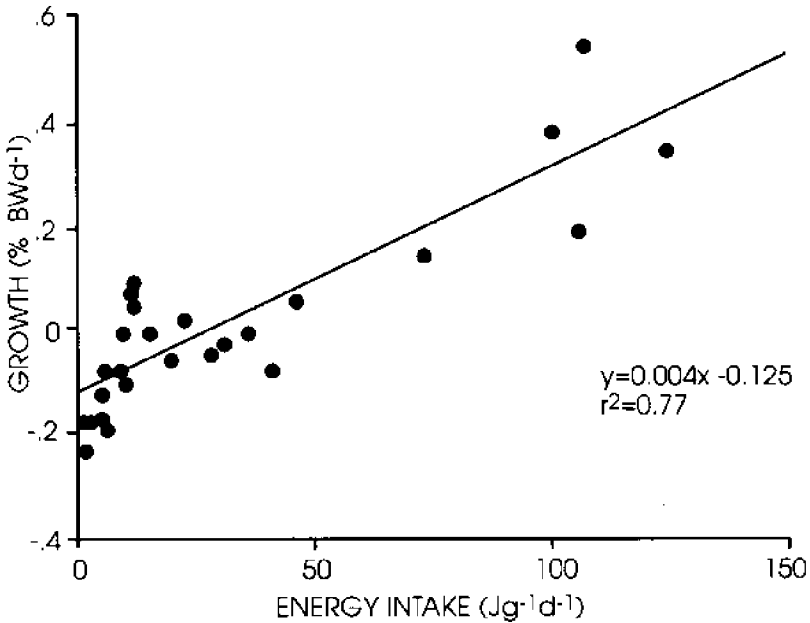


Figure 2. Growth, % BWd⁻¹, of yellowfin sole in the laboratory as a function of energy intake, Jg⁻¹d⁻¹, at 6°C. Fish were fed either herring fillets or chopped octopus.

where y is growth in % BWd⁻¹ and x is energy intake in Jg⁻¹d⁻¹ (Fig. 2). The equation derived from the 3°C experiments (Smith et al. 1990) was:

$$y = 0.0065x - 0.140 (r^2 = 0.72).$$

The rates of energy intake (Jg⁻¹d⁻¹) required to achieve the growth rates seen in Fig. 1 were calculated using the above equations (Fig. 3). Energy requirement versus age in the Bering Sea conforms to the equation $y = 87.6x^{-0.49}$ ($r^2 = 0.97$); the equation for the Gulf of Alaska population is $y = 146x^{-0.62}$ ($r^2 = 0.98$). Fig. 4 illustrates the amounts of three different prey necessary in the Bering Sea (3°C) to meet the expected energy requirement. Fig. 5 is the same exercise for the Gulf of Alaska (6°C).

Yellowfin sole in the Bering Sea exhibit daily growth rates ranging from 0.50% BWd⁻¹ to 0.026% BWd⁻¹ from age 1 to age 15 (Fig. 1 above). During their first year yellowfin sole require from 1.65 to 6.2% BWd⁻¹

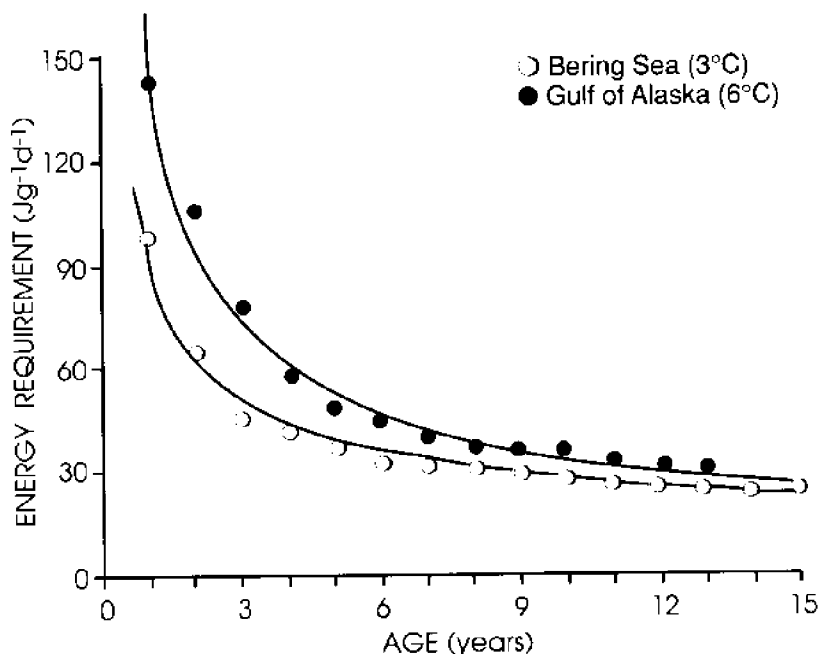


Figure 3. Energy requirement, $Ig^{-1}d^{-1}$, to achieve growth rates observed in the natural populations of yellowfin sole in the Bering Sea and Gulf of Alaska as a function of fish age.

daily ration depending on the energy content of the prey (Fig. 4). A 15 year old fish (375 g) requires from 0.43 to 1.6% BWd^{-1} as a daily ration (Fig. 4). In the Gulf of Alaska, yellowfin sole exhibit daily growth rates ranging from 0.53% BWd^{-1} to 0.020% BWd^{-1} from age 1 to age 13 (Fig. 1 below). During their first year they require from 2.4 to 9.0% BWd^{-1} daily ration depending on the energy content of prey (Fig. 5). A 13 year old fish (505 g) requires from 0.53 to 2.0% BWd^{-1} as a daily ration in order to achieve the growth rate seen in Fig. 1 below. Since yellowfin sole are known to feed on a variety of invertebrates and fish, values in the middle of the above ranges of rations are likely.

Discussion

This exercise is based on a number of assumptions. First, we assume that growth in yellowfin sole is dependent on energy intake irrespective of food type. Differences in digestibility and conversion efficiency

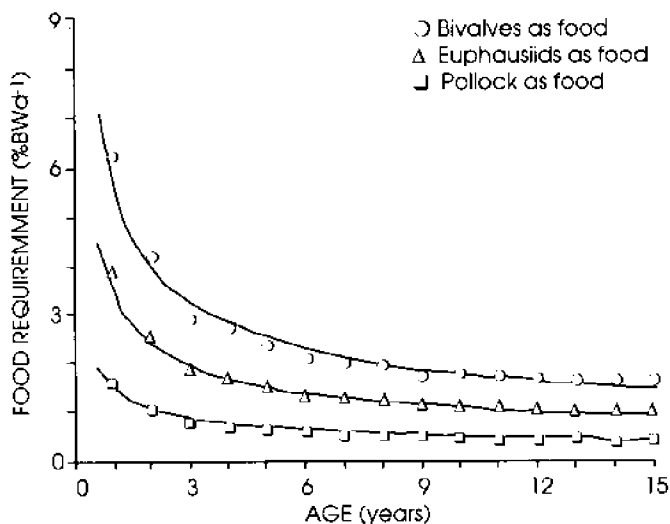


Figure 4. Food requirement, % BWd⁻¹, to achieve growth rates observed in the Bering Sea yellowfin sole population as a function of fish age.

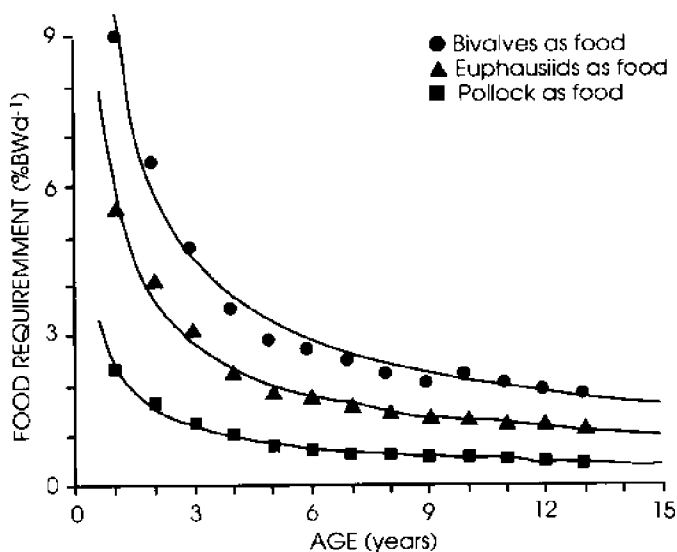


Figure 5. Food requirement, % BWd⁻¹, to achieve growth rates observed in the Gulf of Alaska yellowfin sole population as a function of fish age.

would invalidate this assumption. However, the significant relationship seen in Fig. 2 ($r = 0.877$; $p < 0.01$) supports this assumption. A second assumption is that the energy-growth relationships we use are valid for all fish sizes. Smith et al. (1990) developed the energy-growth curve upon which Fig. 2 is based and found no evidence of size effect within the range of weights used (88-459 g). Presumably, very small fish would require even more energy than our model predicts due to surface to volume relationships. A third assumption is that the temperatures we use in this exercise are representative of the gulf and Bering Sea. Smith et al. (1988) reported Gulf of Alaska temperatures at shelf depths fluctuating around 5-6°C over a year cycle. For the eastern Bering Sea, Livingston et al. (1986) reported bottom temperatures of 1.5-3°C over the annual cycle at stations where yellowfin sole were captured. Thus, our 3°C energy-growth relationship may not be entirely appropriate for the entire annual cycle in the eastern Bering Sea. Finally, we assume that the estimates we derive in this study are conservative. Fish held in the laboratory may be stressed by the artificial environment, including the human manipulations. However, we feel that these potential increases in metabolic rate are more than offset by the savings resulting from not having to actively acquire food or avoid predators. These assumptions require validation by further experimental and field observations.

What is the impact of the Bering Sea yellowfin sole stock on its prey stocks? An estimate can be derived from the findings reported above. One approach is to calculate the mean daily ration for all age classes of yellowfin. Those values are 2.41, 1.50 and 0.64% BWd⁻¹, respectively, for fish fed bivalves, euphausiids or pollock. These rations produce estimates of 880, 548 and 234% of the yellowfin biomass annually for the three food organisms listed. Clearly, these flatfish eat a variety of prey with different energy contents. Perhaps the best single estimate would be one assuming an average prey energy content in the middle of the range, near that of euphausiids.

A further iteration could be made using the relative biomass of the different year classes (Niggol 1982) and the ration requirement specific to that year class (Fig. 4). This method, although it accounts for age-specific differences in food intake, produces estimates (906, 565 and 241% of biomass, respectively) very similar to those obtained with the mean daily ration figures used above. Tominaga et al. (1995) report an annual ration for brown sole, *Pleuronectes herzensteini*, of about

1,060% of body weight. This value is very similar to ours, considering the more temperate habitat (Sea of Japan) of brown sole.

Livingston et al. (1986) reported a daily ration of 0.12% BWd^{-1} for Bering Sea yellowfin sole. The latter estimate was based on examination of stomach contents from trawl-caught fish and on the Elliott and Persson (1978) model. This daily ration estimate is below the minimal food requirements we present above (Fig. 4). Livingston et al. (1986) present evidence that suggests yellowfin sole feeding is restricted to 153 days a year. Thus, one could predict the impact of the Bering Sea yellowfin stock on its prey stocks ($0.12\% BWd^{-1} \times 153d \times \text{biomass}$) at about 18% of the yellowfin biomass annually.

Wakabayashi (1986) used Laevastu and Larkins' (1981) estimate of 1.16% BWd^{-1} as the probable daily ration of yellowfin sole in the Bering Sea. This figure produces an estimate of yellowfin sole's annual impact on prey of about 423% of the yellowfin biomass ($1.16\% BWd^{-1} \times 365d \times \text{biomass}$), assuming a 365d feeding period. This value falls within our range of estimates.

Livingston et al. (1993) abandoned the stomach content approach and used a value of 0.4% BWd^{-1} as the daily ration of Bering Sea yellowfin sole. Thus, annual impact on its prey could be estimated at about 61% of yellowfin biomass ($0.4\% BWd^{-1} \times 153d \times \text{biomass}$).

In comparison to the Bering Sea population, that in the Gulf of Alaska grows faster and requires a larger daily ration. A 1 year old fish has a growth rate of 0.53% BWd^{-1} (Fig. 1b) and requires a ration of 2.4 to 9.0% BWd^{-1} , depending on energy content (Fig. 5). Similarly, a 13 year old fish (505 g) grows 0.020% BWd^{-1} (Fig. 1b), and requires a daily ration of 0.53 to 2.0% BWd^{-1} (Fig. 5).

There are no other estimates of daily ration of yellowfin sole from the Gulf of Alaska. However, other authors have reported daily rations for flatfishes at higher temperatures. Food consumption in the winter flounder, *Pseudopleuronectes americanus*, at 5-7.5°C ranged from 1.8-2.4% BWd^{-1} (Tyler and Dunn 1976; Huebner and Langton 1982). Hatena et al. (1956) found that *Limanda yokohamae* maintained at 13°C had a mean food intake of 3.2-3.3% BWd^{-1} . Daily rations of brown sole from the Sea of Japan fluctuates seasonally from 0.88 to 5.8% BWd^{-1} (Tominaga et al. 1995). Thus, our estimates of the minimal food requirements for yellowfin sole appear to be consistent with food consumption rates in other flatfish species. It appears that use of the previous daily ration estimates based on stomach contents and on

conversion efficiency assumptions for yellowfin sole populations underestimates the ecological impact on their prey stocks.

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Energy Requirements of Fasting Flathead Sole (*Hippoglossoides elassodon* Jordan and Gilbert 1880) Calculated from Respiratory Energy Needs

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Abstract

Measurements of oxygen consumption rates were made for unfed flathead sole, *Hippoglossoides elassodon*, to examine the role of fish weight and temperature on respiration rate. At 5.5°C $\dot{V}O_2$ for 1 to 350 g unfed fish was described by the equation:

$$\text{ml O}_2 \text{ ind}^{-1} \text{ h}^{-1} = 0.013 (\text{live wt. g}) + 0.344; \quad r^2 = 0.93. \quad (1)$$

Measurements of $\dot{V}O_2$ relative to water temperature for 40 to 70 g unfed fish, exhibited a linear increase between 2.0 and 9.5°C described by the following equation based on mean values:

$$\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1} = 3.077(\text{T}^\circ\text{C}) + 1.655; \quad r^2 = 0.99. \quad (2)$$

Based on indirect calorimetry the metabolic energy requirement for fasting 55 g flathead sole at 3°C was estimated to be 5.0 Jg⁻¹d⁻¹. Minimal prey consumption rates to have provided this much energy would be 0.98% body weight d⁻¹ for high energy tissue or 1.96% bw d⁻¹ for low energy tissue if conversion efficiency is assumed to be 12.3. A

feeding individual always requires more energy than fasting fish and thus a higher food intake.

Introduction

Fisheries scientists are using multispecies models to understand changes in population structure of Alaskan groundfishes (Laevastu and Larkins 1981). A prime link between species in these models is mortality through predation. The flathead sole, *Hippoglossoides elassodon* Jordan and Gilbert 1880, is a common benthic fish in both the Gulf of Alaska and the southeast Bering Sea. Because of its abundance it is a key member of the food web (Livingston et al. 1986). Estimates of prey consumption of this species based on an evacuation technique (Livingston et al. 1986) and feeding and growth experiments (Paul et al. 1992) exist. The evacuation method predicted a consumption rate of 0.45% body weight (bw) d^{-1} while the feeding method predicted 0.4 to 6.2% bw d^{-1} depending on fish age. Some errors in the captive feeding method are likely to underestimate consumption because the captive fish did not have to forage or migrate. Alternatively the stress of captivity could elevate metabolic rate and thus estimates of consumption rate. Given the large disparity between these two estimates (Livingston et al. 1986, Paul et al. 1992) we decided to use another approach to estimate ration to see if the consumption rate based on the evacuation rate could sustain flathead sole. This study measured flathead sole minimum energy requirements based on oxygen consumption rates. The method relies on the fact that unfed fish decrease their metabolic rate to the absolute minimum thus minimizing the effects of laboratory conditions on oxygen consumption rates. These oxygen consumption rates were used to estimate minimum metabolic needs associated with the fasting state, and what the consumption rates would have been to store this much energy. The examination of the effects of temperature on respiratory metabolic needs also provides a scaling factor to modify estimates of consumption from Paul et al. (1992) under a variety of thermal conditions.

Methods

Flathead sole used in all experiments were captured by trawl in Resurrection Bay, an embayment of the Gulf of Alaska, near Seward,

Alaska. Experiments were done at temperatures the species normally encounter. In the Gulf of Alaska bottom temperatures of 3 to 6°C are common (Smith et al. 1988) while in the Bering Sea they might reach -1.8 (Bakkala 1981).

To understand the effect of fish size on oxygen consumption rate the following experiment was conducted. Oxygen consumption ($\dot{V}O_2$) was measured for 20 fish of 1 to 350 g at 5.5°C. Fish were kept at the test temperature for at least one month, then feeding was stopped. Fish were acclimated to the chamber for one week prior to measurement of $\dot{V}O_2$. Fish were held in 23.5 L or 128 L black plastic chambers without food. The chambers were kept in the dark and fish rested on bare plastic bottom. Other studies indicate the addition of sediment substrate to the chambers might have modified respiration, but this factor was not described by our experiments. The open chambers were held in 1000 L constant temperature cooling seawater baths with an average temperature of 5.5°C (sd = 0.5). Pilot experiments were done in which sole lowered background oxygen levels to 3 ml L⁻¹ in sealed chambers and no evidence of depressed rates of oxygen consumption were observed. During measurements of $\dot{V}O_2$ the chambers were sealed for 24 hours. Oxygen concentration was measured at the beginning and end of the 24 hrs. Oxygen levels in the experiments did not fall below 3.5 ml L⁻¹ so that background oxygen levels should not have affected oxygen consumption. Measurements of $\dot{V}O_2$ for a fish were made on three separate days and the results averaged to provide an estimate of oxygen consumption.

Measurements of $\dot{V}O_2$ relative to water temperature were accomplished with 40 to 70 g unfed fish using the above methods. For each of four temperatures, five or six fish were acclimated to the temperature for one month during which they were fed daily. Next they were acclimated to individual 23.5 L chambers for one week without food, prior to triplicate $\dot{V}O_2$ measurements. Temperatures were provided by the natural seasonal thermal cycle of Resurrection Bay. Test temperatures ranged from 2.0 to 9.5°C. In all cases the variation of test temperature around the mean value was 0.3°C or less.

All oxygen measurements were made with an electronic probe (Orion 97-08) and meter (Orion 701A) calibrated against Winkler titrations (Parsons et al. 1984). Regressions describing the relationships of fish weight and temperature to oxygen consumption were fitted to log, power, exponential and linear models and the best fit as indicated by the coefficient of determination (r^2) adopted.

Table 1. Changes in oxygen consumption rates of 40 to 70 g fasting flathead sole, *Hippoglossoides elassodon*, based on equation 2.

Temperature °C	Oxygen consumption $\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$	Percent change
2	7.80	—
3	10.88	39
4	13.96	28
5	17.04	22
6	20.12	18
7	23.19	15
8	26.27	13
9	29.34	11
10	32.42	10

Results

The rate of oxygen consumption at 5.5°C for unfed fish weighing 1 to 350 g was described by the equation:

$$\text{ml O}_2 \text{ ind}^{-1} \text{ h}^{-1} = 0.013 (\text{live wt. g}) + 0.344; \quad r^2 = 0.93 \quad (1)$$

(Fig. 1). Measurements of $\dot{V}\text{O}_2$ relative to water temperature for 40 to 70 g unfed fish, exhibited a linear increase between 2.0 and 9.5°C described by the equation based on mean values:

$$\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1} = 3.077(\text{T}^\circ\text{C}) + 1.655; \quad r^2 = 0.99 \quad (2)$$

(Fig.2).

The estimate of respiratory Q_{10} for sole held at 2.0 to 9.5°C was 6.3. Based on equation 2, for every °C increase in habitat (2 to 10°C) the respiratory energy needs increased by 10 to 39% (Table 1). Respiratory rate changes due to warming increased the most at the colder end of the test temperatures (Table 1).

Discussion

No other oxygen consumption estimates were located for *H. elassodon* but estimates exist for *H. platessoides* Fabr. from the North Atlantic (MacKinnon 1973). Generally those estimates, which were termed routine values, were about three times higher than values for flathead

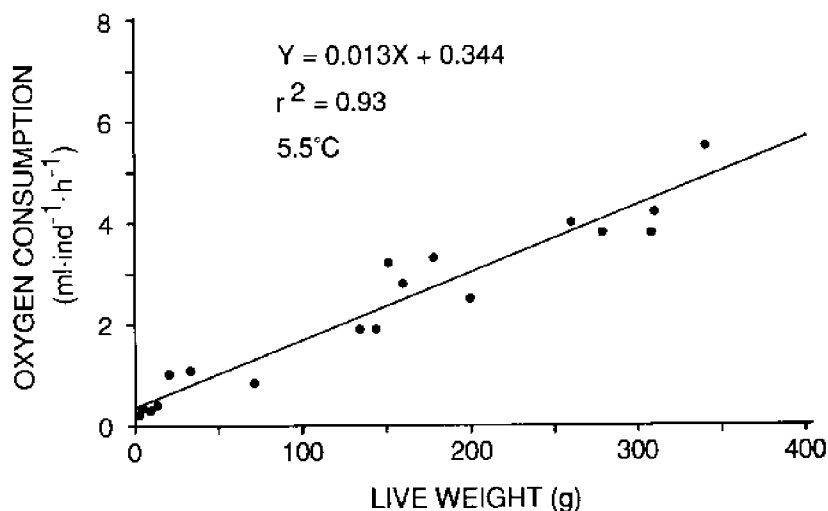


Figure 1. Oxygen consumption at 5.5°C of unfed *Hippoglossoides elassodon* (1-350 g) relative to body weight.

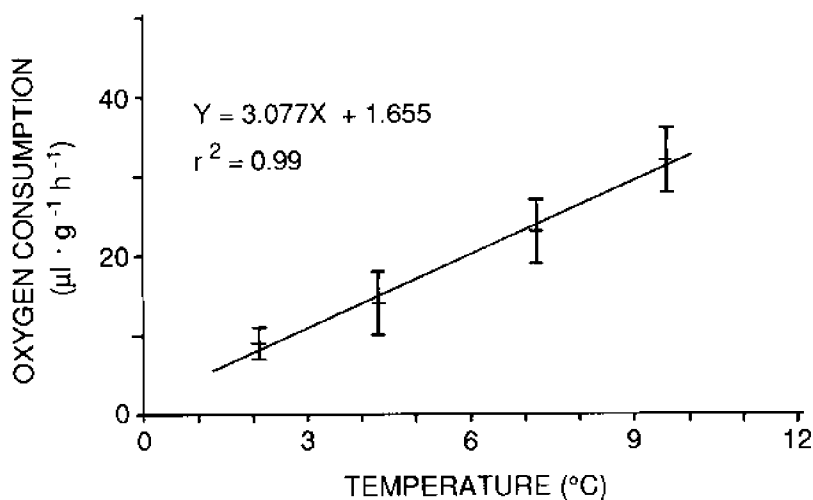


Figure 2. Specific oxygen consumption of unfed 40-70 g *Hippoglossoides elassodon* relative to water temperature: Values are mean \pm 1 sd.

sole. These differences may be the result of variations in methods. For example the plaice were not allowed to acclimate to the chamber for more than 24 hrs. More likely the studies are measuring different activity states. The objective of this study was to estimate the minimum ration based on metabolic measurements of unfed, quiescent fish and compare it to the consumption rate estimate based on stomach analysis (Livingston et al. 1986). The effect of starving the flathead sole would be to cause them to reduce their activity level and conserve energy, and thus lower their respiration rate to the absolute minimum.

The high Q_{10} values for flathead sole suggest it evolved to live in cold water habitats with a relatively narrow thermal range. In the southeastern Bering Sea flathead sole apparently select 2-4°C habitat in preference to warmer or colder strata by altering their depth distribution (Mineva 1964). Minimizing activity level is another strategy that flatfish can use to maintain a positive energy balance when confronted by thermal change.

We used the oxygen consumption values derived above to generate an estimate of minimal food energy required by flathead sole. For the following exercise of estimating a meaningful daily ration we used a 55 g fish as an example. In order to determine prey consumption rates based on metabolic rate derived energy needs it is necessary to know the conversion efficiency rate for a species. A 55 g flathead sole consuming a ration of 42.5 J g d⁻¹ (2,338 J ind⁻¹) would gain about 0.125% bw d⁻¹ (Paul et al. 1992). Assuming that flathead sole bodies contain 4,184 J g⁻¹ this growth rate would produce 0.069 g of tissue with an energy content of 287.7 J. The resulting conversion efficiency would be 12.3% (287.7/2,338). Estimates of energy expenditure due to respiration can be calculated using a conversion factor of 4.63×10^{-3} cal or 0.0194 J μl^{-1} of O₂ consumed (Brett and Groves 1979). At 3°C, 55 g unfed flathead sole (Fig. 2) would need 278.8 J fish⁻¹d⁻¹ for metabolic energy needs alone. With a conversion efficiency of 12.3% the 55 g fish would have to eat 2,266 J ind d⁻¹ to meet just its metabolic energy needs. Assuming the prey were something like walleye pollock which had 4,184 J g⁻¹ (Smith et al. 1986) then consumption would be 0.54 g or 0.98% bw d⁻¹ just for metabolic needs. If the prey was brittle stars with 2,092 J g⁻¹ (Thayer et al. 1973) then all the energy from a consumption of 1.96% bw d⁻¹ would have to have been used for minimal metabolic needs. These ration estimates are of course too low to meet the energy needs of an active growing fish. They are probably too low to be realistic for even a fasting flathead sole since

the starvation periods in the experiment altered the metabolic rate to one much lower than the fish might have in nature.

Based on an evacuation technique (Livingston et al. 1986) estimated that flathead sole under 25 cm have a daily ration of only 0.45% bw d⁻¹ at 3°C. Our oxygen consumption study suggests that this feeding level probably would not provide enough energy for active flathead sole. This conclusion agrees with a laboratory growth study (Paul et al. 1992) which estimated that flathead sole would need 0.4 to 6.2% bw d⁻¹ depending on size of fish and prey type. Even these later estimates may be low since the captive fish were fed high energy food, sparing them the normal energy expenditure associated with foraging.

Currently our understanding of prey consumption by groundfish species is very rudimentary. If species interaction models are ever going to become reliable, then considerable effort will have to be expended on combined field and laboratory studies. One very important aspect of these studies must be the examination of the seasonal aspect of consumption. Flatfishes are noted for active feeding in spring and summer and reduced feeding in winter and energy use cycles that reflect these changes in predation rates. Yellowfin sole for example had an annual energy cycle (Paul et al. 1993) with energy accumulation and growth from May to September. Thereafter they utilized stored energy for metabolic and reproductive needs. Spawning began in late May or early June and fish were spent by August. Whole body energy content for yellowfin sole increased by 28, 33 and 35% between May and June, for females, juveniles, and males, respectively, the most dramatic change during the year long survey. No measurements of the seasonal energy needs of flathead sole exist but their annual energy storage and use cycle is probably just as complex as that of yellowfin sole, so one cannot rely on a single value for consumption rate to estimate annual prey use. One promising approach for estimating consumption rates for flathead sole would be seasonal measurements of somatic energy values combined with assimilation efficiency studies.

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Evaluating a Crystal Pattern in the Microstructures of Juvenile Pacific Halibut Otoliths as a Means for Identifying Nursery Area Location

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Abstract

Like many flatfish, the otoliths of young Pacific halibut (*Hippoglossus stenolepis*) contain distinctive polygon shape patterns in their microstructures which are associated with the transition from late larval to juvenile stages. These patterns, which are derived from the placement of secondary sites of nucleation, mark the boundary between different fields of crystalline growth. Variations in the shape and in the orientation of the patterns were examined to determine if they could be used for stock separation. Sagittal otolith pairs were taken from six newly settled halibut from three widely dispersed nursery areas in Alaska. Fifteen measurements were collected from each otolith using Nomarski interference contrast illumination in conjunction with an image processing system. A partial nested analysis of variance model contrasted the pattern variation between otolith pairs with that between individuals and areas. The results indicated that the mechanisms that cause the pattern formations are not under tight biological control and there is little utility in measuring the patterns to identify halibut population according to their nursery areas. By considering the otolith a crystal, it is suggested that some formations in otoliths stem from a sensitivity to initial conditions, and that happenstance

also needs be considered as a mechanism that can give rise to a diversity of patterns.

Introduction

Pacific halibut (*Hippoglossus stenolepis*) is a large, long-lived flatfish that has a wide-ranging distribution in the North Pacific Ocean. Larval halibut are pelagic for several months (Thompson and VanCleve 1936, St-Pierre 1989) and during that time their transport to nursery areas is dependent on wind- and buoyancy-driven circulation (Parker 1988). From tagging studies of juveniles it is known that a significant proportion of the population may undergo extensive migrations (Hilborn et al. in press). This juvenile migration is thought to be a mechanism by which halibut counteract larval drift and maintain dispersed spawning populations (Skud 1977).

Current management of halibut is based on a catch-quota system that identifies broad regions as separate management units. However, uncertainty about migration rates of halibut between these regions can cause significant adjustments to the population models that are used to estimate yields (Quinn et al. 1990). In addition, by-catch of juvenile halibut by the trawl fishery is of increasing concern because of its potential effects on recruitment to the longline fishery (Sullivan et al. 1994). Estimating this loss requires knowledge of migration rates of the juveniles. Currently, the only estimates of migration of halibut stem from tagging studies (Quinn et al. 1990, Hilborn et al. in press). However, differential tagging mortality, tag-induced behavioral effects, and incomplete reporting of tag recoveries add uncertainty to those estimates. In addition, tagged juveniles are likely to be in the process of migration, making it difficult to identify site-specific patterns to migration.

An ideal tag would be a natural marker that could identify the fish to its nursery area of origin, or the spawning grounds from which it originated. This study was initiated to determine if a microstructure pattern formed in otoliths during the first year of life could be used as a tag to identify halibut according to its area of origin. Otoliths are an ideal candidate for examination, because unlike other sites of calcium deposition, calcium carbonate in otoliths is generally not reabsorbed (Campana and Neilson 1985). The deposition patterns that form early in life can be recovered in older fish by removing the overlying material.

In halibut, similar to other marine fish, the otolith starts to grow from a central nucleus, and in late larval stages form secondary sites

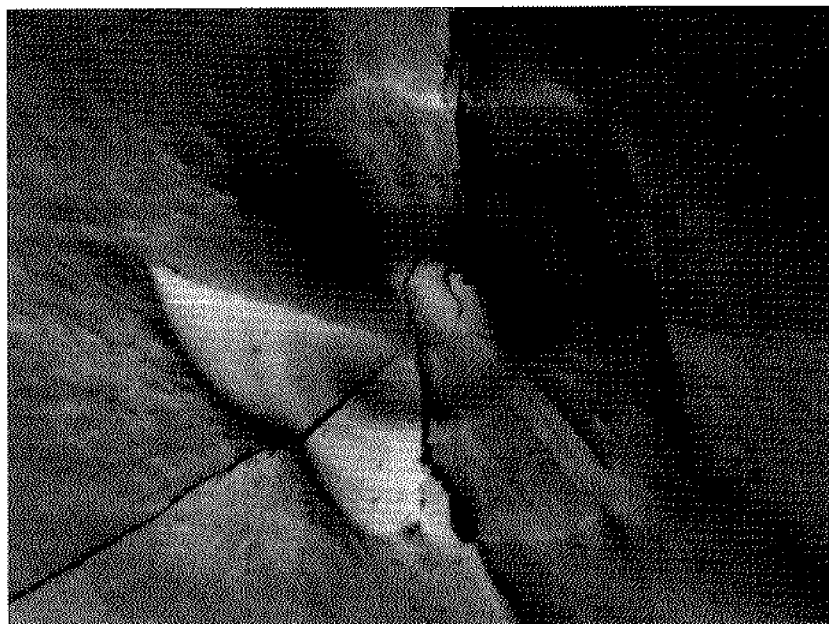


Figure 1. Digitized image of a larval crystal of a halibut otolith using Nomarski interference contrast illumination.

of nucleation (Hagen 1989). Campana and Neilson (1985) referred to these secondary sites as accessory primordia. In other flatfish, these accessory primordia have been shown to correspond to the times of metamorphosis from larval to juvenile stages (Toole et al. 1993, Sogard and Able 1992). Eventually growth from the accessory primordia encases the growth that stems from the central nucleus and a boundary line demarcating the two fields of growth appears as a complex polygon (Figure 1). This line can be quite prominent when viewed along the sagittal plane of the otolith and can be readily recovered from older fish. Variation in this shape and its association with nursery area location are examined in this paper. If the shape can be used to identify halibut to nursery areas, it may be possible to recover that information from adult halibut otoliths which are collected for age-structure population analysis (Quinn et al. 1990).

For the purposes of this paper, the growth stemming from the central nucleus, which is encased by the boundary line, will be referred to as the larval crystals. Correspondingly the growth stem-

ming from the accessory primordia will be referred to as the accessory crystals. This terminology, though not common to otolith discussions, reflects a classification that is similar to the descriptions of other biomineralized structures (Lowenstam and Weiner 1989).

The approach taken here is to extract measurements of halibut larval crystals collected from different nursery areas and include both the left and right otoliths in the analysis. An analysis of variance model is then used to contrast the pattern variation between otolith pairs with that between individuals and areas. By using otolith pairs it is possible to determine the extent that pattern formation is under biological or environmental control or whether it is unrelated to extraneous sources.

Methods

Juvenile halibut (age zero) from three nearshore areas in Alaska were collected for this study. The sites were nursery areas in Bristol Bay, Prince William Sound, and Southeast Alaska. From these collections, both the left and right sagittal otoliths from six individuals from each area were removed and mounted sulcus side up on glass slides using thermoplastic resin. The otoliths were ground using a series of silicon carbide paper (500, 1200 grit), followed by 9 micron lapping paper with a 0.3 micron alumina polish to expose the otolith crystal. The surfaces of the otoliths were examined using reflected bright field and interference contrast (Nomarski) illumination. Under these light sources the boundary lines demarking the larval crystal were easily observed. Interference contrast, in particular, provided a perspective of topographic relief to what is essentially a smooth plane. When it is gradually exposed during the grinding sequence, the larval crystal achieves its largest size when the exposed plane includes the otolith nucleus. To determine an estimate of measurement error that was likely to be encountered with small differences in grinding depth, measurements were made on a subsample of otoliths at various points in the grinding sequence. Based on these observations, there appeared to be less than 2% difference in linear measurements between slightly different grinding planes that included the otolith nucleus. Given this consistency of the measures, a single measurement plan through the nucleus sufficed and for the purpose of this study no attempt was made to quantify the crystal shapes in three dimensions.

Measurements of larval crystal shape were collected with the aid of an image processing program (Optimas Corporation, 190 West Dayton Street, Edmonds, WA, USA 98020). The otolith was oriented

Table 1. Suite of measurements taken for each larval crystal shape.

1.	Area: size of the larval crystal (mm ²)
2.	Circularity: the ratio of the area perimeter squared divided by the area (unitless)
3.	Rectangularity: the ratio of the crystal area to the area of a containing box oriented along the longest axis (unitless)
4.	MajorAxisLength: the length of longest axis through the area (mm)
5.	Breadth: the width of the otolith measured perpendicular to the major axis (mm)
6.	COMdistance: distance from the area center of mass to the nucleus (mm)
7.	COMangle: angle of COMdistance to reference line (degrees)
8.	MinRadi: shortest radial distance from the nucleus to the crystal boundary (mm)
9.	MinRadiAngle: angle of MinRadi from reference line (degrees)
10.	MaxRadi: longest radial distance from the nucleus to the crystal boundary (mm)
11.	MaxRadiAngle: angle of MaxRadi from reference line (degrees)
12.	MeanRadi: mean of all radial distances (n = 360) from nucleus to the crystal boundary (mm)
13.	SDRadi: standard deviation of distribution of radial measurements
14.	SkewRadi: skewness of distribution of radial measurements
15.	KurtRadi: kurtosis of distribution of radial measurements

such that a line drawn from the nucleus to the anterior axis of the otoliths, as indicated by the farthest point along the rostrum, was given an angle of zero. Fifteen measurements were taken on each otolith. Three of the measurements included angles in relationship to the reference line, five were linear measurements of distance, two were indices of shape, one was the measurement of area, and four were the moments of a distribution of linear measurements (Table 1). The data were collected for each otolith by tracing the shape of the larval crystal and identifying the location of the central nucleus. From the outline of the larval crystal, the area contained by the outline was obtained, along with the length of the major axis, its breadth, and the distance and orientation of the nucleus to the area's center of mass (Figure 2). These measures provide a degree of asymmetry in the growth of the crystal. Also obtained from the larval crystal shape were two indices that measure similarities of the shape to a circle and rectangle (Table 1).

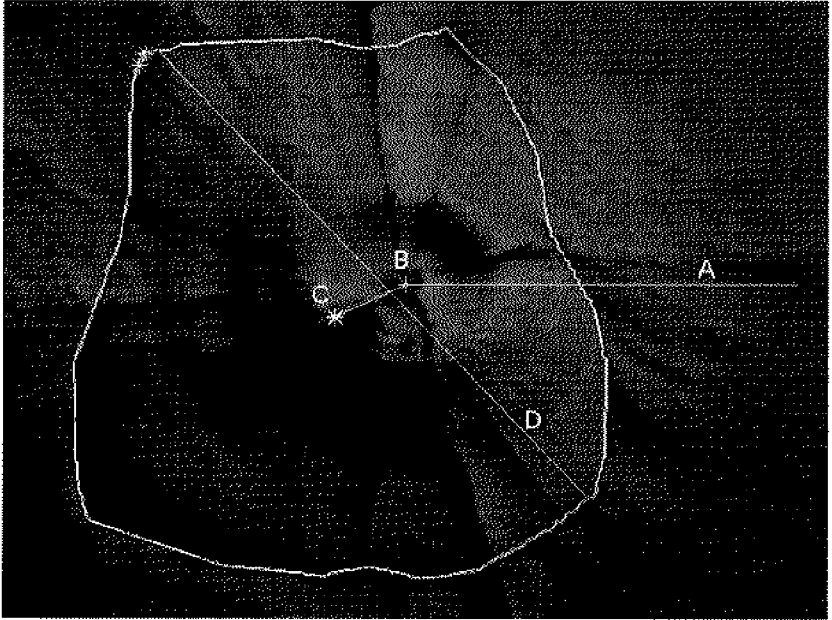


Figure 2. Digitized image of a larval crystal of a halibut otolith using Nomarski interference contrast illumination. Outline of larval crystal shape is indicated by the white line. Reference line A indicates direction toward anterior axis. Point B shows location of central nucleus. Point C indicates the center of mass of the area of the larval crystal. Measurement COMdistance (#6 in Table 1) is the distance C to B. COMangle (#7) is the angle, counterclockwise, of ABC. Line D is the MajorAxisLength (#4), as determined by larval crystal shape. Breadth (#5), not shown, is width of the area at 90 degrees to the MajorAxisLength.

A second series of measurements was obtained by collecting 360 radial measurements in one degree increments from the nucleus to the outline of the larval crystal (Figure 3). The mean, variance, skewness and kurtosis of these measurements was calculated. In addition, the minimum and maximum radial measurements were recorded along with their angles with respect to the reference line.

To analyze the data I used a combination of exploratory data analysis, methods for analyzing directional data, and analysis of variance (ANOVA) models. I used both otoliths in the analysis, even though in halibut, similar to other flatfish, the otoliths are asymmetric with the right otolith being thicker than the left otolith. This asymme-

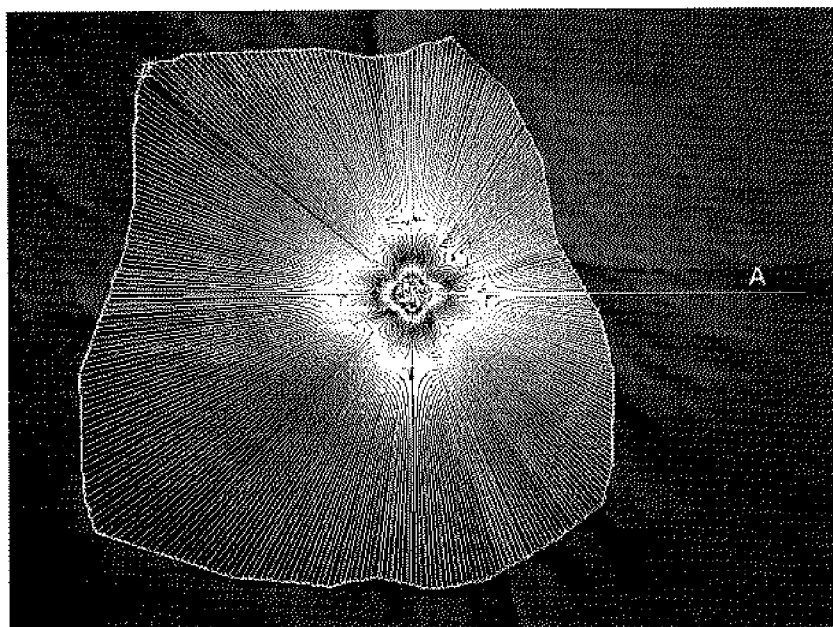


Figure 3. Digitized image of a larval crystal of a halibut otolith using Nomarski interference contrast illumination. The 360 radial lines emanate from the central nucleus and extend to the boundary of the larval crystal. The minimum and maximum length radial lines were extracted including their angle with respect to the reference line A.

try can complicate the model design. The advantage of using both otoliths however, is that it provides a measure of variation found within an individual and this can assist in understanding the processes which may ultimately control the variation in pattern.

Results

Nomarski interference contrast illumination provided a perspective on the otolith morphology distinct from that commonly observed with transmitted light or even with scanning electron microscopes. While the method did not give an indication of daily increment deposition, it did show the boundary of the larval crystal, and in addition brought out other patterns that were unexpected. For example the cone that seems to surround the nucleus in Figure 1 was apparent in all specimens examined. The three dimensional appearance of the structure is

Table 2. Mean Angle α , dispersion s , the Rayleigh test statistic R , and adjusted probability level p , for tests of directedness, for each of the three angle measurements.

	COMAngle	MaxRadiAngle	MinRadiAngle
Mean Angle α	154.02	172.00	47.22
Dispersion s	84.78	81.83	98.76
Test statistic R	12.05	12.98	8.15
Probability level	$0.08 > p > 0.04$	$0.04 > p > 0.02$	$p > 0.40$

somewhat of an artifact of this type of illumination but it does indicate a difference in the refraction of light. Interestingly this feature did not appear to coincide with an event such as metamorphosis or first feeding that might be expected from an examination of larval increments (Hagen 1985). One possible explanation is that it shows the location of the sulcus during the early larval stages, and the pattern is visible with Nomarski lighting because there is a shift or folding in the orientation of the crystalline axes at that point.

Since the purpose of the study was to see, in a practical sense, if there was some simple measure of the larval crystal that could be used to delineate stocks, a variety of measurements were taken from each otolith to ensure that all attributes of the shapes were considered. Many of the measurements were positively correlated with one another. Area was significantly correlated, using a Bonferroni adjustment, with seven of the other variables. Other measures, such as breadth, showed fewer significant positive correlations. The indices circularity and rectangularity were not significantly correlated with any other measurement.

The three angle measurements were considered separately in the analysis due to the difficulties in trying to linearize circular scales (Batschelet 1981). In Table 2, I pooled the left and right otoliths from all nursery areas to see if there was a consistent direction for growth away from the nucleus (COMAngle), for the orientation of the minimum radial length (MinRadAngle) and for the maximum radial length (MaxRadiAngle). As shown in Table 2 there did appear to be a consistent direction associated with maximum radial length, but no indication that the other measurements are different from a random distribution as indicated by Rayleigh's test (Batschelet 1981). When the data are broken down by otolith pair and nursery area (Table 3), Rayleigh's

Table 3. Mean angle with respect to anterior end of the otolith for three measurements of larval crystal shape, by location of capture and otolith side. No measurements were found significant ($p < 0.05$) after applying a Bonferroni adjustment for multiple testing.

	COMAngle		MaxRadiAngle		MinRadiAngle	
	Right	Left	Right	Left	Right	Left
B. Bay	152.6	89.3	146.3	164.7	15.9	125.7
PWS	64.2	169.3	63.8	161.8	75.4	22.2
SE AK	165.2	132.5	162.0	132.7	52.5	24.2

test was not significant for any of the groups, though with the exception of the right otoliths from the Prince William Sound, there was a tendency for the larval crystal to grow more toward the posterior axis of the otolith. In general though, the lack of consistency within any of the angle measures suggests that the orientation of the shapes was quite variable.

To examine the other twelve measurements and the extent to which variation in the shape can be explained by the effects of location, individual, and otolith side, I first checked for normality of each variable and applied a partial hierarchical nested analysis of variance model (Winer 1971). In this design, location L , is treated as a fixed effect, individual I , within location, is treated as a random effect, nested by location, and the otolith side S , is treated as a fixed effect which can have an interactions with location and with individual within location. The model can be written as

$$VAR = C + L + I[L] + S + S * L + S * I[L]$$

where C is a constant and the brackets $[]$ indicate the associated factor is nested, and $*$ indicates an interaction effect between factors. Since there is no within-cell variation (i.e. only one otolith pair per fish) the model is complete and, as written, there is no error term. To test for the effects of location using the F statistic,

$$F_L = MS(L) / MS(I[L]),$$

while to test for the other effects x ,

$$F_x = MS(x) / MS(S * I[L]).$$

Table 4. Unadjusted and (modified Bonferroni adjusted) p -values for model $VAR = C + L + I[L] + S + S * L + S * I[L]$, where L is nursery area location, I is individual, and S is otolith side.

Variable	L	$I[L]$	S	$S * L$
Area	0.67 (1.00)	0.91 (1.00)	0.94 (1.00)	.70 (1.00)
MajorAxisLength	0.64 (1.00)	0.78 (1.00)	0.78 (1.00)	0.75 (1.00)
Breadth	0.50 (1.00)	0.82 (1.00)	0.05 (0.55)	0.01 (0.12)
Circularity	0.14 (1.00)	0.26 (1.00)	0.41 (1.00)	0.05 (0.50)
Rectangular	0.76 (1.00)	0.15 (1.00)	0.003 (0.04)*	0.44 (1.00)
COMdistance	0.10 (1.00)	0.99 (1.00)	0.85 (1.00)	0.74 (1.00)
Min Radi	0.53 (1.00)	0.07 (0.70)	0.37 (1.00)	0.01 (0.12)
Max Radi	0.25 (1.00)	0.80 (1.00)	0.79 (1.00)	0.75 (1.00)
Mean Radi	0.85 (1.00)	0.88 (1.00)	0.78 (1.00)	0.58 (1.00)
SD Radi	0.09 (1.00)	0.98 (1.00)	0.66 (1.00)	0.62 (1.00)
Skew Radi	0.34 (1.00)	0.05 (0.55)	0.94 (1.00)	0.80 (1.00)
Kurtosis Radi	0.52 (1.00)	0.03 (0.36)	0.86 (1.00)	0.14 (1.00)

I applied this model to each of the twelve measurements separately. Applying this model to all measurements simultaneously in a MANOVA test proved problematic with this particular design. The p -values for the test of each effect by variable is shown in Table 4. Because separate testing was done but the measurements are not independent of each other, to be conservative and avoid erroneous conclusions I applied an adjustment to p -values based on a sequential modified Bonferroni procedure (Wright 1992). The adjusted p -values is shown in parentheses next to the model p -values, with a asterisk denoting a significant effect based on an alpha level of 0.05.

From Table 4 there was no significant location effect in any of the measurements. Knowledge of a fish's nursery area of origin does not explain any significant variation in the patterns, and thus the use of any of these patterns as a natural tag does not appear feasible.

Table 4 also shows the p -values for the variation explained by the individuals within location. As with the location effect, using a Bonferroni adjustment there was no significant variation in the patterns that could be attributed to the fact that an otolith pair comes from the same individual. In addition there is insignificant variation explained by the otolith side factor or its interaction with location. The only measure that appeared to have any significance using the

Bonferroni adjustment was the index of rectangularity, in which the left otolith is, on the whole, closer in shape to square than is the right otolith. If that effect is indeed real, it could be a reflection, and an early indication of the asymmetric differences in otolith thickness that is apparent in juvenile and adult halibut otoliths.

The next lowest *p*-values in Table 4 were breadth and minimum radius length in the interaction effect of side and location. In both cases the effect is due to differences in the shape of the Prince William Sound otoliths. For breadth, the left otolith is larger than the other two areas and for the minimum radius length, the right otolith is shorter than the other areas. While these effects are not significant they do suggest that some characteristics may distinguish the Prince William Sound samples from the other samples. The other two areas however, show no distinguishing variables which separate them.

Figure 4 shows the radial lines and the outline of the larval crystal from two pairs of otoliths collected in Prince William Sound. The figure illustrates the variability in shape of the crystalline patterns.

Discussion

Lowenstam and Weiner (1989), in their review of the field of biomineralization, note that organisms from a wide variety of taxa can have large differences in the degree of control exerted during the process of mineralization of various structures. This control is exerted in the number and sites of nucleation, the differential growth of particular crystal facets, and the resulting crystalline morphology. The authors go on to note, that "even straightforward measurements of the dimensions of the individual crystals can provide important clues about the type of control exerted over crystal formation." (p. 105).

From the results of this study, the larval crystal shape was not a useful indication of a halibut's nursery area of origin. Furthermore, the general lack of systematic difference between left and right otoliths and high within-individual variation suggest that the processes that influence the formation of the larval crystal shape are not under tight biological control.

From the measurements in this study and from examining cross-sectioned otoliths, the larval crystals are spatially constrained by the accessory crystals in three dimensions. The shape of the crystals is determined by the relative differences in growth rates between the larval and accessory crystals, and the number, timing, and relative placement of the accessory primordia. Faster growth in the accessory primordia is inferred from the wider growth increments which are

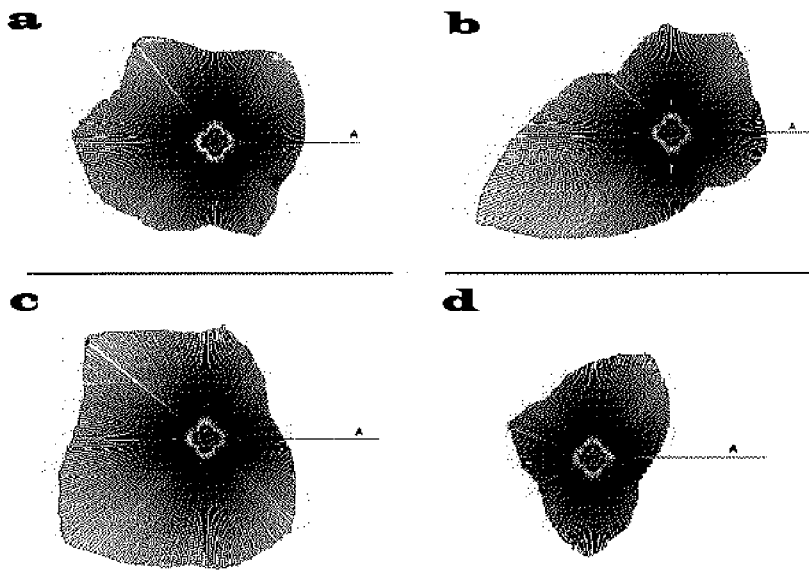


Figure 4. The larval crystal shapes from two halibut collected in a nursery area in Prince William Sound, with the left otolith (a) and the right otolith (b) of one halibut and the left otolith (c) and right otolith (d) of the other halibut. Line A is the reference line indicating the anterior axes of each crystal shape.

common to both crystal fields (P.T. Hagen, unpublished data) and is a common phenomenon with other species (Toole et al. 1993, Campana and Neilson 1985). Faster growth is an indication that the accessory crystals are energetically more favorable sites of ion deposition and it may indicate that a shift has taken place in the direction of ion transport to crystals (Mann et al. 1989). Gaudie and Nelson (1990) propose a pH gradient as the mechanism which directs crystalline growth of otoliths.

The sites of the accessory nucleation were not explicitly measured in this analysis of shape, primarily because it would require a three dimensional perspective. However from Figure 4 it is reasonable to infer that primordia are likely located close to where the outline of the crystal shapes are concave. The relative location of these sites help determine the final crystal shape.

Control over sites of nucleation is one of the primary means organisms use to form shape-specific biomineralized structures. Control is apparently maintained through the organic components. So-called macromolecules can at times inhibit or promote nucleation along particular crystallographic axes (Lowenstam and Weiner 1989). The rapid crystalline growth radiating from the accessory primordias, however, would tend to suggest that the molecular form of control, if it does occur, is inhibitory for the most part. Otherwise, we would expect to see more sites of nucleation than just the three or four which can be inferred from the outline of the larval crystal shape.

One observation from examining halibut larval otoliths (Hagen 1986) is that sites of accessory primordia frequently correspond to radial lines extending from the central nucleus. The central nucleus of halibut otoliths is likely composed of multiple primordia in close proximity which implies that the larval crystal is in fact composed of multiple prisms. The junctures of these different prisms, might be energetically more favorable sites for new nucleation if there is a discontinuity in the crystalline surface. Under this scenario, the location of accessory primordia may in some part be related to the spatial orientation of primordia at the very start of otolith formation. This observation may not be true in all cases of accessory primordia location, but to the extent that it is more than a chance association, it would indicate that final larval crystal shape is sensitive to conditions at the otolith's initial formation.

For halibut it appears that there is likely little functional need to tightly control the sites of secondary precipitation. Indeed given the function of sagittal fish otoliths for use in sound reception (Popper and Combs 1980), it is the outer shape of the otolith that likely provides utility to the fish. Perhaps not as critical are the details of how the otolith achieves that shape.

The results of this analysis may not be applicable to other species. Toole et al. (1993) noted a difference in the occurrence of accessory primordia between the left and right otoliths of Dover sole. Dover sole apparently can have a long and protracted transition from larval to juvenile life stages. Under these conditions, the shape of the otolith during the transitional period may be more critical, and in these instances, the organisms may exhibit greater biological control over the sites of secondary nucleation. What this study does show, however, is the importance of systematically incorporating both the left and right otoliths when extracting information from otoliths.

Despite the results of this study, it may be premature to conclude that there is no utility in examining other otolith patterns of halibut to identify stocks. Hagen and Quinn (1991) found that annulus patterns of young halibut follow broad long-term changes in temperature. To the degree that nursery areas are subject to different environmental conditions, it may be possible to use patterns such as the size of age zero or age one annuli to identify widely separated nursery grounds. In addition, though it may require more detailed preparation, daily increment widths from the first year's growth may also provide a means of distinguishing halibut nursery grounds. In either of these approaches, the results here suggest that within-individuals pattern variation also needs to be identified. Incorporating this variation can help determine the extent to which a pattern reflects extrinsic influences versus being a function of happenstance.

Acknowledgments

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Variations in Relative Abundance and Year-Class Strength of Petrale Sole off Oregon and Washington

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Abstract

Information on relative abundance and year-class strength (YCS) of fish is essential for the long-term management of fisheries. The objectives of this study were to determine interannual changes in relative abundance and year-class strength (YCS) of petrale sole off Oregon and Washington (Pacific States Marine Fisheries Commission, PSMFC, areas 2B: 42°50'N-44°18'N, and 3A: 45°46'N-47°20'N). Non-standardized catch rates of petrale sole (catches at all depths/all bottom trawl effort) and standardized catch rates (catches up to 420 m of depth/directed fishing effort toward petrale sole) were similar within each PSMFC area from 1966 to 1989. Both relative abundance indices showed a substantial decrease in areas 2B and 3A between the late 1970s and 1980s. However, non-standardized catch rates seemed to be increasingly underestimated since the late 1970s due to the greater number of groundfish species landed. Indices of YCS were based on summed-CPUE (catch rates for ages 6+7) and on cohort

analyses (age 6). These two YCS indices tended to be significantly correlated within and between areas 2B and 3A ($r > 0.44$, $P < 0.07$). However, survey data indicated that cohort analyses were more reliable YCS indices than summed-CPUE. Cohort analysis indices of YCS, computed from 1958 to 1977, showed that cohorts born between 1962 and 1965, and between 1973 and 1977 produced average to weak recruitment. Although strong and weak year classes coincided in both PSMFC areas, area 3A showed a more pronounced decline in catch rates and YCS than area 2B, which could be due in part to stock differences between areas. The common decline in YCS for cohorts 1973 to 1977 did not seem consistently associated in both areas with attendant trends in commercial catch rates and parental stock sizes. Thus, fishery independent factors may have been more important than stock size for the initial decrease of YCS in the 1970s. However, the declining trend of YCS for the cohorts born in the 1970s was reflected in the decrease of catch rates since the late 1970s.

Introduction

Petrale sole (*Eopsetta jordani*) is a relatively large flatfish of the family Pleuronectidae. It is reported from Coronado Island, Baja California, to the northern Gulf of Alaska (Miller and Lea 1972). Commercial catches of petrale sole occur between Santa Barbara, California, to Hecate Strait, British Columbia (Pedersen 1975a). The effect of fishing upon the abundance and year-class strength (YCS) of this species is poorly understood. For petrale sole off British Columbia and Washington, decreased yields have been ascribed to fishing (Cleaver 1949), both to heavy exploitation and long-term recruitment failure (Barraclough 1954), and to recruitment variations largely independent of parent stock size (Pedersen 1975a). In addition, Ketchen and Forrester (1966) stated that both fishing and environmental factors could explain long-term changes in yield and recruitment of this species.

Petrale sole start recruiting to the Oregon-Washington trawl fishery at 3 years of age, but full recruitment is not completed until ages 6 or 7. For petrale sole off Oregon, Lenarz (1978) indicated important YCS variations, and Demory (1984) suggested variable recruitment, but no trends for year classes born between 1960 to 1975 off Oregon-Washington. However, he indicated a general decrease in relative abundance of petrale sole since the late 1970s. For petrale sole off the Oregon-Washington coast, Castillo et al. (1994) reported

significant correlations between environmental factors and YCS of cohorts born between 1958 and 1977.

Indices of YCS based on catch tend to be overestimated during upward trends in effort on a stock, and YCS indices based on catch-per-effort tend to be affected by opposite bias (Pedersen 1975a). On the other hand, estimates of YCS derived from virtual population analysis (e.g., Pope 1972) have been considered more reliable than catch-per-effort indices (Hayman et al. 1980). However, only catch rates (Ketchen and Forrester 1966) and landings of partially recruited ages (Demory 1984), have been used as quantitative indices to estimate YCS of petrale sole.

The objectives of this study were to: (1) estimate general changes in relative abundance using two different estimates based on catch rates and (2) determine and compare the magnitude of YCS variations for petrale sole in Pacific States Marine Fisheries Commission (PSMFC) areas 2B and 3A (formerly PMFC areas, Figure 1). areas 2B and 3A have supported the highest landings of petrale sole off Oregon and off southern Washington. On average, females account for 58% of the numbers and 65% of the weight landed of petrale sole in each area (Castillo 1992).

Although over 98% of the catches of petrale sole have come from otter trawling (Pedersen 1975a), the orientation of fishing effort to different species has changed through time, making it difficult to obtain a consistent measure of relative abundance. In addition, landing statistics have not accounted for all groundfish catches taken by offshore foreign fleets. Besides, both fishing depth ranges and fishing power of domestic vessels have increased since the late 1970s. Thus, new analyses on the changes in relative abundance and YCS of this species require the use of alternative methods to those considered in previous studies.

Data and Methods

Indices of YCS derived from fishery data were based on summed-CPUE (Hayman et al. 1980) and on the cohort analysis version II of Jones (1981, after Pope 1972). These two types of YCS indices were estimated separately from fishery data for PSMFC areas 3A and 2B. Age frequencies of petrale sole derived from surveys conducted by the Oregon Department of Fish and Wildlife (ODFW, Robert Demory, unpublished data, Newport, OR 97365) were used to compute relative YCS indices for PSMFC areas 2B and 2C+3A, hereinafter referred to as

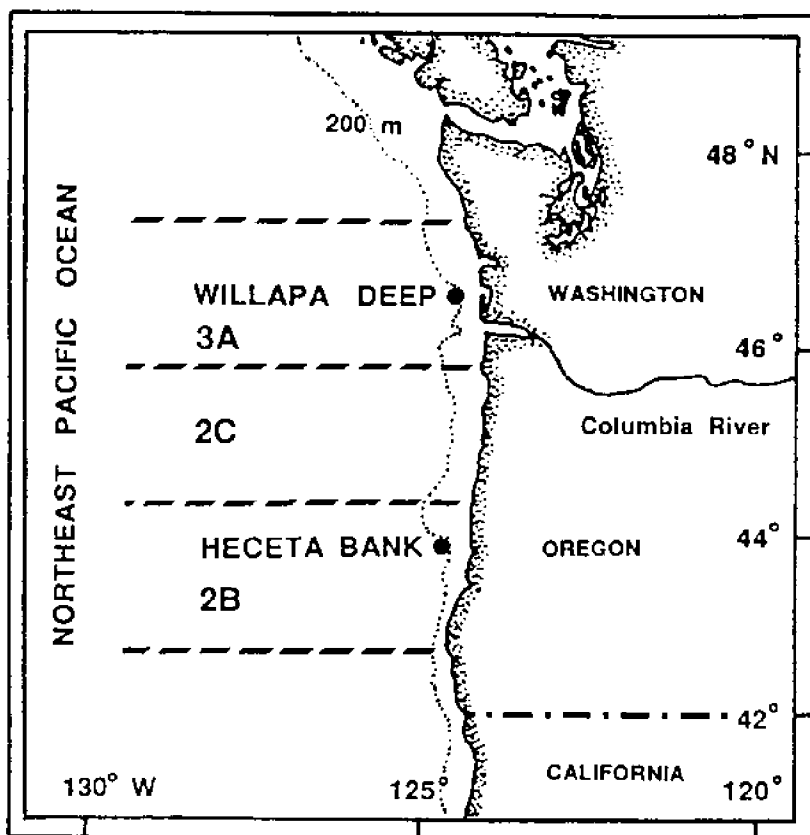


Figure 1. Location of Pacific States Marine Fisheries Commission (PSMFC) areas considered in this study. Also shown are the locations of Willapa Deep and Heceta Bank spawning grounds of petrale sole in areas 2B ($42^{\circ}50'N$ - $44^{\circ}18'N$) and 3A ($45^{\circ}46'N$ - $47^{\circ}20'N$). From Castillo et al. (1994), after Pedersen (1975a).

areas 2B, 2C and 3A. ODFW survey data were also used to evaluate YCS indices based on relative abundance and to correct cohort analysis indices for year classes born from 1960 to 1971.

Age composition of petrale sole used in this study was based on the surface aging method of otoliths (blind side sagitta). However, recent use of the break and burn technique showed that surface aging of otoliths underestimates the age of males if they are over 8 years of age (William H. Barss, ODFW, Newport, OR 97365, unpublished data).

Nevertheless, variation of YCS in females should be reflected in males since male and female numbers were significantly correlated in landings. This conclusion was also supported by age frequencies of males and females obtained from ODFW surveys.

The age composition from commercial bottom trawl landings was provided by ODFW from 1966 to 1981, and for 1987 and part of 1986. Age composition for 1976 in area 3A was obtained from sampling conducted by the Washington Department of Fisheries (WDF). The remaining age composition from 1982 to 1989 was estimated as a part of this study using otolith samples collected by ODFW.

Landing data from 1966 to 1981 were obtained from PMFC (1964 to 1984). Total landing estimates from 1982 to 1989 were obtained from unpublished data furnished by ODFW and WDF.

Data Analyses

Because available age composition from commercial samples was biased by discards of small fish, it was necessary to use age-specific estimates of discard rates (TenEyck and Demory 1975; Robert Demory, ODFW, Newport, OR 97365 unpublished data). No YCS estimates were computed for age groups under age 6 due to potentially higher discard rates for stronger cohorts.

Estimates of YCS indices required data on age-specific mean weight of females from landings. As this information was not available for all years, it was estimated from age-weight relations of females, and length-weight relations for both sexes. The regression of fish weight on fish length used is $W = aL^b$, where W is the total fish weight (g) and L is the total fish length (mm). The parameters a and b were computed from log-transformed weight and length data as: $\ln[W] = \ln a + b \ln [L]$, ($r > 0.90$, $P < 0.01$). There were significant differences between the regression parameters for each area and sex ($P < 0.05$). The transformed regression parameters by area and sex were:

Area 2B:	Females:	$W = 2.67 \times 10^{-6} L^{3.248}$
	Males:	$W = 6.90 \times 10^{-6} L^{3.083}$
Area 3A:	Females:	$W = 1.49 \times 10^{-6} L^{3.348}$
	Males:	$W = 9.78 \times 10^{-6} L^{3.027}$

ODFW survey data used in this study were available within areas 3A and 2C for 1971 and 1973, and within area 2B for 1972 and 1974 (Figure 1). Because annual age frequencies from surveys were not affected by discard rates and were computed from a larger number of samples than those from the fishery, survey data were deemed more

reliable indicators of year to year relative differences in YCS than landing data.

General differences in YCS were estimated from surveys by comparing and following individual brood years through the years (Demory et al. 1976). Only female age composition was utilized to compute relative YCS indices because of the unreliable age estimations of male fish mentioned previously. As age frequencies in areas 2B, 2C and 3A showed common strong year classes in succeeding years, the age frequencies for areas 3A and 2C were combined to increase the representation for years 1971 and 1973.

Changes in relative abundance were estimated using non-standardized and standardized catch rates. Non-standardized catch rates were computed by dividing the total annual landing of petrale sole in areas 2B and 3A by the attendant total annual bottom trawl fishing effort. Since the range of fishing depths increased through the period 1966-1989, standardized catch rates consider a constant depth range of fishing per area, and only include the fishing effort in which petrale sole catches were reported. The latter was done to reduce the effect of changes in orientation of total fishing effort to other species. As the landings of petrale sole in areas 2B and 3A during the middle 1960s occurred at depths shallower than 420 m, this depth was selected as a limit to standardize catch and fishing effort information through time. For each PSMFC area, the standardized annual fishing effort (Oregon-Washington fleets) directed toward petrale sole (f) was computed as fishing days (24 hr/day) by the relation:

$$f = (f_o \times C) / C_o \quad (1)$$

where f_o is the annual Oregon groundfish fishing effort in which attendant Oregon landings of petrale sole (C_o) were reported in logbooks at depths of up to 420 m, and C is the estimated total landing of petrale sole per area (2B or 3A) up to 420 m of depth. C was calculated as the total annual landing of petrale sole at all depths multiplied by the annual proportion of Oregon landings up to 420 m of depth (computed from Oregon fishing logbooks). Since both f_o and C_o were based on partial annual sampling of Oregon logbooks, they do not reflect interannual changes in total fishing effort and landings in equation (1), but changes in their annual ratio (f_o/C_o). However, this procedure allowed to estimate both standardized annual catch rates (C/f), and summed-CPUE indices for cohort born in year t . The latter was computed as:

$$\text{Summed-CPUE}_i = \sum_j^{j+1} (N_j/f_{i+j}) \quad (2)$$

where N_j is the number of females at age j and f_{i+j} is the corresponding standardized fishing effort for year $i+j$. Summed-CPUE indices were computed for ages (6+7) and for ages (8+9).

Cohort analysis required estimates of instantaneous annual rates of natural mortality (M), fishing mortality at a terminal age (F_t) and the numbers of fish caught at different ages for a given year class. The number of females was back-calculated by cohort analysis from age 12 to age 6 for cohorts born from 1960 to 1977, and from age 12 until ages 7 and 8 for cohorts born in 1959 and 1958 respectively. The previous difference in back-calculations is due to lack of age composition prior to 1966.

As indicated by Jones (1981) and evidenced in the present study, potential errors in the estimated catch at older ages in some cohorts prevented the use of a standard method for computing F_t for all cohorts. In the case of most cohorts, F_t was computed as $Z - M$, where Z is the total instantaneous mortality and M is as previously defined. Z was calculated as the slope of the regression: $\ln [N_j/f_{i+j}]$ on age j , where j ranges from age 8 to 12, and f_{i+j} is as described in equation (2).

Available estimates of M used for cohort analyses were the same for areas 3A and 2B ($M = 0.16$; Castillo 1992). However, the F_t values for some of the cohorts were corrected by survey and catch data. Such correction of F_t was required because of: (1) the disagreement between the resultant YCS and the relative YCS determined from surveys, and (2) the improbably low (or high) catch estimates at older ages which could produce large bias in the back-calculated number of fish at smaller ages.

The correction of F_t values was based on two methods: (1) percentages of age frequency derived from surveys, and (2) comparison of summed-catch for individual cohorts. In method 1, age frequencies from age groups 3 to 11 obtained from surveys were computed for cohorts 1960 to 1971. Then, the ratios of age frequencies for adjacent cohorts at the same age were used to estimate YCS ratios for adjacent cohorts (Table 1). The F_t values selected by this procedure were those producing cohort analyses back-calculations of fish numbers at age 6 consistent with the median ratio of percentage of age frequencies for adjacent cohorts.

Table 1. Ratios of percentage of age frequencies between adjacent cohorts ($\text{year}_t/\text{year}_{t-1}$) for a same age group of female petrale sole. Only cohorts with age groups ranging from age 3 (1971 and 1970) to age 11 (1961 and 1960) were compared. (Based on survey data for PSMFC areas 3A+2C and 2B provided by Robert Demory, ODFW, Newport, OR 97365.)

Adjacent cohorts	Years compared			Median
	1971-72	1972-73	1973-74	
1971 / 1970	–	–	1.06	1.06
1970 / 1969	–	3.18	1.63	2.40
1969 / 1968	0.33	0.58	0.43	0.43
1968 / 1967	1.34	1.19	0.65	1.19
1967 / 1966	0.44	0.77	0.60	0.60
1966 / 1965	1.74	1.28	1.84	1.74
1965 / 1964	1.78	2.51	1.24	1.78
1964 / 1963	0.66	0.63	2.61	0.66
1963 / 1962	2.80	0.67	2.61	2.61
1962 / 1961	0.69	0.33	–	0.51
1961 / 1960	2.68	–	–	2.68

Method 2 was used for cohorts in which catch estimates at older ages were questionable, but for which no survey information was available, estimates of F_t were based on values reflecting an increase (or decrease) in summed commercial catches between adjacent cohorts. As catches for younger age groups were not available for all cohorts, only ages 8 to 12 were included in the previous summed-catches.

The agreement between summed-CPUE YCS indices and cohort analyses YCS indices was compared within and between areas 2B and 3A by Spearman-rank difference correlations (Tate and Clelland 1957).

Results

Catch rate estimates

Non-standardized annual catch rates of petrale sole were similar to standardized annual catch rates in each area. However, interannual variations were greater in area 3A than in area 2B (Figure 2). Relative abundance could have been increasingly underestimated by non-

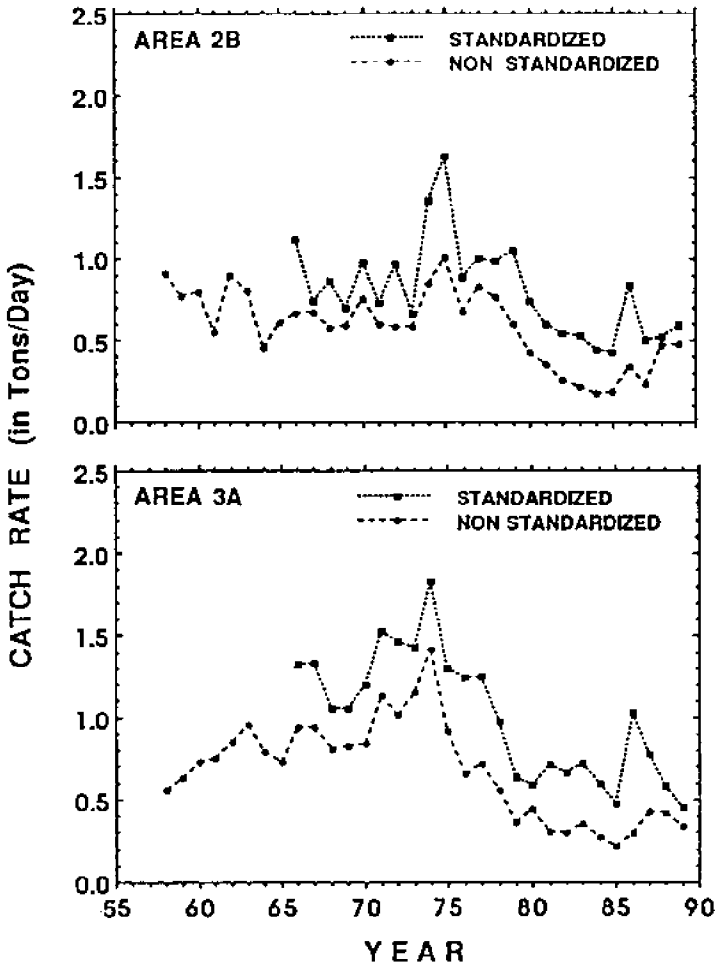


Figure 2. Catch rates of petrale sole in PSMFC areas 2B and 3A. Standardized catch rates consider all fishing effort resulting in petrale sole catches to a depth of 420 m. Non-standardized values consider all groundfish fishing effort and fishing depths per area, including fishing trips that did not capture any petrale sole.

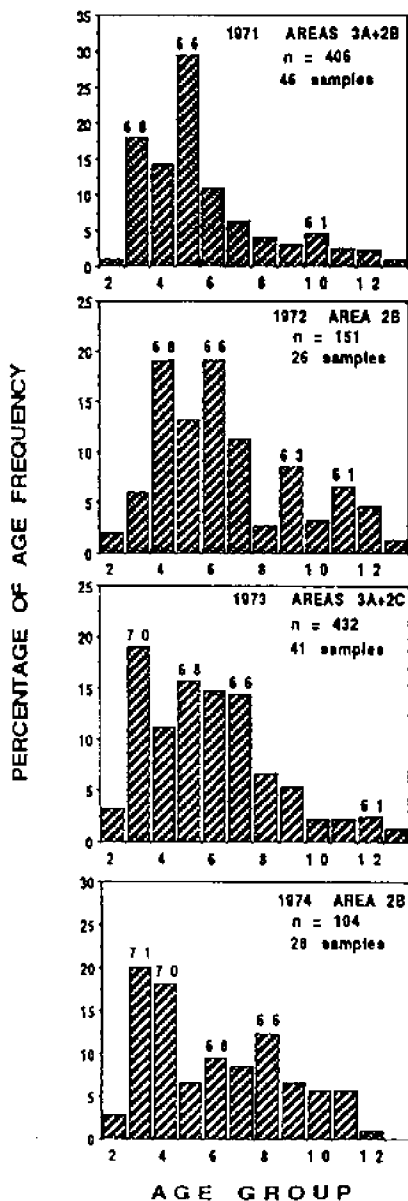


Figure 3. Relative year-class strength indices of petrale sole based on the percentage of age frequency of females obtained from surveys in PSMFC areas 2B and 3A. (Computed from data provided by Robert Demory, ODFW, Newport, OR 97365.)

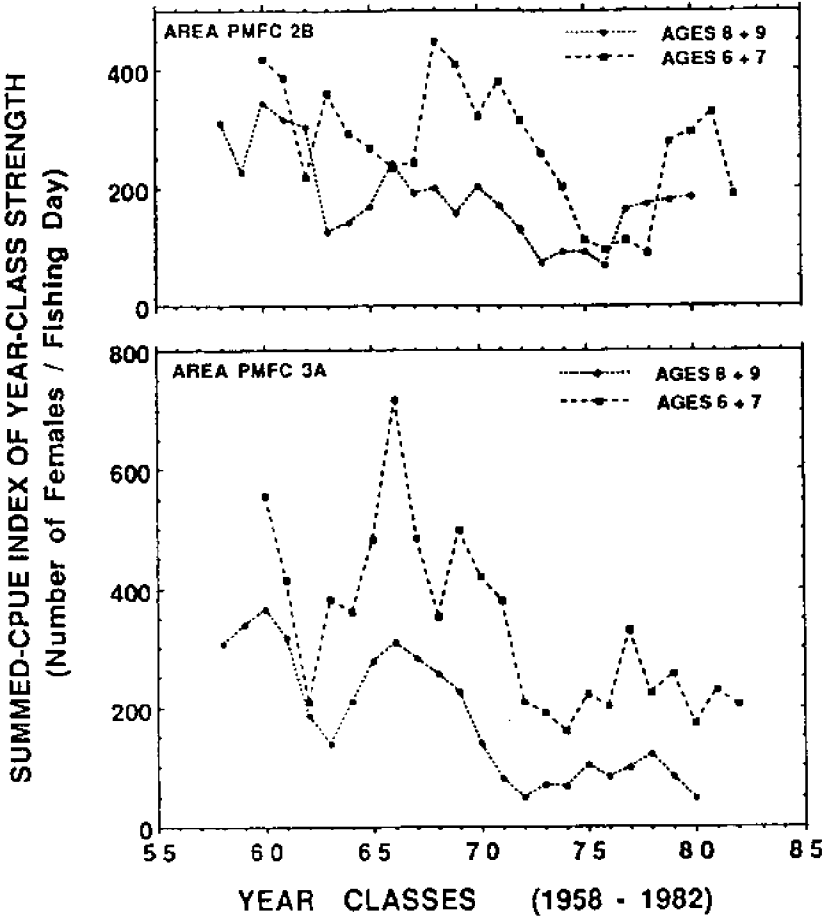


Figure 4. Estimates of year-class strength of petrale sole in PSMFC areas 2B and 3A based on summed-CPUE indices for females of ages (6+7) and ages (8+9).

standardized catch rates from the late 1970s because of the greater number of species landed, or due to the attendant increase in fishing effort. Standardized catch rates also indicated a substantial decrease in relative abundance since the late 1970s in areas 2B and 3A. A slight increase in catch rates was observed in both areas after 1985, but it persisted only in area 2B until 1989.

Relative YCS from surveys

This index was used to compare YCS between adjacent cohorts from year classes born from 1960 to 1971. Large differences in relative YCS were indicated from these age frequencies. Cohorts born in 1961, 1966, 1968, 1970 and 1971 appeared to be consistently strong (Figure 3). These YCS patterns were also supported by ratios of age-frequency percentages between adjacent cohorts (Table 1).

YCS indices based on summed-CPUE

Both the indices for ages (6+7) and ages (8+9) showed a decreasing trend in YCS from cohorts born in the middle 1960s to the middle 1970s. From this last period until 1982, these two indices suggested a small recruitment increase in area 2B (Figure 4). The correlation between Summed-CPUE indices for year classes born from 1960 to 1980 was higher for area 3A ($r = 0.83$, $P < 0.01$) than for area 2B ($r = 0.38$, $P < 0.09$). The lower consistency between indices for area 2B suggested that these could be less reliable than those for area 3A. Despite the differences in each area, older age groups are more susceptible to differences in fishing mortality among cohorts. Thus, the index for ages (6+7) was considered more reliable than the index for ages (8+9). Relative differences in YCS from year to year seen from survey data were generally not reflected in summed-CPUE indices, particularly in area 2B, which further supports the lower reliability of summed-CPUE indices for this area.

Cohort analysis estimates

The F_t values adjusted from survey age frequencies or summed-catches tended to differ from other F_t values (Tables 2 and 3). However, since calculated values of annual instantaneous fishing mortality derived from cohort analyses tend to converge toward younger age groups (Pope 1972), temporal comparisons among fishing mortalities should be more reliable for younger age groups. The F_t values for age 6 suggested that year classes born in the 1970s generally had higher

fishing mortalities than cohorts born in the 1960s (Figure 5). Moreover, the average estimate of annual instantaneous fishing mortality at age 6 for year classes 1960 to 1977 was smaller, and less variable, for area 2B (average = 0.16, s.d. = 0.07) than for area 3A (average = 0.24, s.d. = 0.12).

YCS indices between age 6 and age 8 were significantly correlated in area 3A ($r = 0.93$, $P < 0.001$) and area 2B ($r = 0.94$, $P < 0.001$). Since cohort analysis back-calculations until age 6 were influenced by older age groups, these high correlations are not unexpected. Because of the greater contribution of older age groups needed to estimate the number of fish at age 6, YCS for this age group is considered the most reliable YCS index. However, due to the high correlation between cohort analyses estimates for ages 6, 7 and 8, the numbers of fish at ages 6 and 7 for cohorts 1958 and 1959 were estimated by simple linear regressions of ages 6 and 7 on age 8 ($r > 0.93$, $P < 0.001$, Tables 2 and 3).

Cohorts born from 1962 to 1965 and from 1973 to 1977 were intermediate to weak year classes in areas 2B and 3A (Figure 6). The declining trend of YCS for the cohorts born in the 1970s was reflected in lower catch rates since the late 1970s (Figure 2). Thus, despite the relatively large number of age groups of petrale sole in the Oregon-Washington fishery, the co-occurrence of weak cohorts may have substantial effects on commercial catch rates.

Comparison of YCS indices between areas

Area 3A showed consistently greater summed-CPUE indices and numbers of fish reaching age 6 than area 2B (Figures 4 and 6). With the exception of a marginally significant correlation between the summed-CPUE indices of area 3A and the cohort analysis index for area 2B ($P = 0.06$), all other YCS indices were significantly correlated (Table 4). The previous exception is apparently due to the relatively lower decrease of YCS in area 2B than in area 3A for cohorts born since the early 1970s. The substantial YCS decline beginning from the early 1970s seems to have occurred first in area 3A and next in area 2B and it is supported both by summed-CPUE and cohort analysis indices.

