

# FLATFISHES: A Systematic Study of the Oregon Pleuronectid Production System and Its Fishery

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# 1. INTRODUCTION & BACKGROUND

Pleuronectids--saltwater flatfishes--make up a significant fraction of Oregon's trawl fisheries. [Pleuronectids, according to Webster's third unabridged dictionary, are flatfishes (order Heterosomata) that have the eyes on the right side, the dorsal fin extending well forward on the head, and the mouth terminal.] Oregon's Department of Fish and Wildlife (ODFW) keeps count of more than 13 species of flatfishes landed commercially from state and adjacent waters. Dover, English, and petrale sole make up the greatest poundages and command the highest ex vessel prices. In 1979 flatfishes\* accounted for about 43 percent (by weight) of all trawl landings and approximately \$5.18-million, or 30 percent (by value), of the state's total groundfish catch.

The number of trawlers (including shrimp trawlers) licensed by the State of Oregon has grown geometrically in recent years. ODFW records show 52 Oregon and out-of-state boats licensed for all trawl fisheries in 1952, 65 ten years later, 93 in 1970, 124 in 1975, and 280 by 1979! Their quantity alone does not tell the entire story. While the number of trawlers has been rising ever faster, the typical new boat may be up to twice the length of its predecessor, with proportionally greater fishing capacity. For heavily exploited flatfish stocks, this trend points up urgent need for refining fisheries management capabilities.

From the earliest days, trawl fishermen and biologists have recognized that distributions of flatfishes and other species overlap on Pacific Northwest

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\*Excluding halibut, which may not be taken legally by net under international regulations but includes sanddabs of the Fam. Bothidae

fishing grounds. Although the trawl fleets direct their efforts toward the most marketable species, trawling as a fishing method captures a mixture of species that varies in sizes and ages. Trawlers discard undersize and unsaleable fish overboard. Few survive.

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***"The number of trawlers licensed by the State of Oregon has grown geometrically in recent years."***

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As consumer demand for seafood rose during the 1960s and '70s, social and political pressures mounted to manage fish stocks to perpetuate maximum harvest capabilities. Fisheries management is a relatively young concept, mostly postdating World War II. Owing to ocean fishes' elusive behavior and the opaque, three-dimensional, fluid nature of their habitat, pioneering fisheries scientists have had to deal with one cryptic variable at a time. Nonetheless, the knowledge thus derived has enabled researchers to begin piecing together a functional understanding of critical aspects of fisheries productivity and human exploitation of marine stocks.

Investigators in the Pacific Northwest have been stockpiling catch and effort statistics and biological data for 25 years. Their research has linked fluctuations in key fisheries with variations in physical and biological factors in the fishes' environment. By the early 1970s, with public access to remote sensing data and the advent of third-generation computing technology, some fisheries scientists were coming to believe that the majority of fisheries dynamics will not be adequately explicable without considering multiple, interdependent factors. That is to say, they began to advocate studying fisheries dynamics as a system of interactive variables.

Meanwhile, spiralling demand for seafood prompted growth of local fishing fleets. It compelled foreign operators to range ever farther to sea. Russian trawlers first appeared in Oregon waters in 1966. Their intrusion onto previously uncontested domestic fishery grounds escalated fishing effort in the northeast Pacific and aggravated Americans. Most of the U.S. industry was of the opinion that

unless the unregulated foreign pressure was curtailed, it could and would cut traditional domestic catches. In 1976 the United States unilaterally asserted sovereign claim to the economic resources of its continental shelf. This political initiative redressed a measure of American fishing industry's concern. However, the Fishery Conservation and Management Act has come to be regarded internationally as enlightened legislation. Specifically, it encourages global use of ocean production, while reserving for U.S. fishermen and processors the first rights to ocean stocks within the 200-mile economic zone. Perhaps more noteworthy in the eyes of its critics is what the Act omits—it does not exclude foreign fishing inside the zone, despite lobbying by fishermen for such a ban. Instead, it legitimizes the licensing of foreign vessels (subject to American regulation) to harvest surplus production not taken by U.S. operators. In sum, then, the Act imposes a political solution to social and biological problems. It creates management goals such as "optimum sustainable yields" (OY) but delegates definition of such crucial concepts to management agencies. The Act thus provides a new urgency for fisheries scientists to advance from analyses of historical changes in productivity to bona fide predictive capabilities.

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***"Perhaps more noteworthy in the eyes of its critics is what the (Fisheries Conservation and Management) Act omits—it does not exclude foreign fishing inside the (200 mile) zone, despite lobbying by fishermen for such a ban."***

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From six to ten investigators at Oregon State University had been working independently on aspects of ocean productivity with Sea Grant funding since 1968. In spring 1974 grantees in OSU's Department of Fisheries and Wildlife and School of Oceanography drafted proposals to extend their prior research. With encouragement from the Sea Grant director and logistical aid from Sea Grant's marine advisory agents, they participated in informal meetings in coastal communities. There and

elsewhere the researchers canvassed fishermen, processors, and staff of state and federal agencies in regard to problems besetting local fishing interests, seeking possibilities which might be attacked through applied research. Among issues that they surfaced was a need for investigation of the productivity of underutilized fisheries.

At about the same time, the OSU Sea Grant program was preparing a 5-year plan to guide program administration toward Calendar Year 1979 and the start of its second decade. The director called on Sea Grant's citizen advisory council and community leaders around the state for counsel. One pronouncement in the plan that stimulated the pleuronectid study was its formal encouragement of interdisciplinary research. The plan also called for greater cooperation by university, fisheries, oceanographic, and other disciplinary specialists; coordination with resource management agencies; and joint goal setting with fishing industry. It called for providing new knowledge that could increase, by 15 percent, the production of underutilized fish stocks off Oregon. Objectives for producing food from the sea included:

- continuing to emphasize research relating to the abundance and productivity of both exploited and unexploited ocean stocks.

- attempting to develop understanding of recruitment, survival, and response to management strategems which could lead to increased harvest of groundfish species, and

- investigating some of the economic, social, and cultural effects of the then hoped-for 200-mile economic zone, in cooperation with state and federal agencies.

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***"... the Act imposes a political solution to social and biological problems."***

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The local Sea Grant administration sought to identify opportunities consistent with its 5-year plan where investment of limited resources promised the greatest return. In consultation with the fisheries investigators who had asked for Sea Grant funding, the program administration con-

cluded that a collaborative investigation of factors affecting flatfish productivity was just such an opportunity.

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***"One tentative conclusion is that Oregon pleuronectids offer a potential for greater productivity if managed as assemblages (rather than as individual species)."***

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After screening preliminary proposals for 1975-76, the Sea Grant director met with five senior investigators from OSU and one from ODFW. These principals agreed to shape their research designs in a cooperative, interdisciplinary probe of the systematics of flatfish productivity off Oregon, concentrating on unknowns in the productivity of exploited species. In return, Sea Grant made the commitment to fund their collaborative effort for five years as Project R/OPF-1, the Pleuronectid Production System and its Fishery, beginning July 1975.

The collaboration by R/OPF-1's six principal investigators integrated capabilities in aquatic biology, benthic ecology, biological oceanography, fisheries ecology, and fisheries population and community ecology. Their efforts have since been augmented by the contributions of two more faculty members, two data processing specialists, and 19 student assistants pursuing subprojects under the senior investigators' supervision. By June 1980 study findings had yielded 14 journal articles, four graduate theses, and drafts of at least 17 additional submissions. (A bibliography of literature generated during this investigation appears in the Appendix.) Four computer software packages were completed and available to interested users outside OSU. A parallel Sea Grant study of social, behavioral, and economic characteristics of Pacific Northwest trawl fisheries originated with the beginnings of this project. And owing in large measure to progress posted under R/OPF-1, in late 1978 an OSU team was able to initiate analyses of OY management for a West Coast fishery for Pacific whiting on an expedited schedule for the Northwest and Alaska Fisheries Center of the National Marine Fisheries Service.



OSU Sea Grant administrators did not venture into this multiple-year, interdisciplinary funding commitment without reservations. Against prospects for useful, readily acceptable findings they had to weigh the risks of coming to inconclusive endings and failing on a grand scale. The National Sea Grant Program's amenability to flexible programming encouraged them to proceed. The project has subsequently capitalized on adaptability. As Section 2 documents, the study has seen certain subtasks substantially revised, resources redirected, some inquiries closed, and others opened, and one or two efforts come to dead ends. The mixing of disciplines and need to be adaptable combined at times to frustrate program administrators. Nonetheless, by June 1980 the project clearly had begun illuminating how flatfish reproduction and growth processes affect flatfish productivity and how domestic fisheries use that productivity.

Section 3 digests technical accomplishments through June 1980. One tentative conclusion is that Oregon pleuronectids offer a potential for greater productivity if managed as assemblage units. Trawls do not capture a single target species, but take sections of entire bottom communities. The fishes in these communities interact to significant degrees. In the pleuronectid fisheries, therefore, it appears that it is not possible to manage for maximum productivity of more than one species in a stock at a time. Furthermore, evidence from this project suggests that using traditional yield models to manage species that interact in assemblages will not lead to long-term stability in the fisheries.

R/OPF-1 results to date include:

- 1) developing computer software to analyze species associations and analyzing the species associations in which the commercially valuable flatfishes occur;
- 2) mapping commercial catch locations;
- 3) mapping seasonal shifts in catch patterns and relating those migrations to spawning behavior;
- 4) developing computer software to portray commercial catch statistics as "three dimensional" graphics;
- 5) locating nearshore nursery grounds that are at least as important to productivity as estuarine areas for certain species;

- 6) evaluating the growth rates of juvenile English sole in estuarine and nearshore nursery areas;
- 7) analyzing loss in flatfish yield caused by discarding undersize specimens from trawl catches;
- 8) discovering that flatfishes in the study region grow faster as water temperature drops, which is the inverse of temperature's effects on growth of North Atlantic flatfish stocks;
- 9) demonstrating statistically that upwelling is a dominant determining influence on survival of flatfish larvae and growth of juvenile flatfish;
- 10) discovering a long-term trend in upwelling that is a dominant influence on biological productivity in the region;
- 11) linking fluctuations in flatfish populations to natural variations in oceanic conditions (demonstrating that flatfish productivity varies independently of fisheries effort);
- 12) analyzing feeding selectivity of and the influence of bottom sediments and food on the distribution and abundance of Dover sole;
- 13) analyzing the food web of representative flatfishes and associated species to determine which compete for food and form interactive species associations that should be managed as a group;
- 14) developing computer software for estimating brood strengths of representative species five years later (at age of recruitment) from current data on upwelling;
- 15) proposing that calculation of maximum achievable yields for one flatfish species requires data on six to ten species;
- 16) determining from statistics for the early 1960s and 1970s that calculation of flatfish catch quotas by traditional methods would have damaged local stocks had not economic constraints curtailed markets;
- 17) proposing that managing one flatfish species in an association for maximum productivity precludes achieving maximum productivity for other species in that association;

- 18) proposing that an alternative multiple-species fishery strategy should be to optimize productivity of selected species and maintain species population levels within associations (and not to attempt to optimize yields of all species);
- 19) demonstrating that stock size had little effect on resulting brood strength for a 25-year period; and
- 20) determining that establishment of fisheries strategy for flatfishes requires choosing either constant yield or maximum productivity (which fluctuates with variability in oceanic conditions).

R/OPF-1 investigators speculate that of all their findings the feeding studies may be of greatest long-term value. To continue work on the feeding studies, synthesis of results from the various subprojects, and documentation of findings, the Sea Grant program has extended support for portions of the project through June 1981.

Project R/OPF-1 has been administered by Oregon State University's Sea Grant College Program with funding from the State of Oregon and the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. This work has been supported by federal grants 04-7-158-44085, 04-8-M01-144, and NA79AA-D00106.



## 2. DESCRIPTION OF STUDY

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Project R/UPF-1, the Pleuronectid Production System and Its Fishery, constitutes applied research. In part it is a response to requests from local fishing industry, which the project's principal investigators interpreted as indicative of need for a holistic study of the dynamics of the commercially important flatfish stocks off Oregon.

The primary target species of the Oregon pleuronectid fishery are Dover, English, petrale, and rex sole. Landings of each of the sole species annually amount to millions of pounds. The area for this study extends essentially from southern Washington to Cape Blanco and seaward to the margin of the continental shelf.

Another influence on the focus of the study was availability of pertinent research data previously collected by the Oregon Department of Fish and Wildlife, OSU Sea Grant, OSU School of Oceanography, and other entities active in fisheries research in the northeast Pacific. The predecessor agency to ODFW had gathered data on age-class structure of several flatfish species, including estimates of biomass, growth and mortality rates. In addition to those data, Sea Grant and ODFW personnel had some information on the distribution of bottom dwelling fishes relative to water depth and types of bottom sediments, on food habits of flatfishes, and on distribution of flatfish larvae.

Yet another stimulus was the high priority accorded this research by the Pacific Marine Fisheries Commission and ODFW. Fisheries managers foresaw a need for better understanding of flatfish productivity in anticipation of U.S. extension of its economic zone beyond the then 12-mile limit. More effective management of flatfish stocks off Oregon would require a better informational base than existed at that time.

Flatfishes harvested by trawl are taken in associations with other types of

bottom fishes and with other sea-floor organisms. One of the important objects of the study has been investigation of the biological significances of associations to flatfish productivity. Unknowns when the project was designed included: which species in the association of fishes feed on the same prey; which species prey on flatfishes, and in what phases of the flatfish life cycle; which foods flatfishes prefer in the various phases of their life cycle; and how much of this food is available.

There were gaps in understanding of the critical stages of the flatfish life cycle. All species hatch from egg into planktonic larva and drift with currents in the water column. The larva metamorphoses to fish form, settles to the ocean bottom, and acquires the physical characteristics of flatfishes, including migration of one eye to what becomes the darker, "dorsal" surface. Juveniles mature over a span of three to eight years. Recruitment to the fishery occurs between the third or fourth and the ninth years. The natural life span runs to about 20 years for Dover sole, which is common for northeast Pacific species.

Growth and survival are processes critical to fish production and fishery yields. Data on both processes were scarce. Estuaries were known to serve as important nursery areas for juvenile English sole and starry flounder, but in 1975 no one had evaluated how critical the role of estuaries might be to maintenance of flatfish populations. Also, the food web of flatfishes had received but limited research attention. Fisheries scientists intuitively linked oceanic variables caused by upwelling to locally high fish production, but no one had scientifically demonstrated such relationships. However, other workers had found that sea-surface temperature and transport of larval English sole by water mass influenced brood abundance outside the upwelling region. (Ref. 2-1, 2-2) Measurable oceanic conditions were suspected to be determinants of larval survival and of juvenile growth rates. Such mechanisms still remained to be identified. How interspecific and intraspecific competitions and other interactions within flatfish associations affect recruitment to fishable stocks were unknowns. A question of paramount importance to ODFW was how great the yields from flatfish stocks might be. That interest suggested a complex of possibilities for sampling, analyses, and computer modeling. Whether traditional approaches to stock management were even adequate and suf-

ficient to maximize production and avoid overfishing became timely questions.