Discussion

The decrease in summed-CPUE and cohort analysis YCS indices for year classes born since the early 1970s was reflected in the decline of

Table 2. Terminal fishing mortalities (F_t) and numbers of female petrale sole reaching ages 6 to 12 in PSMFC area 2B. Values were based on cohort analyses. (Ages 6 and 7 of cohort 1958 and age 6 of cohort 1959 are regression estimates based on age 8.)

Cohort	Age group (thousands of fish)							F_t
	6	7	8	9	10	11	12	
1958	208	142	90	53	39	27	16	0.38
1959	278	199	137	103	75	50	34	0.33
1960	309	243	184	130	90	42	29	0.38
1961	385	312	236	175	112	70	53	0.28
1962	231	185	137	64	37	19	8	1.20 ^a
1963	296	233	144	106	74	53	25	0.25 ^a
1964	240	162	110	71	49	31	19	0.45
1965	280	206	139	101	66	41	30	0.08 ^a
1966	487	379	300	230	171	132	107	0.72 ^a
1967	352	284	207	144	103	80	60	0.19 ^a
1968	419	321	211	139	99	63	44	0.25
1969	349	234	149	106	67	37	18	1.20 ^a
1970	426	303	222	146	98	67	43	0.32
1971	421	307	205	132	95	64	47	0.32
1972	373	269	166	113	79	55	34	0.22
1973	356	251	177	127	95	65	44	0.23
1974	259	178	120	80	41	19	5	0.72
1975	193	129	90	52	28	12	6	0.38
1976	157	101	68	45	28	13	10	1.19
1977	223	165	118	78	40	26	11	0.38

^a F_t adjusted by survey data.

standardized and non-standardized commercial catch rates since the late 1970s (Figure 2). YCS indices derived from cohort analysis are deemed the most reliable YCS indices in the present study as they account for differences in fishing mortality among cohorts, as well as differences in YCS based on surveys. On the other hand, summed-CPUE indices may be biased due to temporal differences in mortality rates among cohorts (presumably mainly fishing mortality) and changes in catchability through time, both of which further assume no trends for the comparisons to be reliable. Thus, the present summed-CPUE indices must be considered rough measures of YCS. The fact

Table 3. Terminal fishing mortalities (F_t) and numbers of female petrale sole reaching ages 6 to 12 in PSMFC area 3A. Estimates were based on cohort analyses. (Ages 6 and 7 of cohort 1958 and age 6 of cohort 1959 are regression estimates based on age 8.)

Cohort	Age group (thousands of fish)							F_t
	6	7	8	9	10	11	12	
1958	543	379	247	155	80	45	2	0.48 ^a
1959	544	394	248	134	72	36	7	0.55
1960	624	459	268	150	79	25	14	0.55
1961	692	508	370	243	166	111	76	0.23
1962	333	251	172	114	69	42	24	1.20 ^a
1963	421	288	183	134	91	48	19	0.36
1964	365	245	156	95	51	9	1	0.97
1965	547	365	253	158	92	65	45	0.02 ^b
1966	954	678	482	336	238	191	155	0.11 ^b
1967	703	508	348	227	154	121	75	0.36
1968	737	573	404	280	211	145	103	0.36
1969	558	386	231	146	70	32	15	1.20 ^b
1970	651	503	329	221	147	103	77	0.24
1971	570	382	267	168	124	95	58	0.21
1972	463	327	183	119	92	71	52	0.20
1973	415	209	136	94	57	27	10	0.33
1974	326	188	113	70	40	26	16	0.26
1975	332	213	109	44	18	9	1	0.92
1976	286	168	81	28	11	2	1	0.97
1977	424	241	108	63	41	33	21	0.03 ^a

^a F_t adjusted by summed catch from age 8 to 12.

^b F_t adjusted by survey data.

that similar conclusion was reported by Hayman et al. (1980) for Dover sole (*Microstomus pacificus*), but not for English sole (*Pleuronectes vetulus*) in area 3A, supports their view that species distribution may affect the reliability of summed-CPUE indices. Like Dover sole, petrale sole has wider bathymetric distribution than English sole (Alverson 1960).

The relative YCS indices of Demory et al. (1976), based on both sexes, were similar to the present relative YCS estimates based on females. Their small differences are ascribed mainly to the scarcity of

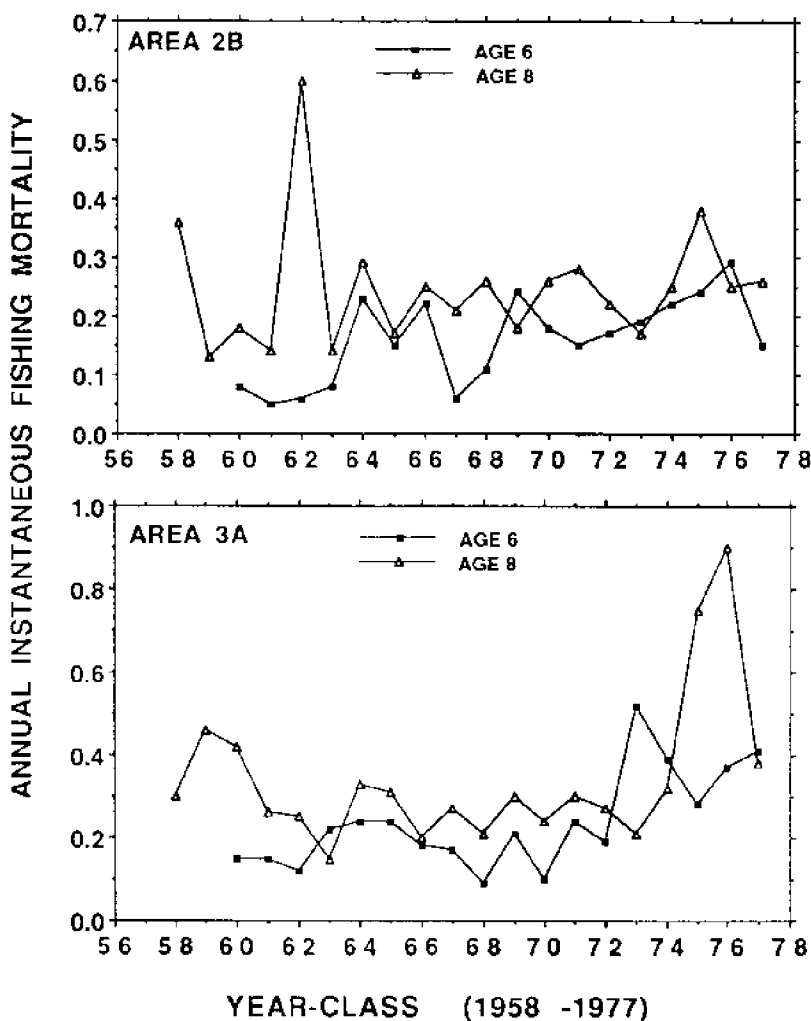


Figure 5. Cohort analyses estimates of annual instantaneous fishing mortalities for female petrale sole of ages 6 and 8 in PSMFC areas 2B and 3A.

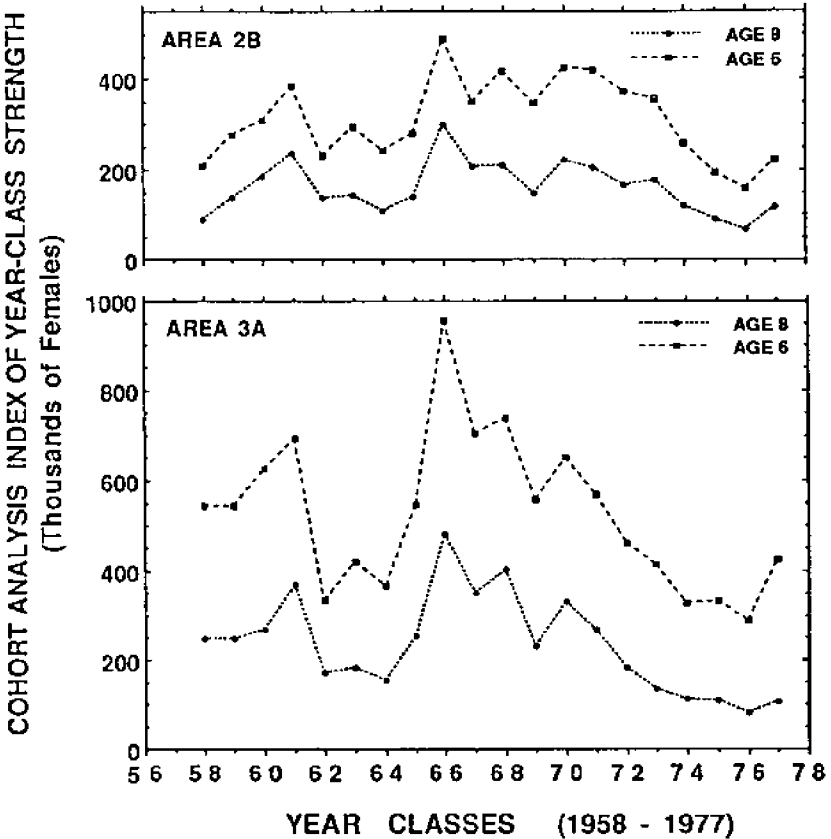


Figure 6. Year-class strength estimates of petrale sole based on cohort analyses of the number of females reaching 6 and 8 years of age in PSMFC areas 2B and 3A.

older males in survey samples. Moreover, Demory's (1984) recruitment index for petrale sole based on summed-catch of females from ages 5 to 7 in the Columbia area (43°N-47°30'N) was correlated with the present cohort analysis indices from 1960 to 1971 (area 2B: $r = 0.82$, $P < 0.01$; and area 3A: $r = 0.65$, $P = 0.03$). For most cohorts born in the 1970s however, Demory's (1984) YCS index may have greatly overestimated recruitment due to a substantial increase in fishing effort and landings in the late 1970s (Castillo 1992). Conversely, the present summed-CPUE indices could have underestimated YCS for cohorts born in the 1970s and 1980s. Yet, the decline in YCS shown by

Table 4. Spearman's correlations among YCS indices of petrale sole in PSMFC areas 2B and 3A. Indices used are the summed-CPUE index for ages 6+7 (Summed-CPUE) and cohort analysis estimates for age group 6 (Age 6). Cohorts included in the correlations were born from 1960 to 1977. (P-values are shown in parenthesis, n = 18.)

YCS Indices	YCS Indices		
	Summed-CPUE Area 3A	Age 6 Area 2B	Age 6 Area 3A
Summed-CPUE Area 2B	0.49 (0.04)	0.61 (0.01)	0.61 (0.01)
Summed-CPUE Area 3A		0.45 (0.06)	0.76 (< 0.01)
Age 6 Area 2B			0.82 (< 0.01)

summed-CPUE indices during the 1970s was consistent with cohort analysis estimates of YCS.

Previous tagging studies in petrale sole are useful to explain differences in recruitment patterns of petrale sole in areas 2B and 3A. Nearly 57% of the recoveries of petrale sole tagged in area 2B during its spawning period in Heceta Bank were obtained in this same area over a nine-year period (Oregon Fish Commission 1970). For area 3A, the attendant recovery over a period of eight years following a tagging in Willapa Deep was nearly 69% (DiDonato and Pasquale 1970). In both tagging studies, most of the remaining percentage of fish showed a northward migration (area 2B: 34%; area 3A: 29%). Moreover, only 2% of the recoveries tagged in area 3A showed southward migration, and only 13.6% of the recoveries tagged in area 2B were captured farther north than area 2C. This tendency for restricted latitudinal movement of fish suggests that YCS variations of petrale sole in areas 2B and 3A are largely due to independent but similar recruitment processes within each area. Tagging of petrale sole in southern and northern spawning areas are also consistent with a "homing" tendency in this species (Alverson and Chatwin 1957; Best 1963; Pedersen 1975b). Thus, tagging studies support the present use of separate YCS indices for areas 2B and 3A.

Although area 2B could have been grouped with area 2C to compute a more representative YCS index for the spawning group of Heceta Bank, insufficient age structure from commercial catches in area 2C prevented the inclusion of this latter area. Despite the greater relative abundance of petrale sole in area 3A than in area 2B, the stock in area 3A may have experienced a more drastic decline in abundance due to higher exploitation. Over the period 1966 to 1989, the average annual total catch of petrale sole was 245.7 tons in area 2B and 504.4 tons in area 3A. For the same period, the average total annual fishing effort was 328 days in area 2B and 576 days in area 3A. On the other hand, the declining trend in catch rates in areas 2B and 3A did not occur until the late 1970s. This suggests that the decrease of YCS detected for cohorts born since the early 1970s may have been initially more related to natural factors than to potential recruitment overfishing. Such possibility is consistent with unrelated trends in potential parental egg production and YCS of cohorts born between 1970 and 1977 (Castillo et al. 1994).

For average to weak year classes born from 1962 to 1965, no associated decline in catch rates was evident when these year classes entered the fishery. A reason for this may be the increased recruitment of cohorts born between 1966 to 1971. Besides, the simultaneous decline in YCS from 1962 to 1964 in both areas (Figure 6) is not explained by inverse trends in catch rates prior to 1966 in areas 2B and 3A (Figure 2). This fact is consistent with the suggestion of Ketchen and Forrester (1966) that the recruitment of petrale sole in some years may have been independent of the exploitation history. However, the combined effect of poor recruitment and increased fishing mortalities in the 1970s may explain the substantial decrease of catch rates seen in areas 2B and 3A between the late 1970s and 1980s.

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Population Dynamics of 0+ English Sole, *Pleuronectes vetulus*, in Estuaries and Nearshore Areas off Washington

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Abstract

Grays Harbor and Willapa Bay estuaries and the nearshore ocean area adjacent to them provide critical nursery habitat for 0+ English sole. Estuaries were far more important nurseries for 0+ English sole than the nearshore waters, as indicated by both higher densities and total population sizes in the estuaries. Significant exchange between estuarine and nearshore systems occurred over the entire study period. This exchange is typified by migration of small fish from the nearshore area to the estuaries and a return migration of large fish from estuaries. Emigration of large fish from the estuaries started as early as June, as indicated by a sudden increase in the mean length within the nearshore population between June and July each year. However, there appeared to be little net immigration into or emigration from the study areas during July through September each year. Therefore, the population of 0+ English sole in the study area can be treated as closed and results from the surveys can be used as an index of year-class strength. Year-class strength of English sole off Washington was established by July of their first year of life, and over the four years of this study, indices of recruitment showed a threefold difference at most. The ranking of the abundance within Grays Harbor, Willapa Bay

and the nearshore area did not vary between years and Willapa Bay consistently contained both the highest density and largest population of English sole during June through August. The significance of these findings in regard to designing long-term surveys of recruitment to the Washington-Oregon English sole stock is discussed.

Introduction

English sole spawn in offshore areas and the survival and transport of eggs and larvae is dependent on oceanographic conditions. Once metamorphosis and benthic settlement have occurred, English sole actively seek out estuarine nursery areas, and oceanographic influence becomes less important. Krygier and Pearcy (1986) demonstrated that Oregon coastal estuaries and nearshore areas are nurseries for 0+ English sole. The estuaries off Oregon are much smaller than those off the Washington coast in terms of space, however. Recent surveys (Shi 1987, 1994; Rogers et al. 1988; Gunderson et al. 1990) have revealed that there are large populations of juvenile English sole in Grays Harbor and Willapa Bay estuaries, as well as the adjacent open coast area.

Analysis of tagging data, distribution of adults, available spawning habitat and egg distribution (Shi 1994) suggests that the Grays Harbor and Willapa Bay estuaries serve as nursery area for English sole that spawn as far south as central Oregon. While further research is required to establish the overall importance of Grays Harbor and Willapa Bay estuaries in the Washington-Oregon production system, it appears likely that they are critical components.

Few studies to date have dealt with juvenile recruitment variation for English sole. In this paper, recruitment, density, spatial distribution and their variability are assessed for English sole in Grays Harbor, Willapa Bay and the adjacent nearshore area.

Methods and Materials

The study area

The study area is situated along the southern Washington coast and is composed of both nearshore and estuarine components (Fig. 1). The nearshore area is bounded to the north at 47°15'N, to the south at about 46°30'N, and extends from the shoreline seaward to a depth of 60 m. It encompasses an area of nearly 146,600 ha. The two major estuaries, Grays Harbor and Willapa Bay, along the Pacific coast of Washington are included in the study area.

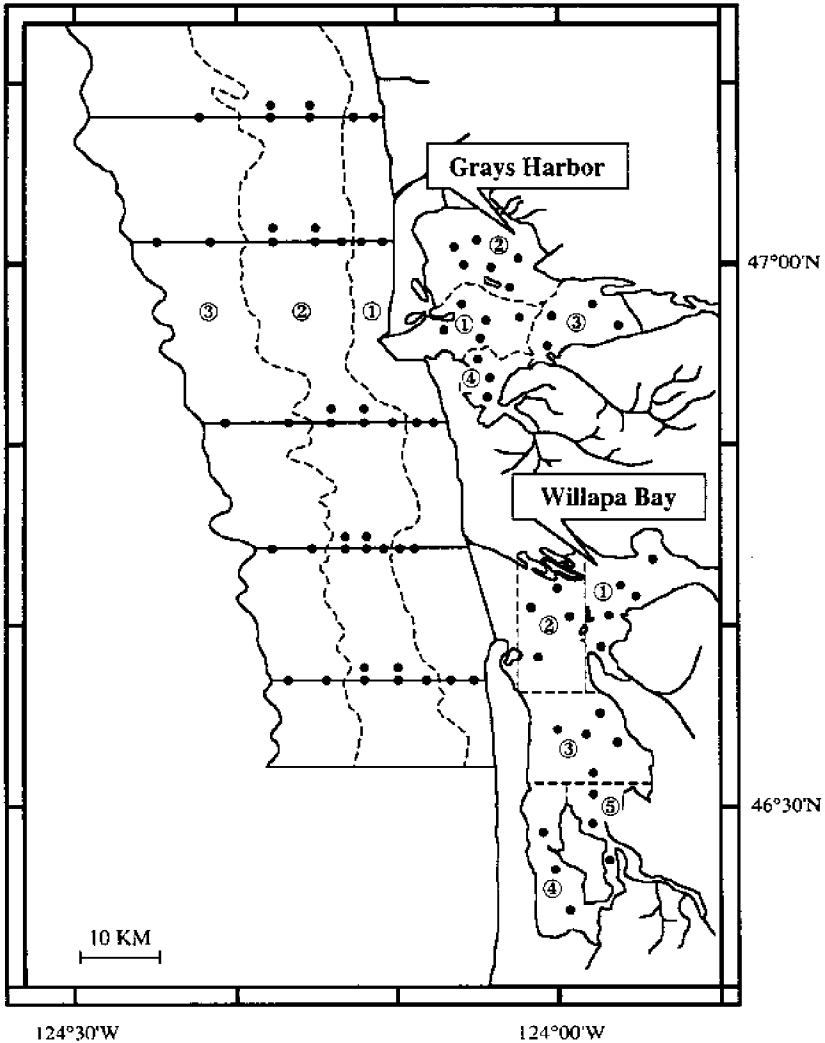


Figure 1. The study area along the southern Washington coast. Shown are subsystem boundaries, nearshore transect lines and trawl stations (filled circles). Dashed lines indicate survey stratum boundaries.

Grays Harbor is one of the significant estuaries located along the U.S. West Coast and is characterized by extensive mudflats, sandbars and low islands. The estuary is triangular in shape with a length of approximately 24 km and is 21 km at its widest point. The average depth is less than 6 m and 63% of its total surface area at Mean Higher High Water (MHHW) is exposed at Mean Lower Low Water (MLLW). Grays Harbor is the drowned valley of the Chehalis River, which supplies 80% of the freshwater input.

Willapa Bay has been described as one of the most productive and unspoiled estuaries along the U.S. West Coast (Hedgepeth and Obrebski 1981). It is an elongate body of water that is separated from the Pacific by a long barrier spit north of the Columbia River mouth. Willapa Bay is roughly 40 km long and 10 km at its widest point and is second in size (MHHW) among the west coast estuaries. At MLLW, over 50% of Willapa Bay is exposed as large expanses of intertidal mudflats, sandbars and low islands. Although the drainage basin is considerably larger than for Grays Harbor, industrial activity in the watershed is low and water quality is high.

Survey design

A stratified random sampling design was developed for both estuaries. Four different geographical strata were delineated within Grays Harbor (Fig. 1). Within each stratum, stations were randomly selected from a 1 km² grid superimposed on nautical charts, with the constraint that no two stations were immediately adjacent to one another. The effort (number of stations) allocated to each stratum was proportional to the abundance of English sole in the 1983 survey (Rogers et al. 1988).

Willapa Bay was divided into five strata (Fig. 1), based on habitat characteristics, i.e. the degree of oceanic influence. Each stratum was divided into 0.5 × 0.5 km grids, and stations were randomly selected with the constraint that no two stations could be immediately adjacent to each other. The number of stations assigned to each stratum was proportional to the anticipated abundance of English sole and Dungeness crab. Restropective analyses of the English sole data for 1985 and 1986 showed that no reallocation was necessary.

The nearshore area was sampled along fixed transects oriented east-west with trawl stations located at discrete depths (Fig. 1). Five transects were established, and sampling stations were located at depths of 5, 9, 18, 27, 36, 46, and 55 m (i.e. 3, 5, 10, 15, 20, 25, and 30 fm, respectively). The 55 m station was not sampled on the northern-

most transect, because of frequent gear damage. Additional effort was permanently allocated to the intermediate stratum, such that two trawl samples were taken at all 27 and 36 m depths. Sampling stations were stratified according to depth when making population estimates. On each transect, three depth strata grouped the two shallowest, the three intermediate and the remaining deeper stations together. The outer boundary for the nearshore study area was the 59 m (32.5 fm) isobath and the MLLW mark was the inner boundary. The boundary separating the inner and middle strata followed the 14 m (7.5 fm) isobath while the boundary between the middle and outer strata was at 41 m (22.5 fm). The northern and southern limits of the survey area were positioned 5 km beyond the northern and southern-most transects.

Each of the three areas was visited once a month. Sampling in estuaries was planned during low spring tides of the month (May/April through September) so that we could navigate easily among unmarked channels which are otherwise difficult to see. Stations in close proximity to intertidal areas were preferentially sampled at low tide so as to minimize bias associated with fish movement onto the tideflats at higher stages of tide. More exposed sites were typically sampled at high water. Trawling operations ceased when tidal currents were judged sufficiently strong that the trawl gear would not tend bottom properly. The nearshore sampling trips were usually made between the two estuary trips in that month.

Sampling gear and sampling procedures

Survey samples throughout the study area were collected using a 3 m plumb staff beam trawl specifically developed for this study (Gunderson and Ellis 1986). This system was scaled for use aboard small boats within estuaries and for larger commercial fishing vessels along the open coast. Effective width of the net was 2.3 m, while the estimated vertical opening was 0.6 m. The body of the net was 7-9 mm (lumen) knotless nylon and the codend was lined with 4 mm stretch mesh. A double tickler chain array was attached to a 9.5 kg wingtip weight at each corner of the net. The tickler chain array, together with the turbulent zone it creates, dislodged small animals from the substrate thus promoting capture by the net. This gear was very effective at capturing small juvenile English sole (total lengths > 15 mm) and Dungeness crab (*Cancer magister*; carapace widths > 6 mm), the primary targets of the larger study (Gunderson et al. 1990). This gear was used without modification throughout the study period.

Nearshore sampling was conducted from the 17 m stern trawler F/V *Karelia*. Tows in the nearshore were taken parallel to isobaths. Scope was routinely 5:1, except at the 5 and 9 m stations where it was 8:1 and 9:1, respectively. Time on bottom was estimated using a trigonometric relationship between water depth and wire out while the minimum linear distance towed (mean: 750 m) was determined from LORAN readings. Tow duration was routinely 20 minutes, except at the 5 and 9 m stations which often yielded excessive quantities of sand dollars (*Dendraster excentricus*) or other substrate; tows in these areas were limited to 5 or 10 minutes at a mean towing speed of 2.6 km hr⁻¹ (1.4 knots).

A 6.4 m Boston Whaler with a 150 hp outboard engine was used for all estuarine trawling. Buoys were deployed at the points where the net first contacted the bottom and subsequently left bottom upon retrieval. The distance towed (mean: 260 m) was estimated with an optical rangefinder. Mean towing speed was 2.8 km hr⁻¹ (1.5 knots) and was thus similar to that in the nearshore area.

Fishes present in nearshore trawl samples were sorted from the catches, frozen and transported to the School of Fisheries where further processing was carried out on English sole. Catches were sorted to species or species group and weighed. Weights, counts and length measurements (nearest 5 mm TL) were taken for all English sole. The upper total length limits for the 0+ age class of English sole were determined by visual inspection of modes in length frequency plots, as well as the results of previous studies on growth of 0+ English sole (Kendall 1966; Rosenberg 1982).

Data analysis

Abundance estimation

Density and population size were estimated by the area swept method. Nautical charts of Grays Harbor, Willapa Bay and the adjacent nearshore were digitized, and the area of each stratum determined. Formulas used for calculating densities, population and size composition by stratum and for all strata combined are presented in Table 1.

Using these procedures, certain simplifying assumptions were made which may bear on the quality of the estimates. A catchability coefficient of 1.0 was used for all sizes of fish, assuming that all individuals in the path of the net were captured and that all sizes were equally vulnerable to the net. All sampling areas were not equally accessible to the trawl gear, and density estimates for trawlable areas

Table 1. Formulas used for calculating densities, populations, and size composition by stratum and for all strata combined.

Calculation	Formula	
	Size composition	All lengths combined
Density for haul <i>j</i> in stratum <i>i</i> , (catch per hectare)	$D_{ijl} = \frac{qC_{ijl}}{wd_{ij}} \times 10,000$	$D_{ij} = \sum_{l=1}^L D_{ijl}$
Mean density for stratum <i>i</i>	$\overline{D}_{il} = \frac{1}{n_i} \sum_{j=1}^{n_i} D_{ijl}$	$\overline{D}_i = \frac{1}{n_i} \sum_{j=1}^{n_i} D_{ij}$
Variance of the mean density for stratum <i>i</i>	$Var(\overline{D}_{il}) = \frac{\sum_{j=1}^{n_i} (D_{ijl} - \overline{D}_{il})^2}{n_i(n_i - 1)}$	$Var(\overline{D}_i) = \frac{\sum_{j=1}^{n_i} (D_{ij} - \overline{D}_i)^2}{n_i(n_i - 1)}$
Population for stratum <i>i</i>	$P_{il} = A_i \overline{D}_{il}$	$P_i = A_i \overline{D}_i$
Variance of population for stratum <i>i</i>	$Var(P_{il}) = A_i^2 Var(\overline{D}_{il})$	$Var(P_i) = A_i^2 Var(\overline{D}_i)$
Total population	$P_t = \sum_{i=1}^s P_{il}$	$P_{tot} = \sum_{i=1}^s P_i$
Variance of total population	$Var(P_t) = \sum_{i=1}^s Var(P_{il})$	$Var(P_{tot}) = \sum_{i=1}^s Var(P_i)$

Parameters:

C_{ijl} = catch for length group

d_{ij} = distance fished in meters

w = effective width of the net opening (2.3 m)

q = catchability assumed equal to 1

n_i = number of hauls in stratum *i*

A_i = area of stratum *i* in hectares

were extrapolated to the entire survey area. However, it is unlikely that this introduced substantial bias into the estimates since most of the survey area was trawlable.

Recruitment

Recruitment includes both settlement and immigration of young fish into the study area. Therefore recruitment success is measured by the magnitude of increase in number of small fish inhabiting the study area over a defined period. In this study, recruitment success is measured by the average abundance of 0+ English sole in the study area during July through September of each year, that is,

$$R_i = \frac{1}{3} \sum_{j=7}^9 P_{ij}$$

where R_i = recruitment index; i = year (1985 through 1988); j = month (July through September); and P_{ij} = abundance of 0+ English sole in year i and month j .

It is assumed that this index better reflects recruitment success than an estimate based on a single month, given the patchy distribution of the 0+ juveniles and interannual variability in the timing of settlement. July through September is probably the only time period when the English sole population in the study area is closed. Previous studies of egg, larval and juvenile distribution indicate that June is the last month that English sole postlarvae settle in this study area (Doyle 1992; Hewitt 1980; Rosenberg 1982; Laroche et al. 1982; Krygier and Percy 1986). NMFS ichthyoplankton surveys off the coast of Washington, Oregon and California showed that there were no English sole eggs or larvae in neuston or bongo samples after June (Kendall and Clark 1982a and b; Clark 1984). After July, the only significant migration would be emigration from the study area. Results of a growth and survival study (Shi et al. in prep.) indicate that emigration is insignificant during this period.

Statistical analysis

One means of assessing interannual variability in recruitment is to statistically compare the fish densities in the study area during July through September. To do so, a three-factor ANOVA was implemented using log-transformed density data collected in this study. Because of unequal sample sizes, the ANOVA regression approach is utilized. Specifically the proposed full model is:

$$D_{ijk} = \mu + \alpha_i y_i + \beta_j m_j + \gamma_k a_k + (\alpha\beta)_{ij} y_i m_j + (\alpha\gamma)_{ik} y_i a_k + (\beta\gamma)_{jk} m_j a_k + \epsilon_{ijk}$$

where D_{ijk} = log-transformed density in year i (1985, 1986, 1987, and 1988), month j (July, August and September), and area k (nearshore, Grays Harbor, and Willapa Bay); y_i, m_j, a_k are dummy variables for year, month and area, and ϵ_{ijk} = the residuals. The dummy variables y_i were used to examine the year effect and defined as follows:

$$y_1 = \begin{cases} 1 & 1985 \\ -1 & 1988 \\ 0 & \text{otherwise} \end{cases}, \quad y_2 = \begin{cases} 1 & 1986 \\ -1 & 1988 \\ 0 & \text{otherwise} \end{cases},$$

$$y_3 = \begin{cases} 1 & 1987 \\ -1 & 1988 \\ 0 & \text{otherwise} \end{cases};$$

dummy variables m_j are used to examine the month effect and defined as:

$$m_1 = \begin{cases} 1 & \text{July} \\ 0 & \text{August} \\ -1 & \text{September} \end{cases}, \quad m_2 = \begin{cases} 0 & \text{July} \\ 1 & \text{August} \\ -1 & \text{September} \end{cases};$$

and a_k s are used to investigate the area effect and defined as:

$$a_1 = \begin{cases} 1 & \text{nearshore} \\ 0 & \text{Grays Harbor} \\ -1 & \text{Willapa Bay} \end{cases}, \quad a_2 = \begin{cases} 0 & \text{nearshore} \\ 1 & \text{Grays Harbor} \\ -1 & \text{Willapa Bay} \end{cases}.$$

The SYSTAT GMLH (Wilkinson 1989) algorithm was used here to test for the presence of interaction effects and main effects. The effects of interest are: (1) the interannual variation in juvenile recruitment; (2) the interannual variation in the distribution of recruits by area; (3) the variation in the distribution of recruits by month each year. The first effect is of special interest in establishing year class strength indices, which can be used to study the correlation between juvenile recruitment and future adult recruitment when estimates of adult population sizes or commercial catch statistics are available. The significance of the other two effects lies in providing information for

Table 2. A summary of three factor ANOVA to assess year, month, area effects on 0+ juvenile English sole density in July through September, 1985-1988.

Sources	SS	DF	MSE	<i>p</i>
year	105.94	3	35.31	< 0.001
month	53.30	2	26.65	< 0.001
area	2,945.87	2	1,472.93	< 0.001
year × area	1.23	6	0.21	0.999
year × month	40.99	6	6.83	0.109
month × area	124.05	4	31.01	< 0.001
error	3,745.68	942	3.98	

the design of future studies on juvenile English sole recruitment in the study area. If there is no year-area interaction present, then future studies aimed at monitoring recruitment success can be carried out in a single estuary, and will be more cost-effective. If the month-area interaction is not significant then the population in each area can be considered as temporally closed, indicating no significant net migration from one area to another during summer.

In order to ascertain the significance of the effects listed above, a stepwise regression approach was taken. First, log-transformed density was regressed against the simple main factors of year, month and area. If all terms were significant in explaining the variation in density, then two-factor interaction terms were included in the model and their significance tested. If all interaction terms associated with the year effect were nonsignificant, then pairwise comparisons of annual mean densities were carried out using a Bonferroni procedure (Neter et al. 1985) to adjust probabilities for the effect of multiple comparison.

Results

Population, density and variation

Results from ANOVA on density show that there was a significant year, month, area, and month-area interaction effect (Table 2). The significant year effect indicates that recruitment of 0+ English sole in the study area varied interannually. Significant month and area effect indicates that density of juvenile English sole varied seasonally, and

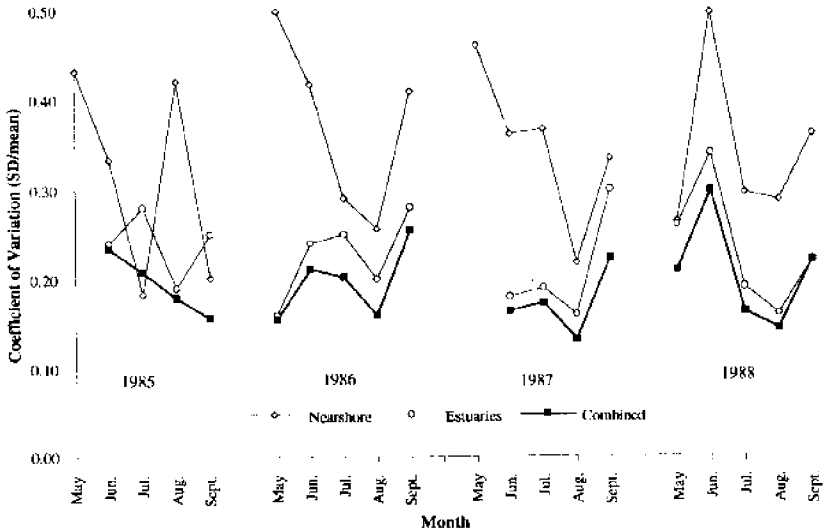


Figure 2. Changes in coefficient of variation (CV) with season each year, 1985-1988. Note the CVs were usually lowest in August each year, except in the nearshore area August 1985.

between areas. The month-area interaction effect reflects the fact that fish migrated between areas. The results from ANOVA also show that there was no significant year-area interaction effect ($p > 0.11$, Table 2), indicating that interannual trends in density were synchronous in all three areas.

The distribution of 0+ English sole was quite patchy, as indicated by the wide range of estimated density in the same stratum during the same sampling period. In stratum 2, Grays Harbor, July 1985, for example, density varied from 190 fish/ha at one station to 14,125 fish/ha at a nearby station, a difference of two orders of magnitude. In stratum 4, Willapa Bay, September 1987, the estimated density ranged from 9,928 fish/ha to 30 fish/ha. Patchiness was more prominent in the nearshore area than in estuaries, as indicated by CV values of mean densities (Fig. 2).

Spatial variation

The abundance of English sole varied considerably between areas as indicated by significant area effect in the ANOVA ($p < 0.01$, Table 2). Figure 3 presents estimated population by month and area. On the

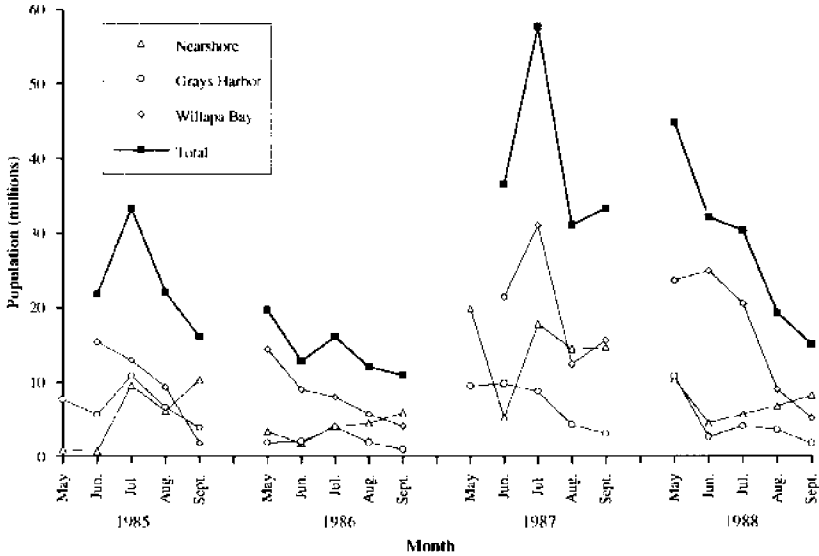


Figure 3. Seasonal trend of total estimated 0+ English sole population.

average, the estimated abundance of 0+ English sole in the two estuaries combined was 2.4 times as high as that in the coastal study area, even though the total area of estuaries (19,700 ha, Grays Harbor and Willapa Bay combined) is less than 14% that of the nearshore study area (146,600 ha). The estimated population was usually highest in Willapa Bay during May through August, but nearshore in September.

Density of English sole varied with stratum in Grays Harbor. Strata 1, 2 and 4 (Fig. 1) were the most important habitats for newly recruited juvenile English sole in May through July (Fig. 4a). Stratum 3 provided a habitat for large juveniles during August through September. Densities in Stratum 3 were always far lower than in the other strata, although they tended to increase during August and September.

In Willapa Bay overall mean densities (all years and months combined) by stratum were not significantly different among Strata 1 through 4, 1,145 (SE = 206), 1,083 (SE = 180), 1,084 (SE = 188) and 885 (SE = 291), respectively. These are equally important habitats for 0+ age English sole in Willapa Bay. Stratum 5 typically had lower densities than the others (Fig. 4b).

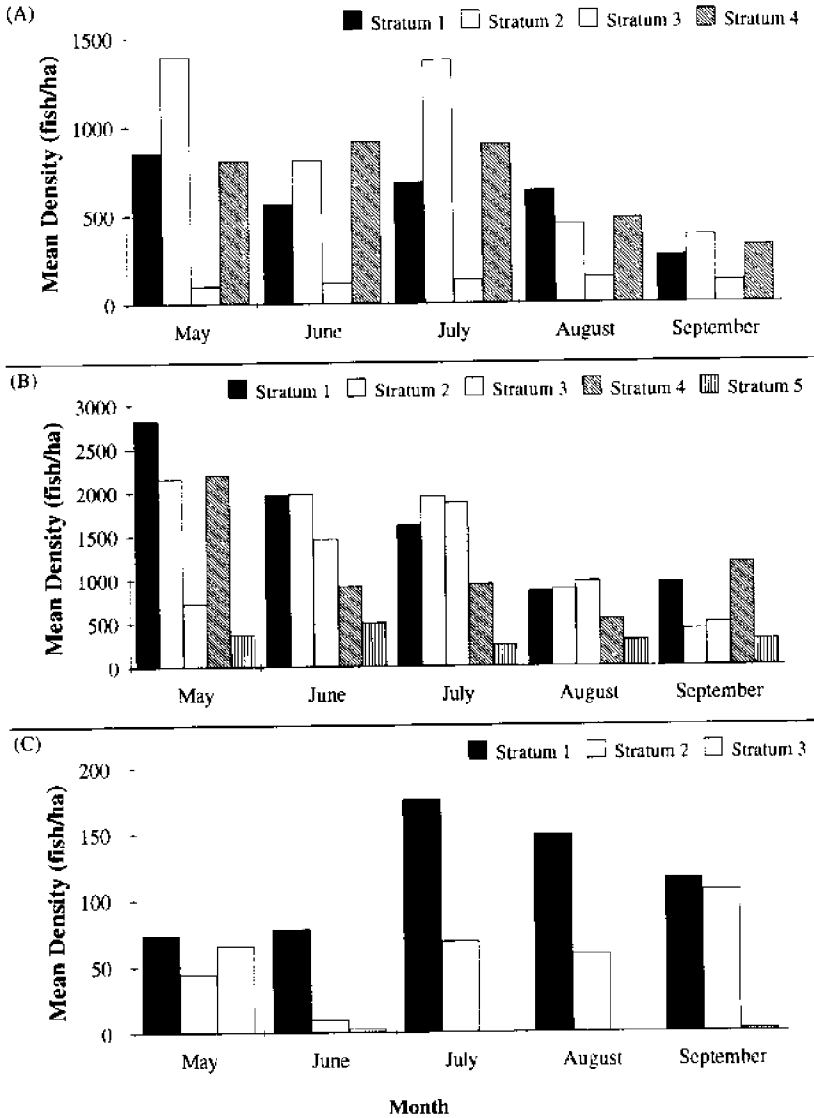


Figure 4. Mean density (fish/ha) by stratum in Grays Harbor (A), Willapa Bay (B), and nearshore area (C) during May through September, 1985-1988.

Overall, Strata 1 and 2 (0-41 m, Fig. 1) provided habitat for over 99% of the 0+ English sole in the nearshore study area during July through September, and the mean density of English sole decreased with depth (Fig. 4c). No clear latitudinal distribution pattern was observed.

Seasonal variation

No consistent trend in estimated population of 0+ English sole was observed before July each year (Fig. 3). However, density of English sole varied significantly and in a consistent manner as indicated by the significant month effect, and nonsignificant year-month interaction in the ANOVA (Table 2).

The general pattern of change in the total estimated population (estuarine and nearshore area combined) from July to September was a sharp decline from July to August followed by a less severe decrease from August to September each year (Fig. 3). An abnormal situation occurred in 1987, when the estimated 0+ English sole population increased by 2.3 million from August (31.1 million) to September (33.4 million). However, this increase was not statistically significant ($p = 0.38$).

After July, the population in the nearshore area typically increased with the decline in estuarine population (Fig. 3). In June each year, the estimated population of 0+ English sole in estuaries was at least 85% of the estimated total population, and there were at least six times as many juvenile English sole in estuaries as in the nearshore study area. By September each year, the total number of 0+ English sole in estuaries was usually less than that in the coastal study area, 1987 being an exception. The average size of 0+ English sole (78 mm TL) in September 1987 was small relative to other years (95 to 102 mm TL) in the same month, and their seaward emigration from the estuaries was evidently delayed as a consequence.

Table 3 shows monthly change in total estimated population (estuaries and nearshore area combined) from July to August, August to September and the overall change from July to September. In general, the magnitude of the changes decreased with season, as did their statistical significance. From July to August, the declines in population were significant in 1987 and 1988 ($p < 0.02$), nonsignificant in 1985 and 1986 ($p > 0.07$), while from August to September, changes were nonsignificant for all four years ($p > 0.09$). However, if we look at a longer time span, i.e. from July to September, then the declines in population were either significant ($p < 0.03$) or marginally significant

Table 3. Results of approximated randomization tests on the total population decrease (millions of fish) July to August, August to September and overall decrease July to September.

		1985	1986	1987	1988
July-August	Change	11.26	4.03	26.51	10.98
	<i>p</i>	0.07	0.12	0.01	0.01
August-September	Change	6.03	1.12	-2.25	4.29
	<i>p</i>	0.09	0.37	0.61	0.17
July-September	Change	17.29	5.15	24.27	15.28
	<i>p</i>	0.02	0.09	0.03	0.01

($p = 0.09$, 1986) (Table 3). These significant decreases in population size indicate that the total population in the study area was declining due to natural mortality and/or emigration from the survey areas.

Settlement

Settlement was determined by estimating the abundance of recently metamorphosed fish (< 25 mm TL). Even though the recruitment of juvenile English sole was protracted, backcalculations from growth rate data indicated that there were two major settling periods, one in January-February and the other in April-May (Shi 1994; Shi et al. in prep.). Timing of settlement was quite variable over the four year period. In 1985, most 0+ English sole probably settled in January-February and were represented by the high occurrence of fish in the size range of 45 to 75 mm in May (Fig. 5). Settlement in 1986 was quite different from other years. The clear bimodal length frequency pattern apparently resulted from two different recruitment influxes. The mode with larger fish consists of those fish that had settled in the survey areas in about January-February, while the mode of smaller fish consists of fish that had settled during April, May and to a lesser extent in June. Settlement in 1987 and 1988 followed more or less the same pattern, with a large number of newly transformed juveniles settling in both nearshore and estuarine areas during May. Most of the May settlers disappeared before the June survey in 1988, while in 1987 they were abundant in surveys conducted the following months (Fig. 5). Clearly, successful initial settlement does not always guarantee recruitment success.

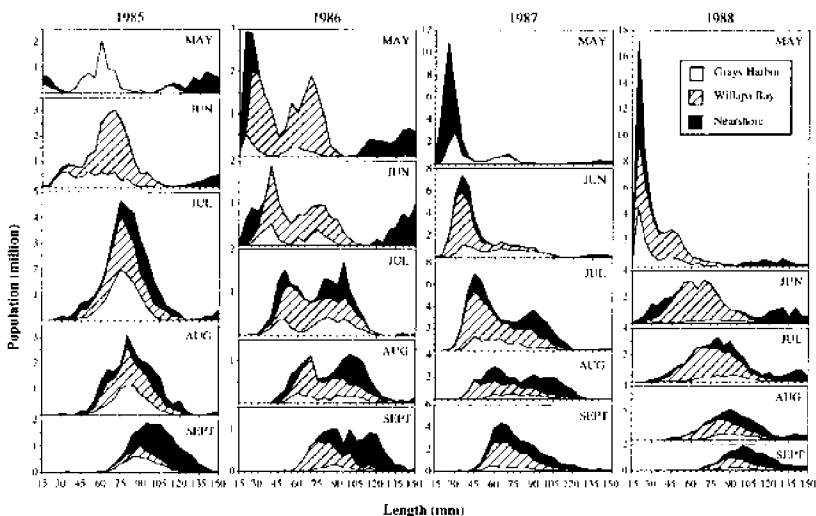


Figure 5. Population estimates of 0+ English sole, *Pleuronectes vetulus*, in Grays Harbor, Willapa Bay and nearshore study areas by size, 1985-1988.

Transformation and settlement took place in both coastal and estuarine waters in all years studied (Fig. 5). Newly transformed juveniles (< 25 mm TL) settled in coastal waters as well as in estuaries (Table 4), and mean length at settling was the same in all areas. Generally, settlement terminated in June in both estuaries and nearshore waters.

Discussion

Spatial distribution and migration

Results from the ANOVA on density show that there was a significant month-area interaction effect ($p < 0.001$, Table 2), indicating significant migration and redistribution of fish between estuarine and nearshore areas during the year. Typically transformation and settlement took place in both coastal and estuarine waters through June in all years studied. In later months, young juveniles which had settled in the nearshore area moved into estuaries as they grew. The use of estuaries off Washington by 0+ English sole is seasonal. Each year the percentage of 0+ English sole in estuaries consistently declined from more than 85% in June to less than 50% in September, except during August 1985 and September 1987. This decrease in the percentage in

Table 4. Settlement (millions) of juvenile English sole (< 30 mm TL) in estuaries and nearshore areas.

Month	1985		1986		1987		1988	
	ES	NS	ES	NS	ES	NS	ES	NS
May	0.46	0.68	0.60	2.32	0.25	5.38	10.07	7.54
June	0.02	0.10	0.02	0.56	0.16	0.08	0.04	0.30
July	0	0	0	0	0	0	0	0.03

estuaries is probably caused by emigration of large English sole from estuaries to the nearshore waters.

Migration of 0+ English sole within the study area appeared to be size dependent. Most fish that settled in nearshore waters at a size < 25 mm TL, eventually migrated into estuaries. By the time fish had reached a length of 55 mm TL, the majority (78 to 98%, during 1985-1988) were found in estuarine waters of Grays Harbor and Willapa Bay (Figs. 5 and 6). At about 70-80 mm, fish began to emigrate from estuaries. Most fish greater than 125 mm had emigrated from the estuaries and 86%-95% of English sole larger than 125 mm were found in coastal waters during 1985-1988 (Figs. 5 and 6). By combining the monthly population estimate for each size group, annual mean length frequency distributions (Fig. 6), can be generated to examine length-dependent migration to and from the estuaries. Mean length frequency distributions for all four years (Fig. 6) reflect gains in the coastal population of 75-120 mm fish and corresponding losses from the estuarine population as a result of emigration. The data for all four years also show increases in estuarine population over the size ranges of 20-70 mm as smaller fish immigrate from the coastal area and corresponding decreases in coastal populations over the same size ranges were seen in 1986 through 1988. This supports the hypothesis that 20-70 mm 0+ English sole were leaving the nearshore area and moving into estuaries.

Estuarine-nearshore migration is also reflected by changes in mean lengths by month and area. Before July, mean lengths (weighted by abundance in each stratum) in the nearshore waters were always smaller than in estuarine waters. After July, the reverse was true, and the mean lengths in the nearshore area were always greatest (Fig. 7). An increase in the weighted mean length (WML) of 40-50 mm between June and July surveys was evident in the nearshore area every

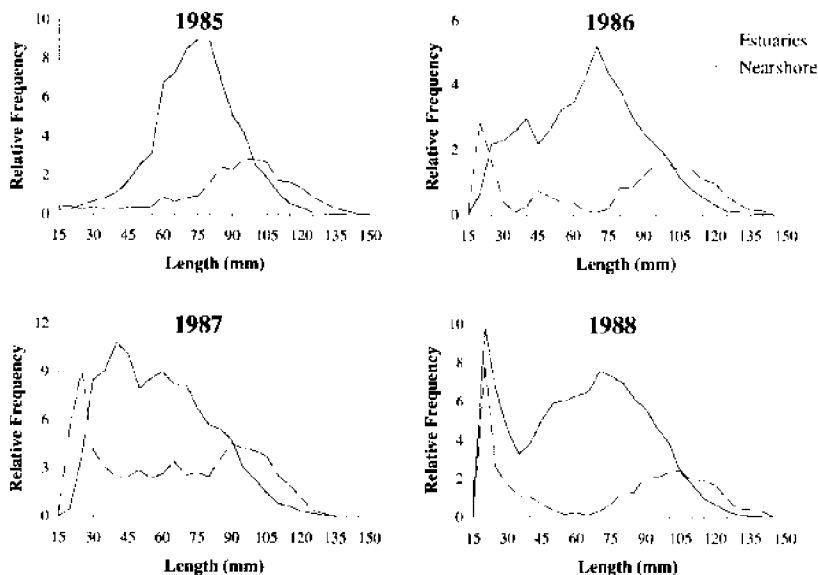


Figure 6. 0+ English sole catch curves for nearshore and estuarine (Grays Harbor and Willapa Bay combined) study areas, based on cumulative population estimates, all months combined.

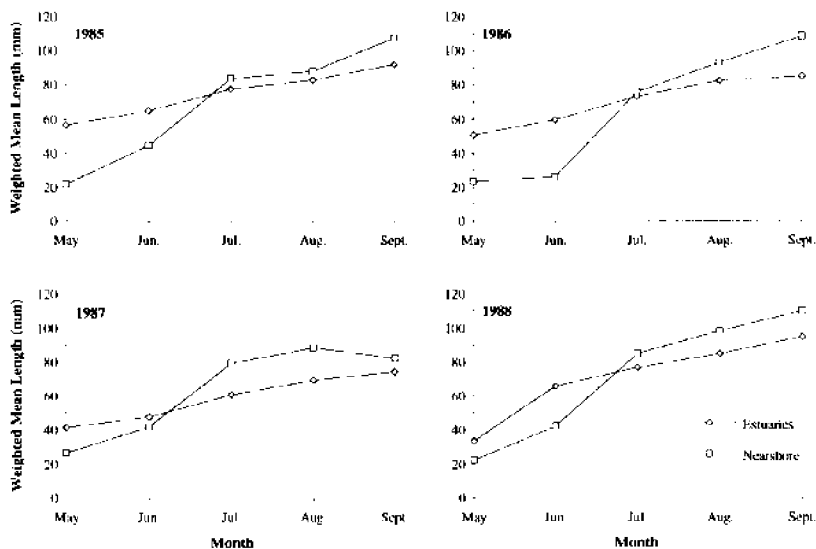


Figure 7. Changes in weighted mean lengths for nearshore and estuarine 0+ English sole.

Table 5. Significance value (after Bonferroni adjustment) of paired comparison (contrast) tests based on ANOVA model. Numbers in parentheses are the significance value before Bonferroni adjustment.

	1986		1987		1988	
1985	0.454	(0.076)	0.004	(0.001)	- 1.0	(0.856)
1986	—		< 0.001	(< 0.001)	0.288	(0.048)
1987			—		0.007	(0.001)

year, 1985-1988. These unusually large increments in WML probably resulted from immigration of large fish from estuaries to the nearshore area and emigration of small fish from the nearshore area to estuaries.

Interannual variation in density and year class strength

Juvenile (0+) English sole density varied significantly between years, months and areas (significant year, month and area effects), while the density distribution pattern and seasonal dynamic trends did not differ interannually (nonsignificant year-area and year-month interaction effects, Table 2). Results from the analysis of variance show that all interaction terms associated with the year effect were nonsignificant, so that paired comparisons (contrasts) between annual mean densities were straightforward. The results of the pairwise comparisons of annual recruitment indices indicate that 0+ English sole density in 1987 was significantly higher than other years. No significant difference in juvenile English sole density was detected between 1985, 1986, and 1988 (Table 5) using ANOVA. However, an approximate randomization test (Noreen 1989) which took the stratified nature of the survey design into account showed that the recruitment index for 1986 was significantly lower than that for all other years ($p < 0.008$).

Recruitment success in this study was measured by the mean abundance estimates of 0+ English sole during July through September each year. The 0+ English sole population in the study area is most likely closed during this period. Three levels of recruit success were identified on the basis of estimated mean population during July through September (Fig. 8). Strong recruitment occurred during 1987 with an overall mean abundance estimate of 40.7 ± 8.6 million fish. Moderately strong recruitment during 1985 and 1988 was reflected by

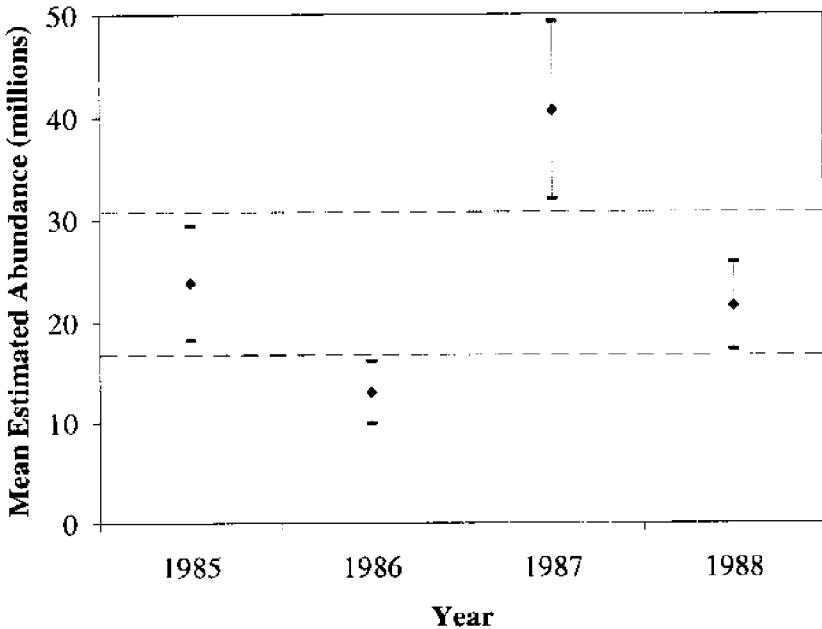


Figure 8. Means and 95% confidence limits for average population size of 0+ English sole in July through September, as an indicator of recruit success.

intermediate mean abundance estimates (23.8 ± 5.6 and 21.6 ± 4.3 million, respectively). A substantially lower mean abundance (13.0 ± 3.1 million) was observed in 1986.

Even though settlement terminated in June each year (except 1988), immigration from waters outside the study area continued into July. Increases in abundance in both nearshore and estuarine population from June to July support the hypothesis that immigration continued (Fig. 3). The magnitude of the immigration varied substantially over the four year period (Fig. 3). The estimated total abundance increased more than 21 million from June to July in 1987, while it decreased about 2 million from June to July in 1988. Nevertheless, it is clear that year class strength of English sole off Washington is not established until July.

Year class strength can be indexed by recruit success which in turn can be measured by the mean estimated abundance from July through September each year. There are two considerations that justify the use of the mean estimated abundance from July through

September as a measure of recruit success. First, during the July-September period, migration of 0+ English sole in and out the study area was most likely minimal, and in most years the population in the study area might even be assumed to be closed. Second, it would be ideal to use estimated abundance in September as an index of year class strength, for it is closest to the time when the fish recruit to the fishery. However, due to the patchy distribution of 0+ English sole in September (Fig. 2) and interannual variability in the timing and pattern of settlement (Gunderson et al. 1990, Shi 1994), the mean estimated abundance during July through September might better reflect the recruit success than an estimate based on a single month. It is recommended that future surveys of 0+ English sole recruit success be carried out during July through September.

The fact that no significant year-area interaction was detected indicates that it may not be necessary to conduct trawl surveys in all three areas (Grays Harbor, Willapa Bay, and nearshore) in order to obtain an index of recruitment. Interannual trends in density are evidently synchronous in all three areas. Furthermore, abundance in Willapa Bay tends to dominate the recruitment index for all areas combined, and surveys of Willapa Bay alone would probably suffice to provide a recruitment index for 0+ English sole for the entire study area.

Such a survey might well serve as an index of recruitment success for all English sole off Washington and Oregon. Analysis of commercial trawl landings, adult tagging, availability of spawning habitat, and egg distributions (Shi 1994) support the hypothesis that most English sole in the Washington-Oregon region spawn off central and northern Oregon. Further, estimated coastal geostrophic and Ekman alongshore transport showed relatively strong northward transport during years when eggs and larvae were abundant off Washington and Oregon. Reconstructions of egg drift trajectories (Shi 1994) using an oceanographic model provided further evidence that the eggs and larvae found off southern Washington were advected from spawning grounds as far south as central Oregon. While many estuaries along the coast of Washington and Oregon are known to support populations of juvenile English sole (Kryger and Pearcy 1986), those along the Oregon coast are much smaller than Grays Harbor and Willapa Bay. The Columbia River estuary is also large in surface extent, but its physical processes are dominated by freshwater input, and it appears to provide relatively poor habitat for juvenile English sole (C. Simenstad, University of Washington, pers. comm.). We assume that northerly

transport of eggs and larvae spawned off Oregon maximizes opportunity to recruit to estuaries in southern Washington.

Although further studies of egg drift, synoptic coastwide trawl surveys of Washington and Oregon estuaries, and tagging studies on juvenile English sole would be desirable to define the importance of Grays Harbor and Willapa Bay more clearly, it appears likely that they may serve as the primary nursery grounds for the Washington-Oregon stock of English sole. As such, juvenile surveys in these areas may prove invaluable in providing recruitment indices that serve in monitoring environmental quality, determining what suite of environmental characteristics result in favorable recruitment and as an aid in tuning catch-at-age models (Sampson 1993).

Acknowledgments

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Spatial Patterns Associated with an Increase in the Abundance of English Sole (*Parophrys vetulus*) off Oregon and Washington

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Abstract

A recent assessment for the stock of English sole (*Parophrys vetulus*) off Oregon and Washington (USA) indicates a large and steady increase in the numerical abundance, biomass, and annual recruitment of females during the period 1977-1992. Abundance and biomass levels in 1992 were approximately ten times the 1977 levels. This paper analyzes the time series of research trawl data to examine how the spatial distribution of this resource changed as the stock increased. There appears to have been an increase in the density of the fish but relatively little expansion of their range. The results are discussed in relation to MacCall's basin model for the dynamic geography of marine fish populations.

Introduction

Variations in a population's abundance will necessarily result either in changes in the population's density (the number of organisms per unit area), its geographic range, or some combination thereof. It is important to understand how the spatial distribution of an exploited fish stock responds to changes in abundance, because of its influence on catch rates, which are sometimes used as indices of stock abundance. If variations in abundance do not alter a stock's range, but only its density, then changes in catch rates will be directly proportional to

total abundance (Figure 1, upper panel). However, if changes in abundance alter a stock's spatial distribution, then catch rates will no longer be strictly proportional to abundance, and in the extreme can be independent of abundance (Figure 1, lower panel).

This paper examines changes in the geographic distribution of the stock of English sole (*Parophrys vetulus*) that occurs off the West Coast of the United States (Figure 2). A recent assessment (Sampson 1992) indicates that the portion of this stock found off Oregon and Washington has increased roughly ten-fold since 1977 (Figure 3). In the current study I analyze in detail data from six National Marine Fisheries Service trawl surveys, spanning the period 1977 to 1992, with regard to changes in the percentage of tows with English sole, the number of English sole per tow, and the average weight of a fish.

Materials and Methods

NMFS triennial trawl survey data

Every third year beginning in 1977 the National Marine Fisheries Service (NMFS) has conducted a bottom trawl survey of most of the continental shelf off the U.S. West Coast from the Mexican to the Canadian borders. Although these surveys were designed primarily to monitor the stocks of rockfish (*Sebastes* sp.), flatfish were also routinely caught in the standardized survey trawl. Data collected during the surveys include the weights and numbers of fish by species caught at each station.

For each survey the shelf area from 30 fathoms to 200 fathoms (from 50 to 250 fathoms for the 1977 survey) was stratified by depth and latitude, and the survey vessels conducted randomized tows within strata, along systematically placed transects. Tows were generally 30 minutes in duration and extended roughly 1.5 kilometers. The stratum boundaries were not identical for all six surveys, and the sampling densities were not uniform across strata and surveys. Dark and Wilkins (1994) concisely summarize the survey designs for the first four surveys; Weinberg et al. (1994) give details for the 1989 survey. The 1992 survey followed the same design as the 1989 survey (pers. comm., Mark Wilkins, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA 98195, April 1993.)

Statistical methods

For my analysis of the spatial distribution of English sole I grouped the NMFS trawl survey data into geographic regions based on 20

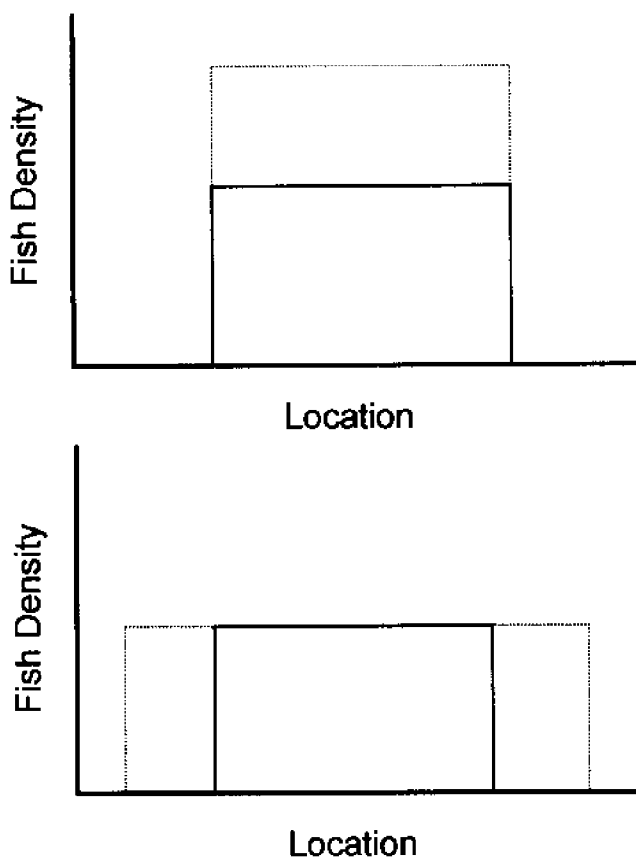


Figure 1. The practical importance of spatial distribution in fisheries. If changes in a fish stock's abundance do not affect the stock's geographic range, then fish density and catch rates will reflect total stock abundance (upper panel). If changes in abundance do not affect a stock's density, then catch rates will be independent of stock abundance (lower panel). Abundance here is represented by the area of the rectangles and density is represented by their height.

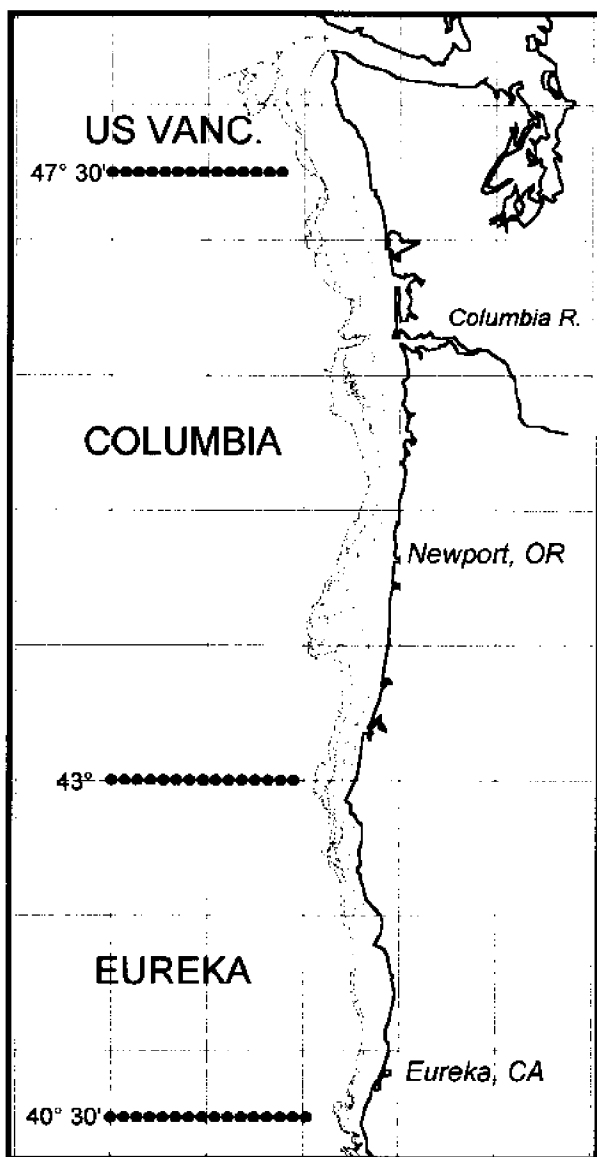


Figure 2. Map of the study area. The study analyzed standardized research survey data, which were collected by the U.S. National Marine Fisheries Service, from the Eureka and Columbia statistical areas and the U.S. portion of the Vancouver area. The depth contours on the map represent the 50, 100, 150, and 250 meter isobaths.

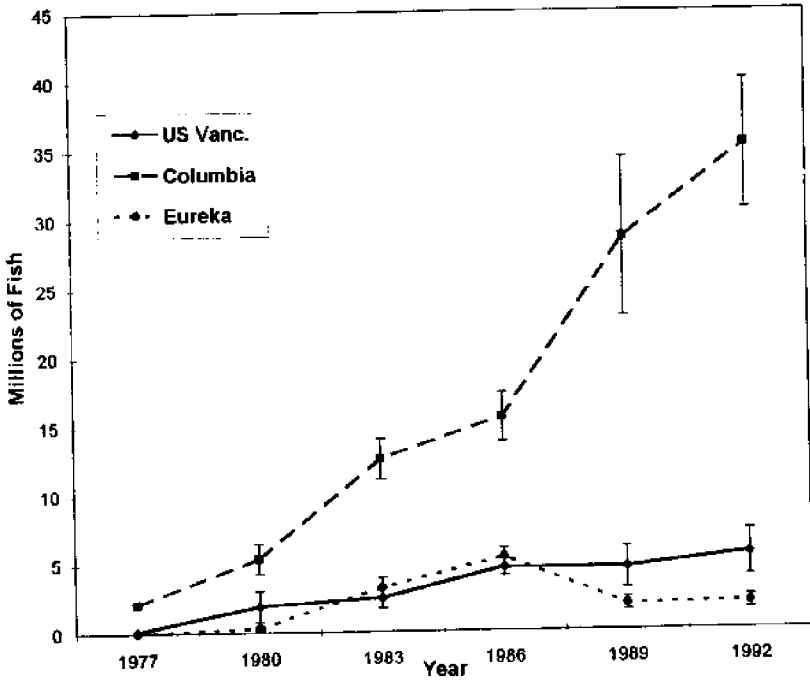


Figure 3. Numerical abundance of English sole as estimated from the NMFS triennial trawl survey data. The error bars depict the estimated abundance plus and minus one standard error. (Pers. comm., Mark Wilkins, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA 98195, April 1993.)

latitudinal zones and 8 depth zones (Table 1). Because the sampling densities were not uniform across surveys and sampling strata, I was careful to establish the boundaries of the 160 regions so that strata receiving high-density sampling during a given survey were not mixed with strata receiving less intense sampling on the same survey.

Percent occurrence of English sole

To examine changes in the percent occurrence of English sole I tabulated by geographic region and survey the number of tows that caught at least one English sole and the total number of tows. I analyzed the resulting data set by fitting the data with a hierarchical set of logistic regression models using GLIM 3.77, a statistical program for fitting generalized linear models using maximum likelihood (Baker

Table 1. Geographic regions for the statistical analyses. Tow by tow data for each survey were grouped into 160 categories on the basis of 8 depth zones and 20 latitudinal zones.

				Depth zone boundaries	
				Fathoms	Meters
				30 - 50	54.9 - 91.4
				50 - 75	91.4 - 137.2
				75 - 100	137.2 - 182.9
				100 - 120	182.9 - 219.5
				120 - 140	219.5 - 256.0
				140 - 160	256.0 - 292.6
				160 - 180	292.6 - 329.2
				180 - 200	329.2 - 365.8

				Latitudinal zones	
INPFC area	Latitude bounds	INPFC area	Latitude bounds		
Eureka	40°30' - 41°	Columbia (Northern)	45°30' - 46°		
	41° - 41°30'		46° - 46°16'		
	41°30' - 42°		46°16' - 46°30'		
	42° - 42°50'		46°30' - 46°44'		
	42°50' - 43°		46°44' - 47°		
Columbia (Southern)	43° - 43°30'	U.S. Vancouver	47° - 47°20'		
	43°30' - 44°		47°20' - 47°30'		
	44° - 44°18'		47°30' - 47°50'		
	44°18' - 44°40'		47°50' - U.S./Canada Border		
	44°40' - 45°				
	45° - 45°30'				

and Nelder 1985). I treated the variables Year, Latitude Zone, and Depth Zone as factors rather than as continuous variables. To reduce the number of spatial categories I also included a factor Area. Each of the four areas was a collection of adjacent latitudinal zones (Table 1).

To assess the statistical significance of different factors and factor combinations and their influence on the percent occurrence of English sole, I conducted forward stepwise analyses, and examined the relative improvement in fit that occurred as I added factors to a model. In GLIM a statistic known as the "deviance" measures how well a statistical model fits the observed data. When the model is correctly

specified, the deviance, which is a linear function of the log-likelihood, is approximately distributed as a chi-square random variable (McCullagh and Nelder 1983).

Numerical density of English sole

To examine changes in the density of English sole first I divided the number of English sole caught in each tow by the distance covered by the tow, then I excluded tows that did not catch any English sole, and finally I applied a logarithmic transformation to the remaining non-zero observations. I analyzed the resulting data set using the Statistical Analysis System (SAS) procedure known as GLM (SAS 1988). To assess the statistical significance of different factors on the density of English sole, I used the technique of "backward elimination" (Draper and Smith 1966) and examined the relative degradation in fit that occurred as I removed factors from a model.

Average weight of English sole

To examine changes in the average weight of English sole I excluded tows that did not catch any English sole, and then I divided the total weight of English sole caught at each tow by the corresponding number of fish caught. I analyzed the resulting data using the SAS procedure GLM. To account for differences in the precision of the observed values of average weight, I used the number of English sole caught at each tow as a weighting variable. This procedure gave greater influence to samples that contained large numbers of fish.

Results

Percent occurrence of English sole

During the forward selection of a model for the percent occurrence of English sole I was unable to find a completely adequate model because of computer memory constraints on the size of the model. The "best" model that I was able to fit included main effects for Area, Depth, and Year, and an interaction between Area and Depth (Table 2). However, the model with Latitude, Depth, and Year provided a significantly improved fit over the model with Area, Depth, and Year. If I had been able to examine the interactions with Latitude, I suspect that the best model would have included Latitude, Depth, and Year and one or more interactions between these factors. The model with Area contains many fewer parameters than the model with Latitude, and consequently is much simpler to interpret.

Table 2. Results from a logistic regression analysis of the percent occurrence of English sole in six NMFS trawl surveys.

Model	Deviance	d.f.	Effect	Deviance	d.f.	F	Prob.
intercept	1463.0	590					
Area (A)	1437.8	587	Area	25.2	3	3.43	0.017
Depth (D)	911.2	583	Depth	551.8	7	50.44	0.000
Latitude (L)	1366.0	571	Latitude	97.0	19	2.13	0.004
Year (Y)	1274.3	585	Year	188.7	5	17.32	0.000
Area+Depth	851.4	580	Area Depth	59.8	3	13.58	0.000
A+D+A.D	799.3	559	A.D A+D	52.0	21	1.73	0.023
Area+Latitude	1366.0	571	Latitude Area	71.8	16	1.88	0.020
Area+Year	1249.9	582	Area Year	24.5	3	3.80	0.010
A+Y+A.Y	1223.4	567	A.Y A+Y	26.4	15	0.82	0.659
Depth+Latitude	802.3	564	Latitude Depth	108.9	19	4.03	0.000
Depth+Year	808.0	578	Year Depth	103.2	5	14.77	0.000
D+Y+D.Y	754.0	544	D.Y D+Y	54.0	34	1.14	0.266
Latitude+Year	1186.2	566	Latitude Year	88.1	19	2.21	0.002
Area+Depth+Year	751.2	575	Area D+Y	56.8	3	14.49	0.000
Depth+Lat.+Year	701.5	559	Latitude D+Y	106.5	19	4.46	0.000
			Latitude A+D+Y	49.7	16	2.47	0.001
A+D+Y+A.D	696.6	554	A.D A+D+Y	54.6	21	2.07	0.004
A+D+Y+A.Y	722.1	560	A.Y A+D+Y	29.1	15	1.51	0.098
A+D+Y+D.Y	693.9	541	D.Y A+D+Y	57.3	34	1.31	0.113

"A.B" denotes the interaction of effect A with effect B.

The percent occurrence of English sole predicted by the model with terms for Area, Depth, Year, and an Area.Depth interaction suggest that the English sole stock expanded its range into deeper waters between the 1980 and 1983 surveys, but thereafter the stock made no further expansions in its range (Figures 4a and 4b). In all four areas there were English sole present in nearly 100% of the tows in the shallowest depth zone (30-50 fathoms), but the percent occurrence rapidly declined with increasing depth. In all areas there was also a secondary peak in percent occurrence around the 140-160 fathom depth zone.

Table 3. Results from a linear regression analysis of the log density of English sole (no. fish/km) in six NMFS trawl surveys.

Model	Error SS	d.f.	Effect	SS	d.f.	F	Prob.
Simple model							
Area*Depth*Year	1984.9	971	A.D.Y	84.4	50	0.83	0.801
A+D+Y+A.D+A.Y+D.Y	2069.2	1021	D.Y	69.8	29	1.19	0.229
A+D+Y+A.D+A.Y	2139.0	1050	A.Y	75.3	15	2.46	0.001
			A.D	76.0	19	1.96	0.008
			Y	94.9	5	9.32	0.000
			D	570.0	7	39.97	0.000
			A	19.0	3	3.12	0.025
Alternate model							
Latitude*Depth*Year	1464.9	746	L.D.Y	194.3	127	0.78	0.960
L+D+Y+L.D+L.Y+D.Y	1659.2	873	D.Y	39.0	28	0.73	0.842
L+D+Y+L.D+L.Y	1698.2	901	L.Y	199.4	87	1.22	0.096
L+D+Y+L..D	1897.6	988	L.D	302.0	80	1.97	0.000
			Y	185.4	5	19.31	0.000
			D	514.2	7	38.25	0.000
			L	77.1	19	2.11	0.004

"A*B*C" denotes a model with three main effects and all possible interactions between those effects.

"A.B" denotes the interaction of effect A with effect B.

Numerical density of English sole

The observed data on the density of English sole were reasonably well fitted by a model with main effects for Area, Depth, and Year, and interactions between Area and Depth and between Area and Year (Table 3). However, a more complex model with Latitude, Depth, Year, and an interaction between Latitude and Depth provided the best fit to the data. For simplicity I only provide details for the simpler model with Area.

The numerical density of English sole predicted by the model with terms for Area, Depth, and Year, and Area.Depth and Area.Year interactions indicates that in the northern Columbia area there was a

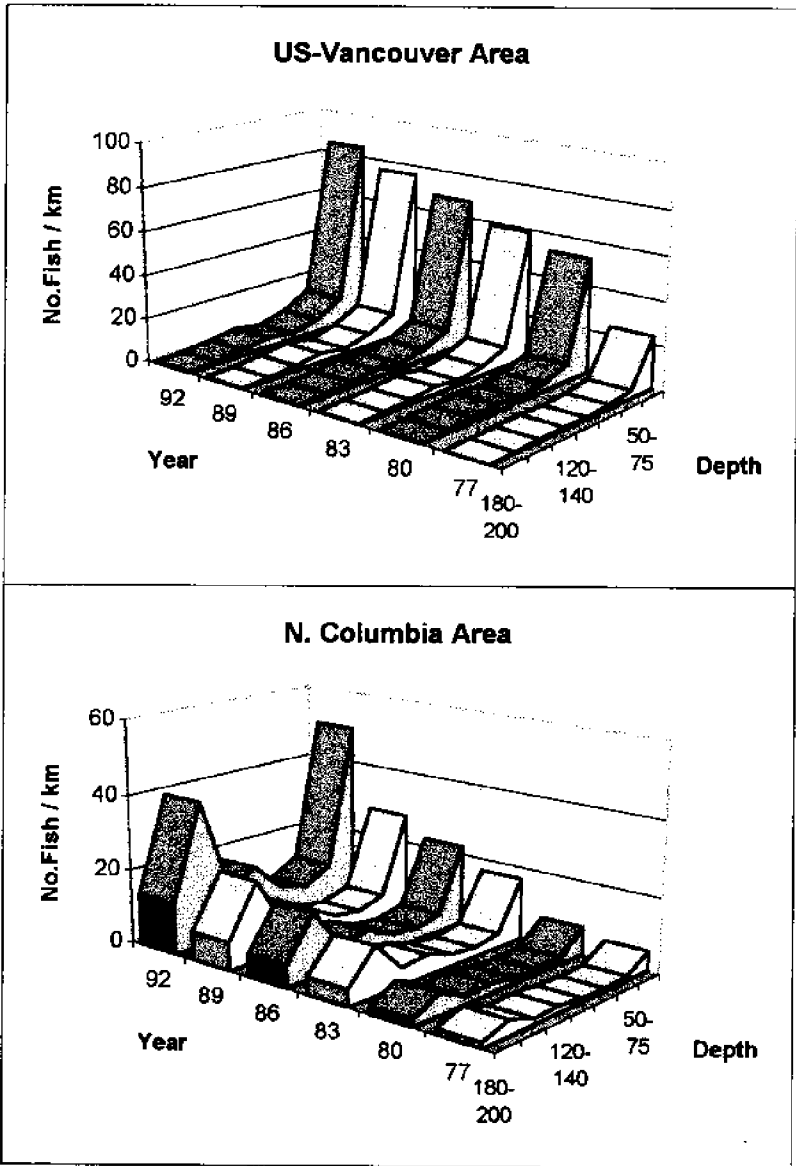


Figure 5a. Predicted density of English sole in the two northern areas, based on a linear regression model with factors for Area, Depth, Year, and Area.Depth and Area.Year interactions. The predicted values have been back-transformed from a logarithmic scale, but without corrections for transformation bias.

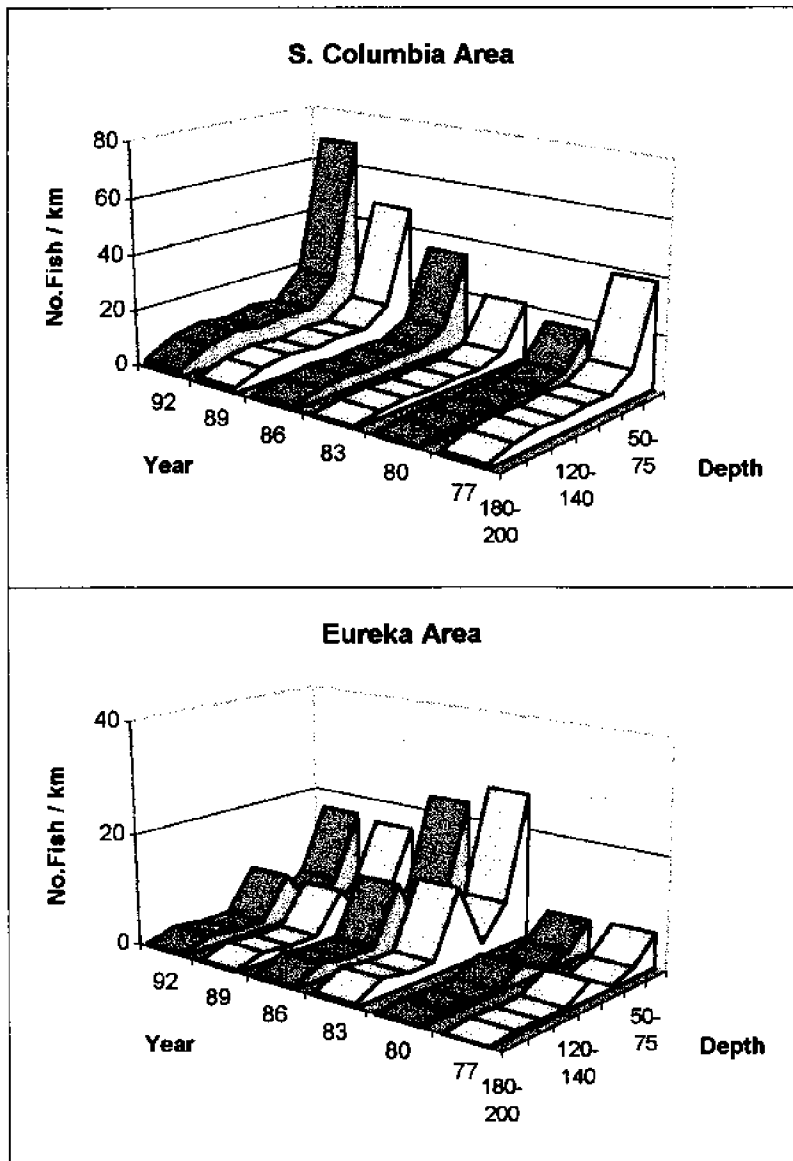


Figure 5b. Predicted density of English sole in the two southern areas, based on a linear regression model with factors for Area, Depth, Year, and Area.Depth and Area.Year interactions. The predicted values have been back-transformed from a logarithmic scale, but without corrections for transformation bias.

Table 4. Results from a weighted linear regression analysis of the average weight of English sole in six NMFS trawl surveys.

Model	Error SS	d.f.	Effect	SS	d.f.	F	Prob.
Simple model							
Area*Depth*Year	1984.9	971	A.D.Y	84.4	50	0.83	0.801
Area*Depth*Year	667.7	971	A.D.Y	43.6	50	1.27	0.104
A+D+Y+A.D+A.Y+D.Y	711.3	1021	D.Y	17.6	29	0.87	0.665
A+D+Y+A.D+A.Y	728.9	1050	A.Y	26.1	15	2.51	0.001
			A.D	135.0	19	10.24	0.000
			Y	37.5	5	10.82	0.000
			D	374.8	7	77.14	0.000
			A	7.7	3	3.68	0.012
Alternate model							
Latitude*Depth*Year	494.5	746	L.D.Y	75.3	127	0.89	0.783
L+D+Y+L.D+L.Y+D.Y	569.8	873	D.Y	19.4	28	1.06	0.378
L+D+Y+L.D+L.Y	589.2	901	L.Y	86.9	87	1.53	0.002
L+D+Y+L.D			L.D	136.9	80	2.62	0.000
			Y	32.5	5	9.95	0.000
			D	97.4	7	21.29	0.000
			L	13.7	19	1.10	0.341

"A*B*C" denotes a model with three main effects and all possible interactions between those effects.

"A.B" denotes the interaction of effect A with effect B.

substantial and steady increase from survey to survey in the numbers of English sole per kilometer towed (Figure 5a). The increase was most pronounced in the 30-50 fathom and 160-180 fathom depth zones. In the southern Columbia area there was also a reasonably steady increase in fish density in the 30-50 fathom depth zone (Figure 5b).

Average weight of English sole

The observed data on the average weight of English sole were also reasonably well fitted by a model with main effects for Area, Depth, and Year, and interactions between Area and Depth and between Area and Year (Table 4). However, as with the previous analysis, a more complex model with Latitude, Depth, Year, and an interaction between Latitude and Depth provided the best fit to the data. Again, for simplicity I only provide further details for the simpler model with Area.

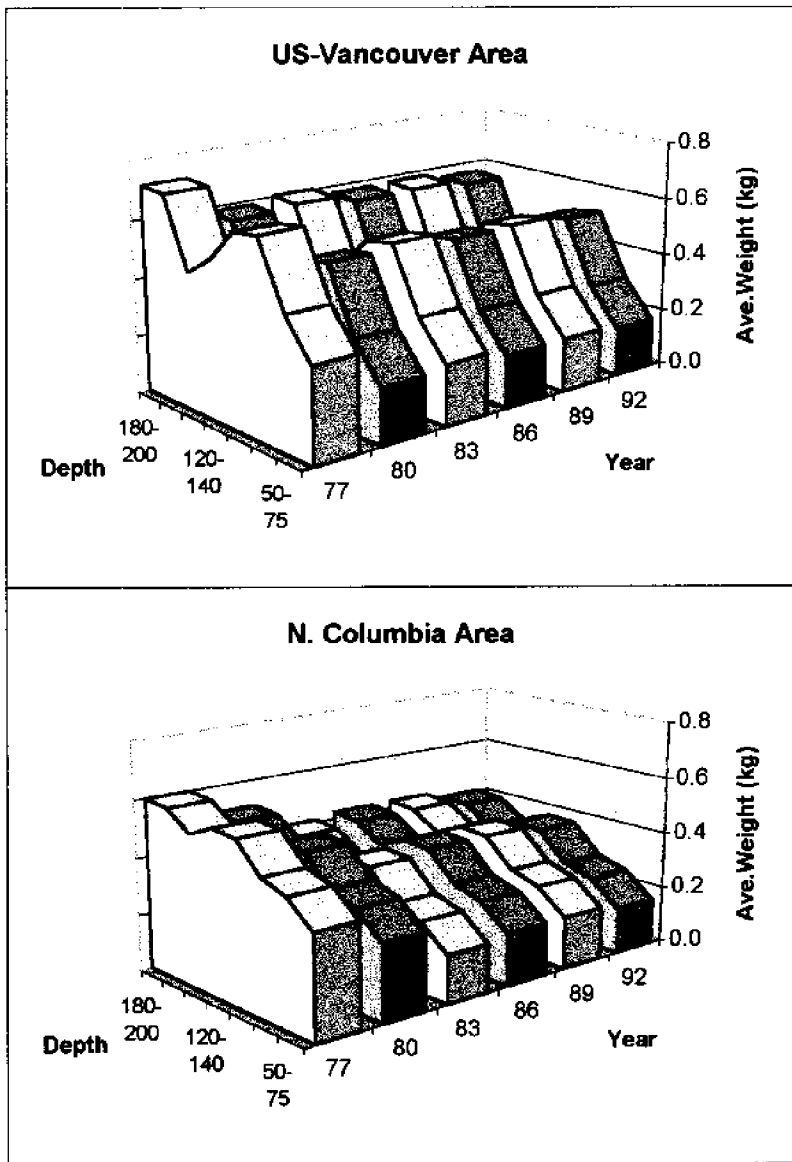


Figure 6a. Predicted average weight of English sole in the two northern areas, based on a weighted linear regression model with factors for Area, Depth, Year, and Area.Depth and Area.Year interactions.

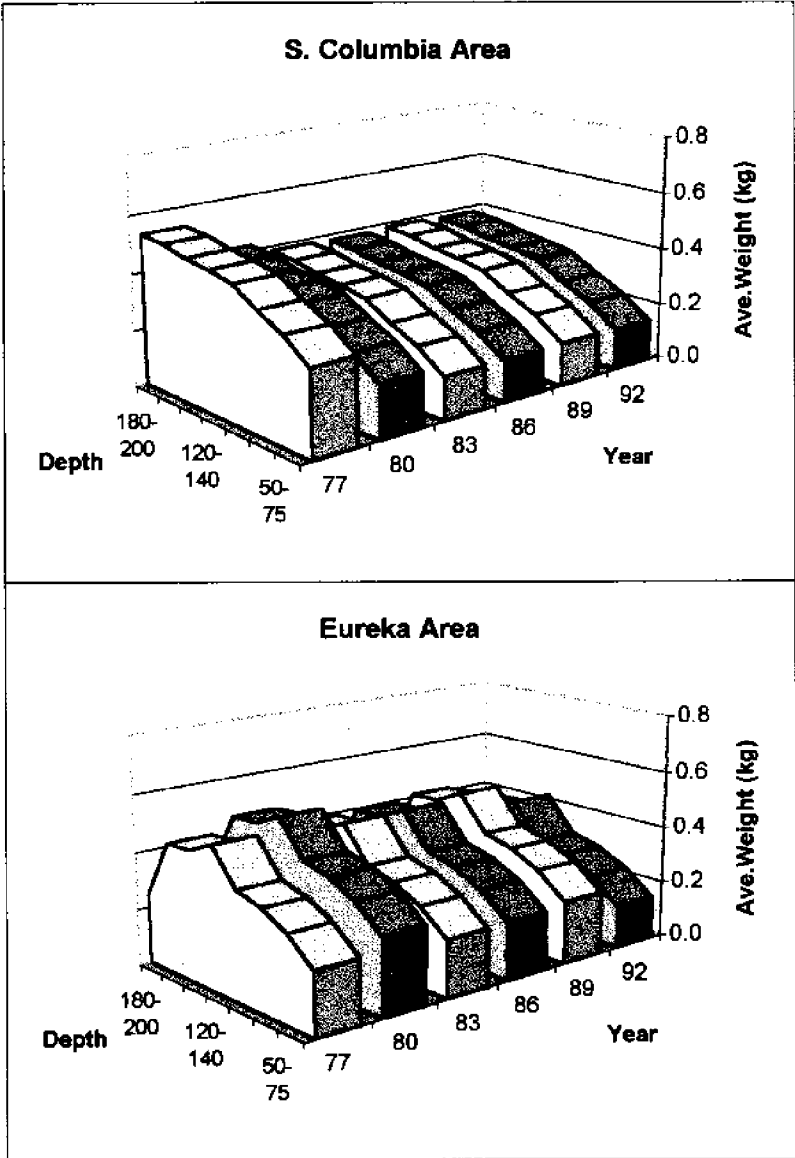


Figure 6b. Predicted average weight of English sole in the two southern areas, based on a weighted linear regression model with factors for Area, Depth, Year, and Area.Depth and Area.Year interactions.

The average weight of English sole predicted by the model with terms for Area, Depth, and Year, and Area.Depth and Area.Year interactions indicates that there was a drop in average weight between the 1977 and 1980 surveys, but little change between subsequent surveys (Figures 6a and 6b). In all areas there is a general tendency for the shallowest depth zones to have the lightest weight fish.

Discussion

The predicted values for English sole density and average weight are consistent with the notion that there has been a general increase in recruitment to this stock over the period 1977-1992. English sole have planktonic larvae that metamorphose, settle to the bottom, and assume their demersal form about two months after hatching (Kruse 1983). The 0-age fish occur in estuaries and in shallow waters along the open coast (Krygier and Pearcy 1986). As the fish grow they move into deeper water where the adult population is found. A steady increase in recruitment would result over time in greater numbers of small fish in the shallows, which is the general pattern shown in Figures 4 and 5.

Based on a simple model for density-dependent habitat selection MacCall (1990) developed a theoretical model that relates a population's geographic distribution with its overall size. In this model the population is analogous to liquid in a basin. Depending on the topography of the basin, changes in the volume of the liquid (the population's abundance) will alter the depth of the liquid (the population's density) and the location of the shoreline (the population's range). If the basin has very steep sides, then changes in the volume of the liquid result primarily in changes in the depth of the liquid rather than the location of the shoreline. This seems to be the appropriate model for the West Coast stock of English sole. A ten-fold increase in stock abundance resulted in relatively little change in the occurrence of English sole but substantial increases in fish density in those areas where fish occurred.

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Changes in Geographic Dispersion of Eastern Bering Sea Flatfish Associated with Changes in Population Size

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Abstract

Trawl survey estimates of flatfish abundance in the eastern Bering Sea were used to evaluate the relationship between population size and spatial dispersion of populations. According to MacCall's "basin" hypothesis, fish may utilize suboptimal habitats in response to density-dependent interactions. Not only are there potential negative effects on individual fitness, but a relationship between stock area and abundance also influences catchability and could thus confound the resource assessments.

Numbers of arrowtooth flounder (*Atheresthes stomias*), Greenland turbot (*Reinhardtius hippoglossoides*), yellowfin sole (*Pleuronectes asper*), rock sole (*Pleuronectes bilineatus*), Alaska plaice (*Pleuronectes quadrituberculatus*) and flathead sole (*Hippoglossoides elassodon*) were estimated using standard stratified sampling procedures. These estimates were compared with an index of dispersion based on the catch per unit effort-weighted average distance of a population from its calculated center of abundance during each year (1982-1993). Annual maps were examined and linear regressions were performed to evaluate the nature of the abundance-dispersion relationship for each species. Direct relationships were apparent for arrowtooth flounder ($P = 0.08$), Greenland turbot ($P = 0.04$), flathead sole ($P = 0.01$) and yellowfin sole ($P = 0.17$). No relationship was evident for rock sole ($P = 0.93$) and an inverse relationship was observed for Alaska plaice

($P = 0.002$). Examination of the temporal cross correlations between abundance and dispersion indicated a delayed (+1 year) response to increased abundance by Alaska plaice. Possible mechanisms are described, including a multi-species interpretation of the abundance-dispersion relationship for Alaska plaice.

Introduction

Changes in the spatial distribution of fish stocks may reflect underlying changes in population size. MacCall (1990) proposed that geographical expansions and contractions of fish stocks in response to changes in abundance were the result of density-dependent habitat selection. That is, as a population increases within a given area, elevated levels of interference and competition eventually relegate subordinate individuals to marginal and perhaps suboptimal habitat. When population size decreases at a later time, inhabitants of outlying areas reoccupy more suitable areas as competitive pressures ease. In effect, the overall density of individuals remains relatively constant while total geographic area expands and contracts.

Aside from possible negative effects on individual fitness related to suboptimal habitat, a relationship between stock size and area occupied can profoundly affect the ability to assess the resource. Quantitative stock assessments generally assume a constant and proportional relationship between catch per unit of effort (i.e., C/f , or CPUE) and underlying stock abundance (N) at any given time t . That is:

$$(C/f)_t = q \times N_t \quad (1)$$

The presumed constant of proportionality is the catchability coefficient (q):

$$q = e \times (a/A) \quad (2)$$

which is comprised of two components, namely the gear efficiency (e), or the fraction of individuals in the path of the net that are retained by the net, and secondly the area sampled by one unit of effort (a) relative to the area occupied by the full population (A). In practice, the parameter A may be defined as a stratum area and the parameter t may actually be an interval of time sufficiently long that averages are used for $(C/f)_t$ and N_t :

$$(\overline{C/f})_t = q \times \overline{N}_t = e \times (a/A) \times \overline{N}_t \quad (3)$$

As such, the catchability coefficient is inversely proportional to the area (A) occupied by the full population (Paloheimo and Dickie

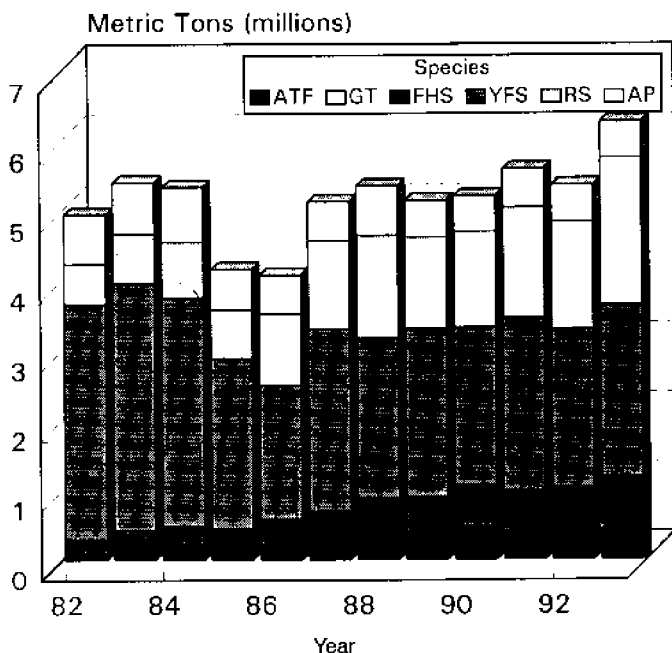


Figure 1. Total biomass of major flatfish species over the continental shelf of the eastern Bering Sea. Estimates are based on annual bottom trawl surveys conducted by the National Marine Fisheries Service. (ATF = arrowtooth flounder; GT = Greenland turbot; FHS = flathead sole; YFS = yellowfin sole; RS = rock sole; AP = Alaska plaice; note that the white band for GT, above ATF, is imperceptibly narrow.)

1964; Winters and Wheeler 1985; Crecco and Overholtz 1990). Therefore, CPUE is not a reliable indicator of abundance when the geographic range of the stock varies.

Flatfish stocks in the eastern Bering Sea varied considerably during the period 1982-1993 (Fig. 1) and, because of their commercial and ecological importance (Bakkala 1993), an investigation of the abundance-dispersion relationship has been undertaken. The combined flatfish biomass has ranged from 4.1 million metric tons (mt) in 1986 to 6.3 million in 1993. Except for 1985-1986, the combined biomass has been relatively constant around its long-term average of 5.18 million mt. Individual stocks, on the other hand, have varied

according to their own unique long-term patterns. Biomass of rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), and arrowtooth flounder (*Atheresthes stomias*) have increased steadily during the period; the biomass of yellowfin sole (*Pleuronectes asper*) and Alaska plaice (*Pleuronectes quadrituberculatus*) has generally declined in abundance during the same period; and Greenland turbot (*Reinhardtius hippoglossoides*) biomass has recently increased after a period of sharp decline. If changes in dispersion accompany these changes in abundance, then there are a number of important implications and these are discussed.

Data and Methods

Estimation of abundance

Research trawl surveys are conducted annually in the eastern Bering Sea (EBS) by the Resource Assessment and Conservation Engineering Division of the Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service, to provide data for stock assessments and management of the fishery resources in the region. The surveys are pursued each June-August in a 463,400 km² region of the EBS shelf (Fig. 2) at depths ranging from approximately 20 to 200 m. An 83-112 Eastern otter trawl is deployed from chartered vessels within each of 355 standard stations defined by a 20 by 20 nautical mile (nmi) sampling grid. This sampling frame is divided into 10 strata defined on the basis of depth and geography (Walters and McPhail 1982; Walters 1983). Each sample consists of a 30 minute tow taken at a speed of 3 knots. The catch is individually processed to determine total weight and numbers by species and sex and a variety of measurements and biological samples are collected from individual specimens. Sex is determined by visual inspection of the body cavity.

Population estimates for each species are generated from catch weights and numbers using standard area-swept procedures (Alverson and Pereyra 1969). The population estimates that result can be partitioned according to sex/life history stage (i.e., male, female, juvenile) and stratum. Prior to 1988, area swept by the net was determined using LORAN fixes and a standard net width. Since that time, SCANMAR (Aasgaardstrand, Norway) electronic net mensuration gear has been used to monitor net configuration and beginning in 1992 a geographic positioning system (GPS) has been used to determine geographic position (reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA).

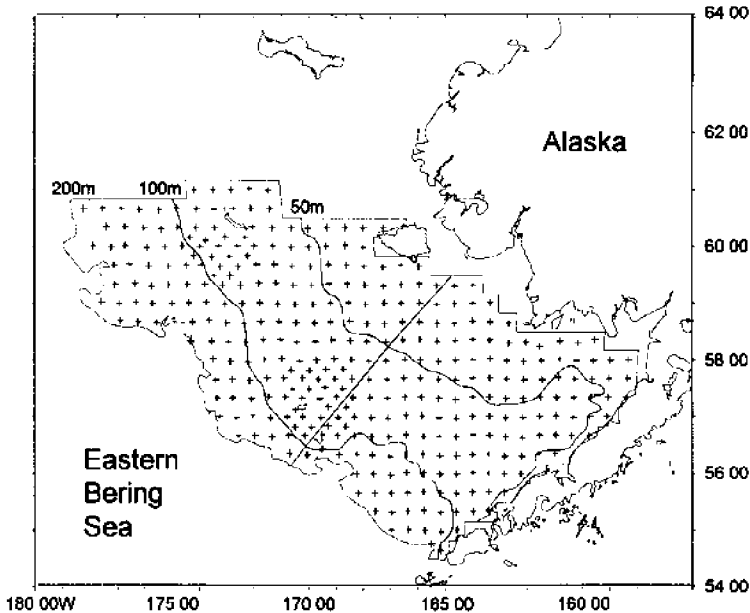


Figure 2. Schematic diagram of the annual National Marine Fisheries Service bottom trawl survey of the eastern Bering Sea continental shelf. Stations are generally located 20 nmi apart at depths generally between 20 and 200 m. Higher density sampling occurs in the vicinity of the Pribilof Islands.

For purposes of this study, abundances of rock sole, flathead sole, arrowtooth flounder, yellowfin sole, Alaska plaice and Greenland turbot are reported as the total number of males and females within the study area. This grouping was an attempt to exclude juveniles from analyses with older fish because of potential age-specific differences in spatial distribution (Swain and Wade 1993; Marshall and Frank 1994; Fig. 3).

Dispersion index

Dispersion is defined as the state of being distributed in space as a result of scattering in various directions. For this study, an annual index of dispersion was determined for each flatfish population based on a weighted mean distance of the population from its center of abundance. That is, the population center (*pc*) was defined as the

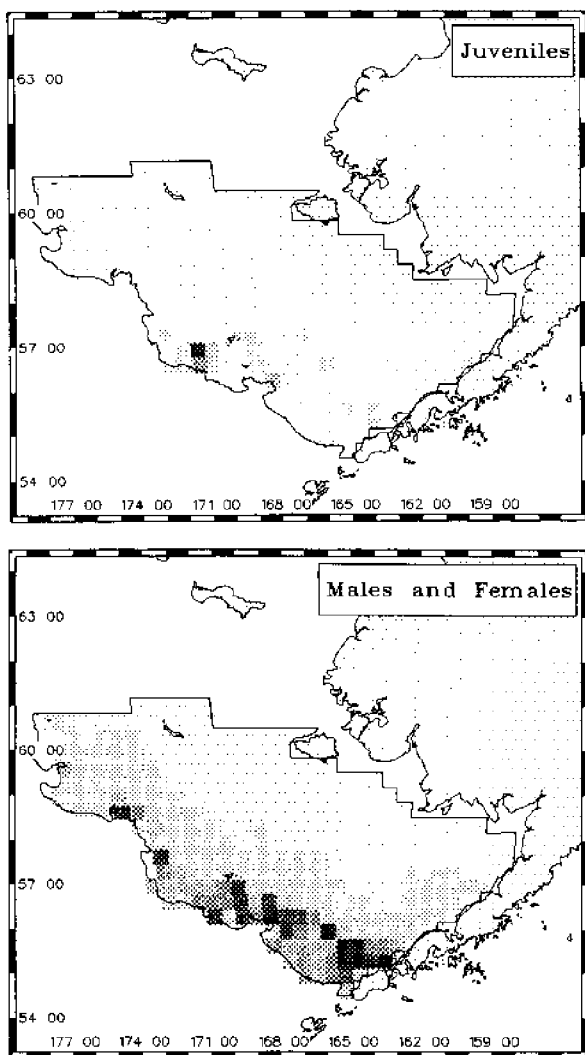


Figure 3. Distribution maps for arrowtooth flounder demonstrating the pattern of age segregation in eastern Bering Sea flatfish. Plotted values represent average densities (no./unit area) for the period 1982-1993. Higher densities are represented by denser shade patterns, with zero-catches shaded the same as the land mass. Approximately 20% of the total population is contained in each of the five non-zero density classes.

intersection of the CPUE-weighted average latitude and CPUE-weighted average longitude of all samples (i) taken during a given year:

$$\overline{pc}_{lat} = \frac{\sum(C/f \times lat)_i}{\sum(C/f)_i}, \quad \overline{pc}_{long} = \frac{\sum(C/f \times long)_i}{\sum(C/f)_i} \quad (4)$$

Dispersion of a flatfish population during a particular year ($dispop_{sp,yr}$) was estimated by calculating the CPUE-weighted average distance between each survey station visited and the population center for a species during each year. Distances ($dist$) between the latitude-longitude pairs were determined using an unpublished algorithm (Compact) on the AFSC's mainframe computer:

$$dispop_{sp,yr} = \frac{\sum \left\{ (C/f)_i \times dist \left\{ (lat_i, long_i), (\overline{pc}_{lat}, \overline{pc}_{long}) \right\} \right\}}{\sum (C/f)_i} \quad (5)$$

Distribution maps

Graphical representations of dispersion were produced using Camris, a PC-based mapping and resource inventory system (Ecological Consulting, Inc., Portland, OR). Standardized numbers of individuals caught at each station were represented using the survey mapping module with the original 20 by 20 nmi grid in a Mercator projection. Fixed intervals (except as noted) were used to plot the abundance data so as to represent absolute changes in the dispersion of a population.

Statistical analysis

The relationship between abundance and dispersion for each of the six flatfish stocks was evaluated using standard linear regression (c.f., Rose and Leggett 1991). The regressions were structured with abundance as the independent variable and dispersion as the dependent variable, in keeping with the underlying density-dependent mechanism. The resulting models were examined for unusual residuals and excessive leverage. An asymptotic model (c.f. Swain and Wade 1993) was not utilized since there was no evidence by 1993 of biological saturation in the EBS survey area.

Cross-correlations between abundance and dispersion were calculated to evaluate temporal aspects of the stock-area relationships. The correlation coefficients, however, were not used to evaluate the fundamental abundance-dispersion relationships because of the

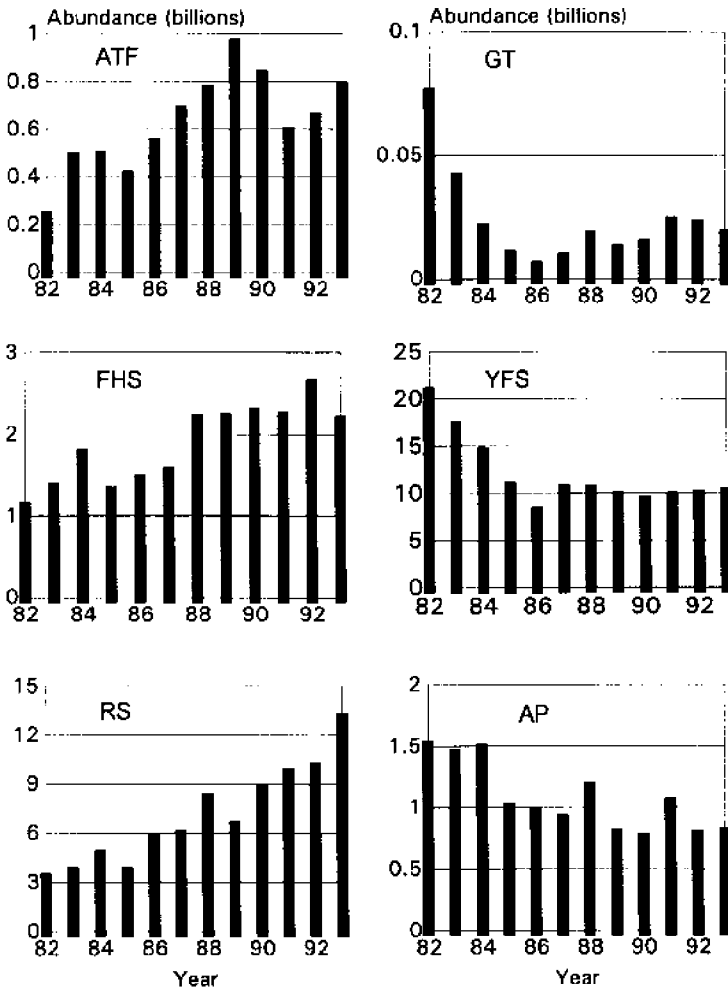


Figure 4. Numbers of combined male and female flatfish over the continental shelf of the eastern Bering Sea. Estimates are based on annual bottom trawl surveys conducted by the National Marine Fisheries Service. (ATF = arrowtooth flounder; GT = Greenland turbot; FHS = flathead sole; YFS = yellowfin sole; RS = rock sole; AP = Alaska plaice.)

functional dependence between the variables (Sokal and Rohlf 1981). Statgraphics Plus for Windows (ver. 1.0) and Statgraphics Plus for DOS (ver. 6.1) (Manugistics, Inc., Rockville, MD) were used to perform the statistical analyses.

Results

Population abundance

The abundance of male and female flatfish in the EBS survey area varied substantially during 1982-1993. In keeping with the trend in combined biomass (Fig. 1), the numbers of male and female rock sole, flathead sole and arrowtooth flounder have generally increased, yellowfin sole and Alaska plaice have generally declined while Greenland turbot have recently increased following a period of sharp decline (Fig. 4). Rock sole abundance increased over four-fold, ranging from a low of 3.23 billion fish in 1982 to 13.03 billion in 1993. Except for temporary declines in 1985 (-22%) and 1989 (-21%), the population has grown steadily larger, averaging 19% year⁻¹ during the period of interest. Flathead sole abundance has doubled from 1.11 billion males and females in 1982 to 2.16 billion in 1993. The steady increase in the flathead sole population in the Bering Sea was punctuated by two intervals of decline, 1984-1985 (-26%) and 1992-1993 (-17%). An especially large (+42%) increase in numbers of males and females occurred during 1987-1988. Numbers of arrowtooth flounder have increased from 0.23 billion males and females in 1982 to 0.78 billion in 1993. The population increased during eight of the eleven yearly intervals and declined temporarily during the other three intervals (-17% during 1984-1985; -39% overall during 1989-1991). Maximum abundance of arrowtooth flounder occurred during 1989 with an estimated 0.96 billion males and females on the shelf. Yellowfin sole numbers in the EBS during 1982-1993 have declined substantially from a high of 20.68 billion males and females in 1982 to 7.96 billion in 1986. The population increased (30%) to 10.04 billion in 1987 and has remained relatively constant ever since. Notwithstanding the overall decline, yellowfin sole was the dominant flatfish species in the EBS during 1982-1993, both in terms of biomass and number of individuals. (Preliminary estimates for 1994, however, indicate that rock sole is now the most abundant species; Pers. comm., G. Walters, Alaska Fisheries Science Center, NMFS, 7600 Sand Point Way N.E., Seattle, WA 98115-0070/ waltersg@afsc.noaa.gov, Oct. 1994). The Alaska plaice population in the EBS declined 48%, from 1.50 billion

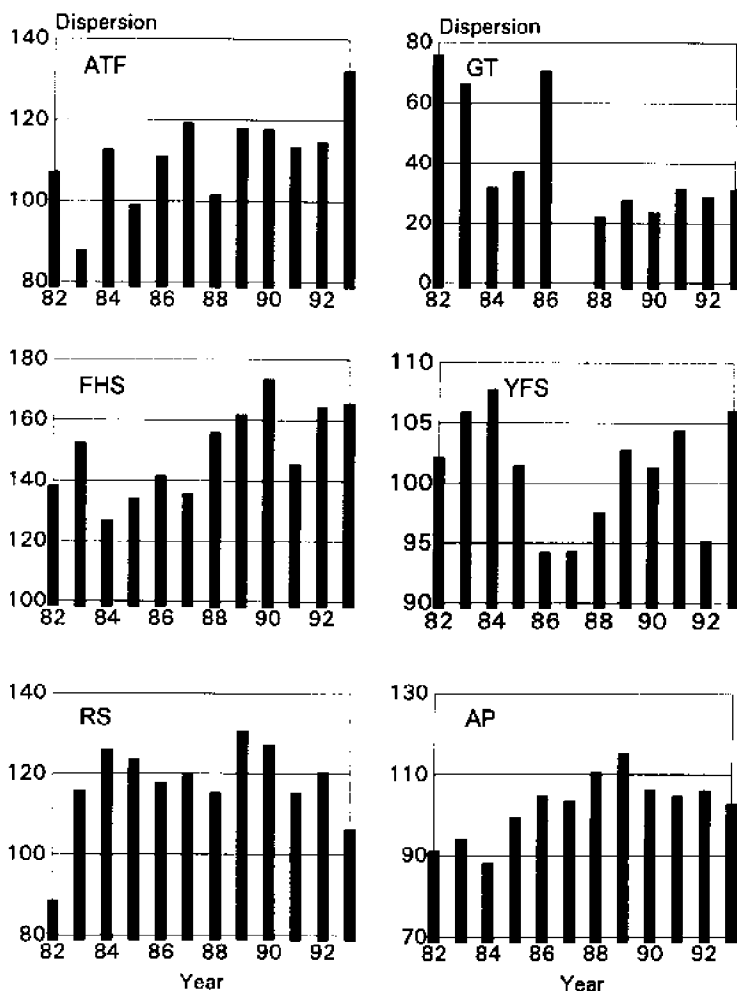


Figure 5. Dispersion of eastern Bering Sea flatfish populations based on CPUE-weighted mean distances of each population from its annual center of abundance. (ATF = arrowtooth flounder; GT = Greenland turbot; FHS = flathead sole; YFS = yellowfin sole; RS = rock sole; AP = Alaska plaice.)

Table 1. Average and coefficient of variation for the annual indices of dispersion (nmi) of flatfish populations in the eastern Bering Sea, 1982-1993. Remember these are means of estimates and that each species was not independently observed.

Species	Average	Coefficient of variation
Alaska plaice	100.9	7.8
Arrowtooth flounder	110.0	10.3
Flathead sole	147.9	10.0
Greenland turbot	35.6	62.1
Rock sole	115.9	9.6
Yellowfin sole	100.6	4.7

males and females in 1982 to 0.78 billion in 1993. Overall, the trend was steadily downward with the single greatest drop (-33%) occurring during 1984-1985. There were, however, two sizable upswings during the period: 1987-1988 (+30%) and 1990-1991 (+39%). The abundance of Greenland turbot males and females declined precipitously (-93%) from 1982 (0.075 billion) to 1986 (0.005 billion). The annual rate of decline, however, decreased gradually through this period. The population began to increase slightly in 1987, with an upward trend continuing to 0.18 billion in 1993.

Population dispersion

Dispersion of EBS flatfish populations varied interannually with some notable differences among the species (Fig. 5). Average dispersion for the 1982-1993 period was greatest for flathead sole, followed by rock sole, arrowtooth flounder, Alaska plaice, yellowfin sole and Greenland turbot (Table 1). There was an apparent lack of association between average abundance and average dispersion when examined at the species level for all years combined, suggesting species-specific differences in average population densities. For example, yellowfin sole consistently was the most abundant of the six flatfish species in the EBS (Fig. 4), yet ranked fifth overall in average dispersion (Table 1). Flathead sole, on the other hand, demonstrated the greatest average dispersion of the species studied, yet was only the third largest population during 1982-1993. Overall, dispersion was clearly lower for Greenland turbot which were consistently least abundant (Fig. 4), however variability of the annual index was notably greater for

Table 2. Coefficients, significance levels and coefficients of multiple determination (R^2) for standard linear regressions between numeric abundance of eastern Bering Sea flatfish and an index of dispersion based on CPUE-weighted average distance from the annual population center.

Species	Slope $\times 10^9$	Intercept	<i>P</i> -value	R^2
Alaska plaice	-2.2	123.3	0.002	0.61
Arrowtooth flounder	3.0	91.6	0.076	0.28
Flathead sole	2.2	107.6	0.009	0.51
Greenland turbot	70.0	20.1	0.037	0.37
Rock sole	0.01	115.2	0.930	< 0.01
Yellowfin sole	0.05	94.5	0.172	0.18

this species (Table 1). The dispersion of arrowtooth flounder and flathead sole populations in the EBS generally increased during 1982-1993. Dispersion of Alaska plaice populations also generally increased although there was evidence of a slight decline late in the interval. Rock sole dispersion during 1982-1993 was relatively constant, excluding the very low value during 1982. Dispersion of yellowfin sole varied between high and low values without a clear trend while dispersion of Greenland turbot generally declined, except for a dramatic increase during 1986.

Abundance-dispersion analysis

The linear regression analysis demonstrated major differences in both type and strength of the abundance-dispersion relationship (Table 2; Fig. 6). Direct relationships between stock abundance and dispersion were apparent for flathead sole ($P = 0.009$), Greenland turbot ($P = 0.04$), arrowtooth flounder ($P = 0.08$) and yellowfin sole ($P = 0.17$), indicating that dispersion of the stock increased with increased abundance. No relationship was evident for rock sole ($P = 0.93$) while an inverse relationship resulted for Alaska plaice ($P = 0.002$), indicating that dispersion increased as abundance decreased. There were two instances of excessive leverage (i.e., leverage values more than three times the average leverage value) in the set of abundance-dispersion regressions. The Greenland turbot population in 1982 was characterized by relatively high levels of both abundance and dispersion, associated with the peak population of the study period. Rejection of

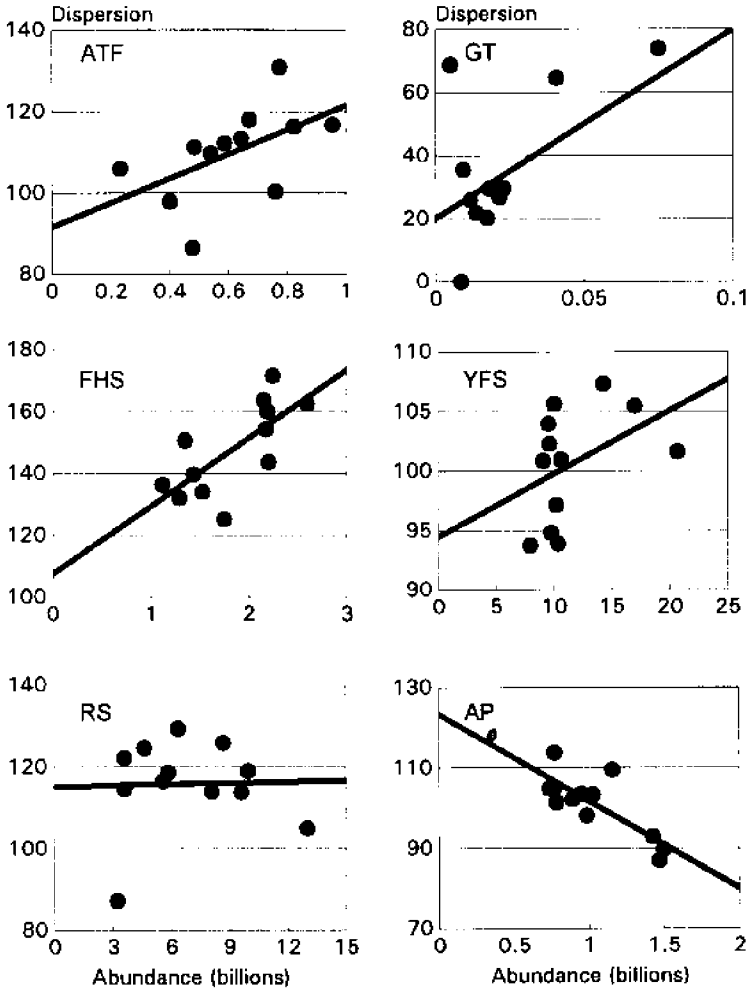


Figure 6. Least squares linear relationships between numbers of eastern Bering Sea flatfish and an annual index of spatial dispersion. (ATF = arrowtooth flounder; GT = Greenland turbot; FHS = flathead sole; YFS = yellowfin sole; RS = rock sole; AP = Alaska plaice.)

this point had a modest effect on the slope (reduced to 62.5×10^{-9}), but changed the P -value (0.35) and R^2 (0.10) appreciably. The 1982 data point for yellowfin sole also was highly influential, with a nominal effect on the slope (0.10×10^{-9}) and R^2 (0.33) but a relatively large effect on the P -value (0.07). Since 1982 was the period of highest abundance for these stocks (Fig. 4), it is likely that additional data from preceding years would reduce the influence of these points and improve the strength of the overall relationships between abundance and dispersion. However, these earlier data were collected using different gear and calibration of the catches is required.

The cross-correlation analysis indicated that time lags may need to be considered in studies of the relationship between stock abundance and dispersion. The analysis identified a significant correlation ($r = -0.66$) between abundance and dispersion of Alaska plaice at a lag of 1 year suggesting that abundance declines "immediately" as well as 1 year after an increase in dispersion.

Discussion

An "ideal free distribution" exists when all individuals in a population are capable of choosing the most suitable habitat and are free to occupy it (Fretwell and Lucas 1970). This implies that individuals will occupy the most suitable habitat at low levels of abundance and "spill out" (to use the image of a "basin" suggested by MacCall (1990)) into increasingly marginal/less suitable habitat as a population grows. Field investigations suggest that increased dispersion is the result of interference and competition for resources among individuals with overlapping niches (MacCall 1990; Swain and Wade 1993; this study). If stock abundance decreases at some later time, then theory predicts that the population will contract in space and retreat toward the most suitable habitat available to it. This could be the same area occupied during the period of lowest abundance or may be an entirely new location when habitat is defined by spatially dynamic variables such as temperature. Detecting these changes in dispersion is a complex task particularly when resource gradients are not smooth and biological responses are protracted. Nevertheless, because critical information about habitat requirements can be inferred from changing patterns of distribution and because of the impact spatial changes may have on conventional stock assessments and resource management success (Paloheimo and Dickie 1964; Winters and Wheeler 1985;

Crecco and Overholtz 1990), studies of the relationship between stock abundance and dispersion are important.

The analyses described here suggest that the geographic area occupied by a population (i.e., its degree of dispersion) can vary as a result of changes in abundance. Populations of arrowtooth flounder, Greenland turbot, flathead sole and yellowfin sole in the eastern Bering Sea, to varying degrees, showed increased dispersion as a result of increased abundance. These results are consistent with theory (MacCall 1990) and with previously published studies of demersal fish in the northwest Atlantic (Crecco and Overholtz 1990; Rose and Leggett 1991; Swain and Wade 1993). The strong inverse relationship between abundance and dispersion of Alaska plaice in the EBS, on the other hand, apparently contradicts theory when considered in the conventional single-species context. This result suggests that dispersion actually decreases as population size increases. However, an explanation using the standard arguments of reduced fitness in marginal areas and density-dependent dispersion away from centers of strong competition (in this case involving other species) seems more reasonable.

Increased dispersion and declining populations of Alaska plaice in the EBS may have been the result of unsuccessful competition with large and increasing populations of congeners. Not only is there significant overlap in the spatial distributions of Alaska plaice, rock sole and yellowfin sole (Fig. 7), but recent evidence indicates that there is considerable overlap in the diets of the three species and, furthermore, that the Alaska plaice diet is the most restricted of the group (Lang et al., 1995). Whereas rock sole consume polychaetes (45% by weight), other marine worms (sipunculans/eciurids; 16%) and gammarid amphipods (7%), the Alaska plaice diet is almost exclusively polychaetes (57%) and other worms (23%). Similarly, the yellowfin sole diet has a relatively large (18%) polychaete component and thus may compete with Alaska plaice for food. During 1982-1993, the rock sole population grew dramatically and, when considered together with the yellowfin sole population (the most abundant flatfish in the EBS from 1982 to 1993), greatly outnumbered Alaska plaice even in areas of relatively low abundance. Thus, increasing dispersion of Alaska plaice may have been a response to crowding by dominant (both in terms of dietary flexibility and sheer numbers) congeners. The sustained decline in numbers would be indicative of reduced fitness in increasingly marginal habitat. This scenario suggests that the "basin" theory

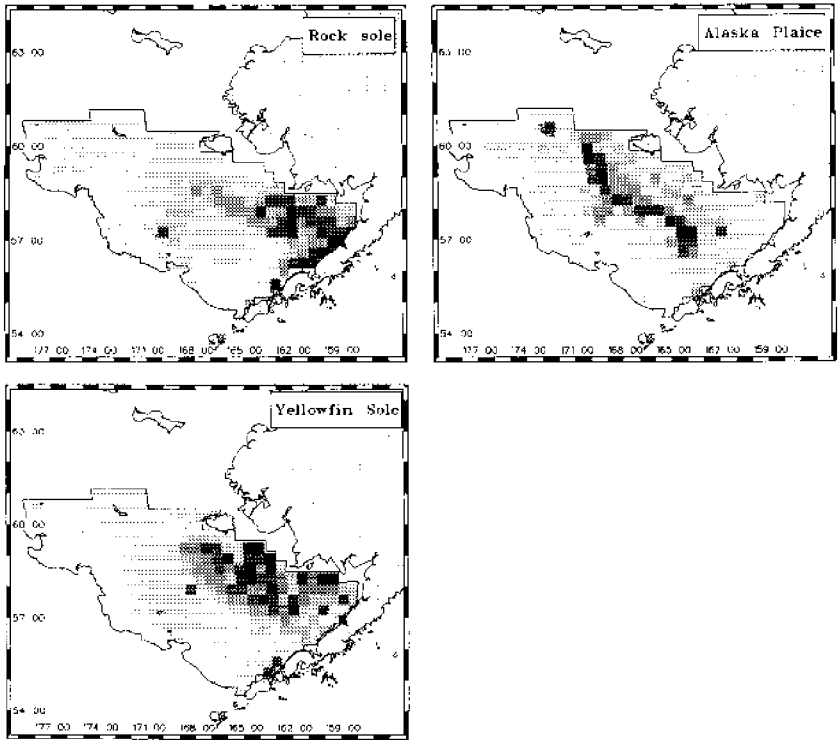


Figure 7. Distribution maps for rock sole, Alaska plaice and yellowfin sole demonstrating spatial overlap and the potential for interference and competition in the eastern Bering Sea. Plotted values represent average densities (no./unit area) for the period 1982-1993. Higher densities are represented by denser shade patterns, with zero-catches shaded the same as the land mass. Approximately 20% of the total population is contained in each of the five non-zero density classes. Because of substantially larger yellowfin and rock sole populations, there may be considerable interaction with Alaska plaice even in areas of relatively low abundance.

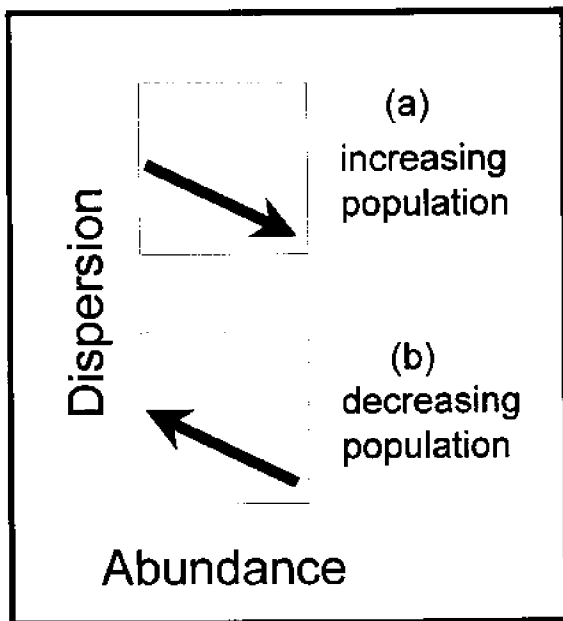


Figure 8. Schematic diagrams of inverse abundance-dispersion relationships demonstrating alternative interpretations based on consideration of the time path (indicated by arrow) of an abundance time series. The relationship for population (a) suggests that dispersion is decreasing as abundance increases, suggesting some form of aggregative behavior whereas relationship (b) suggests that dispersion is increasing as abundance declines (as suggested for Alaska plaice in the eastern Bering Sea).

could be extended to include interspecific competition, as well as a temporal component which accounts for the path along the abundance-dispersion line (Fig. 8).

Other factors may complicate investigations of abundance-dispersion relationships in marine fish. One obvious concern is the inverse relationship between dispersion and catchability (eq. 2). For example, the magnitude of the decline in Alaska plaice abundance may have been amplified somewhat by unaccounted for changes in catchability as the stock dispersed. Existing stock assessment tech-

niques do not address this problem. Also, previous studies generally have not considered time lags, although it seems reasonable that some temporal offset in the variables occurs. In the case of the declining Alaska plaice population, cross-correlation analyses suggested that declining abundance associated with competition for food persisted through the following year. For direct relationships and increasing populations (e.g., flathead sole), positive time lags might reflect delayed dispersion due to slow depletion of food resources or a delayed influx of progeny from a nursery area that is spatially discrete. Although positive time lags are probably more prevalent, negative time lags (i.e., changes in dispersion prior to changes in abundance) are also conceivable if, for example, juveniles and adults intermingle and compete for a limiting resource, but juveniles are not retained by the sampling gear until a certain minimum size is reached. As a result, several time periods could pass before smaller individuals are detected and prior dispersion is explained. Appropriateness of the sampling frame also needs to be considered when survey data are used to estimate abundances. Abundance-dispersion relationships would obviously be weakened if large and variable components of a population occurred outside the study area. New evidence suggests, for example, that the relatively weak yellowfin sole relationship reported here may have been influenced by estimation errors caused by repeated migrations of fish into shallow water for batch spawning (as proposed by Nichol 1995).

Abundance-dispersion studies would probably benefit from an improved index of stock distribution. For example, Marshall and Frank (1994) discussed contradictory results in the literature for Georges Bank haddock (*Melanogrammus aeglefinus*), which were attributed to differences in the dispersion index used. Also, the apparent disagreement between the distribution maps for rock sole which depict a strong abundance-dispersion relationship (Fig. 9), and the results of the statistical analysis which clearly are not supportive, suggests that further refinement is necessary. Other studies have estimated stock distribution using measures based on presence/absence or indices based on the magnitude of catch-per-tow (reviewed by Marshall and Frank 1994). Some indices scale positively with abundance (e.g., frequency of non-zero samples) while others may unnecessarily obscure fine-scale patterns (e.g., integrating stratum areas based on median catch levels therein). The index used here, while avoiding some of these problems, is sensitive to the definition of the population center. If multiple centers exist initially and grow together over

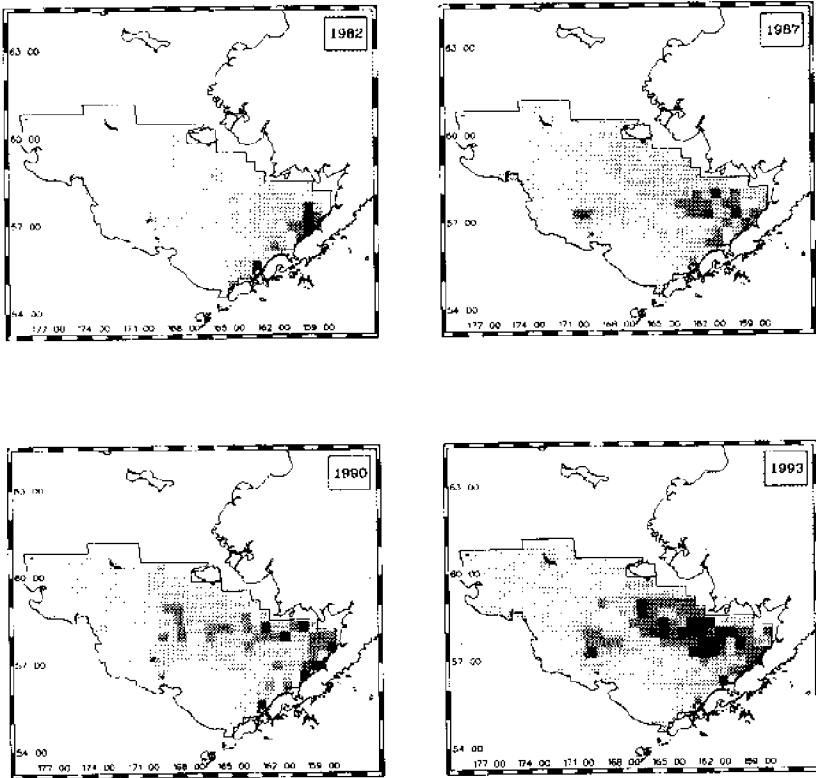


Figure 9. Distribution maps for eastern Bering Sea rock sole demonstrating increasing levels of dispersion during a period of steadily increasing population size (1982-1993). Plotted values represent average densities (no./unit area) for the period 1982-1993. Fixed cutpoints (0, 100, 500, 1000, 1500, > 1500) are used to indicate absolute changes in abundance. Higher densities are represented by denser shade patterns, with zero-catches shaded the same as the land mass. Note in particular that expansion of the high density area over time and the concurrent movement into previously unoccupied habitat proceeded in a generally northwesterly direction.

time, dispersion would probably be overestimated at first and underestimated thereafter. This effect could mask an otherwise strong abundance-dispersion relationship. This apparently was not the case for rock sole ($P = 0.93$), however, since there is no evidence of multiple population centers (Fig. 9). Directionality has not generally been incorporated into the various indices used to date (except perhaps as it pertains to the location of the population center relative to land masses; Marshall and Frank 1994), although it would probably contribute to an understanding of the dispersion process.

In addition to analytical methodology, future work with EBS flatfish will focus on aspects of the density-related dispersion mechanism. In particular, group attributes (e.g., size/sex/species) in marginal areas and the evolution of these groups as expansion and contraction occurs will be examined. In addition, spatial modeling of differences in abundance over time will help define the dispersion process and species-specific differences based on life history characteristics (e.g., mode of egg dispersal) could be evaluated. Based on recurring patterns of habitat use, the critical suite of factors which define habitat quality could ultimately be described.

Acknowledgments

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Greenland Turbot (*Reinhardtius hippoglossoides*) Stock Assessment and Management in the Eastern Bering Sea

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Abstract

The fishery for Greenland turbot, *Reinhardtius hippoglossoides*, in the eastern Bering Sea has increased in the past few years, prompting renewed interest in the condition of the stock. Data on this species has been collected by the National Marine Fisheries Service (NMFS) domestic fishery observer program and by surveys using trawl and longline gear. However, because Greenland turbot have not been the focus of a directed research program, the value of any single data source is limited. In this assessment, we use all available information in a size-based model and evaluate the consequences of different plausible interpretations of survey biomass estimates. These alternatives are then used to project future conditions. Because the fishery is executed by longline and trawl gear which target different age groups, the projections are evaluated under different gear-specific harvest levels. A stochastic recruitment model was used in the projection analysis. Fishing mortality specific to gear and sex was monitored. Results indicate that if future harvests are dominated by longline gear, a more immediate decline in female spawner biomass will occur. However, in this strategy, the expected increase in spawners would occur sooner. This is due to the current state of the population which is composed of mostly large fish from the strong year classes of the 1970s and relatively few intermediate-aged fish from the poor year

classes of the 1980s. We attempt to develop an appropriate strategy which considers the potential competition between gear types.

Introduction

Greenland turbot (*Reinhardtius hippoglossoides*) within the U.S. 200 mile exclusive economic zone are mainly distributed in the eastern Bering Sea (EBS) and Aleutian Islands regions. Juveniles spend the first 3 or 4 years of their lives on the continental shelf and then move to the continental slope (Alton et al. 1988). Juveniles are absent in the Aleutian Islands region, suggesting that the population in this area originates from the EBS or elsewhere. In this study, we assumed that the Greenland turbot found in the two regions represent a single management stock. Because of similarities in appearance and early markets for Greenland turbot and arrowtooth flounder (*Atheresthes stomias*), these two species were managed together until 1985. In recent years, the markets for these species have specialized and the conditions of the stocks have diverged (Wilderbuer and Sample 1992). The American Fisheries Society uses "Greenland halibut" as the common name for *Reinhardtius hippoglossoides* instead of Greenland turbot. To avoid confusion with the Pacific halibut, *Hippoglossus stenolepis*, we retain the common name of Greenland turbot which is also the "official" market name in the United States and Canada (Robins 1991).

Catches of Greenland turbot and arrowtooth flounder were not reported separately during the 1960s. During that period, combined catches of the two species ranged from 10,000 to 58,000 metric tons (t) annually and averaged 33,700 t. Beginning in the 1970s the fisheries for Greenland turbot intensified with catches of this species reaching a peak from 1972 to 1976 of between 63,000 t and 78,000 t annually (Fig. 1). Combined catches declined after implementation of the Magnuson Fisheries Conservation and Management Act (MFCMA) in 1977, but were still relatively high in 1980-83 with an annual range of 48,000 to 57,000 t. Since 1983, however, harvests have declined steadily to a 1986-1994 average harvest equal to 8,100 t. This overall decline was due mainly to catch restrictions placed on the fisheries. For example, during 1992-1994, a total allowable catch (TAC) of 7,000 t was set by the North Pacific Fisheries Management Council due to concerns over low recruitment levels in the 1980s. Also, a comprehensive evaluation of available information on the status of the EBS Greenland turbot stock has not been available since the work of Alton et al. (1988). In this paper, we present results of our investigations of

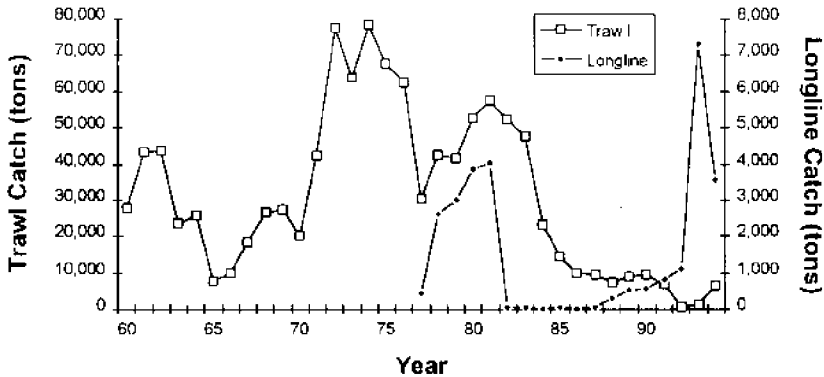


Figure 1. Comparison of trawl (1960-93) and longline (1977-93) catches of Greenland turbot.

available fishery and survey data to be used for the management of the Greenland turbot resource.

Methods: Population Assessment Using a Size-Based, Age-Structured Model

A version of the stock synthesis program (Methot 1989, 1990) to model the Greenland turbot stock was initially presented in Ianelli et al. (1993). Prior to that time, stock assessments of Greenland turbot in the EBS and Aleutian Islands had relied in part on stock reduction analysis (SRA) to provide historical trends in the fishery (Wilderbuer and Sample 1992). In the following sections, we describe the model structure and estimation procedure, and then present information used to model the population dynamics of Greenland turbot in the EBS.

Model structure

Stock synthesis functions by simulating both the dynamics of the population and the processes by which the population is observed. This simulation is first based on available information on the biology and demographics of the species. Namely, the length-weight relationship, maturity at size, fecundity, natural mortality, and growth information. For Greenland turbot, females grow to a larger size than males, information in the model that is specific to sex is retained. The simulated population is used to predict expected values for observa-

tions. These expected values are then compared with the actual observations (data) from surveys and fisheries. The results of the comparisons between expected values and the observations are then used to obtain a statistical likelihood value. This likelihood is maximized via a numerical derivative "hill climbing" algorithm (Methot 1989) to update the simulation model parameters, which continues until no further improvements can be made by "tuning" the simulation.

Catch data from 1960 to 1994 were used in the stock synthesis model. The last four years of data were adjusted to include discards. It was assumed that the stock was at or close to its virgin biomass level when the catch statistics started.

Numbers at age at the beginning of a year (N_a) were calculated by a deterministic population model. The N_a values were transformed to provide expected values for comparison to the observed data. The basic population dynamics equations that describe the catch in numbers at age C_a and total catch biomass Y in a given year are

$$C_a = \frac{N_a F s_a}{F s_a + M} (1 - e^{-F s_a - M})$$

and

$$Y = \sum_{a=1}^{n_{ages}} W_a C_a$$

where s_a is selectivity at age a , F is the fishing mortality rate for fully selected age groups (i.e., where $s_a=1.0$), and W_a is weight at age.

We chose to begin our model in 1960—the first year that catch data were available. The early catches included Greenland turbot and arrowtooth flounder together. To separate them, we assumed that the ratio of the two species in the catch for the years 1960-64 was the same as the mean ratio caught by Soviet vessels from 1965 to 1969. In our model, total catch biomass was also assumed to be known precisely.

This initial numbers at age were modelled using the Beverton-Holt (1957) stock-recruitment model as parameterized by Kimura (1988). In addition, annual recruitments were estimated as parameters in the model and can be thought of as deviations from the underlying stock-recruitment curve. These recruitment deviations were treated as process errors from the mean stock-recruitment curve caused by natural variation in the recruitment process.

Table 1. Data sets used in the stock synthesis model for Greenland turbot in the eastern Bering Sea. All size and age data are specified by sex.

Data component	Years of data
Survey size at age data	1975, 1979-82
Shelf survey: size composition and biomass estimates	1979-1994
Slope survey: size composition and biomass estimates	1979, 1981-82, 1985, 1988, 1991
Longline survey: size composition and abundance index	1984-1993
Total fishery catch data	1960-1994
Trawl CPUE index	1978-1984
Trawl catch size composition	1980-1993
Longline catch size composition	1977, 1979-85, 1992-93

A dome-shaped size-based selectivity function (Methot 1990) was estimated for each survey and fishery described below. Selectivity in our paper indicates a combination of the physical gear retention, that is, as typically determined by mesh or hook size, and availability. For example, if a survey operates in areas where large/older fish are absent due to movement or habitat specificity, then the selectivity estimates would reflect that only the small/young fish typically retained by the gear are expected. For the trawl fishery, the time periods of length frequency data collections from the domestic and foreign fleet did not overlap. Consequently, we treated the foreign and domestic trawl data as from a single fishery and simply let the selectivity pattern be different between the respective periods. Recently, larger/older fish than normal have been observed in the EBS shelf region trawl surveys. Consequently, selectivity for the two most recent years was estimated separately from the earlier data.

Model parameters were estimated by maximizing the log likelihood (L) of the predicted observations given the data. Data were classified into different components. For example, age composition from a survey and catch per unit effort (CPUE) from a fishery were different components. The individual likelihood components were weighted by emphasis factors and summed to get the total likelihood (L). In this paper, emphasis factors are used to evaluate the impact of potentially conflicting data sources. For Greenland turbot in the EBS the model

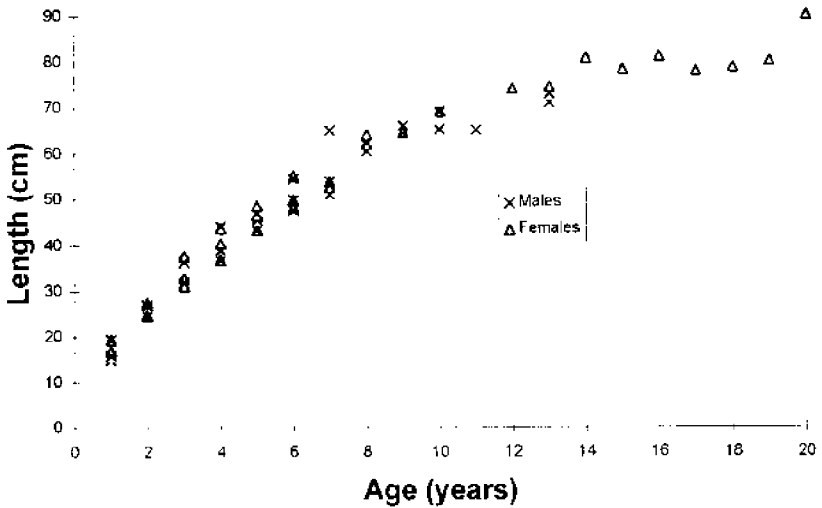


Figure 2. Average annual length at age data for Greenland turbot by sex from the eastern Bering Sea.

included two fisheries and three surveys. Table 1 summarizes the extent of the data used in the different likelihood components.

Biological data

Data on the distribution of Greenland turbot suggest an age-specific spatial pattern. Age data from earlier years show that Greenland turbot on the continental shelf were mainly 1- to 3-year-olds while the fishery on the continental slope caught fish ranging from 3 to 19 years (Alton et al. 1988). Greenland turbot taken by the commercial fishery have been aged as old as 21 years using break-and-burn methods (J. Lyons, pers. comm., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle WA 98115). The von Bertalanffy length-age relationship for Greenland turbot was estimated using all of the available size-at-age data (Fig. 2) and the progression of length frequency distributions within the assessment model.

The length-weight relationship for Greenland turbot as estimated by Ianelli et al. (1993) was:

$$W = 2.69E-06 L^{3.3092} \text{ for females}$$

and

$$W = 6.52E-06 L^{3.068} \text{ for males}$$

where L = length in mm, and W = weight in grams.

Maturation and fecundity by size or age is poorly understood for Greenland turbot in the EBS region. Alton et al. (1988) presented the results from studies of Greenland turbot in different areas in addition to the EBS region. For this analysis, we used a logistic size-maturity relationship which has 50% of the female population mature at 60 cm; 2% and 98% of the females were assumed to be mature at about 50 and 70 cm respectively. This was based on an approximation from Dyakov's (1982) study in the western Bering Sea. The natural mortality rate of Greenland turbot was assumed to be 0.18. This preliminary estimate was selected based on values estimated from other flatfish species. Alternative values for natural mortality were not pursued in this assessment but are planned for future analyses.

Survey data

Age and size composition

Size-at-age information is available from surveys conducted between 1976 and 1982. Time series of estimated size composition of the population was available for the shelf and slope trawl surveys and for the longline survey for various years (Table 1). These are presented in the form of estimated length frequencies of the population that was vulnerable to the survey sampling gear. The slope surveys typically sample more Greenland turbot than the shelf trawl surveys, consequently, the number of fish measured in the slope surveys is greater. The time series of length frequencies from all the surveys (and fisheries) are presented in the results section where model predictions are compared.

Abundance estimates

Abundance estimates for juvenile Greenland turbot on the EBS shelf are provided annually by National Marine Fisheries Service (NMFS) trawl surveys. The older juveniles and adults on the slope have been assessed every third year since 1979 (also in 1981) using various trawl survey gear (Wilderbuer and Sample 1992). The time series of estimates are presented in Table 2.

Biomass estimates from the trawl slope surveys are believed to underestimate the absolute Greenland turbot biomass (Wilderbuer and Sample 1992). Thus, the estimates are essentially indices of relative abundance. They also provide some indication of the minimum stock biomass. The combined estimates from the shelf and slope indicate that abundance in the EBS declined in 1985 to 25% of the

Table 2. Estimated biomass levels from National Marine Fisheries Service, Alaska Fisheries Science Center, demersal trawl surveys.

Year	Eastern Bering Sea			Aleutians
	Shelf	Slope	Shelf and slope combined	
1975	126,700	—	—	—
1979	225,600	123,000	348,600	—
1980	172,200	—	—	48,700
1981	86,800	99,600	186,400	—
1982	48,600	90,600	139,200	—
1983	35,100	—	—	63,800
1984	17,900	—	—	—
1985	7,700	79,200	86,900	—
1986	5,600	—	—	76,500
1987	10,600	—	—	—
1988	14,800	42,700 ^a	57,500 ^a	—
1989	8,900	—	—	—
1990	14,300	—	—	—
1991	13,000	40,500	53,900 ^a	12,000 ^b
1992	24,000	—	—	—
1993	30,399	—	—	—
1994	48,771	—	—	—

^aThe 1988 and 1991 estimates are from 200 to 800 m whereas the earlier slope estimates are from 200 to 1,000 m.

^bThe 1980, 1983, and 1986 surveys sampled 1-900 m whereas the 1991 survey sampled only 1-500 m.

level in 1979. In 1988 and 1991 the slope biomass estimates and the 1991 Aleutian Islands estimate are not comparable to previous years due to differences in depths sampled (Table 2). The interpretation of the CPUE data from these surveys, however, suggests a moderate decline in abundance between 1985 and 1991. The recent increase of biomass in the shelf region is partly due to the presence of larger fish found there (see Fig. 5). Biomass estimates from trawl surveys in the Aleutian Islands region show an increasing trend from 48,700 t in 1980 to 76,500 t in 1986 (Table 2).

The EBS longline survey was used as a relative abundance index. The survey methods and results are presented in Zenger and Sigler

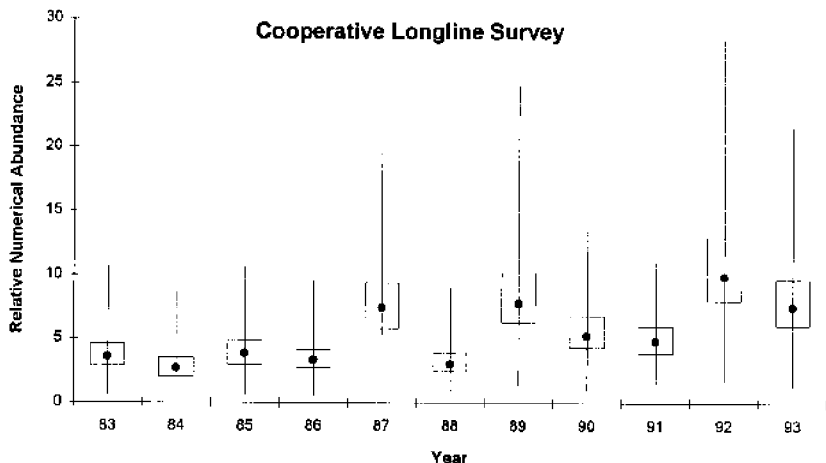


Figure 3. Abundance index estimated from the cooperative longline survey. Boxes represent 25% of the bootstrap estimates around median values (solid dots) and vertical lines represent nominal 90% confidence bounds.

(1992). A log-linear modelling method similar to Kimura (1988) was used to estimate an abundance index as:

$$\log Y_{ijk} = \mu + \alpha_i + \beta_j + h(X_{ijk}) + \varepsilon_{ijk}$$

$$\varepsilon_{ijk} \sim N(0, \sigma^2)$$

where Y_{ijk} is the number of Greenland turbot caught per unit of 900 hooks (20 skates), μ is the mean effect, α_i is the effect of location (survey station i), β_j is the year effect in year j (relative abundance) and $h(X_{ijk})$ is a smooth function of the average hook depth for the k^{th} unit of effort. This type of model (referred to as a general additive model or GAM) with alternative applications of error structures was presented in Chambers and Hastie (1992). The years of available data ranged from 1983 to 1993. Bootstrap resampling of the original data (5,556 observations) and replicate model estimates were used to provide confidence bounds on the annual relative abundance estimates (Fig. 3). We used the median values of the bootstrap estimates as our relative population index. This index represented numerical abundance whereas the shelf and slope surveys represent biomass indices.

Table 3. Catch per unit effort indices from the early trawl fishery (Alton et al. 1988) and recent National Marine Fisheries Service observer data (present study). The recent data were not used in the assessment model for reasons discussed in the text.

Year	78	79	80	81	82	83	84
CPUE Index (Alton et al. 1988)	291	316	449	409	235	195	335
Year			90	91	92	93	94
Trawl CPUE > 300m depth			13.7	11.3	1.6	10.4	19.0
N			1,502	1,306	627	317	67
Trawl CPUE Greenland turbot > 30% of catch			33.0	27.4	77.6	85.5	42.8
N			585	455	9	32	26
Longline CPUE > 500m depth			111.9	107.4	130.5	188.0	118.3
N			747	924	773	2,063	39

CPUE = an index of Greenland turbot catch rate by weight

> 300m signifies fishing operations greater than 300 meters depth

> 30% signifies fishing operations in which Greenland turbot comprised more than 30% of the catch by weight.

Fishery data

Catch and catch per unit effort (CPUE)

The catch data as presented in the introduction were used for both the longline and trawl fisheries. A standard CPUE index derived in Alton et al. (1988) for the years 1978-84 for the trawl fishery was used as an index of abundance in the stock synthesis model (Table 3). Recent NMFS fishery observer data were also examined for changes in catch-rate patterns of Greenland turbot. A preliminary analysis of recent observer data indicates that Greenland turbot catch rates were highest in 1993 but that problems remained in how to handle the data (Table 3). For example, in 1992, 627 trawl operations were observed at depths greater than 300 meters but only 9 of those yielded Greenland turbot in quantities representing more than 30% of the total catch weight. Clearly, this is due to unaccounted for differences in the trawl

target species. At this time, we feel a more rigorous analysis of these data is required before they can be used for assessment purposes.

Size and age composition

No age composition information is available from the fisheries. However, extensive length frequency data are available from the NMFS observer program for the period from 1980 to 1991. The length composition data from the trawl and longline fishery (and the expected values from the assessment model) are presented below in Fig. 5. This information is used in the assessment model and provides an indication of the selectivity of these fisheries and the recruitment strengths.

Results and Discussion

Model selection

Since the model begins in 1960 and size composition data are not available until 1977, resolution of recruitment strength estimates during the early part of the simulation was poor. Initially, we set the individual recruitment estimates from 1960 to 1969 equal to that predicted by an equilibrium stock-recruitment relationship. This yielded a poor fit to the size composition data and estimated a virgin recruitment level which implied a mean unfished biomass of more than 1.8 million metric tons. When all recruitment deviations were estimated (the full model), a single large deviation resulted in the early part of the time series. This indicated a year class more than an order of magnitude greater than the mean estimated recruitment since 1970. Both the full model and the equilibrium recruitment models were therefore unsatisfactory. To compensate, we pooled recruitment deviation estimates from 1965 to 1968 as in Ianelli et al. (1993).

Initial model runs with the shelf survey biomass estimates configured as an absolute biomass index and the slope surveys as a relative index resulted in model fits with unreasonable parameter values. The best fit occurred when the slope abundance index represented only about 5% of the biomass available to the slope survey. That is, a slope survey biomass estimate of 50,000 t would expand to 1,000,000 t of actual biomass available to the survey. This value of "Q" or catchability for the slope survey is unreasonably low compared with values of Q common for other flatfish species. Consequently, we investigated the effect of different fixed values of slope survey Q on the fit to individual

Table 4. Description of three alternative models selected for this stock assessment.

	Assumed slope survey catchability	Implication on current biomass	Total likelihood
Model 1	0.25	High	-2,392
Model 2	0.50	Moderate	-2,452
Model 3	0.75	Low	-2,482

data components. Ianelli et al. (1993) found the majority of likelihood components to be consistent with a low Q value for the slope survey, but that the likelihood surface was relatively flat with respect to Q . Given this uncertainty, we chose to present results for the following three models which have different conclusions about current biomass levels (Table 4).

Selectivity

Selectivity of Greenland turbot varied considerably between all of the surveys and fisheries. The shelf survey selected only small fish whereas the slope survey caught much larger fish. A similar pattern was observed between the trawl and longline fisheries with the longline fishery consistently catching larger Greenland turbot (Fig. 4). Note that the average selectivity estimates for the slope and shelf surveys indicate that our surveys do not sample intermediate size fish (35-50cm) very well. The reason for this is not clear, however, we feel that it is related to the apparent bi-modality in the size distribution observed in the trawl fishery.

Model fit to size composition data

Size composition observations from the fisheries and surveys are generally poorly matched by the model predictions (Fig. 5). This lack of fit can be attributed to several causes. First, the influence of size composition data on the total likelihood for a given gear type and year depends on the number of Greenland turbot measured. In some years, relatively few fish were measured so adjustments of the model to those data would depend on the trade-off in fitting other data, which may have had more extensive sampling. Second, unaccounted for fish movement and hence changing availability affects fits to size composition data when an "average" gear selectivity is used. Finally, natural

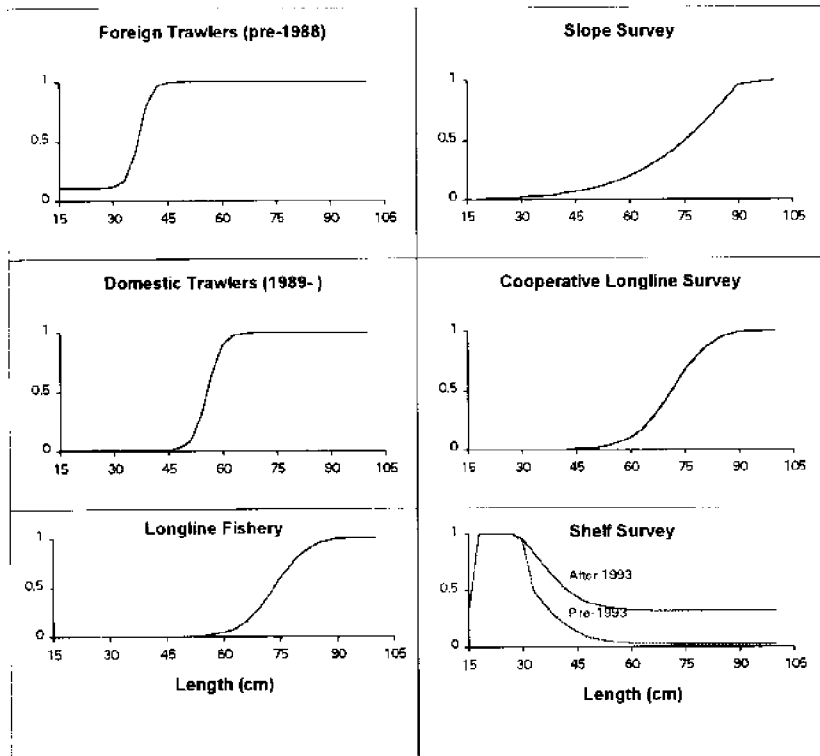


Figure 4. Size-specific selectivity patterns for the surveys and fisheries.

mortality rate is undoubtedly variable among cohorts and years, the extent of which would affect our ability to model the age structure of the population accurately. The nature of the inconsistencies among data types is presented below, particularly as they pertain to assessing the current stock status.

Trends in abundance

For the three models presented in Table 4, the historical biomass trajectory varies considerably (Fig. 6). For Model 3, the model fit to the different abundance indices is also variable (Fig. 7). The assessment model predictions for shelf survey biomass are far below the observed estimates during the early years and subsequently track the survey estimates well. These data are consistent with the conclusion of Alton et al. (1988) that recruitment of juveniles in the EBS has been low

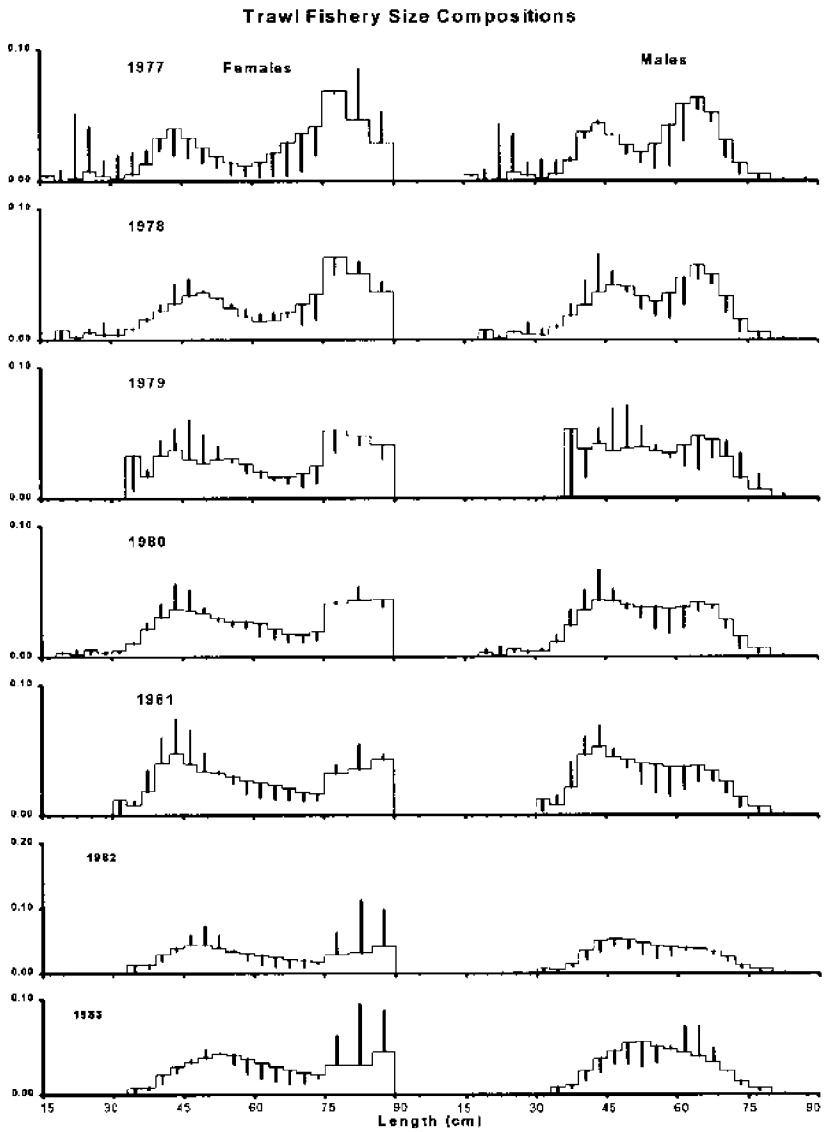


Figure 5. Observed (continuous line) length frequencies and deviations (vertical bar) for the different fisheries and surveys used in the model.