The project's systematic study of flatfish productivity, with its implications to the fishery, reflects the combined breadth of skills offered by the six senior investigators. These six were:

Andrew G. Carey, Jr.  
Biological Oceanographer  
OSU School of Oceanography

Robert L. Demory  
Aquatic Biologist  
Oregon Dept. of Fish and Wildlife

William G. Percy  
Biological Oceanographer  
OSU School of Oceanography

Sally L. Richardson  
Biological Oceanographer  
OSU School of Oceanography

Albert V. Tyler  
Fisheries Ecologist  
OSU Dept. of Fisheries  
and Wildlife

Charles E. Warren  
Aquatic Ecologist  
OSU Dept. of Fisheries  
and Wildlife

Richardson's ability to identify flatfish larvae was indispensable to answering questions about the larval phase of the pleuronectid life cycle. Earlier Sea Grant work by Percy and Carey had dealt with bottom sediments' characteristics that affect flatfishes and bottom-dwelling invertebrates. These studies provided a basis for probing flatfish feeding habits and availability of food. Demory's study of the distributions of flatfishes from ODFW research cruises gave the team an empirical basis for its planning and provided the initial data for analyzing species assemblages. Tyler's experience with population dynamics of North Atlantic stocks facilitated the adaptation of general theory to specific West Coast fisheries dynamics. Warren's work in general systems ecology broadened the study's approaches to problems in management of multiple species. The family of subprojects which the six have subsequently headed, accordingly, represents a composite of complementary OSU and ODFW capabilities.

The principal investigators' general objectives for the project, as defined in

their first-year proposal, were:

1. to define species assemblages associated with Dover sole and other pleuronectids on the commercial trawling grounds on Oregon's continental shelf;
2. to determine ecological interactions among associated species and factors influencing the productivity of the demersal (bottom-dwelling) phase;
3. to identify critical factors in the pelagic (water column-dwelling) phase of pleuronectids that may influence survival and year-class strength; and
4. to enable more effective fisheries management through modeling and simulation of populations, fishery effects, cost-benefits and multiple species interactions.

Work on 15 of the project's eventual 31 component subprojects began in July 1975. Figure 2-1 traces a simplified and idealized flow of efforts comprising the project. The timing and phasing of subtasks have depended, in part, on the status of research data that each requires. Thirteen subprojects have been done by utilizing pre-existing data. However, the existence of empirical information has not meant easy access to it. Certain of the subtasks that drew on existing data exacted appreciable investment of research time to locate that information. The work directed at correlating year-class strength of juvenile and adult flatfishes with oceanic conditions, for example, necessitated a search that led to dealing with six agencies spanning the nation.

Six subprojects requiring supplemental sampling along with nine others that have depended entirely on original sampling necessitated 69 cruises using all three of the university's research vessels between July 1975 and November 1978. Cruises varied in duration from three hours to 16 days, for an accrued total of some 2,358 hours of ship time. Table 1 identifies which of the subprojects required gathering data.

Tyler has been principal investigator for the portions of the project devoted to synthesizing computerized simulations and management models. Because of the study's size and complexity, he also has doubled as coordinator for cooperation among the departments and disciplines involved. He credits the resulting collaboration with synergistic dividends. Questions that

likely would have gone unaddressed for protracted periods have, instead, been dealt with promptly. Each of the senior researchers has been able to direct questions impinging on other fields of specialization to colleagues who were willing to give them prompt attention. Throughout the first year of the project, the principal investigators met monthly to coordinate their efforts. Thereafter, the team met formally at annual, internal symposia to present their current findings and to plan remaining subtasks. They maintained communications by numerous informal meetings and when they met to review graduate student degree programs.

Reflective of the complexities of its subject, multiple participants, and flexible administrative handling, the study traced out a labyrinthine genealogy. Figures 2-2 through 2-5 portray interrelationships and evolution of the study's subtasks. The time spans over which they have been active can be read from the date scale at the top of each diagram. New subprojects were begun as their prerequisites became available. Early in the second year, for example, Carey, graduate assistant Kaskan, and research assistants Jones and Gish began a more intensive study of flatfish prey because studies done during the first year revealed the need for additional sampling of sediments. Similarly, Hayman and Tyler had to correlate flatfish year-class strengths with ocean conditions and to discover that there is no relationship between stock size and recruitment before they could move ahead on simulation of sole populations.

Questions raised by one subproject prompted short-term, specialized, but unanticipated subinvestigations. Carey and Hogue undertook their study of invertebrate prey of coastal juvenile flatfish to answer questions raised by Percy's work with Richardson and Krygier on flatfish nursery areas and juvenile survival rates. The early attention given to simulating fishery effects on flatfish production and evaluating cost-benefit ratios for management alternatives led to an expansion and the transfer of these thrusts to a separate, related Sea Grant project (R/PPA-8, "NETS") headed by Courtland Smith of the OSU Department of Anthropology. That transition occurred in July of the third year. Richardson's departure from Oregon State University at the end of the fourth year obliged curtailments and adjustments in thinking on some of the hoped-for studies of the larval phase of productivity.

### SUBPROJECTS BASED ON EXISTING DATA

#### Mapping of Distribution of Flatfishes and Associated Stocks

- Analysis of distribution of flatfish stocks and associated species - Tyler
- Analysis of distribution of flatfish stocks and associated bottom fishes - Percy
- Analysis of distribution of invertebrates associated with flatfish stocks - Carey

#### Investigation of Bottom-dwelling Phase

- Analysis of feeding habits of flatfishes - Hancock, Kravitz, Percy

#### Investigation of Water Column-dwelling Phase

- Investigation of distribution and duration of larval phases for Dover, rex, and petrale soles - Percy, Hosie, Richardson
- Correlation of year-class strength of flatfishes with oceanic conditions - Hayman, Tyler
- Simulation of processes affecting English sole year-class strength and spawning time - Kruse, Tyler

- Determination of relationships between stock size and resulting year-class strength - Hayman, Tyler
- Determination of distribution and abundance of flatfish larvae in coastal waters - Richardson, Percy
- Determination of sea bottom temperature from sea level data - Kruse, Huyer

#### Synthesis of Relationships Between Productivity and Fisheries

- Simulation of Dover sole populations (based on catch per unit effort) - Tyler
- Simulation of Dover sole populations (based on year-class strength) - Tyler
- Simulation of English sole populations - Hayden, Tyler
- Application of innovations in isocline phase-plane theory to flatfish production systems - Liss, Warren
- Inclusion of economic factors in application of isocline phase-plane theory to flatfish production systems - Thompson, Liss

### SUBPROJECTS REQUIRING SUPPLEMENTAL DATA

#### Mapping of Distribution of Flatfishes and Associated Stocks

- Analysis of distribution and movement of juvenile vs. adult English sole - Hewitt, Percy

#### Investigation of Bottom-dwelling Phase

- Investigation of the food web within an assemblage of fishes on the Oregon shelf - Wakefield, Percy

#### Investigation of Water Column-dwelling Phase

- Relation of year-class strength of

- larval English sole and other flatfishes to oceanic conditions - Richardson, Laroche, Mundy

#### Synthesis of Relationships Between Productivity and Fisheries

- Analysis of yield loss from discarding small flatfishes at sea - TenEyck, Demory
- Simulation of fishery effects and evaluation of cost-benefit ratios for management alternatives - Tyler
- Development of models for multiple-species management strategies - Tyler

### SUBPROJECTS REQUIRING ORIGINAL DATA

#### Investigation of Bottom-dwelling Phase

- Investigation of feeding habits and selectivity of Dover sole - Gabriel, Percy, Carey
- Intensive study of invertebrate communities preyed on by flatfishes on sites chosen by distribution studies - Carey
- Measurement of juvenile English and Dover sole and correlation with oceanic conditions - Kreuz, Tyler
- Measurement of growth rates of newly settled juveniles - Rosenbergg, Percy
- Study of invertebrate prey of flatfishes and juvenile flatfishes in

- coastal waters - Hogue, Carey
- Analysis of vertical distribution of invertebrate prey of flatfishes on the Oregon shelf - Carey
- Analysis of vertical distribution of invertebrates in Dover sole environment - Carey, Kaskan
- Mapping of nursery areas for bottom-dwelling phase and study of juvenile survival distributions, movements, and growth - Percy, Krygier

#### Investigation of Water Column-dwelling Phase

- Determination of larval growth, survival, and mortality of English sole - Richardson, Laroche

TABLE 1. Data requirements for R/OPF-1 subprojects

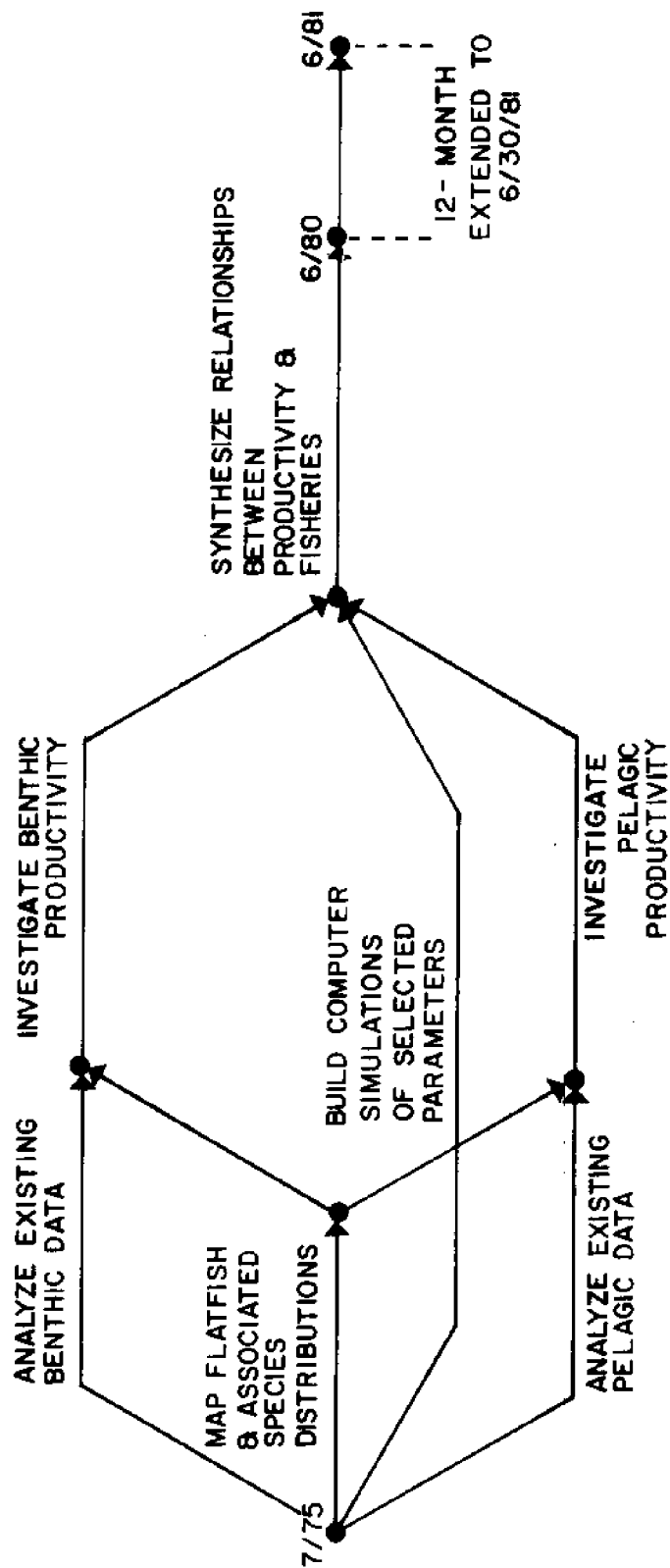


FIGURE 2-1. Flow of R/OPF-1 Subprojects



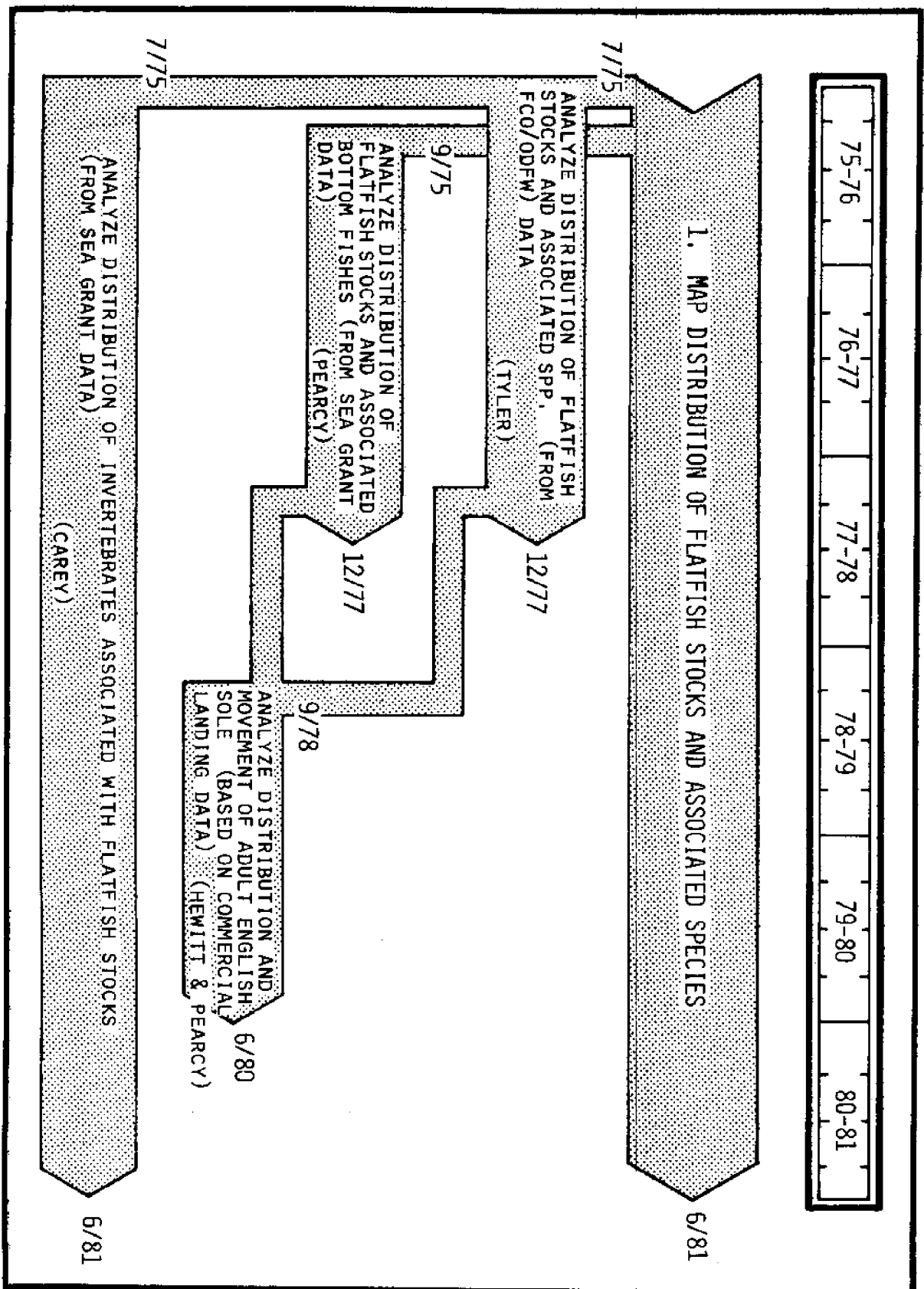


FIGURE 2-2. Chronology of subprojects investigating the distribution of flatfish stocks and associated species

FIGURE 2-3. Chronology of subprojects investigating the productivity of the bottom-dwelling phase of the flatfish life cycle

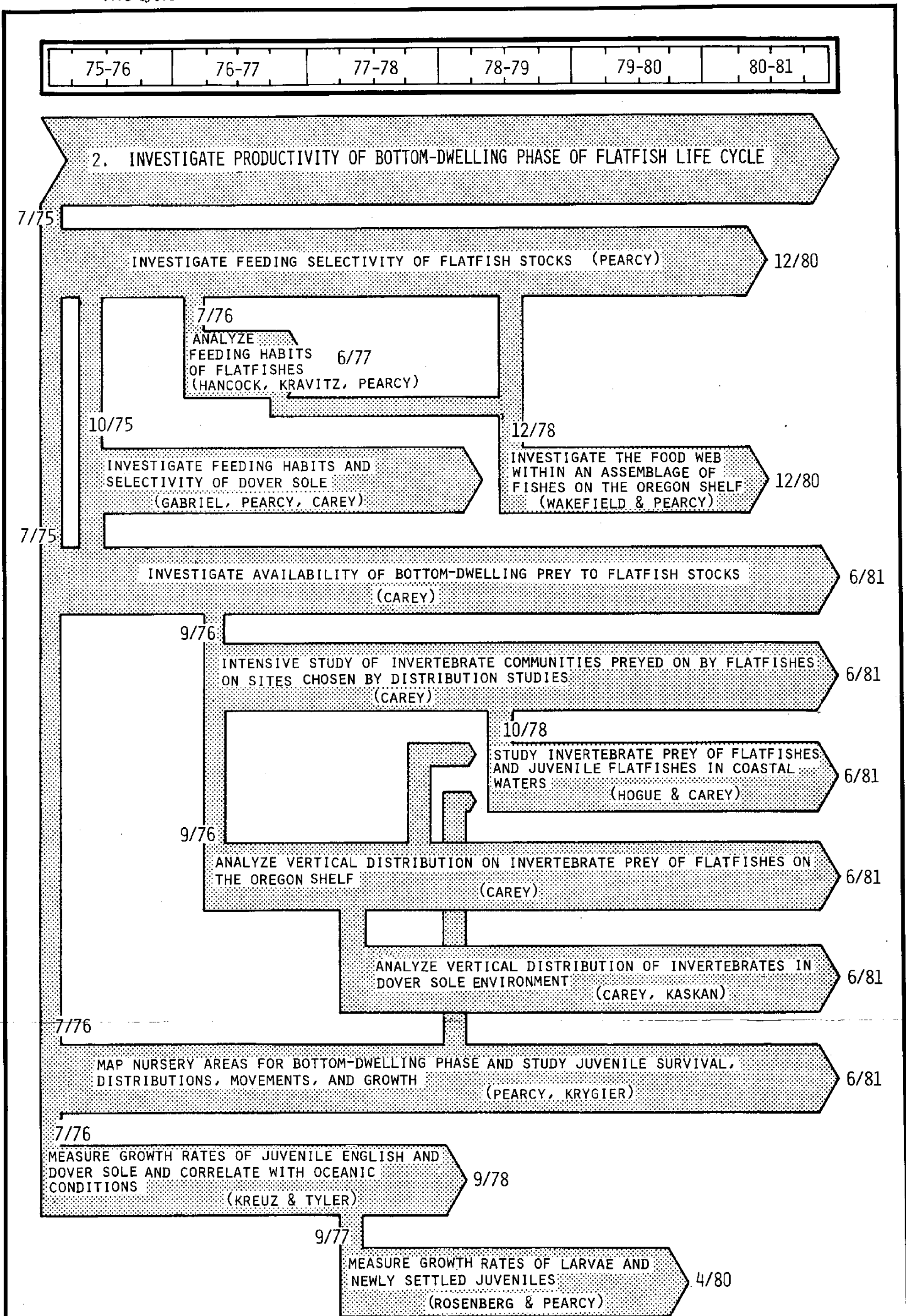


FIGURE 2-4. Chronology of subprojects investigating the productivity of the water column-dwelling phase of the flatfish life cycle

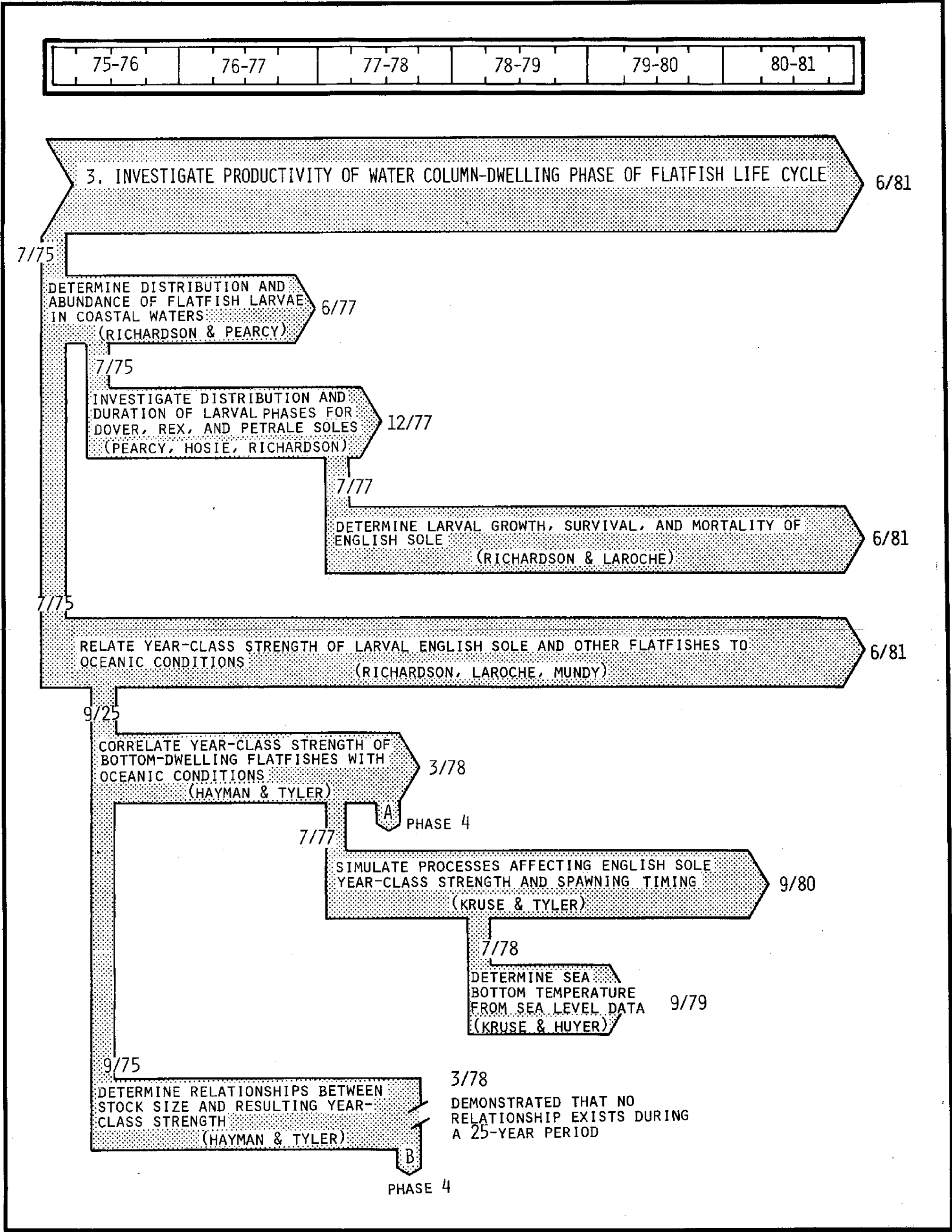
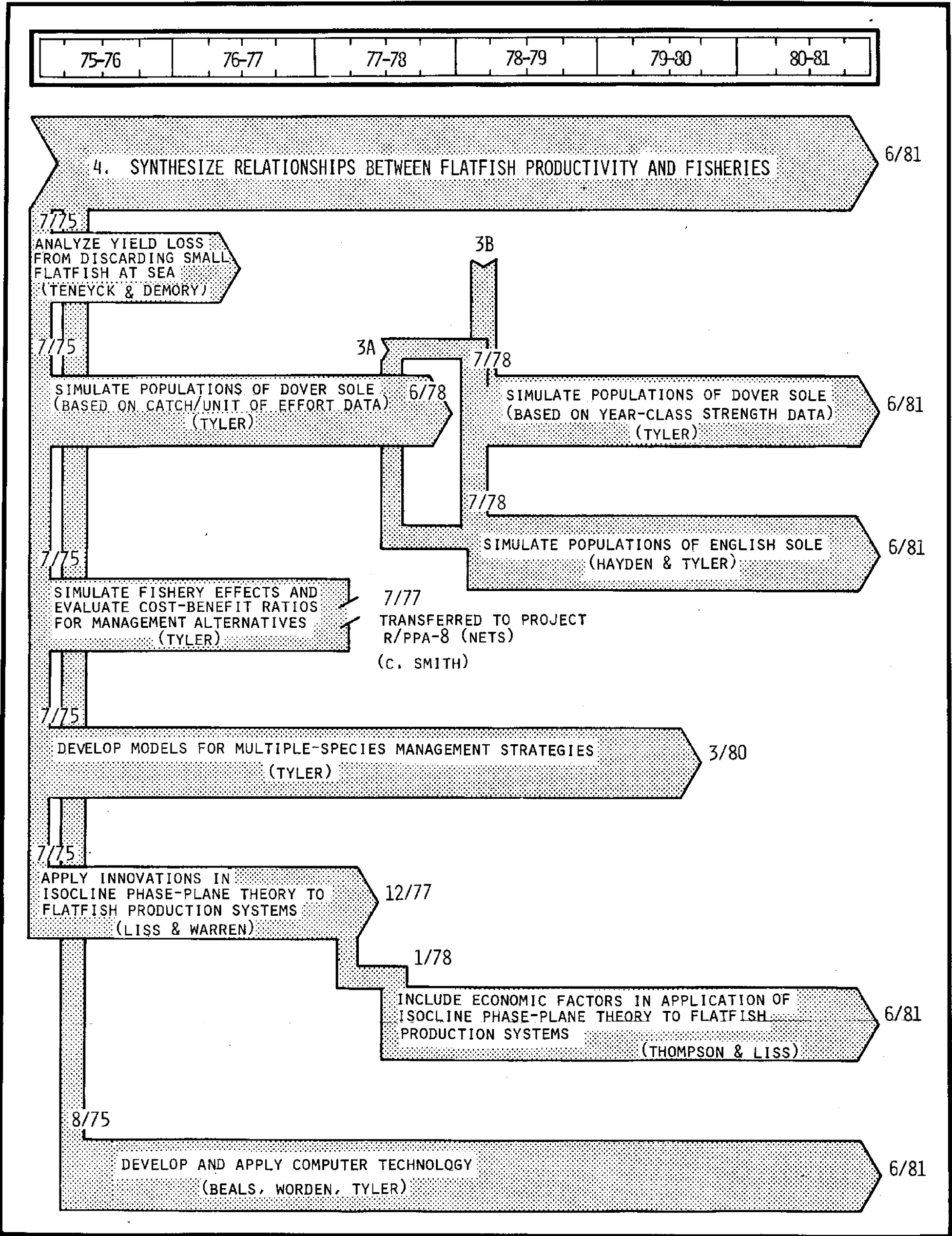


FIGURE 2-5. Chronology of subprojects attempting to synthesize relationships between flatfish productivity and fisheries



In addition to coordinating their efforts, the principal investigators periodically reported their progress to the OSU Sea Grant program office. They wrote reports annually and documented their planning for remaining effort by preparing materials for Sea Grant's proposals for renewal of funding from 1976 through 1980. While the feasibility of continuing the pleuronectid study was not re-evaluated each time, progress--and changes--under the project were evaluated by the local Sea Grant administration, the national Sea Grant monitor, and Sea Grant site visit teams. Results to date have been documented in Sea Grant annual reports and in the summaries of accomplishments for the project in each of the renewal proposals prepared since 1975-1976. Scientific reporting on subprojects began appearing in the literature in 1977 and can be expected to continue with regularity for at least the next two years. In July 1980, Sea Grant director Wick granted a 12-month extension to the original 5-year term of the project. The extension recognizes the greater than anticipated volume of data developed under the project and provides the participants continued support for analysis and documentation of findings. A summary of results for the original 5-year period appears in the following section.

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### 3. RESULTS

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The project has been an attempt to investigate aspects of the natural productivity of commercially valuable flatfish stocks off Oregon by treating the stocks within the context of a larger system. The investigators have examined both the structure and dynamics of the multiple-species, flatfish communities, what affects the productivity of these stocks, and how the local trawl fishery exploits them. This section summarizes the result of the work.