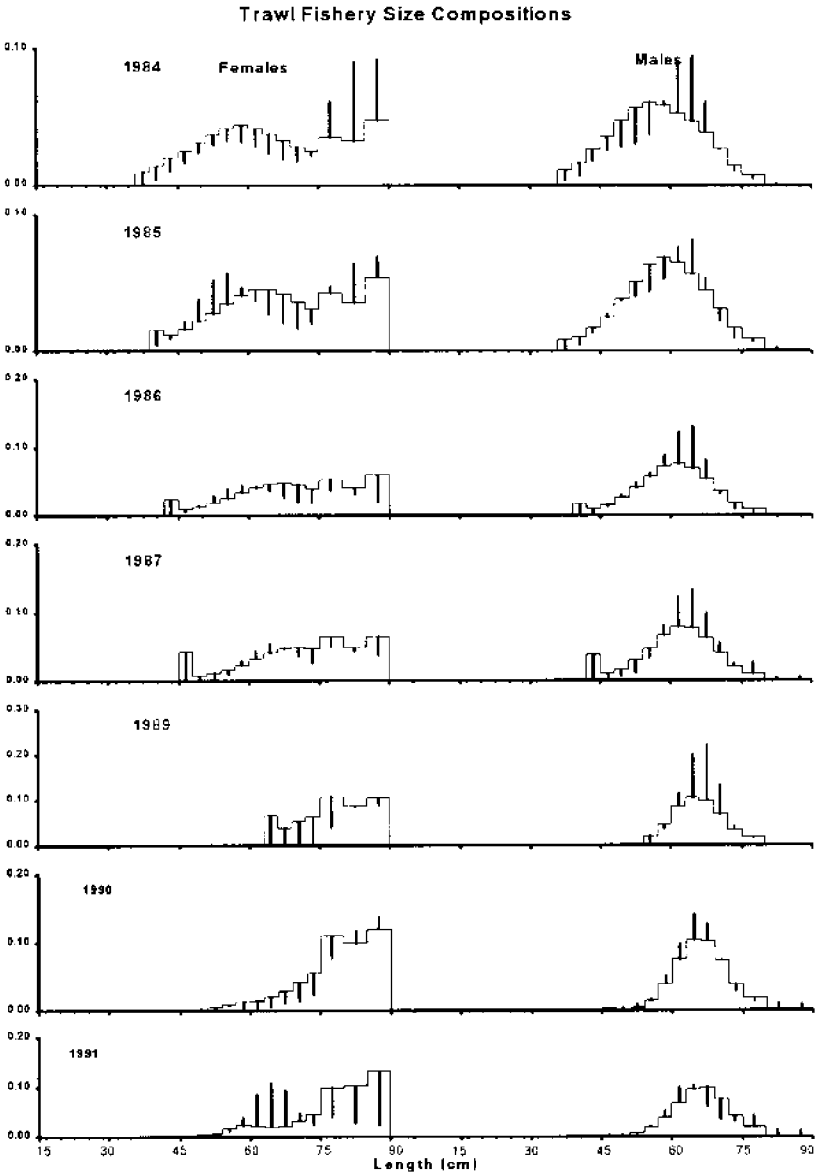


Figure 5. (continued.)

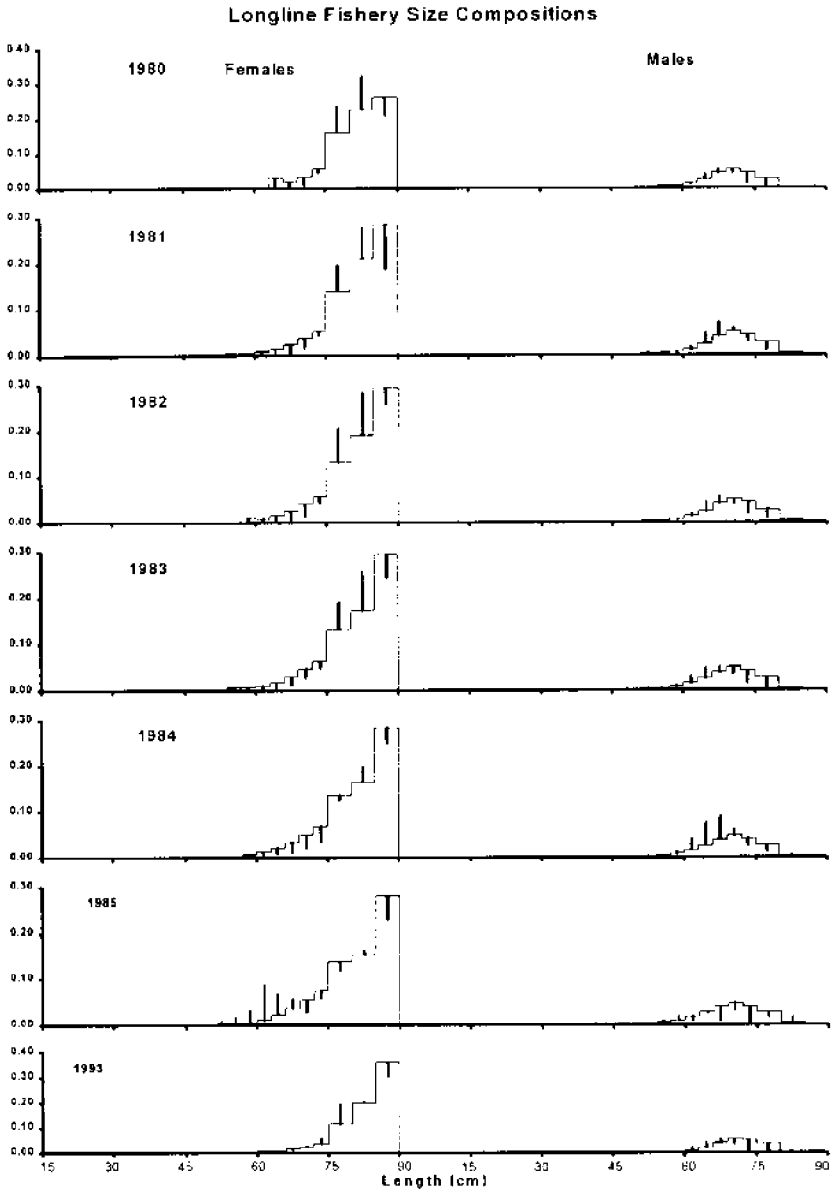


Figure 5. (continued.) Observed (continuous line) length frequencies and deviations (vertical bar) for the different fisheries and surveys used in the model.

Shelf Trawl Survey Size Compositions

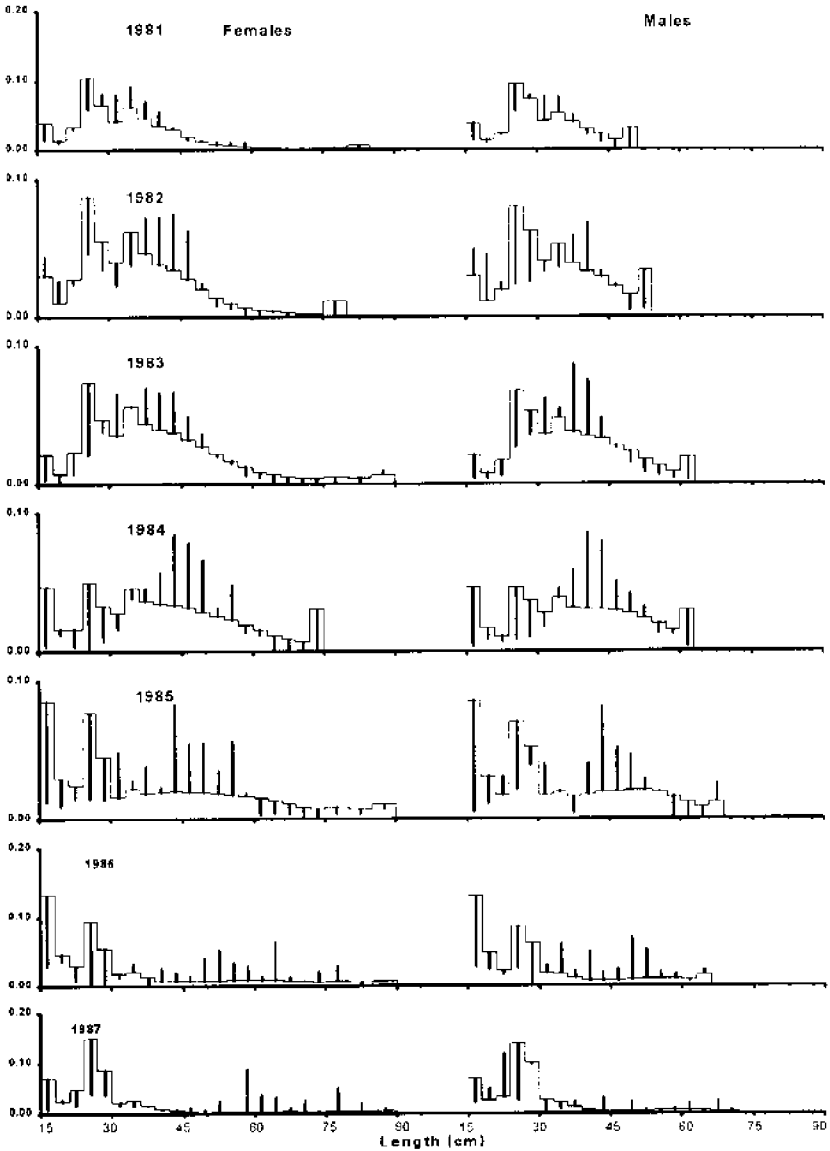


Figure 5. (continued.)

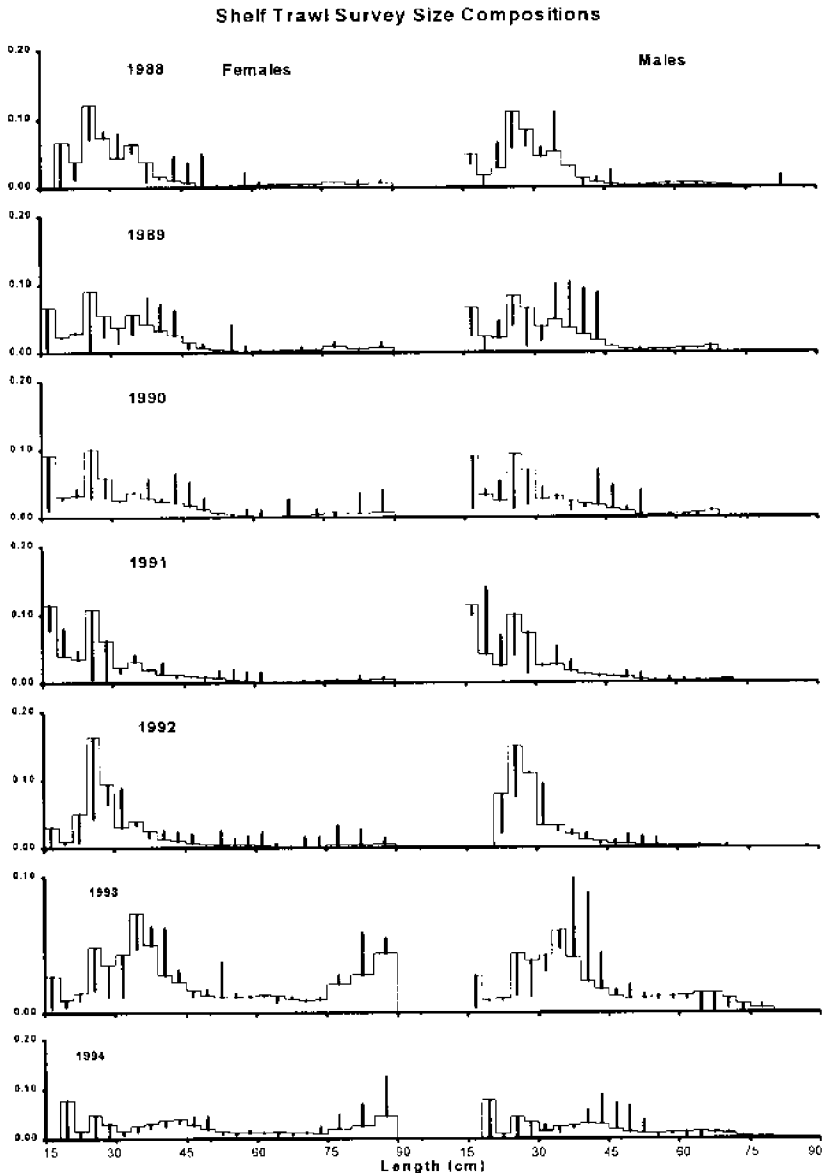


Figure 5. (continued.) Observed (continuous line) length frequencies and deviations (vertical bar) for the different fisheries and surveys used in the model.

Slope Trawl Survey Size Compositions

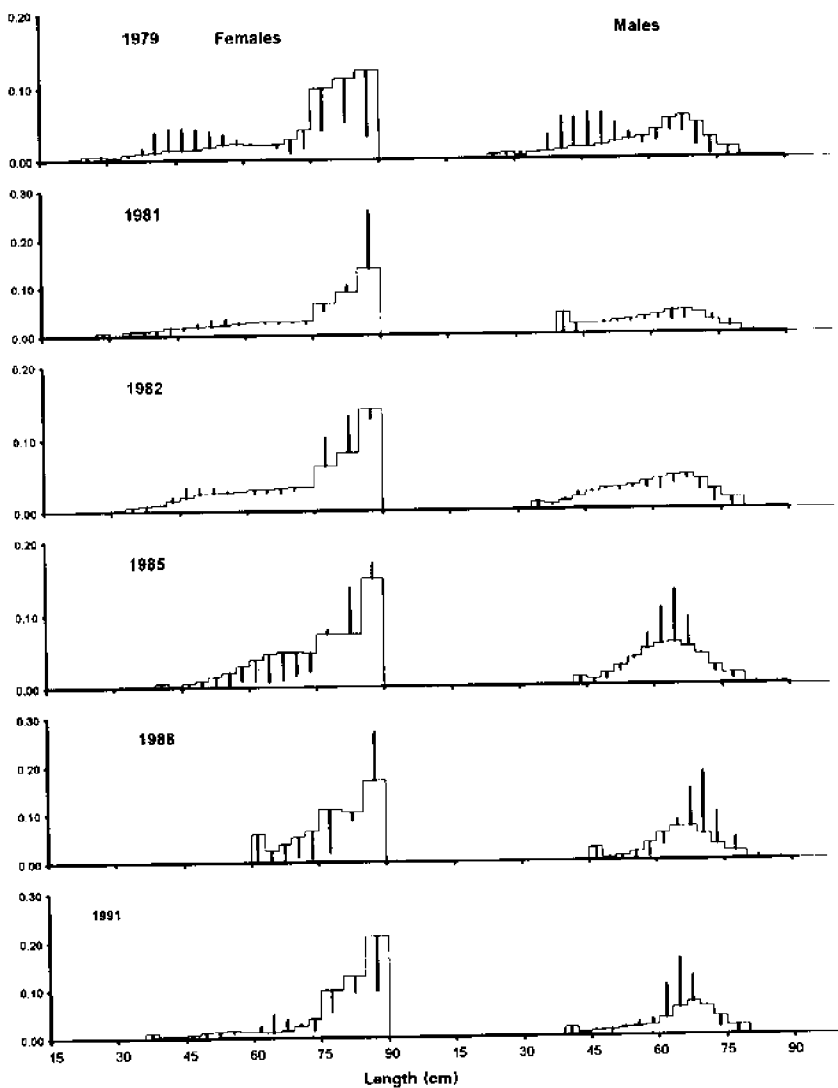


Figure 5. (continued.)

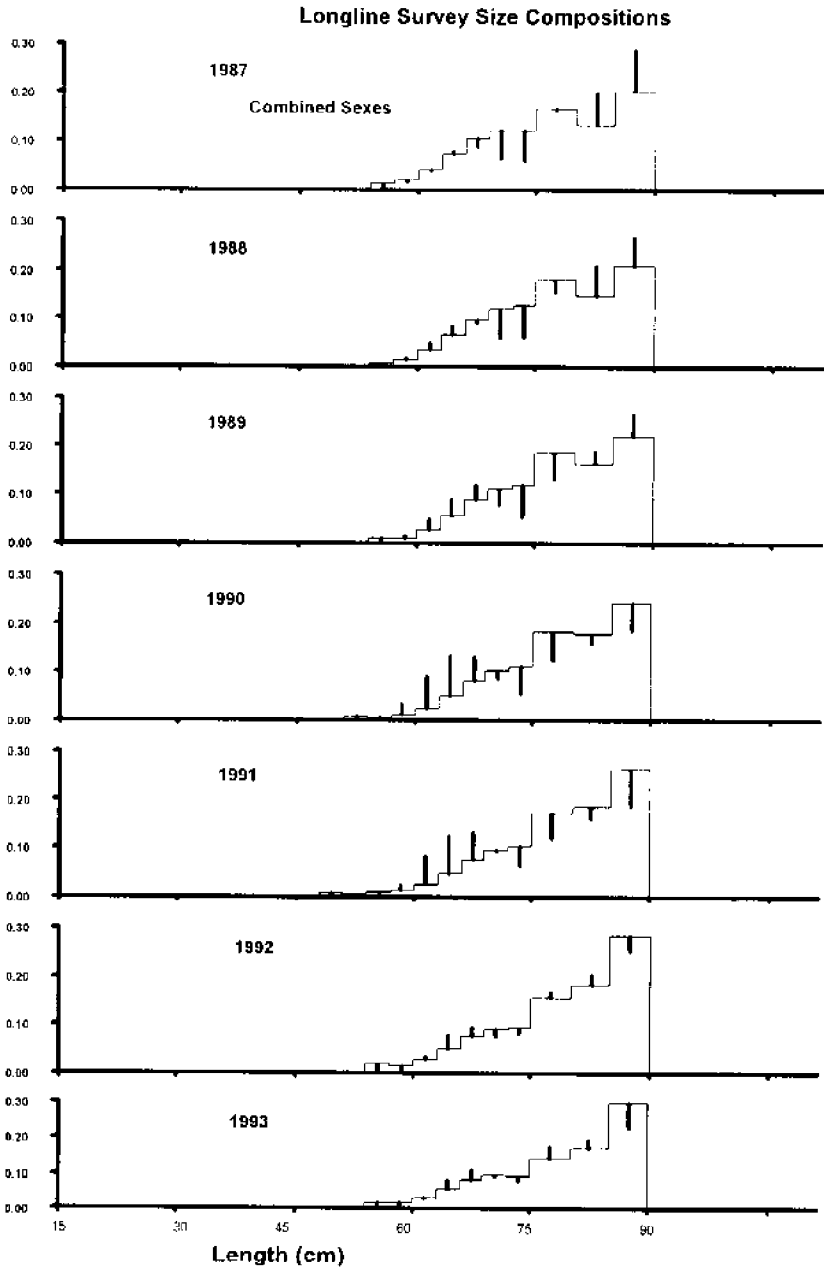


Figure 5. (continued.) Observed (continuous line) length frequencies and deviations (vertical bar) for the different fisheries and surveys used in the model.

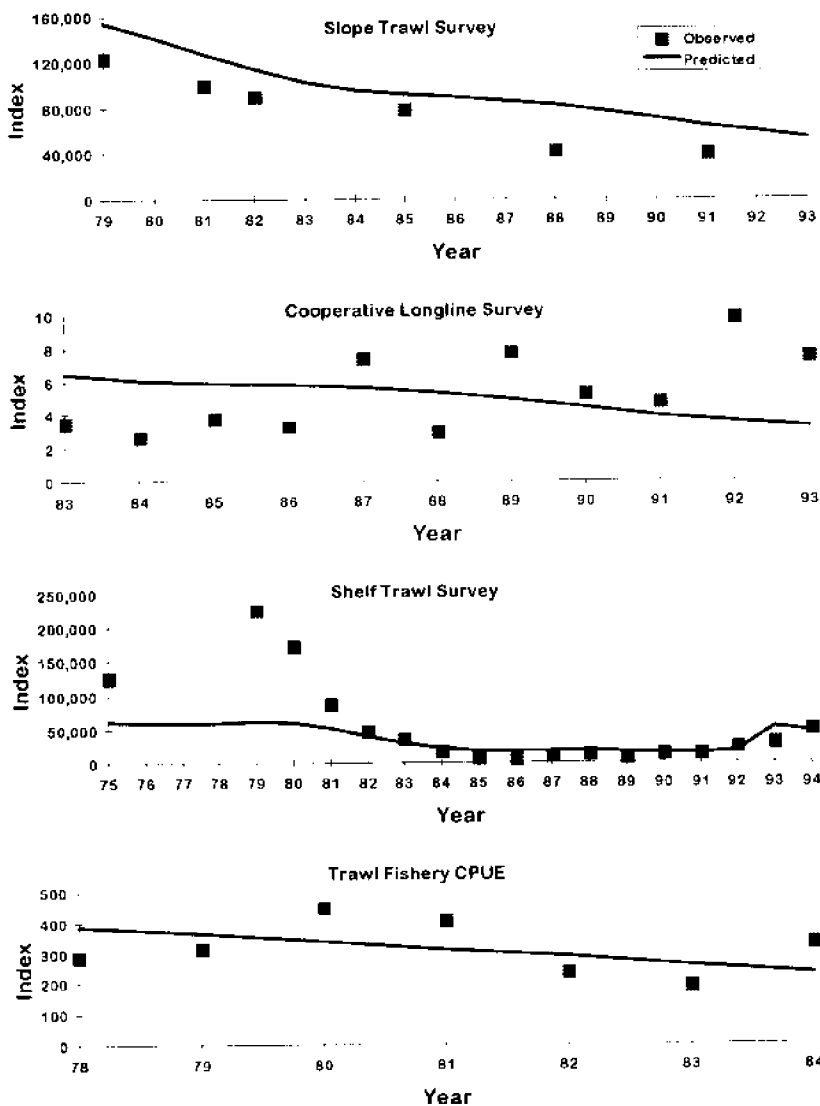


Figure 6. Model fits to the different survey and fishery indices.

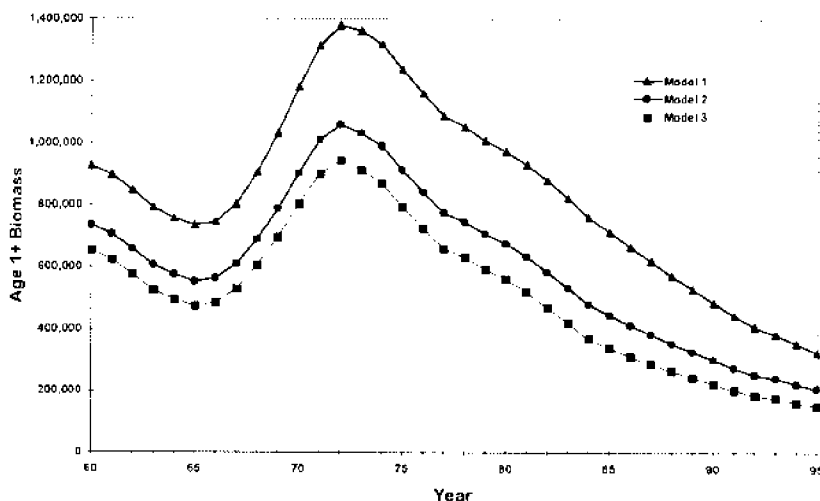


Figure 7. Total age 1+ biomass trend for the individual models.

since the early 1980s. The model fits the early period of the shelf trawl survey index poorly because high levels of recruitment are inconsistent with observations of numbers of older fish later in the time series. The overall trend for the slope survey estimates is mimicked by the assessment model, but indicates biases based on the fixed Q values used in each model for the slope survey. The general trend of the longline survey index shows increasing numbers while the model predicts declines. The model's reluctance to fit the apparent increasing trend from the longline survey data reflects the relatively large standard errors associated with this index. If we increase the model emphasis on the survey longline trend, the fits to the other surveys degrades considerably as indicated by the change in likelihood (Fig. 8). The effect of high emphasis (> 10) on the longline survey (increasing biomass trend) would indicate a much higher level of current spawner biomass (Fig. 8).

The biomass of Greenland turbot has roughly doubled during the 1970s from the early 1960s level and is currently about one-half of the unfished level. The 1995 total beginning of the year biomass (age 1 and older) ranges from about 325,000 to 150,000 t with slope survey Q set to 0.25 and 0.75, respectively (Fig. 6). The estimated historical numbers at age based on Model 3 show the change in the age structure over time (Table 5).

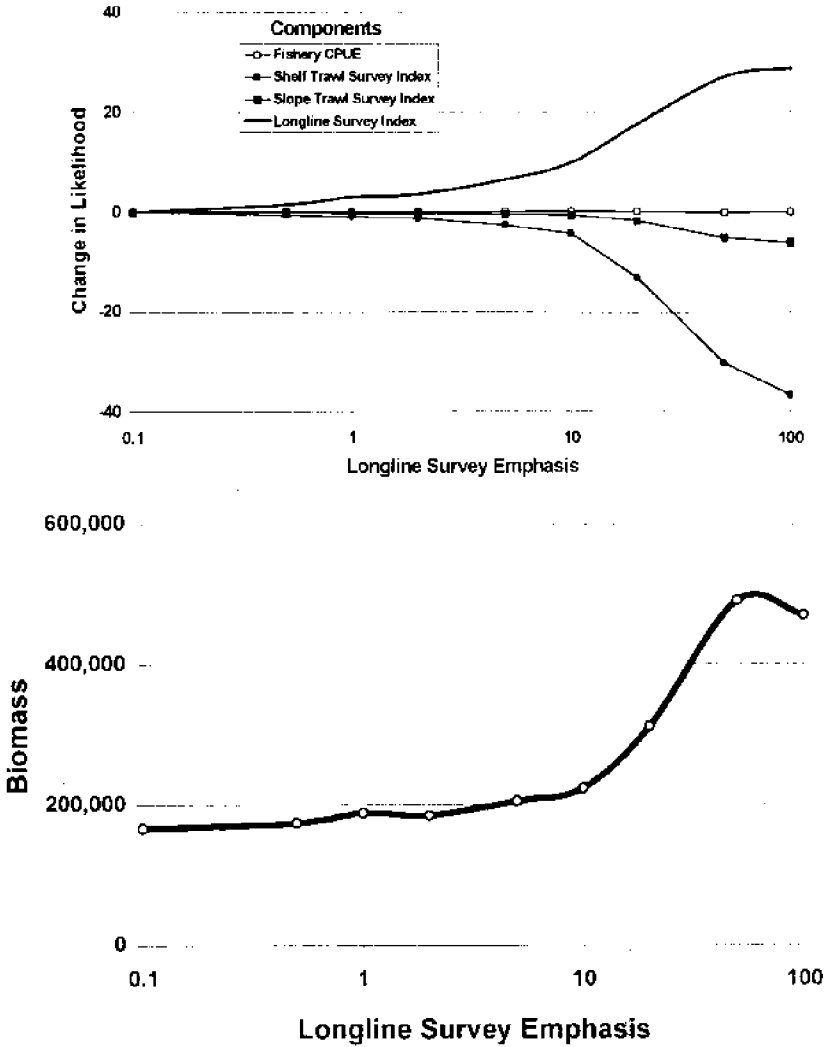


Figure 8. Change in likelihood by data component (upper panel) and current total biomass level (lower panel) when emphasis on fitting longline survey abundance index is increased.

Table 5. Estimated beginning of year numbers at age and sex (10,000s) estimated for Model 3.

Year	Females																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21+
70	2,417	2,960	13,006	10,751	8,660	6,896	1,259	568	464	370	283	392	306	245	202	168	140	117	97	81	405
71	1,637	2,013	2,465	10,794	8,778	7,035	5,600	1,022	462	377	300	238	319	249	199	164	137	114	95	79	395
72	2,335	1,376	1,672	2,035	8,653	6,973	5,584	4,445	811	366	289	238	189	253	197	158	130	108	90	75	376
73	4,192	1,931	1,138	1,368	1,580	6,611	5,321	4,261	3,391	619	280	228	182	144	193	151	120	99	83	69	344
74	6,300	3,472	1,599	934	1,073	1,223	5,109	4,112	3,293	2,621	478	216	176	141	111	149	116	93	77	64	319
75	3,373	5,203	2,867	1,305	718	810	921	3,850	3,098	2,481	1,975	361	163	133	106	84	112	88	70	58	289
76	5,240	2,787	4,299	2,342	1,006	544	613	697	2,912	2,344	1,877	1,494	273	123	101	80	64	45	66	53	262
77	4,318	4,329	2,302	3,509	1,802	760	410	462	526	2,198	1,769	1,416	1,127	206	93	76	60	48	64	50	238
78	6,642	3,586	3,595	1,900	2,811	1,431	603	326	367	417	1,742	1,402	1,122	893	163	74	60	48	38	51	228
79	4,402	5,504	2,971	2,953	1,496	2,195	1,111	468	252	284	322	1,345	1,081	864	687	123	57	46	37	29	214
80	2,669	3,647	4,559	2,440	2,321	1,160	1,692	859	362	195	219	248	1,033	829	662	526	96	43	35	28	186
81	1,423	2,205	3,012	3,720	1,875	1,751	874	1,273	646	271	146	163	185	768	615	491	390	71	32	26	156
82	705	1,173	1,817	2,447	2,817	1,389	1,295	646	939	475	199	107	119	134	538	448	356	282	51	23	133
83	309	581	966	1,474	1,842	2,072	1,020	950	474	689	349	146	78	87	89	409	328	261	207	38	115
84	438	254	478	783	1,106	1,352	1,518	747	696	347	505	256	107	57	64	72	300	240	191	152	112
85	838	363	211	393	618	863	1,053	1,182	582	542	270	393	199	83	45	50	56	233	187	149	205
86	1,527	696	301	174	316	492	687	838	940	463	431	215	313	158	66	36	40	45	186	149	281
87	1,000	1,270	579	250	141	255	397	554	675	758	373	348	173	252	128	53	29	32	36	150	347
88	625	832	1,057	480	202	114	205	319	445	543	610	300	280	139	203	103	43	23	26	29	399
89	714	521	692	877	391	164	92	166	259	361	440	494	243	226	113	164	83	35	19	21	346
90	989	596	435	578	732	326	135	75	133	207	288	351	394	194	180	90	131	66	28	15	292
91	1,625	835	498	363	483	609	267	108	59	105	162	226	275	308	151	141	70	102	52	22	239
92	492	1,357	697	416	303	402	500	214	86	47	82	127	177	215	240	118	110	55	80	40	204
93	436	411	1,133	582	347	253	334	414	177	71	38	68	104	145	176	197	97	90	45	65	199
94	808	364	344	946	486	290	210	275	336	142	56	30	52	80	110	133	148	73	67	33	196

Table 5. (continued.) Estimated beginning of year numbers at age and sex (10,000s) estimated for Model 3.

Year	Males																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21+
70	2,417	2,960	13,005	10,747	8,671	6,813	1,262	589	464	371	294	394	307	245	202	168	140	117	97	81	405
71	1,657	2,013	2,465	10,791	8,784	7,048	5,614	1,025	462	377	301	238	320	250	199	164	137	114	95	79	395
72	2,335	1,376	1,672	2,034	8,667	6,983	5,595	4,456	813	367	299	238	189	254	198	158	130	108	90	75	376
73	4,192	1,931	1,138	1,367	1,585	6,631	5,330	4,269	3,400	621	280	228	182	144	194	151	121	99	83	69	344
74	6,300	3,472	1,599	933	1,076	1,228	5,126	4,119	3,299	2,628	480	216	177	141	112	150	117	93	77	64	319
75	3,373	5,203	2,867	1,304	720	813	925	3,883	3,104	2,486	1,980	361	163	133	106	84	113	88	70	58	289
76	5,240	2,787	4,299	2,340	1,009	547	615	700	2,922	2,348	1,881	1,498	273	123	101	80	64	85	67	53	262
77	4,318	4,329	2,302	3,506	1,808	764	413	464	528	2,205	1,772	1,419	1,130	206	93	76	61	48	64	50	238
78	6,642	3,586	3,595	1,899	2,815	1,436	806	327	368	419	1,749	1,405	1,125	896	164	74	60	48	38	51	229
79	4,402	5,504	2,971	2,952	1,500	2,190	1,115	470	254	286	325	1,356	1,089	872	694	127	57	47	37	29	216
80	2,669	3,647	4,559	2,438	2,326	1,164	1,696	863	364	197	221	251	1,048	841	673	536	98	44	36	29	190
81	1,423	2,205	3,012	3,717	1,881	1,758	877	1,277	650	274	148	166	189	787	631	505	402	73	33	27	163
82	705	1,173	1,817	2,445	2,827	1,397	1,301	649	944	480	202	109	123	139	579	465	372	296	54	24	140
83	309	581	966	1,472	1,849	2,084	1,025	955	476	693	352	149	80	90	102	425	341	273	217	40	120
84	438	254	478	782	1,112	1,360	1,527	751	700	349	508	258	169	59	66	75	312	250	200	159	117
85	838	363	211	393	619	868	1,059	1,189	585	545	272	395	201	85	46	51	58	243	195	166	215
86	1,527	696	301	174	316	493	690	843	946	465	433	216	315	160	67	36	41	46	193	165	295
87	1,000	1,270	579	250	141	255	398	557	679	763	375	349	174	254	129	54	29	33	37	156	362
88	625	832	1,057	479	203	114	205	320	448	546	613	302	281	140	204	104	44	24	26	30	417
89	714	521	692	877	391	164	92	166	239	363	443	497	245	228	114	165	84	35	19	21	362
90	999	596	435	578	732	327	137	76	136	210	292	356	399	196	182	91	132	67	28	15	306
91	1,625	835	498	363	483	610	270	112	61	168	166	231	281	314	154	143	71	104	53	22	252
92	492	1,357	697	416	303	403	506	221	90	49	86	132	182	221	247	121	113	56	82	41	216
93	436	411	1,133	582	347	253	336	421	183	75	41	71	109	151	182	204	100	93	46	67	211
94	808	364	344	946	486	290	211	270	346	150	61	33	58	88	121	147	163	80	74	37	222

Recruitment of young juvenile Greenland turbot has been poor since the early 1980s as indicated by trawl surveys on the EBS shelf. There is evidence from slope surveys that this poor recruitment has reduced abundance of the exploitable stock which will continue to reduce the exploitable stock into the 1990s. As presented in Ianelli et al. (1993), there were several strong year classes through the 1970s, which were followed by a series of poor recruitment of Greenland turbot since the early 1980s (Fig. 9). Preliminary analyses on fitting the stock-recruitment relationship indicated that the residuals were highly autocorrelated. Because of statistical problems with autocorrelated errors, we feel that environmental conditions may play an important role in explaining recruitment variability. Therefore, analyses of stock-recruitment relationship to estimate maximum sustainable yield were not pursued.

Yields and projected biomass

During the past five years the relative fishing mortality between longline and trawl fishing has ranged from over 80% for trawl gear to less than 20% in recent years. Consequently, the three models presented above are also broken down by alternative fishery contributions to the total fishing mortality rate. The three relative rates of 80%, 50%, and 20% between trawl and longline gear were used. Harvests of several North Pacific groundfish species depend on estimates of the fishing mortality rate which determines the reduction of spawner biomass levels per recruit (Clark 1991). For example, harvests set to the $F_{35\%}$ fishing mortality rate would indicate a level of fishing that would reduce the amount of reproductive output per recruit to 35% of the unfished expectation. The value of such a rate thus depends on the age-specific selectivity of the fishing gear, the somatic growth rate, natural mortality, and the age-specific fecundity. The North Pacific Fishery Management Council has established that the $F_{30\%}$ rate represents a measure of overfishing which should not be exceeded and that the $F_{35\%}$ or $F_{40\%}$ rates are robust rates for sustainable yields. However, because this rate depends on assumed selectivity, future yields are sensitive to relative gear-specific harvest levels. For example, if we assume next year's fishery will be predominately longline harvests (e.g., sub-model a), then the yield recommendation in the next year is much higher than if sub-model c) was assumed to be true (Table 6). Furthermore, if we assume sub-model a) which gives a quota of 26,512 t ($F_{35\%}$), and the fishery actually harvests as in sub-model c), then we would exceed the overfishing level of that scenario

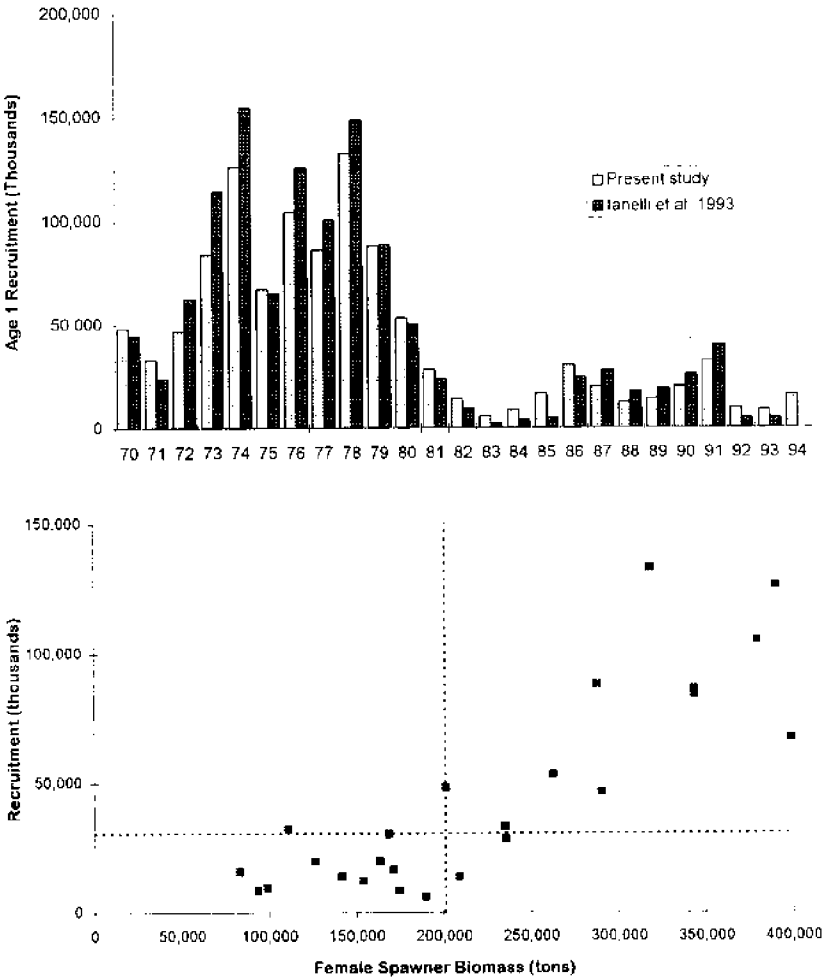


Figure 9. Estimated recruitment to age 1 for Model 3 compared with estimates from Ianelli et al. (1993) (upper panel) and the observed stock-recruitment pattern (lower panel). Dashed lines represent median recruitment and spawner biomass levels.

Table 6. Fishing mortality rates, yield, and mean exploitable biomass for different harvest fraction sub-models of Model 3 in 1995.

Submodel	Relative <i>F</i> contribution		$F_{40\%}$	$F_{35\%}$	$F_{30\%}$
	Longline	Trawl			
			<u><i>F</i> Multiplier</u>		
a	80%	20%	0.361	0.457	0.588
b	50%	50%	0.241	0.297	0.369
c	20%	80%	0.184	0.223	0.274
			<u>Yield</u>		
a	80%	20%	21,572	26,512	32,817
b	50%	50%	18,542	22,361	27,170
c	20%	80%	17,101	20,427	24,564
			<u>Mean exploitable 1995 biomass</u>		
a	80%	20%	59,756	58,013	55,811
b	50%	50%	76,938	75,290	73,631
c	20%	80%	92,940	91,601	89,650

(24,564 t). Because harvests of this resource is not allocated by gear type, the unpredictable nature of future harvests between gears is an added source of uncertainty. However, this uncertainty is considerably less than uncertainty related to treatment of survey biomass levels, that is, factors which contribute to estimating absolute biomass (Table 7).

Summary

In addition to using the cooperative longline survey data within the assessment model, we also used this time series to examine inter-specific and spatial patterns of abundance. The longline gear used in this survey regularly catches eight species or species groups: sablefish (*Anoplopoma fimbria*), rockfish (primarily *Sebastes aleutianus* and *S. borealis*), Pacific halibut, shortspine thornyheads (*Sebastolobus alascanus*), Pacific cod (*Gadus macrocephalus*), grenadier (*Albatrossia pectoralis*), arrowtooth flounder, and Greenland turbot. The survey is designed to fish at depths between 100 and 1,000 m. These depths are ideal for catching sablefish, however, Greenland turbot and shortspine thornyheads are consistently caught at these depths as well (Fig. 10).

Table 7. Yield and exploitable biomass values for 1995 based on different fishing mortality rates and model assumptions. In this case we assumed that the relative contribution to the overall fishing mortality would be equal between trawl and longline fisheries (sub-model b).

<i>F</i>	Model 1 <i>Q</i> = .25	Model 2 <i>Q</i> = .50	Model 3 <i>Q</i> = .75
	1994 Yield (t)		
<i>F</i> _{40%}	43,152	26,277	18,542
<i>F</i> _{35%}	51,881	31,662	22,361
<i>F</i> _{30%}	62,831	38,423	27,170
	Mean exploitable biomass (t)		
<i>F</i> _{40%}	185,666	110,590	76,938
<i>F</i> _{35%}	182,197	108,499	75,290
<i>F</i> _{30%}	177,788	105,841	73,631

Pacific cod, arrowtooth flounder, and Pacific halibut are found at the shallow range of these depths while grenadiers are common at the deepest depths and rockfish are intermediate (Fig. 10). The spatial distribution of Greenland turbot and sablefish shows that in the mid-1980s, the proportion of sablefish caught by the survey gear was relatively high and then substantially declined in recent years (Fig. 11). Apparently the sablefish abundance in the EBS slope region has declined while the abundance of Greenland turbot has remained steady or increased.

In this assessment we have adopted the hypothesis proposed by Alton et al. (1989) regarding the stock structure of Greenland turbot in the EBS and Aleutian Islands regions. Briefly, spawning is thought to occur throughout the adult range with post-larval settlement occurring on the shelf in shallow areas. The young fish on the shelf begin to migrate to the slope region at about age 4 or 5. In our treatment, the spawning stock includes adults in the Aleutian Islands and the EBS regions. This hypothesis was further supported from length compositions data between these areas (Ianelli et al. 1993). Small Greenland turbot have not been found in the Aleutian Islands region. McConnaughey (1995) has shown considerable inter-annual variability in concentration of Greenland turbot in the EBS shelf region suggesting stock distribution is variable.

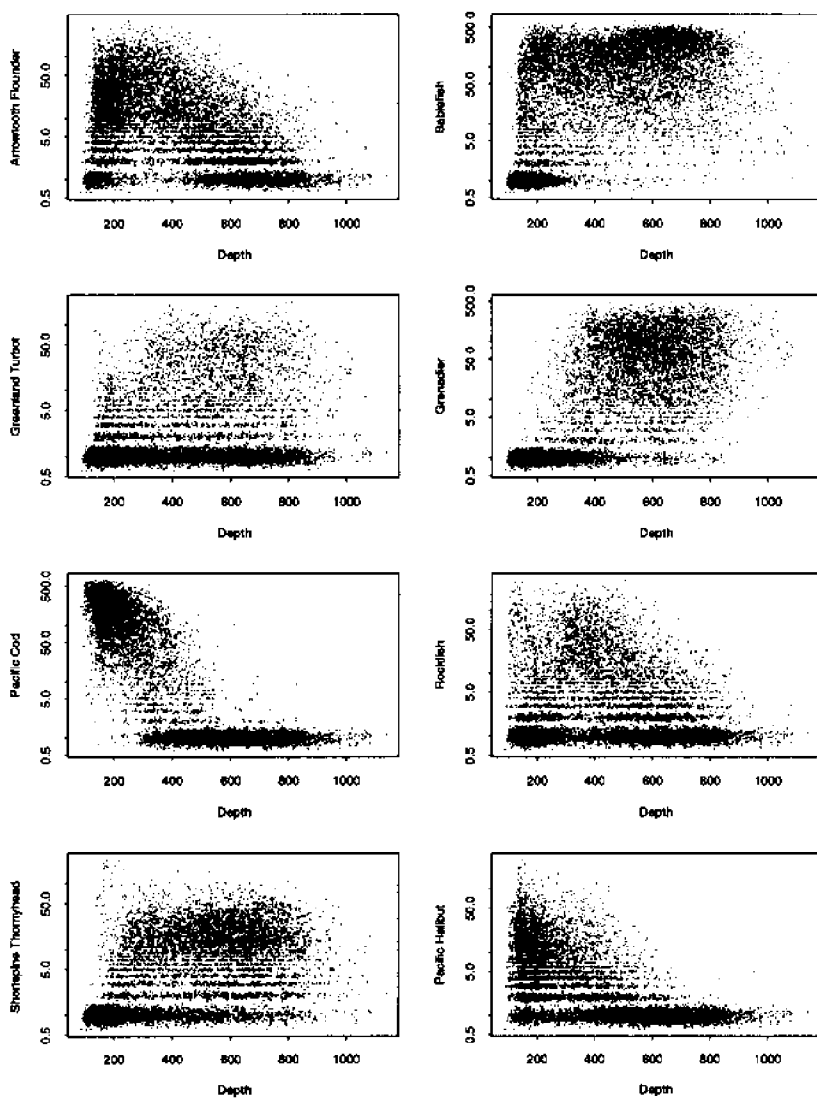


Figure 10. Species-specific catch rates (number of fish +1 per 900 hooks) by depth. Points have been randomized slightly to show density.

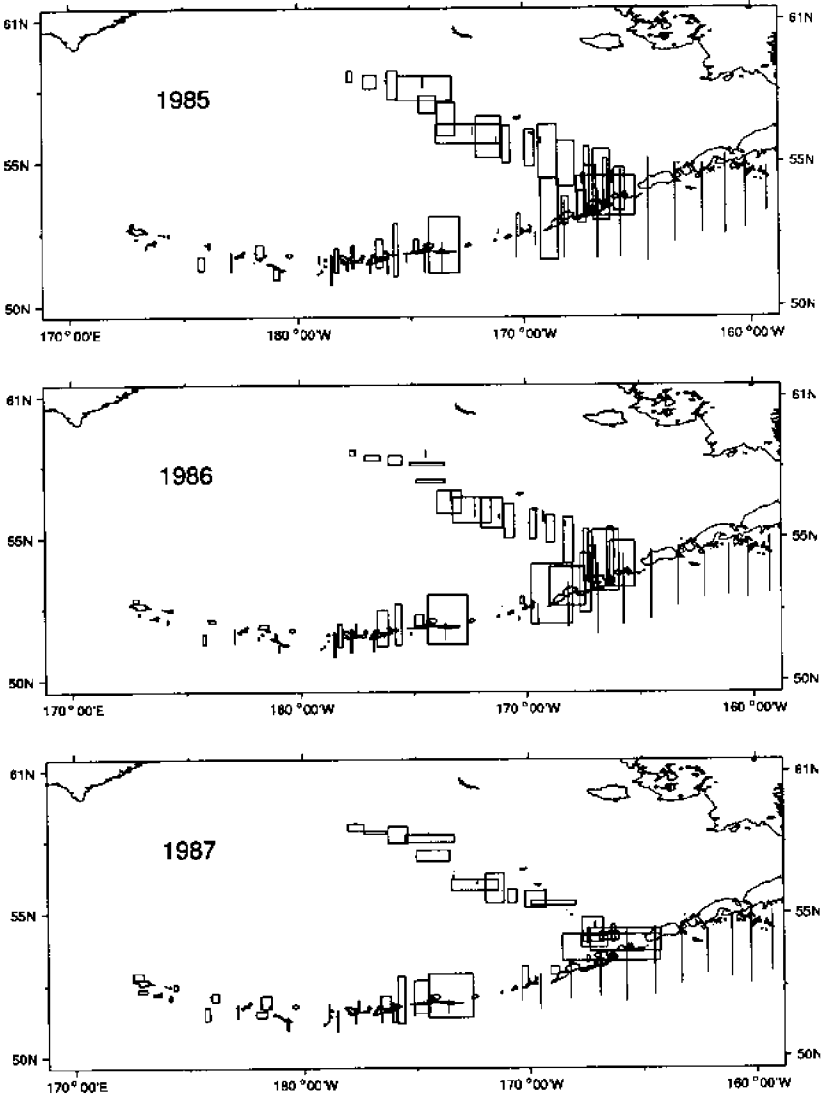


Figure 11. Map showing the relative abundance of Greenland turbot (horizontal dimension of boxes) and sablefish (vertical dimension of boxes) from the cooperative longline survey, 1985-1987.

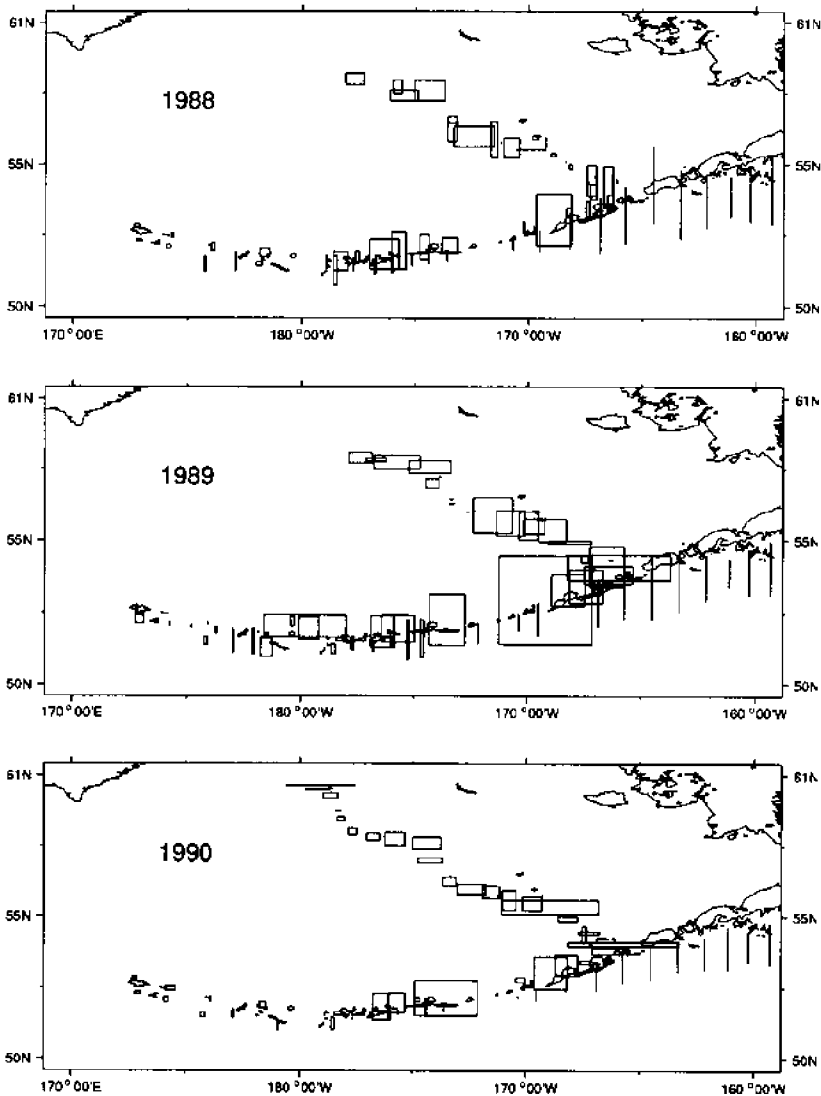


Figure 11. (continued.) Map showing the relative abundance of Greenland turbot (horizontal dimension of boxes) and sablefish (vertical dimension of boxes) from the cooperative longline survey, 1988-1993.

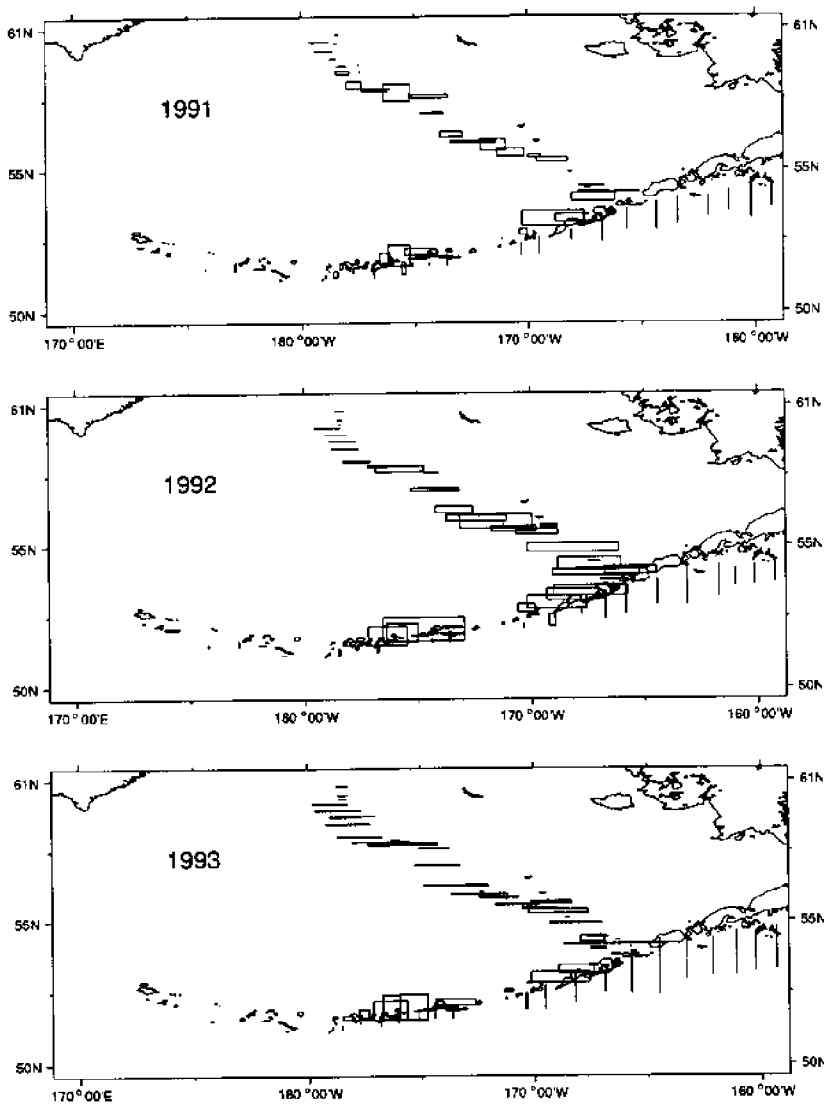


Figure 11. (continued.)

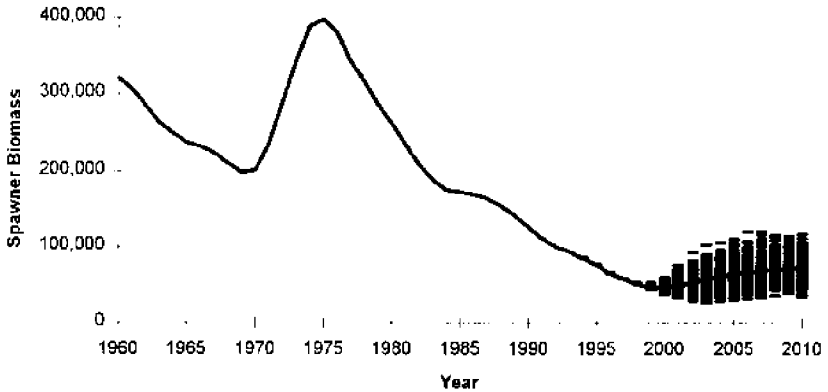


Figure 12. An estimated trajectory of female spawner biomass and projected levels for $F_{40\%}$ harvest rate. These runs are based on Model 3 with even relative fishing mortality rates between longline and trawl fishing gear (sub-model b).

In summary, the current biomass of Greenland turbot in the EBS is estimated at about one-half of the unfished level (Fig. 6). The 1995 total beginning of the year biomass (age 1 and older) ranges from 325,000 to 150,000 t depending on the interpretation of survey data. In past years, harvest levels were conservatively restricted because of poor recruitment observed during the 1980s. We argue that the more conservative assumptions of Model 3 presented here are appropriate for quota recommendations. The projected abundance under the recommended fishing strategy shows a continued decline over the next few years with increases expected by about the turn of the century (Fig. 12).

Acknowledgments

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Dynamics of the Flounder Populations in the Northwest Japan Sea

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This report provides information on changes in species composition under varying fishing intensities over time, and dynamics of some flounder stocks in the northwest Japan Sea from the 1960s to the 1990s.

In the northwest Japan Sea (specifically Peter the Great Bay), flounders have been an important target of the coastal fishery for more than 60 years. In Peter the Great Bay, the flounder fishery has been carried out since 1929, after the appearance in the Far East of steam-driven trawlers (Moiseev 1953). From the outset, the fishery has been vigorously developed, the regions and seasons of harvest as well as fishing technologies have changed, and the fishing power of the fleet has increased every year. Historically, the number of flounders in the bay was quite high as evidenced by the catch. For example, in 1942 the catch was 10,200 tons, and reached 12,800 tons in 1955.

Twelve species of flounders are captured in the fishery, but the species composition of flounders changed over the years. In the 1930s, when the flounder fisheries began, the most abundant species in the catch was yellowfin sole (*Limanda aspera*) (60-70%) and pinewood flounder (*Cleisthenes herzensteini*) (10-15%) (Table 1). In the 1950s, the Yokohama flounder (*Limanda yokohama*) was most abundant (up to 40%) while in the 1960s Korean flounder (*Glyptocephalus stelleri*) dominated (up to 50%) (Moiseev 1953, Minjova 1967, Ivankova 1975). In the last 15 years, yellowfin sole (up to 50%) as well as Korean flounder (up to 25%) and Yokohama flounder (up to 15%) predominated again (Ivankova 1988). The variations in the species composi-

Table 1. Species composition of flounder catch in Peter the Great Bay (average percent).

Species	1930-1931	1951	1955-1959	1964-1968	1972-1979	1981-1985	1986-1990	1991-1992
<i>Limanda aspera</i>	60-70	4	1	13.0	18.5	48.8	32.2	25.7
<i>Glyptocephalus stelleri</i>	17	30	37.5	38.0	16.9	28.9	28.3	
<i>Limanda yokohama</i>	48	16	10.2	2.9	8.5	12.1	19.4	
<i>Limanda herzensteini</i>	3-4	10	2.2	5.7	4.3	9.0	9.0	8.2
<i>Cleisthenes herzensteini</i>	10-15	5	3.6	9.2	13.4	3.9	4.0	3.6
<i>Limanda punctatissima</i>	10-15	4	3.4	5.2	5.7	3.8	4.6	3.8
<i>Hippoglossoides dubius</i>	+	11	26.1	11.5	14.7	6.3	6.8	7.7
<i>Acanthopsetta nadeshnyi</i>	+	+	16.1	7.7	2.5	0.9	0.4	0.8
<i>Platichthys stellatus</i>	+	1	+	+	+	1.2	1.3	1.4
Other species	1.6	+	+	0.2	0.1	1.1		

tions are explained both by the fishery and climatic factors. From 1930 to 1960 the fishery was intense, but it has been regulated and stabilized in the last 30 years. The long-term regulation of the fishery and its stabilization, as well as the warming of the Sea of Japan, have created favorable conditions for reproduction of yellowfin sole, one of the basic commercial species of Peter the Great Bay (Ivankov and Ivankova 1983). At the same time, there has been heavy silting in Peter the Great Bay in recent years, changing the dimensions of the forage base and the qualitative composition of forage organisms (Klimova 1974, Klimova and Ivankova 1977), thus restraining increases of yellowfin sole and other flounders.

Along with variations in the species composition, noticeable variations in the size-age composition of the flounder population have been observed. Since yellowfin sole and Korean flounder play a major

Table 2. Body length and age of yellowfin sole in Peter the Great Bay.

Year	Length, cm			Age		
	min	max	mean	min	max	mean
1930-1931	20	44	31.1	4+	12+	6.1
1958	16	34	24.2	2+	6+	3.8
1964	20	32	23.7	2+	9+	4.0
1966	18	40	24.6	2+	7+	4.1
1968	16	38	25.2	2+	7+	4.7
1972	17	42	26.7	5+	13+	5.4
1980	13	46	26.2	3+	13+	5.7
1982	16	44	28.9	2+	18+	6.1
1984	16	46	29.6	3+	18+	6.7
1986	16	44	27.7	3+	19+	5.8
1990	18	45	27.6	2+	15+	5.7
1992	13	41	26.7	2+	12+	5.5

role in the fishery, we focused on catch-at-age and growth data for these species.

During the early phase of the fishery the catch was dominated by yellowfin sole which varied in length from 16 to 44 cm with an average of 31.1 cm (Table 2; Moiseev 1953). As the trawl fishery in Peter the Great Bay developed, the body length decreased and by 1964 averaged 23.7 cm. Maximim life expectancy of yellowfin sole during the early phase of the fishery was 14 years and the average age of the fish was 6.1 years. By 1964, corresponding numbers were 9 and 4 years.

During this time similar variations were found for Korean flounder, one of the most common flounders in the bay. In the early phase of the fishery, when the stock was near natural conditions, the body length of individuals varied from 26 to 50 cm with an average of 39.9 cm (Table 3; Moiseev 1953). By 1964, these figures were reduced to 46 cm and 30.2 cm, respectively. The life expectancy of Korean flounder in the 1930s was 15 years with an average age of 7.4 years. By 1964, the corresponding figures were reduced to 12 and 5.7 years.

In recent years both the average length and age in the populations of these commercial species have increased due to a stable fishery, indicating the condition of the stocks to be satisfactory. Yellowfin sole aged 3 to 19 years appear in the catches (Table 2). Seventy percent of

Table 3. Body length and age of Korean flounder in Peter the Great Bay.

Year	Length, cm			Age		
	min	max	mean	min	max	mean
1930-1931	26	50	39.9	5+	15+	7.4
1951	18	48	32.1	2+	10+	6.0
1964	18	46	30.2	3+	12+	5.7
1966	18	46	29.1	3+	11+	5.5
1968	21	45	30.3	3+	13+	5.8
1972	16	50	31.8	5+	18+	7.6
1980	16	50	34.2	5+	21+	8.0
1982	18	48	32.9	5+	20+	8.4
1984	18	54	35.1	3+	24+	8.8
1986	20	48	32.3	3+	21+	8.1
1990	17	48	33.1	4+	20+	7.6
1992	25	45	32.7	5+	16+	7.6

the catch is composed of individuals aged 6 to 9 years. From 1968 (when fishery management was introduced) to 1984, the average length and age increased from 25.2 cm to 29.6 cm and from 4.7 to 6.7 years, respectively (Table 2). Maximum age increased from 10 to 19 years. Up to 17 age groups of fishes are found in catches.

Korean flounder has a longer life expectancy than yellowfin sole. Individuals up to 25 years old are found in catches (Table 3). Catches are dominated by individuals aged 7 to 10 years (up to 80%). After the introduction of fishery management, average length and age increased from 30.2 to 35.1 cm and from 5.8 to 8.8 years, respectively. Maximum ages increased from 12 to 25 years for Korean flounder as in the case of yellowfin sole. Up to 20 age groups of fishes are found in catches.

By 1992, minor decreases of the average length and age for yellowfin sole and Korean flounder were observed, to 27.6 cm and 5.7 years and to 32.7 cm and 7.6 years, respectively.

As noted earlier, intense fisheries for flounders for more than 30 years has led to sharp reduction in their numbers and changes in the population patterns. This precipitated strict fisheries management measures for Peter the Great Bay. The first management step (1967-1974), a full ban on fishing, led to a threefold increase in the number

of flounders, increasing the maximum and average values of body sizes and aggregation of older age groups (Ivankova 1975). The second phase, from 1975 to present, included limited fisheries. Annual harvest quotas, based on stock condition and flounder population patterns, are specified. The conservation measures, which initially were a complete ban on fishing (only controlled harvest of flounders using two MRS-80 type vessels), were followed by limiting access of large trawlers to the resource and establishing periods and areas for fishing. These measures have allowed stabilization of the flounder population in Peter the Great Bay (Ivankova 1988).

The abundance of flounders is estimated by various methods. The biostatistical method is based on data obtained from catches. The instantaneous mortality rate of flounders is determined using the Baranov method (1960), while the instantaneous coefficient of catch mortality and annual loss are determined by the Beverton and Holt technique (1969). The mortality rates for yellowfin sole and Korean flounder during the fishery vary slightly.

The flounder population is also estimated using the virtual population approach (VPA) (Ricker 1979) and the results of station trawl surveys (Aksyutina 1968). These analyses show that the numbers of flounders early in the fishery, when the populations were in their natural condition, were quite high at 30,000-35,000 tons.

As a result of intense fishing, the commercial reserve of flounders was reduced to 5,700 tons by the mid-1960s (Minjova 1970). Management of the fishery positively affected the restoration of stocks. The commercial reserves of all flounder species in Peter the Great Bay have maintained a level of 22,000-25,000 tons for the last 20 years.

However, when considering individual species, the abundance of yellowfin sole was three times higher from the late-1970s to the mid-1980s than from the 1960s to the mid-1970s. During the late 1980s to early 1990s the stock decreased back to its previous level (Figure 1).

A different picture was observed for Korean flounder. From the late-1970s to mid-1980s, abundance decreased substantially from the previous period. At present, an increase in abundance of this species is observed (Figure 1). Somewhat lesser variations of commercial reserves during this period are also noted for other species of flounders in Peter the Great Bay. For example, in recent years, stocks of Yokohama flounder increased from 2,000-3,000 tons in the early 1980s to 5,000-7,000 tons in the late 1980s.

In conclusion, the management of the flounder fisheries led to stabilization of populations. In addition, the cyclic variations in

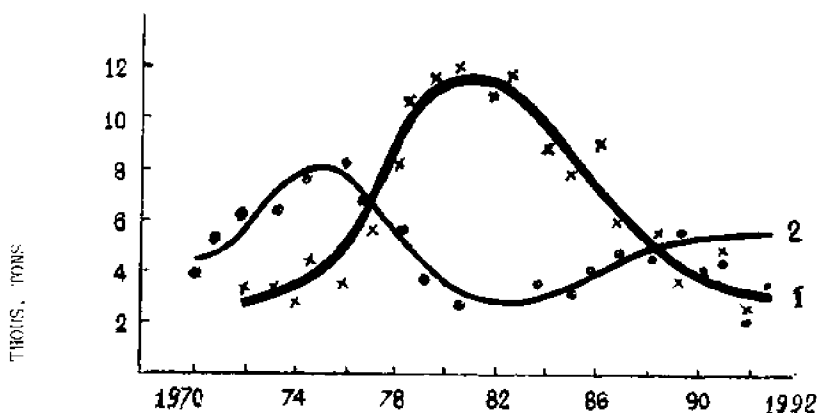


Figure 1. Abundance of yellowfin sole (1) and Korean flounder (2) in Peter the Great Bay.

abundance of individual flounder species are reported. These variations are evidently caused by climatic and anthropogenic factors.

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Stock Condition of Greenland Turbot (*Reinhardtius hippoglossoides matsuurae* Jordan et Snyder) in the Northwestern Bering Sea

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Abstract

Pacific turbot is abundant in both the Okhotsk and Bering seas close to the Kuril and Aleutian islands, and forms a single population in the Bering Sea. Juveniles of the 0+ to 2+ age groups are distributed in the northeastern Bering Sea shelf in Anadyr Bay and the adjacent American zone, and then settle along the eastern Bering Sea shelf. Immatures aged 3-6 migrate to the northern part of the continental slope, including the Russian waters in the northwest. This is determined by the relative abundance of juveniles aged 2+ to 7+ in this area. In the 1980s the Bering Sea stock was very depressed, probably due to both the natural decrease in abundance and the uncontrolled bycatch of juveniles in fisheries for other species. Currently there are indications of population rebuilding.

Systematics

When Greenland turbot were first seen in Pacific waters off Japan the fish was described as a separate species, *Reinhardtius matsuurae* Jordan et Snyder (Ishikawa and Matsuura 1987). Taranets (1933) disputed the designation of a separate species. In 1937, based on morphometric analysis, Panin and Vernidub designated it as an independent species. Researchers currently hold different points of view. For example, Fedorov (1971) insisted there was a lack of differ-

ences necessary to define a subspecies; but Fairbairn (1981) used genetic analysis to conclude that subspecies differences exist.

Distribution

The work of the 1930s (Shmidt 1933, Andriyashev 1935 and 1937) indicated turbot abundance in the Okhotsk and Bering seas. Shmidt recorded Greenland turbot as a valuable incidental catch in trawl fisheries. New data showed its distribution ranged from areas near California (Best 1963, Hubbs and Wilimovsky 1964, Schott 1966) to Sagami Bay near Japan (Abe 1966 and 1967), the Chukotsk (Alton et al. 1988) and Japan seas (Mikawa 1963). Nevertheless, all of these authors designated the specimens collected to the south accidental and isolated from their main region.

Thus, Greenland turbot occupies an area from the shelf and continental slope off Asia (Sagami Bay [Honshu]) to North America (California) northward of 66° latitude in the Chukotsk Sea. Greenland turbot is abundant in waters north of Hokkaido, in the Okhotsk Sea near the Kuril and Aleutian islands, and in the Bering Sea. Most scientists presume that turbot occur eastward of Kadjak and Japan due to drift of incidental eggs and larvae or migration of mature specimens. During TINRO's vessel surveys in the Chukotsk Sea, only fingerlings, which probably grew from eggs and larvae carried by currents, were observed. The ability of these juveniles to return and rejoin their stock is rather doubtful.

Life History

TINRO and VNIRO began regular investigations of the Bering Sea continental slope in 1957. In 1959 Japanese fishermen began developing the continental slope resources. The scientific literature (Novikov 1960, 1961, and 1974; Shuntov 1965, 1966, 1966a, and 1971) describes the environmental condition, biology, length-age structure, and abundance of Greenland turbot occupying the continental slope in this area. Annual assessments of the condition of eastern Bering sea Greenland turbot stocks are forecast in Russia by TINRO and in the U.S. by NOAA.

Dyakov (1981) studied the intraspecies structure of Pacific Ocean Greenland turbot. Based on analyses of blood polymorphism, body structure, and biological characteristics, he was convinced of the genetic heterogeneity of the Bering and Okhotsk seas turbot. According to his data, there are weakly intermingled populations within the

Table 1. Length composition of Greenland turbot in the trawl catch in the northwest region of the Bering Sea.

Year	Length (cm)															N	M		
	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95			100	105
1984	-	-	0.1	2.7	12.6	21.8	23.9	21.7	9.0	4.3	2.4	1.0	0.2	0.3	0.4	-	-	1,435	53.8
1985	-	-	-	14.9	20.3	13.1	15.8	7.9	10.5	7.0	3.5	2.6	2.6	1.8	-	-	-	114	52.8
1986	-	-	-	-	0.4	4.6	13.6	21.4	29.1	16.3	8.4	4.4	1.6	0.2	-	-	-	1,400	62.8
1987	1.3	7.3	25.3	18.0	11.3	6.0	6.7	14.7	4.0	4.0	4.0	1.3	-	-	-	-	-	150	48.1
1989	0.1	1.5	6.7	6.2	2.0	3.7	19.1	24.2	11.1	6.1	10.3	6.2	2.5	0.4	-	-	-	594	62.2
1990	-	-	0.4	4.9	12.9	6.0	2.8	12.7	34.0	12.7	4.5	3.6	2.2	0.7	0.4	-	0.2	537	58.9
1992	-	-	-	0.3	0.8	3.5	8.7	16.5	29.5	19.9	8.5	7.2	2.4	1.8	0.7	0.1	0.1	1,187	64.2
1993	0.1	1.0	1.4	3.4	5.6	9.0	10.2	21.5	21.9	10.1	10.1	8.6	4.3	1.7	0.6	0.5	0.1	1,569	64.9

Table 2. Age composition of Greenland turbot catches at the depth of 300-1,000 m in the northwest part of the Bering Sea, percent.

Year	Age														N
	2	3	4	5	6	7	8	9	10	11	12	13	14		
1976	26.7	43.9	15.3	5.7	2.9	1.9	1.5	0.8	0.6	0.4	0.2	0.2	-	524	
1978	-	27.9	30.2	23.2	11.6	4.7	2.3	-	-	-	-	-	-	43	
1981	-	26.4	43.3	10.7	8.8	3.1	1.9	2.5	0.6	2.5	0.6	0.6	-	159	
1982	-	7.1	35.0	24.1	15.0	8.6	6.2	2.4	4.7	4.7	-	2.4	-	419	
1983	-	-	3.9	14.2	25.6	16.6	19.7	11.8	10.2	-	-	-	-	117	
1984	0.1	4.1	22.1	21.4	16.5	16.5	9.9	16.8	1.8	0.7	0.3	0.2	-	1,435	
1985	0.4	15.8	25.4	13.6	9.1	8.3	9.2	9.2	3.7	2.9	1.3	1.0	-	114	
1986	0.1	2.9	8.3	11.9	18.9	24.2	22.6	6.9	3.0	1.0	0.2	-	-	1,400	
1987	4.1	29.8	23.5	8.5	4.6	7.1	10.5	8.5	2.5	0.7	0.2	-	-	150	
1989	0.7	7.8	7.0	2.8	7.0	15.3	19.8	17.8	9.1	7.9	3.1	1.6	0.3	594	
1990	0.3	6.2	16.0	5.4	5.0	13.7	24.6	19.0	4.9	2.9	1.1	0.5	0.4	537	
1992	+	0.3	4.3	4.9	7.8	15.7	24.6	25.2	8.7	4.8	1.9	1.0	0.8	1,187	
1993	0.4	2.3	7.6	6.1	6.2	11.1	19.6	25.5	10.4	6.3	2.4	1.1	1.0	1,569	

Age composition is determined by I. P. Hikolenko

Bering and Okhotsk stocks, while the greater component of the turbot in the Russian economic zone eastward of Shirshov ridge belong to the single eastern Bering Sea population. We don't deny the reproductive segregation of the Bering and Okhotsk turbot; but at the same time we don't agree with the belief that there is a smaller self-reproductive population in the Bering Sea.

Greenland turbot grow quite quickly and reach 16-20 cm in body length during the first year. By the third year the length doubles, after which the growth in length decreases. Greenland turbot live about 20-25 years (Panin and Vernidub 1937) and reach 130 cm in length and 16-17 kg in weight (Moiseev 1953, Panin and Vernidub 1937), although large individuals cannot be reliably aged. Individuals more than 100 cm in length and 13 years old have been caught in trawls accidentally (Tables 1 and 2, Figure 1).

Males predominate in younger age groups since females join commercial stocks at a more advanced age. Males older than 11 are rarely found in catches. According to Novikov (1974), Greenland turbot males mature at the age of 5-9 and 50-70 cm in body length, and females mature at the age of 5-10 and 50-80 cm in body length. In 1978 mature fishes were already noted in the third age group (30-40 cm in body length).

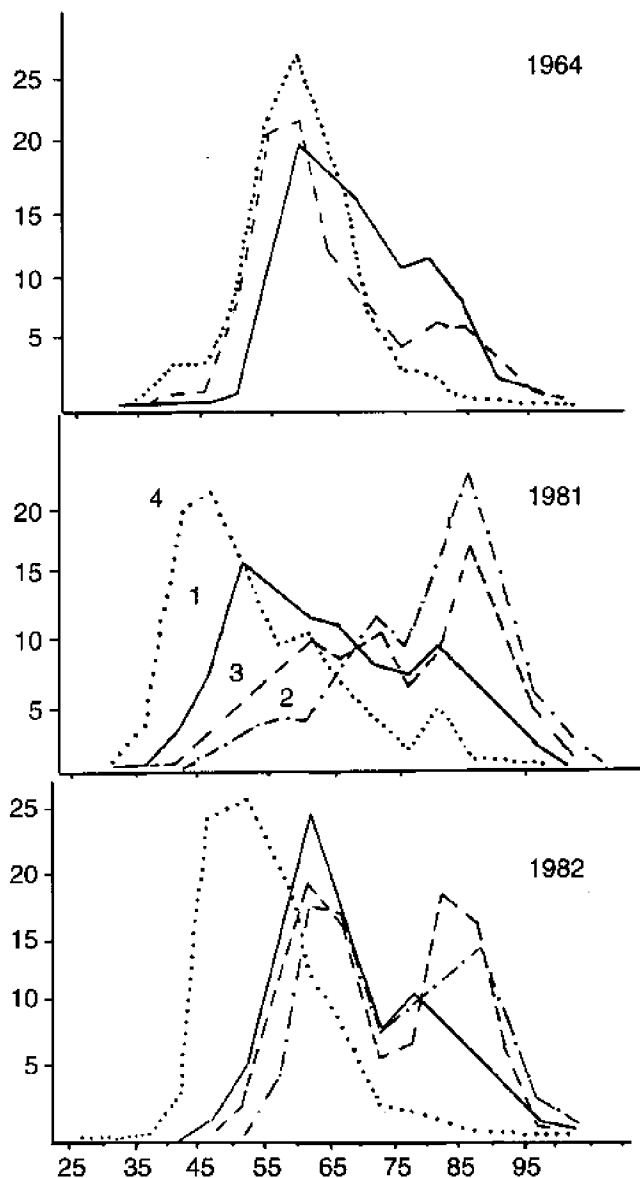


Figure 1. Length composition of Greenland turbot along the continental slope of the Bering Sea. 1 is Northeastern Area, 2 is Central Area, 3 is Southeastern Area, and 4 is Northwestern Area.

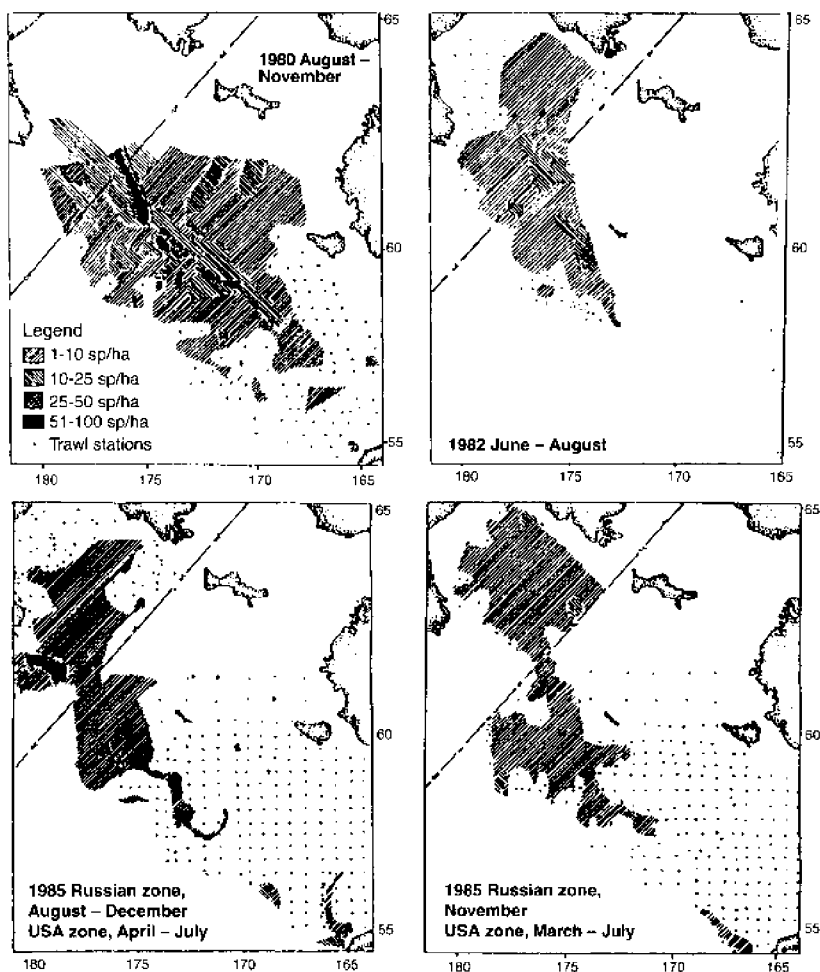


Figure 2. Distribution of Greenland turbot in the eastern Bering Sea shelf and Anadyr Bay.

Greenland turbot spawn in the Bering Sea from September to March, peaking in November-February (Shuntov 1970, Bulatov 1983). Novikov observed some females even in the last half of August.

Spawning has been recorded along the entire continental slope. Panin and Vernidub (1937), and Pertseva-Ostroumova (1961) observed spawning along the continental slope of the Koryakskiy coast and from Cape Navarin to Saint Matthew Island. Novikov observed spawn-

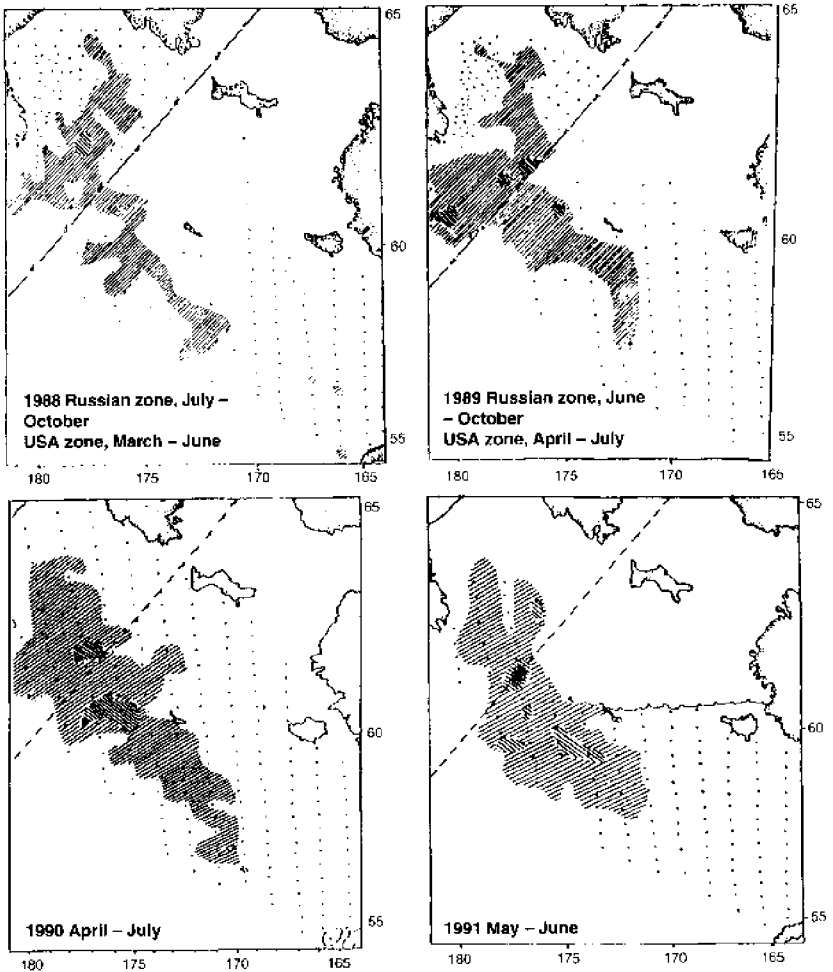


Figure 2. (continued)

ing along the east Bering Sea continental slope between the Krenitsyn Islands and Cape Navarin at a depth of 550-680 m. According to Alton et al. (1988), the continental slope between Unimak Island and the Pribilof Islands is the basic spawning region. In 1992-1993, turbot spawning was observed between Cape Navarin and Cape Olyutorskiy.