The study team subdivided their research on pleuronectid productivity into parallel investigative efforts of reproductive processes and of body growth characteristics. Examination of reproductive processes began with a study of the distribution of spawning flatfishes. This effort aimed at expanding upon available data describing that phase of the flatfish life cycle when stocks are most vulnerable to capture by trawlers. Fisheries managers regard better understanding of this phase of productivity as one requisite for managing the stocks to perpetuate the fishery. The work on this aspect of productivity also has application in the determination of spawning times. Study efforts to determine distribution and mortality of flatfish eggs and larvae have contributed to locating important spawning grounds, a second critical requisite for effective management. Findings from this subtask have improved understanding of larval survival rates and spawning times. Locating flatfish nursery areas has helped round out the still incompletely understood life cycle of pleuronectids. Measurement and analysis of data regarding physical influences on spawning time related to the goal of determining the variables that influence the pronounced fluctuations in flatfish year-class strengths. (Year-class strength is a measure of the young fish surviving after a given spawning season.)

The investigation of influences affecting hatching of eggs and survival of larvae has the same goal. Attention has also been paid to distinguishing fishery-

related effects on stocks so that these can be factored out when analyzing brood strength yields.

The purpose of investigating body growth of newly settled juvenile flatfishes has been to develop reliable means for assessing the relative importance of the portion of the flatfish life cycle spent in bay or nearshore nurseries. By comparing growth rates of juvenile pleuronectids in these areas researchers are seeking to determine which environment contributes more to flatfish growth. Project personnel have incorporated data from this subtask into a computer simulation of English sole populations. Investigation of growth rates in sub-adult flatfishes required sampling over a wide area to develop confidence in the extent of sampling required for making reliable stock projections. An additional purpose of the survey sampling has been to develop understanding of seasonal variation in flatfish growth processes. Study of flatfishes' food web has contributed new understanding of feeding preferences of and availability of foodstocks to the commercially valuable flatfishes.

The second main category of research has focused on how the local trawl fishery exploits the stock off Oregon. A substantial share of the effort along this line has been devoted to developing computer models of productivity. One of the preliminary tasks here has been mapping of locations from which the commercial catch comes, to find where the trawl fishery concentrates effort. Other preliminary tasks have been the development of yield estimates using traditional surplus-production and yield-per-recruit methods. These have provided a basis for comparison of results derivable with the modeling techniques developed under this project. To determine whether traditional management models would allow under- or overfishing of target species, investigators have developed a simulation of a Dover sole stock that accommodates the uncontrollable fluctuations observed in year-class strength and growth rate. For related reasons, investigators have developed a conceptual model that argues that management of species that interact in a complex fishery requires sustaining assemblage characteristics as well as individual target stocks that are part of the assemblage. To test an alternative management approach to the same hypothesis, other members of the project have been applying isocline theory to derive yield estimates. Influences accommodated in their methods include social and economic factors operating on the fishery.

### 3.1 PRODUCTIVITY AS A FUNCTION OF REPRODUCTIVE PROCESSES

#### 3.1.1 Distribution of Spawning Flatfishes

The mapping of commercial catch locations reported under paragraph 3.2.1 has revealed an annual shift in location of trawling effort for English sole. The fleet alternates effort between nearshore and deeper, offshore waters on a seasonal basis. To project researchers this bimodal pattern suggested that the trawlers' target species may migrate between these regions on a seasonal basis. The prospect posed the question whether such movement, if consistent, might be a manifestation of spawning behavior. G. Hewitt, under W. Pearcy's supervision, examined commercial fishery catch statistics from 0 to 80 fathoms for the area between Coos Bay and Cape Lookout for the years 1973, 1975, and 1976 to analyze English sole distributions on an annual basis. His goal has been to determine if the species migrates seasonally. He has searched for any detectable link between their seasonal movements and what is known about the life cycle of the species. Concurrently, he has assessed problems inherent in using commercial catch records as an index of abundance for one species in a multiple-species fishery.

Hewitt has found that any longshore movement of English sole is obscured by month-to-month fluctuations in fishing effort caused by factors such as adverse weather. (Market restraints also influence fishing effort.) He has found consistent evidence in all three years' data that English sole stocks off Oregon do move inshore and offshore seasonally. Average water depth at time of capture and catch per unit of fishing effort increase during fall and early winter, suggesting a movement of target stocks into deeper water.

Oregon's fishery for English sole exploits primarily females, owing to the differential growth rates for the two sexes. Hewitt's examination of the condition of ovaries from English sole caught near Heceta and Stonewall Banks, off the central Oregon coast, suggests that the concentrating of females in these areas and their subsequent movement offshore do correlate with spawning cycles. The average depths of catches increase, and larger and more frequent, commercially exploitable aggregations begin appearing in the fall, just prior to commencement of spawning in late fall and winter. The stocks' spring dispersal and slight inshore movement may be components of long-shore migrations that may alleviate intraspecific

competition for food. One effect of their seasonal dispersal is greatly reduced fishing pressure. (Ref. 3-1)

### 3.1.2 Distribution and Mortality of Eggs and Larvae

Richardson began work under the study by analyzing planktonic fish larvae collected from 2 to 111 km off Yaquina Bay between January 1971 and August 1972. Plankton from 287 bongo net tows contained 23,578 fish larvae representing 90 taxonomic groups. Richardson identified 78 of these groups to the species level. (The data collection from which she worked also includes temperature and salinity measurements at the sampling stations.) (Ref. 3-2) Richardson and Percy have analyzed these larvae as coming from two distinct assemblages of larval fishes: a "coastal" assemblage occurring 2 to 28 km offshore and an "offshore" assemblage at 37 to 111 km. (Richardson has recently identified a third, "transitional" assemblage existing between the coastal and offshore groups.) Three fish species, including English and butter sole, dominate the coastal assemblage. Slender sole is the only pleuronectid found among the offshore dominants. More than 90 percent of all larvae collected were netted between February and July. Distribution patterns were similar in both years. Adult spawning locations and current and circulation patterns probably account for the observed separation of the assemblages. Species in the coastal assemblage are similar to those found inside Yaquina Bay except that differing individual species dominate in the two locations. The coastal zone is an important spawning area for the English sole, which uses Yaquina Bay estuary as a nursery ground during part of its early life. (Ref. 3-3)

Percy, Hosie, and Richardson have analyzed 593 bongo net tows and more than 2,200 Isaacs-Kidd midwater trawls from the study area for distribution and larval phases of Dover, rex, and petrale soles. Dover sole larvae were present in all months. They appear to remain in the water column for their first year of life and are most common beyond the continental slope in the uppermost 50 m. Large larvae probably remain in the water column for more than a year and exhibit low recruitment to bottom-dwelling populations. Rex sole larvae increase in size and advance in development from March through February. Juvenile fish are common on the bottom during winter on the outer shelf. Their pelagic phase usually lasts about a year.

Both species may use the outer continental shelf and upper slope region as a nursery during the early bottom-dwelling phase of life. Petrale sole larvae were rare. Those that were present were taken from March to June and appeared to spend about six months in the water column. Young-of-the-year rex sole, uncommon in the trawl collections, appeared on the inner continental shelf only in the fall. (Ref. 3-4)

Laroche and Richardson analyzed larval collections from the region between the Columbia River and Cape Blanco primarily for abundance of English sole (but also for butter sole, starry flounder, and sand sole). Abundance, distribution and size composition of English sole larvae (but not butter sole, starry flounder, and sand sole) varied widely between late winter and early spring of the four years studied. In 1973 English sole larvae occurred more frequently, were more widely distributed, and made up a greater proportion of the collection than in any of the other three years. Weather in the winter of 1973 was unseasonably milder, precipitation was lower, winds were lighter but more variable, and sky cover was less than in the other study years. The fluctuations in larval patterns may have been related to variations in spawning times and differences in food availability. Unusual wind and weather conditions may have affected the timing and intensity of the winter phytoplankton bloom, leading to optimal larval feeding conditions and good survival that year. (Ref. 3-5)

In investigating distribution and mortality of English sole eggs and larvae, Laroche, Richardson, and Rosenberg have established and validated a technique for determining that age of larvae and metamorphosing planktonic juveniles by counting daily growth increments of otoliths. They developed a mathematical model depicting the growth of larval English sole in the ocean off Oregon, based on size-at-age data for larvae caught in the field. Growth rates decreased from 0.3 mm per day at eight to nine days of age to less than 0.1 mm per day between 73 to 74 days. The latter age is about that at which English sole larvae in the water column transform to bottom-dwelling juvenile fish. Knowing estimated age and rates of growth, when combined with abundance data, enabled them to compute mortality rates to estimate larval mortality in the ocean more accurately. (Ref. 3-6) Richardson and others have also traced development of butter sole from egg through bottom-dwelling juvenile fish



by collecting at sea and by rearing specimens in the laboratory. The species is of potential interest because it may be a main competitor with English sole in the larval phase. (Ref. 3-7)

Richardson, Laroche, and Richardson have found the patterns of larval fish distribution to be consistent throughout the winter and spring months. From additional work on the collections they have now distinguished coastal, transitional, and offshore assemblages that are present in each period sampled. The region of transition from coastal to offshore assemblages corresponds approximately to the break between the continental shelf and the continental slope. Species in the coastal and offshore groups do not overlap. The consistency of these patterns may be related to the spawning location of the adults and to predominant longshore coastal circulation patterns. They believe differences in offshore distribution of coastal assemblages may reflect differences in local coastal wind patterns. Differences in dominant taxa and their relative abundances within assemblages may reflect variation in timing of spawning and survival of larvae in the planktonic phase of their life cycle. Despite the differences observed, the persistent occurrences of three major assemblages and of three major species groups supports the idea that these patterns of larval fish concentration are constant over the continental shelf region off Oregon. (Ref. 3-8)

### 3.1.3 Identification of Nursery Areas

W. Laroche and Holton have discovered zero-age English sole along the open coast off Oregon. They have identified zero-age specimens in samplings collected off Moolach Beach and have analyzed the seasonality, depth distribution, and length-frequency patterns of these groups. Whereas the estuary has long been recognized as an important nursery ground for the species, Laroche's and Holton's findings suggest that at least some portion of this year-class may spend its first year in shallow, open coastal areas instead of exclusively in estuaries as previously postulated (Ref. 3-9). Considering the vast extent of shallow, sandy bottom, unprotected nearshore waters and relatively limited estuarine area along the coast, it is possible that even low-density or localized use of these grounds may play a significant role in total production of English sole within the study area. (Ref. 3-10)

Pearcy and Krygier have derived length-frequency histograms for larval and juvenile English sole in the lower Yaquina Bay estuary at three stations sampled with a 1.6 m beam trawl over six years and from three stations sampled with a beach seine in 1977 and 1978. They have found recently metamorphosed juveniles or late metamorphosing larvae from January through June. In some years recruitment of these small fish begins as early as October or November and continues as late as July or August, suggesting prolonged spawning times.

Abundance of zero-age specimens within the bay has been fairly consistent, although in 1977 and 1978 catches were above average. The average size of juveniles in the estuary may decrease in autumn, apparently because the larger young-of-the-year may emigrate from the bay. Small juveniles apparently occur commonly at Moolach Beach stations, often appearing a month or so earlier or persisting a month or so later than in the bays. The investigators' May 1978 sampling of other estuaries shows highest abundances of zero-age juveniles occurring in Tillamook Bay, followed by Yaquina, Siletz, Alsea, and Winchester Bays. Trawling along the open coast in summer and fall 1978 confirmed the occurrence of juveniles on open-coast, nearshore nursery grounds and reinforces the possibility that these areas contribute importantly to total productivity. (Ref. 3-11)

### 3.1.4 Influences on Spawning Times

Kruse and Tyler have tested hypotheses about possible recruitment mechanisms by developing a computer simulation that treats selected empirical data as independent variables. When egg production is correlated with either water temperature records and egg survival data or larval transport indices, their simulation model can account for 64 and 58 percent, respectively, of the variability observed in English sole recruitment. The paradigm they have used in their simulation explains the variation in terms of water temperature changes and water mass transport. These factors being characteristic of the prevailing upwelling phenomenon leads investigators to be optimistic about the model serving as a useful estimator of stock strength. For example, it predicts increased availability of English sole in the 1980s on the basis of recent, favorable environmental conditions for egg and larval survival. Using the simulation, fishery

managers should now be able to predict when to reduce future fishing effort to protect the stocks, based on measurable physical conditions that have been shown to be unfavorable to brood survival. The model, additionally, can distinguish when low recruitment follows from unfavorable conditions rather than from fishery pressure. (Ref. 3-12)

In developing the simulation capability, Kruse and Huyer searched the available record of physical data for variables which related to little documented bottom water temperatures on the continental shelf off Oregon. They have shown that sea level correlates closely with bottom temperatures at key locations--even more so than does the upwelling index. Using regression analysis, Kruse has demonstrated that near-bottom temperatures can be assessed from sea level data for application in predicting future stock strength. (Ref. 3-13)

Kruse and Tyler examined possible causes of variability in the English sole spawning season and found the phenomenon to be related to bottom temperature. They inferred spawning times from 13 years' data on gonadal conditions of female sole, on planktonic larvae, and on juveniles. They have deduced three hypotheses that collectively account for much of the observed variability: the rate of gonadal development is inversely related to near-bottom water temperatures in summer; no spawning occurs at temperatures below about 7.8° C; and rapid increases in bottom water temperatures delay spawning. (Ref. 3-14) Their simulation model indicates that both stock strength and environmental factors contribute to recruitment strength. Using the simulation they have been able to account for 68 percent of the variability that occurred in English sole brood strengths from 1960 through 1966 (Figure 3-1). (Ref. 3-15)

### 3.1.5 Influences on Egg and Larval Survival

Hayman and Tyler examined relationships between cohort strengths of Dover and English soles and environmental variables that might influence spawning success or survival. Variables that they have evaluated include measures of spawning capacity, monthly means of oceanic and Columbia River conditions, and measurements of short-term weather variability. A multiple factor statistical correlation incorporating two oceanographic factors, upwelling in early summer and offshore water movement the previous winter, explained 65 percent of the cohort strength

variation for Dover sole between 1946 and 1962 (Figure 3-2). Upwelling may have influenced food availability for newly feeding larval fishes, and offshore water movement may have influenced the location of larval settling. For English sole early fall (pre-spawning) values of upwelling, and also barometric pressure, showed statistically significant correlation with cohort strength and accounted for 84 percent of cohort strength variability between 1955 and 1966. Fall upwelling delayed warm-up of inshore bottom temperatures, which may have delayed spawning or improved egg condition, both of which are limited to stronger cohorts.