According to Novikov (1974) Greenland turbot females spawn 61,000-281,000 eggs; moreover, fecundity depends on the age and

Table 3. Length composition of Greenland turbot in trawl catches in Anadyrskiy Bay, percent.

Year	Length, cm																	100 N	mln.sp				
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85			90	95		
1985	-	17.8	1.8	23.3	36.6	7.4	7.4	3.1	1.3	1.3	-	-	-	-	-	-	-	-	-	-	-	163	11.0
1986	25.7	14.9	30.9	11.8	3.9	6.0	4.4	1.5	0.4	0.4	0.2	-	-	-	-	-	-	-	-	-	-	482	13.6
1989	-	7.6	12.6	10.1	6.5	26.6	25.2	10.1	0.7	0.3	0.3	0.3	-	-	-	-	-	-	-	-	-	278	12.8
1990	1.7	28.5	3.4	6.7	10.4	10.1	6.4	9.4	10.7	2.0	0.3	1.0	2.0	1.3	1.7	1.0	2.0	2.0	0.7	0.7	0.7	298	13.2

Table 4. Greenland turbot abundance in Anadyrskiy Bay (million fish).

Years	Area	Age										Total	
		0	1	2	3	4	5	6	7	8	9		10
1983	1*	0.15	2.17	0.86	1.34	1.54	5.18	-	-	-	-	-	11.24
	2	0.09	4.70	1.91	0.49	17.23	13.15	-	-	-	-	-	45.57
1985	1	1.78	1.99	4.91	1.65	0.44	0.14	0.07	0.02	-	-	-	11.00
	2	0.15	2.17	0.86	1.34	1.54	5.18	-	-	-	-	-	11.24
1988	1	5.26	5.32	1.5	0.61	0.56	0.26	0.05	0.04	-	-	-	13.60
1989	1	1.02	2.28	2.45	5.42	16.48	0.06	0.01	-	0.03	0.04	0.01	12.80
1990	1	4.0	— age not determined —										13.20

* 1 - Anadyrskiy Bay; 2 - Eastern Bering Sea north of 58°, Alton et al. 1988.

length of the female. Dyakov (1965) estimated Greenland turbot to be less fecund with 24,000-149,000 eggs, with an average of 61,000-80,000 eggs depending on location.

Greenland turbot eggs are bathypelagic, and 3.9-4.1 mm in diameter (Mikawa 1963). Larvae move to the surface and drift to the shallows where they settle at the bottom after completion of metamorphosis. The larval period is long—probably months (Novikov 1974). Greenland turbot fingerlings 34-65 mm in length occurred in Anadyrskiy Bay at a bottom temperature of 0.8-5.6°.

Samples of Greenland turbot 25-115 cm in length and 2-17 years old are collected with trawls along the continental slope of the north-western Bering Sea (Tables 1 and 2).

A great number of immature fish occupy the vast area of the eastern Bering Sea shelf, including Anadyrskiy Bay (Shuntov 1965 and 1966, Novikov 1974, Alton et al. 1988).

According to Alton (1988) about 90% of the juveniles are concentrated north of 58°. Unfortunately, these data were collected only within the U.S. economic zone. Our observations show that a great number of Bering Sea Greenland turbot juveniles, especially of the first age group, are found in the northern Bering Sea primarily in Anadyrskiy Bay (Figure 2, Tables 3 and 4). Moreover, the recorded abundance of fingerlings in Anadyrskiy Bay collected with comparable fishing gear is higher than in the rest of the eastern Bering Sea shelf area, and the abundance of yearlings and 2-year-old specimens is comparable (Table 4). Evidently, the first age groups concentrate in Russian and adjacent U.S. waters and then settle along the eastern Bering Sea shelf, which they inhabit for their first four years. Mature

Table 5. Greenland turbot catch in the western Bering Sea (tons).

	1978	1979	1980	1981	1982	1983	1984	1985
Turbot and halibut catch	943	2834	2949	6285	2908	2087	2121	2671
Turbot only *	943	2834	2087	6285	2908	2087	2121	1300-1700
Targeted turbot catch		no date	1207	4200	1371	1337	1076	956

	1986	1987	1988	1989	1990	1991	1992
Turbot and halibut catch	4619	3340	1499	1655	2094	1537	1138
Turbot only *	2500-3500	1600-2400	900-1200	300-1000	400-1200		no date
Targeted turbot catch	1312	1563	891	272	327	-	-

* 1985-1993 assessment of experts

fish of age 5-6 drift to the continental slope (Shuntov 1965 and 1966, Novikov 1974, Alton et al. 1988). According to Alton et al. such fish move to the continental slope in areas east and southeast of St. Matthew Island.

Comparison of lengths of turbot collected along the continental slope in the northwestern and eastern areas indicates a deficiency of large fish in the Russian economic zone (Figure 1). Specimens that attain maturity for the first time along with immature specimens of the 5-9 year age group and 50-70 cm in length form the basis of the catch (60-70%), while larger fish predominate along the continental slope of the eastern area. This distribution by length provides every reason to assume that recruits to the Bering Sea commercial stock run to the continental slope of the northern area. Some of these fish stay in the Olyutor-Navarinskiy area, while others drift along the continental slope to the southeast. A sharp decline in the concentration density and catch per effort, corresponding to an increase in concentration density along the U.S. continental slope, is caused by Greenland turbot drifting away (Kodolov 1992).

Table 6. Relative assessment of Greenland turbot juvenile abundance in the eastern Bering Sea shelf (million fish).

Year	1979	1980	1981	1982	1983	1984	1985	1990	1991
Alton's date, 1988	903.6	725.7	280.3	81.1	48.9	22.1	15.6	-	-
Our date	-	240.6	105.2	-	58.3	13.6	30.1	54.8	107.0

The Fisheries

All known commercial concentrations of Greenland turbot in the Bering Sea are distributed east of Cape Olyutorskiy. Nevertheless, the bottom contour of the Russian area is more complex and less convenient for Greenland turbot trawl fishing. This is why the fisheries started by Japanese fishermen in the northeastern area moved quickly east to the present U.S. zone. Secondary data show the Greenland turbot and Arrowtooth flounder fishery in the northwestern area reached its maximum in 1961-1962 when only 12,000 tons were harvested annually. Greenland turbot made up about 70% of the catches. Evidently, such harvests were too intensive, and the Greenland turbot and Kamchatka and arrowtooth flounder catch reached only several thousand tons up to the mid-1960s. Commercial stocks of these fish near Asian shores disappeared altogether in 1974.

Greenland turbot fishing resumed in this area in 1978, after the eastern area was closed to Russian vessels. Target fisheries were conducted with medium refrigerator trawlers making up part of the fleet. Harvest transshipment and vessel supply are carried out at sea. Greenland turbot is a valuable commercial fish and its exploitation rate in Russian waters was probably due to dense commercial concentrations.

Harvests peaked at 6,000 tons until 1981 (Table 5), when they began decreasing. In 1990 target fishing was stopped on TINRO's recommendations.

Target fisheries removed only 28-68% (average 53%) of the harvested Greenland turbot. Significant removal was due to the incidental catch in trawl fisheries for walleye pollock and other species fished

along the upper continental slope, or by large refrigerator trawlers in areas of Greenland turbot concentrations.

Dynamics of Abundance

No marked changes in Bering Sea Greenland turbot stock abundance were noted from the 1960s to the 1970s. Although the Greenland turbot and Kamchatka flounder annual total catches varied from 132,000 to 103,000 tons, the reasons are not clear. This variation is explained only in part by changes of commercial stock biomass and concentration density. Problems of organization and market relating to the eastern shelf are also a large contributing factor. Exhausted commercial concentrations and a sharp decrease in recruitment in the northwestern area caused the loss of the fisheries.

According to Alton et al. (1988), the maximum abundance of immature fishes (904 million individuals) was recorded in 1979. Juvenile abundance decreased while areas of juvenile settling and distribution density decreased from 1979 to 1989 (Tables 2 and 3, Figure 2). TINRO data show juvenile abundance along the eastern shelf, including Anadyrskiy Bay, to have decreased 20-fold; U.S. data show a 40-fold decrease. Alton et al. (1988) recorded a decrease in the abundance of age groups 1 and 2 from 1979 to 1985 to the second order. It is curious that there was insignificant change in the abundance of juveniles of the first age group in Anadyrskiy Bay (Table 3). By 1988, Greenland turbot catches decreased 11-fold to 7,000 tons in the eastern area (Wilderbuer and Sample 1990).

We believe that the Japanese surimi fishery in the 1980s is one of the main reasons for the sharp decline in Greenland turbot. Alton et al. report that from 1977 to 1980 bycatch of Greenland turbot juveniles in the walleye pollock fishery amounted to 9,000-12,000 tons annually. In 1980 the mean length of harvested juveniles was 27 cm (body weight 110-180 g). According to data collected by Russian research vessels in the northern Bering Sea, where the majority of Greenland turbot was caught, the mean juvenile body weight was 20 g at depths down to 50 m and 67 g at depths of 50-100 m. Indications are that 60 to 120 million individuals, a great number of which were age 1-2 years, were caught by these ships annually.

There is good reason to suppose that in the early 1970s the abundance of Greenland turbot juveniles was lower than in 1979-1980. The increase of juvenile abundance during this period is demonstrated by the abundant harvest of 1976-1978. The fish from these

years evidently contributed to the increased Greenland turbot catch in the eastern and western areas in 1981 (Table 2).

Since 1979 the juvenile population density along the eastern Bering Sea shelf decreased sharply. The earlier abundant broods provided relatively high levels of biomass and catch in the eastern Bering Sea until 1983, when the population in Russian waters decreased sharply.

Results of trawl surveys at depths of 200-800 m during 1982-1990 showed a change in Greenland turbot biomass from 5,000 to 10,000 tons. The proportion of the stock concentrated at great depths is unknown, but it can't exceed 20-25%.

There is good reason to assume that the decrease of Greenland turbot abundance has stopped. Judging by juvenile length composition in Anadyrskiy Bay and by its assessment along the eastern Bering Sea shelf in 1990 and 1991 (Tables 3 and 6), the harvest of 1985, 1986, and 1990 were of relatively high abundance.

Conclusion

Changes in the Greenland turbot catch in the Bering Sea during 1960-1980 are connected with the natural cycle of abundance and market condition. Stock depression in the 1980s is also probably in response to harvest and uncontrolled juvenile catch. The first indications of depression appeared in the northeastern Bering Sea in the early 1970s. In our opinion, a great number of specimens of the young (0+ to 2+ years) fish are distributed through the Anadyrskiy Bay and adjacent U.S. waters and then settle along the eastern Bering Sea shelf. This distribution holds especially when turbot abundance is low; during periods of high abundance, the area where the first age groups settle probably expands. Evidently, a great number of the Bering Sea stock recruits run toward the continental slope (including Russian waters) northeast of Saint Matthew Island. Juvenile bycatch in this area influences all Bering Sea commercial stocks. To prove these assumptions it is necessary to have a joint program with the Northwest Fisheries Center for Greenland turbot tagging.

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Dynamics of Abundance and Biomass of Greenland Turbot (*Reinhardtius hippoglossoides*) in Western Kamchatka in 1976-1993

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Abstract

The Greenland turbot has been commercially fished in the Okhotsk Sea since 1976. Stocks inhabiting waters off western Kamchatka comprise the majority of the total catch. Some scientists believe there are several populations of turbot in the Okhotsk Sea, two of which are in the region off western Kamchatka.

Based on analysis of turbot stock data (CPUE, number, biomass and age at length composition) collected between 1974 and 1993, and comparing data from the traditional turbot fishing region and the other parts of the Okhotsk Sea, we conclude that the southwestern Kamchatka stocks are replenished by fish migrating from the Sakhalin slope, and from the northern areas of the Okhotsk Sea. The strength of the turbot stocks inhabiting waters off southwestern Kamchatka was high from the mid-1980s to the early 1990s. The tendency toward decreasing biomass was first seen in 1988. This decrease was caused by the gradual reduction in recruitment beginning in 1977, and by large catches of mature turbot in the Okhotsk Sea between 1986 and 1991.

Introduction

The Greenland turbot (*Reinhardtius hippoglossoides*) is widely distributed in the Okhotsk Sea. Russian fishermen harvest this species mainly off western Kamchatka where the annual catch ranges from 2,600 to 16,200 tons.

Population structure of the western Kamchatka turbot is a matter of speculation. It has been suggested that there are at least two populations of the species in this region (Dyakov 1981, Dyakov et al. 1981, Dyakov 1991). One population occupies the TINRO hollow and is entirely isolated from the other populations. The reproductive area of the second population is confined to the waters off southwestern Kamchatka. Genetic similarity between groups in the southwestern Kamchatka region, the northern part of the TINRO hollow, and the area off eastern Sakhalin is explained by the passive transport of eggs and larvae by currents.

Analysis of fishery statistics, dynamics of stock abundance and biomass, and changes in the age-at-length structure of the catches make it uncertain whether separate populations really exist near southwestern Kamchatka, and suggest that mature turbot actively migrate into this region.

Long distance migrations could explain genetic similarity of turbot from different areas of the Okhotsk Sea, the considerable fluctuations of biomass and abundance of the commercial stocks on the continental slope near southwestern Kamchatka, and the differences in length-at-age.

In our research we considered the following: (1) the history of the turbot fishery in the Okhotsk Sea; (2) dynamics of number and biomass of turbot near southwestern Kamchatka and other regions of the Okhotsk Sea in 1977-1993; (3) changes in distribution of turbot in the Okhotsk Sea in 1977-1989; and (4) identification of the areas that supply the majority of turbot stocks harvested off southwestern Kamchatka.

Understanding these matters may be useful for answering questions about population structure of turbot in the Okhotsk Sea and the western Kamchatka region. This knowledge may be helpful in working out rational approaches to fishing strategy.

Results and Discussion

The turbot fishery in the Okhotsk Sea began in 1976, and developed very rapidly. In early 1976 only four trawlers fished for this species,

Table 1. Changes in the annual catch (1,000 mt) and catch per day per vessel (mt) of Greenland turbot on the continental slope of western Kamchatka in 1976-1993.

Year	1976	1977	1978	1979	1980	1981	1982	1983	1984
Catches	10.0	16.2	5.9	3.3	2.6	4.8	6.8	10.0	11.2
CPUE	3.0	3.0	2.5	-	2.2	2.5	3.5	3.6	3.4

Year	1985	1986	1987	1988	1989	1990	1991	1992	1993
Catches	10.5	12.8	8.7	9.0	9.2	9.0	5.0	4.4	2.6
CPUE	3.5	3.5	3.9	4.2	3.9	3.8	3.3	2.9	2.6

and by the end of the year the number of vessels reached 29. The total catch of this species exceeded 10,000 tons in 1976. In 1977 the annual catch amounted to 16,200 tons, which was the largest catch in history for the turbot fishery in the Okhotsk Sea. By the third year of stock exploitation, 1980, catch per day per vessel (CPUE) dropped to a critical level of 2.2 tons. This led to the termination of the commercial fishery for this species in 1980 when the total annual catch constituted 2,600 tons (Table 1). The CPUE increased over the next two years. By 1982-1983 the CPUE estimate exceeded the number for the first year of the fishery. The catch increased until 1988, then gradually began to decline, and is still decreasing.

Understanding the causes for rapid changes in the catch per unit effort and annual catch is possible only by summarizing data on changes in abundance, biomass, and size-age structure in the catches. No abundance and biomass assessments of the turbot stock were made prior to the harvest by the fishery off the southwestern coast of Kamchatka. As revealed by the length-at-age structure analysis, specimens 55-80 cm in length, aged 6+ to 10+ dominated, and comprised 70-80% of the total catch in 1974-1975 (Figure 1). Older animals comprised up to 20% of the total catch. At the same time, stock recruitment was low and the proportion of fish younger than 6 years did not reach 10%. Therefore, the major portion of the stock consisted of large, sexually mature fish, which provided a good harvest, but at the same time recruitment to the stock was weak.

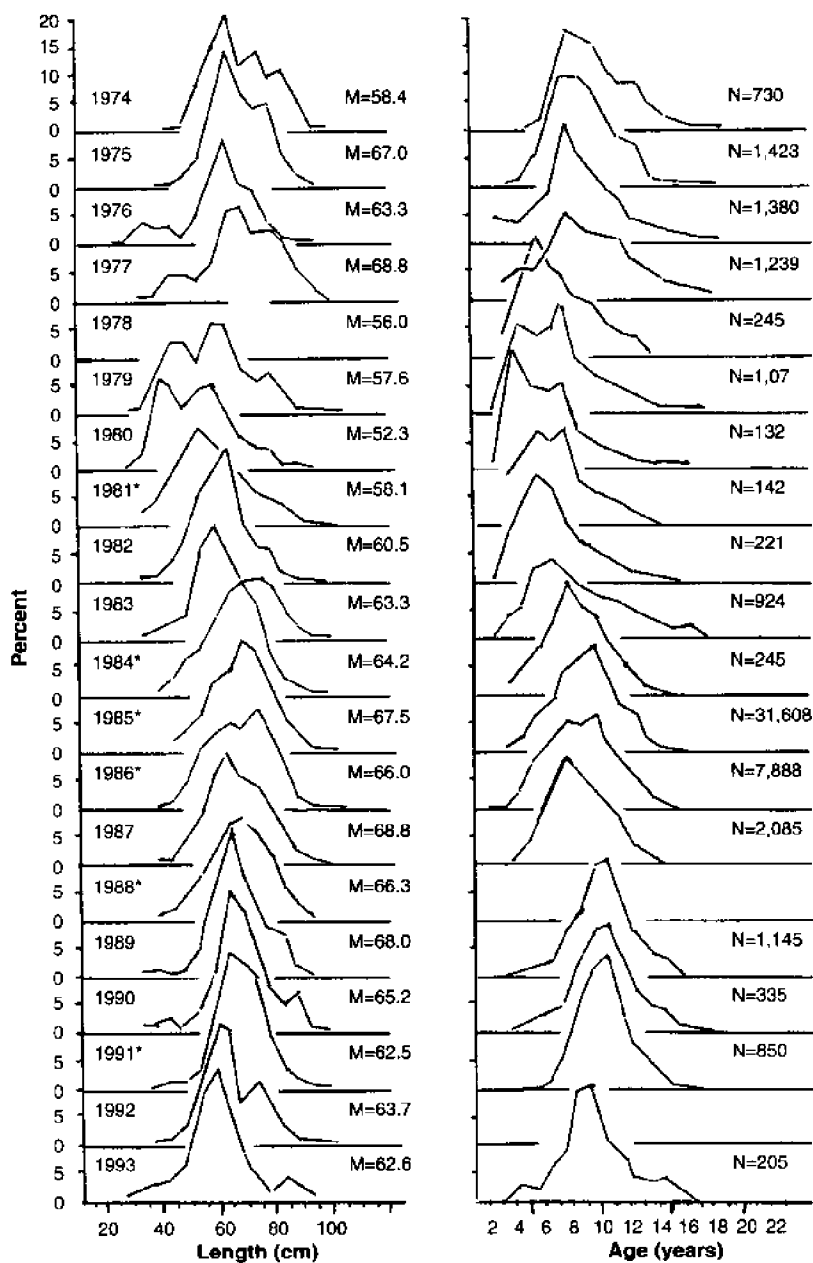


Figure 1. Length and age composition of Greenland turbot of southwestern Kamchatka from 1974 to 1993 (trawl). * Commercial catches.

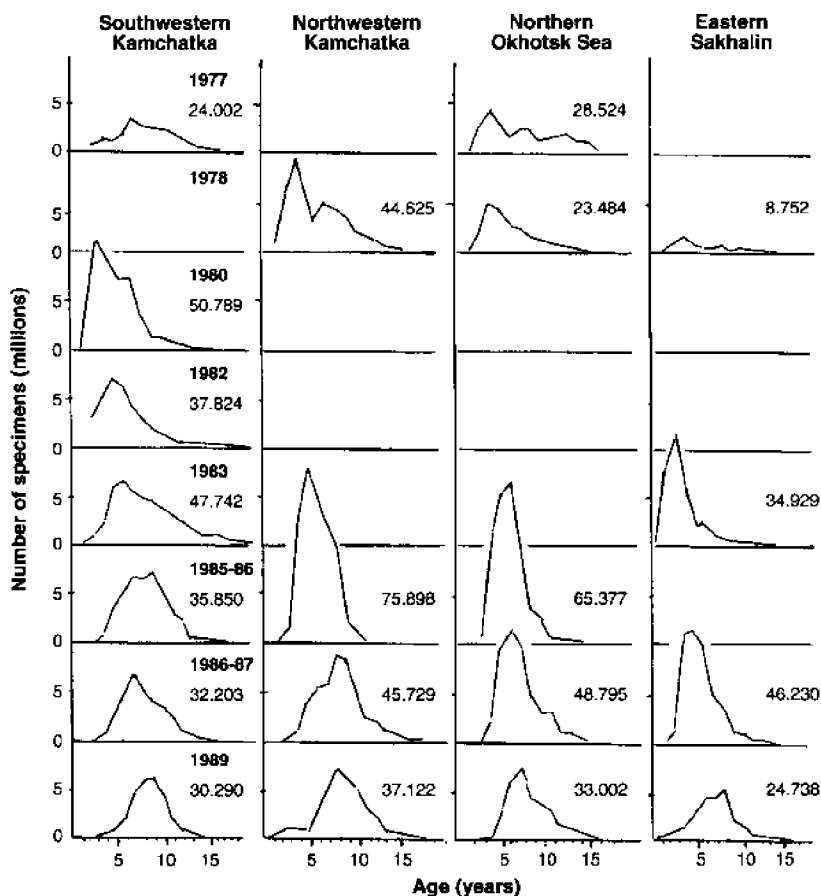


Figure 2. Age composition and abundance of Greenland turbot on the continental slope in different regions of the Okhotsk Sea from 1977 to 1989 (depths 500-1,000 m).

Table 2. Change in biomass (1,000 mt) abundance of the Greenland turbot on the continental slope of southwestern Kamchatka in 1977-1989.

Year Seasons	1977 Summer	1980 Winter	1982 Winter	1983* Spring	1985-1986 Autumn- winter	1986-1987 Autumn- winter	1989 Summer
Biomass	79.2	60.5	83.7	114.5	86.3	92.8	89.7
Abundance	24.0	50.8	37.8	47.7	35.8	32.2	30.3
Surveyed area	11.2	5.0	20.3	25.2	21.3	25.2	25.2

All the calculations are adjusted to the whole area of the continental slope (25.2 thousand square miles).

- * Increase in biomass and abundance is caused by specific distribution of turbot in spring. That's why these characters are not considered in analysis of interannual stock fluctuations.

In 1977, the second year of the turbot fishery, the species biomass near southwestern Kamchatka was estimated at 79,200 tons with 24 million fish (Table 2); 12.4 million fish were 9+ years old, comprising the greatest portion of the catch (Figure 2). The numbers fell to 5.8 million fish by 1980. Biomass and abundance calculations for the years 1977-1989 were made by the method of squares (Aksyutina 1968) with 0.4 coefficient of efficiency of catch. The reason for such a rapid decline in the number of mature fish was the unregulated harvesting of the stocks between 1976 and 1979. During this period the target fishing vessels alone caught 35,400 tons, or nearly 14.5 million turbot. The commercial stock biomass dropped to 60,500 tons by 1980, which had an impact on the overall fishery.

The juvenile population began to increase in 1978 and reached a peak in 1980 (Figure 2). The overall number of fish in the commercial stock appeared to be 50.8 million by 1980, which was twice the 1977 abundance. The most abundant age groups were 1976 and 1977, which produced 11.1 and 9.2 million fish respectively. In fact, the 1976 and 1977 age groups had the highest yield throughout our investigations, and constituted 2,071 and 2,126 conventional units respectively (Table 3). For Table 3, the relative strength of a year class is the sum of all the fish of that year class caught per effort during its lifetime (Kodolov et al. 1986, Kodolov et al. 1987).

Turbot aged from 3 to 6 were weakly represented in the catches off southwestern Kamchatka. The appearance of numerous recruits and

Table 3. Change in relative abundance of year classes of Greenland turbot, in 1966-1982, in conventional units.

Year class	1966	1967	1968	1969	1970	1971	1972	1973	1974
Abundance	1,406	1,195	1,129	1,107	960	893	1,094	1,428	1,603
Year class	1975	1976	1977	1978	1979	1980	1981	1982	
Abundance	1,703	2,071	2,126	1,696	1,525	1,558	1,466	1,305	

juvenile fish hatched during 1978-1980 had several causes: (1) large numbers of young fish, (2) decrease in number of mature fish, and (3) comparatively severe hydrological conditions during the winter of 1978-1979 and 1979-1980 (Khen 1991, Chernyavskiy 1992).

The large concentration of recruits and juveniles in the waters off southwestern Kamchatka had practically no effect on the stock biomass in 1979-1980 due to the low individual weight of the fish. Subsequent high-yield age groups provided good potential for an increase in harvest. From the winter of 1980-1981 to 1983 the number of fish older than 9+ years increased noticeably, and by 1983 there were 19.8 million fish (Figure 2).

Size at age composition of the catches show that by 1983 fish 55-80 cm long and 6-11 years old comprised 60-80% of all turbot caught (Figure 1). The reappearance of both young and mature fish resulted in the rapid growth of turbot biomass, which allowed for increased harvest again. Research trawls on the continental slope of the Okhotsk Sea suggest that the influx of turbot in 1977-1983 came from the northern region of the sea (Figure 3). Figure 4 shows the distribution of turbot on the continental slope of the Okhotsk Sea in 1985-1989.

The increase in turbot biomass near southwestern Kamchatka, which began in 1981 and continued for several years, was accompanied by a decrease in juvenile migrations. The number of recruits into the commercial stock aged 2+ to 5+ was 8.6 million fish in 1985-1986, 8.1 million in 1986-1987, and declined to 6.3 million by 1989 (Figure 2).

In the late 1970s and early 1980s, the stock biomass grew due to an increase in length and weight of fish from high-yield 1976-1977 age groups, and the migration of mature turbot from other regions. Turbot

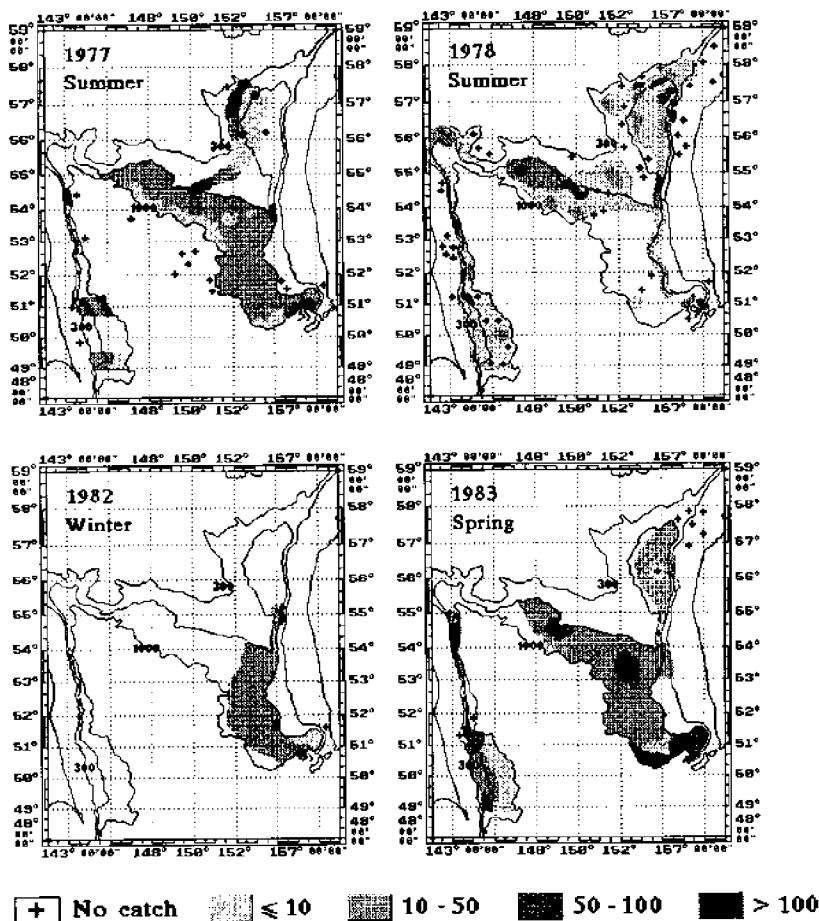


Figure 3. Distribution of Greenland turbot on the continental slope of the Okhotsk Sea from 1977 to 1983 (sp/ha).

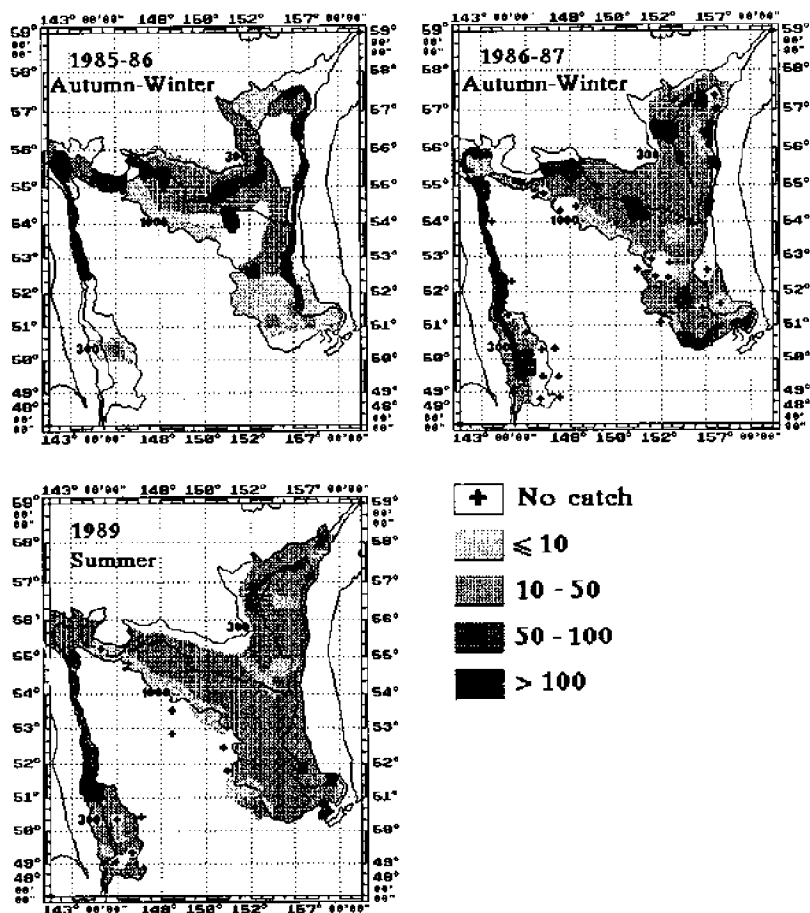


Figure 4. Distribution of Greenland turbot on the continental slope of the Okhotsk Sea from 1985 to 1989 (sp/ha).

biomass was at its maximum of 92,800 tons by the winter of 1986-1987 (or by 1988, based on commercial catch data), and then began to decline.

We estimated a comparatively high yield of 1978-1980 age groups; their strength was 1,696 conventional units for 1978 and 1,558 for 1980 (Table 3). These age groups were recorded mainly in the northern region of the Okhotsk Sea and in the region off the eastern Sakhalin Island. But the individuals of this age group on the continental slope of southwestern Kamchatka were essentially not observed until the mid-1980s. They appeared in high numbers only in 1985-1986 at ages 6+ to 7+ and in later years fish of these age groups occupied a dominant position. Therefore, in the 1980s the commercial catches were made up primarily of mature fish, not juveniles.

In 1985-1987, turbot ages 3+ to 6+ (the 1978-1980 age groups) were abundant on the slope of Sakhalin Island, near the northwest coast of Kamchatka, and in the northern Sea of Okhotsk (Figure 2). By 1989 the abundance of turbot in all of these region had decreased to half: on the Sakhalin slope the abundance decreased from 42.6 to 25 million individuals from fall 1986 to summer 1989. Abundance in the northern Sea of Okhotsk decreased from 65.4 to 33 million individuals from winter 1985-1986 to summer 1989, and from 75.8 to 37.1 individuals for the same period near northwestern Kamchatka. However, near southwestern Kamchatka, despite intense fishing mortality, the decreases in density were lower, from 35.8 million individuals in 1985 to 30.2 in 1989, less than 15% decline.

Considering these data, there appears to be a fairly constant supply of turbot for the commercial fishery near southwestern Kamchatka due to the migration of individuals into the region from other parts of the sea.

One of the reasons for the decrease in abundance and biomass of the turbot stocks near southwestern Kamchatka after 1988 is the drop in yield, which began in 1977 and led to the decline in turbot abundance in the entire Okhotsk Sea (Table 2).

In 1988, 33 million turbot were recorded on the northern shelf, the main feeding ground for young fish (Table 4). This estimate is almost half the estimate for 1982, though a larger area was covered. Judging from the size composition of turbot on the northern shelf and near the coast of Kamchatka, young fish had almost disappeared. Mostly mature fish were covered by the fishery.

Another reason for a decrease in mature turbot abundance in the Okhotsk Sea and near western Kamchatka is the increased fishing

Table 4. Greenland turbot abundance (millions) on the shelf of the northern Okhotsk Sea in summer, 1982 and 1988

	1982	1988
Abundance	62.4	33.0
Covered area square miles	28,600	35,700
Presence of turbot in the area square miles	27,625	19,680

pressure on the stocks during recent years. The annual catch of Russian and Japanese fishermen, excluding joint ventures and bycatch, totaled 15,000-19,000 tons. The specialized vessels alone caught more than 150,000 tons or about 60 million fish from 1983 to 1993, which probably exhausted the high-yield classes. A decrease in fish smaller than 50 cm and larger than 80 cm in length was detected both near the southwestern Kamchatka and in Japanese catches (Figure 5).

Based on the hypothetical migration of mature turbot from the western and northern areas to the eastern area of the Okhotsk Sea, the decrease in biomass should not have occurred until 1990-1992, when turbot from the high-yield age groups all matured at the same time.

The turbot fishery in the neutral sector of the Okhotsk Sea and in waters off eastern Sakhalin, where gillnets cross the turbot migration routes, could provide an additional reason for the reduced strength of stocks migrating to southwestern Kamchatka.

It was not possible to assess turbot biomass and abundance by the methods of squares, but judging from the CPUE, the species biomass and abundance continue to decline (Table 1).

In general, the turbot inhabiting the slope of Sakhalin Island and the northern Okhotsk Sea are small; mature fish are scarce in this area (Nikolenko 1993). The largest turbots reported in the Okhotsk Sea were near the southwestern Kamchatka, despite intense harvesting by the fishery. Observation of genetic and morphometric similarities between turbot of the northern region and the Sakhalin slope (Dyakov 1981, Dyakov et al. 1981, Dyakov 1991) suggest that some fish migrate from the western and northern areas of the Okhotsk Sea to the eastern area as they grow and mature.

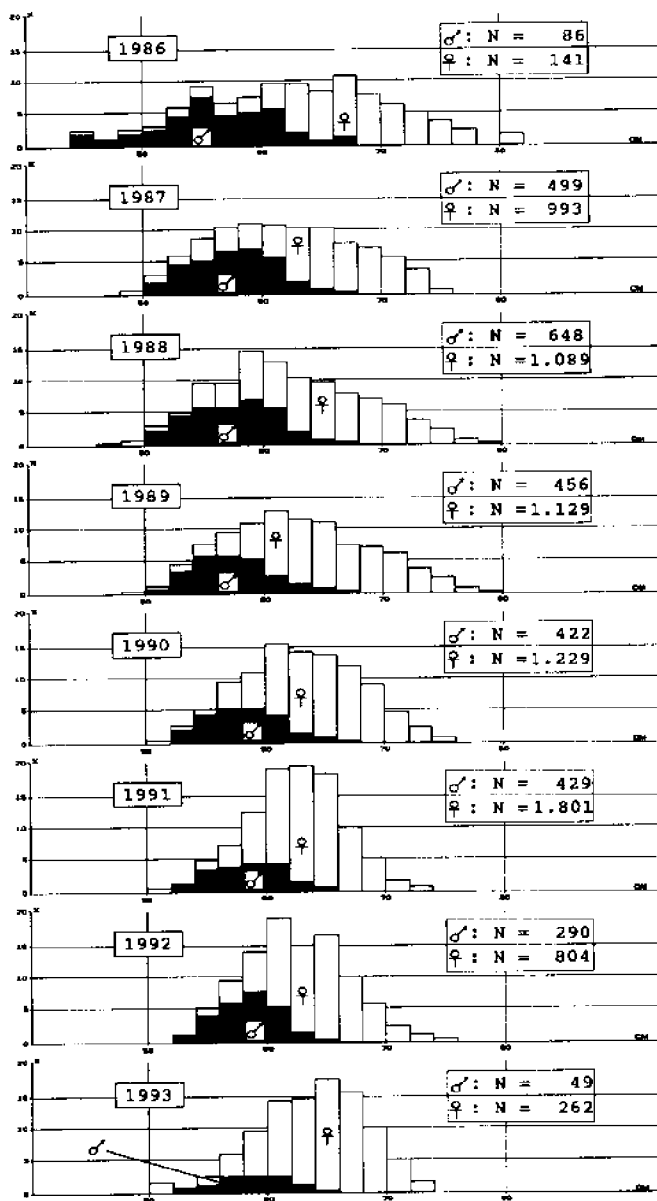


Figure 5. Length composition of catches of Greenland turbot in neutral part of the Okhotsk Sea, commercial gillnet fishery, according to Japanese Department of Fisheries.

Table 5. Changes in annual catch (thousand tons) and catch per day per vessel (tons) during the Greenland turbot fishery in neutral waters by gillnets in 1985-1993 (data provided by Japanese Department of Fisheries).

Year	1985	1986	1987	1988	1989	1990	1991	1992	1993
Catch	0.26	6.0	5.7	7.4	8.2	8.0	10.1	5.0	2.3
CPUE	-	10.1	7.2	8.0	9.6	11.0	12.9	10.8	7.8

The increase in turbot catch by Japanese fishermen during 1987-1991 (Table 5) is primarily connected to the onset of mass-maturation and increased migration in the eastern Sakhalin region. Turbot abundance dropped to 25 million on the Sakhalin slope. Abundance was especially low for fish in the 9+ age group at the age of mass-maturation (Figure 2). However, biomass declines began near southwestern Kamchatka in 1988 due to a substantial decline in the immigration of the juvenile and mature fish.

Conclusion

Our research revealed that during the time of this investigation, turbot near southwestern Kamchatka changed from 24.0 to 50.8 million specimens, and the biomass changed from 60.5 to 92.8 thousand tons (excluding spring season). The stocks inhabiting waters off western Kamchatka primarily consist of large, mature fish with few young fish. Stock replenishment is provided mainly by recruits and mature fish migrating from the western and northern areas of the Okhotsk Sea. This explains why the biomass and abundance of turbot stocks near western Kamchatka depend on the stock strength of turbot in the entire Okhotsk Sea.

In our opinion, the decline in stock abundance and biomass near southwestern Kamchatka, which began in 1988, is related to the decrease in age group yield from 1977 to 1982, and intensive harvesting by trawl and gillnet fisheries of mature fish near western Kamchatka and in the neutral zone of the Okhotsk Sea during 1985-1991.

Because of the genetic similarity of turbot from Sakhalin, the northern Okhotsk Sea, and the southwest Kamchatka region, we conclude that fish inhabiting the slope off western Kamchatka constitute the major mature portion of a single Okhotsk Sea population,

consisting of local groups as discussed by Dyakov (1981, 1991). Thus the commercial stock of turbot in the Okhotsk Sea should be considered of a single stock, and therefore the fishery for turbot should be regulated for the entire Okhotsk Sea.

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Stock Condition of Pacific Halibut (*Hippoglossus stenolepis*) in the Northwestern Bering Sea

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Abstract

From the 1960s to the early 1970s commercial concentrations of Pacific halibut near Asian shores disappeared, and for about 20 years this species occurred in catches only as individuals. In the 1980s, a rapid increase in halibut abundance was noted both in Russian waters and the eastern Bering Sea. Few studies on halibut in Russian waters have been made due to the low abundance. This has resulted in the absence of data in the scientific literature on the present Asian stock. TINRO's data on the Pacific halibut of the western Bering Sea, missing from the International Pacific Halibut Commission data, are presented here.

Population Structure

Pacific halibut (*Hippoglossus stenolepis*) is one of the most valuable fishes in the North Pacific. The International Pacific Halibut Commission (IPHC) is engaged in studying biology, stock condition, and fishery management in the eastern Bering Sea. The latest data on Asian halibut were published in 1974 (Novikov 1974). More recent information on Pacific halibut of Asian waters in TINRO records is presented here.

Pacific halibut occupies the shelf and upper continental slope north of Japan and California waters to Saint Lawrence Island in the Bering Sea. The population structure has evidently been investigated only in the area to the east of 180° longitude. Genetic analysis of blood

protein (Tzuyuki et al. 1969) demonstrated the genetic homogeneity of halibut samples of the eastern Pacific Ocean and Bering Sea. Scud (1977) reached an analogous conclusion based on enzyme studies. Hall et al. (1977) noted significant differences in the mercury content of muscles and questioned population homogeneity. Investigations of U.S. ichthyologists showed that within the eastern Bering Sea, halibut disperse widely during ontogenetic and other migrations. Best (1968) considers that the currents in the Gulf of Alaska are able to carry eggs and larvae long distances. Some juveniles inhabiting the Bering Sea descend from eggs that drifted from the spawning grounds off Alaska. Scud (1977) suggests that some eggs spawned in British Columbia reach the Aleutian Islands and Bering Sea, and the number carried from the spawning grounds off Alaska to the Bering Sea is rather significant. Moreover, he believes that a large segment of the Bering Sea halibut stock descends from eggs spawned off the Pacific shore (this probably excludes the northwestern area). Likewise, some portion of the eggs may drift from the southeastern spawning grounds of the Bering Sea toward the Asian coast. Pacific halibut spawn in all of these areas. Accordingly, it can be assumed that a certain portion of halibut in each area descend from eggs and larvae drifting from spawning grounds with swifter currents, i.e., from the east. Of the 20,435 individuals tagged in the Bering Sea, only 1,223 returned, 467 of them (38.2%) to the Gulf of Alaska and British Columbia (Scud 1977). Reverse return of adult fishes was not observed. It is assumed that some portion of the mature halibut return to the areas where their parents spawned (Scud 1977). Thus, the anticyclonic system of currents connecting the Gulf of Alaska and Bering Sea allows intensive intermingling of Pacific halibut stocks.

The Fisheries

Until 1958 not many Pacific halibut were caught with hooks and seines by the Kamchatka fishery cooperative companies during the coastal cod fisheries. In 1958, only Ust-Kamchatsk vessels caught 385 tons of halibut in the east Kamchatka region. According to data on halibut abundance close to the Kamchatka coast (Polutov 1960), this catch was not incidental. In 1958 Japan's fishermen began commercial longline fishing near the Russian coast of the Bering Sea. In 1958 Japan's fishermen caught 1,300 tons of halibut in waters west of 175° longitude, in what is now mostly the Russian zone (Hoag 1976). The fisheries developed intensively and in 1961 the catch reached 11,100 tons. The commercial longline fishery's share of the catch began to

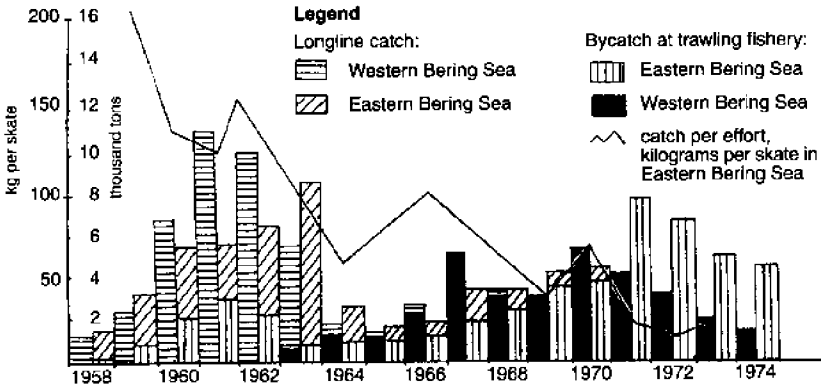


Figure 1. Pacific halibut catch in Bering Sea (after Hoag 1976).

decrease (Figure 1) and the fishery was closed in 1966. This closure was probably due to depletion of mature fish. However, the incidental halibut catch, mainly of immature fish, in trawl fisheries for other target species continued to be high (3,000-5,600 tons a year) until 1972 when halibut disappeared from catches near the Asian coast.

From 1977 to 1989 only Russian vessels fished close to Asian shores. Official Russian statistical data on Greenland turbot (*Reinhardtius hippoglossoides*) and Pacific halibut catches, combined as "halibut," are shown in Table 1. A large amount of these halibut occurred as incidental catch in fisheries for walleye pollock, flounder, and other species by large refrigerator trawlers in the Olyutor-Navariniski region. The catch of Pacific halibut was low until 1985: 5-7% of the total catch of "halibut" according to survey vessel data. Beginning in 1986 the halibut catch began to increase intensively shown by the incidental catch of juveniles in areas of walleye pollock, cod, and flounder concentrations. Based on survey vessel data taken in the late 1960s, Pacific halibut made up about 17% of the trawl catches on the upper slope and outer margin of the shelf; 7% in 1982; and 64-68% in 1989-1992. Target fisheries for Greenland turbot were conducted by medium refrigerator trawlers until 1990, then stopped due to commercial stock depression. Up to 1985 Greenland turbot was the basis of the catch (more than 90%) in targeted trawl fishing of all "halibut," as was Pacific halibut in seine and longline fishing. After 1987 Pacific halibut made up an estimated 40-60% of the remainder of the catch harvested during walleye pollock and cod fisheries. During

Table 1. Greenland turbot and Pacific halibut catch in western Bering Sea by Russian vessels.

	1982	1983	1984	1985	1986	1987
Olyutor-Navarin area	2908	2087	2121	2671	4619	3340
Turbot commercial catch	371	1377	1076	956	1312	1563
Seine and cod longline catch	—	10	—	n.i.	110	53
Eastern Kamchatka	—	10	21	7	174	57
Estimated halibut catch		n. i.		300-500	500-1000	500-1000

	1988	1989	1990	1991	1992	1993
Olyutor-Navarin area	1499	1655	2094	1537	1138	n.i.
Turbot commercial catch	891	272	327	—	—	—
Seine and cod longline catch	n.i.	159	461	347	560	316
Eastern Kamchatka	96	64	204	555	551	83
Estimated halibut catch	500-1000	500-1000	800-1500	1000-2000	2500-3000	3000-4000

Data on joint enterprises and foreign vessels fishery are not included in total catch of 1991-1992, n.i. = no information.

1991-1993 some vessels, especially those which shared their raw fish with foreign processing ships, did not give exact information on catch composition, and catch data by foreign vessels are not included in these statistics.

TINRO's data shows that during cod longline fisheries, the incidental catch of Pacific halibut varies from 0.6 to 4.4% (Table 2) depending on the season. In 1991-1992, 19,000 and 29,000 tons of cod, and therefore 500-800 tons of Pacific halibut, were harvested by longlines. Thus, during longline and seine fisheries for cod, the incidental catch of halibut was between 900 and 1,300 tons.

The incidental catch of halibut due to seine fishing may be significant. Thus, in Karaginskiy Bay from June 5 to 10, two small seine

Table 2. Seasonal changes of Pacific halibut bycatch during cod longline fishing in the northwestern Bering sea in 1992, by month.

Area	IV	V	VI	VII	VIII	IX	X	XI	XII
1	-	-	2.1	0.6	3.7	4.4	1.6	1.0	-
2	21	4.7	3.6	3.6	1.4	n.i.	0.7	1.6	n.i.

1 = Olyutor-Navarinский area westward of Olyutor Cape; 2 = Olyutorskiy Bay; n.i. = no information

boats delivered 128 tons of cod and 8 tons of halibut (0.7 tons per vessel per day of fishing) to Sintoku-Maru; and in Olyutorskiy Bay, from July 1 to 10, 100 tons of cod and 27 tons of halibut (1.7 tons per vessel per day of fishing).

Beginning in 1990 longline fishing for halibut was resumed by the Russian and American joint-venture vessels and later by Russian vessels. Abundant commercial concentrations were found in the Olyutor-Navarinский area during fall-winter 1990-1993, and in summer near eastern Kamchatka. These concentrations provided stable daily catches (4-10 tons per vessel and 400-1,500 kg per 1,000 hooks). We assume that halibut, as both the target species and the incidental catch, made up 3,000-4,000 tons a year in 1992-1993. The majority of halibut caught were immature.

Length-age Composition.

Data on length-age composition of catches was collected by trawl and longline cod and halibut vessels. About 60% of the fish caught by trawlers and more than 50% of those caught by cod longlines were less than 80 cm in body length (Table 3) and comprised approximately one-third of catch by biomass. In 1991, a large number of immature halibut appeared near the Olyutor-Navarinский area; they made up 94% of the total trawl catch and 73% of the cod catch. Therefore, until 1992 about 60% of harvested halibut were immature. Beginning in 1992, the proportion of mature fish has increased due to implementation of target fishing by the Russian and American joint ventures.

Data on age-determining structures of halibut were collected only in 1991. Because of this, the inferred age structure of the population during other years should be used for general orientation only (Table 4). The rate of halibut growth changed significantly. Thus, according to

Table 3. Pacific halibut length composition in the western Bering Sea, by percent.

Year	Gear	Area	Season	Length, cm																	N	M				
				10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170			180	190	200	210
1986-87	trawl	1	winter		4.3	14.4	16.0	34.9	25.2	6.6	2.5	0.2	0.5	0.2	0.1	0.2									759	53.39
1986-87	trawl	2	winter				0.8	36.5	24.6	19.0	8.0	3.2	0.8	1.6	1.6	1.6	0.8	0.8		0.7					126	71.04
1988-89	trawl	2	winter		0.7		6.1	33.1	16.9	23.6	6.7	4.0	3.4	1.4											149	69.75
1993	trawl	2	spring				6.6	44.1	27.4	9.3	5.7	2.7	1.6	1.2	0.3	0.9	0.3								335	64.53
1993	trawl	2	winter		2.8		14.2	35.5	15.4	10.0	6.4	5.6	2.1	3.6	2.4	1.7	1.2	0.5	0.7	0.5		0.2			100	68.3
1983	trawl	3	winter				5.8	30.9	18.7	17.4	8.0	4.8	7.1	2.4	5.6			0.8							126	81.80
1985	trawl	3	summer				2.2	23.8	35.7	21.6	12.7	2.8	0.9	0.3											360	67.60
1986-87	trawl	3	winter	6.1	0.5	1.4	13.3	21.2	18.3	9.2	10.7	6.1	4.3	3.9	1.2	0.9	1.2	0.2	0.7	0.2	0.4	0.2			413	68.96
1990-89	trawl	3	winter		0.1	0.8	9.7	21.4	15.4	15.0	10.3	8.2	7.7	4.0	2.4	1.5	2.2	0.6	0.2	0.2	0.2	0.1			940	83.22
1990	trawl	3	summer		0.6	2.2	2.8	5.6	19.6	27.5	21.2	10.1	2.3	1.7	2.8	1.2	0.6	0.6	1.2						178	80.38
1991	trawl	3	summer		0.4	1.1	34.4	38.9	7.9	6.6	4.9	3.0	1.0	0.5	0.6	0.5									3190	43.86
1993	trawl	3	spring		0.4	2.5	3.6	18.4	11.2	15.1	13.7	10.3	8.9	6.3	3.9	2.0	1.4	1.4	0.2	0.7					795	82.87
1993	trawl	3	summer				1.2	16.7	18.5	17.6	23.8	10.8	5.1	4.5	0.3	0.3	0.6	0.3							355	77.7
1993	trawl	3	summer				1.0	13.4	16.4	17.2	24.6	11.7	6.2	4.5	1.2	0.7	1.2	1.0	0.2	0.5					419	82.47
1993	trawl	3	fall				0.6	7.2	13.5	22.3	19.4	15.5	8.1	4.9	3.4	1.4	2.0	0.5	0.6	0.3	0.1	0.1		0.1	1003	86.98
1993	trawl	3	winter			1.4	6.9	29.8	29.5	13.1	6.0	4.2	3.8	2.4	1.2	0.9	0.6	0.2							1368	68.81
1991	longline	2	winter				4.4	14.4	31.0	23.0	16.2	7.0	3.1	0.9											229	72.01
1991	longline	3	winter				2.4	27.5	23.6	18.2	14.9	7.1	3.9	2.4											127	71.29
1992	longline	3	winter				0.1	4.4	19.0	26.1	22.3	12.0	5.8	2.1	2.1	1.3	0.8	0.5	0.4	0.1	0.1				935	82.82
1990	longline	3	winter				1.3	13.4	24.4	27.4	18.1	10.6	3.1	1.3	0.2	0.2									1268	74.94
1992	longline	2	summer				+	+	2.6	9.1	16.3	18.7	19.8	13.2	7.6	6.0	3.8	1.9	0.7	0.1	+				2057	103.55
1992	longline	3	summer				1.3	16.9	25.8	25.3	16.6	8.2	3.6	1.3	0.9	0.1									949	73.90
1992	longline	4	summer					5.9	38.2	23.9	9.7	8.4	6.4	4.5	2.6	1.2									155	79.69

1 = Eastern Kamchatka; 2 = Olyutorsky Bay; 3 = Olyutorsky area (eastward of Olyutorsky Cape); 4 = Little Strait.

Table 5. Rate of Asian halibut growth, 1991-92, in cm.

Age	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+
Min	35	34	44	47	50	54	63	72	70	76	72
Max	50	56	61	72	80	79	98	97	108	117	108
Mid	42.5	43.5	52.7	61.6	64.4	70.1	75.7	82.5	89.1	93.3	99.7
Number of ind.	2	4	11	20	28	24	22	22	14	15	11
Age	14+	15+	16+	17+	18+	19+	20+	21+	22+	23+	
Min	88	116	129	154	153	155	152	160	155	156	
Max	119	116	153	168	163	177	169	163	155	156	
Mid	100.0	116.0	143.0	160.3	158.0	162.8	158.0	161.5	155	156	
Number of ind.	7	1	4	3	2	5	5	2	1	1	

Table 6. Frequency of occurrence and Pacific halibut catch in the northeastern Bering Sea (Olyutor-Navarinskiy area).

	1962	1972	1984	1985	1986	1989	1990	1991	1992
Frequency of occurrence	38.0	23.6	14.2	39.6	72.1	30.8	39.4	55.1	73.7
Catch (sp/hour of trawling)	1.8	0.4	0.36	4.2	7.4	1.4	2.4	3.2	17.2
sp/sq. km	48	11	10	111	109	31	53	47	147
Number of trawls	83	55	61	48	43	65	66	49	80

Investigations were done by Japanese vessels with highly efficient fishing gears in 1992.

the 1991 data, same-age individuals in the Gulf of Alaska were 10% smaller, or approximately the same as in the 1950s (IPHC 1991). In the 1970s age 10 females and males averaged 95 cm and 115 cm in body length, and 9,060 g and 16,761 g of biomass respectively. In the 1920s these indices were 72.5 and 80.0 cm, 3,624 and 4,530 g (Best and Hardman 1982). The rates of Pacific halibut growth near the Asian coast are given in Table 5. Specimens of age 5-11 in trawl catches and age 6-14 in longline catches made up 75% of the total fish, excluding 1991, when 6-year-old fish predominated in trawl catches, and 10-year-old fish predominated in longline catches.

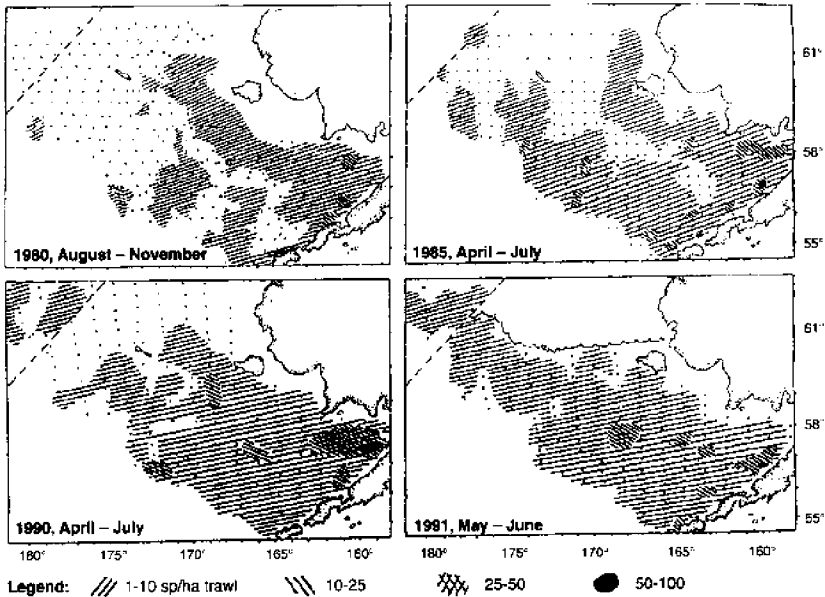


Figure 2. Distribution of Pacific halibut juveniles based on TINRO's trawl surveys, 1980-1991.

Dynamics of Abundance

During the period of low abundance, halibut distribution along the shelf and on the upper slope of the Bering Sea was scattered. Concentrations were located mainly in the southeastern area of the sea. Only small areas with limited halibut distribution were observed near the Asian coast. During the 1980s halibut were distributed along the western Bering shelf (Figures 2, 3, and 4). Research vessel data on changes in halibut catches along the shelf and upper slope of the Olyutor-Navarin'skiy area during 1962-1992 are given in Table 6. The surveys were conducted by vessels trawling at various speeds and with different rigs and parameters. Nevertheless, these data suggest definite changes in Pacific halibut distribution (density) in the northeastern Bering Sea.

Based on catch per effort and frequency of occurrence, Pacific halibut abundance decreased at least 4-fold during the 1960s and 1970s. In the mid 1980s it increased again due to the harvest from 1978 to 1983. The super refrigerator trawler *Gnevniy* found the first indications of increased abundance in Pacific halibut while surveying

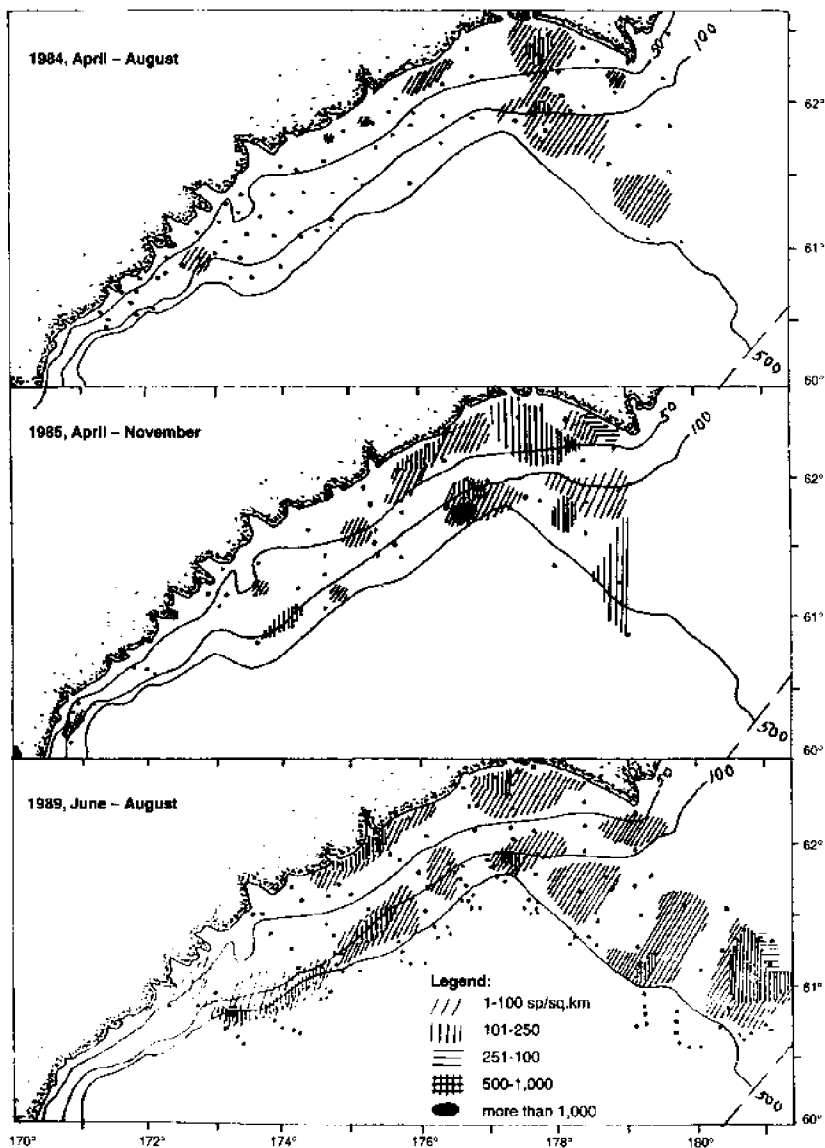


Figure 3. Pacific halibut distribution in Olyutor-Navarin'skiy area during summer.

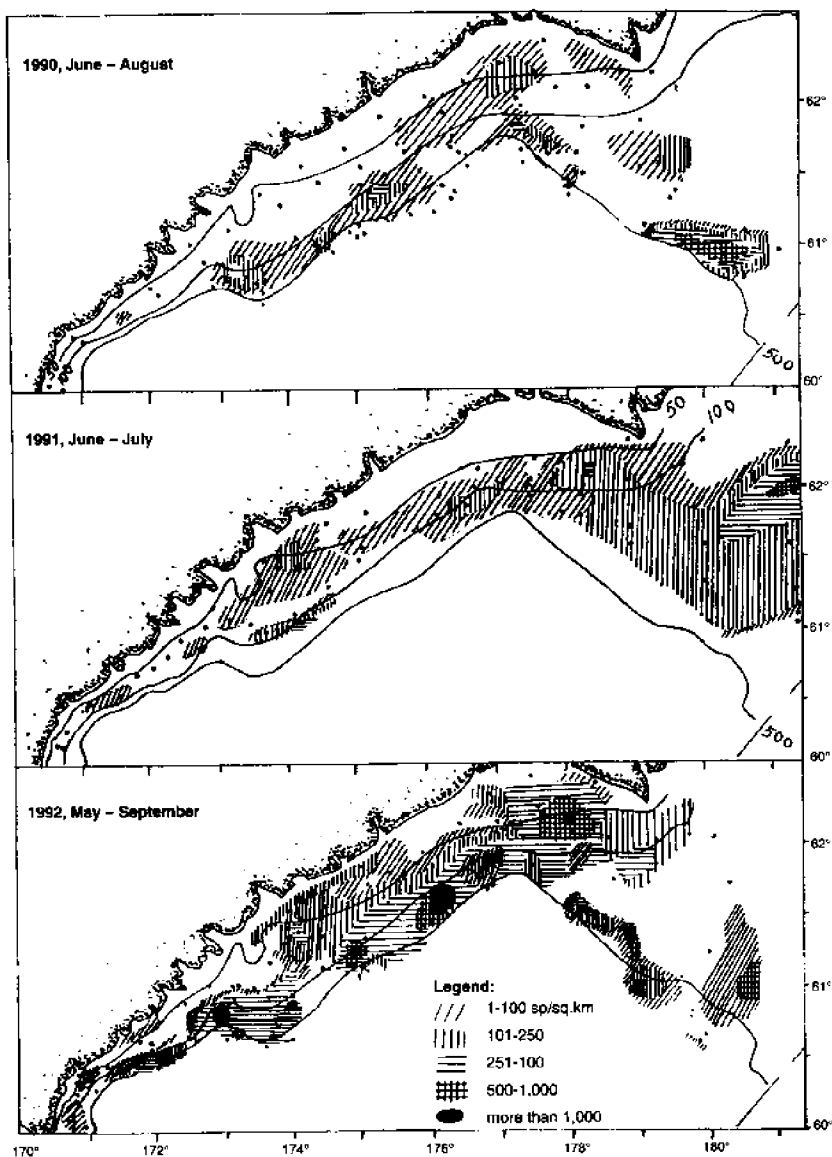


Figure 3. (continued.)

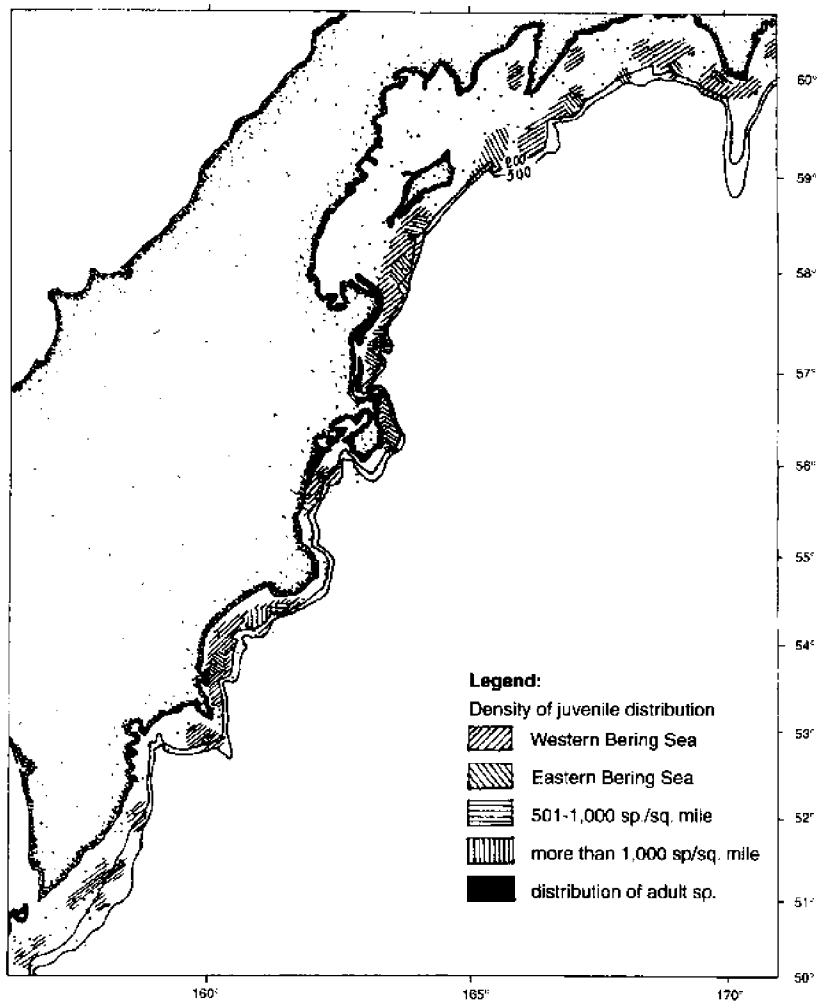


Figure 4. Pacific halibut distribution in eastern Kamchatka, 1992.

Table 7. Frequency of Pacific halibut occurrence and catch by trawlers in the western Bering Sea at 50-250 m depth.

Area	1986-87, winter			1991, summer			
	Frequency of occurrence, %	catch, sp/hr	Hauls	Sp. length less 50 Sm, %	Frequency of occurrence, %	catch, sp/hr	Hauls
Western Kamchatka	70	18.1	20	64.4	58	6.5	79
Olyutorskiy Bay	22	1.1	9	37.3	42	5.1	43
Eastward area of Olyutorskiy Cape	57	3.2	21	21.3	51	2.4	49

along the upper slope of the Bering Sea during winter 1982-1983. About 70% of the catch was 45-85 cm in body length (age 5-9). Nevertheless, 1984 summer research on Pacific halibut abundance showed it to be rather poor. Evidence of increased settling density of Pacific halibut was noted on the shelf and slope of the Olyutor-Navarinskiy region in summer 1985. Bottom survey and commercial trawl harvests were conducted only in unconnected areas of the western Bering Sea because of complex bottom relief. These areas proved to be the best habitat for halibut survival. In control areas of eastern Kamchatka, the average Pacific halibut caught was 30 kg in 1980, 42 kg during winter 1982-1983, and 55 kg in 1986.

The frequency of occurrence of Pacific halibut in catches near eastern Kamchatka during winter 1986-1987 was 3 times higher than in Olyutorskiy Bay, and higher than in the primary area of its commercial concentrations—the Olyutor-Navarinskiy area (Table 7). The proportion of juveniles is much higher near eastern Kamchatka.

Interannual variations of the youngest part of the population are significant in the Olyutor-Navarinskiy area, and this isn't explained only by the natural process of abundance dynamics. Most likely, the variability and degree of increase in halibut abundance in the Olyutor-Navarinskiy area is due to significant intensive settling of both mature and immature fishes from the eastern and western areas (see Figures 3 and 4). Figure 4 shows relatively high occurrence, and Figure 3 shows rapid settling of the northern area and relative abundance of juveniles west of Cape Olyutorskiy. Prespawning and postspawning halibut were observed in the Olyutor-Navarinskiy area during fall and winter 1990-1993. An evident scarcity of the younger age groups is noted in this area, except in 1991. The majority of the eggs and larvae is probably

carried west of Olyutorskiy Bay and eastern Kamchatka by the Kamchatka current, and to the east by the Navarinskiy current.

We are concerned about the intermixing of halibut stocks from Asian and U.S. waters in the Olyutor-Navarinskiy area, but the rate of individual intermingling among areas is as yet unknown. The dynamics of Pacific halibut abundance in these areas is evidently similar. Data on surveys in Bristol Bay from 1973 to 1980 indicate strong year classes in 1973-1974 and especially in 1977-1978 (Best and Hardman 1982). Judging by the age structure samples collected in the eastern Bering Sea (Table 4), year classes of 1978-1983 provided for high abundance of the present commercial stock, though all following year classes, especially 1988, were also of high productivity.

The halibut abundance decrease in the 1960s and increase in the 1980s were both observed all over the area (abundance increasing in the 1980s was also observed near western Kamchatka and the Kuril Isles). Based on the value and dynamics of the halibut catch (37,200 tons in 1958-1963, 31,300 tons by longline) (Hoag 1976), the commercial halibut stock in the area west of 175°W longitude was estimated at 25,000-30,000 tons. The stock depression was probably caused not only by cyclic natural events but also and most significantly by the nearly total harvest of spawners in the western Bering Sea and the significant harvest of spawners and recruits in the eastern Bering Sea.

During 1989-1990 over 19,000 tons of Pacific halibut were recorded only in the Olyutor-Navarinskiy region by area. Taking into account the selectivity of bottom trawls, true stock figures were 30-50% higher during that period. Unfortunately, we failed to obtain sufficient data for population stock assessments during the following years.

Conclusion

In the 1960s Pacific halibut abundance in the western Bering Sea decreased significantly due to the influence of cyclic natural events and uncontrolled catch. In the early 1980s, the number of harvested juveniles began to increase first in eastern Kamchatka and then eastward of Cape Navarin. The majority of the age 1+ juveniles of the western Bering Sea stock is assumed to concentrate in eastern Kamchatka, in Karaginskiy and Olyutorskiy bays, then migrate east of Cape Olyutorskiy. Abundance of juveniles increases on the eastern Bering Sea shelf, probably due to the feeding migration of the mature fishes. The proportion of eastern and western fishes migrating is not

known; this question demands further study by use of tagging and genetic techniques.

In 1990 target fisheries were resumed east of Cape Olyutorskiy, and in 1992 in eastern Kamchatka. Unfortunately, most of the harvested Pacific halibut have been caught during cod longline and trawl fisheries for other species and consist of immature individuals. This can cause another depression in the commercial stock.

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Abundance and Composition of Flatfish in Kachemak Bay, Alaska

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Abstract

The harvest of flatfishes from Kachemak Bay, Alaska, has generally been limited to incidental harvests during Pacific cod, halibut, and other fisheries despite a relatively high flatfish abundance. However, interest in flatfish species has increased in recent years as traditional fisheries such as salmon, crab, and sablefish have encountered biological or economic declines and shorter seasons. During October 1989, commercially important flatfish species in Kachemak Bay were sampled for the first time as part of a multispecies trawl survey by the Alaska Department of Fish and Game. Flatfish population estimates for Kachemak Bay included 14.2 million flathead sole (2,415 tonnes), 9.2 million butter sole (1,374 tonnes), 8.8 million rock sole (895 tonnes), 6.9 million arrowtooth flounder (1,559 tonnes), 1.6 million Dover sole (612 tonnes), 1.4 million rex sole (375 tonnes), 1.3 million halibut (757 tonnes), 0.6 million yellowfin sole (198 tonnes), 0.2 million starry flounder (356 tonnes), 0.1 million sand sole (62 tonnes), 0.03 million Alaska plaice (14 tonnes), and 0.01 million English sole (128 tonnes). Flatfish catch rates (kg/nm) from both the shallow (< 91 m) and deep (≥ 91 m) strata in Outer Kachemak Bay were twice that of Inner Kachemak Bay. Age composition summaries and Schnute's general four-parameter size-age growth model were presented for

arrowtooth flounder, Dover sole, and flathead sole. Arrowtooth flounder were represented by ages 0 through 4 and 6 but 1 and 3 year old fish predominated. Dover sole ranged from age 2 to 5 but age 3 and 4 fish predominated. Flathead sole ages ranged from 1 through 12 with most specimens between ages 2 and 6.

Introduction

Many traditional Alaskan salmon and crab fisheries have recently been subjected to biological or economic declines in the northwestern Gulf of Alaska (Bechtol 1994). At the same time, market conditions for groundfish species have improved because of collapses in many North Atlantic groundfish resources and a desire by many Alaskan fish processors to diversify their businesses. Greater gear efficiency has increased the economic viability in targeting groundfish, resulting in greater effort for many species that were previously limited to incidental catches (Blackburn et al. 1983; Bechtol and Morrison in press). Little is known about the abundance and distribution of flatfishes in Kachemak Bay, Alaska.

Although numerous Outer Continental Shelf (OCS) projects were initiated during the 1970s to assess marine resources off the coast of Alaska, most studies focused on salmon, shellfish, and the shallow subtidal resources. Although some OCS studies examined marine resources, little survey effort occurred in Kachemak Bay (Blackburn 1978), and few of the OCS surveys conducted in Kachemak Bay were directed at groundfish (Lees et al. 1980). Lower Cook Inlet was also surveyed in 1990 as part of the triennial bottom trawl surveys conducted in the western and central Gulf of Alaska by the National Marine Fisheries Service (NMFS), but Kachemak Bay was not included (Payne and Stark 1991). Resource assessment studies following the 1989 *Exxon Valdez* oil spill in Prince William Sound provided the first opportunity to collect basic information on a variety of resources along the northern Gulf of Alaska. A trawl survey conducted by the Alaska Department of Fish and Game (ADF&G) as part of those assessment studies provided a unique opportunity to estimate species composition and absolute abundance of commercially important fish and shellfish species in Kachemak Bay (A. Kimker, Alaska Department of Fish and Game, Homer, Alaska, personal communication). This report summarizes the flatfish species composition, biomass, and abundance estimates from that Kachemak Bay trawl survey.

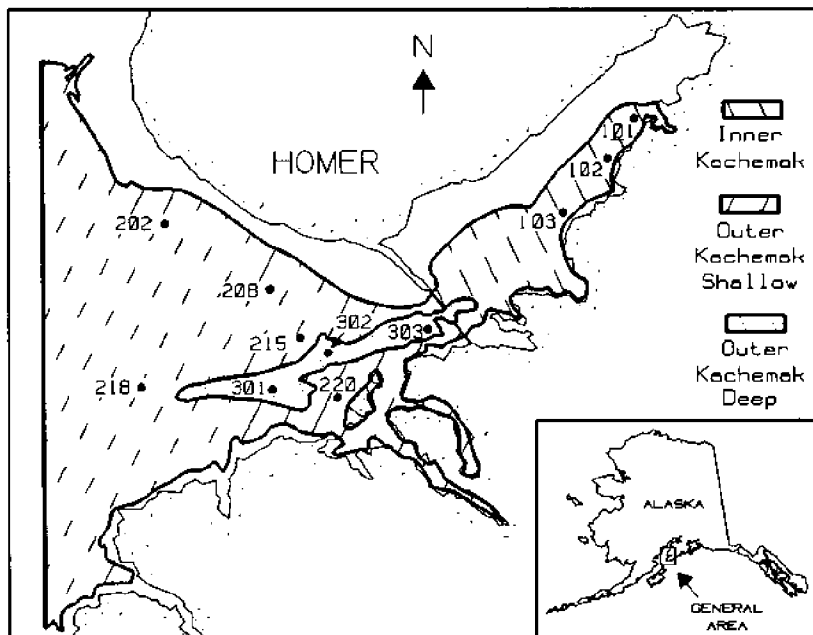


Figure 1. Study area and sample stations for October 1989 trawl survey of Kachemak Bay, Alaska.

Methods

Fish samples were collected from Kachemak Bay, an embayment centered approximately at $59^{\circ}35'N$, $151^{\circ}52'W$ in the northern Gulf of Alaska (Figure 1). The 20.1 m ADF&G research vessel *Pandalus* towed a 400-mesh eastern trawl with 364 kg, 152 cm \times 213.3 cm Nor'Eastern Astoria V trawl doors. The trawl mesh was 10.2 cm in the wings and body, 8.9 cm in the intermediate, and 3.2 cm in the cod end. With headrope and footrope lengths of 71 m and 29.0 m, the estimated fishing height and width of the trawl were 2.7 m and 12.1 m, respectively.

The survey followed a stratified random design and divided areas of Kachemak Bay deeper than 18 m (10 fathoms) into 3 strata (Figure 1). The Inner Kachemak stratum had depths between 18 and 91 m (10 and 50 fathoms) and a surface area of 35.7 square nautical miles

Table 1. Sample site and tow characteristics from the 1989 Kachemak Bay multispecies trawl survey.

Haul	1	2	3	4	5	6
Area	Outer Shallow	Outer Deep	Outer Deep	Inner Bay	Inner Bay	Inner Bay
Station number	208	301	302	101	102	105
Date	10/03	10/03	10/04	10/07	10/08	10/08
Longitude	151°41.2'	151°39.8'	151°30.3'	151°05.4'	151°09.2'	151°14.4'
Latitude	59°36.6'	59°31.4'	59°33.6'	59°43.7'	59°41.3'	59°38.9'
Heading (deg.)	270	240	45	200	210	210
Avg. depth (fm)	16	57	84	33	28	31
Duration (min)	24	27	32	24	26	27
Distance (nm)	1.0	1.0	1.0	1.0	1.0	1.0

Haul	7	8	9	10	11
Area	Outer Shallow	Outer Shallow	Outer Shallow	Outer Shallow	Outer Deep
Station number	202	218	215	220	303
Date	10/09	10/09	10/10	10/10	10/25
Longitude	151°50.8'	151°51.3'	151°36.8'	151°34.1'	151°28.2'
Latitude	59°39.8'	59°30.5'	59°33.4'	59°30.9'	59°33.8'
Heading (deg.)	195	250	30	230	220
Avg. depth (fm)	14	35	48	53	90
Duration (min)	21	25	24	25	27
Distance (nm)	0.6	1.0	1.0	1.0	1.0

Note: See text for specific descriptions of areas.

(nm²). The Outer Kachemak Shallow stratum was also between 18 and 91 m deep and was the largest in area at 194.0 nm². The Outer Kachemak Deep stratum had depths ≥ 91 m (50 fathoms) and was the smallest in area at 17.3 nm². Table 1 lists the individuals tows within each stratum. Within each stratum, 6.25 nm² (2.5 nm × 2.5 nm) were delineated within bottom contour constraints. Stations were selected randomly and tow paths were based on the vessel captain's determination of trawlable substrate from NOAA nautical charts and hydro-acoustic assessment of the bottom contour, as well as tide and weather constraints. A total of 11 tows were made between 3 October and 25 October 1989, with three tows each in the Inner Kachemak and

Table 2. Flatfish species captured during the October 1989 trawl survey of Kachemak Bay, Alaska.