## 3.2 PRODUCTIVITY AS A FUNCTION OF BODY GROWTH PROCESSES

### 3.2.1 Growth of Early Juveniles

Rosenberg and Percy have estimated the ages and growth rates of juvenile English sole from Yaquina Bay estuary and from Moolach Beach nearshore nursery grounds. While the average growth rates have been similar for the two areas, they appear to be more variable in juveniles from the estuary. Rosenberg reports an average rate of growth for specimens from both areas is about 10 mm in 20 days. His calculation of individual growth rates from radial measurement of growth rings on otoliths removed from the specimens suggests that growth proceeds linearly, with specimens from the estuary showing slightly faster rates in 1979 than 1978. (Ref. 3-16) Percy and Krygier have obtained slightly faster growth rate estimates for juveniles from Yaquina Bay by an alternative technique employing progression of length modes of specimens taken throughout the year by trawling in the bay. (Ref. 3-11)

Rosenberg has linked findings on juvenile growth rates with data on larval growth rates measured by Laroche to derive an understanding of growth processes during the metamorphic period. The species appears to experience a prolonged interruption to growth in length between 60 and 120 days of age. Over this interval the fish undergo extensive morphological change but add no length. (Ref. 3-18) Apparently settlement from water column to bottom habitat occurs in winter and spring in the nearshore nursery grounds but mostly only in early winter in the estuary. (Ref. 3-17)

### 3.2.2 Growth of Sub-adults

Kreuz, Tyler, Kruse, and Demory have

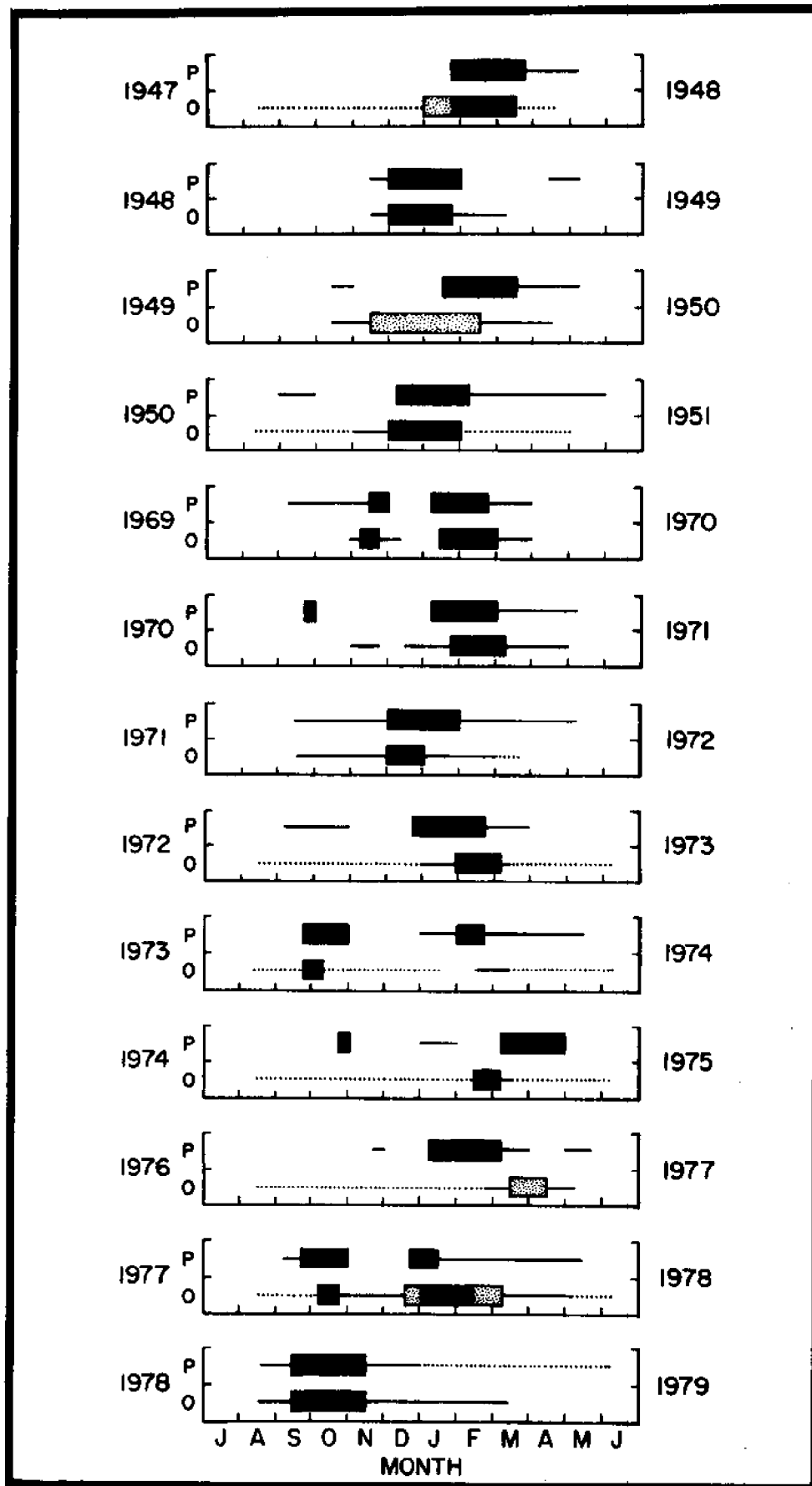


FIGURE 3-1. Comparison between observed (O) spawning records and those predicted (P) when all three temperature hypotheses are incorporated into a simulation model driven with bottom temperature estimates. A distinction is made between spawning (solid line), peak spawning (solid shaded areas) and probable peak spawning (stippled areas). A dotted line indicates no data.

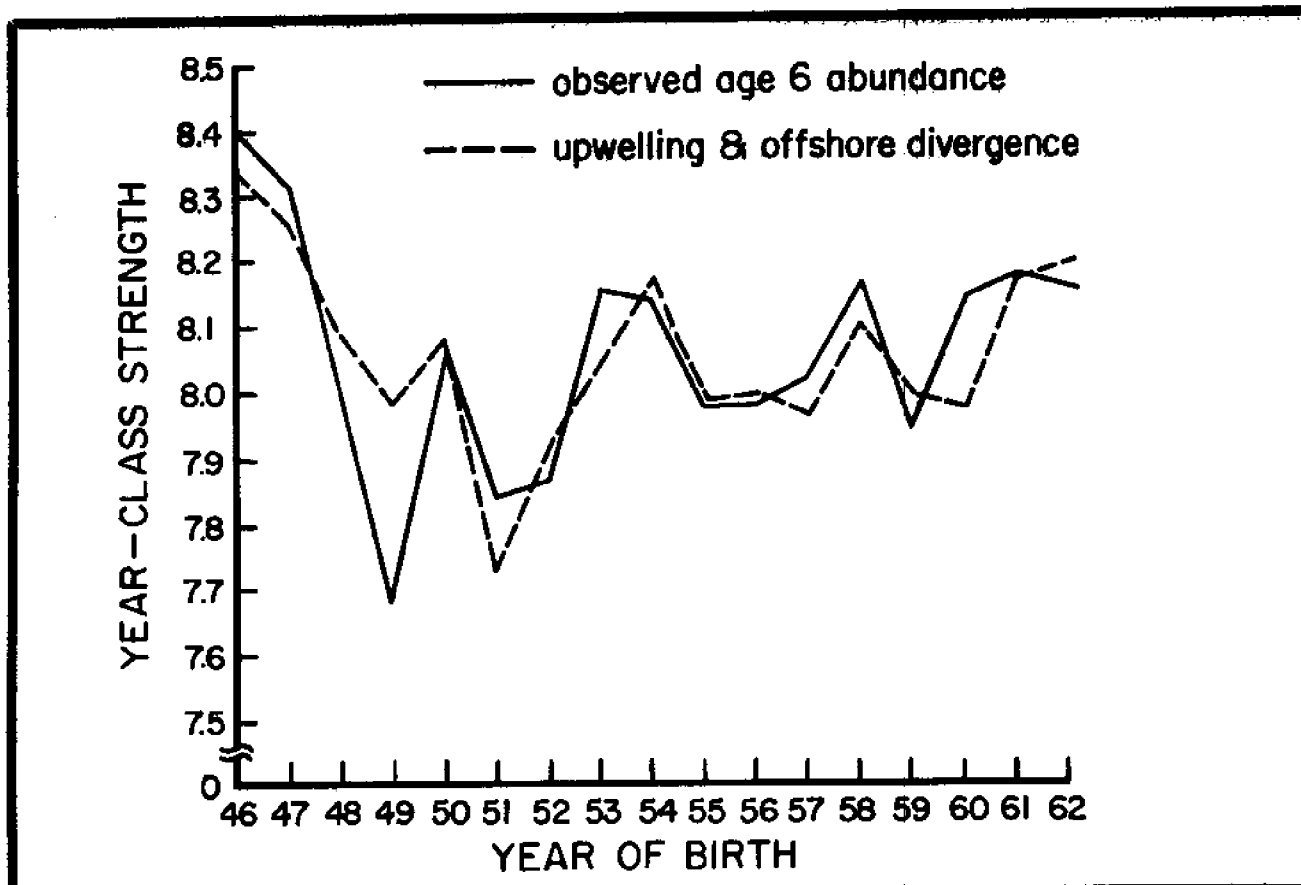


Figure 3-2. Numbers of age-6 Dover sole (year-class strength in natural logarithms) estimated by cohort analysis (solid line) compared to estimates of numbers based on environmental variables.

collaborated on a study of growth rates of Dover sole off Astoria and Brookings and of English sole off Astoria and Coos Bay. They measured increments of growth between annuli on scales and on interoperculum bones for Dover and English soles, respectively. Also, the age-specific rate of growth for Dover sole varied significantly year by year--by up to 19 percent from the average rate over the period from 1961 to 1974. Dover and English sole captured off Astoria exhibited good growth and poor growth in the same respective years as did Dover sole from waters off Brookings 460 km south of Astoria and English sole captured off Coos Bay 300 km to the south of Astoria. Dover sole taken off Astoria grew significantly faster than samples of the same species captured off Brookings. English sole from off Astoria and Coos Bay exhibited no such differential growth. Growth rates for Dover sole from off Astoria showed a general long-term increase between 1958 and 1966, followed by a gradual decrease through 1969 (Figure 3-3). Their average rate then fluctuated widely through the mid-1970s. Data for English sole exhibit a similar long-term trend that is less apparent because the information base does not cover a correspondingly long period. (Ref. 3-19)

The growing season for English sole begins in March and extends through September. Growth is most rapid during May and June (Figure 3-4). For these months the correlation between fluctuations in growth rates for both species and variation in near-bottom water temperatures is significant. Water in the area occupied by sub-adult English sole is cooler in summer due to upwelling. But the cooler water is associated with faster growth. It appears from work at another laboratory that cool temperatures may promote growth by acting directly on physiological processes governing growth (Ref. 2-2). Also, the cooler upwelled water is richer in nutrients and promotes productivity of algae and hence food animals of the sub-adult soles. Both annual fluctuations and long-term trends in upwelling and bottom temperature show strong relationship to growth rates of English and Dover sole. Growth does not appear to be associated with stock density of either Dover or English sole for the time period that was tested. (Ref. 3-19)

### 3.2.3 Food Web and Food-Energy Pathways in the Natural Production System

Tyler has contributed to baseline

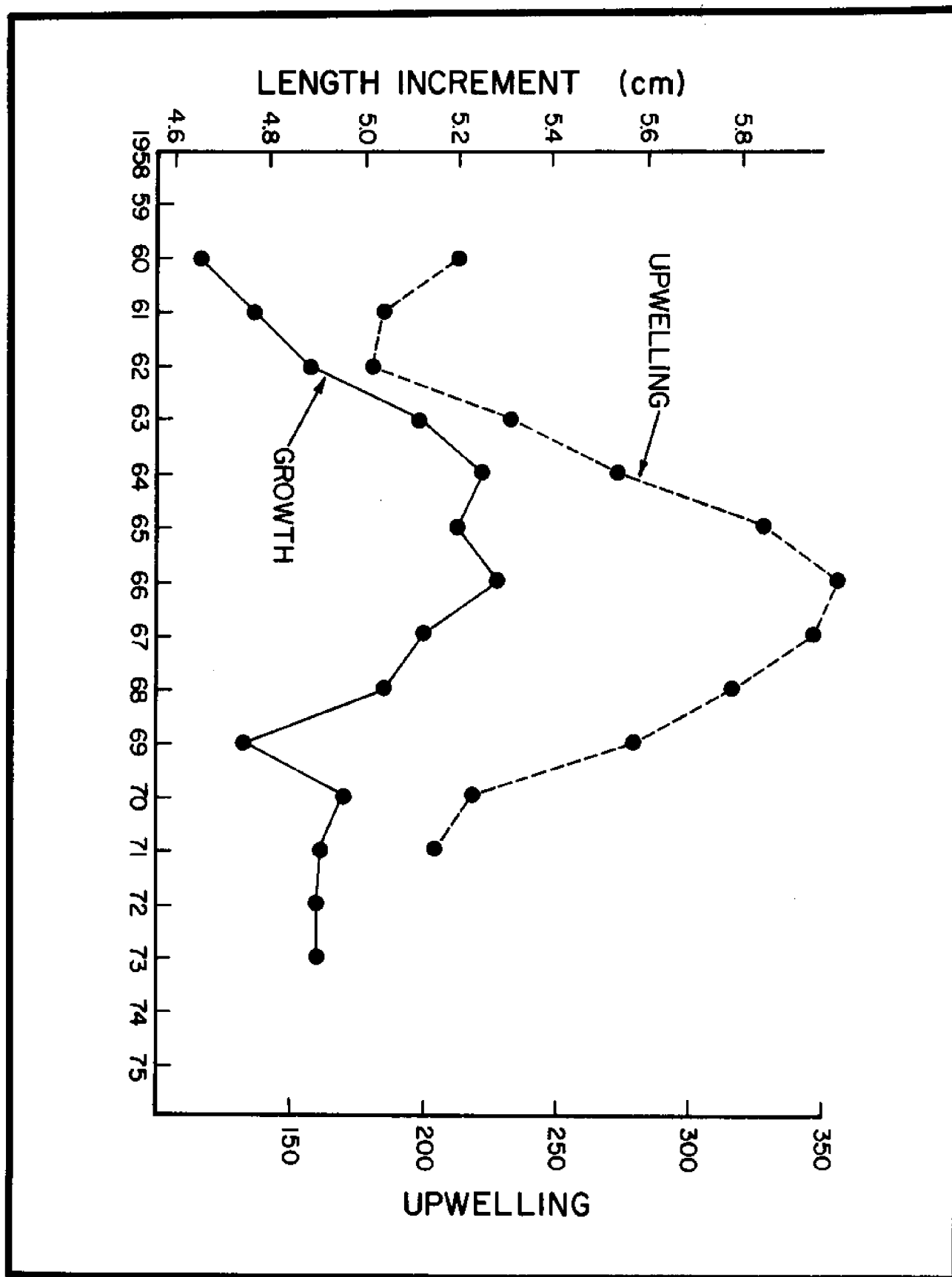


FIGURE 3-3. Upwelling is given as vertical transport of cubic meters of water each second along 100 meters of coastline summed for April through September. Five-year moving averages smooth both of the lines.