Common name	Scientific name
Alaska plaice	<i>Pleuronectes quadrituberculatus</i>
Arrowtooth flounder	<i>Atheresthes stomias</i>
Butter sole	<i>Isopsetta isolepis</i>
Dover sole	<i>Microstomus pacificus</i>
English sole	<i>Parophrys vetulus</i>
Flathead sole	<i>Hippoglossoides elassodon</i>
Halibut	<i>Hippoglossus stenolepis</i>
Rex sole	<i>Glyptocephalus zachirus</i>
Rock sole	<i>Lepidopsetta bilineata</i>
Sand sole	<i>Psetichthys melanostictus</i>
Starry flounder	<i>Platichthys stellatus</i>
Yellowfin sole	<i>Limanda aspera</i>

Outer Kachemak Deep strata and five tows in the Outer Kachemak Shallow stratum. For any tow in which the trawl became tangled in the substrata to the extent that the trawl and the vessel were stopped, the tow was deemed unsuccessful, the catch was discarded, and the tow was repeated. Each station was sampled by a 1.0-nm tow, except for station 2-2 which was sampled by a 0.6-nm tow because the bottom terrain reduced the likelihood of a successful long tow.

Each successful tow was brought aboard, weighed, and all crabs and large fish were counted and weighed or measured. For tows totaling < 450 kg, the remaining catch was sorted by species, counted, and weighed or measured (Hart 1973; Lee 1979; Kramer and O'Connell 1986). For tows \geq 450 kg, the composition of the smaller species was extrapolated from a 2-bushel subsample which was sorted, counted, and weighed by species. All tows were expressed in catch per nautical mile and later converted to biomass and abundance estimates for each stratum, and for all of Kachemak Bay. The species of flatfish caught during the October 1989 survey are listed in Table 2. Most halibut were measured for length, and weight was later estimated from a standardized length-weight key (Quinn et al. 1983). For each tow, length, sex, and sexual maturity were recorded for 20-50 individual arrowtooth flounder, Dover sole, flathead sole, and rex sole. Ages for these samples were later determined in the laboratory from

otoliths preserved in a glycerin solution (Chilton and Beamish 1983). Length frequency data were also collected for halibut, rex sole, and rock sole.

Schnute's (1981) general four-parameter model was used to examine length-at-age relationships for arrowtooth flounder, Dover sole, and flathead sole, and weight-at-age for Dover sole:

$$y_t = [y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}}]^{1/b}, \quad (1)$$

where y_t = length or weight at age t , t_1 = youngest observed age, t_2 = oldest observed age. The model parameters to be estimated were: y_1 = size at t_1 , y_2 = size at t_2 , a , and b . Initial values were y_1 = observed size at t_1 , y_2 = observed size at t_2 , $a = 0.2$, $b = 1.0$. Special cases of this general model included the von Bertalanffy curve where $a > 0$, $b > 0$; the logistic curve where $a > 0$, $b = -1$; and the exponential curve where $a < 0$, $b = 1$.

Catch by area

Let $c_{a,i}$ = catch, either number of individuals or weight per nautical mile, from the i th tow in area a , and n_a = number of tows within area a . Mean catch by species per nautical mile by area, \bar{c}_a , was

$$\bar{c}_a = \frac{\sum_{i=1}^{n_a} c_{a,i}}{n_a}. \quad (2)$$

The associated standard error, which did not account for tow measurement error when the total catch was extrapolated from a single 2-bushel subsample, was

$$s_a = \sqrt{\frac{\sum_{i=1}^{n_a} (c_{a,i} - \bar{c}_a)^2}{n_a - 1} / \frac{1}{n_a}}. \quad (3)$$

Total catch within a stratum, T_a , either in numbers of individuals or weight by species, was calculated from the mean catch by area, \bar{c}_a , the surface area, A_a , in square nautical miles, and a factor of 151.9 (to extrapolate from the area swept by the trawl) as

$$T_a = 151.9 \bar{c}_a A_a. \quad (4)$$

The associated standard error was

$$s_{T_a} = \sqrt{(151.9A)^2 s_a^2}$$

Assuming normally distributed measurement errors, lower and upper 95% confidence limits, which did not account for measurement errors when total catch was extrapolated from single 2-bushel subsamples, were:

$$T_a - 1.96s_{T_a} \leq T_a \leq T_a + 1.96s_{T_a} \tag{6}$$

Catch for all areas combined

For the combined areas of Kachemak Bay, mean catch by species per nautical mile, C , weighted by the surface area of each stratum, A_a , was

$$C = \frac{\sum_{a=1}^3 \bar{c}_a A_a}{A} \tag{7}$$

where A = the combined surface area. The standard error of C , either in numbers of individuals or by weight, was similar to that given by Sokal and Rohlf (1969):

$$s_C = \sqrt{\sum_{a=1}^3 \left(\frac{A_a}{A}\right)^2 s_a^2} \tag{8}$$

Total catch, T , by species in numbers of individuals or weight for the entire study area was calculated from C and the combined surface area, A , in square nautical miles:

$$T = 151.9CA \tag{9}$$

The associated variance was

$$s_T = \sqrt{(151.9A)^2 s_C^2}$$

Lower and upper 95% confidence limits, which do not account for measurement errors when total catch was extrapolated from 2-bushel subsamples, were

$$T - 1.96s_T \leq T \leq T + 1.96s_T \tag{11}$$

Results

Three successful tows were made in the Inner Kachemak, five in the Outer Kachemak Shallow, and three in the Outer Kachemak Deep

Table 3. Flatfish catches (fish per nautical mile) by species and trawl station in Kachemak Bay during October 1989.

Species	Inner Kachemak Bay					Outer Kachemak Shallow					Outer Kachemak Deep				
	Station no.					Station no.					Station no.				
	101	102	105	Mean	202	208	215	218	220	Mean	301	302	303	Mean	
Alaska plaice	0	0	1	0	0	0	5	0	0	1	0	0	0	0	
Arrowtooth flounder	0	7	91	33	0	111	358	25	569	213	368	81	10	153	
Butter sole	0	0	0	0	0	936	0	618	0	311	0	0	0	0	
Dover sole	0	0	18	6	0	19	104	0	73	39	324	87	16	142	
English sole	0	0	0	0	0	0	1	0	1	0	0	0	0	0	
Flathead sole	336	54	625	338	0	26	407	0	1,586	404	179	293	50	174	
Hallbut	22	15	13	17	150	14	1	36	5	41	11	2	1	5	
Rex sole	0	0	14	5	0	38	66	1	60	33	444	4	0	149	
Rock sole	0	4	18	7	65	1,406	0	18	1	298	0	0	0	0	
Sand sole	0	1	0	0	0	18	0	5	0	5	0	0	0	0	
Starry flounder	39	12	5	19	0	19	0	0	0	4	0	0	0	0	
Yellowfin sole	59	32	57	49	0	56	0	0	0	11	0	0	0	0	
Total	457	125	842	475	215	2,644	942	703	2,296	1,360	1,326	467	77	623	

strata (Table 1). A total of 1,199 specimens were collected, with 600 sampled for age, sex, and size and the remaining 599 for lengths only. Halibut occurred most frequently and were caught in all successful tows. Arrowtooth flounder and flathead sole ranked second in frequency of occurrence, both being caught in 82% of the tows.

The mean catch rate in numbers of flatfish (all species) was greatest in Outer Kachemak Shallow, at 1,360 fish/nm, followed by Outer Kachemak Deep, at 623 fish/nm, and Inner Kachemak at 475 fish/nm (Table 3). The mean catch rate by species was greatest for flathead sole at 133 fish/nm. A maximum of 1,586 flathead sole/nm occurred at a single station in Outer Kachemak Shallow.

An estimated 44.3 million flatfish were in Kachemak Bay during October 1989 (Table 4). Flathead sole were the most abundant species at 14.2 million fish, followed by butter sole at 9.2 million, rock sole at 8.8 million, and arrowtooth flounder at 6.9 million. More than 80% of the Kachemak Bay flatfish population was in Outer Kachemak Shallow where arrowtooth flounder and butter, flathead, and rock soles were most abundant. Within Inner Kachemak, flathead sole was most abundant; arrowtooth flounder and Dover, flathead, and rex soles were most abundant in Outer Kachemak Deep.

The biomass of fish caught per nautical mile was greatest for flathead sole with an average of 64.3 kg/nm across all strata. The mean biomass catch rate of all species was greater in Outer Kachemak Deep (259 kg/nm) and Outer Kachemak Shallow (249 kg/nm) than within Inner Kachemak (133 kg/nm; Table 5).

The aggregate flatfish biomass in Kachemak Bay was estimated to be 8,746 tonnes (Table 6). Flathead sole (2,415 tonnes) predominated the Kachemak Bay biomass, followed by arrowtooth flounder (1,559 tonnes) and butter sole (1,374 tonnes). Most of the flatfish biomass was concentrated in the Outer Kachemak Shallow stratum where arrowtooth flounder, butter sole, and flathead sole comprised over half of the estimated biomass. Within the Inner Kachemak stratum, flathead sole, halibut, starry flounder, and yellowfin sole contributed most of the biomass. Within the Outer Kachemak Deep stratum, arrowtooth flounder and Dover, flathead, and rex soles provided most of the biomass.

Arrowtooth flounder ranged from ages 0 through 6 but were primarily ages 1 to 3; no age 5 fish were in the samples (Table 7; Figure 2). Arrowtooth flounder averaged 276 mm in length, with larger mean lengths observed for Outer Kachemak Deep stations 301, 302, and 303. Dover sole ranged from ages 2 through 5 but were primarily

Table 4. Estimated flatfish abundance ($\times 1,000$) with 95% confidence limits for areas of Kachemak Bay sampled during October 1989.

Species	Inner Kachemak stratum			Outer Kachemak Shallow stratum			Outer Kachemak Deep stratum			All strata combined		
	1,000	95% C.I.		1,000	95% C.I.		1,000	95% C.I.		1,000	95% C.I.	
	Fish	Lower	Upper	Fish	Lower	Upper	Fish	Lower	Upper	Fish	Lower	Upper
Alaska plaice	2	0	5	29	0	85	0	0	0	31	0	87
Arrowtooth flounder	177	0	488	6,271	0	12,587	403	0	968	6,851	502	13,200
Butter sole	0	0	0	9,161	0	20,533	0	0	0	9,161	0	20,533
Dover sole	33	0	96	1,155	0	2,372	375	0	856	1,562	252	2,873
English sole	0	0	0	12	0	26	0	0	0	12	0	26
Flathead sole	1,838	83	3,592	11,902	0	29,556	458	96	821	14,198	0	31,943
Halibut	91	61	120	1,214	0	2,824	12	0	29	1,317	0	2,927
Rex sole	26	0	77	975	0	1,788	393	0	1,154	1,395	280	2,509
Rock sole	40	0	98	8,785	0	24,805	0	0	0	8,825	0	24,845
Sand sole	2	0	5	138	0	345	0	0	0	140	0	347
Starry flounder	101	0	212	110	0	326	0	0	0	211	0	453
Yellowfin sole	268	175	361	330	0	976	0	0	0	598	0	1,251
Total	2,577			40,082			1,642			44,301		

Table 5. Flatfish catch rates (kg per nautical mile) by species and Kachemak Bay trawl station during October 1989.

Species	Inner Kachemak					Outer Kachemak Shallow					Outer Kachemak Deep			
	Station no.					Station no.					Station no.			
	101	102	105	Mean	202	208	215	218	220	Mean	301	302	303	Mean
Alaska plaice	0	0	2	1	0	0	2	0	0	0	0	0	0	0
Arrowtooth flounder	0	1	9	3	0	22	50	3	160	47	122	45	5	58
Butter sole	0	0	0	0	0	106	0	127	0	47	0	0	0	0
Dover sole	0	0	3	1	0	1	44	0	29	15	134	49	8	64
English sole	0	0	0	0	0	20	0	0	1	4	0	0	0	0
Flathead sole	34	16	136	62	0	3	55	0	266	65	38	127	23	63
Hallbut	28	22	18	22	31	5	2	47	16	20	33	5	4	14
Rex sole	0	0	0	0	0	2	19	0	15	7	181	2	0	61
Rock sole	0	0	0	0	44	102	0	5	1	30	0	0	0	0
Sand sole	0	0	0	0	0	8	0	3	0	2	0	0	0	0
Starry flounder	49	14	7	23	0	39	0	0	0	8	0	0	0	0
Yellowfin sole	26	15	20	20	0	15	0	0	0	3	0	0	0	0
Total	137	68	196	133	75	324	173	185	488	249	508	229	40	259

Table 6. Estimated flatfish biomass (tonnes) with 95% confidence limits for areas of Kachemak Bay sample during October 1989.

Species	Inner Kachemak stratum			Outer Kachemak Shallow stratum			Outer Kachemak Deep stratum			All strata combined		
	1,000 Fish	95% C.I.		1,000 Fish	95% C.I.		1,000 Fish	95% C.I.		1,000 Fish	95% C.I.	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Alaska plaice	3	0	10	11	0	32	0	0	0	14	0	36
Arrowtooth flounder	19	0	49	1,388	0	3,101	152	0	329	1,559	0	3,281
Butter sole	0	0	0	1,374	0	3,035	0	0	0	1,374	0	3,035
Dover sole	5	0	15	439	0	971	168	0	360	612	45	1,178
English sole	0	0	0	128	0	360	0	0	0	128	0	360
Flathead sole	336	0	734	1,915	0	4,885	165	0	333	2,415	0	5,417
Halibut	121	91	152	599	116	1,082	37	0	85	757	0	1,244
Rex sole	1	0	2	214	0	443	160	0	469	375	0	760
Rock sole	2	0	3	893	0	2,033	0	0	0	895	0	2,034
Sand sole	1	0	2	62	0	148	0	0	0	62	0	149
Starry flounder	126	0	265	230	0	681	0	0	0	356	0	828
Yellowfin sole	110	74	146	88	0	261	0	0	0	198	22	375
Total	724			7,340			682			8,746		

Table 7. Length-at-age of arrowtooth flounder caught during October 1989 in Kachemak Bay, Alaska.

	Age	Length (mm)		Sample size	Percent of total
		Mean	SD		
Station 302	2	297	41.6	3	10.7
	3	354	41.5	16	57.1
	4	399	50.9	9	32.1
Total		363	53.0	28	100.0
Station 102	1	178	12.6	4	57.1
	2	325	7.1	2	28.6
	4	390	0.0	1	14.3
Total		250	93.5	7	100.0
Station 105	1	192	15.2	15	41.7
	2	218	39.6	13	36.1
	3	314	65.5	7	19.4
	4	360	0.0	1	2.8
Total		230	62.8	36	100.0
Station 218	0	97	5.8	3	11.5
	1	164	20.9	17	65.4
	2	298	9.6	4	15.4
	3	340	28.3	2	7.7
Total		190	74.0	26	100.0
Station 215	1	206	10.8	34	60.7
	2	278	30.1	18	32.1
	3	338	25.0	4	7.1
Total		238	47.8	56	100.0
Station 220	1	210	8.2	4	7.0
	2	302	43.6	17	29.8
	3	346	31.1	28	49.1
	4	406	67.8	7	12.3
	6	380	0.0	1	1.8
Total		331	60.5	57	100.0
Station 303	2	300	14.1	2	22.2
	3	346	45.1	5	55.6
	4	435	21.2	2	22.2
Total		356	59.2	9	100.0
Combined stations	0	97	5.8	3	1.4
	1	192	22.3	74	33.8
	2	276	48.0	59	26.9
	3	344	39.8	62	28.3
	4	403	52.8	20	9.1
Combined total	6	380	0.0	1	0.5
		276	84.4	219	100.0

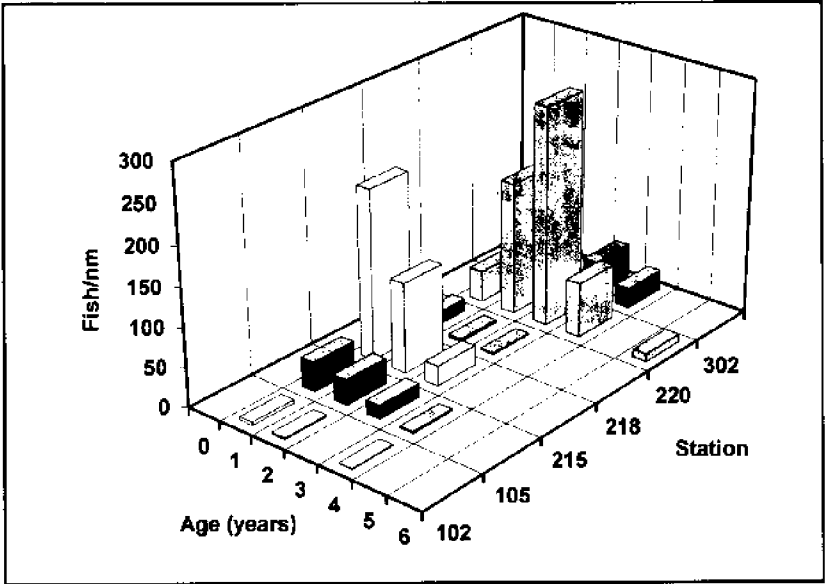


Figure 2. Arrowtooth flounder abundance (fish/nm) and age composition by Kachemak Bay sample station during 1989.

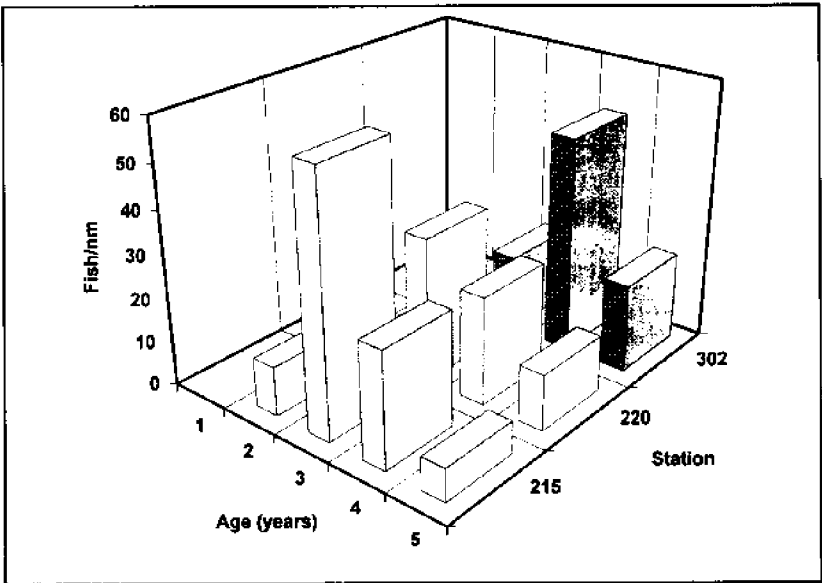


Figure 3. Dover sole abundance (fish/nm) and age composition by Kachemak Bay sample station during 1989.

Table 8. Length-at-age of Dover sole caught during October 1989 in Kachemak Bay, Alaska.

	Age	Length (mm)		Sample size	Percent of total
		Mean	SD		
Station 302	3	324	20.9	6	20.0
	4	350	22.3	17	56.7
	5	384	19.1	7	23.3
Total		353	29.0	30	100.0
Station 215	2	298	33.1	6	10.9
	3	327	25.3	31	56.4
	4	342	29.7	14	25.5
	5	370	29.4	4	7.3
Total		331	31.5	55	100.0
Station 215	2	290	28.3	2	3.2
	3	328	21.5	28	45.2
	4	354	18.6	21	33.9
	5	381	28.4	11	17.7
Total		345	31.0	62	100.0
Combined stations	2	296	30.2	8	5.4
	3	327	23.1	65	44.2
	4	349	23.2	52	35.4
	5	380	25.3	22	15.0
Combined total		341	31.8	147	100.0

ages 3 and 4 (Table 8; Figure 3). Dover sole averaged 341 mm in length and 545 g in weight. Individual weights were not measured for other species. Flathead sole ages 1 through 12 were found in the samples but most were between ages 2 and 6 (Table 9; Figure 4).

Schnute's (1981) general four-parameter size-age growth model produced different growth curves for each species. Arrowtooth flounder length-age was best described by a logistics type curve (Figure 5). In our initial fit of the arrowtooth flounder data, a was positive and b was -0.56 ; b was constrained to -1 in our final fit as is required for the logistic curve. The Dover sole length-age relationship appeared to be an exponential curve for the ages examined as a was negative and $b = 1$ in our first and only fit (Figure 6). Dover sole weight-age relationship also appeared to be an exponential curve (Figure 7). In our initial fit, a was negative and $b = 1.11$; b was con-

Table 9. Length-at-age of flathead sole caught during October 1989 in Kachemak Bay, Alaska.

	Age	Length (mm)		Sample size	Percent of total	
		Mean	SD			
Station 101	1	130	0.0	1	3.6	
	2	193	19.9	15	53.6	
	3	258	11.7	6	21.4	
	4	270	0.0	1	3.6	
	6	280	0.0	1	3.6	
	7	315	7.1	2	7.1	
	9	390	0.0	1	3.6	
	13	380	0.0	1	3.6	
Total		233	63.1	28	100.0	
Station 102	2	188	32.4	12	22.2	
	3	245	28.1	6	11.1	
	4	267	33.3	6	11.1	
	5	285	52.8	10	18.5	
	6	320	43.4	6	11.1	
	7	335	85.4	4	7.4	
	8	368	61.8	4	7.4	
	9	400	0.0	1	1.9	
	10	380	56.6	2	3.7	
	11	380	56.6	2	3.7	
	12	320	0.0	1	1.9	
	Total		281	76.9	54	100.0
Station 105	2	220	0.0	1	2.5	
	3	253	33.5	7	17.5	
	4	286	31.0	13	32.5	
	5	298	40.7	6	15.0	
	6	340	66.8	4	10.0	
	8	375	21.2	2	5.0	
	9	343	20.8	3	7.5	
	10	375	21.2	2	5.0	
	11	390	0.0	1	2.5	
	13	420	0.0	1	2.5	
	Total		305	56.0	40	100.0
	Station 218	3	250	0.0	1	20.0
		6	350	0.0	1	20.0
9		390	26.5	3	60.0	
Total		356	63.5	5	100.0	
Station 215	1	180	60.8	3	5.4	
	2	175	55.4	6	10.7	
	3	228	38.6	19	33.9	
	4	257	24.5	11	19.6	
	5	264	13.0	8	14.3	

Table 9. (continued.)

	Age	Length (mm)		Sample size	Percent of total
		Mean	SD		
	6	299	14.6	7	12.5
	7	300	0.0	1	1.8
	9	270	0.0	1	1.8
Total		242	49.2	56	100.0
Station 220	1	130	0.0	1	1.8
	3	260	55.0	9	16.1
	4	270	34.0	10	17.9
	5	293	22.1	10	17.9
	6	309	28.4	11	19.6
	7	323	16.3	6	10.7
	8	318	21.4	6	10.7
	9	300	0.0	1	1.8
	10	300	84.9	2	3.6
Total		290	45.0	56	100.0
Station 303	2	340	0.0	1	2.0
	4	295	7.1	2	4.1
	5	298	34.3	6	12.2
	6	325	46.5	4	8.2
	7	334	21.3	9	18.4
	8	369	32.7	8	16.3
	9	359	28.0	8	16.3
	10	348	22.2	4	8.2
	11	383	9.6	4	8.2
	12	393	20.8	3	6.1
Total		346	38.5	49	100.0
Combined stations	1	160	51.0	5	1.7
	2	193	40.9	35	12.2
	3	244	38.9	48	16.7
	4	272	30.8	43	14.9
	5	287	36.2	40	13.9
	6	315	37.8	34	11.8
	7	328	37.0	22	7.6
	8	354	41.5	20	6.9
	9	357	38.6	18	6.3
	10	350	47.6	10	3.5
	11	383	24.3	7	2.4
	12	375	40.4	4	1.4
	13	400	28.3	2	0.7
Combined total		286	66.8	288	100.0

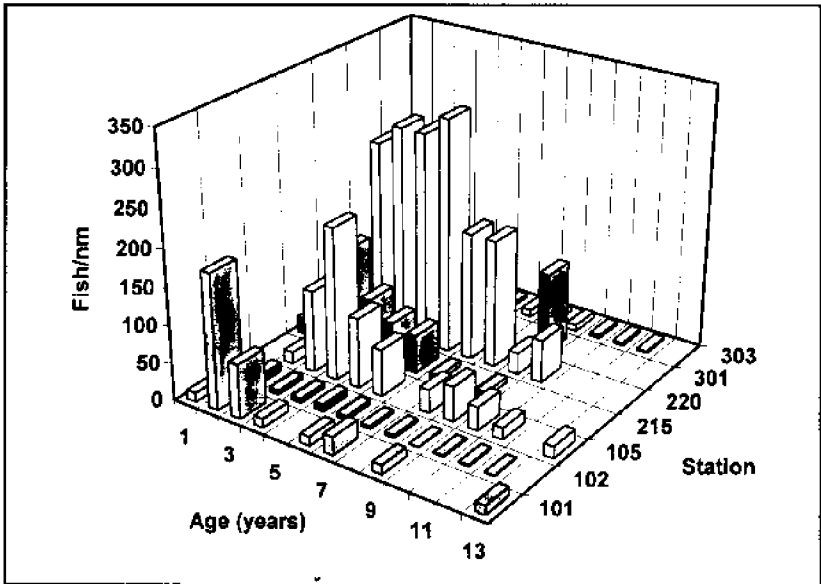


Figure 4. Flathead sole abundance (fish/nm) and age composition by Kachemak Bay sample station during 1989.

strained to a value of 1 in our final fit. The flathead sole length-age model was a von Bertalanffy type curve where a and b were both positive and initial parameter values were retained as the final values (Figure 8).

Length frequency data indicated halibut were generally larger than 270 mm except for Outer Kachemak stations 202 and 208 where a greater frequency of smaller fish were found (Figure 9). Across all stations, halibut lengths ranged from 90 to 1,200 mm. Most of the rex sole length samples were from one station where fish ranged from 240 to 410 mm (Figure 10). Rock sole from Outer Kachemak Shallow ranged from 80 to 440 mm, although there appeared to be segregation by size between stations (Figure 11).

Discussion

Halibut were caught in 100% of our tows versus 68% of the tows by Blackburn (1978) and 67% of the successful NMFS tows (Payne and Stark 1991). Our study found flathead sole to be the predominant

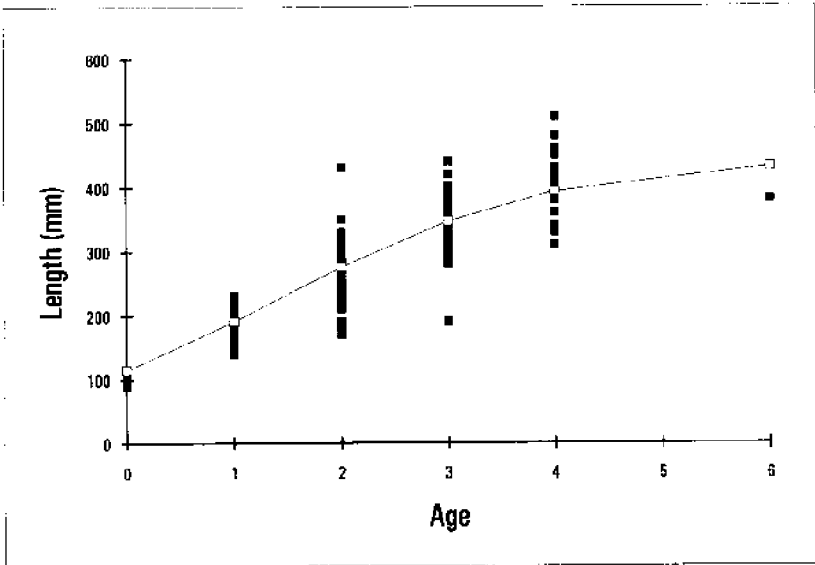


Figure 5. Schnute's general four-parameter length-age model for arrowtooth flounder in Kachemak Bay describes a logistic growth curve where $a = 0.78$, $b = -1.00$, $y_1 = 114.30$, and $y_2 = 432.18$.

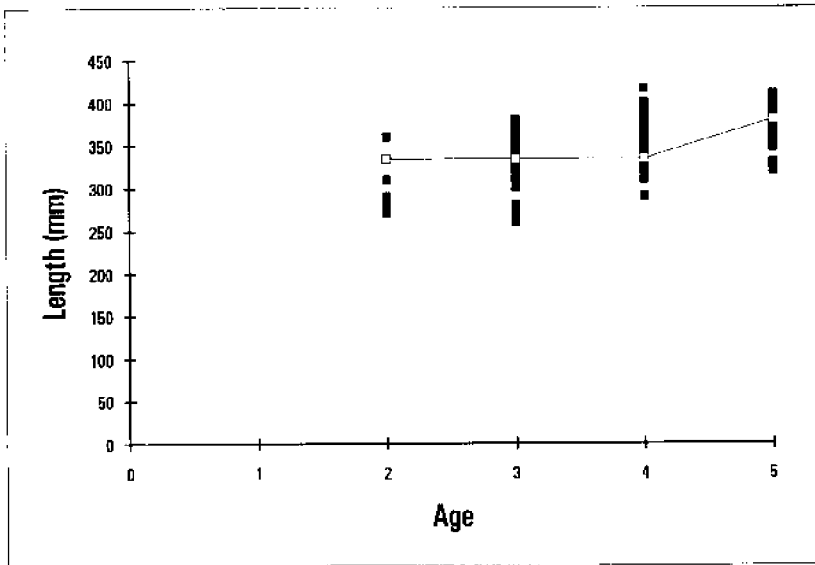


Figure 6. Schnute's general four-parameter length-age model for Dover sole in Kachemak Bay describes an exponential growth curve where $a = 112.14$, $b = 1.00$, $y_1 = 334.26$, and $y_2 = 379.86$.

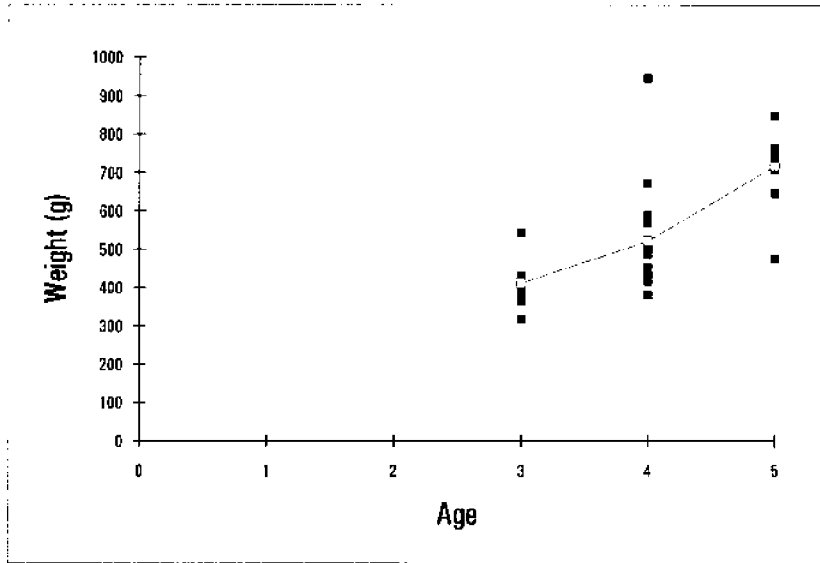


Figure 7. Schnute's general four-parameter weight-age model for Dover sole in Kachemak Bay describes an exponential growth curve where $a = -0.58$, $b = 1.00$, $y_1 = 412.13$, and $y_2 = 719.29$.

flatfish species in Kachemak Bay, Alaska, with arrowtooth flounder ranked second in both abundance and biomass (Tables 3-6). In contrast, flathead sole was not predominant in a NMFS survey involving six tows in lower Cook Inlet during August 1990 (Payne and Stark 1991). Instead, the NMFS study found arrowtooth flounder as the predominant flatfish biomass in two deep water tows, followed by halibut, Dover sole, and rex sole, whereas halibut predominated the shallow tows, followed by starry flounder, rock sole, and Alaska plaice.

The average catch rate (kg/nm) of flatfish from the shallow NMFS tows was < 8% of that from the deep tows. Our study, on the other hand, found similar average catch rates in the Outer Kachemak Deep and Outer Kachemak Shallow strata. The Inner Kachemak stratum catch rates were nearly half that of Outer Kachemak (Table 5). Our more consistent catch rates relative to the NMFS study are mainly attributed to flathead sole catches which were relatively consistent across all areas. In addition, greater catch rates of starry flounder and yellowfin sole moderated a lack of arrowtooth flounder in the Inner Kachemak stratum.

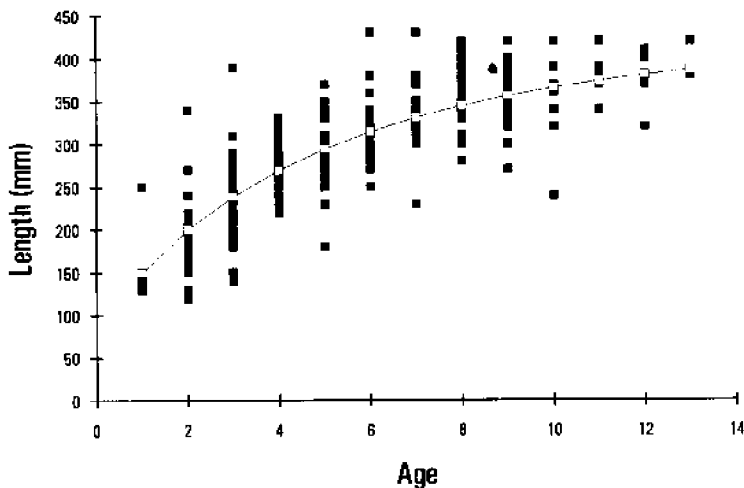


Figure 8. Schnute's general four-parameter length-age model for flathead sole in Kachemak Bay describes a von Bertalanffy growth curve where $a = 0.17$, $b = 1.46$, $y_1 = 149.87$, and $y_2 = 386.60$.

Blackburn's (1978) 58 otter trawl tows made during the summer of 1976 and 18 otter hauls made during March 1977 found yellowfin sole to be the most abundant flatfish, followed by rock sole and halibut. In both our surveys and those conducted by NMFS, yellowfin sole was generally found at depths < 35 fathoms (64 m), including all the Inner Kachemak stratum tows. This is consistent with observations in the eastern Bering Sea that yellowfin sole tend to be at depths > 50 fathoms (91 m) in winter and < 50 fathoms (91 m) in summer (Wilderbuer et al. 1992). It is notable that the location of greatest yellowfin sole abundance during Blackburn's Cook Inlet study corresponded to the location of a relatively intense, but short-term, commercial fishery for this species in the mid-1980s (unpublished data).

The growth curves developed by Schnute's general four-parameter model represent an initial analysis of size-at-age for the available data. The von Bertalanffy curve described for flathead sole appeared to be a reasonable fit to the data (Figure 8). On the other hand, the Dover sole size-age curves, especially the length-age curve, were of limited usefulness in describing the size-age relationships because so few

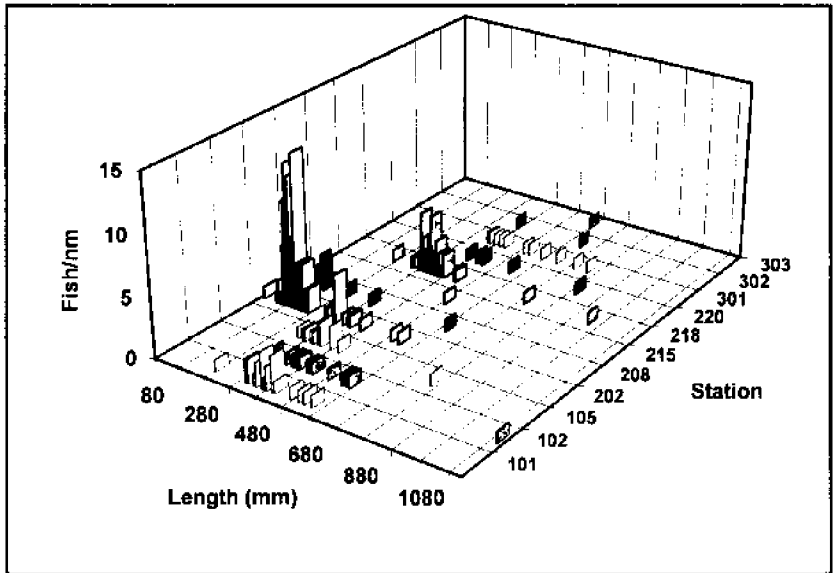


Figure 9. Halibut length frequency by Kachemak Bay sample station during 1989.

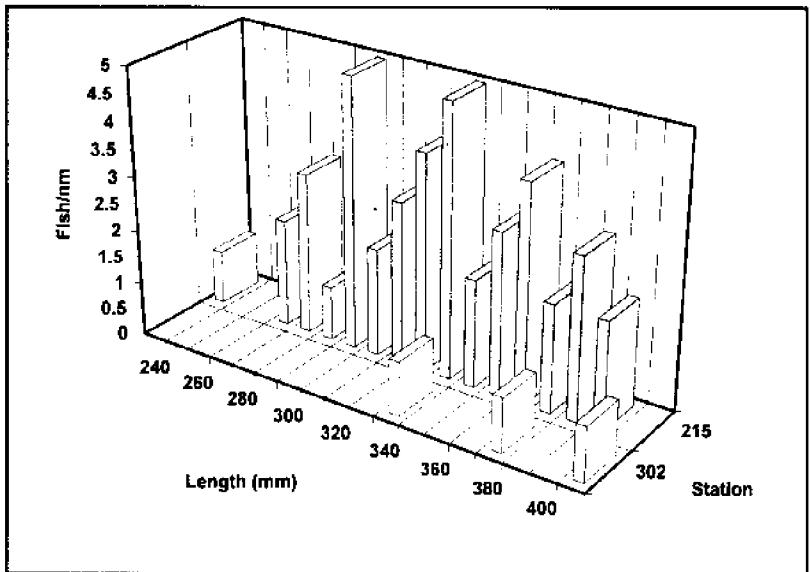


Figure 10. Rex sole length frequency by Kachemak Bay sample station during 1989.

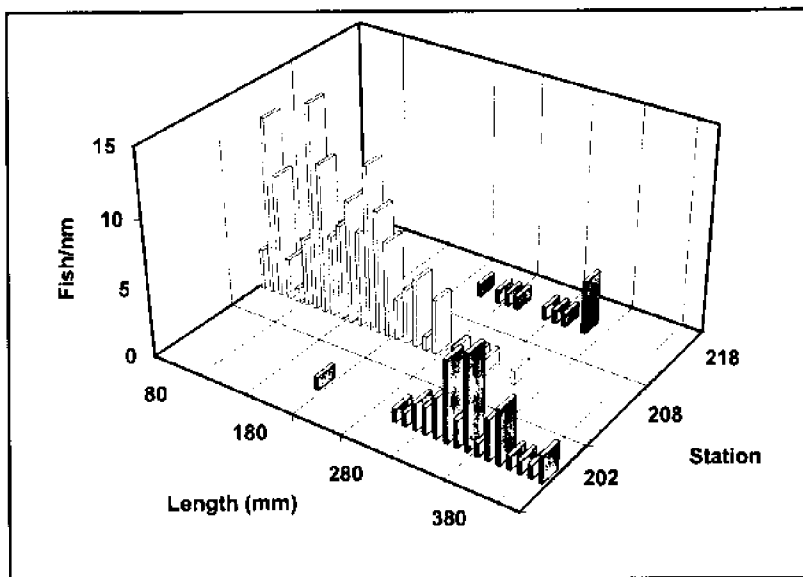


Figure 11. Rock sole length frequency by Kachemak Bay sample station during 1989.

ages were represented (Figures 6 and 7). Larger sample sizes over a wider range of ages is needed to adequately model the growth characteristics of Dover sole.

While several studies have examined bias associated with the use of trawl gear, trawl gear remains one of the more comprehensive and least selective gear types for resource assessment (Klein 1986; Dickson 1993). Our study did not take gear bias into account. In addition, flatfish resources at depths < 18 m were not examined in this study (Figure 1). For the area surveyed, the variation in abundance and biomass, both between strata and between stations within strata, and as evidenced by the wide 95% confidence intervals, indicated patchy distributions for most flatfish species (Tables 3-6). Figures 9 and 11 also provided evidence of station-specific size distributions for halibut and rock sole. Studies emphasizing habitat use are needed to better understand flatfish production and distribution in this area.

Conclusions

This study advanced our understanding of flatfish in nearshore areas. Because halibut has produced the only major flatfish fishery in

southcentral Alaska, little was known about other flatfish in this area. Concerns about the impacts of fishing mortality on low-value, high-volume groundfish species, such as flatfish, continue to increase (Pacific Associates 1994). Fishing fleets are increasingly capable of removing surplus production, and the removal is often poorly defined for species that are not retained. This study provided a "snapshot" of the flatfish in Kachemak Bay, Alaska. However, surplus production was not determined, and the flatfish contribution to the Kachemak Bay resource energy budget remains unknown. Although marine ecosystems are rarely static, having a view of the past will lead to a better understanding of how an ecosystem evolves and a better evaluation of potential "risk" of a particular fishing strategy. While unveiling many new questions about the interactions and distributions of flatfish resources, this study will provide input into future management decisions and direction for future studies.

Acknowledgments

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Characteristics and Trends in the Recreational Halibut Fishery of Southcentral Alaska, 1991-1993

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Abstract

A major recreational fishery has developed for Pacific halibut *Hippoglossus stenolepis* in southcentral Alaska over the last 20 years. Harvest in the International Pacific Halibut Commission Regulatory Area 3A increased from about 18,000 fish in 1977 to 225,000 fish in 1993. This fishery accounted for about 60% (by weight) of recreational halibut landings on the entire North American west coast in 1992. Lower Cook Inlet fisheries accounted for about 80% of the south-central Alaska harvest in recent years. Area 3A anglers released 32-49% of the halibut they caught during the period 1991-1993. Growth in the fishery necessitated collection of recreational harvest data for accurate stock assessment. Most of the sport harvest from the major ports of Kodiak, Homer, Seward, and Valdez was 5-15 years old and 50-170 cm long. Females dominated the harvest at all ports. Seasonal trends in harvest data suggested onshore-offshore movement of adult fish in Cook Inlet. Anglers on charter boats accounted for the majority of harvest at all ports except Kodiak. Halibut was the primary species targeted by bottomfish anglers, and most halibut were taken using bait. Observed differences in age, size, and sex composition among ports suggest the existence of localized stocks, subpopulations, or aggregations that are subject to varying exploitation rates. As stock biomass declines and sport harvest increases, management concerns include size limits for the sport fishery, localized depletion of stocks,

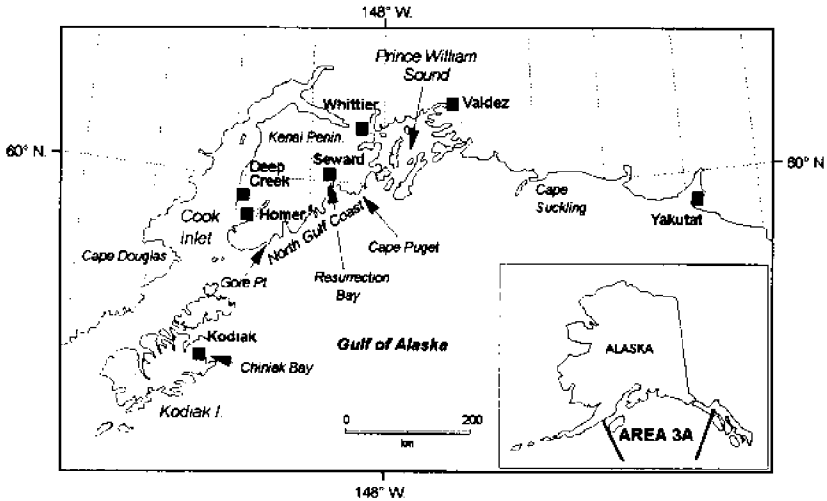


Figure 1. Coastal waters and major ports of recreational halibut landings in IPHC Regulatory Area 3A.

allocation of harvest among user groups, and increased competition on fishing grounds.

Introduction

Pacific halibut *Hippoglossus stenolepis* are distributed along the west coast of North America from southern California to western Alaska (IPHC 1987). Abundance is highest in the central Gulf of Alaska near Kodiak Island and the Kenai Peninsula (Trumble et al. 1993), adjacent to the most densely developed and populated region of Alaska. Because halibut are large, desirable food fish that are relatively enjoyable and easy to catch in nearshore waters, a major recreational fishery has developed in southcentral Alaska. The primary waters fished include Prince William Sound, Cook Inlet, and the Gulf of Alaska from Kodiak to Cape Suckling (Figure 1). Recent sport harvests in this area made up about 70% (in number) of the total Alaskan sport halibut harvest (Mills 1993, 1994) and about 60% (by weight) of the sport halibut harvest for the entire North American west coast (Blood 1994a).

The halibut sport fishery and regulatory structure have developed largely within the last 20 years. Although the commercial fishery of

southcentral Alaska escalated in the 1920s and 1930s, recreational fishing for halibut at that time was practically nonexistent. Skud (1975) estimated the total Alaskan sport harvest at only 10,000 fish annually, and did not consider the sport fishery an important source of removals. The sport fishery was not officially recognized or regulated by the International Pacific Halibut Commission (IPHC) until 1973 and regulations were not adopted by the State of Alaska until 1981. The Alaska sport fishery is restricted by daily bag and possession limits of 2 and 4 halibut per person and is closed during January. Although the commercial fishery is subject to an 81 cm (32 inch) minimum size limit, there is no minimum size limit for the sport fishery.

The recreational fishery is of vital economic importance to southcentral Alaska. Over 470,000 angler-days of fishing effort were expended in this area for all marine finfishes in 1993 (Mills 1994). The proportion of fishing effort spent targeting halibut is unknown, but more halibut were harvested than salmon, and halibut made up 45% (in number) of the marine finfish harvest in 1993. Although similar data are not available for recent years, halibut were the target species for nearly 11% of all resident and 14% of all nonresident fishing trips in southcentral Alaska in 1986 (Jones and Stokes 1987). The same study showed that anglers spent \$18.6 million to harvest 85,200 halibut in Cook Inlet fisheries, and indicated a willingness to pay an additional \$25.2 million to ensure the continued availability of halibut fishing opportunities. The charter boat industry is an economically important component of the fishery and can have great impacts locally. For example, the Homer charter boat industry generated \$9.1 million in gross income and an equivalent of 64 full-time, year-round jobs in this small community in 1985 (Coughenower 1986).

Responsibility for management of the Pacific halibut resource and fishery rests with the IPHC and the North Pacific Fishery Management Council (NPFMC). The IPHC manages Pacific halibut in state and federal waters of Alaska for optimum sustained yield under authority of the Halibut Convention of 1953 and its 1979 Protocol. The IPHC annually estimates stock biomass and other population and fishery characteristics and determines allowable harvest using a constant exploitation rate strategy. Responsibility for allocation of the allowable harvest among user groups was delegated to the NPFMC under the Magnuson Fisheries Conservation and Management Act of 1976.

Although the State of Alaska does not have direct management authority over halibut fisheries, it is nonetheless concerned with the

wise, long-term management of the resource for the maximum economic benefit to the state. The Alaska Department of Fish and Game (ADF&G), Division of Sport Fish, gathers and provides annual sport fishery statistics to the IPHC, the NPFMC, and the public to aid in management and allocation decisions. This paper summarizes recent statistics and trends in the southcentral Alaska recreational fishery.

Data Sources

Two ADF&G research programs provide halibut sport fishery information: (1) a postal survey generates annual estimates of effort, catch, and harvest (Mills 1979-1994), and (2) port sampling provides estimates of harvest composition and other fishery characteristics (Meyer 1992, 1993, 1994).

Postal survey

The ongoing postal survey provides a cost-effective means to estimate recreational harvest throughout Alaska. Halibut harvest has been estimated since 1977. Effort (in angler-days) was also estimated for all marine finfish combined, but effort targeted specifically on halibut was not separable. Sport halibut catch, or fish harvested as well as released, has been estimated since 1990. Catch and harvest were estimated separately for charter anglers (those utilizing charter boats to access the fishery) and non-charter anglers only in the Cook Inlet and North Gulf Coast fisheries described below.

Survey questionnaires are mailed to a random sample of resident and nonresident license holders. Data are gathered for each surveyed angler's entire household. At least 30,000 surveys were mailed in recent years, and the response rate was 50-60%. All estimates were corrected for non-response bias. Postal survey harvest estimates were shown to be comparable to on-site creel survey estimates for fisheries with a large number of respondents (Mills and Howe 1992). Over 10,000 responses were used to generate the 1992 halibut harvest estimate for southcentral Alaska, resulting in a relative precision of $\pm 3.5\%$ (with 95% confidence). The accuracy of these estimates is probably sufficient for management under the current system.

For purposes of this report, southcentral Alaska is defined as IPHC Regulatory Area 3A (Figure 1). Area 3A extends from Cape Spencer (lat. 58°12'N, long. 136°38'W) to Cape Trinity (lat. 56°45'N, long. 154°9'W). Postal survey estimates are presented for five major fisheries within

Area 3A: (1) Kodiak—waters surrounding the Kodiak Island archipelago, (2) Cook Inlet—waters of Cook Inlet and the Gulf of Alaska between Cape Douglas and Gore Point, (3) North Gulf Coast—all waters between Gore Point and Cape Puget, (4) Prince William Sound—all waters between Cape Puget and Cape Suckling, and (5) Yakutat—all waters fished from the port of Yakutat. The Kodiak, Prince William Sound, and Yakutat areas correspond closely to reporting areas used by the postal survey. Estimates for the Cook Inlet and North Gulf Coast fisheries were obtained by apportioning postal survey estimates for the Kenai Peninsula area based on reported locations fished. The Cook Inlet estimates also include harvest from the postal survey's West Cook Inlet reporting area.

Accuracy of the postal survey estimates is limited by several potential reporting errors of respondents. Some anglers, particularly guided nonresidents, often do not know or can't remember exactly where they were fishing and are likely to report harvest by port of origin. Site-specific estimates were grouped into the larger areas described above to alleviate this problem. Some anglers may occasionally confuse arrowtooth flounder *Atheresthes stomias* and other flounders with halibut. Port sampling data indicate that flounder harvest is minimal, negating this concern. Finally, halibut are often reportedly taken from shore. Given the lack of road-accessible halibut habitat, the reported harvests are probably flounders taken from shore or halibut taken by boat anglers fishing near shore. Because the reported shoreline harvest represented less than 1% of all harvest, it was combined with non-charter boat harvest in this paper.

Port sampling

Collection of recreational halibut harvest data in southcentral Alaska has increased in recent years. Other than a marine creel survey at Valdez in 1988 (Roth and Delaney 1989) and creel surveys at several ports following the Exxon Valdez oil spill in 1989 (Roth 1990), most halibut data were collected on an opportunistic basis prior to 1991. As a result, the data were gathered incidental to sampling for other species or objectives and may not have accurately represented the sport harvest composition. A long-term program began in 1991 to estimate the recreational harvest composition of halibut and other groundfishes at major ports in Area 3A. Homer, Seward, and Valdez were sampled during the period 1991-1993, and Whittier and Deep Creek were sampled in 1991. Data from Whittier and Deep Creek will not be presented; the number of halibut landed at Whittier was

insignificant, and the age, size, and sex composition of the Deep Creek harvest was similar to that of Homer. Sampling was discontinued at Whittier and moved to Kodiak in 1992 and 1993. The ports of Kodiak, Homer, Seward, and Valdez are the major ports representing the Kodiak, Cook Inlet, North Gulf Coast, and Prince William Sound harvest reporting areas. They accounted for about 65% of the Area 3A sport harvest in 1993, while the Deep Creek area accounted for most of the remainder (Mills 1994).

The primary objectives of port sampling were to estimate age, length, and sex composition of the sport harvest (Meyer 1992, 1993, 1994). Mean weight was also estimated to determine the biomass of the sport harvest. The 1993 objectives also included estimation of the user group, target species, and gear type composition of (1) effort for all bottomfish, and (2) halibut harvest. The spatial distribution of recreational bottomfishing effort (in angler-days) was estimated each year, and the spatial distribution of halibut harvest was estimated in 1993. Spatial data were recorded for the same statistical areas used in commercial groundfish harvest reporting. Each year a sampling plan was reviewed by the IPHC to ensure that the data and estimates met the requirements of their annual stock assessment.

A single sampler assigned to each port collected data five days per week, including weekends and holidays, from late May through mid-September. All sampling was conducted during the late afternoon and evening hours when most sport fishing boats return to port, to ensure interception of the majority of the harvest. Sampling was designed to accommodate high daily and seasonal variation in the number of fish harvested. Peak harvests generally occurred during July and on good boating days in any summer month. Systematic sampling with seasonally varying rates was employed to ensure that the sampler was not saturated during peak harvest periods and that data were representative of all landings.

Halibut were measured from the tip of the snout to the center lobe of the caudal fin to the nearest millimeter. Sex was determined by visual inspection of gonads. Ages were determined from whole left sagittal otoliths (Chilton and Beamish 1982). Otolith subsamples were also examined by the IPHC to ensure consistency between agencies. Anglers targeting groundfish were interviewed to determine the number of anglers per boat, the user group (e.g., civilian or military charter boat, private boat, etc.), target species, gear type, statistical area fished, and the number of halibut (and other species) harvested. Skippers or deck hands provided most information for charter boats.

Composition was expressed as the proportional contribution of any class (e.g., age, length, sex, gear type) to the harvest. All proportions were estimated using standard normal procedures. The mean weight of harvested fish was computed using the IPHC length-weight relationship (Clark 1992) and length data for individual fish (Nielsen and Schoch 1980). Chi-square contingency tests were used to detect differences in proportions for discrete data, and Anderson-Darling tests (Scholz and Stephens 1987) were used to detect differences in length composition. When estimates differed significantly between months or locations and sample size was not proportional to harvest, estimates were stratified post-seasonally and weighted by the estimated fraction of the harvest that occurred each month. Weighting of estimates did not always cause significant improvements because some differences were statistically, but not functionally, different. Weighted estimates were presented only when they differed from unweighted estimates by more than 10%.

Findings

Harvest and catch

The estimated recreational harvest in Area 3A increased from about 18,000 fish in 1977 to 225,000 fish in 1993 (Table 1). The Cook Inlet fishery accounted for 72-83% of the annual harvest over this period. The North Gulf Coast and Prince William Sound harvests have been roughly similar in magnitude and have grown in parallel fashion. Much of the growth in these two fisheries has occurred since 1991, reducing the Cook Inlet share of the Area 3A harvest from a peak of 83% in 1990 to 72% in 1993. Harvest in the Kodiak and Yakutat fisheries has been relatively stable since the mid-1980s.

The number of halibut harvested by charter anglers has grown consistently in the Cook Inlet and North Gulf Coast fisheries (Figure 2). In addition, the share of the overall harvest taken by charter anglers in Cook Inlet increased steadily from 28% in 1986 to 55% in 1993 (Figure 2). There was no similar trend, however, in the North Gulf Coast fishery. The share of the harvest by charter anglers in the North Gulf Coast fishery averaged 45%, and ranged from a minimum 36% in 1989 to a maximum of 55% in 1991.

A large fraction of the halibut caught by anglers were released. The number of fish caught since 1990 ranged from about 277,000 to 443,000, and anglers released from 88,000 to 218,000 fish (Table 2). The fraction of the catch that was released ranged from 32% in 1991 to

Table 1. Estimated number of halibut harvested by recreational fishery in IPHC Regulatory Area 3A, 1977-1993 (Mills 1979-1994).

Year	Kodiak	Cook Inlet	North Gulf Coast	Prince William Sound	Yakutat	Area 3A total
1977	994	13,466	1,705	1,247	428	17,840
1978	1,721	25,577	2,723	933	24	30,978
1979	3,013	26,997	2,902	1,691	78	34,681
1980	3,651	29,985	3,017	3,143	34	39,830
1981	6,858	38,721	3,443	2,495	65	51,582
1982	9,180	39,532	2,954	2,735	398	54,799
1983	8,545	60,126	2,619	3,493	682	75,465
1984	8,179	61,202	3,267	4,428	241	77,317
1985	7,303	63,158	5,934	4,527	520	81,442
1986	10,960	85,153	10,398	8,331	777	115,619
1987	9,869	78,431	7,171	4,379	1,194	101,044
1988	7,749	137,252	11,696	9,845	1,673	168,215
1989	10,435	126,917	7,251	8,697	772	154,072
1990	9,134	148,538	9,500	10,851	1,459	179,482
1991	12,089	148,646	13,818	12,733	2,112	189,398
1992	10,860	143,094	18,595	17,855	1,861	192,265
1993	14,169	162,413	25,525	19,716	2,752	224,575

49% in 1993. Anglers in the Kodiak and Cook Inlet fisheries released a larger percentage of their catch, while a smaller fraction was released in the Yakutat fishery.

Harvest characteristics

Age composition of the sport harvest varied among ports and years during the period 1991-1993. Despite these variations, certain properties were evident at all ports and in all years. Sport-caught halibut ranged from 3 to 22 years old, but the vast majority of the harvest was between 5 and 15 years old (Figure 3). The modes of age distributions generally ranged from 8 to 10 years. Relatively strong and weak year-classes tracked well from year to year. The strong 1987 year-class identified in Bering Sea trawl surveys (Clark and Bakkala 1992) was

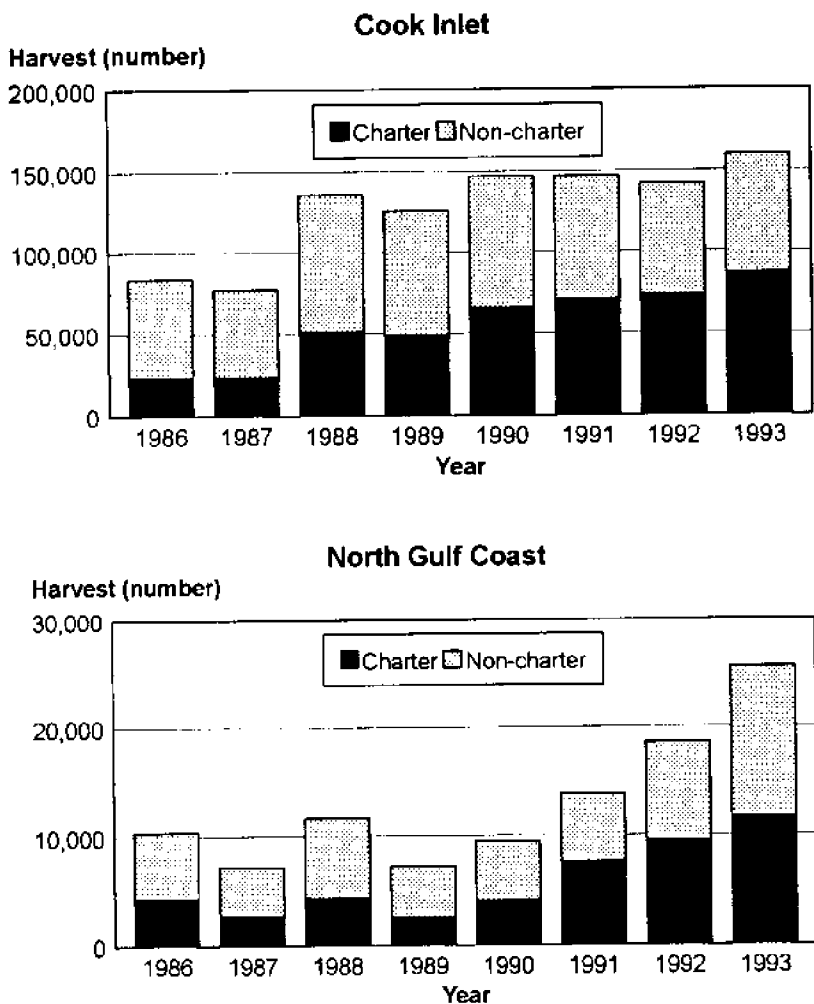


Figure 2. Recreational halibut harvest by charter and non-charter anglers in the Cook Inlet and North Gulf Coast fisheries, 1986-1993 (Mills 1979-1994).

Table 2. Estimated number of halibut caught and released and proportion released in the Area 3A recreational fishery, 1990-1993 (Mills 1991-1994).

Year and component	Kodiak	Cook Inlet	North Gulf Coast	Prince William Sound	Yakutat	Total Area 3A
1990:						
Catch	16,846	280,826	16,310	18,897	2,052	334,931
Release	7,712	132,288	6,810	8,046	593	155,449
% Released	45.8	47.1	41.8	42.6	28.9	46.4
1991:						
Catch	18,757	221,043	17,266	17,769	2,567	277,402
Release	6,668	72,397	3,448	5,036	455	88,004
% Released	35.5	32.8	20.0	28.3	17.7	31.7
1992:						
Catch	20,216	256,477	28,537	27,511	2,597	335,338
Release	9,356	113,383	9,942	9,656	736	143,073
% Released	46.3	44.2	34.8	35.1	28.3	42.7
1993:						
Catch	29,212	330,623	43,149	36,136	3,710	442,830
Release	15,043	168,210	17,624	16,420	958	218,255
% Released	51.5	50.9	40.8	45.4	25.8	49.3

evident as 5- and 6-year-olds in the Kodiak harvest in 1992 and 1993, and as 6-year-olds in the Valdez harvest in 1993.

Seasonal variations in age composition lacked a consistent pattern at most ports. Differences in age composition among months were not significant at Kodiak, and were significant at Seward only in 1993 and at Valdez only in 1991. In Cook Inlet, however, age composition shifted seasonally in a consistent pattern, with progressively older fish taken early in summer and younger fish taken in late summer. This pattern was evident at Deep Creek in 1991 and at Homer every year (Figure 4).

As with age, length and weight of the sport harvest varied among ports and years. Lengths of sampled fish ranged from 27 to 221 cm, but most were 50-170 cm (Figure 5). Mean length and weight were consistently lowest at Seward, and decreased each year (Table 3).

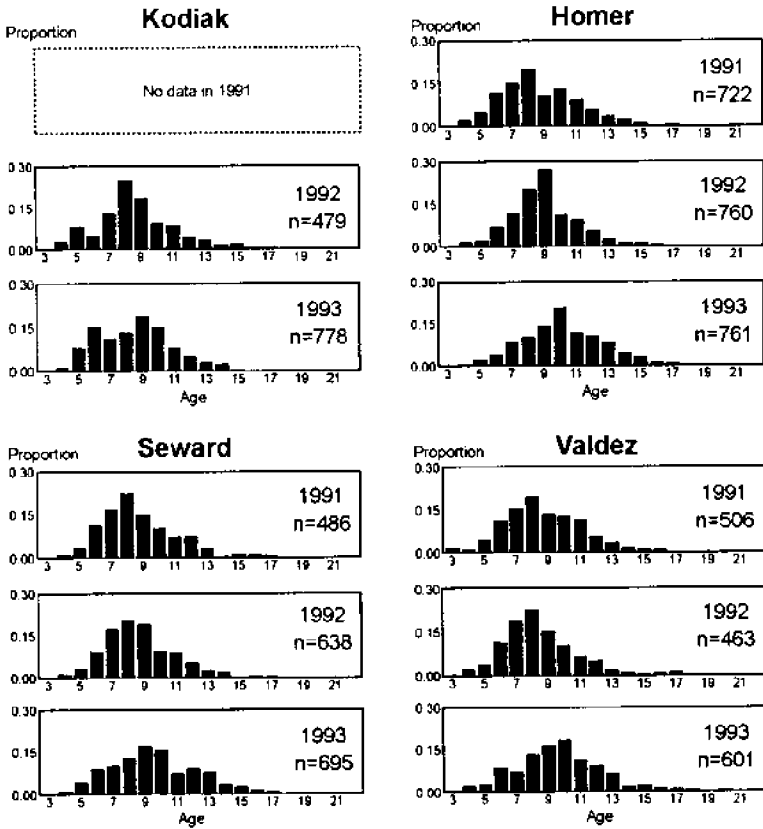


Figure 3. Age composition of the recreational halibut harvest landed at Kodiak, Homer, Seward, and Valdez, 1991-1993.

Depending on port and year, from 17 to 65% of the sport harvest was under the commercial size limit of 81 cm. Length composition varied seasonally in Cook Inlet in a manner similar to age composition (Figure 4). Harvested fish were largest in July at Deep Creek in 1991 and at Homer each year. Differences were most pronounced at Homer in 1991.

Length composition varied among user groups. In general, anglers on charter boats tended to harvest larger halibut than other anglers (Figure 6). Notable exceptions were that non-charter anglers landing fish at the U.S. Coast Guard base in Kodiak caught the largest halibut, and anglers on military charter boats at Seward harvested smaller

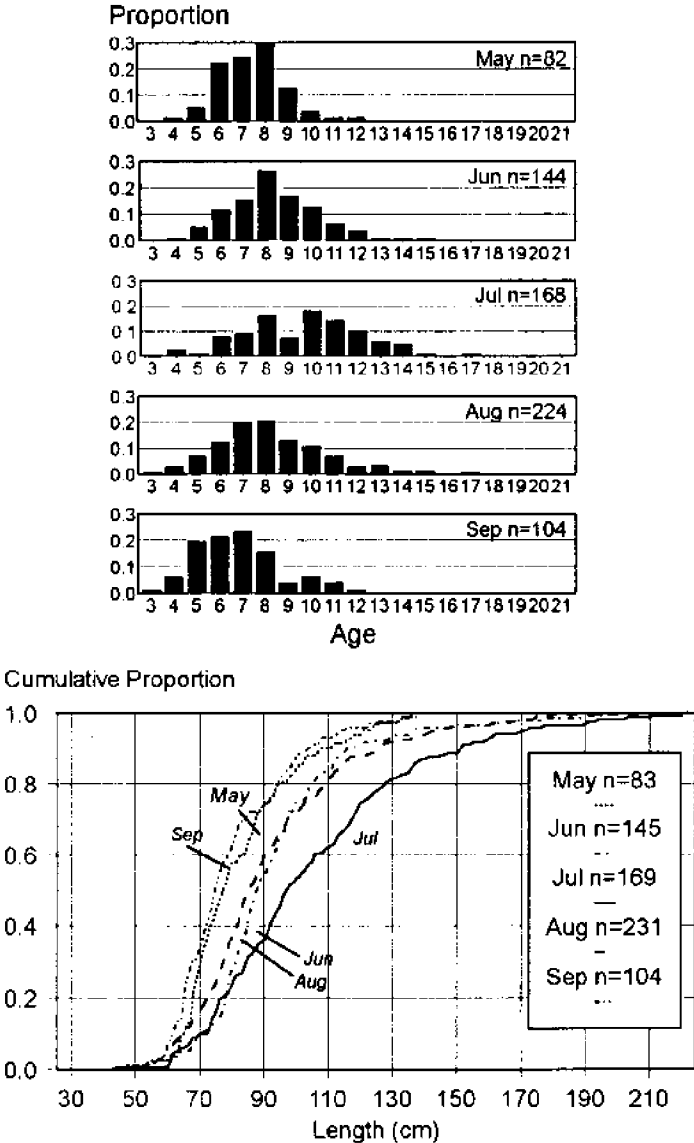


Figure 4. Monthly variation in age composition (upper graphs) and length composition (lower graph) of the recreational halibut harvest landed at Homer in 1991.

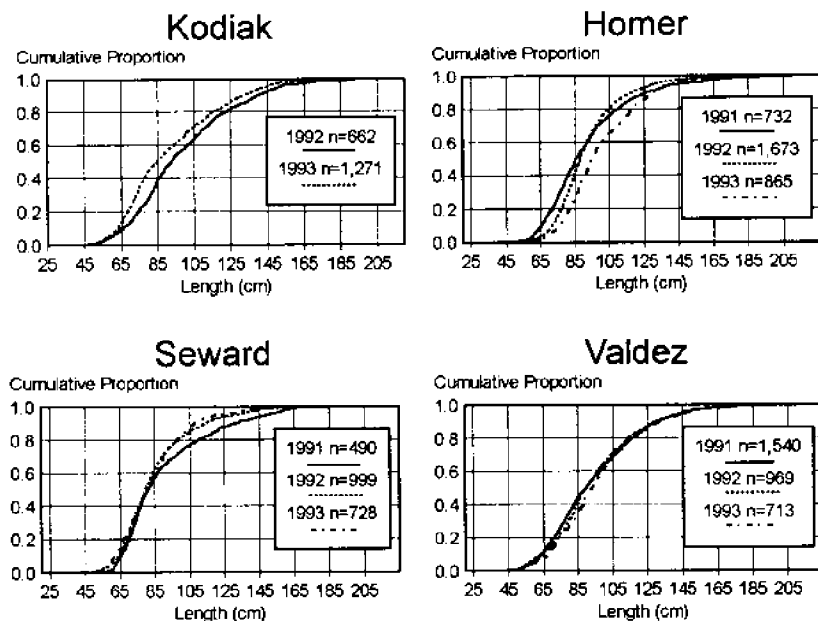


Figure 5. Length composition of the recreational halibut harvest landed at Kodiak, Homer, Seward, and Valdez, 1991-1993.

Table 3. Mean length and net weight (eviscerated, head off) of halibut harvested by the sport fishery at Kodiak, Homer, Seward, and Valdez, 1991-1993. NA indicates data are not available.

Year	Kodiak	Homer	Seward	Valdez
Length (cm):				
1991	NA	93.0	90.9	94.7
1992	99.1	92.8	85.4	95.4
1993	92.4	100.1	84.4	97.3
Net weight (lb.):				
1991	NA	22.5	20.7	23.0
1992	27.1	19.9	15.9	23.6
1993	21.5	24.9	14.6	24.2

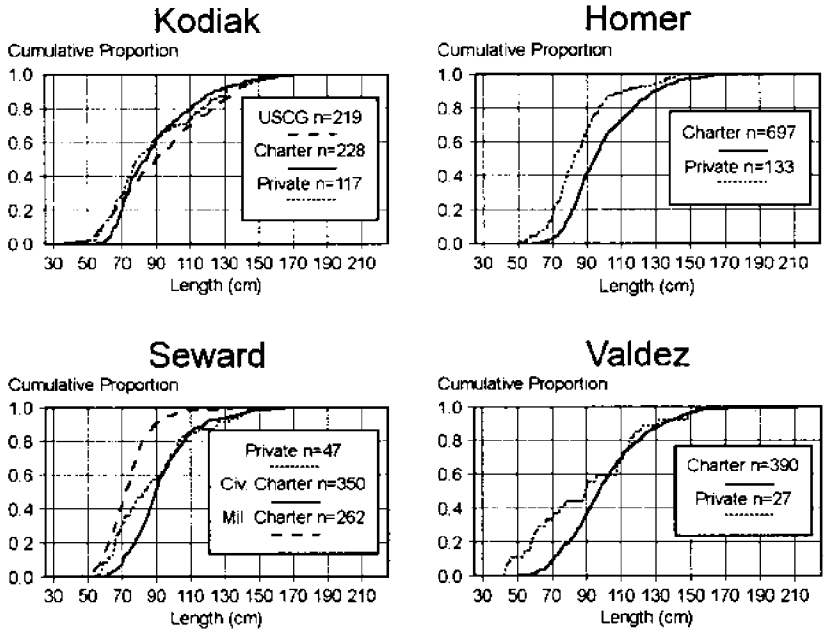


Figure 6. Length composition, by user group, of the recreational halibut harvest landed at Kodiak, Homer, Seward, and Valdez in 1993.

halibut than all other user groups in 1993. Differences in length composition among user groups were more pronounced at Homer and Seward than other ports.

The sport fishery harvested primarily female halibut. Females made up at least 80% of the sport harvest at Kodiak, Homer, and Valdez, but only 55-63% of the fish landed at Seward. In 1992 and 1993 there were significant differences in sex composition among months at some of the ports. For example, the proportion of females in the harvest was lowest in July at Seward and Kodiak in 1992. For ports that did show differences, there did not appear to be any clear patterns within or among seasons.

User group composition of effort and harvest varied widely by port. At all ports, charter anglers accounted for a greater percentage of the harvest than of the effort. Charter anglers accounted for 77% of the fishing effort for bottomfish and 88% of the halibut harvest at Homer (Table 4). Charter anglers at Valdez were similarly responsible for 69% of the effort and 85% of the harvest. In contrast, charter

Table 4. User group composition of the recreational bottomfishing effort (in angler-days) and halibut harvest (in number of fish) at selected southcentral Alaska ports, 1993.

Port	Percent of effort by user group		Percent of harvest by user group	
	Private	Charter	Private	Charter
Kodiak	75.8	24.2	66.8	33.2
Homer	23.1	76.9	12.2	87.8
Seward (civilian)	54.0	46.0	43.6	56.4
Valdez	31.0	69.0	15.2	84.8

Table 5. Composition of the recreational bottomfishing effort (in angler-days) and halibut harvest (in number of fish) by target species category at selected southcentral Alaska ports, 1993. Data are from interviews with anglers targeting bottomfish for any portion of their angling day.

Port	Percent of effort by target			Percent of harvest by target		
	Halibut only	Halibut + other	Other	Halibut only	Halibut + other	Other
Kodiak	81.7	18.3	0.0	80.2	19.8	0.0
Homer	99.6	0.0	0.4	100.0	0.0	0.0
Seward (civilian)	66.6	25.2	8.2	76.8	22.4	0.8
Valdez	95.9	2.7	1.5	99.0	0.8	0.2

anglers accounted for only 24% of the effort and 33% of the harvest at Kodiak. Since the Seward Military Recreation Camps annually report total effort and harvest, user group composition was estimated only for the civilian fleet at Seward. Anglers on civilian charter boats made up 46% of the effort but 56% of the civilian harvest at Seward. The 1993 reported harvest by military charter anglers made up 25% of the total harvest estimated by Mills (1994). Therefore, military and civilian charter anglers together accounted for approximately 68% of the total Seward halibut harvest.

Halibut was the primary species targeted by bottomfish anglers at all ports (Table 5). About 67-100% of the bottomfish effort was di-

Table 6. Composition of the recreational bottomfishing effort (in angler-days) and halibut harvest (in number of fish) by gear type category at selected southcentral Alaska ports, 1993. The "other" category includes jig, troll, lure, and fly.

Port	Percent of effort by gear type			Percent of harvest by gear type		
	Bait only	Bait + other	Other	Bait only	Bait + other	Other
Kodiak	84.5	13.0	2.5	86.0	12.2	1.8
Homer	98.4	1.2	0.4	98.9	1.1	0.0
Seward (civilian)	67.3	25.5	7.3	70.2	28.2	1.6
Valdez	94.1	3.0	2.9	92.7	2.8	4.5

rected at halibut exclusively, and 77-100% of the halibut harvest was taken by anglers targeting halibut exclusively. Anglers also targeted halibut in connection with other species, usually rockfish *Sebastes* and salmon *Oncorhynchus*, particularly at Kodiak and Seward. About one-fifth of the halibut harvest at Kodiak and Seward was taken while targeting halibut along with other species.

Anglers employed a wide variety of gear types, often used them in combination (e.g., jig with bait), and often used more than one during a day. Bait, however, was clearly the favorite method. Gear type categories were therefore simplified to (1) bait only, (2) bait combined with another gear type or used the same day, or (3) other gear types. Anglers using bait exclusively accounted for 67-98% of the total bottomfishing effort and 70-99% of the halibut harvest (Table 6). The typical setup for anglers using bait consisted of a circle hook baited with herring, salmon entrails, or octopus. Bait was more likely to be combined with another gear type at Kodiak and Seward than at other ports.

Recreational fishing effort was spread over an extremely large area, with some boats making day trips of up to 230 km round-trip. The Kodiak recreational fleet rarely ventured more than 30 km from port. Roughly 75-80% of angler-days by the Kodiak fleet were spent within Chiniak Bay 1992 and 1993. The Homer fleet, however, generally spent only about 20% of its effort within Kachemak Bay (east of a line from Anchor Point to Point Pogibshi), and the vast majority of that was by private boats. Most of the effort by private and charter boats was in Kennedy Entrance or Cook Inlet south of Anchor Point.

The Seward fleet fished from Nuka Bay to Montague Island, with boats commonly traveling over 100 km round-trip per day. Favorite areas included the Chiswell Islands and Johnstone Bay. The Valdez fleet distributed its effort over most of eastern and central Prince William Sound, but the majority of effort was in a north-south corridor between Valdez Arm and Hinchinbrook Entrance. Surprisingly, 20-45% of the effort by Valdez boats was in waters near or south of Hinchinbrook Entrance, over 100 km from Valdez.

The spatial distribution of fishing effort was either relatively stable or varied annually with no clear trend at Kodiak, Homer, and Valdez. At Seward, however, there was a definite eastward trend among civilian boats. The portion of angler-days spent east of Cape Mansfield increased from 11% in 1991 to over 40% in 1992 and 1993. Concurrently, the portion of effort spent closer to Seward in Resurrection Bay and Day Harbor dropped from 52% in 1991 to 34% in the next two years, and effort in the Cape Aialik/Chiswell Islands area decreased from 37% to about 18%.

Halibut harvest was generally distributed farther from port than was effort. Harvest at Kodiak was dispersed similarly to effort, with 85% of the halibut taken in Chiniak Bay. At all other ports the ratio of harvest to effort was generally highest in statistical areas farthest from port. For example, Kachemak Bay accounted for only 9% of the halibut harvest, but 24% of the effort by the Homer fleet. The more distant central waters of Cook Inlet, on the other hand, accounted for 41% of the harvest compared to 31% of the effort. The Resurrection Bay/Day Harbor area close to Seward accounted for 25% of the harvest but 34% of the effort. More popular waters east of Cape Mansfield, 45-90 km from Seward, accounted for 62% of the harvest compared with 46% of the effort. Finally, 21% of the halibut harvest and 42% of effort were from northeastern Prince William Sound, within 90 km of Valdez. Waters south of Hinchinbrook Entrance, however, accounted for 41% of the harvest compared with 27% of the effort.

Information from an ADF&G marine creel survey at Seward in 1972 (unpublished data on file at ADF&G, Anchorage) was examined to compare harvest trends over a 21-year span. Although total harvest was not estimated, interviewed anglers harvested only 61 halibut in 1972 (455 boat-trips) compared with 1,223 fish in 1993 (311 boat-trips). Not only was there a major increase in the magnitude of harvest over this interval, but effort and harvest were redistributed eastward. Seventy-two percent of the recreational harvest was taken in the

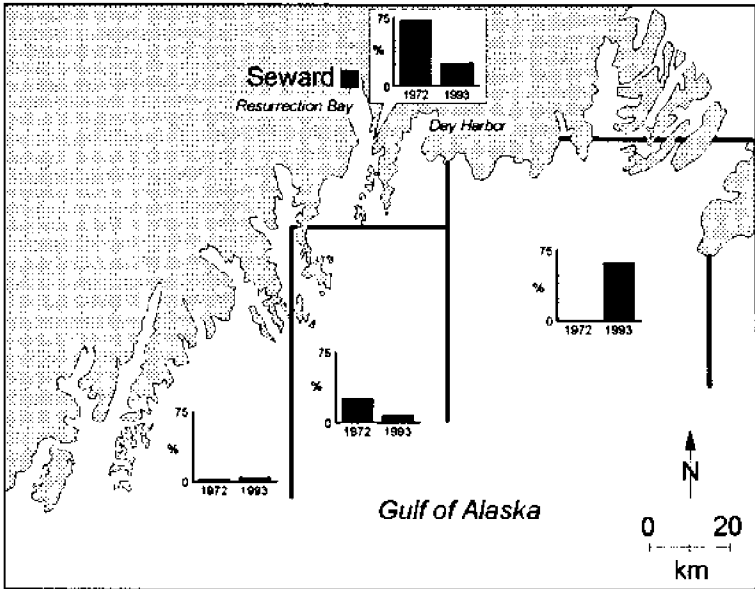


Figure 7. Changes in the spatial pattern of recreational halibut harvest in the North Gulf Coast fishery. Bar graphs show the percent of the harvest taken in 1972 versus 1993 in each of four areas.

Resurrection Bay/Day Harbor area in 1972, compared with only 25% in 1993 (Figure 7). The fraction of harvest taken east of Day Harbor jumped from zero to 62% over the same period.

Discussion

The increasing trend in halibut harvest has for the most part reflected growth in the human population and tourism in southcentral Alaska. Increased competition in road-accessible freshwater fisheries is also responsible for increased effort in some marine fisheries. For example, much of the rising effort in the Deep Creek marine fishery in the last few years was probably due to weak returns and subsequent catch-and-release restrictions on Kenai River chinook salmon *Oncorhynchus tshawytscha*. In the marine fishery, anglers could harvest chinook salmon along with halibut for the lower cost of a half-day trip.

In a review of the halibut sport fishery, Skud (1975) concluded that the sport harvest was not a critical factor in determining fluctuations

in halibut abundance. The sport fishery has since become a considerable source of fishing mortality. For example, inclusion of sport harvest data in the 1991 stock assessment led to a 10-15% increase in the overall harvest and a 10% decrease in estimated biomass over preceding years (Sullivan et al. 1992). The 1993 harvest made up about 15% of all sources of removals in Area 3A. Meanwhile, Pacific halibut biomass is declining coastwide. The Area 3A exploitable biomass peaked in 1989 at about 196 million pounds and dropped 5-12% per year to about 137 million pounds in 1993 (Sullivan and Parma 1994). The recruitment of 8-year-old halibut is very low and the stock is expected to decline at a rate of 10-15% per year for the next several years (Sullivan 1994). Growth in the sport harvest during a time of stock declines has led to conservation and allocative concerns.