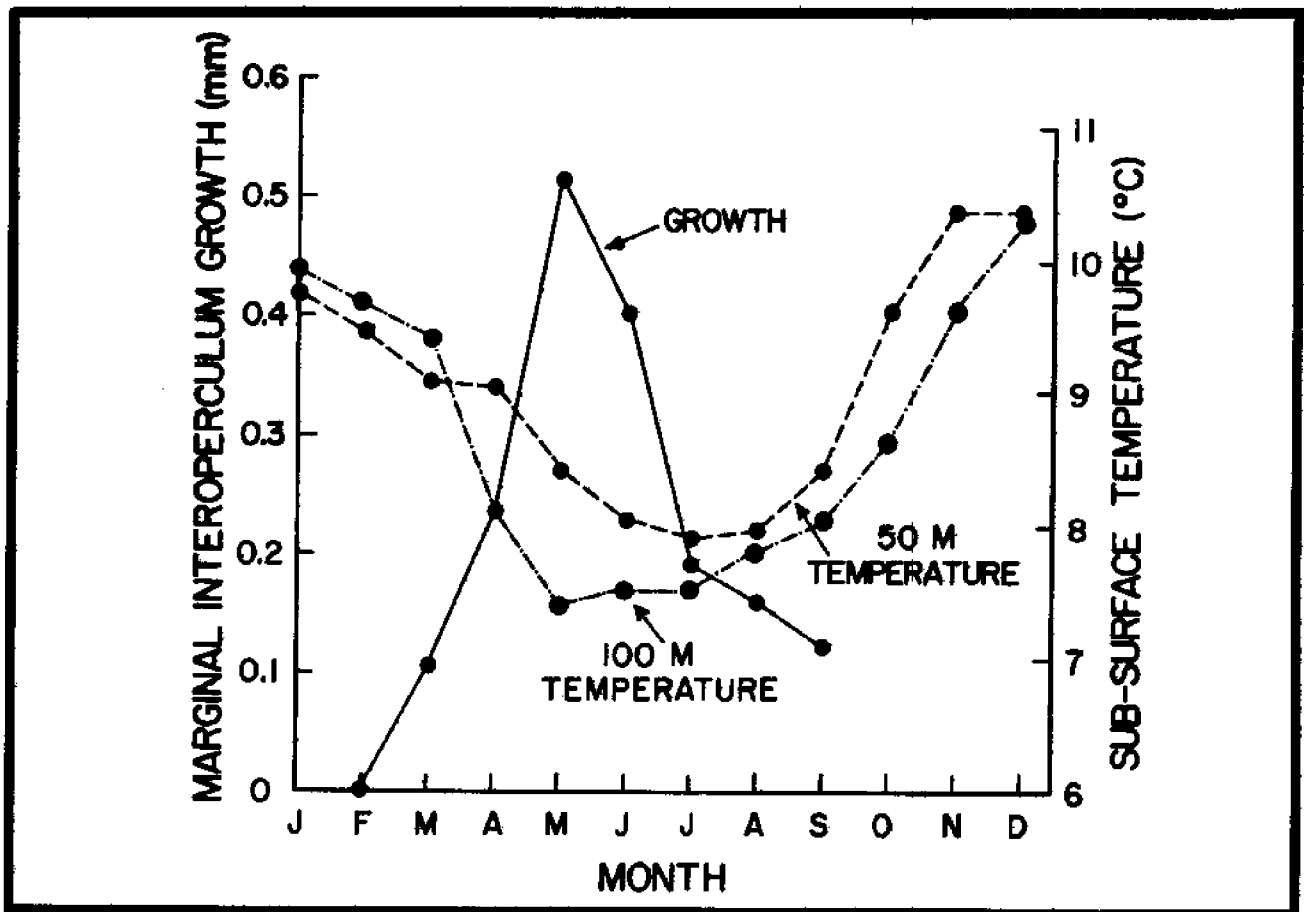


FIGURE 3-4. Changes in seasonal growth increment for English sole with bottom temperature

findings for the pleuronectid project through study of the stomach emptying rates of Atlantic cod. He found that juvenile fish obliged to swim at controlled speeds after consuming measured quantities of food showed no relationship between swimming speed and rate of emptying their stomachs, except at the highest swimming speed. His work suggests that gastric emptying rate is independent of swimming activity at normal swimming rates. This finding facilitates estimating daily rations of fish in nature. (Ref. 3-20) He subsequently has done work to determine if diet choice changes abruptly about some threshold size of prey for a determinate size of predator. He succeeded in developing a technique for classifying predators into size strata corresponding to sizes of prey taken. There apparently exists a threshold size relationship between predator and prey. (Ref. 3-21) Tyler also has found food resource partitioning to be influenced by a combination of predator-prey effects and disturbance of habitat by physical influences. The larger the degree of disturbance, the weaker the degree of food partitioning observed. The combined effects of natural perturbation and human

disturbance of habitat apparently reduce food resources partitioning. Regularly repeated disturbances, such as intermittent ocean pollution, may favor the increase of populations of prolific, shorter lived species, may reduce food partitioning, and may support predator populations that otherwise would not occur. (Ref. 3-22)

Carey, Hogue, and Kaskan have investigated the availability of prey to predators and food sources for juvenile English sole. They sampled bottom-dwelling organisms at six stations transecting selected fishing grounds to measure the physical availability of prey to pleuronectids. Sectioning of box core samples from these stations has yielded data on the composition, abundances, and vertical distribution of prey species inhabiting bottom sediments. Most species of invertebrate prey inhabit the upper few centimeters of sediments; only a few forms exist deeper in the layers sampled at most stations. Juvenile sand sole, English sole, butter sole, and speckled sanddab use the nursery ground off Moolach Beach. The amounts and types of prey available to them are important determinants of their growth rates and, perhaps,

year-class success. The investigators examined gut contents of zero-age juvenile flatfish from the nearshore area to identify which bottom-dwelling species they take; to monitor seasonal changes in feeding habits; to determine distribution of prey species in time and space; and to relate gut contents to types of bottom sediment. They have found that the four species studied represent a trophic continuum. Juvenile English sole feed exclusively on the bottom, butter sole feed on bottom-dwelling invertebrates and prey in the water column, speckled sanddab generally take prey from the water column but sometimes feed on organisms in bottom sediment, while sand sole feed exclusively in the water column. The feeding behavior of juvenile English sole changes seasonally as a result of changes in the availability of prey. (Ref. 3-23)

From earlier Sea Grant-supported research Bertrand and Carey report four distinct communities of invertebrate prey organisms in the sediments of the central shelf. They correspond to four distinct types of sediment that more or less parallel the coastline. The four zones are distinct substrates of beach sand, mixed silt and sand, silt, and glauconitic sand. The animal species occupying these habitats are low in diversity, abundance, and biomass despite the high productivity of the overlying waters. No significant change in composition or numbers is evident through the seasons at any station from 75 to 450 m. Sediment characteristics such as content of organic carbon, organic nitrogen, and sediment particle size similarly show no significant seasonal change. The differences occurring in biomass and abundance of individuals in the four zones, in comparison to those in other areas on the continental shelf, probably reflect the effects of submarine topography and consequent current patterns and distributions of sediments. (Ref. 3-24, 3-25)

Pearcy and Hancock have studied feeding habits of Dover, rex, and slender soles and Pacific sanddab at seven stations on the continental shelf. They have determined that Dover sole feed on a large variety of invertebrate species dwelling in and about the bottom sediments. Diets vary with depth and type of sediment. Pelecypods are the most important prey at shallow depth (74 m) in well-sorted sandy bottom communities. To depths of about 100 m ophiuroids, sea pens, sea anemones, and pelecypods are the main prey in silty sand and sandy silt communities. Polychaetes make up more than 90 percent of the diet at

depths to 195 m in clayey silt and silty sand sediments. The food habits of Dover sole show similarities at stations of similar depth but not among stations at differing depths but similar sediments. Dover sole taken in winter had the highest percentage of empty stomachs, suggesting that this species may feed more intensively in summer. Small rex sole were found to feed mainly on amphipods and other crustaceans. Large rex sole fed chiefly on polychaetes. This species is less diverse in its feeding preferences than Dover sole and overlaps little in its selection of prey with that of Dover sole. Pacific sanddab, the most numerous common species at shallow sand sites, and slender sole, the most common species at three deep, soft sediment stations, prey principally on open-ocean crustaceans such as euphausiids, shrimps, and amphipods. Pacific sanddab feed mainly on open-ocean crustaceans and fishes. (Ref. 3-26)

Kravitz, Pearcy, and Guin have described food selectivity for co-occurring English sole, rex sole, rock sole, petrale sole, and Pacific sanddab. English sole takes a diverse diet of polychaetes and amphipods that also includes mollusks, ophiuroids, crustaceans, and pelecypods. Rock sole take principally ophiuroids plus some polychaetes and mollusks, and occasionally shrimps, other crustaceans, herring, sandlance, echinoderms, and amphipods. Petrale sole prey on fishes and decapod crustaceans but not on polychaetes and amphipods. Other researchers have reported finding euphausiids, herring, sandlance, shrimp, and open-ocean fishes among their stomach contents. The indications suggest that the species feeds largely on open-ocean prey. (Ref. 3-27)

Wakefield and Pearcy have investigated feeding among an assemblage of bottom fishes on the inner continental shelf off Newport. They studied food partitioning among fishes, possible predation on juvenile English sole, and species composition and size range of fishes in shallow and deep waters. Trawling off Moolach Beach has revealed differences in assemblages at shallow and at intermediate depths. Species showing up in deeper tows, in decreasing order of abundance, were Pacific sanddab, English sole, butter sole, Dover sole, petrale sole, rex sole, and rock sole. The tows at shallow and intermediate depths were dominated by sand sole, butter sole, and starry flounder. In shallow water big skate, ratfish, and Pacific tomcod were abundant. (Ref. 3-28)

Gabriel has examined feeding selectivity of Dover sole from two areas of the central continental shelf. She has identified 35 principal prey taxa from specimens taken at 119 m and 25 taxa from fish netted at 426 m. At both depths polychaetes and ophiuroids are more important prey than mollusks and crustaceans. Stomach contents indicate that larger fish are increasingly selective in their feeding preferences. The body size of prey, as reported by Tyler, increases with predator size. Success in capturing prey appears to vary with the size of the predator. It may be energetically advantageous for larger fish to extract a few large bottom-dwelling organisms from below two cm in the sediment than to hunt many small, surface prey. It is also possible that small flatfishes may be physically unable to extract prey from deep within the sediment. (Ref. 3-29, 3-30, 3-31)

Wakefield has described the food web centering on English sole in an attempt to summarize potential feeding interactions within this flatfish assemblage (Figure 3-5). He has synthesized information from original observations with published and unpublished reports of the distribution and food habits of Pacific Northwest coastal fishes, marine mammals, and sea birds. Figure 3-5 depicts the main links directly involving English sole as solid lines and potential overlaps between this species and associated fishes and invertebrates as dashed lines. The diagram distinguishes relationships in open-ocean and estuarine nursery areas from those on somewhat deeper water feeding grounds for subadult and adult fishes. Nursery areas and feeding grounds constitute separate subsystems. Energy flows through three trophic levels at each and may or may not end with English sole. The figure represents the complexities of this relationship.

Production in open coast and estuarine nursery areas is based on phytoplankton, bottom algae, and land and aquatic detritus. Newly settled and older juvenile flatfish feed on intermediate size sedimentary species including copepods, larger species such as amphipods, polychaetes, and cumaceans, as well as regenerated parts such as polychaete tentacles and mollusk siphons. Polychaetes, crangonid shrimp, and other invertebrates prey on principal prey of English sole. It appears that major food resources of juvenile English sole are also common in the diet of similar size butter sole. Other juvenile fishes generally feed off the bottom but sometimes return to the bottom to take prey similar

to that of juvenile English sole.

Production at offshore feeding and spawning grounds is based on detritus and phytoplankton. Subadult and adult English sole there feed on a broad spectrum of organisms occurring in and on the bottom, as described above. An assemblage of fishes and invertebrate carnivores may compete for food with English sole. These pathways represent overlapping food consuming groups that terminate with carnivores at higher trophic levels. Slim sculpin, blackbelly eelpout, Pacific tomcod, and ratfish display food habits that are more like those of English sole than are any other roundfishes. Some predatory invertebrates also divert energy from English sole production.

English sole, in turn, are prey to a number of carnivores at different stages of their life cycle. Recent studies of food habits of juvenile salmonids and wolf-eels show that larval and metamorphosing flatfishes are a principal prey of these species. (Ref. 3-32, 3-33) Invertebrate predation may be an even more significant source of mortality for settling English sole. Abundant crangonid shrimp prey heavily on juvenile flatfishes in all nursery areas. Lingcod and big skate feed on juvenile flatfishes in shallow, open coast areas. In deeper waters, subadult and adult English sole are prey of lingcod, longnose skate, and petrale sole. Undoubtedly other fishes are also pleuronectid predators. Finally, English sole are a principal component of harbor seals' diet in the estuary and on the continental shelf. (Ref. 3-34)

### 3.3 USE OF NATURAL PRODUCTIVITY BY DOMESTIC FISHERY,

#### 3.3.1 Mapping and Characterizing Commercial Catches

Tyler and others have developed a computer graphics capability for digesting trawlers' logbook data and portraying them as "three-dimensional" plots of catch concentration or fishery effort. The resulting graphics can facilitate interpretation and application of the statistics by resource managers. Figures 3-6 and 3-7 illustrate the capability of this routine to translate quantitative information to easy-to-interpret visuals. (Ref. 3-35)

ODFW collected data from trawlers' logs from the Astoria fleet during 1975. Using computer processing, Tyler has coded and analyzed the data for seasonal patterns of fishing effort and for catch compositions



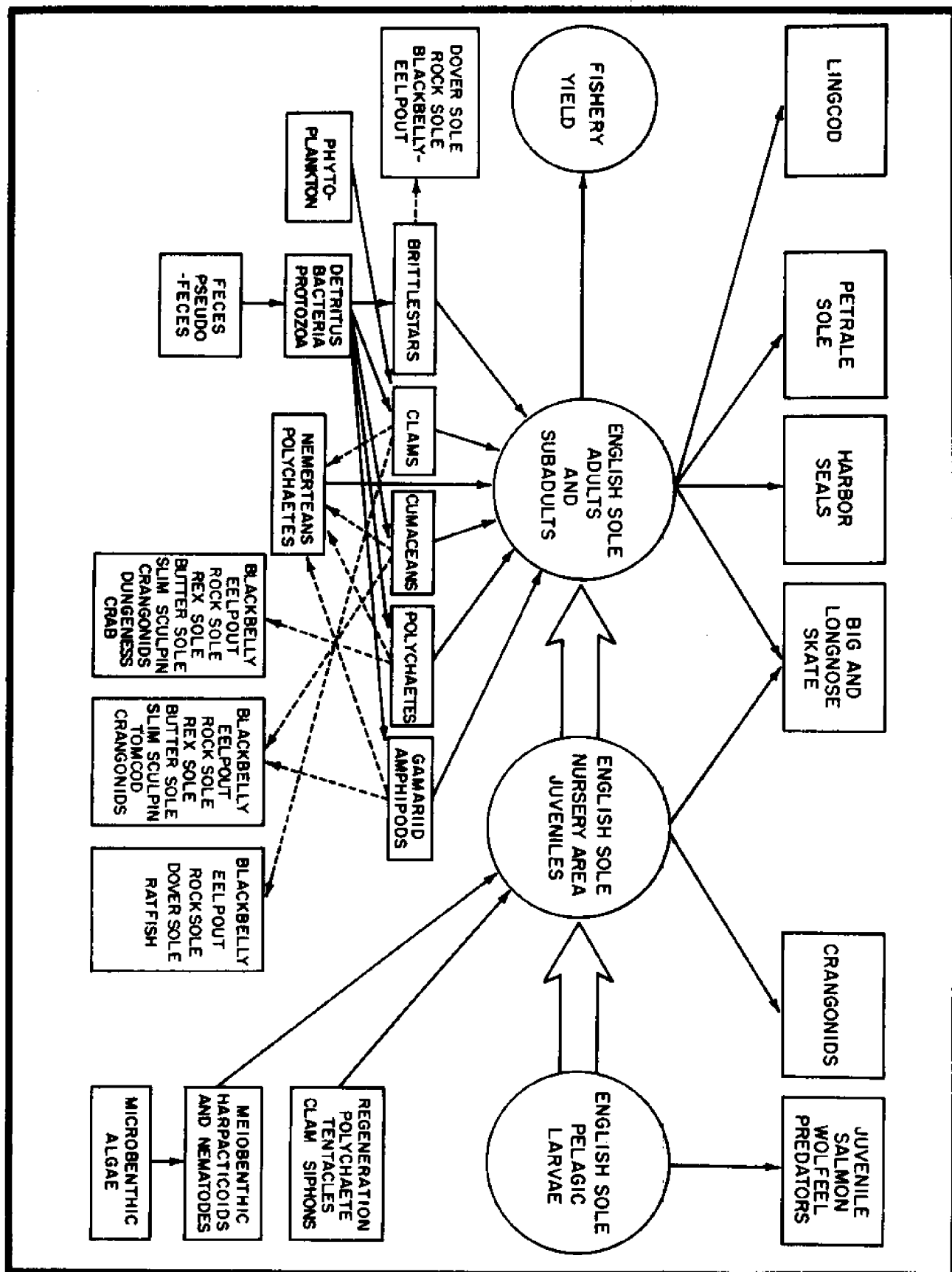


FIGURE 3-5. Portion of food web off Oregon and Washington showing direction of food-energy flow for English sole and associates. Dashed lines show potentially competitive transfer away from English sole.

DISTRIBUTION FOR ENGLISH SOLE  
 YEAR 1975  
 MAXIMUM PEAK REPRESENTS 76165 POUNDS

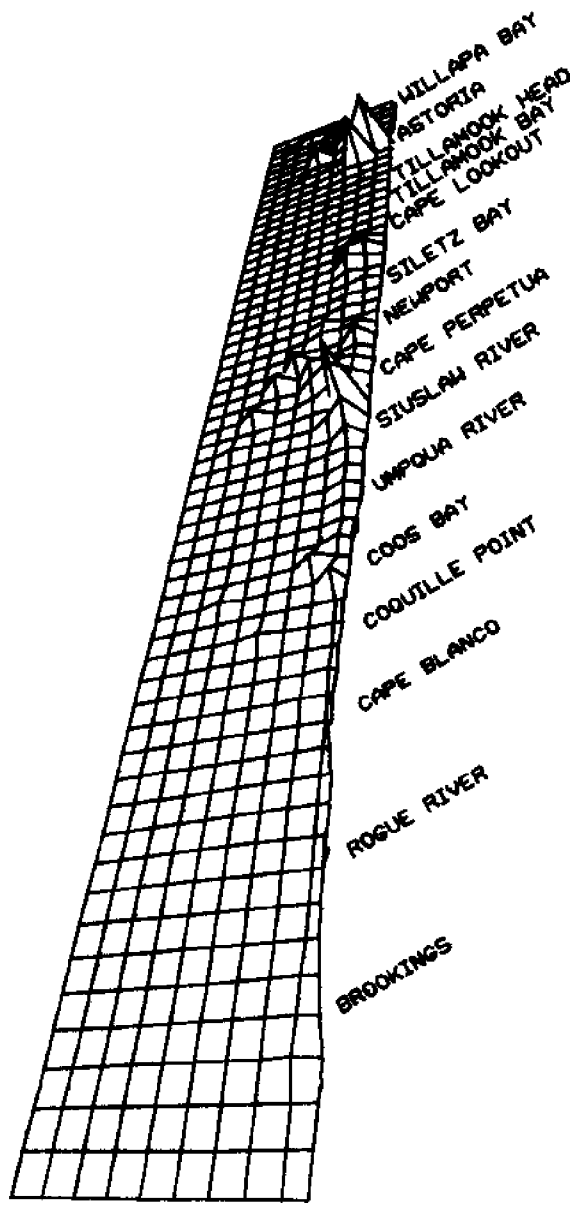


FIGURE 3-6. Computer maps of Oregon catches for English sole

DISTRIBUTION FOR DOVER SOLE  
 YEAR 1975  
 MAXIMUM PEAK REPRESENTS 105055 POUNDS

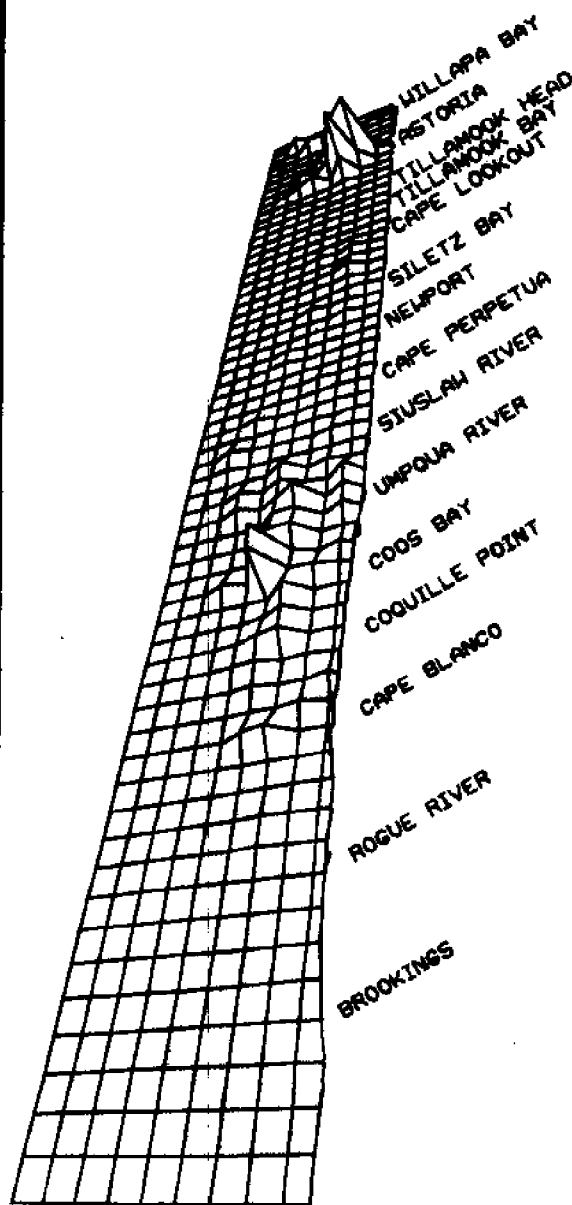


FIGURE 3-7. Computer maps of Oregon catches for Dover sole

for eight groundfish species, including six pleuronectids. He has defined and described eight catch composition classes or recurrent species mixes. The analysis has identified the proportion of monthly effort directed to each recurrent species mix. And it has led to a separate investigation under contract with Courtland Smith. (Ref. 3-36)

### 3.3.2 Yield Estimates from Traditional Models

Hayman, Tyler, and Demory have calculated indices of year-class strength, stock size, and sustainable fisheries yield for female Dover and English sole by catch-per-unit-effort (CPUE) and cohort analysis methods. Effort data for Dover sole were shown to be unreliable for indexing CPUE abundance. Cohort analysis estimates show a gradual decline in female stock size in the 1950s, a leveling off at lower abundance in the 1960s, and an increase in the 1970s. These trends in stock size appear to lag parallel trends in recruitment. Estimates of yield from parabolic surplus production models indicate that only slightly higher yields may be achievable by increasing fishing effort.

For English sole CPUE was shown to be a useful index of abundance of fish. Female stock size increased when the 1961 year-class was recruited but has since declined.

Inadequacies in the effort data for Dover sole seem to correspond to fluctuating market demand and technique used to assign effort to discrete species in a multiple species fishery. The investigators believe that cohort analysis, therefore, is a better determinant of year-class strength than CPUE analysis. For English sole, nonetheless, CPUE analysis apparently is as reliable as cohort analysis. (Ref. 3-37, 3-38)

### 3.3.3 Yield Estimates from Simulations Showing Trade-Off Between Constant Landings and Maximum Landings

On a national basis traditional management methods have attempted to target the same catch quotas every year by manipulating or otherwise accommodating biological, economic, and social factors affecting fish production. This approach calls for balancing rates of fishery-induced mortality and natural mortality against biological productivity at a determinable level. The methods used traditionally, however, do not take into account uncontrollable

variables that influence natural productivity. Tyler and others believe that adjusting allowable fishing effort and landing quotas yearly can lead more realistically to maintaining desired stock levels. Actually, some governmental management agencies, (e.g., Northeast Fisheries Center, NMFS, and Canadian Fisheries and Oceans Assessment Group, Halifax) have been setting different quotas annually. In developing their simulation model for northern Oregon Dover sole, Tyler and his associates have found that an appreciable annual adjustment to landings quota is required to reach maximum yields without overfishing (Figure 3-8). Variability in recruitment productivity necessitates such adjustment. They believe that catch and effort quotas developed from average dynamic bases could lead to underfishing (or overfishing) within a single five-year period in the immediate future. Tyler's computerized stock assessment model for the northern Oregon Dover sole stock accepts data on actual variations in year-class strength and growth rate and predicts lower yield levels than do traditional methods based on empirical modelling. (Ref. 3-39.)

### 3.3.4 Managing Fisheries to Maintain Assemblage Units Instead of Optimum Yields

Tyler and fellow investigators have come to believe that fishery management objectives must embrace not only traditional goals for target species but also goals of maintaining fish assemblage units. They and others suggest that the paramount concern for managing a renewable resource has to be preservation of management options. Fishery management aimed at attaining maximum sustainable yield will likely result in simplification of the production system and domination by species exhibiting highest reproductive rates. They maintain that there is no empirical basis for assuming that simplified, high productivity in portions of formerly diverse fish assemblages can persist in the ocean environment. They also suggest that managing one species for optimum yield risks perturbing the assemblage such that it will not return to its original species composition when fishing effort is reduced.

Effort under the pleuronectid project indicates that geographic assemblages of fishes exist off Oregon. (Figures 3-9 and 3-10.) The make-ups of most assemblages are consistent with the depths at which they exist. There may be four to six assemblages across the range of 20 to 400 meters' depth. (Ref. 3-40) Project members propose that each assemblage may be

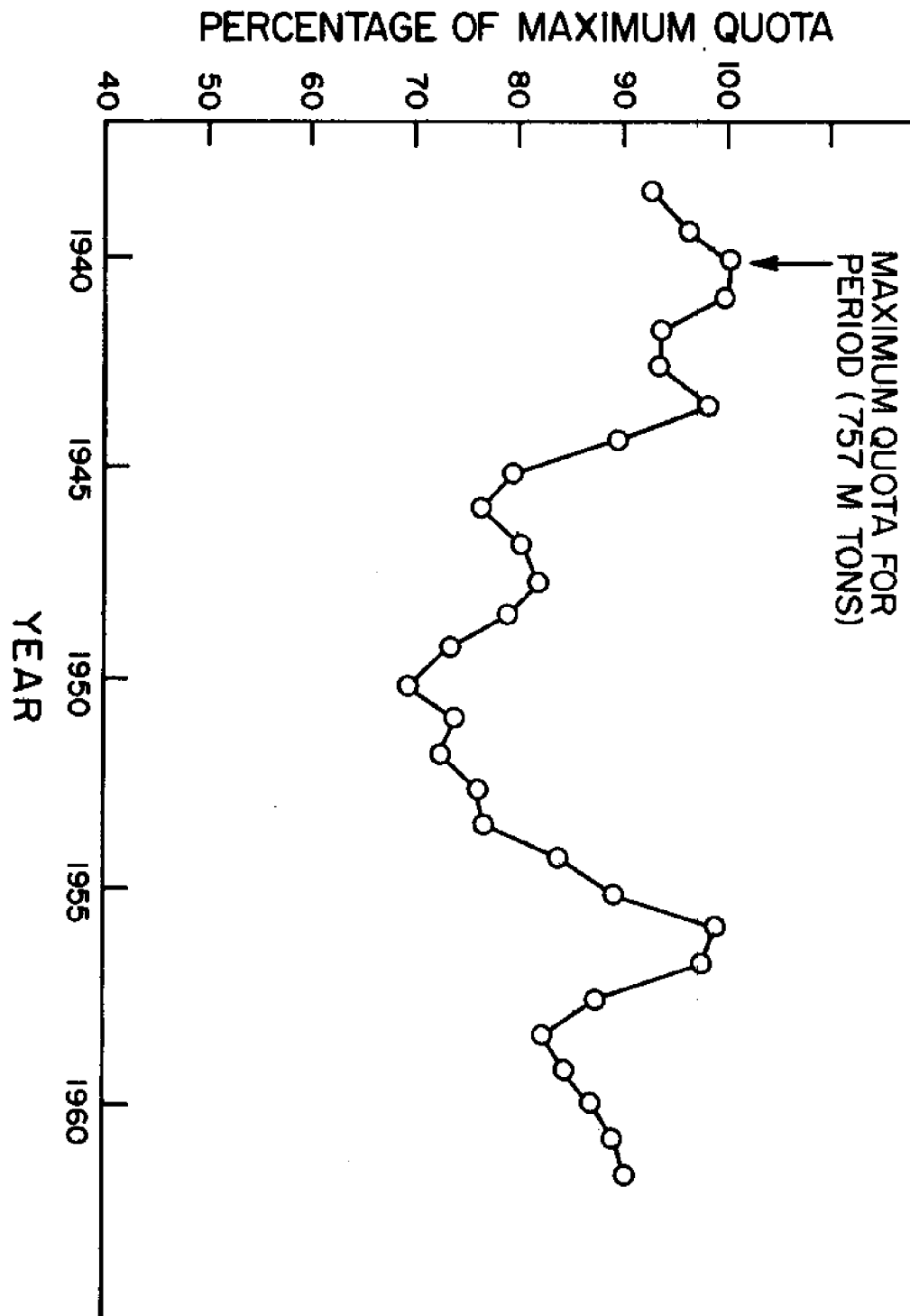


FIGURE 3-8. Variation in quota necessary for maximization of yield for the Dover sole stock off northern Oregon and southeastern Washington for the period 1946-1962