Recruitment overfishing by the sport fishery is one conservation concern. The sport fishery, unrestricted by a minimum size limit, takes younger, smaller fish than the commercial setline fishery. Over the last three years, the bulk of the sport harvest was 5-15 years old, compared to 7-20 years for the commercial harvest (Blood 1992, 1993, 1994b). Clark and Parma (1993) examined the effects of size limits on yield per recruit (YPR) and female spawning biomass per recruit (SPR). Using data from Homer, the primary port of sport harvest, they concluded that the selectivity was such that size limits had little effect on either variable at the level of fishing mortality exerted by the sport fishery. This analysis may need to be repeated to incorporate recent changes in age and size composition, as well as reductions in the halibut growth rate.

Another conservation concern is the threat of localized depletion of halibut stocks. Halibut are managed as a single stock on the basis of relatively large regulatory areas such as Area 3A. The observed differences in age, size, and sex composition of the sport harvest among ports, combined with information on the spatial distribution of effort and harvest, suggest that there may be localized stocks, subpopulations, or even aggregations that are subject to varying exploitation rates. For example, halibut taken near Seward are significantly smaller and contain a higher percentage of males. Segregation of fish by size and sex is commonly observed over rather large areas in Bering Sea surveys (Pers. comm., W. Clark, IPHC, P.O. Box 95009, Seattle, WA 98145, 11/94) and Area 3A charter operators have reported the same phenomenon. The observed differences in mean weight among ports must be accounted for in estimation of sport harvest biomass. In addition, the seasonal pattern of change in length and age composi-

tion in Cook Inlet, but not other areas, also suggests regional differences. The onshore-offshore movement of large fish is consistent with tagging studies (Skud 1977), but the reason for the lack of this pattern at some ports is unclear. Harvest composition and fishery use patterns must continue to be examined to address the potential for localized overharvest.

Growth in the sport harvest has also led to several allocation issues. The halibut resource is fully exploited, yet the emerging sport fishery has no catch quota. The sport harvest, subsistence and personal use harvest, bycatch mortality, and waste directly reduce the commercial quota under present management. The commercial quota is threatened by growth in unregulated removals combined with decreasing stock size. As a result, the NPFMC is currently considering a proposal by the setline industry to limit sport harvest by charter anglers.

User groups exploiting nearshore waters are also concerned over the implementation of an individual fishery quota (IFQ) system for the setline fishery in 1995. Direct competition, as well as localized overharvest, are anticipated as setline vessels move inshore to target halibut on summer feeding grounds. Setline vessels tended to fish closer to port after a similar program was implemented in Canada, even though catch per unit effort was often lower.

Conservation and allocation issues will intensify as long as sport harvest increases in the face of declining stock biomass. Sport harvest surveys must be continued and improved in order to make accurate stock assessments, inform managers considering allocation decisions, and provide for long-term sustained yield of the resource.

Acknowledgments

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Contaminant Effects on Reproductive Output in North Pacific Flatfish

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Abstract

In a series of laboratory and field studies conducted in Puget Sound, Washington, we have investigated the impact of chemical contaminants on reproductive function in several common pleuronectid species, including English sole (*Pleuronectes vetulus*) and rock sole (*Lepidopsetta bilineata*). We have found that exposure to and uptake of chemical contaminants such as aromatic and chlorinated hydrocarbons is associated with several types of reproductive dysfunction. Inhibited gonadal development, depressed plasma concentrations of reproductive steroids, reduced spawning success, reduced egg size, and reduced egg and larval viability, appear to be most closely correlated with exposure to aromatic hydrocarbons (AHs), although polychlorinated biphenyls (PCBs) and other chlorinated hydrocarbons may also be involved, particularly in altered egg development and reduced egg viability. Although the long-term impact that reproductive impairment might have on the survival and abundance of affected fish is not known, preliminary results of a population modeling study with English sole from polluted sites in Puget Sound suggest that contaminant-related declines in reproductive output may have the potential to reduce the growth rate of English sole subpopulations in urban areas. In general, North Pacific flatfish stocks would probably not be affected by contaminant-associated declines in survival or reproductive success because levels of chemical contaminants in the

areas where animals typically reside are relatively low. However, flatfish in Prince William Sound were exposed to high concentrations of AHs during the *Exxon Valdez* oil spill (EVOS) in 1989. In laboratory studies, rock sole and flathead sole treated with Prudhoe Bay crude oil (PBCO) exhibited elevated concentrations of fluorescent aromatic compounds (FACs) in bile, reduced plasma estradiol concentrations, and reduced endogenous ovarian estradiol production, indicating that short-term exposure to PBCO has the potential to alter reproductive function in these fish. Consequently, we measured several indicators of reproductive development in yellowfin sole (*Limanda aspera*) from Prince William Sound during the 1990 and 1991 spawning season, 15 and 27 months after the spill. The majority of animals sampled showed little evidence of altered gonadal development or reduced plasma estradiol levels. However, plasma estradiol concentrations were depressed in a small number of individuals with extremely high levels of biliary FACs. These findings suggest that while the EVOS did not appear to have a dramatic long-term impact on flatfish reproduction, exposure to AHs in crude oil or related materials could inhibit reproductive function in North Pacific flatfish if exposure levels were sufficiently high.

Introduction

In recent field and laboratory studies, exposure to xenobiotic compounds has been shown to have detrimental effects on reproduction in several marine and freshwater fish species. Among the effects observed in laboratory exposures to compounds such as pesticides, PCBs, dioxins and aromatic compounds are inhibition of oocyte development and maturation, increased follicular atresia of both yolked and previtellogenic oocytes, abnormal yolk deposition and yolk formation within oocytes, and abnormal egg maturation and egg production (see Lam 1983; Susani 1986; and Donaldson 1990 for reviews). Similar types of impairment also have been reported in field studies with fish from polluted sites. For example, Hose et al. (1989) showed that white croaker (*Genyonemus lineatus*) and kelp bass (*Paralabrax clathratus*) collected from contaminated waters of California had reduced fecundity. Similarly, white sucker (*Catostomus commersoni*) collected from contaminated lakes of Ontario, Canada, showed a decrease in egg size, fecundity, and spawning success (Munkittrick et al. 1991).

Flatfish are an important component of the northwest Pacific groundfish fishery. The impact of contaminants on the ability of flatfish species to reproduce in the north Pacific is of concern because of increased population and urbanization which ultimately leads to increased pollution. Since 1985, the Environmental Conservation Division of NOAA/NMFS has been conducting a series of field and laboratory studies to examine the effects of contaminants on reproductive parameters in several flatfish species widely available in Puget Sound, Washington, including English sole (*Pleuronectes vetulus*), rock sole (*Lepidopsetta bilineata*). Moreover, after the Exxon Valdez oil spill (EVOS) in 1989, we expanded our research program to examine the effect of the Prudhoe Bay crude oil (PBCO) on reproductive processes of yellowfin sole (*Limanda aspera*) in Alaska. This paper summarizes the results of ongoing field and laboratory studies that examine the effects of contaminants on reproductive parameters of several north Pacific flatfish species from Puget Sound, Washington, and from Alaska.

Industrial Pollution and Flatfish Reproduction (Puget Sound)

Initial studies on flatfish reproductive toxicology were conducted on English sole from Puget Sound, Washington. English sole was chosen as our target species because previous studies had shown that this species took up and metabolized or accumulated chemical contaminants from sediments, and was particularly sensitive to their impact, as demonstrated by high prevalence of liver lesions and other pathological conditions (Malins et al. 1984; Myers et al. 1987). The first of these studies (Johnson et al. 1988; 1993) investigated ovarian development in prespawning English sole from four sites in Puget Sound differing in levels of contaminants (Figure 1). Two sampling sites, the Duwamish Waterway and Eagle Harbor, had high concentrations of xenobiotic compounds in the sediment. The Eagle Harbor site was the former location of a creosote plant and extremely high levels of PAHs in sediment were found, whereas the Duwamish Waterway sediments were contaminated with a variety of industrial pollutants including PCBs and PAHs. The other sites, Port Susan and Sinclair Inlet, had lower contaminant concentrations in sediments. A number of factors associated with ovarian recrudescence were measured, including plasma concentrations of estradiol and vitellogenin, gonadosomatic

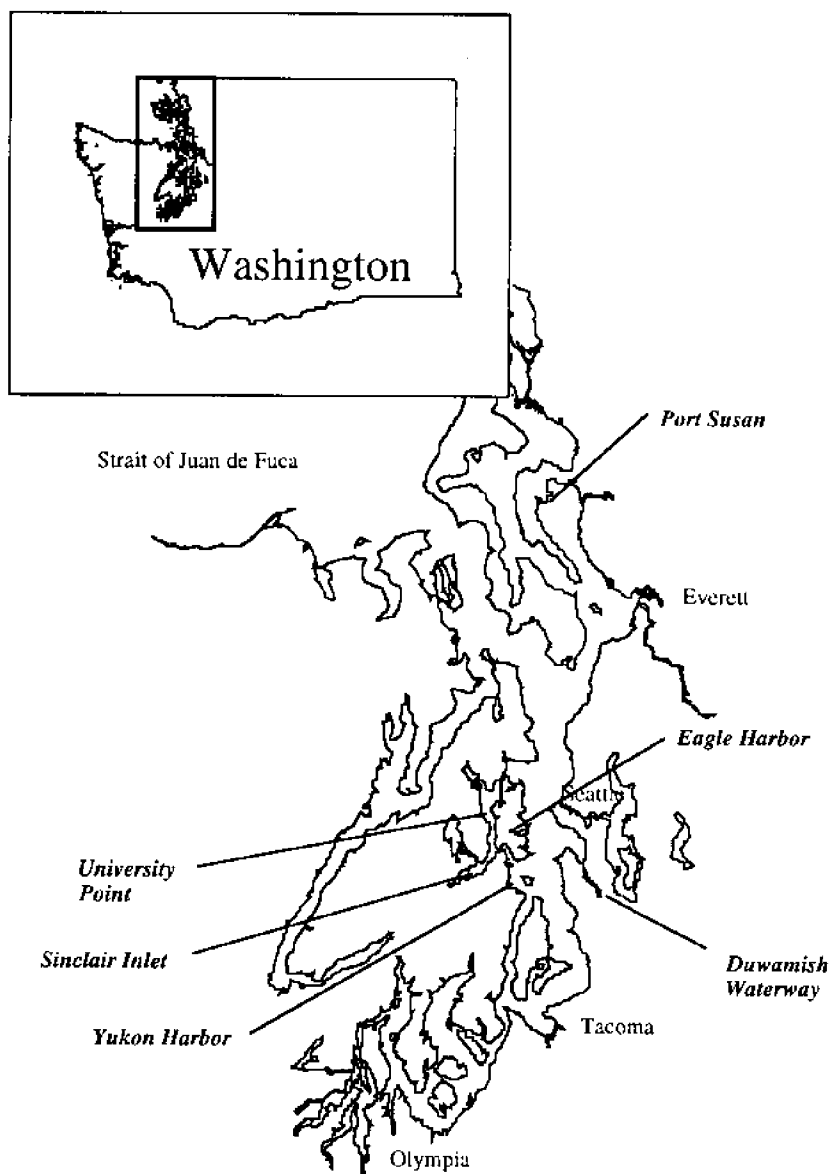


Figure 1. Map of Puget Sound, Washington, showing sites of sample collection.

Table 1. Survival rate and indicators of reproductive success in English sole from four sites in Puget Sound, Washington. Data compiled from Johnson et al. 1988; Casillas et al. 1991; Landahl and Johnson 1993; Johnson and Landahl 1994.

	Port Susan	Sinclair Inlet	Duwamish Waterway	Eagle Harbor
Sediment	Least polluted	Moderately polluted	High organics	High PAHs
Survival rate (3+ years)	0.62	0.62	0.62	0.80
% maturing	80	90	64	57
% spawning	90	75	54	35
% fertilization	52	35	44	24
% normal larvae	74	54	59	68
% overall reproductive success	28	13	9	3.2

index (GSI), oocyte maturation stage, and ovarian atresia. Results showed that female English sole from the contaminated sites had lower plasma estradiol levels and lower *in vitro* production of estradiol by ovarian tissue than fish from minimal to moderately contaminated sites, and were less likely to enter vitellogenesis and undergo normal ovarian development (Table 1). At the minimally to moderately contaminated sites approximately 80-90% of adult females underwent gonadal development, while at the highly contaminated sites, the percentage declined to 57-64% (Table 1). In addition, significant correlations were found between the probability of ovarian development and concentrations of fluorescent aromatic compounds (FACs) in the bile, an indicator of exposure to PAHs. Laboratory experiments support our field observations that sole exposed to environmental contaminants may have reduced concentrations of estradiol in plasma and associated reproductive impairment. For example, injection of gravid female English sole from a non-urban area with extracts of contaminated sediment from the Duwamish Waterway led to a significant reduction in circulating estradiol levels in comparison with untreated controls (Stein et al. 1991).

Additional studies suggested that a significant proportion of English sole from contaminated areas that did successfully enter vitellogenesis experienced inhibited spawning ability and reduced viability of eggs and larvae (Casillas et al. 1991). When gravid English sole from Port Susan, Sinclair Inlet, Eagle Harbor, and Duwamish Waterway were brought into the laboratory and artificially induced to spawn with LHRHa (luteinizing hormone releasing hormone analogue), spawning success was significantly lower in fish from Eagle Harbor and Duwamish Waterway. Also, when naturally spawning populations of English sole were examined, animals with elevated levels of contaminants in tissues were rare, even at spawning sites adjacent to industrial waterways, suggesting that fewer animals from polluted sites were migrating to spawning areas (Collier et al. 1992).

While these studies showed an impact of contaminants on the reproductive success of individual sole, a more critical question was whether this could affect fish abundance. In a preliminary attempt to answer this question, field and laboratory data on English sole mortality and fecundity at clean and contaminated sites were incorporated into a Leslie matrix model (Landahl and Johnson 1993) and population growth rates were estimated. Results suggested that the decline in reproductive potential associated with inhibited gonadal development and impaired spawning success in fish from the contaminated sites (Duwamish Waterway, Eagle Harbor) could significantly decrease the population growth rates of sole subpopulations in these areas if the loss of recruits were not offset by other compensating mechanisms.

After observing that contaminants could affect the reproductive parameters in English sole, we expanded our research program to investigate the effects of contaminant exposure on reproductive processes of other pleuronectid species, including rock sole. Rock sole were captured at Eagle Harbor, Yukon Harbor, and Sinclair Inlet (Figure 1). Preliminary results of this field study showed that plasma estradiol concentrations of female rock sole from Eagle Harbor were significantly lower than in fish from Sinclair Inlet (Johnson et al. 1993). In addition, vitellogenic female rock sole collected from various areas in Puget Sound (Eagle Harbor, Sinclair Inlet, University Point, and Yukon Harbor (Figure 1)) were artificially induced to spawn with LHRHa. Results of this study showed that the fish from Eagle Harbor took longer to spawn (Figure 2a), and had less chance of spawning and producing fertile eggs (Figure 2b) than the fish from the reference site University Point. Also, in the fish that did spawn, percent fertilization and percent normal larvae were lower in fish from Eagle Harbor.

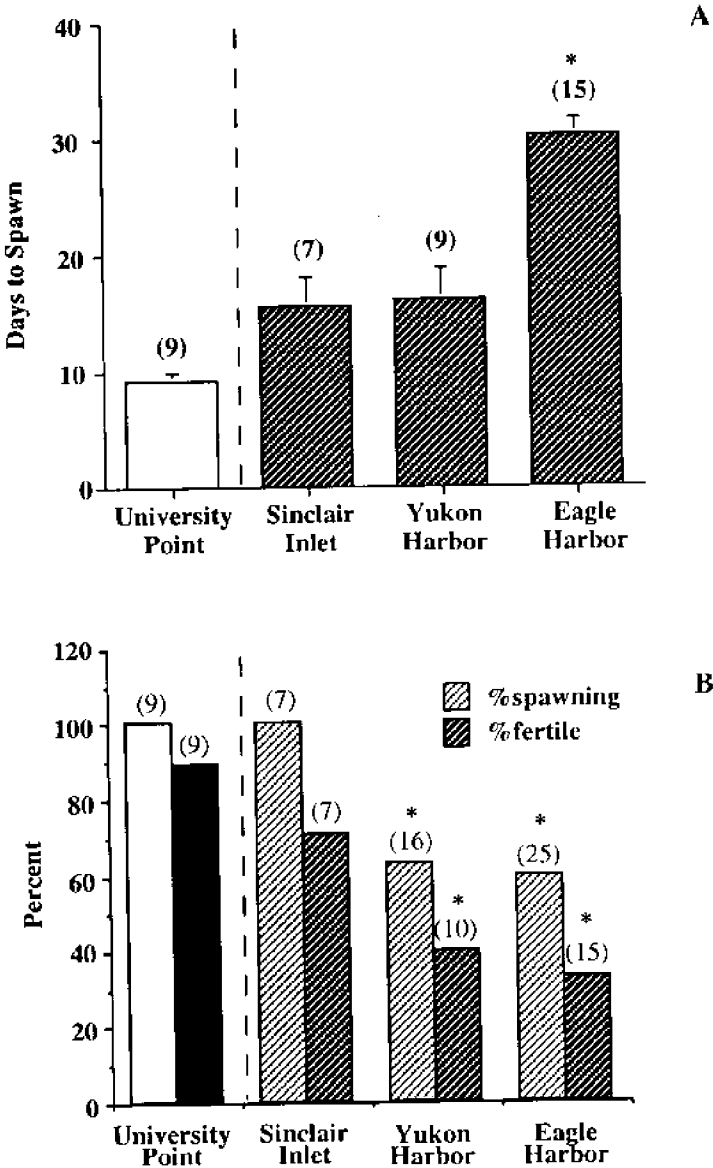


Figure 2. Mean \pm (SE) of (A) average number of days to spawn, and (B) % spawning and % fertile of rock sole from four sites of Puget Sound injected with LHRHa. Numbers in parentheses represent numbers of animals tested from each site. * represents significant difference from the reference site University Point (ANOVA, Fishers PLSD, 95% CI).

Moreover, egg weight and larval weight of the fish from Eagle Harbor were lower than in the fish from the reference site, University Point.

Results of these studies suggest that industrial pollution poses a potential threat to fish stocks in urban sites, and may become an increasing problem in other areas of the North Pacific if urban growth continues unchecked.

Oil Pollution and Flatfish Reproduction (Prince William Sound)

Although industrial pollutants may impact flatfish stocks near urban waterways, for much of the undeveloped North Pacific a greater problem is acute exposure to pollutants from oil or chemical spills. The 1989 *Exxon Valdez* oil spill (EVOS) in Prince William Sound, Alaska, is a prime example of such an incident.

After the EVOS, we conducted a series of field and laboratory studies to assess the impact of exposure to Prudhoe Bay crude oil (PBCO) on reproductive function in flatfish. One of these studies (Johnson et al. 1994) was a controlled laboratory exposure which examined the effects of short-term exposure to PBCO on plasma estradiol levels in rock sole and flathead sole, two species common throughout the North Pacific, including Prince William Sound. In this study, gravid female fish collected from Port Susan were injected intramuscularly with a 1:1 mixture of PBCO and acetone:emulphor carrier at dosages of 0.1, 0.5, and 1.0 mg oil/kg body weight. A group of animals injected with carrier alone served as controls. Treated animals received two injections, on days 1 and 4 of the experiment. On day 7, blood samples were collected for analyses of plasma estradiol concentration, and fish were necropsied and samples collected for chemical and histological analyses. Uptake of PBCO was assessed by measurement of FAC levels in bile. In both species, FACs-PHN concentrations (ng/mg of protein) in exposed fish increased in a dose-dependent fashion, while circulating plasma estradiol levels decreased. In flathead sole, exposure to weathered PBCO also appeared to inhibit ovarian estradiol production in a dose-dependent manner (*in vitro* estradiol production in rock sole was not examined). Reductions in ovarian estradiol production were associated with depressed plasma estradiol concentrations in the same fish, suggesting that reduced ovarian steroidogenesis may contribute to decreased endogenous steroid levels in contaminant-exposed fish. The results of this study suggested that acute exposure to PBCO could alter endocrine

function in both rock sole and flathead sole, but the possible impact of short-term disruption of endocrine function on reproductive success remained to be determined.

To assess the effects of PBCO exposure on reproductive function in wild Prince William Sound flatfish, we examined adult female yellowfin sole from several oil impacted areas of Prince William Sound for evidence of oil exposure and associated reproductive dysfunction (see Collier et al. 1993 for a complete list of sites sampled). Yellowfin sole was chosen as the target species for these studies primarily because it spawns in late summer and early fall, when weather conditions were optimal for sampling; rock sole and flathead sole, which are winter spawners, were not feasible target species. Several indicators of reproductive development were measured during the reproductive cycle, including concentrations of estradiol in plasma, gonadosomatic index (GSI), and ovarian maturation stage, as well as oil exposure as indicated by biliary FAC levels. Results of the study showed that in fish sampled in 1990, levels of biliary FACs in fish from Snug Harbor and Squirrel Bay, two areas heavily impacted by the spill, were significantly higher than the levels found in fish from the reference site at Olsen Bay. By 1991, the levels of FACs in fish from Snug Harbor and Squirrel Bay had decreased dramatically, and were comparable to the levels found in fish from Olsen Bay (Figure 3a) (Collier et al. 1993). In general, reproductive function of fish from Snug Harbor and Squirrel Bay did not seem to be affected by exposure to petroleum. Neither GSI nor plasma estradiol concentrations of the fish from Snug harbor and Squirrel Bay were found to be different than in the fish from Olsen Bay (Figure 3b, c), and little correlation was found between GSI or plasma estradiol concentrations and exposure to oil, as estimated from biliary FAC levels (Figure 4a, b). The intersite differences that we observed were due mainly to differences in the size and age of the fish collected at the sampling sites. These findings suggest that yellowfin sole collected in the Prince William Sound field study were not exposed to sufficiently high concentrations of oil to affect reproductive parameters at the time they were sampled (1-2 years following the spill). In the laboratory study, decreased plasma estradiol concentrations were observed in fish injected with oil at doses greater than 0.5 mg oil/kg body weight (biliary FACs-PHN > 78,000 ng/g bile protein) for flathead sole and doses greater than 0.1 mg/kg body weight (biliary FACs-PHN > 110,000 ng/g bile protein) for rock sole. Most of the fish collected in the field had biliary FACs-PHN levels about one-tenth of these levels. When biliary FACs-PHN values

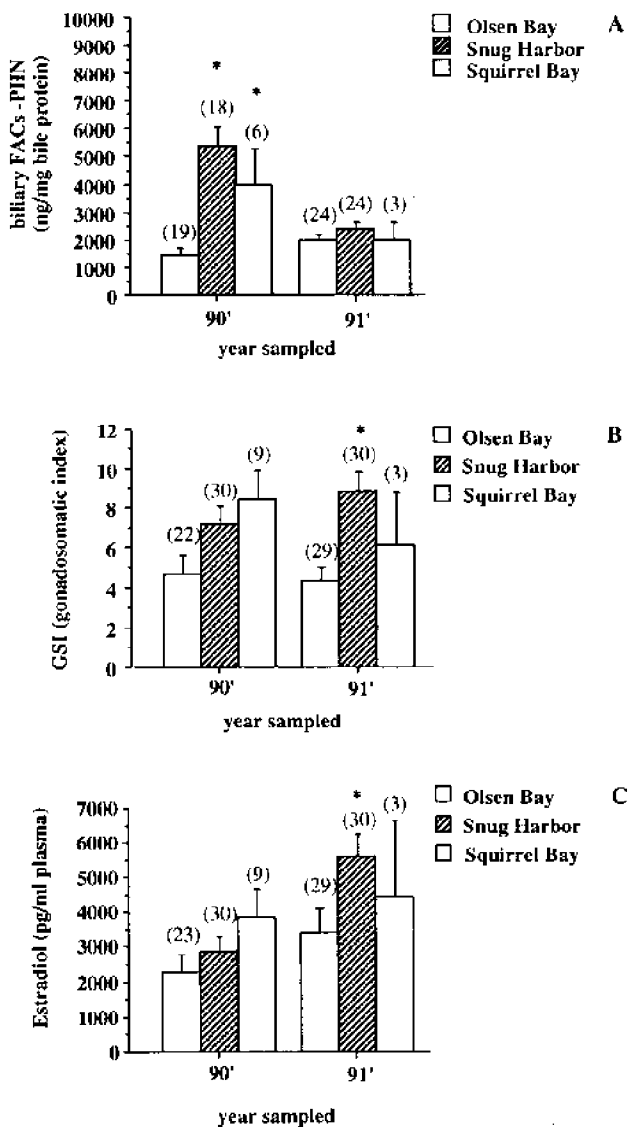


Figure 3. Mean \pm (SE) of (A) biliary FACs-PHN, (B) GSI, and (C) plasma estradiol concentration of yellowfin sole captured from Olsen Bay, Snug Harbor, and Squirrel Bay during sampling years 1989, 1990, and 1991. Numbers in parentheses represent numbers of animals tested at each site. * represents significant difference from the fish injected with carrier (NOVA, Fishers PLSD, 95% CI).

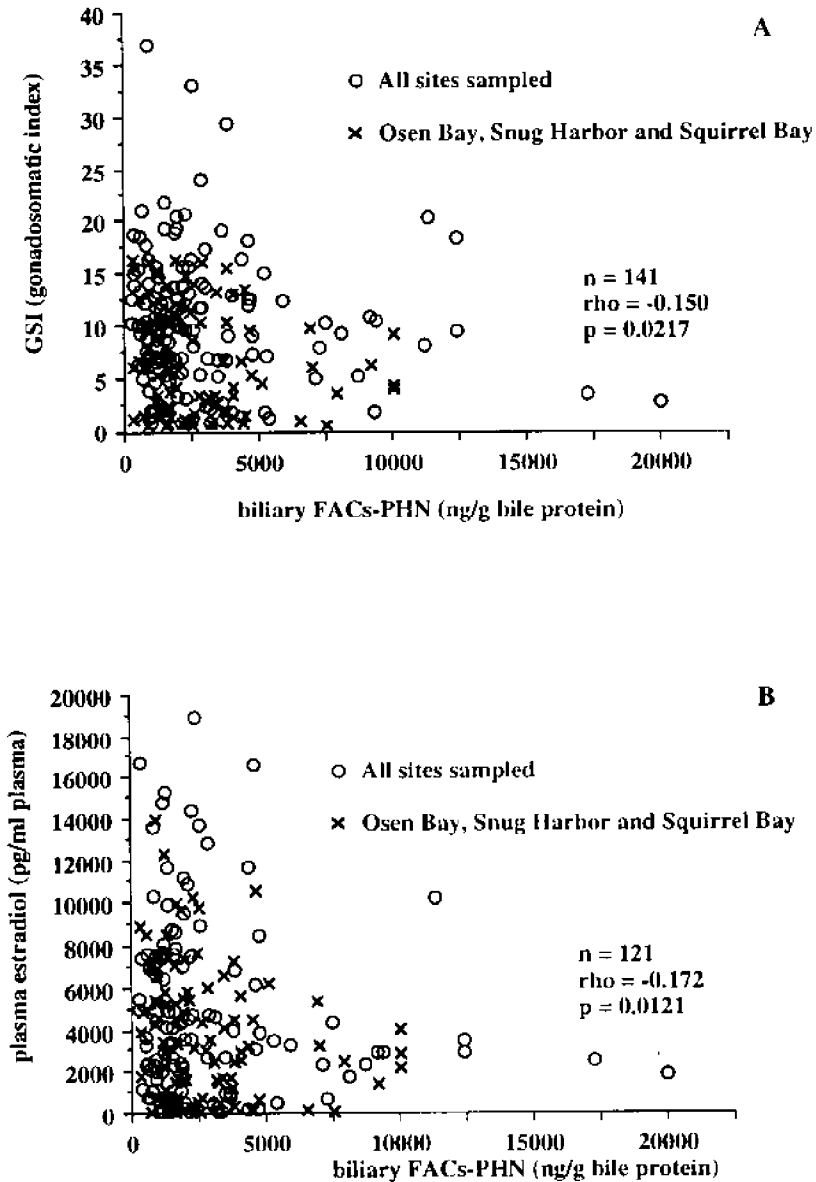


Figure 4. Relationships between biliary FACs-PHN and (A) GSI and (B) plasma estradiol concentrations of yellowfin sole captured from Prince William Sound, Alaska (Spearman rank correlation, 95% CI).

of the fish sampled at other sites were compared to the GSI value, only a few fish showed possible reproductive dysfunction (low GSI and plasma estradiol concentrations at biliary FACs-PHN levels > 15000 ng/g bile protein) (Figure 4a, b).

Interspecies differences in sensitivity to or uptake and metabolism of oil may also have contributed to the different responses of sole exposed to oil in the field and in the laboratory. Both rock sole and flathead sole showed higher exposure levels and more sustained P-450 induction after the EVOS than yellowfin sole collected from the same sites (Collier, unpublished data), suggesting that yellowfin sole may differ somewhat from these other two species in their uptake and metabolism of aromatic compounds. Ecological differences between these species, such as diet or migration patterns, could also affect exposure levels. Studies on multiple species may help us to identify physiological and ecological characteristics that make particular fish species especially vulnerable to contaminant-associated reproductive impairment.

Conclusion

The quality of the marine environment in the North Pacific and its impact on commercially important fish stocks in this region is a major concern to fisheries managers. As the population in nearshore marine areas and discharges to the marine environment continue to increase, these impacts can pose a threat to health of flatfish stocks residing in these areas. On the basis of research conducted to date, there is considerable evidence that anthropogenic contaminants are impairing the health and reproduction of Puget Sound flatfish species (Casillas et al. 1991; Johnson et al. 1988, 1991, 1993, 1994), and may have similar impacts on these species in other urbanized areas. For much of the North Pacific, however, chemical or oil spills, rather than industrial pollution, are the main concern. Although results of laboratory studies indicate that flatfish exposed to high concentrations of oil may show altered endocrine function, yellowfin sole collected following the Prince William Sound oil spill appeared to be recovering well from the oil exposure and showed few signs of altered gonadal development. Apparently, the relatively short-term acute exposure to oil that these fish received at the time of the spill did not result in long-term disruption of reproductive function, at least for those indicators measured in this study.

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Tumors, Lesions, and an Eye Parasite in Flatfish from Resurrection Bay, Alaska

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Abstract

Five species of flatfish from depths of 5-40 m in Resurrection Bay, Alaska, were examined to determine frequency and intensity of external lesions and parasites. Skin tumors were observed in 20% of the yellowfin sole, *Pleuronectes asper*, 67% of the flathead sole, *Hippoglossoides elassodon*, and 20% of the Dover sole, *Microstomus pacificus*. No skin lesions were observed on either English sole, *Pleuronectes vetulus*, or arrowtooth flounder, *Atheresthes stomias*. Fin necrosis was seen in 4% of the yellowfin sole.

Frequency of tumors and parasites was greater at 5-20 m than at 30-40 m. Incidence of tumors is discussed and compared to incidence in highly polluted nearshore waters elsewhere. Our results suggest that undetermined xenobiotics in subtidal sediment may be the underlying cause of the lesions.

A parasitic, pennellid copepod, *PhrEXOcephalus cincinnatus*, was observed attached to the eye of arrowtooth flounder. These parasites appear to be specific to this flatfish and occurred in 40% of the

individuals caught. Mean intensity of occurrence of this parasite was 2.1 per fish with some individuals carrying up to five copepods.

Introduction

Fish inhabiting pristine habitats generally have few external abnormalities and exhibit few or no effects of parasitism. In contrast, fish living in inland and coastal waters degraded by anthropogenic pollutants exhibit a variety of external lesions such as fin necrosis, skin tumors and increased numbers of external parasites (Kimura et al. 1984; Murchelano and Wolke 1985; Khan et al. 1992). Subtle, stress-related changes including physiological, behavioral and reproductive, have also been reported in fish inhabiting polluted waters (Myers et al. 1987; Schreck 1990; Munkittrick et al. 1991). Several studies have reported that petroleum aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), heavy metals and pesticides, acting singly or collectively, can cause severe and irreversible abnormalities in fish (Malins et al. 1984). Most reports on the effects of pollutants originate from industrialized areas such as Puget Sound, Washington (Malins et al. 1984), the Great Lakes (Baumann et al. 1991), and Boston harbor (Marchelano and Wolke 1985). However, there is also evidence of pollution-induced lesions from high latitude, sparsely populated habitats (Khan et al. 1992).

We conducted a preliminary survey of the shallow water flatfishes of Resurrection Bay, Alaska (Figure 1), looking for external parasites and lesions as general indicators of fish health. This glacial fjord exhibits a modest level of human impact in the forms of the city of Seward (population 4,000), a small boat harbor, a coal loading facility, a lumber mill, a ship repair facility and two fish processing plants. In addition, there are several creeks and rivers that inject fresh water mixed with glacial sediments into the bay.

Materials and Methods

Sampling was conducted with a 3 m otter trawl towed from an 8 m aluminum work boat. Trawling proceeded along the 5 m, 30 m and 40 m depth contours. Five species of flatfish were captured: yellowfin sole (*Pleuronectes asper* Pallas 1814), flathead sole (*Hippoglossoides elassodon* Jordan and Gilbert 1880), Dover sole (*Microstomus pacificus* [Lockington, 1879]), English sole (*Pleuronectes vetulus* [Girard, 1854]) and arrowtooth flounder (*Atheresthes stomias* [Jordan and Gilbert, 1880]).

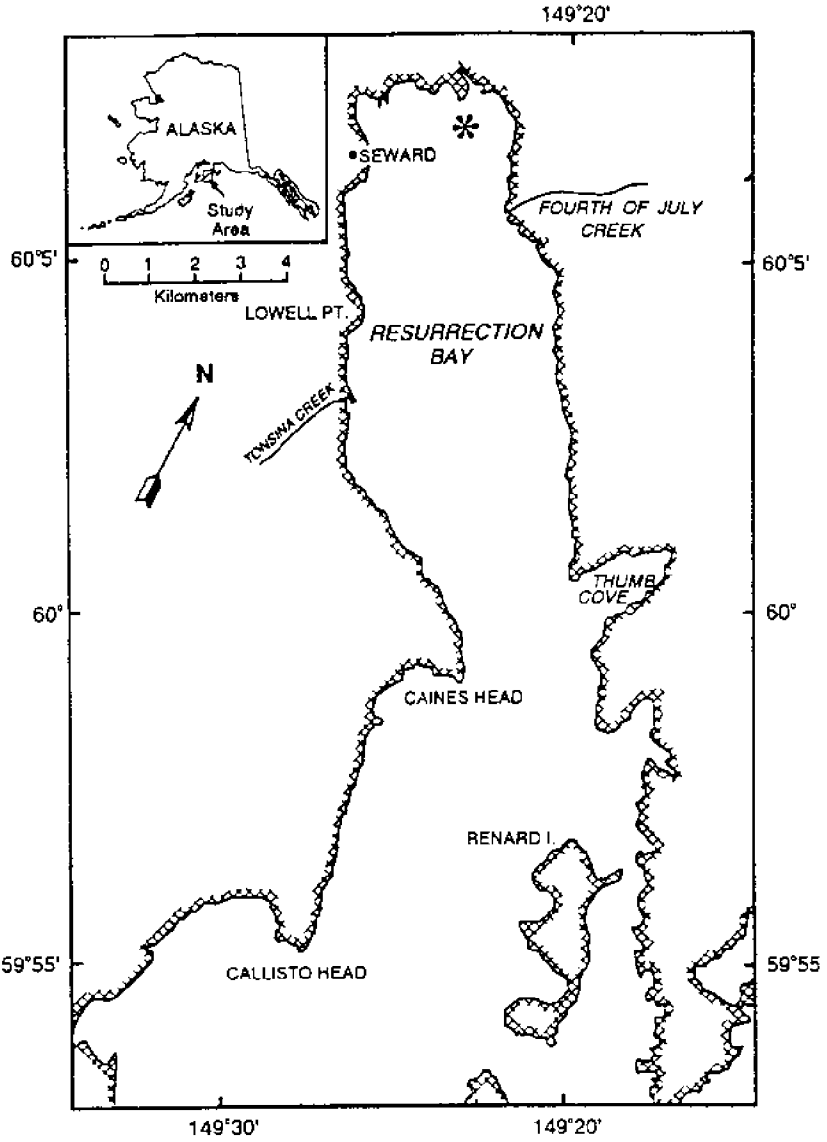


Figure 1. Site near Seward (asterisk) from which flatfish were collected in Alaska.

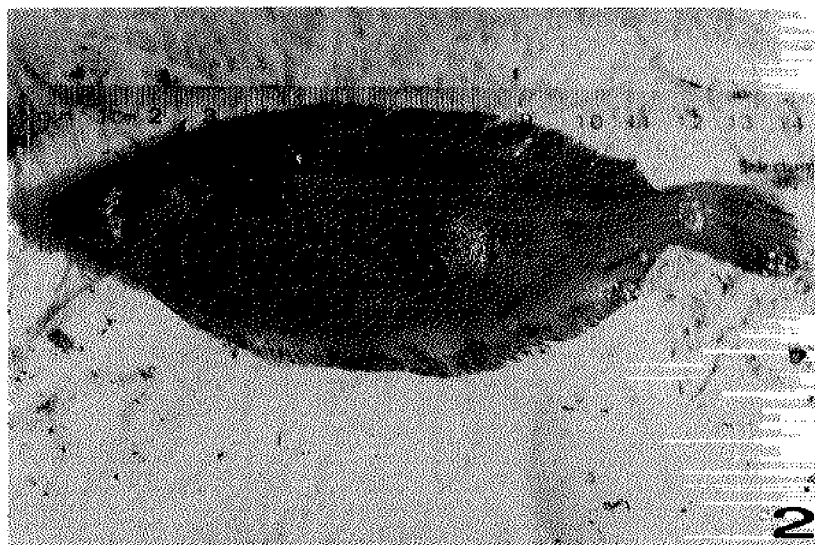


Figure 2. Tumor on the right side of a Dover sole.



Figure 3. Tumor on the left side of a flathead sole.

Table 1. Prevalence of epidermal tumors in species of flatfish captured in Resurrection Bay, Alaska, at 5 and 30-40 m depth.

Fish species	5 m		30-40 m	
	# with tumors/ # examined	%	# with tumors/ # examined	%
Flathead sole	4/6	67	0/12	0
Yellowfin sole	2/10	20	0/10	0
Dover sole	1/5	20	0/7	0
English sole	1/7	14	0/2	0
Arrowtooth flounder	0/19	0	0/9	0
Total	8/47	17	0/40	0

Fish were measured and examined macroscopically for lesions and ectoparasites. Tumors were excised, fixed in 10% formalin and subjected to conventional histological methods. Histological sections of 6 μ m were prepared and stained with hematoxylin and eosin. Other tissues were removed and preserved in 10% formalin for further histological study.

Results and Discussion

Skin tumors were observed in four of the five species captured at 5 m depth. None of the fishes from 30-40 m depth exhibited skin tumors (Table 1). Highest incidence of tumors occurred in flathead sole (67%) followed, in descending order, by yellowfin sole (20%), Dover sole (20%) and English sole (14%). Overall, 17% of the 47 fish examined had skin tumors. Tail necrosis (fin rot) was observed in two species; one of 10 yellowfin sole examined (10%) and one of six flathead sole examined (17%).

The size (to mm in diameter) of the tumors was variable as was the location. Tumors were present on both the right (eyed) side and the left (blind) sides. Some tumors were located toward the center of the body (Figures 2 and 3); others were associated with the fins (Figure 4). Only small Dover and English sole had tumors while both large and small yellowfin and flathead soles were affected.

Microscopic examination of the tumors revealed that these were epidermal papillomas consisting of hyperplastic epidermal cells with a papilliform arrangement developing above the connective tissue.



Figure 4. Tumors on the tails of a yellowfin and a flathead sole.

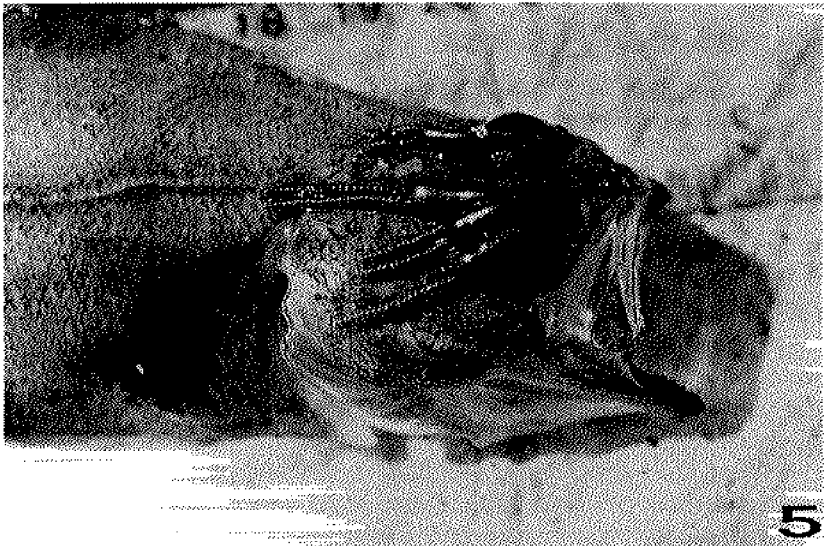


Figure 5. Copepods, *Phrixocephalus cincinnatus*, parasitizing the eyes of an arrowtooth flounder.

Inflammatory and epidermal cells were also observed in the connective tissue itself.

A penellid copepod, *Phrixocephalus cincinnatus* (Copepoda: Penellidae) parasitized the eye of arrowtooth flounder in Resurrection Bay (Figure 5). Seven of 19 fish examined (37%) harbored an intensity of 2.1 ± 0.4 parasites per fish. As many as five parasites were imbedded within the eye of a single flounder and one fish had multiple parasites attached to both eyes. Three of the affected fish had opaque eyes; the remaining four had hematomas associated with the point of entry of the copepod into the eye.

Results of this preliminary survey have revealed the presence of epidermal tumors (epitheliomas) in at least four species of flatfish inhabiting Resurrection Bay. Skin tumors described as epitheliomas or epidermal papillomas might consist of connective tissue nodules or true papillomas derived from the epidermis (Wellings et al. 1965). Epizootics of skin tumors have been reported previously in several species of flatfish including Dover, English and flathead sole inhabiting the north Pacific Ocean (Mawdesley-Thomas 1972). Nigrelli et al. (1965) examined flatfishes of the coast of British Columbia and observed that 32% of 726 sand sole (*Psettichthys melanostictus*) had epidermal tumors. These tumors also occurred in rock, English and butter sole (*Isopsetta isolepis*). The authors speculated that a cytomegalovirus was the causative agent. Wellings et al. (1977) suggested that an X-cell might be the underlying cause. More recently, Goyetter et al. (1988) reported epidermal papillomas in English sole captured in Vancouver Harbor, British Columbia, which receives both urban and industrial discharges containing toxic and carcinogenic wastes. The presence of hepatic lesions in 30% of 106 fish was suggestive of exposure to xenobiotics which could occur in the sediment and water column.

Recent work on the diseases of flatfish in the Dutch Wadden Sea by Vethaak (1992) indicate that fish exposed to strong salinity fluctuations are much more likely to develop skin diseases. That is, salinity fluctuation is a stress factor. In this study, the only fish exhibiting skin tumors were sampled from the 5 m depth contour, where significant salinity fluctuations occur depending on the tides, extent of freshwater runoff and wind mixing.

If, on the other hand, physical and biological variables in the ecosystem did not cause tumors in the species of flatfish in Resurrection Bay, their induction may well be associated with pollutants that are present at shallow depths. Flatfish tend to submerge themselves in

sediment when not foraging for food and are more likely to be affected by contaminated sediment than are other benthic fishes. Moreover, the occurrence of epitheliomas in both juvenile and adult flounder suggests that exposure to carcinogens may occur at an early age and most likely in the shallow, nursery area.

Most studies which have reported tumors in fish indicate that they occur more often in large or old fish (Malins et al. 1984; Murchelano and Wolke 1987). Maccubbin and Erising (1991), for example, noted that epidermal papillomas in bullheads (*Ictalurus nebulosus*) and fibromas in the skin of walleye (*Stizostedion vitreum*) were found primarily in older or large specimens, but Nigrelli et al. (1965) noted them in young (1-2 year old) sand soles. Wellings et al. (1977) observed at certain sites in Puget Sound that the prevalence of epidermal papillomas in young-of-the-year flatfish exceeded 50%. These fish were smaller, weighed less and disappeared earlier in collections than normal fish. Moreover, the prevalence of tumors in flatfish in Resurrection Bay is comparable and, in some instances higher than in fish taken from industrialized areas such as Boston Harbor, Puget Sound, the Great Lakes, the Hudson River, New York, and the Elizabeth River, Vermont (Malins et al. 1984; Murchelano and Wolke 1987; Bowser et al. 1990; Vogelbein et al. 1990; Baumann et al. 1991). A wide range of chemicals have been reported in these studies from several species of fish including polychlorinated aromatics in bullheads, PCBs in Atlantic tomcod (*Microgadus tomcod*), PAHs in English sole and creosote in mummichog, *Fundulus heteroclitus* (Smith et al. 1979; Malins et al. 1984; Vogelbein et al. 1990; Baumann et al. 1991). These and other studies have also shown more subtle changes such as elevated levels of detoxifying enzymes, such as mixed function oxygenase, which might culminate in the release of benzo (a) pyrene, a carcinogen (Vogelbein et al. 1990).

The findings reported in this pilot study indicate that further attention to fish health in Alaskan fjords is warranted. Future studies on flatfish in Resurrection Bay should focus not only on skin lesions but also on tissue contaminants, detoxifying enzyme activity and histopathology to assess the impact of xenobiotics on fish health and populations.

From this study, the presence of single, opaque eyes in three juvenile arrowtooth flounder infected with the copepod, *P. cinnatus*, indicates that the parasite causes blindness. Kabata and Forrester (1974) observed that the infection was more common in young fish and it diminished in prevalence with age and depth. The

authors also reported that the small, juvenile parasite penetrates the eye, then the retina and eventually embeds itself in a blood vessel. With growth, it moves backwards through the eye forming a large hematoma and ultimately causing blindness. Kabata and Forrester (1974) speculated on the basis of diet, that destruction of one eye does not impair foraging but might influence avoidance of predators. Binocular infection appeared to be fatal. In view of these findings, an in-depth study on the host parasite relationship of *P. cincinnatus* in the Gulf of Alaska seems warranted.

The higher prevalence of *P. cincinnatus* in arrowtooth flounder captured at 5 m than at 30-40 m suggests that a focus of infection occurs at shallow depths. Some copepods such as *Lernaecocera branchialis* infect more young than older Atlantic cod (*Gadus morhua*) and infections are more prevalent inshore than offshore (Khan 1988). Similar results were also reported in arrowtooth flounder captured in Canadian Pacific waters (Kabata and Forrester 1974). Both field and laboratory studies support the view of increased parasitism in fish living in polluted waters (Khan and Thulin 1991). It is also likely that the high prevalence of *P. cincinnatus* in arrowtooth flounder might be related to the presence of pollutants which are known to impair host's defense mechanisms and increase susceptibility to ectoparasites (Anderson 1990; Khan and Thulin, 1991).

Acknowledgments

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Management of Flatfish Fisheries in the North Pacific

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Abstract

An overview of management strategies for flatfish fisheries off Alaska is provided. Fisheries for all flatfish species, with the exception of Pacific halibut, are managed by the North Pacific Fishery Management Council through the National Marine Fisheries Service. Harvest of groundfish species, including flatfish, is regulated by the implementation of two fishery management plans: one in the Gulf of Alaska (GOA), and the other for the Bering Sea and Aleutian Islands (BSAI) area. The relative biomass of flatfish species differs greatly between these areas. In the GOA, arrowtooth flounder comprise 72% of the total exploitable flatfish biomass, which was estimated to be about 2.6 million mt for 1994. In the BSAI, yellowfin sole and rock sole together comprise a majority (67%) of exploitable flatfish biomass (6.1 million mt). Biomass of GOA and BSAI flatfish stocks has increased as a result of good recruitment and low exploitation. Annual quotas, called total allowable catches (TACs), are set for individual species or species complexes, and may be apportioned among regulatory areas based on biomass distribution to prevent localized depletion. With the exception of BSAI Greenland turbot, fisheries have been unable to fully harvest the exploitable biomass of any of the flatfish species or complexes due to halibut and crab bycatch limits and conservative quotas. Historically, flatfish TACs have been set much lower than the acceptable biological catch (ABC) levels. In the GOA, this is done to protect the available bycatch for more economically valuable fisheries such as pollock, Pacific cod, and rockfish. Total harvest of all finfish in the BSAI is limited by an optimum yield cap of two million metric tons per year; consequently, most TACs of flatfish are reduced well

below ABC levels to allow for larger harvests of more valuable species, particularly walleye pollock and Pacific cod. Discarding of flatfish has been prevalent in both areas due to relatively low economic returns in the race for fish, and the council is evaluating potential regulatory changes to reduce discarding.

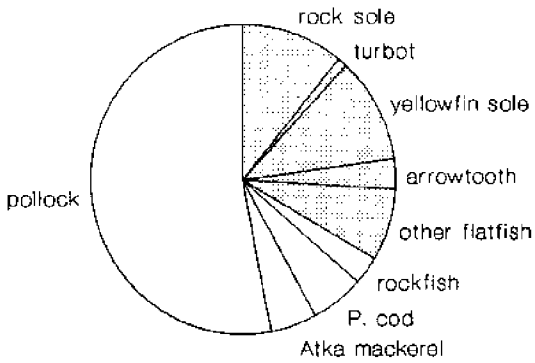
Introduction

The Magnuson Fishery Conservation and Management Act gave the United States management authority over all the living resources within the Exclusive Economic Zone (EEZ), which is the area from 3 to 200 nautical miles offshore of the U.S. coast. The Act created eight regional fishery management councils, one of which is the North Pacific Fishery Management Council (NPFMC), to provide local and regional input into fisheries management. With the exception of Pacific halibut (*Hippoglossus stenolepis*), flatfish and other groundfish fisheries in the North Pacific are managed under two fishery management plans, one for the Gulf of Alaska (GOA) and one for the Bering Sea and Aleutian Islands (BSAI) area (NPFMC 1991, 1993a). The groundfish plans were implemented in 1978 (GOA) and 1982 (BSAI), and have since been amended many times to meet changing management needs; consequently, the plans and their implementing regulations have become quite complex. This paper is intended to provide a brief overview of the management plans as they currently relate to flatfish fisheries.

Stocks and Fisheries

Flatfish species comprise a large proportion of groundfish exploitable biomass in the GOA and BSAI (Figure 1). Dominant species include arrowtooth flounder (*Atheresthes stomias*) in the GOA, and yellowfin sole (*Pleuronectes asper*) and rock sole (*P. bilineatus*) in the BSAI. In the GOA, arrowtooth flounder comprise 72% of the total exploitable flatfish biomass, which was estimated to be about 2.6 million mt for 1994. To a lesser extent, flathead sole (*Hippoglossoides elassodon*), shallow water flatfish (primarily rock sole and yellowfin sole), and deep water flatfish (primarily rex sole *Errex zachirus*, and Dover sole *Microstomus pacificus*) are also found in commercial quantities in the GOA. In the BSAI, yellowfin sole and rock sole together comprise a majority (67%) of exploitable flatfish biomass (6.1 million mt). Other abundant or commercially important BSAI flatfish species include arrowtooth flounder, flathead sole, Alaska plaice (*Pleuronectes quadri-*

Bering Sea and Aleutian Islands



Gulf of Alaska

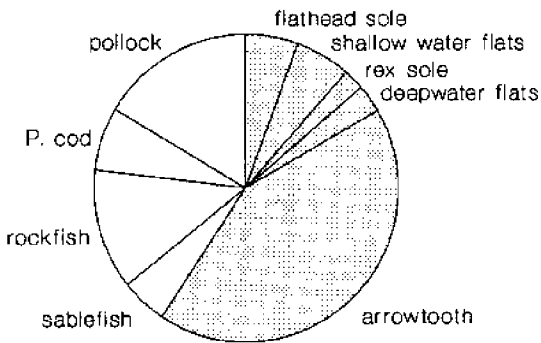


Figure 1. Species composition of groundfish exploitable biomass in the Gulf of Alaska and Bering Sea/Aleutian Islands area, 1994.

tuberculatus), and Greenland turbot (*Reinhardtius hippoglossoides*). Biomass of most GOA and BSAI flatfish stocks is relatively high and increasing as a result of good recruitment and low exploitation (NPFMC 1993b, 1993c).

Harvests of most flatfish species have remained at low levels despite high abundance. Until 1984, flatfish were harvested at low to moderate levels by foreign fisheries operating in the North Pacific. After passage of the Magnuson Act, foreign fisheries were gradually replaced with joint ventures, then superseded by domestic fishermen and processors. Since 1990, groundfish fisheries have been conducted entirely by the domestic fleet (Figure 2), with flatfish caught and processed primarily by offshore trawl operations. Catches in the BSAI have been variable since 1978, with yellowfin sole and rock sole serving as primary target species. Catches have been increasing in the GOA, and have consisted mainly of arrowtooth flounder taken as bycatch in the pursuit of other target species. With the exception of BSAI Greenland turbot, fisheries have been unable to fully harvest the exploitable biomass of any of the flatfish species or complexes due to halibut and crab bycatch limits and conservative quotas.

Although flatfish have remained underutilized, they are nonetheless valuable fisheries. Total ex-vessel revenue for flatfish landed increased through the 1980s, with 1992 landings worth 7.2 million dollars from GOA flatfish and 48.4 million dollars from BSAI flatfish (Kinoshita et al. 1993). Flatfish fisheries are not as valuable as trawl fisheries for pollock and Pacific cod, and hook and line fisheries for sablefish, however (Table 1). Overall flatfish landings comprised only 4.9% of the 1992 ex-vessel value of all GOA groundfish fisheries and 9.2% of the 1992 ex-vessel value of all BSAI groundfish fisheries. Nevertheless, 1992 BSAI flatfish landings were more valuable than any of the GOA fisheries.

Management Measures

The fishery management plans allow for control of flatfish and other groundfish fisheries by limited entry, quotas for target and bycatch species, seasons, in-season adjustments, gear restrictions, closed waters, allocations, regulatory areas, reporting requirements, and permits. Not all of these management measures are applicable to current fisheries for flatfish, however. For example, there are no explicit allocations of flatfish among gear types, as is the case with sablefish and BSAI Pacific cod. Also, there are no minimum size restrictions on flatfish or other groundfish managed by the NPFMC.

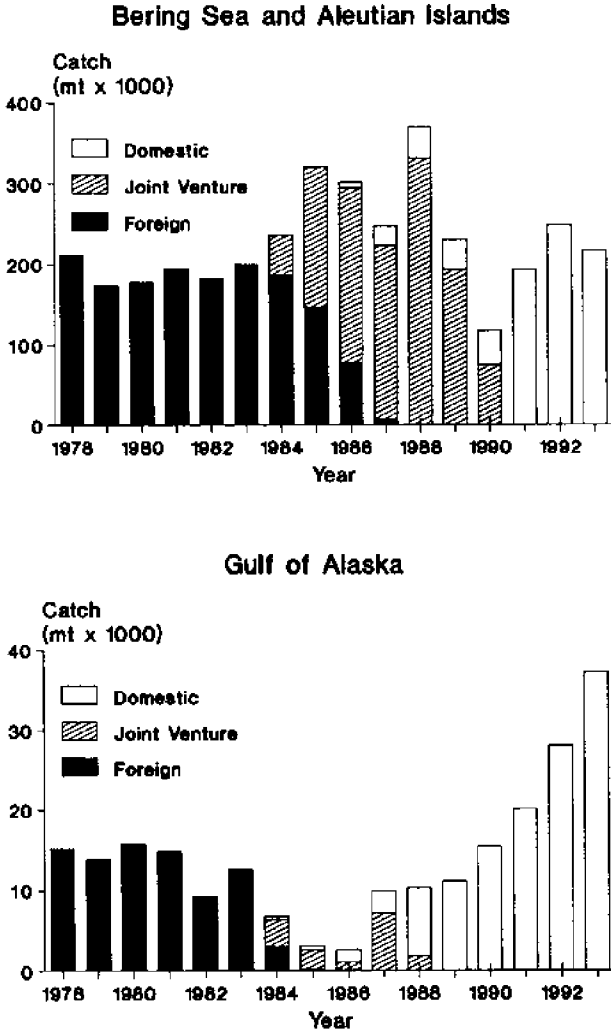


Figure 2. Landings of flatfish in the Gulf of Alaska and Bering Sea/Aleutian Islands area by foreign, joint venture, and domestic fisheries, 1978-1993.

Table 1. Average ex-vessel price (\$/lb, round weight) and total ex-vessel value for 1992 groundfish fisheries off Alaska, by area and species complex (from Kinoshita et al. 1993).

	Average price	GOA value	BSAI value	Total value
Pollock	0.126	28.2	360.5	388.7
Sablefish ¹	1.024	47.9	5.2	53.1
Pacific cod	0.231	42.2	85.3	127.5
Flatfish	0.107	7.2	48.4	55.6
Rockfish	0.242	16.1	4.9	21.0
Atka mackerel	0.125	3.8	12.7	16.5
Total		145.4	517.0	662.4

¹Sablefish are harvested primarily by hook and line gear.

Management measures currently applied to flatfish fisheries are described in this section.

Permits and limited entry

Federal fishing permits are required for vessels fishing in the EEZ of the BSAI and GOA. These permits, which are issued annually and are nontransferable, allow for fleet monitoring and overall fishery management. The NPFMC has taken steps to limit entry of new vessels into the groundfish fisheries by adopting a vessel moratorium in 1992, and revised to be more restrictive in 1994. The number of boats participating in groundfish fisheries had increased dramatically from slightly over 2,000 boats in 1977 to a fleet size of 4,963 boats in 1991. The large number of vessels fishing for a limited resource had created a "race for fish," characterized by short seasons and economic inefficiency. Although a moratorium may not resolve the underlying problems of existing overcapitalization and excess effort in the groundfish fisheries, the intent of the moratorium was to prevent these problems from worsening while comprehensive solutions are being developed. To resolve these problems, the NPFMC is currently in the process of examining ways to rationalize the groundfish and crab fisheries by using other forms of limited access such as license limitation or individual fishing quotas (IFQs). IFQ management of the hook and line halibut and sablefish fisheries off Alaska is scheduled to begin with the 1995 fisheries.

Regulatory areas

For management purposes, the NPFMC has split up the North Pacific into management units (BSAI and GOA) and regulatory areas (Figure 3). Regulatory areas allow for management measures to be regionally applied. Quotas, bycatch limits, seasons, and gear restrictions may be specific to regulatory areas, and in-season adjustments can be applied to more discrete areas than the entire management unit. For example, bycatch limits for *Chionoecetes bairdi* Tanner crab are set for Zone 1 (which includes regulatory areas 511, 512, and 516) and Zone 2 (regulatory areas 513, 517, and 521). If bycatch limits are reached in one of these zones, only those regulatory areas encompassed by the zone are closed to the affected fishery.

Quotas

Total removals of flatfish and other groundfish are controlled by quotas. Each year, the NPFMC makes recommendations to the Secretary of Commerce on annual harvest levels for target, prohibited, and other species categories. Harvest levels are based on annual stock assessments, which are reviewed by the NPFMC's groundfish plan teams and scientific and statistical committee, and other relevant information on the fisheries. For target species, such as flatfish, three harvest levels are set, corresponding to the overfishing level (OFL), the acceptable biological catch (ABC) and total allowable catch (TAC). TACs are essentially annual quotas for the fishery, ABCs generally define acceptable harvest levels from a stock perspective, and OFL defines the unacceptable harvest level. These quota specifications account for all fish harvested, including those fish landed and those discarded (100% mortality for all discards is assumed). To evenly distribute catch and effort, ABCs and TACs may set for specific regulatory areas, particularly in the GOA. The total TACs of all species, within all regulatory areas, must fall within the optimum yield (OY) range of 116,000 to 800,000 mt for the GOA and 1.4 to 2.0 million mt for the BSAI. The 1993 ABCs, TACs, and subsequent catch (including discards) of flatfish in the GOA and BSAI areas are listed in Table 2. The NMFS is responsible for in-season management of the fisheries, and closes directed fisheries for each species or complex when the TAC is taken. Following a directed fishing closure, species may be retained as bycatch or specified as non-retainable. As such, management has been relatively effective at maintaining catches of flatfish and other groundfish within biologically acceptable levels.

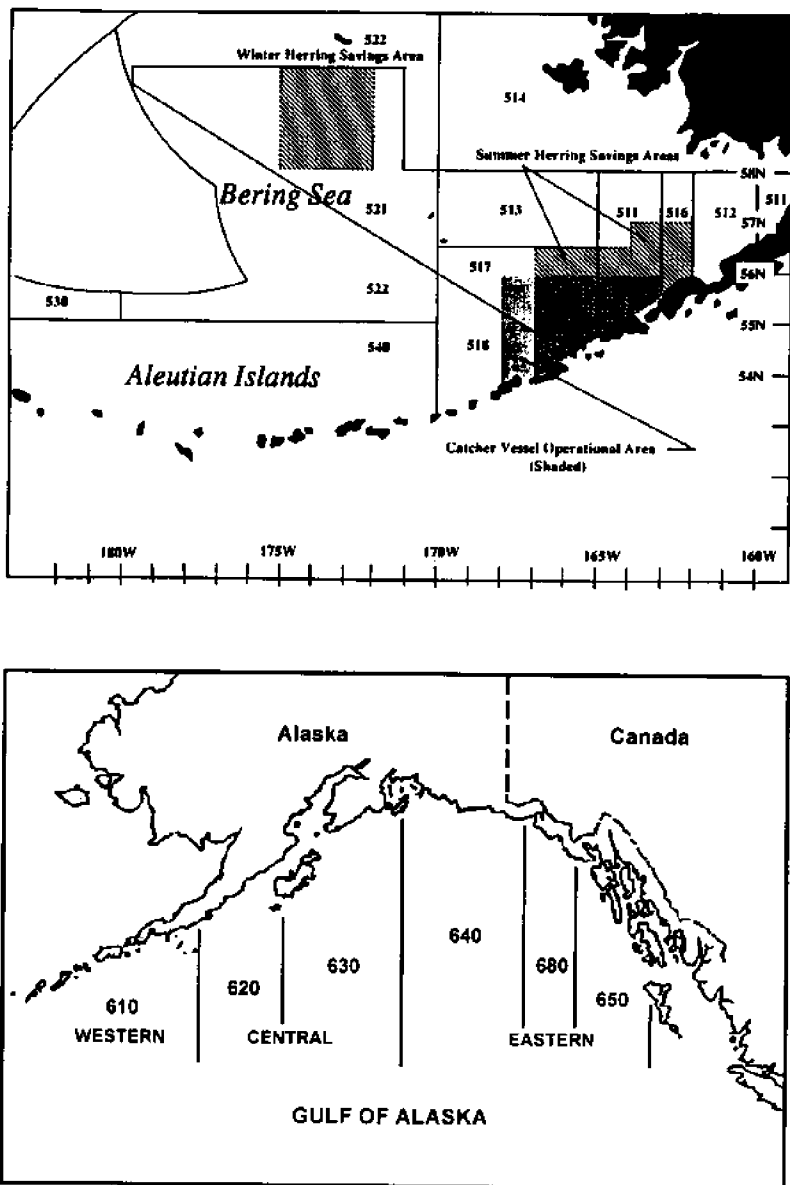


Figure 3. Regulatory areas for groundfish fisheries in the Gulf of Alaska and Bering Sea /Aleutian Islands area.

Table 2. Harvest specifications (in metric tons) for the 1993 flatfish fisheries in the Gulf of Alaska and Bering Sea/Aleutian Islands area, including exploitable biomass, Overfishing Level (OFL), Allowable Biological Catch (ABC), Total Allowable Catch (TAC), and 1993 catches.

Species complex	Exploitable biomass	OFL	ABC	TAC	Catch
Bering Sea/Aleutian Islands					
Yellowfin sole	2,500,000	275,000	238,000	187,000	106,101
Greenland turbot	292,000	10,500	7,000	7,000	8,447
Arrowtooth	480,000	96,000	72,000	10,000	9,338
Rock sole	1,550,000	270,000	185,000	75,000	63,953
Other flatfish	1,250,000	228,000	191,000	67,150	29,073
Total BSAI	6,072,000	879,500	693,000	346,150	216,912
Gulf of Alaska					
Shallow water flatfish	261,720	70,860	50,480	16,240	9,148
Deep water flatfish	227,660	59,650	45,530	19,740	6,179
Flathead sole	247,250	64,780	49,450	10,000	2,821
Arrowtooth	1,889,920	451,600	321,290	30,000	19,091
Total GOA	2,626,550	646,980	466,750	75,980	37,239

Historically, flatfish TACs have been set much lower than the acceptable biological catch (ABC) levels. In the GOA, this is done to protect the available bycatch for more economically valuable trawl fisheries for pollock, Pacific cod, and rockfish. Total harvest of all finfish in the BSAI is limited by an optimum yield cap of two million metric tons per year; consequently, most TACs of flatfish are reduced well below ABC levels to allow for larger harvests of more valuable species, particularly walleye pollock and Pacific cod.

Seasons

The fishing year is defined as January 1 through December 31, with seasonal restrictions by fishery. In the GOA, all groundfish fishing with fixed gear may begin on January 1 with the exception of the sablefish longline fishery, which begins mid-May depending on tides. Trawl fisheries open on January 20 in both the GOA and BSAI (beginning in 1994). Flatfish fisheries no longer occur on a year-round basis, but

instead are concentrated over several months when TAC and bycatch are available.

Gear restrictions

Legal gear types for harvesting flatfish and other groundfish in the GOA and BSAI include hook and line, jig, troll, longline, longline pot, pelagic trawl, pot and line, Danish seine, and trawl. Undefined gear, including sunken gillnets, seines, and others are not legal for directed fishing for groundfish. However, vessels participating in non-groundfish fisheries (e.g. salmon fisheries) using undefined gear are allowed to retain bycatch amounts of groundfish consistent with existing directed fishing standards. In addition to restricting gear types, the NPFMC has also instituted marking requirements, mandatory escape panels for pot gear, and maximum size of pot tunnel openings. A six inch minimum mesh size was recently adopted for codends used in the BSAI rock sole trawl fishery.

Closed waters

Some areas have been designated as waters closed to fishing to offer protection for particular marine organisms and habitats. These areas may prohibit fishing with certain gear types or fishing during certain months. In the Gulf of Alaska, several areas around Kodiak Island are closed to bottom trawling to protect juvenile and molting red king crab (*Paralithodes camtschatica*). A larger area in the BSAI around the Pribilof Islands restricts all trawling to protect juvenile blue king crabs (*P. platypus*) and their habitat. Until 1994, some trawling for yellowfin sole occurred in the Pribilof area. Closed areas have also been designated to protect Pacific herring (*Clupea harengus pallasii*). Attainment of a herring bycatch cap, set at 1% of the herring biomass, will trigger trawl closures in two areas north of the Alaska Peninsula and an area northwest of the Pribilof Islands. Yellowfin sole trawl fisheries have some potential to be affected if BSAI herring biomass declines in the future. To protect Steller sea lions (*Eumetopias jubatus*), a threatened species under the Endangered Species Act, trawling is prohibited year-round within 10 nautical miles of numerous Steller sea lion rookeries. Currently, there are 14 rookery closures in the Gulf of Alaska, 8 in the Bering Sea, and 19 in the Aleutian Islands area. Some sea lion rookery closures extend out to 20 nautical miles on a seasonal basis. To protect Pacific walrus (*Odobenus rosmarus*), seasonal closures extending out to 12 miles around Round Island, The Twins, and Cape Pierce have also been implemented. Many areas within state waters have also

Table 3. Gulf of Alaska halibut PSC apportionments and seasonal allowances for 1994 trawl fisheries. Target fisheries in the shallow water complex are pollock, Pacific cod, shallow water flatfish, Atka mackerel, and other species. Deep water complex fisheries include those for deep water flatfish, rockfish, flathead sole, sablefish, and arrowtooth flounder.

Quarter	Shallow complex	Deep water complex	Total
1st quarter	500 mt	100 mt	600 mt
2nd quarter	100 mt	300 mt	400 mt
3rd quarter	200 mt	400 mt	600 mt
4th quarter	—No apportionment—		400 mt
Total			2000 mt

been closed to trawling to protect marine resources and habitats. These numerous federal and state time/area closures may serve as refugia for adult and juvenile flatfish, but the benefits have not been assessed from this perspective.

Bycatch caps

Bycatch caps were designed to restrict the amount of halibut, herring, red king crab, and *C. bairdi* Tanner crab that can be caught incidentally in the pursuit of other fisheries. These caps are called prohibited species catch (PSC) limits. When the vessels to which a PSC limit applies have caught an amount equal to that PSC, bottom trawling or longlining may be prohibited altogether to minimize further impact on halibut or other prohibited species. In the GOA, a PSC cap is set for halibut only, and the cap has been the limiting factor to increasing harvests of flatfish in the GOA (Davis and Baldwin 1994). In 1994, the PSC limit for halibut in the GOA trawl fisheries was 2,000 mt (Table 3). This PSC cap was further apportioned among seasons and specific fisheries, depending whether they targeted species belonging to a shallow water or a deep water complex. Species in the shallow complex were walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), shallow water flatfish, Atka mackerel (*Pleurogrammus monpterygius*), and other species. Deep water complex

Table 4. Bering Sea/Aleutian Islands trawl fisheries PSC apportionments and seasonal allowances for 1994.

Fishery group	Halibut mortality rate	Halibut mortality cap (mt)	Herring bycatch (mt)	Red king crab Zone 1	<i>C. bairdi</i> crab Zone 1	<i>C. bairdi</i> crab Zone 2
Yellowfin sole	70%	592	332	40,000	175,000	1,275,000
May 1-Aug 2		230				
Aug 3-Dec 31		362				
Rocksole/ other flatfish	70%	688		110,000	475,000	260,000
Jan 1-Mar 29		428				
Mar 30-Jun 28		180				
Jun 29-Dec 31		80				
Turbot/arrowtooth/ sablefish	40%	137				5,000
Rockfish	60%	201	8			10,000
Jan 20-Mar 29		40				
Mar 30-June 28		120				
Jun 29-Dec 31		41				
Pacific cod						
Jan 20-Jun 28	60%	1,200	25	10,000	175,000	200,000
Pollock/mackerel/ "o. species"	60%	957	178	40,000	175,000	1,250,000
Jan 20-April 15		430				
April 16-Dec 31		527				
7 MW pollock (herring)			1,419			
Total		3,775	1,962	200,000	1,000,000	3,000,000

species included deep water flatfish, rockfish, flathead sole, sablefish (*Anoplopoma fimbria*), and arrowtooth flounder.

In the BSAI, PSC caps for trawl fisheries apply to halibut, herring, red king crab, and *C. bairdi* Tanner crab, and are apportioned seasonally among specific target fisheries (Table 4). Crab caps are set for two areas, Zone 1 and Zone 2, and attainment of the cap will close the zone to trawling. Together with a two million mt OY, halibut and crab PSC caps are the limiting factor to increasing the harvest of flatfish in the BSAI. For example, the 1994 rock sole and other flatfish fisheries were affected when Zone 1 was closed on February 25 with the attainment of the red king crab PSC cap and Zone 2 was closed on

May 7 with the attainment of the *C. bairdi* PSC cap. All areas were closed to directed fishing for rock sole and other flatfish on July 5, when the halibut PSC cap was reached. As a result of these closures, approximately 8% of the rock sole TAC and 45% of the other flatfish TAC remain unharvested.

Bycatch rates

In addition to limiting the total bycatch of PSC species, the NPFMC has also attempted to reduce bycatch rates through a vessel incentive program (VIP). This program was instituted in 1991 to discourage vessels from having excessive bycatch rates and, if possible, to temporarily remove vessels that have high bycatch rates. Specifically, a vessel with a bycatch rate substantially above a fishery average would be fined or prohibited from further fishing for a specified period of time. The VIP rate standards are set each year for halibut and red king crab taken in trawl groundfish fisheries. Rates are based on kg halibut or number of crab per mt of groundfish. For example, the 1993 BSAI yellowfin sole fisheries VIP rate standards were set at 5 kg halibut and 2.5 red king crab per metric ton of groundfish. The VIP rate standard for all GOA trawl fisheries, except midwater pollock trawl fishery, was set at 40 kg of halibut per metric ton of groundfish.

Monitoring and Enforcement

Recordkeeping and reporting requirements have been implemented to keep track of fishing effort, landings, processing, and transfers. Fishing vessel operators making landings in Alaska and, if requested, the purchasers of the catch, must report the catch on Alaska Department of Fish and Game (ADF&G) fish tickets within one week of the landing. Landings to other states or outside the EEZ must be reported on ADF&G fish tickets or the equivalent within one week of the landing. Catcher/processor and mothership/processor vessel operators are required to have a federal permit and must also submit ADF&G fish tickets or the equivalent within one week of transferring fish. There are numerous other requirements for recordkeeping and reporting, to ensure timely and effective in-season management of individual groundfish stocks.

Information on fishery catch, bycatch, discards, abundance, and species composition is collected through the domestic observer program. This type of information is invaluable for effective in-season management and used in stock assessments. Observers are contracted

through independent agencies, and the program is paid for by participants. The current fisheries observer program calls for observers at shore plants, on floating processors and motherships, and trawl and longline groundfish vessels. The amount of observer coverage required depends on operation, vessel type and size. Larger vessels have generally required more observer coverage. For example in 1993, vessels larger than 125' required observers to be onboard at all times; vessels 60' to 125' required observers on 30% of their fishing days per month, and vessels less than 60' in length did not require an observer. Changes in observer coverage are made through a regulatory amendment process.

The structure of the observer program will change somewhat with the implementation of the North Pacific Fisheries Research Plan. The research plan, when it becomes effective, will provide the flexibility to adjust coverage requirements annually. For the first twelve months of the program, fishing operations will continue to carry and pay for observers as currently required; those not carrying and paying for observers will pay a percentage fee of their ex-vessel fish value (up to 2%) into a research fund. After the first year, all vessels will pay into this fund, and observer costs will be paid for out of the fund.

Enforcement of EEZ fishery regulations is the responsibility of the U.S. Department of Commerce and the Coast Guard, in cooperation with other federal and state agencies. The Coast Guard supplies at-sea enforcement using both vessel and air surveillance. The Department of Commerce enforces regulations through the National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NOAA/NMFS) agents and prosecutors. State enforcement agents assist these agencies when possible.

Future Management Issues

Further development of the fisheries for flatfish is constrained by bycatch and processing technology. Halibut bycatch caps have limited the amount of flatfish that can be taken under the current management strategy, and significant increases in flatfish landings in the future may only be possible with increases in halibut bycatch caps (Davis and Baldwin 1993). However, development of fishing gears that catch flatfish in commercial quantities, with low halibut bycatch rates, may allow higher catches of flatfish even under the current management strategy. Improved processing technology may result in higher retention rates for flatfish and generate more revenues from flatfish

catches. Significant progress has been made for processing arrowtooth flounder into surimi (AFDF 1993).

Another issue, and perhaps more pressing, is the public concern regarding discarding (and perceived waste) of groundfish in the North Pacific and elsewhere. Discarding of flatfish has been prevalent in the GOA and BSAI due to low economic returns relative to other target species in the race for fish and available bycatch. Because larger amounts of flatfish are captured by trawl gear, discarding by this gear type in particular, receives the most public scrutiny. Flatfish are also captured in pots and longlines, and represent a large proportion of the finfish discarded by these gear types. Flatfish discards from all gear types and all target fisheries in 1993 amounted to 48.4% of the total flatfish catch (Table 5). Discarding varied by area, processing mode, and species complex. Although arrowtooth flounder had the highest discarding rates (92% average), total discards were highest for BSAI rock sole (41,411 mt). Flatfish species with the lowest discard rates were GOA deep water flatfish and BSAI Greenland turbot.

Potential regulatory changes to reduce discarding of flatfish and other groundfish are currently being evaluated. Strategies under consideration range from technological changes to operational changes and restrictions. An example of a technological change is the measure recently adopted that regulates minimum mesh size of trawl codends, that may reduce the catch of juvenile and non-target species. The other extreme would be to reduce or eliminate discarding by requiring mandatory retention or processing of all fish captured by any gear type. A less restrictive option under consideration may encourage processing of those fish already caught by slowing down the race for fish, or allowing fishermen with low bycatch rates access to additional quota as incentive.

The NPFMC is in the process of developing a comprehensive rationalization plan that may address some of the limitations to the developing flatfish fishery. One of the options being considered is an individual fishing quota (IFQ) program, similar to one adopted for U.S. halibut and sablefish fisheries. Under an IFQ program, the annual quota (total allowable catch in weight) would be distributed based on the amount of quota share held by each share holder. Actual poundage value assigned to each quota share would vary slightly each year with the total allowable quota, which is based on exploitable biomass. Problems that may be addressed by an IFQ program include allocation conflicts, gear conflict, deadloss from lost gear, bycatch loss, discard mortality, excess harvesting capacity, product wholesomeness, safety,

Table 5. Catch and discard of flatfish in the 1993 Gulf of Alaska and Bering Sea/Aleutian Island fisheries, by harvesting mode.

	Shoreside			Mothership		Catcher/proc		Totals	
	Total catch	At-sea discard	Plant discard	Total catch	Discard	Total catch	Discard	Total catch	Percent discard
Bering Sea and Aleutians									
Arrowtooth	487	437	28	131	129	8,721	8,079	9,339	8,673 92.9
Greenland turbot	1,151	450	6	27	3	7,270	1,315	8,448	1,774 21.0
Other flatfish	1,477	1,212	117	379	353	27,216	17,455	29,072	19,137 65.8
Rock sole	5,635	5,213	405	893	641	57,426	35,152	63,954	41,411 64.8
Yellowfin sole	692	375	74	132	132	105,276	28,992	106,100	29,573 27.9
Total BSAI	9,442	7,687	630	1,562	1,258	205,909	90,993	216,913	100,568 46.4
Gulf of Alaska									
Arrowtooth	6,164	4,783	1,088	12	3	12,915	11,676	19,091	17,550 91.9
Deep water flats	2,223	111	383	14	0	3,941	615	6,178	1,109 18.0
Shallow water flats	8,356	718	1,748	14	14	778	342	9,148	2,822 30.8
Flathead sole	1,538	142	359	2	1	1,282	421	2,822	923 32.7
Total GOA	18,281	5,745	3,578	42	18	18,918	13,054	37,239	22,404 60.2
Total GOA and BSAI	27,723	13,441	4,208	1,604	1,276	224,825	104,047	254,152	122,972 48.4

and economic stability. Fishermen may have more time to process captured flatfish, and increase flatfish catch by fishing in the most efficient manner possible.

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Methods to Improve Survival of Pacific Halibut Bycatch Discarded from a Factory Trawler

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Abstract

Mortality of Pacific halibut (*Hippoglossus stenolepis*) caught as bycatch in groundfish fisheries causes economic losses to both groundfish and halibut fisheries. Restrictions on groundfish fisheries to reduce bycatch may cause closures before available groundfish are harvested, and halibut killed as bycatch are not available to the halibut fishery. Increasing survival of halibut bycatch, which must be discarded, is one way of benefiting groundfish and halibut fisheries. Factory trawlers fishing for Pacific cod (*Gadus macrocephalus*) cause a large proportion of halibut bycatch mortality in the Bering Sea, and have experienced fishery closures by exceeding halibut bycatch mortality limits. An experiment on board a factory trawler to sort and discard halibut on deck, using a grid over the hold, removed 40% by number and 52% by weight of the halibut that previously had all been dumped to the hold. Overall mortality of halibut from hauls sorted and discarded on deck decreased 13% and 24% from two alternate sorting methods that occurred in the factory. Time required to dump fish to the hold increased from 1 to 3 minutes for hauls dumped directly to the hold to 10-15 minutes for deck-sorted hauls. Reductions in discard mortality of halibut from factory trawl fisheries for Pacific cod and other groundfish could potentially add thousands of metric tons to

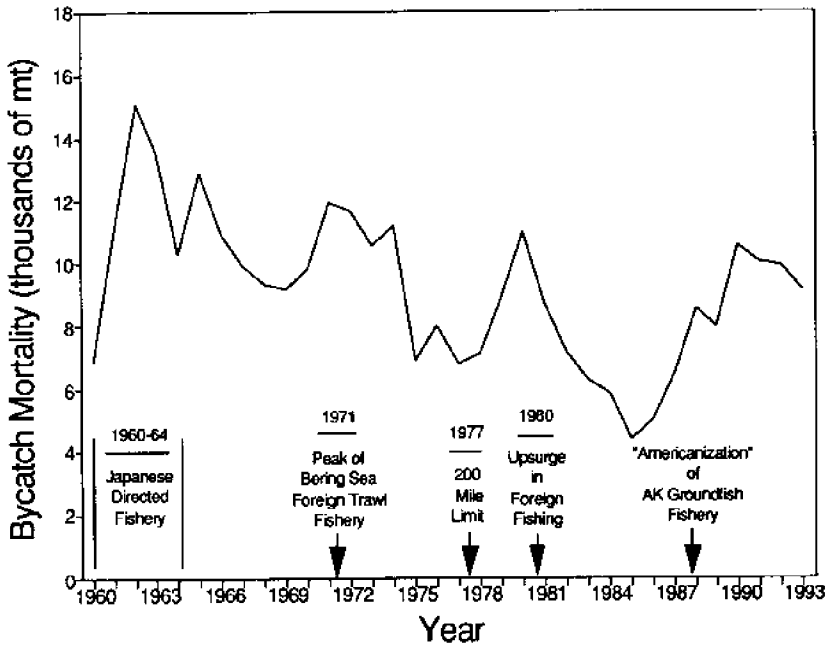


Figure 1. Pacific halibut bycatch mortality from 1960 through 1993.

the groundfish harvest, several hundred tons to the halibut fishery, and millions of dollars in revenues. Implementation of a regulation to require factory trawlers to sort on deck is under review. A final decision on deck-sorting will require policy makers to prioritize among competing demands for observer duties, recognize incompatibility with an existing program, and determine an acceptable level of observer coverage.

Introduction

Commercial fishing for Pacific halibut (*Hippoglossus stenolepis*) began in 1888, and has been a fully utilized domestic fishery of the United States and Canada since early in its history. When groundfish fisheries by foreign nations began the late 1950s and early 1960s, bycatch of Pacific halibut became a serious management issue. The foreign groundfish fleets agreed to discard halibut and other prohibited species, to prevent targeting. The foreign fleets killed over 12,000 mt

round weight of halibut bycatch annually (Fig. 1) before controls were implemented. Through bilateral negotiations and, after extended jurisdiction following the Magnuson Fishery Conservation and Management Act (MFCMA), foreign halibut bycatch was placed under limits (Fredin 1987, Freeburg 1991, Trumble 1992). Regulation of halibut bycatch and bycatch of other species slowly spread to the domestic fisheries of the United States and Canada. Discard of halibut and other prohibited species continued for the domestic groundfish fleets. Bilateral negotiations initially placed observers on board foreign vessels that fish for groundfish. After the MFCMA, regulations for Alaskan waters required observers first on foreign and joint venture vessels, and then on fully domestic vessels. Observers collect biological and fishery data for groundfish and prohibited species. These data are integral to bycatch management.

Bycatch regulations are most highly developed in Alaskan waters under the jurisdiction of the North Pacific Fishery Management Council (NPFMC) (Blackburn and Davis 1992). The NPFMC set bycatch limits of halibut and other species in most of the groundfish fisheries, that when reached, caused the fishery to close. The closures of the groundfish fisheries occurred prior to obtaining the allowable groundfish harvest. These closures have left unharvested thousands of metric tons of groundfish worth millions of dollars. The millions of pounds of halibut killed as bycatch deprived the halibut fishery of harvest and revenue. A cost effective method of bycatch reduction would be in the best interest of groundfish and halibut fleets. The groundfish fleets, however, have difficulty implementing bycatch controls because of competition for fish that develops under open access fishing: any voluntary action on the part of an individual vessel to reduce bycatch that slows down fishing will reduce harvest compared to vessels that do not participate in the bycatch reduction.

Under the race for fish, management agencies have a difficult time reducing bycatch rates. However, regulatory action to reduce the mortality of discarded halibut is feasible. In 1993, the NPFMC established a requirement for careful release of halibut by hook and line fisheries, and prescribed specific, acceptable methods (NPFMC 1992).

The desirability of reducing discard mortality from trawlers became clear. The survival of halibut returned to the sea from trawlers is very dependent on the time out of the water (Hoag 1975, NPFMC 1993): The more quickly that halibut are returned, the better they survive. While survival may exceed 75% for halibut returned immediately after capture, survival drops to near zero for halibut on deck for

more than 30-45 minutes. Williams and Wilderbuer (1994) used modifications of Hoag's methods to estimate discard mortality rates of halibut discarded from trawls. Current U.S. federal regulations for trawls are silent on halibut release methods, except that halibut must be returned to the sea with a minimum of injury. Conflicting U.S. federal regulations, however, prohibit discard of prohibited species until after the federal observer on board, if any, has had an opportunity to sample the catch. On factory trawlers and shore-based trawlers that dump directly to the hold before sorting, halibut and other prohibited species may remain in the hold for several hours while observers sample the catch in the factory. Mortality of discarded halibut will approach 100% in these cases.

The International Pacific Halibut Commission, the Highliners Association (with Natural Resources Consultants), and the National Marine Fisheries Service (NMFS) Alaska Fishery Science Center conducted an experiment to evaluate methods of increasing survival of discarded halibut bycatch from bottom trawls. The experiment involved sorting and discarding halibut from the groundfish catch more rapidly than is now current practice, and estimating the savings in halibut discard mortality rates. The experiment took place aboard the F/T *Northern Glacier* from October 6 through 29, 1993.

Halibut are caught as bycatch by most gear types used in North Pacific groundfish fisheries, but the majority are taken by trawls, especially those targeting on Pacific cod. Bycatch mortality could be reduced by improving survival and several methods have been suggested to accomplish this goal. One way would be to sort the halibut from the catch on deck, before groundfish and halibut are dumped into the below-deck holding tanks. A screen or grid has been suggested as a means of filtering halibut, particularly large halibut, from the catch. Another possibility is to improve the sorting methods used in the factory, in a manner that returns halibut to the sea more quickly than is currently practiced. Termed enhanced sorting, this practice could improve survival for the smaller fish that previously passed through the grid. This experiment was designed to address these issues.

Experimental Design

The vessel targeted Pacific cod in a normal commercial manner over the full 24-hour period. The experiment focused on the bottom trawl Pacific cod fishery because it is allotted the greatest portion of bycatch

in the Bering Sea. The vessel operated in the eastern Bering Sea and in the Gulf of Alaska. Considerable exploratory fishing occurred in an attempt to find areas of good groundfish fishing with moderate amounts of halibut bycatch. Two NMFS observers, one supplied by the vessel and one by the NMFS, determined halibut viability from each haul and sampled the groundfish catch on most hauls.

Two specific experiments were conducted. The first experiment (the Grid Sorting Experiment) evaluated two improved methods of sorting halibut from groundfish against a control method. For many factory layouts, halibut and other prohibited species and discards transit a series of conveyor belts to reach the exit chute. Forty-five minutes or more may elapse for the discards to move from the hold to the exit chute. We considered this procedure for handling discards to be the control method. The second experiment (Live Tank Holding) examined the relative survival of halibut within the established condition categories of excellent, poor, and dead.

For the Grid Sorting Experiment, three treatments were performed: (1) deck sorting with a grid; (2) enhanced sorting of the catch in the factory; and (3) normal sorting in the factory (the control). On the *Northern Glacier*, a single, short conveyor led from the hold to the exit chute. Retained fish were selected from the conveyor, and all else was quickly discarded. The regular procedure on the *Northern Glacier* was designated the enhanced treatment, while the control treatment was simulated by delaying processing for 45 minutes. Thirty hauls for each treatment were conducted, for a total of 90 hauls. We randomized the order of treatments. Other factors monitored were tow duration, haul size, time on deck, and fish size.

The Live Tank Holding Experiment was conducted to test relative differences in survival of the three condition categories. Halibut sorted from the catch on deck and in the factory were placed in holding tanks with running seawater for 3 days (72 hours) until the end of the trip, when holding time was reduced to about 12 hours. Approximately 20 halibut at a time were selected for placement into a tank.

The two grid dimensions examined were 9 inches by 11 inches and 11 inches by 14 inches (Fig. 2). These are based on an even division of the deck opening, the first yielding a grid 3 openings deep and 6 wide. The second provided 2 openings deep by 6 wide. Tow duration was not predetermined, but two duration strata of ≥ 3 hr and < 3 hr were established. The distribution of tow times was adjusted so that equal numbers of short and long hauls occurred for each treatment.

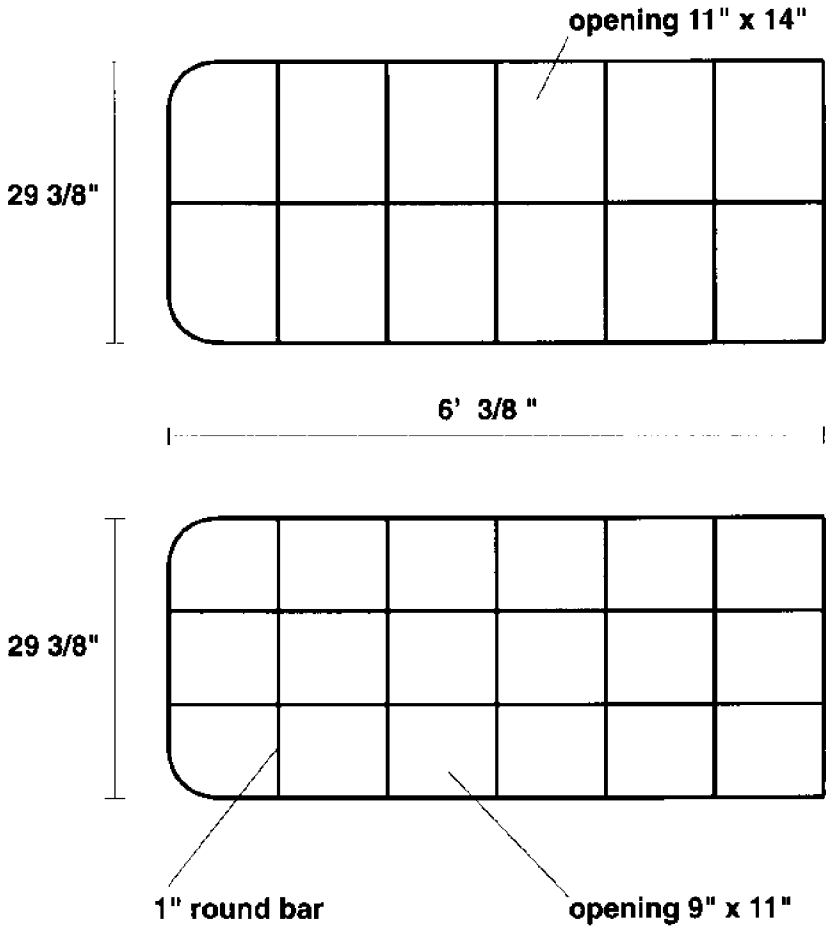


Figure 2. Sorting grids used during the grid sorting experiment. The bottom grid proved to be most appropriate.

Data Collection

During this experiment, data on length (cm), condition factor (excellent, poor, or dead) observations, and time of observation from the net coming on board were collected from each halibut encountered. NMFS observers conducted basket sampling to define the groundfish catch and determined halibut condition, so that these data are consistent with data collected in commercial fishery situations.

A schedule of the treatment for each haul alerted the bridge and the factory so that hauls could be made with factory processing capacity available. As each codend came on board, a biologist started a stopwatch; time of each halibut was recorded to the nearest minute. The observer and the skipper each estimated the groundfish catch. For grid sort treatments, the grid was placed over the hold, and the deck crew grabbed halibut prior to the hatch and on the grid and passed them to biologists for measurement and viability determination by the observer. When deck sampling was completed, the biological team moved to the factory where length, viability, and time data were collected for all remaining halibut. For enhanced and control treatments, the sampling process started in the factory. Enhanced treatments started processing groundfish and sorting halibut quickly after dumping to the hold, while control treatments started processing 45 minutes after dumping to simulate the time needed for halibut to transit the factory to the exit chute typical of most layouts.

Results

Groundfish and halibut catch

Ninety-five hauls made during the experiment included four test hauls, one invalid haul caused by a ripped net, and the ninety hauls specified in the experimental design. Catch weight ranged from about 5 mt to 35 mt per haul, but most were in the 10 to 15 mt range. The experimental hauls were divided into 30 hauls for each treatment, and the hauls of each treatment partitioned equally among < 3 hr and ≥ 3 hr tows. Groundfish harvest totalled 1,189 mt, of which the retained portion was 243 mt of Pacific cod and 496 mt of walleye pollock (*Theragra chalcogramma*). The remaining 450 mt, mostly arrowtooth flounder (*Atheresthes stomias*), other flatfish, and Atka mackerel (*Pleurogrammus monoptyerygius*), were discarded. Total Pacific cod was significantly below the anticipated catch of 1,500 mt, but pollock and discarded groundfish somewhat exceeded the 700 mt anticipated for other groundfish.

Table 1. Catch totals of Pacific halibut during the *Northern Glacier* bycatch experiment.

Treatment/ location	Numbers of halibut		Weight of halibut		Average weight (kg)
	No.	%	kg	%	
Grid Sort					
Deck	1,924	40.5	5,988	52.0	3.11
Factory	2,827	59.5	5,521	48.0	1.95
Overall	4,751	34.2	11,509	34.3	2.42
Enhanced Sort	4,903	35.3	12,437	37.1	2.54
Control Sort	4,223	30.4	9,575	28.6	2.27
Total	13,877	100.0	33,521	100.0	2.42

The number of halibut caught reached 13,877, at an estimated weight of 38,000 kg (2.74 kg/halibut). Approximately equal numbers of halibut were caught in each of the three treatments, with 4,751 in the Grid Sorting, 4,223 in the Control Sorting, and 4,903 in the Enhanced Sorting (Table 1). The halibut bycatch rate was 32 kg/mt. Bycatch rates in numbers of fish were higher than expected, but the total quantity of halibut bycatch was less than the anticipated maximum of 50 mt. Had the anticipated 2,200 mt of groundfish been harvested, halibut catch would have reached approximately 70 mt.

Deck sorting of halibut bycatch

In the Grid Sorting, 1,924 halibut (41%) were collected on deck. The larger sizes of halibut sorted on deck put the proportion of deck-sorted halibut at 52% by weight. At levels of 150 halibut or higher per tow, the sorting proportion remained about 40%, while sorting proportions were highly variable at lower numbers.

The grid selected for use, although the smaller of the two available, did not directly filter out many of the halibut. The high proportion of deck-sorted halibut was due to the slower rate of dumping catch from the codend to the hold, and the opportunity for the deck crew to sort out halibut pouring from the codend to the hatch. Sorting efficiency by the deck crew increased as the codend was placed further from the hold. About 3 to 4 m seemed an efficient distance as halibut passed too quickly past the sorters at shorter distances. Time required to dump a codend after the net came on board normally

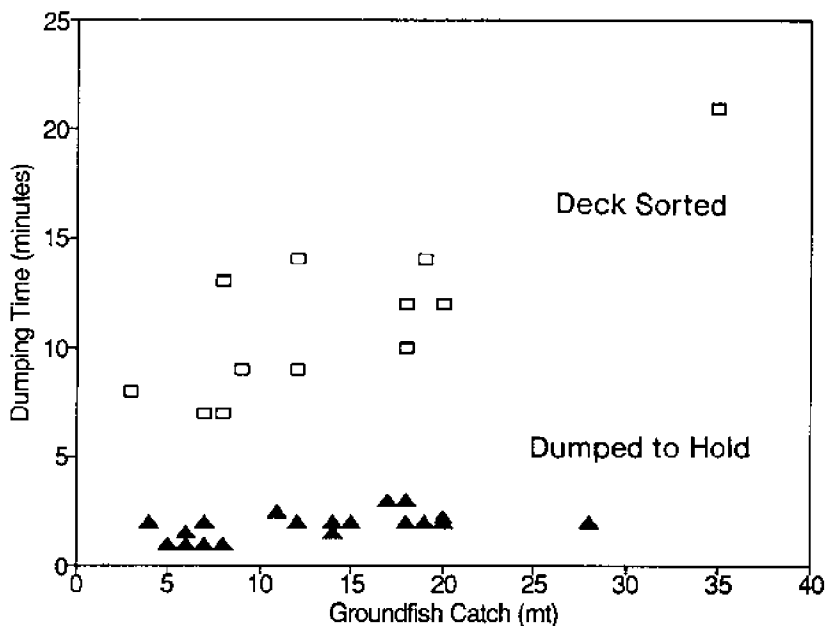


Figure 3. Comparison of the amount of time required to dump the codend when the catch was deck-sorted (open squares) and when the catch was dumped directly to the hold (closed triangles).

ranged from about 90 seconds to 2½ minutes, while a grid sort took about 10 to 15 minutes to dump. Grid Sort dumping time tended to increase with increased catch (Fig. 3), but the relationship was not strong. The deck crew would slow down dumping if more halibut appeared, but let the fish pour across the deck if halibut were not visible.

The ability to sort halibut on deck is dependent upon being able to find the halibut as the catch is being dumped. Larger halibut are more easily spotted and captured than small halibut (Fig. 4). For example, only 15% of the halibut less than 39 cm (0.6 kg, or 1-pound fish) were sorted on deck. The proportion at 50% or greater was not reached until roughly 65-70 cm (3-4 kg). The size distribution of deck-sorted and unsorted halibut captured during the experiment was very similar (Fig. 5), and the mode of the distributions was slightly smaller (50-55 cm), to the sizes most effectively sorted by the grid. As the size of halibut in the bottom trawl bycatch decreases, however, the effectiveness of grid sorting requirements for various fisheries also de-

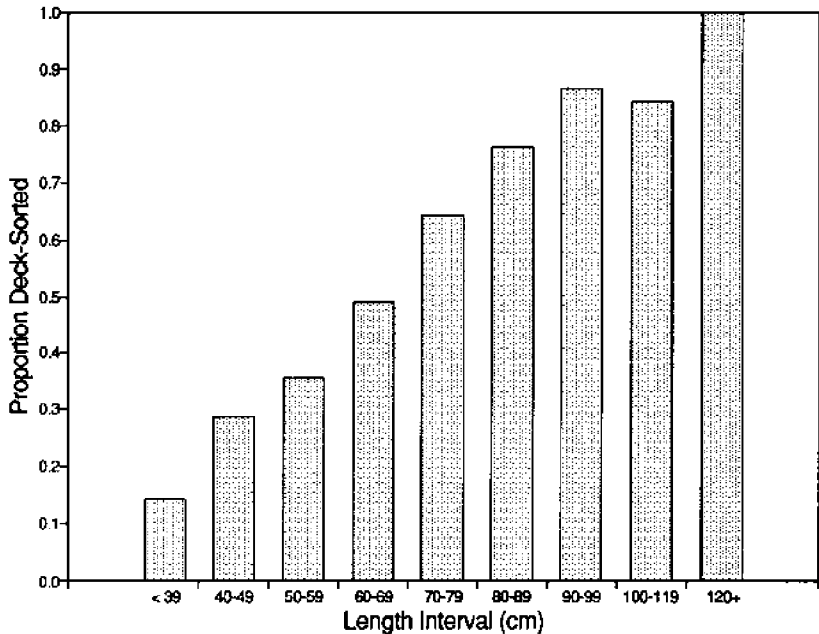


Figure 4. Proportion of halibut sorted on deck by 10-cm length interval. From Grid Sort tows only.

clines. Those fisheries with primarily smaller (< 50-60 cm) halibut may not gain much halibut survival by grid sorting, unless slower dumping speeds or smaller grid dimensions are practical to reach the level of deck sorting experienced in the experiment.

Halibut viability

All halibut caught were examined for condition (excellent, poor, or dead) by one of two NMFS observers, using the same criteria as employed by NMFS fishery observers. The number of halibut by condition category and calculated discard mortality rate for each treatment is summarized in Table 2. Halibut were in the best overall condition when sorted on deck, as was expected, with the percentage of halibut judged to be in excellent and poor condition similar. Halibut in dead condition were rarely seen. Condition factor (Fig. 5) and calculated survival of halibut sorted on deck were improved over the values from observer data in the 1992 Pacific cod trawl fishery in the

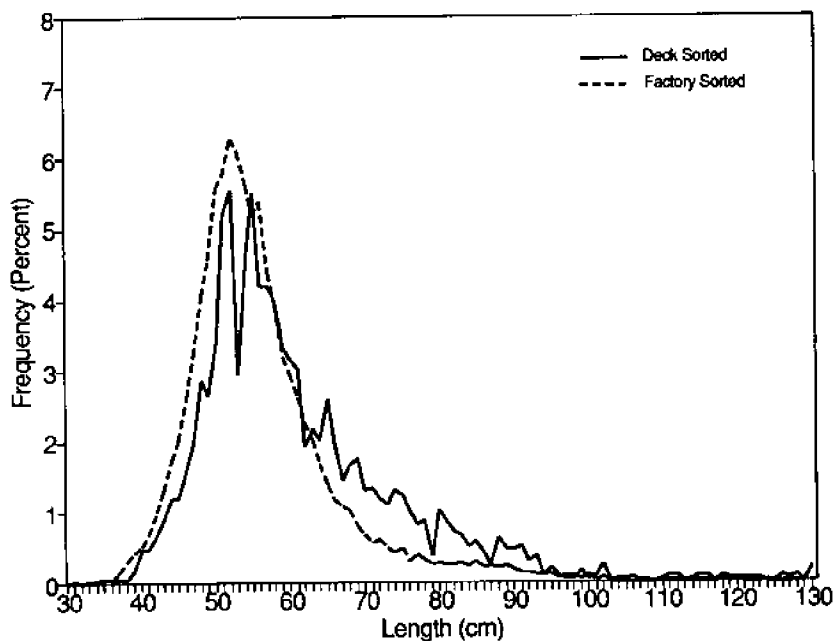


Figure 5. Size distribution of halibut in unsorted catches (Enhanced and Control tows) and of halibut sorted on deck (Grid Sort tows).

Bering Sea. Once the fish were dumped below deck, the condition worsened considerably. The calculated discard mortality rates for halibut sorted in the factory were higher than the 60% rate used by NMFS in the Bering Sea/Aleutian Islands bottom trawl pollock and Pacific cod fisheries, and the combined deck mortality and factory mortality of the grid sorted halibut were comparable to the NMFS rate.

Only 9% of the halibut caught in Enhanced Sort tows were in excellent condition, much lower than the Grid Sort tows. This was much lower than expected, considering that sorting and discard began as soon as the catch was below deck. Halibut in Control Sort tows were in worse condition yet, illustrating the benefits that can be gained by sorting and discarding the catch as soon as is possible, rather than letting the catch sit in holding tanks or spend time traveling through the factory. In this experiment, Enhanced Sort and Control Sort tows had discard mortality rates 15% and 30% higher, respectively, than the Grid Sort tows.

Table 2. Summary of halibut viability by sorting method, and calculated discard mortality rate from the Northern Glacier bycatch experiment.

Treatment/ location	No. of halibut	% Exc	% Poor	% Dead	Calculated disc. mortt. rate (%)
Grid Sort					
Deck	1,924	45	48	7	42
Factory	2,827	3	14	83	83
Overall	4,751	20	28	52	66
Enhanced Sort	4,903	9	22	69	76
Control Sort	4,223	1	7	92	87

For Enhanced Sorting or Grid Sorting in the factory, excellent condition halibut were found mainly during the first 20 minutes after the net came on board, in numbers near or slightly below the numbers of poor condition fish (Fig. 6). Few dead halibut occurred in this period. From 20 to 40 minutes, nearly all halibut were in poor condition. A few excellent and dead halibut were noted. For control sorting and for enhanced or grid sorting after about 40 minutes, nearly all halibut were in dead condition, with occasional poor and the rare excellent halibut.

Economic considerations

In the Bering Sea-Aleutian Islands (BSAI) management area, the directed Pacific cod bottom trawl fishery and the bottom trawl pollock fishery closed prior to achieving TACs in 1990, 1991, 1992, 1993, and 1994 because halibut bycatch mortality exceeded mortality limits. In the Gulf of Alaska (GOA), the directed Pacific cod fishery closed for intermittent periods before achieving TACs in 1990 (5/29-6/30 and 11/20 through the end of the year) because of halibut bycatch mortality, but was not affected in 1991, 1992, 1993, or 1994. Under status quo, future BSAI Pacific cod trawl fisheries will likely leave a large portion of their Pacific cod allocation unharvested. The GOA may be less severely affected, with intermittent closures that do not restrict total harvest. If halibut abundance increases or Pacific cod abundance

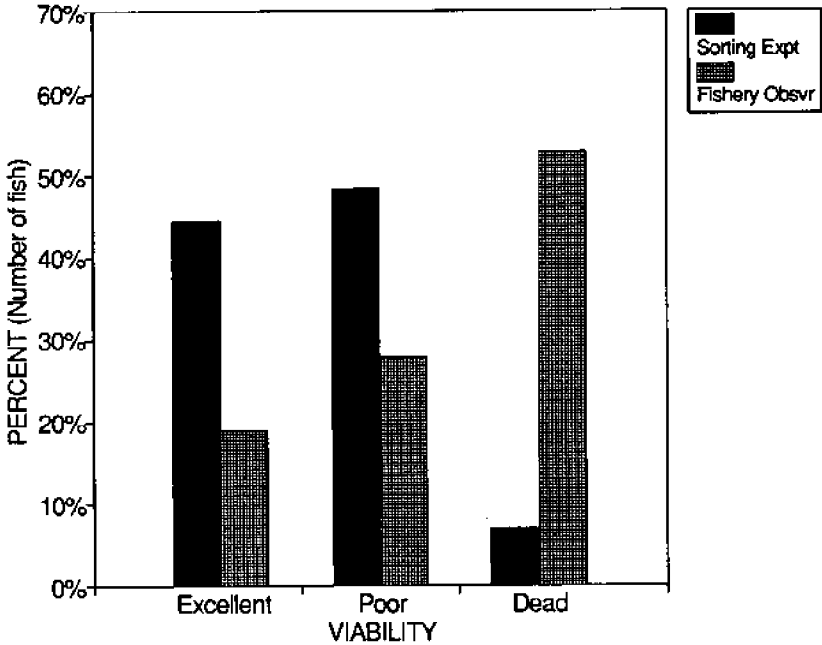


Figure 6. Condition factors of Pacific halibut sorted on deck compared to condition factors recorded by observers in the 1992 Pacific cod trawl fishery in the Bering Sea.

decreases, or both, Pacific cod trawl TACs in particular and groundfish TACs in general will become increasingly difficult to achieve.

A grid sorting requirement in the commercial bottom trawl fishery would to some degree alter operations on board affected vessels by: (1) increasing codend dumping time, (2) establishing on-deck halibut handling procedures for both deck crew and the observer, (3) decreasing fishing time, and (4) decreasing the amount of halibut the processing crew and observer must handle in the factory.

The vessels in the groundfish fleets affected by grid sorting will differ substantially between the BSAI and the GOA management areas. In the BSAI, all bottom trawl factory trawlers could be affected because these vessels dump catch from the codend into stern holding tanks prior to sorting and processing. This fleet component numbers about 70 vessels. In addition, at least three at-sea processing

motherships and fewer than five large shoreside catcher vessels would be affected. These alternatives would not apply to catcher vessels that normally sort on deck before moving fish below into refrigerated seawater for delivery shoreside. Under current regulations, factory trawlers and motherships in the GOA are prohibited from directed pollock and Pacific cod fisheries, so would not be subject to a sorting requirement involving these fisheries.

Time required to dump catches through the grid and into the below-deck tanks will be increased compared to present operations. Increased codend dump times will vary by fishery, size of tow, and the amount of halibut bycatch. During the *Northern Glacier* grid tests, up to 25-ton tows of primarily pollock and Pacific cod required 10-12 minutes longer to sort using the grid than was required when dumping similar amounts directly into the stern tanks. Vessel personnel believe that the dumping and sorting time can be reduced with practice and by bringing people from the factory to the deck for sorting during the codend dumps. Time lost to grid sorting could commensurately reduce fishing time for vessels trying to reset gear as rapidly as possible. Fishing time could be reduced as much as one hour per 24-hour period, assuming 10 minutes delay per tow and six tows per day. Immediate setbacks are not always possible or desirable, however, given fishing conditions and the amounts of fish already on board for processing. Crew costs will not be affected.

Crew time on deck will be increased during grid sorting to effectively remove halibut and pass them to the observer on deck. The crew will have an incentive to sort halibut quickly and efficiently and to assist the observer with the halibut. Crew assistance will decrease the sorting time, increase halibut survival, and lessen time delays before gear can be reset. Increased crew work on deck to prevent halibut from entering the factory will decrease both crew and observer handling of halibut in the factory where work spaces are often cramped and halibut difficult to remove and return to the sea.

Increased survival of discarded halibut will increase the trawl fisheries ability to harvest the TAC under existing halibut mortality limits, and thereby achieve the allocation set by the North Pacific Fishery Management Council. Halibut mortality limits could be decreased with larger groundfish harvest. Experience from the *Northern Glacier* suggested that halibut discard mortality rates may decline 25% for Pacific cod or pollock fisheries. Fisheries for other species will experience reductions in the discard mortality rates, but we cannot predict the magnitude of those savings without research on the effect of deck sorting in those fisheries.

In 1994, the 191,000 mt Pacific cod TAC in the BSAI was split 54% trawl (103,140 mt), 44% fixed gear (84,040 mt), and 2% jig (3,820 mt). The trawl fishery closed May 7 with a catch of 70,919 mt. Halibut bycatch rates were lower in 1994 than in previous years, yet the directed fishery closed with more than 30,000 mt remaining unharvested. The trawl fisheries will end the year at least 10,000 mt short of their Pacific cod allocation after incidental Pacific cod catch in other fisheries is considered. If grid sorting had been required in 1994 with a 25-50% reduction in discard mortality rates, the Pacific cod fishery would have harvested the directed Pacific cod fishery TAC of 83,000 mt, while using only 1,058 mt of halibut bycatch mortality. The 1994 directed Pacific cod fishery harvested about 70,000 mt of Pacific cod using 1,224 mt of halibut mortality, or 0.017 mt of halibut mortality per mt of Pacific cod. This would have saved 142 mt of halibut mortality below the 1,200 mt mortality limit.

Implementation of a deck sorting requirement will reduce or prevent reallocation of Pacific cod from bottom trawl to longline. Ten thousand metric tons of Pacific cod lost from the trawl allocation in 1994 would be worth approximately \$11,000,000 at \$1,086 to \$1,166 per mt (NPFMC 1993). Longline harvest of these fish would be worth approximately \$8,700,000 at \$841 to \$894 per mt (NPFMC 1993).

The BSAI pollock fishery harvested about 1.25 million mt of pollock in 1994 with a halibut mortality limit of 1,257 mt. The bottom trawl fishery closed when it attained its halibut mortality allocation of 314 mt; the pelagic trawl fishery, in spite of the pelagic trawl definition for much of the season that allowed on-bottom fishing, closed for TAC. At a 25% reduction in discard mortality rates, the bottom trawl harvest could have occurred for about 900 mt of halibut mortality, or a savings of 300 mt of halibut.

As indicated above, the savings for other fisheries cannot yet be predicted. However, BSAI groundfish harvest for species other than Pacific cod and bottom pollock was not constrained by halibut bycatch mortality limits in 1993. Therefore, any halibut bycatch savings that result from deck sorting would be available for use by the Pacific cod or bottom pollock fisheries, or for the directed halibut fishery.

Discussion

The experiment aboard the *Northern Glacier* was designed to simulate as close as possible the fishing practices of the bottom trawl fishery for Pacific cod. For the most part, this effort seemed very successful.

However, several differences occurred. The experiment occurred in October, a period that has not been fished for Pacific cod in many years. The location of fishing may not have been where a commercial fishery would operate at that time, in spite of extensive exploration of the grounds in the Bering Sea and Gulf of Alaska. The crew was very aware of the nature of the operations and the emphasis on improving survival of discarded halibut. We could not evaluate if the crew acted in different manner than would have occurred in the absence of the scientific party. The experimental design had originally intended for the treatment order to be unknown to the Captain prior to haulback, but this was abandoned. It was necessary to coordinate with the factory to keep product available, but without overwhelming the holding capacity. Observers collected data from the start to the finish of every haul, and condition factor was collected for each halibut. As a result, the distribution of halibut conditions factors during the experiment may be somewhat different from a distribution collected periodically through the haul as done by observers.

The discard mortality rates observed on the *Northern Glacier* were higher than expected, relative to the discard mortality rates used to manage the bottom trawl pollock and the Pacific cod fisheries. The overall discard mortality rate of 66% for the Grid Sorting is slightly higher than the discard mortality rate used by NMFS for the 1994 Bering Sea Pacific cod and bottom trawl pollock fisheries (60%), and about the same as the 65% rate for the Pacific cod fishery recommended by the IPHC to the NPFMC for 1995 (Williams 1994). However, the overall Grid Sorting discard mortality rate is less than the 77% rate recommended for the bottom trawl pollock fishery in 1995. Enhanced sorting (76%) is similar to the recommended bottom trawl pollock rate, and control sorting (87%) is higher than presently recommended for either fishery.

The reason for the higher than expected experimental rates is not clear, but may be related to the mix of Pacific cod and pollock in the catch, and the way sorting by species and size occurred on the *Northern Glacier*. Because the experiment occurred outside the normal race for fish, the vessel was able to process Pacific cod and pollock in an atypical manner. Pacific cod was sorted from the holding bin by size onto separate lines, and pollock was sorted to a third line. The sorting process was slower than normal aboard the vessel, and average sized hauls of 15 to 20 mt took up to 2 hours to complete. Occasionally, the sorting line had to slow down if Pacific halibut came down the line faster than could be sampled. A normal, commercial Pacific cod

operation on the *Northern Glacier* normally took 30 to 45 min to complete. The longer sorting time during the experiment likely contributed to discard mortality rates higher than observed during commercial fishing for Pacific cod.

However, the relative rates for the three experimental treatments, and the pattern of mortality over time demonstrate the advantage of quickly returning halibut to the sea (Fig. 7). While these results may not be directly applicable to the normal Pacific cod or bottom trawl pollock fishery, we conclude that discard mortality rates in these fisheries may decline 25% on factory trawlers that practice grid sorting. Experience and learning through continued use of grid sorting may well enable the deck crew to sort out a higher proportion of halibut than was the case for the crew of the *Northern Glacier*.

Industry proponents of grid sorting and the IPHC propose a 50-50 sharing of halibut mortality reductions that result from deck-sorting between bottom trawl groundfish fisheries and directed halibut fishery. If savings in the BSAI trawl fishery average 25%, then approximately 700 mt of halibut mortality limit reductions could occur: $3,775 \text{ mt limit} \times 0.25 \text{ reduction} \times 0.5 \text{ sharing} = 722 \text{ mt}$. The trawl fishery would benefit by more efficient use of bycatch equivalent to an increased mortality limit of 700 mt. Halibut bycatch mortality reductions would be proportionally less for discard mortality rate savings less than 25%. Less savings would occur in the GOA where more groundfish are currently sorted on deck.

The demonstrated reductions in halibut discard mortality rates and the proposed sharing of benefits from lower bycatch among trawl and halibut fisheries suggests an expectation of widespread support for a requirement to sort and discard halibut on deck. A wide spectrum of the North Pacific fishing industry has supported the concept. However, some non-trawl groups express concern that trawl operators may find the grid sorting requirement onerous, and will thereby try to avoid using the grid when observers are not watching. They demand either that two observers be placed on board if grid sorting occurs, or that the higher un-sorted rate be applied to unobserved hauls. The level of coverage in specific fisheries may increase after 1995 when a fee payment program by the fishing industry will finance observers. A limitation in overall number of observers will mean increases in one fishery will mean reductions in others. A decision on the grid-sorting requirement is scheduled for spring of 1995.

Data collected by observers in the North Pacific groundfish fisheries are used to quantify the catch of groundfish and prohibited

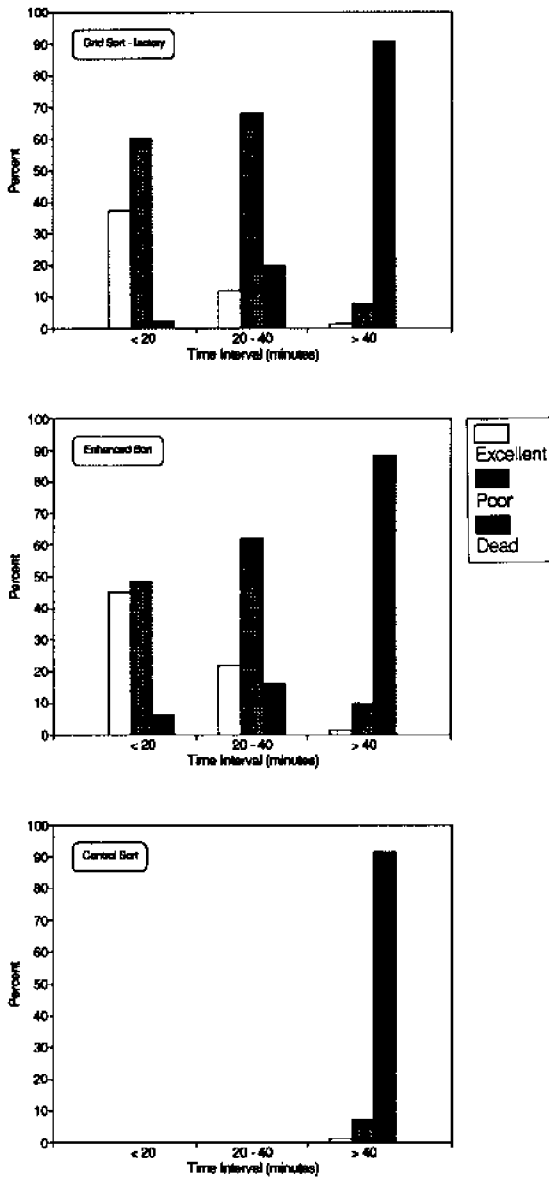


Figure 7. Condition of halibut observed in the factory during three 20-min time intervals for all sorting treatments.

species, including halibut. These estimates form the basis for management of groundfish catch quotas and prohibited species limits. Observer data are also used to estimate halibut discard mortality rates. The existing sampling protocol is structured around a sampling station in the processing factory of catcher/processor vessels. Grid sorting would disrupt the sampling protocol, require fundamental changes in observer sampling, and increase the time necessary for observers to collect data. Data collected under grid sorting will be incompatible with sampling protocols used in an ongoing program to provide an incentive to vessel operators to reduce halibut bycatch. A policy decision will be needed to prioritize competing demands for data. Grid sorting would also require observers to increase time spent on deck, which raises serious safety concerns.

The holding experiment provided less information than expected, but did demonstrate that survival of halibut categorized in the dead condition is possible. The number of halibut held during periods of good and moderate weather was too low to draw quantitative conclusions on survival for condition factors, but clearly indicate the importance of research to improve the definition of condition factors and to develop new methods of estimating discard mortality rates.

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Discard Mortality Rates of Pacific Halibut Bycatch: Fishery Differences and Trends During 1990-1993

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Abstract

In groundfish fisheries off Alaska, fishery observers routinely determine the condition (excellent, poor, or dead) of incidentally caught Pacific halibut (*Hippoglossus stenolepis*) shortly before being returned to the sea. The discard mortality rate (DMR) for halibut can be calculated using estimates of mortality for the three stages of condition. The data indicate that DMRs vary among target fisheries according to differences in gear and fishery characteristics. During 1990-1993, discard mortality rates were fairly stable among trawl fisheries, but variable in hook-and-line and groundfish pot fisheries.

Introduction

Pacific halibut (*Hippoglossus stenolepis*) are commonly captured incidentally in most fisheries operating in the northeast Pacific and eastern Bering Sea. Estimates of the incidental catch, or bycatch, from data collected by fishery observers indicate that the quantity is substantial, exceeding 20 million pounds several times since 1960 (Hoag and French 1976, Williams et al. 1989). Several studies have shown that not all halibut caught as bycatch actually die; survival may be quite good in some cases (Hoag 1975, Neilson et al. 1989). For this reason and also to discourage overt targeting, domestic regulations of

the United States require that halibut caught incidentally be immediately returned to the sea with a minimum amount of injury to the fish regardless of its condition (50 CFR Parts 672.20(e)[2] and 675.20(c)[3]).

Assessing the probability of survival of a bycaught halibut requires determining the extent of injuries due to the capture process and other causes. Fishery observers closely examine the fish, looking for injuries incurred during capture or from improper handling during release, and classify the fish as in excellent, poor, or dead condition. For the groundfish fisheries off Alaska, data on release condition, or viability, were collected by observers from foreign and joint venture fishery operations from the late 1970s through their expiration in the late 1980s, and from domestic operations since 1990. By using mortality rates for the different release condition categories, an overall discard mortality rate (DMR) can be calculated (Hoag 1976).

This paper reviews the procedures used by fishery observers in the groundfish fisheries off Alaska for determining condition of halibut and calculating DMRs for trawl, hook-and-line, and groundfish pot gear. The results are shown for each target fishery in the Gulf of Alaska and eastern Bering Sea, noting differences between fisheries.

Description of Observer Data

The duties of a fishery observer are numerous, but one of the required tasks is to record the condition of halibut when released. Observers are instructed to make this determination immediately prior to discard in the commercial handling process. Condition is determined to be excellent, poor, or dead, based on the physical condition and/or stress indicators shown in Table 1. These categories and supporting criteria have been in use since the beginning of observer activities in the late 1970s, and are largely based on the results of Hoag (1975).

Data collected by fishery observers were obtained from the National Marine Fisheries Service (NMFS) Domestic Observer Program, Alaska Fisheries Science Center, Seattle. For each trawl haul, or hook-and-line or pot set, the information available included the area, fishing depth, catch of groundfish by species, the duration of the haul for trawls or soak time for hook-and-line gear and pots, and number of halibut by condition category.

We used the species composition of a vessel's weekly catch (Sunday through Saturday) as the basis for determining target fishery (Table 2). These fishery criteria were established by National Marine Fisheries Service (NMFS) during 1990-1991 for monitoring of fishery

Table 1. Criteria used in 1993 by NMFS observers to determine halibut condition. Adapted from Hoag (1975).

Trawl and pot fisheries

- (1) *Excellent*: No sign of stress
 - (a) Injuries, if any, are minor.
 - (b) Muscle tone or physical activity is strong.
 - (c) Gills are red (not pink) and fish is capable of closing gill cover (operculum) tightly.
- (2) *Poor*: Alive, but showing signs of stress
 - (a) Moderate injuries may be present.
 - (b) Muscle tone or physical activity is weak.
 - (c) Gills are red (not pink) and fish is capable of closing gill cover (operculum).
- (3) *Dead*: No sign of life or, if alive, likely to die from severe injuries or suffocation
 - (a) Vital organs may be damaged.
 - (b) No sign of muscle tone or physical activity.
 - (c) Severe bleeding may occur.
 - (d) Gills may be pink and fish is not able to close gill cover (operculum).

Hook-and-line fisheries

- (1) *Excellent*: No sign of stress
 - (a) Hook injuries are minor and located in the jaw or cheek.
 - (b) No sign of severe bleeding; gills are red (not pink).
 - (c) No sign of sand fleas.
 - (2) *Poor*: Alive, but showing signs of stress
 - (a) Hook injuries may be severe, but vital organs are not injured.
 - (b) Moderate bleeding may be observed, but gills are still red (not pink).
 - (c) No sign of sand fleas.
 - (3) *Dead*: No sign of life or, if alive, likely to die from severe injuries
 - (a) Vital organs may be damaged.
 - (b) Sand fleas may be present (they usually first attack the eyes).
 - (b) Severe bleeding may occur, gills may be pink.
 - (c) No sign of muscle tone.
-

Table 2. Target fishery definitions based on total catch excluding prohibited species, non-allocated species, and arrowtooth flounder for Gulf of Alaska targets.

Bering Sea/Aleutians

Greenland turbot: $\geq 35\%$

Pacific cod: $\geq 45\%$

Rock sole & other flatfish: if (rock sole + yellowfin sole + other flats) $\geq 40\%$
and rock sole $>$ (yellowfin sole + other flats)

Yellowfin sole: (yellowfin sole + rock sole + other flats) $\geq 40\%$

Arrowtooth flounder: $\geq 20\%$

Rockfish: $\geq 20\%$

Atka mackerel: $\geq 20\%$

Midwater trawl pollock: $\geq 95\%$

Bottom trawl pollock: $\geq 20\%$

Other: anything else

Gulf of Alaska

Pacific cod: $\geq 45\%$

Rockfish: $\geq 30\%$

Shallow water flatfish: rock sole + yellowfin sole $\geq 20\%$

Deep water flatfish: greenland turbot + other flatfish $\geq 20\%$

Bottom trawl pollock: $\geq 20\%$

Midwater trawl pollock: $\geq 95\%$

Other: anything else

catches and bycatch of prohibited species, such as halibut and other specified species, which groundfish fishermen cannot retain.

Procedures for Calculating Discard Mortality Rate

Trawls

The baseline study which provides mortality rates by release condition was conducted by Hoag (1975). This experiment, using shore-based Canadian and U.S. trawlers fishing off Canada in 1970, used the recovery rates from more than 2,000 tagged halibut to estimate the mortality that occurs during trawl-capture and release. Observers on

commercial vessels noted the condition of each halibut prior to release.

Clark et al. (1992) reviewed Hoag's results and recommended revising the mortality rates to the following: 20% for excellent condition fish, 55% for poor fish, and 90% for dead or likely-to-die fish. These rates have been used since 1992 and are used in this paper. Clark et al. (1992) observed that a fourth category with zero survival may be necessary for large volume trawl fisheries that display lag periods before halibut are discarded.

The discard mortality rate for a particular fishery is calculated by applying the mortality rate by condition category to the proportion of fish in that category, shown in Table 3, and summing the products across all categories.

Hook-and-line

For hook-and-line gear, studies of discard mortality comparable to Hoag's (1975) trawl analysis have not been completed. However, data are available from studies by the International Pacific Halibut Commission (IPHC) which suggest that (1) handling mortality of hook & line caught halibut in excellent condition ranges from 2% to 5% (Peltonen 1969), and (2) survival of poor condition fish is approximately half that of fish in excellent condition (Myhre 1974). Additionally, it is assumed that (1) all fish judged as dead actually die and (2) all fish judged as excellent survive, except for those killed through handling mortality (2% to 5%). Using these relationships, mortality rates were 3.5% for excellent condition fish (midpoint of the 2% to 5% range), 52% for poor condition fish (midpoint of 51% to 53%), and 100% for dead or likely-to-die fish.

Pots

There is no information on the mortality of pot-captured halibut occurring from release. Causes of mortality have been suggested, such as size of catch, pot soak time, and the presence of certain species, particularly those with spines (e.g., rockfish or crabs). But it is unknown how much mortality these sources may create.

From our understanding of halibut in excellent, poor, and dead condition in other gear types, it is likely that some fraction of the excellent and poor fish die from capture-related injuries following release and that some small fraction of the dead fish probably survive. Although it is unknown what fraction actually survive in each cat-

Table 3. Results from stratification of halibut condition data by region, gear, and target fishery.

Fishery	1990				1991			
	# Halibut examined	% Exc	% Poor	% Dead	# Halibut examined	% Exc	% Poor	% Dead
BSA trawl								
MWT pollock	7,563	7	10	83	3,258	7	12	81
Atka mackerel	3,536	16	27	57	2,631	9	30	61
Rock sole/ O. flats	12,603	36	19	45	17,106	17	29	54
Pacific cod	83,487	20	22	58	55,389	27	31	42
BT Pollock	40,686	25	22	53	27,571	30	29	41
Rockfish	5,937	27	28	45	2,732	39	26	35
Yellowfin sole	8,338	16	16	68	8,798	19	9	72
Greenland turbot	6,484	38	16	46	2,122	62	24	14
Arrowtooth flndr.	1,481	34	25	41	3,945	62	16	22
GOA trawl								
MWT Pollock	1,305	30	17	53	366	12	22	66
Rockfish	16,547	26	32	42	3,092	21	29	50
BT Pollock	1,373	25	29	46	337	25	46	29
Shallwtr. flatfish	3,970	12	54	34	877	28	28	44
Pacific cod	28,729	28	28	44	28,741	34	33	33
Deepwtr. flatfish	1,507	38	16	46	566	45	18	37
BSA hook-&-line								
Pacific cod	59,689	79	16	5	26,842	69	26	5
Sablefish	1,272	85	12	3	335	82	8	10
Grnld. turbot	2,882	86	11	3	588	50	21	29
GOA hook-&-line								
Pacific cod	5,555	84	13	3	7,934	79	15	6
Sablefish	36,814	88	9	3	3,271	60	29	11
Rockfish	4,303	82	14	4	190	75	15	10
BSA pot								
Pacific cod	1,066	93	6	1	1,215	97	1	2
GOA pot								
Pacific cod	1,890	90	4	6	714	95	2	3

Table 3. (Continued.)

Fishery	1992				1993			
	# Halibut examined	% Exc	% Poor	% Dead	# Halibut examined	% Exc	% Poor	% Dead
BSA trawl								
MWT Pollock	3,968	1	5	94	392	0	1	99
Atka mackerel	774	31	17	52	608	36	26	38
Rock sole/ O. flats	4,346	7	20	73	6,231	18	16	66
Pacific cod	17,520	19	28	53	13,635	25	31	44
BT Pollock	20,805	12	17	71	31,991	10	15	75
Rockfish	1,215	18	52	30	2,308	10	15	75
Yellowfin sole	5,683	11	13	75	5,241	13	16	71
Greenland turbot	-	-	-	-	-	-	-	-
Arrowtooth flndr.	-	-	-	-	-	-	-	-
GOA trawl								
MWT Pollock	215	14	32	54	252	14	49	37
Rockfish	1,113	16	27	57	934	32	17	51
BT Pollock	630	17	22	61	1,783	18	21	61
Shallwtr. flatfish	787	23	34	43	6,353	21	27	52
Pacific cod	5,933	27	31	42	7,992	28	41	30
Deepwtr. flatfish	2,025	26	37	37	6,060	28	33	39
BSA hook-&-line								
Pacific cod	32,584	75	19	6	28,599	78	16	7
Sablefish	221	78	11	11	187	80	19	1
Grnld. turbot	346	76	19	5	1,709	70	24	6
GOA hook-&-line								
Pacific cod	1,945	63	19	18	1,538	91	7	2
Sablefish	3,697	71	19	10	4,809	69	16	15
BSA pot								
Pacific cod	3,637	88	6	6	422	96	1	3
GOA pot								
Pacific cod	3,069	84	4	12	789	80	16	4

egory, the following assumptions have been made: (1) all excellent fish survive (0% mortality); and (2) all poor and dead/likely-to-die fish die (100% mortality).

This may overestimate the actual mortality, because some of the poor fish may survive even though it is assumed all die. However, it is also likely that a small fraction of the excellent condition fish die and that a small fraction of the dead/likely-to-die fish survive. There is currently no way to quantify these errors, but they have only a small effect on the overall estimate of discard mortality given the high proportion of fish that are in excellent condition. Consequently, this approach is conservative, but is reasonable until data can be obtained on post-release mortality.

Results

We aggregated the data into year/region/gear/fishery strata. We excluded fishery targets which were determined by the North Pacific Fishery Management Council as "bycatch-only," or targets which were artifacts of the target classification process. For example, this included a trawl fishery for sablefish in the GOA, and hook-and-line fisheries in some years for pollock, arrowtooth flounder, greenland turbot, and deep water flatfish. In most cases, the number of hauls or sets for these categories in any given year was less than 10. The results are shown in Table 3.

The number of halibut examined by observers in most fisheries was quite large, often exceeding 1,000 fish, but ranging as low as 100-200. The largest sample sizes typically occurred in the major fisheries, i.e., Bering Sea bottom trawl pollock fishery. Trawl fisheries generally had the greatest number of fish, followed by hook-and-line fisheries and pot fisheries. The total number of fish examined annually in all fisheries declined, from over 337,000 fish in 1990 to approximately 115,000 in each of 1992 and 1993. The cause of the decline is unknown, but may be related to the increasing work load of fishery observers, with less time available to devote to viability sampling. Despite the noted decline, sample sizes were sufficiently large enough for calculation of DMRs.

The breakdown by condition category varied among fisheries, but the differences between gear types was pronounced. For example, the percentage of excellent condition halibut for trawl fisheries was usually less than 40%, most often 20%-30%. In contrast, excellent condition halibut in hook-and-line fisheries were 70% to almost 90%,

and pot-caught halibut were 85% to 97%. For halibut classified as dead, the range in the results were 50% to 95% for trawls, 15% or less for hook-and-line, and 6% or less for pots. These results indicate the halibut caught in trawls are in the poorest condition of the three gears, followed by hook-and-line gear and pots.

We used the percentages reported in Table 3 to calculate a DMR for each fishery, using the procedures previously outlined. The results, shown in Table 4, can be summarized as follows. The DMR for trawl fisheries generally fell within a 60% to 90% range; a range of 10% to 25% for hook-and-line fisheries; and 5% to 15% for groundfish pots. In addition, trawl fishery DMRs tended to be higher in Bering Sea fisheries; hook-and-line and pot fishery DMRs tended to be higher in Gulf of Alaska fisheries.

Discussion

Release condition of halibut varied significantly across the strata we examined, but the most pronounced was gear. Of the three dominant gear types used in the groundfish fisheries, trawl gear results in halibut in the poorest condition and the highest discard mortality rates. In Hoag's (1975) study of the Canadian trawl fishery, size of catch, fish length, and time on deck were found to be the most important factors contributing to halibut condition. In particular, time on deck was the most significant factor: condition declined considerably when the time on deck statistic was higher than about 20 minutes.

For trawls, the poorest condition factors and highest DMRs are seen in midwater fisheries. For example, the midwater fishery for pollock in the Bering Sea consistently displayed the highest DMR each year. To a large degree, this is a product of the excessively large catches typical for this fishery: for example, average catch size was over 60 mt in the 1992 fishery. Catch size is important for several reasons. First, large catches create greater crushing within the trawl net while it is being towed. Second, large catches inherently take longer to sort once dumped on board the vessel, meaning that it will take longer before halibut are returned to the sea. Hence, the opportunity for injury and high time on deck statistics are much greater than in other trawl fisheries.

Catch size in other trawl fisheries is not widely different, but other factors come into play. Fish size differs among trawl fisheries, and the effect of this can be seen in the flatfish fisheries. Some of the smallest

Table 4. Calculated halibut discard mortality rates by year, region, and target fishery for groundfish fisheries off Alaska.

Region/target	Discard mortality rate (%)				1990 - 1993 average
	1990	1991	1992	1993	
BSAI trawl					
Midwater trawl pollock	81	81	88	90	85
Atka mackerel	69	73	62	56	65
Rock sole/Other flats	58	68	78	72	69
Pacific cod	68	60	67	62	64
Bottom trawl pollock	65	59	76	78	70
Rockfish	62	54	59	78	63
Yellowfin sole	73	74	77	75	75
Greenland turbot	58	38	—	—	48
Arrowtooth flounder	57	41	—	—	49
GOA trawl					
Midwater trawl pollock	63	74	69	63	67
Rockfish	61	65	69	62	64
Bottom trawl pollock	62	56	70	70	65
Shallow water flatfish ¹	62	61	62	66	63
Pacific cod	61	55	60	56	58
Deep water flatfish ²	57	52	59	59	57
BSAI hook-&-line					
Pacific cod	16	21	19	18	19
Sablefish	12	17	19	14	16
Grnld. turbot	12	42	18	21	23
GOA hook-&-line					
Pacific cod	13	17	30	9	17
Sablefish	11	28	22	26	22
Rockfish	14	20	—	—	17
BSAI pot					
Pacific cod	7	3	12	4	7
GOA pot					
Pacific cod	10	5	16	20	13

¹ Shallow water flatfish complex is composed of rock sole (*Pleuronectes bilineatus*), yellowfin sole (*Pleuronectes asper*), starry flounder (*Platichthys stellatus*), butter sole (*Pleuronectes isolepis*), English sole (*Inopsetta ischyra*), Alaska plaice (*Pleuronectes quadrituberculatus*), and sand sole (*Psettichthys melanosictus*).

² Deep water flatfish complex is composed of Dover sole (*Microstomus pacificus*), Greenland turbot (*Reinhardtius hippoglossoides*), and deepsea sole (*Embassichthys bathybius*).

halibut caught as bycatch are taken in the Bering Sea rock sole fishery. For example, the average size was 0.75 kg and 0.89 kg in 1991 and 1992, respectively, considerably smaller than the overall average size of 1.1 kg and 1.7 kg in the same years. This small size means that condition is poor, and a relatively high DMR of 70%-75%.

Halibut condition and DMRs were much better in hook-and-line fisheries, primarily because each halibut caught is handled and released individually. Injuries from the hook and injuries from the release method are the main sources of mortality, although in some cases amphipod predation on hooked fish can be significant. The widespread use of circle-type hooks has lessened the potential for hook injuries, because halibut are predominantly hooked in the forward part of the mouth (Kaimmer in press). Thus, hook removal and fish release method are the crucial factors.

Among hook-and-line fisheries, differences between target fisheries are not great, with a few exceptions. The high percentage of excellent condition halibut (70%-90%) created DMRs in the range of 15%-20%. The major exception is the Gulf of Alaska fishery for sablefish, where the DMR has been 22% or higher since 1991. Several factors have created an environment in this fishery whereby fishermen are more concerned with maximizing the catch of sablefish before a fishery closure. Since 1990, this fishery has been subject to a limit on the amount of halibut bycatch mortality that can be incurred: once the limit is reached, the fishery is closed. In addition, the fishery has been considered overcapitalized for many years and the excess effort has pushed fishermen onto grounds where halibut bycatch is high (NPFMC 1992). These factors have created a "race for fish," as fishermen attempt to maximize the catch before the fishery closes. The use of hook strippers, which mechanically pull the hook from the fish, cause numerous injuries, many of which are severe or fatal (Kaimmer in press). Hence, a poorer than average condition, and high DMR, is demonstrated by the fishery.

Groundfish pot fisheries, primarily for Pacific cod, demonstrate the best condition factors and lowest DMRs (Table 4). Pots are typically fished individually and retrieved at least once every 24 h in an attempt to maintain high quality of the catch. Unless a halibut injures itself in the pot, the condition should be excellent upon release. However, injuries do occur, caused by abrasions created when coming in contact with certain crab species which are also taken incidentally, and from friction against the mesh of the pot. Also, pot soak times greater than 24 h can worsen condition, thereby increasing the DMR.

Long soaks may occur if adverse weather conditions prevent the vessel from retrieving the pots, or a mechanical breakdown keeps the vessel in port for an extended period. Problems with weather are likely contributing to the overall higher DMRs in the Gulf of Alaska pot fishery.

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Commercialization of Arrowtooth Flounder: The Next Step

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Abstract

Arrowtooth flounder (*Atheresthes stomias*) is one of the last, large resources off Alaska that the seafood industry has not been able to profitably exploit. This vast supply of protein has not been used for a dramatic reason—the flesh turns to mush when cooked. Recently, however, researchers have identified several food grade additives that are successful in inhibiting the proteolytic enzyme that breaks down the flesh.

The Alaska Fisheries Development Foundation recently applied this information in a demonstration project to produce arrowtooth flounder surimi on a commercial scale. Samples have been tested by numerous surimi analog companies, and one company is blending 80,000 lbs of arrowtooth flounder surimi with pollock surimi to market as analog products. The surimi is low to medium grade, white, free from defects and has a mild flavor and odor. Gel strengths range from 300 to over 400 g × cm.

The final roadblocks to commercial utilization of arrowtooth flounder are market conditions and bycatch. Surimi prices are currently low. Harvesting arrowtooth flounder to produce low value surimi would consume bycatch limits that also apply to higher valued groundfish species. Current production economics even prohibit the surimi production of incidentally harvested arrowtooth flounder. Circumstances may change, however, if prices for surimi rebuild and as public concern about fish discards grows.

Table 1. Allowable biological catch (ABC) and total allowable catch (TAC) for arrowtooth flounder in the Gulf of Alaska and Bering Sea/Aleutian Islands for 1993.

	Gulf of Alaska	Bering Sea/Aleutian Islands
1993 ABC	321,290 mt	72,000 mt
1993 TAC	30,000 mt	10,000 mt

Source: North Pacific Fishery Management Council

Introduction

Arrowtooth flounder (*Atheresthes stomias*) constitute one of the last large seafood resources off Alaska that industry has not been able to profitably exploit. Utilization of the arrowtooth flounder resource was identified in 1990 by the National Fisheries Institute as one of the keys to achieving their goal of twenty pounds of annual seafood consumption per person in the United States by the year 2000 (Frozen Food Age 1990). Roadblocks to the development of this resource include processing difficulties, high bycatch levels and poor market conditions. For the past four years the Alaska Fisheries Development Foundation, a nonprofit organization working to promote the seafood industry, has been investigating solutions to the constraints to creating a commercial product from arrowtooth flounder. This paper provides an overview of the progress to date and the steps remaining in the commercial development of arrowtooth flounder.

The Resource

Arrowtooth flounder is the third largest biomass among the flatfishes of the North Pacific and make up fully half of the Gulf of Alaska flatfish. The most recent National Marine Fisheries Service survey information estimates the arrowtooth flounder biomass at 1.9 million metric tons in the Gulf of Alaska. Biomass of arrowtooth flounder in the Bering Sea is considerably smaller, at 480,000 metric tons, although still more plentiful than all other species in that region except pollock, cod and yellowfin sole (NMFS 1994). Over 300,000 mt of arrowtooth are available for commercial harvest per year.

Since markets for arrowtooth flounder are virtually nonexistent, the Total Allowable Catch (TAC), set by the North Pacific Fishery Management Council is a fraction of the allowable biological catch

Table 2. Catch and discard of arrowtooth flounder in the 1993 Gulf of Alaska and Bering Sea/Aleutian Island fisheries (metric tons).

	Total catch	Total discard	Percent discard
Bering Sea/ Aleutian Is.	9,339	8,673	93%
Gulf of Alaska	19,091	17,500	92%
Total	28,430	26,173	92%

Source: North Pacific Fishery Management Council

(ABC) (Table 1). The vast majority of the resource is discarded. In 1993, the catch of arrowtooth flounder comprised 51% of all flatfish harvested in the Gulf of Alaska; however, 93% of the arrowtooth were discarded. That was the equivalent of a discard of 22,565 metric tons of useable protein (Table 2).

Development of a Marketable Product

This vast supply of protein has not been used for a specific and, to the consumer, rather dramatic reason—the flesh turns to mush when cooked. Arrowtooth flounder have a flesh softening problem caused by a heat activated proteolytic enzyme that exists in the flesh. This enzyme is active between the temperatures of 40 and 80°C. This activation zone allows arrowtooth flounder to be harvested, processed and transported to the consumer without any flesh softening, if no temperature abuse occurs. But, upon cooking, this white, firm fillet softens unacceptably. The seafood industry has avoided the production of arrowtooth flounder for good reason—the only possible product was one that would guarantee no repeat buyers.

The Alaska Fisheries Development Foundation began to address this problem in 1990 as an extension of a three-year flatfish development project that pushed the creation of a shore-based flounder and sole fishery in the Gulf of Alaska.

Drs. Diana Wasson and Jerry Babbitt at the National Marine Fisheries Service in an AFDF-directed project, funded by the Alaska Science and Technology Foundation, identified the site on the protein that is used by the enzyme to break down the texture of the flesh. Myosin, the main structural protein of fish muscle, is the primary target of the enzyme (Wasson et al. 1992). That myosin was the main

target of proteolytic activity also had particular important implications for the manufacture of surimi from arrowtooth flounder, since the gel-forming properties of surimi are a direct result of myosin's ability to form a strong cross-linked network. Only unbroken strands of myosin will form the matrix referred to as "gel."

Once the site was isolated, appropriate food grade inhibitors were tested under laboratory and plant conditions to determine their effectiveness. Bovine plasma powder and dried egg white were effective in inhibiting the arrowtooth protease. Results have indicated that a properly applied inhibitor can block all proteolytic activity in arrowtooth flounder (Wasson et al. 1992).

Arrowtooth flounder surimi was produced for the first time in July 1990 from trawl caught (F/V *Dusk*) fish. Since then, Dr. Babbitt has produced sample amounts of arrowtooth flounder surimi using a potato-based inhibitor used with hake, which also faces similar enzymatic degradation. Produced by a commercial seafood plant, the product was evaluated by Louis Kemp Seafood Company. The surimi was blended with pollock surimi in the production of analog type products at levels of up to 50%. While the arrowtooth surimi worked well in a blended analog production, when compared to pollock surimi, it had a higher oil content, its texture was softer, the flavor was different and the color was slightly darker (Babbitt et al. 1993).

A pilot full-scale commercial flounder surimi project, managed by AFDF and funded by the National Marine Fisheries Service, produced approximately 40 tons of market grade arrowtooth flounder surimi in 1993. Samples of the surimi was sent to five analog producers across the country for evaluation.

Following the sample production phase, 40 tons of surimi was produced from arrowtooth flounder harvested by boats targeting other species. The surimi was shipped to Sea Blends Food Company in Seattle for blending with pollock surimi in the production of commercial analog products.

The project produced a low to medium grade surimi that was able to blend successfully with pollock surimi (Table 3). At a 10% blend, arrowtooth flounder surimi was undetectable when mixed with pollock surimi. However, at levels of 25%, some detectable differences in flavor, odor and softness were apparent when compared with pollock surimi. AFDF is planning to produce approximately 9 tons of arrowtooth surimi this winter in conjunction with Sea Blends to analyze these product property changes.

Table 3. Moisture and gel characteristics of arrowtooth surimi with a 4% potato inhibitor or 1.2% AMP (powdered bovine plasma).

	Control	P-1	P-2	AMP-1	AMP-2
Moisture %	76.00 ±0.04	73.39 ±0.06	73.84 ±0.03	76.84 ±0.04	76.55 ±0.12
Punch force g	Too weak	345 ±19	345 ±5	278 ±10	213 ±15
Punch deflection mm	Too weak	8.8 ±0.3	8.7 ±0.2	10.4 ±0.3	10.3 ±0.6
Gel strength g×cm	Too weak	304 ±24	300 ±8	290 ±16	219 ±18
L*	86.0 ±0.4	80.2 ±0.1	79.6 ±0.1	84.5 ±0.3	84.1 ±0.6
a*	-3.2 ±0.1	-3.7 ±0.1	-3.5 ±0.1	-3.6 ±0.1	-3.5 ±0.2
b*	1.7 ±0.4	3.4 ±0.1	3.1 ±0.4	4.3 ±0.2	4.6 ±0.4
Whiteness	86.5 ±0.3	80.8 ±0.1	80.1 ±0.1	85.5 ±0.3	85.2 ±0.4
Stress kPa	17.9 ±3.1	55.7 ±5.0	54.2 ±12.4	34.9 ±5.9	30.2 ±2.0
Strain	1.15 ±0.08	2.19 ±0.20	2.05 ±0.20	2.17 ±0.15	2.03 ±0.13

Produced September 1993 by All Alaska Seafoods, Kodiak, for the Alaska Fisheries Development Foundation. Testing by Dr. Jerry Babbitt, NMFS, Kodiak.

Thus, the results to date demonstrate that the technology is now available to produce a commercial grade of surimi from arrowtooth flounder. Refinement of a number of elements in the manufacture of the surimi are necessary and possible. However, just reaching this level of commercial feasibility breaks through one significant barrier to the utilization of arrowtooth flounder—the degradation of the flesh by proteolytic enzymes.

Several other methods of inhibiting the protease and creating a commercial product from arrowtooth flounder have also been explored. AFDF has investigated the use of microwave cooking as a

means to inactivate the arrowtooth muscle protease. Research showed that microwave cooking increases the temperature of the fish at such a speed that it bypasses the sensitive temperature range of 55°C to 60°C (131°F to 140°F) fairly quickly. When the temperature rises above 80°C (176°F) the arrowtooth muscle protease is inactivated and texture damage is minimized (AFDF 1992). Investigations into the potential for a marketable microwave-cooked arrowtooth product indicated that a fillet, packaged in an acid pH sauce, like tomato, may provide a marketable product. At this stage, however, it is not a cost effective product option.

Mechanical injection of fillets with a protease inhibitor was also tested. While the technique successfully inactivated the enzyme, the texture of the fillets was considered to soft for commercial sales (AFDF 1992).

International Seafoods of Alaska has also been experimenting with the production of a powdered fish protein from arrowtooth flounder. The product is designed to be used as a human protein supplement, primarily intended for the third world (D. Rogers, pers. comm).

Commercialization of Arrowtooth Flounder: The Next Step

The ability to inactivate the proteolytic enzyme was a critical breakthrough that needed to occur before any marketable product from arrowtooth flounder could be created. Having crossed that barrier, the economics of the harvesting and processing of arrowtooth flounder for surimi are still, at this point, preventing the commercial utilization of this vast resource.

The harvest of arrowtooth flounder is now primarily an incidental catch by hard on bottom trawls targeting other flatfish, cod or rockfish. Inherent in that fishing technique, at this point in time, is the bycatch of halibut. Currently, with no commercial market for arrowtooth flounder, the TAC is set much lower than the ABC for arrowtooth. By limiting the TAC, fishermen in the Gulf of Alaska are able to expend their halibut bycatch limit while targeting on more valuable species such as Pacific cod, rockfish and other flatfish species.

Arrowtooth flounder have never been targeted by vessels and are currently avoided since virtually all of them are either dumped over the side or discarded by processors, often at a cost to the fisherman. What remains unknown is the potential for fishermen to target

arrowtooth flounder while avoiding the capture of halibut, crab and salmon. A pilot test that allows fishermen to target arrowtooth flounder while using observers to record bycatch, in conjunction with further surimi production refinement would be a valuable next step.

The current low price of surimi is also another major roadblock to the development of arrowtooth flounder. Right now, economics prohibit the manufacture of arrowtooth surimi, even when delivered as incidental harvest. Arrowtooth flounder range in size from 12 inches to 30 inches, making automatic filleting machines that are limited to 19 inch flatfish, ineffective and requiring expensive hand filleting. The cost of the enzymatic inhibitor also adds costs to typical surimi production.

Arrowtooth surimi, produced under commercial conditions, produces a low to medium grade surimi useful when blended with pollock surimi. However, market price and demand at this stage are still quite low for this product, making it more economical to continue to discard arrowtooth flounder. The creation of product standards for arrowtooth surimi designed to meet the needs of the market have still be developed. Continued dialogue between producers and analog manufactures and continued refinement of arrowtooth surimi products are the next steps.

Right now, in 1994, the commercial utilization of arrowtooth flounder is still on hold. However, the technical information is available to produce a marketable arrowtooth flounder product if circumstances change. That could come about if surimi prices rise and the need develops for a low to medium grade surimi for blending purposes. More likely, the commercial viability of arrowtooth flounder will occur when the public decides that the discard of thousands of tons of viable protein is no longer acceptable. Mandated utilization of arrowtooth flounder may come eventually, providing the processing industry with the incentive to bring in the highest return for the resource. While that may at first be simply fish meal, the tools are in place for arrowtooth surimi to provide an alternative.

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Future Research Needs

R.L. Smith, Moderator

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R. SMITH: I've been asked to conduct this final discussion session, focusing on research needs. As a reminder, the session topics included reproduction of flatfishes; early life history; general biology; feeding and growth; abundance, biomass and distribution; pollution, parasites and disease; and management and economics.

Our keynote speaker, Dr. Don McCaughran, gave us some research needs as he perceived them. I'll quickly mention them so they'll be on the record. Anyone can amplify on these research needs if they wish. Dr. McCaughran spoke about a need for spatial analysis of cost per unit effort. He mentioned harvest strategies as an area needing additional research, and he mentioned more survey data was needed along with an attempt to correlate those data with commercial catch data. Scott Meyer, in his talk, mentioned the potential conflict and the resolution of conflict between commercial and sport halibut uses. One final point that comes to mind is that additional research activity should be focused on the entire issue of bycatch and the regulatory and economic discards.

I'd now like to open this session for comment on future research needs and flatfish.

J. IANELLI: I'm with the Alaska Fisheries Science Center. I want to suggest collaboration with Russian and Japanese scientists in terms of sharing data, for the species that I'm working on, Greenland turbot. We are seeing very similar patterns in our recruitment processes and I would like to see data sharing. The stocks really are very similar, and the movement between areas and the environmental parameters would be important.

- R. TRUMBLE:** I'm from the International Pacific Halibut Commission. One of the things I thought was particularly useful as an approach was the series of spatial talks we heard on a variety of scales, from very small-scale radio tagging such as the McCall Basin Theory approach to distribution as abundance goes up and down. Some things we didn't have a chance to talk about are being done in our office, such as looking at commercial catch per effort compared with surveyed catch per effort. We're also looking for an opportunity to start combining several levels of spatial analysis and having an opportunity to evaluate some of these problems such as: Does catchability change as distribution changes? We heard a little bit about that. Do populations move horizontally or vertically? The opportunity to combine these various levels of spatial studies into some of the basic parameters for stock assessment is going to be a real opportunity for those of us who are managing stocks, to improve our assessments.
- B. BRACKEN:** I'm with the Alaska Department of Fish and Game. I'd like to speak from the perspective of a Gulf Plan Team member for a number of years. One of the ideas that you've seen demonstrated in several talks is the high abundance of arrowtooth flounder. We also heard that it is a currently underutilized species primarily because of what's perceived to be a marketing problem. There are also some other problems inherent with the target fishery for arrowtooth flounder, particularly related to bycatch. I'd like to see some research, through the Alaska Fishery Development Foundation or some other agency, to investigate whether or not arrowtooth flounder can be harvested in any quantity without undue costs to some of the other resources we're trying to protect.
- A.J. PAUL:** I'm with the University of Alaska. I'd like to follow up on Barry's comments. One thing I was hoping to see is some information on regime shifts. For example, we see arrowtooth coming up in the Gulf of Alaska; what are the consequences of that? Is it displacing some other species from a practical point of view? This is a topic that wasn't discussed and I think it's a big information gap.
- R. SMITH:** That's perhaps why the ecologists call changes in major species abundance ecological succession.
- G. KRUSE:** I'm with the Alaska Department of Fish and Game. I was very intrigued with some of the studies on reproductive biology we heard about. I see this as an area that could really use some

more research, from some species that apparently skip spawn under certain conditions to other species that have batch spawning. I think as we try to evaluate very different trends in flatfish abundances, both up and down, that perhaps some of the keys to understanding it might lie in the reproductive biology.

C. BLOOD: I'm with the Halibut Commission. I'd like to remind researchers that many of the flatfish species haven't been age validated yet. We should remember that Beamish and McFarlane pointed out in the early 1980s that age validation has been a forgotten requirement. Some of the university people might be able to help the agencies, especially the agencies that are production-type units and don't have the opportunity or the time to do this kind of work.

P. HOOGE: I'm from the National Biological Survey. I was encouraged to see a start at looking into some of the multi-species relationships. I think this is one of the biggest holes in fisheries biology. We need to look at the cross comparisons between species and understand their effect on both the commercial and noncommercial fish species.

R. TRUMBLE: We have a list up here of some pretty serious topics, and we probably can find more as we go along, but identifying a series of projects is only part of it. Where do we go from here? Are we going to try to put together some additional meetings to highlight some of these activities? Are we going to try to get together on a personal basis with people who have similar interests, or are we going to see if we can get a couple of people who are here from different agencies and put a little pressure on to find ways to start research in these activities? If anybody has any ideas on how to move forward toward solving these problems, or at least starting the solution process, we'd help ourselves a lot by figuring out where we're going to go and how we're going to get there, instead of just identifying where we want to be.

R. SMITH: Then our first order of business would be to form a working group to advance flatfish research.

P. HOOGE: I want to add one thing to that last comment. All of us right now are facing shrinking budgets and I think it's a fine time to start looking at cooperative research projects. There's a lot of overlap here, and that was one of the things that really hit me.

- R. SMITH:** Whether a working group will come out of this workshop depends on someone stepping forward to take an active role.
- B. BRACKEN:** Another approach might be an addendum to the proceedings outlining some of these research needs. It could also be put together in the form of an executive summary and made available to the agencies, so when you are looking for research needs or objectives you have a starting point for discussion. That would help us get a broader audience for these concerns. Each agency would know how they could best contribute to the process.
- A.J. PAUL:** In the other Wakefield symposia, on crab for example, we're further along; we're into our third one next year (1995). In our workshops we've actually gotten to the point where we're putting pretty detailed lists together of types of projects that need to be done. We're not identifying who's going to do it, but a lot of people have come to us to say this is really useful. I can go to my boss or I can go to my funding agency and I've got a prioritized list the scientific community has thought about and put together, and it's been very useful. That's one model.
- R. TRUMBLE:** As the guy who suggested spatial analysis as one of these topics, I would like to have Dave Sampson, Bob McConnaughey, Phil Hooge, and a couple of the people who talked about this problem express some idea of where they think a good place to start some cooperative research would be. For the others of you involved with the other topics, your input would be really useful as we put together A.J.'s model of making some lists of topics we want to look at. The topics listed so far are so broad as to be virtually useless. We need to identify some specific approaches. I don't want to get into your pet research and I don't want to cut out what your next project is going to be, but there's certainly more out there to be done than we're going to be able to do individually over the next couple of funding cycles. So to the degree that we can identify some key topics, I hope you can help us fill in the details.
- P. HAGEN:** There's been a lot of discussion of nursery area dynamics in this conference. There's probably a lot of information to be gathered about spatial distribution in the nursery area that might be important or useful, at least by analogy, to what the adults are

doing. There may be implications in terms of how we manage these fish. That might be another useful or interesting topic to follow.

L. KODOLOV: The university and the Pacific Research Institute started investigating Bristol Bay and the Columbia Bay area in the 1960s. At that time the Americans were not very interested in their fish resources. The Pacific Institute of Fisheries and Oceanography has a tremendous amount of material and data about the fish resources in this region since the 1960s. Unfortunately, publication of our findings was very difficult; we didn't have enough experience, but we have all these very valuable data and materials in our archives.

You have a high abundance of arrowtooth flounder. The proteolytic enzymes are the result of protozoans, myxosporidean parasites. The institute has knowledge relating to the use of these products. The problem, as we see it, is to not allow these specimens to be in high temperature waters. My main point is we have to cooperate and use the archived materials in order to conduct joint research in this vast area.

It was extremely interesting to participate in this conference. Many reports, in spite of lack of knowledge of the English language, raise our professional interest. I hope that the next symposium will take place in Vladivostok.

A.J. PAUL: We need to add "analyze or examine historical data," or "archived data," to the list of future research needs.

R. SMITH: I'm also adding myxosporidean parasites of arrowtooth flounders, a possible area for interaction between our Russian participants and the Alaska Fishery Development Foundation researchers who have been looking at marketability and processing of arrowtooth flounder into commercially useful products.

R. TRUMBLE: On the topic of international cooperation, I want to acknowledge that Dr. McCaughran from the Halibut Commission and Dr. Kodolov have been discussing some joint genetic analysis of Pacific halibut, and we are hoping that we'll be able to exchange samples for analysis on both sides. Also, Dr. Minami has volunteered to provide some halibut from Japanese waters. Perhaps by the next time we get together for another meeting, we will be able to report on the genetic analysis of Pacific halibut all the way around the Pacific Rim.

- C. BLOOD:** I'm also a member of CARE, which is the Committee of Age Reading Experts. We'll be meeting probably in spring of 1996. If anyone is interested in taking up some of this work on age validation in flatfish, feel free to call me, and if I can, I'll put you in touch with the appropriate people so we can get some of this work started.
- A.J. PAUL:** I wonder if it's dangerous to focus exclusively on flatfishes, because flatfishes don't live in a vacuum, they live with other fishes, and when we do things like catch pollock, for example, that might affect populations of flatfishes. This was a good start to get flatfish biologists together and have our own little forum, but maybe we need to think in a bigger way.
- R. SMITH:** Certainly that bigger way does have to do with the multi-species interactions. There were a number of presentations that outlined comparative food habits of flatfishes in the Bering Sea and the extent of depredations that particular flatfish species or stocks make on their prey. When you have a host of predators—some flatfish, some round fish, some not even fish—all targeting on a series of invertebrates and fishes, it's one of those classical exercises in drawing a food web diagram with arrows pointing in every direction. Those kinds of multi-species ecological interactions certainly do extend far beyond flatfish into plenty of related areas. Flatfish eating crabs and crabs eating flatfish is a simple example of how complicated the tasks before us really are.
- G. CASTILLO:** At this conference I have been looking at all the studies and I find that there is something missing which some of you have mentioned: the importance of multi-species relations. There are few data available for the prey items that these organisms eat in relation to their availability, and pollution and introduction of a species could be a big factor that could change the food base. That is a topic that has been neglected. In addition, predation on other juvenile flatfish could be important. Dr. Tanaka mentioned that as an important factor on the coast of Japan and here, but I haven't seen any studies.
- P. HAGEN:** I'd like to make a case for flatfish in general as being something unique. I'd hate to see them get totally swallowed up in a multi-species approach because, in general, flatfish are different from other fish. It is my understanding that recruitment fluctuations aren't exhibited in flatfish like they are in many other fish. Certainly there have been notions of a density-dependent mecha-

nism happening somewhere in fish but flatfish appear to level the population out. That's certainly something that's part of the uniqueness. While we can view flatfish as part of the bigger ecosystem, there's something inherently unique about these critters we're studying.

List of Flatfish Research Needs

The topics are listed as they were provided and no effort has been made to rank them in order of importance.

- Spatial analysis of catch per unit effort for Pacific halibut.
- Additional survey data to be correlated with commercial catch data.
- Potential conflict between commercial and sport halibut fisheries and its resolution.
- Bycatch and relationship with regulatory and economic discards.
- Cooperative research on Greenland halibut.
- Potential for arrowtooth harvest in Gulf of Alaska with acceptable bycatches.
- Does reproductive biology of flatfish drive abundance?
- Age validation of flatfishes.
- Multi-species interactions of flatfishes with their prey, competitors and predators.
- Assessment of archived data on flatfishes.
- Myxosporidean parasite as a cause of arrowtooth soft flesh.
- Genetic analysis of Pacific halibut.
- Human perturbations such as pollution and introduction of alien species.

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