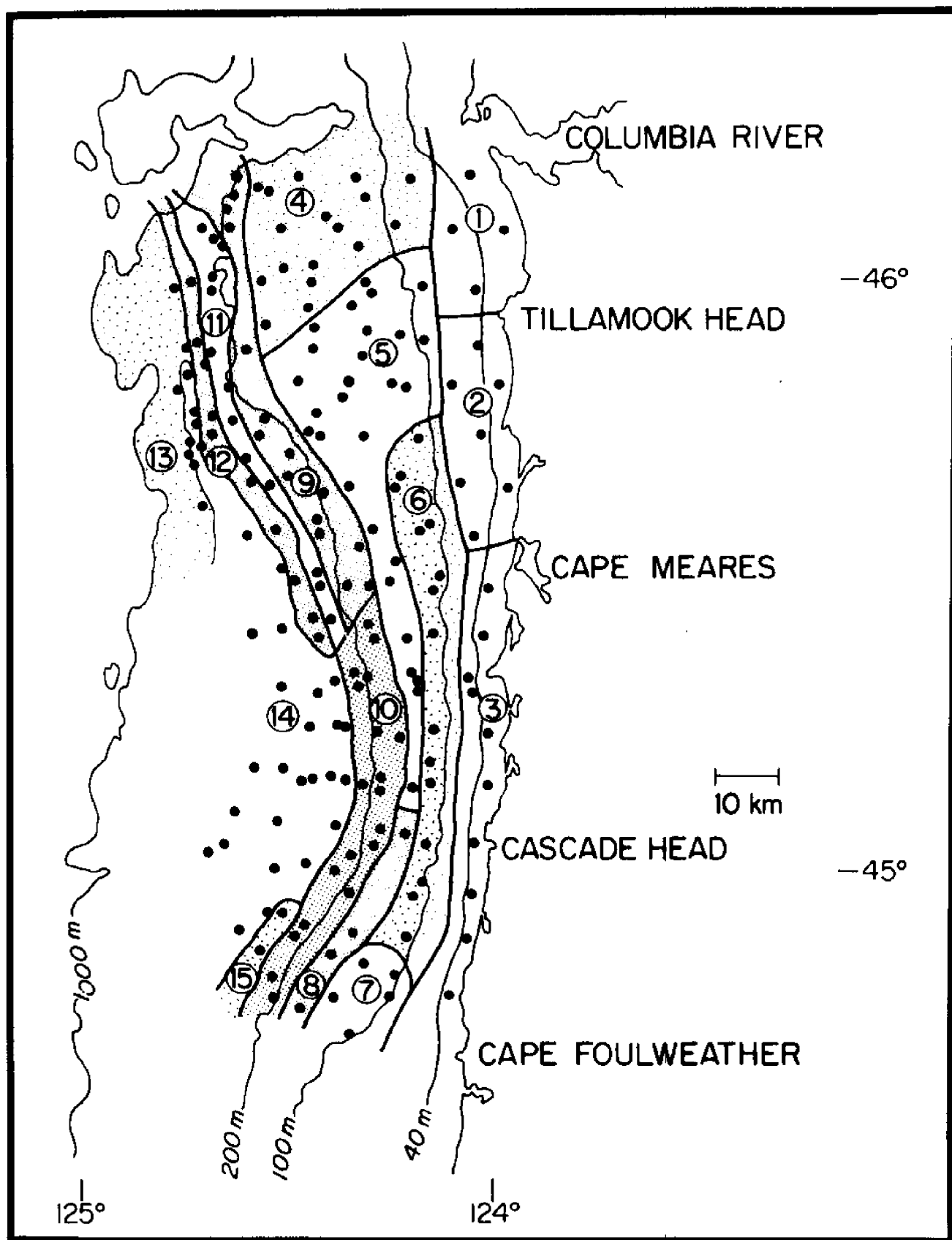


FIGURE 3-9. Fish assemblage maps for the continental shelf off Oregon

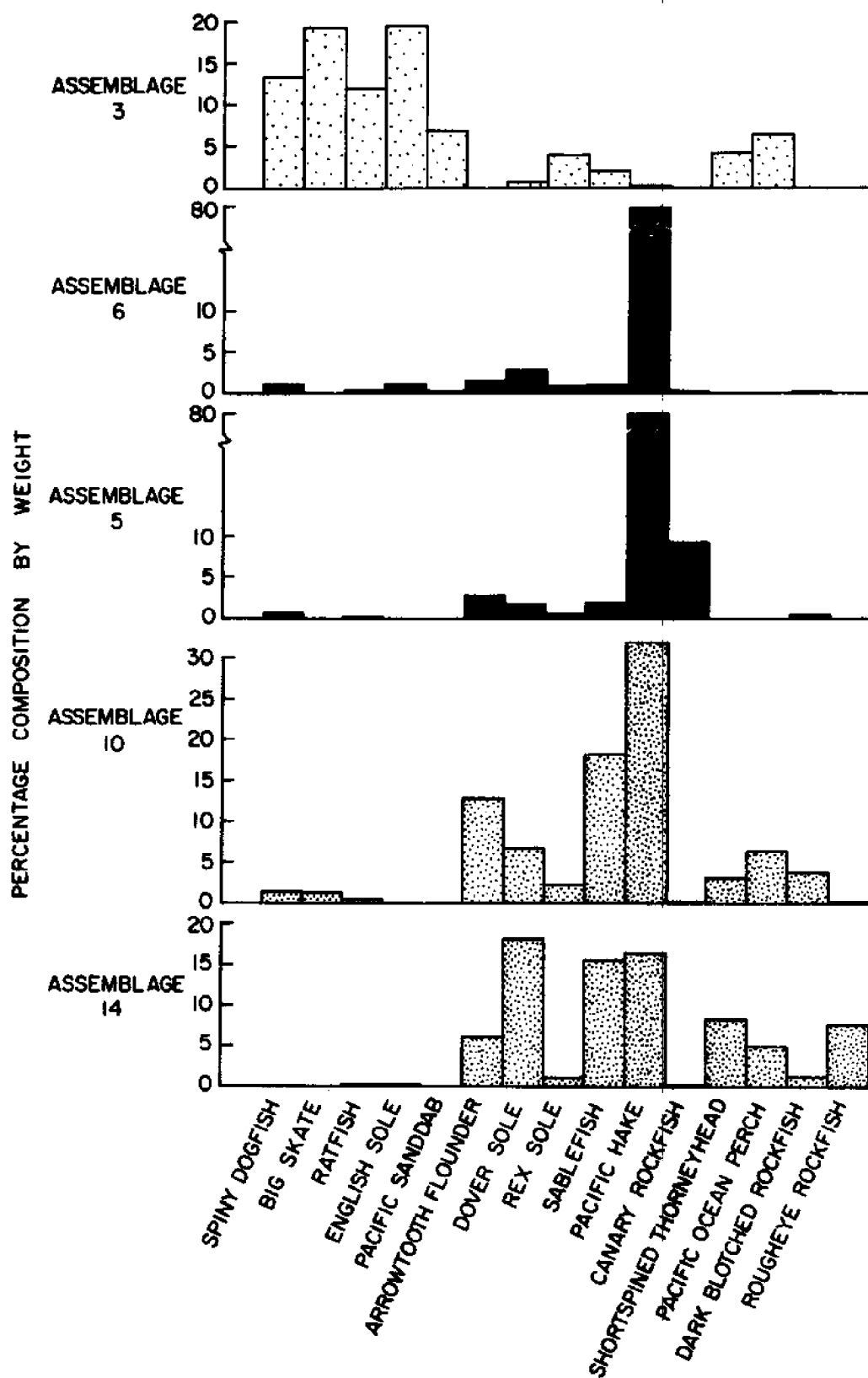


FIGURE 3-10. Assemblage composition along a transect east to west from points between Cape Meares and Cascade Head

part of a geographically definable natural production system of interacting organisms that they label a "community." Species found in the same area that do not interact with the organisms of the community are not part of that functional assemblage. Species occurring year-round within the community comprise its "assemblage production unit." The assemblage production units are analagous to fishery stocks for single-species fishery management concerns. (Ref. 3-41)

Apparently the community and its component assemblage production unit (APU) are influenced by physical and chemical factors that are often driven by forces such as upwelling (which is a result of atmospheric dynamics). They are also subject to biotic driving factors. The production processes of species that are regular components of the assemblage production unit likely are driven by effects of species moving seasonally or occasionally through the area. Accordingly, the investigators treat the seasonal species as driving factors. To model them as species would require modeling regions and processes outside the area occupied by the assemblage production unit.

Rather than basing assemblage-production-unit management strategy on equilibrium or the average state, the APU model represents a transition state. In fact, the transition state may be the only reality for many systems of species. Perturbation of a system by internal, density-dependent factors or by interspecific limit cycles may induce wide, cyclic fluctuations. A growing literature suggests that oceanic trends often dominate fish productivity. Under such influences an equilibrium yield would never even be approached.

Monitoring the transition states following controlled, pulsed fishing by the trawl fleet may offer a means of exploring and maintaining the viability of assemblage production units. Instead of watching a range of APU yields and component escape-ments during periods of constant fishing effort, the fishery manager could monitor the recovery of assemblage structure following fishing pulses of various magnitudes. The pulses could be applied simultaneously to a group of APUs. A research goal would be to find out if all species of the APU recover despite the magnitude of the pulse. Thus, the goal would be to find the limits of repetitive pulsed fishing that allow the APU to persist. Project investigators suggest that this type of management be carried out in a

region set aside for a demonstration fishing. (Ref. 3-38, 3-42)

Pearcy has described species associations, biomass and sizes of fishes, and their relationship to sediments, depth, and season off the central Oregon coast. (Ref. 3-43) Gabriel and Tyler have described bottom-dwelling fish assemblages on the Oregon continental shelf between the mouth of the Columbia River and Yaquina Head, based on data regarding species biomass collected during a 1977 survey of rockfish. They compared these assemblages with those described from data collected in 1973 by ODFW otter trawl survey. The species dominating each are consistent for the two with but one exception. Assemblages occur off Oregon in four major zones: the neritic, from nearshore to 90 m; intermediate shelf zone, 90 to 145 m; the deep shelf zone, 145 to 220 m; and the slope, beginning at 220 m. Over these four zones they have identified 12 assemblages: The Columbia Shallows, Falcon Shallows, Nestucca Shallows, Columbia Intermediate, Tillamook Intermediate, Nestucca Intermediate, Tillamook Deep, Falcon Shale, Nestucca Deep, Tillamook Slope, Cascade Slope, and Columbia Slope. Many of the species in these assemblages undertake seasonal movements or migrations, so Gabriel's and Tyler's description of them relates primarily to their condition in summer. The shallow water assemblages are characterized mainly by differences in pleuronectids present and in abundances. The intermediate shelf assemblages are dominated by Pacific whiting (or hake) in the summer and by species whose distributions overlap from the shallow shelf and deep shelf zones. The deep shelf assemblages are characterized by combinations of rockfish species. Pacific ocean perch, Pacific whiting, arrowtooth flounder, Dover sole, sablefish, and darkblotched rockfish tend to be more abundant throughout the deep shelf and slope zone assemblages. The slope assemblages are set apart chiefly by combinations of rockfish species. (Ref. 3-40)

Tyler, Gabriel, and Overholtz have commented on the difficulties of managing ocean fisheries on a species-by-species basis where the fishing method takes mixes of species. Data requirements for applying management models based on yield models are prohibitive. Problems exist because of interactions among species. (Ref. 3-41)

### 3.3.5 Application of Isocline Theory to Fishery Yield Estimates

Liss, Thompson, and Warren have

explored assemblage maintenance prospects by adaptation of game management isocline theory. This subtask constitutes a long-term investment aiming at eventual development of more adequate management capabilities. Isocline theory involves a graphic calculus that can be used to derive generalizations about interacting fish populations. The researchers adapted techniques from game management applications. As applied to game management, isocline theory commonly has not accommodated influences of environmental variables. The study group has refined the method, relating the theory to factors that affect the dynamics of a fish community. They have examined the effects of changing environmental conditions, of changing composition of a fish assemblage, and how a hypothetical fishery responds to such fluctuations. Among the variable factors evaluated were: energy entering the production system, demand for the fish in the economy, and the characteristic costs that differing levels of effort incur. They have analyzed components of the hypothetical fishery to investigate how each may affect the multiple-species assemblage on which it is based. By varying aspects of trophic structure the investigators have been able to test the effects of the lower feeding levels on productivity of the assemblage.

Accommodating a sport fishery's effects has enabled them to model how the exploited stock's loss rate increases under this perturbation, how such activity competes with trawling effort, and how non-monetary benefits influence fishery management. Including a competing exploited population in their analyses has enabled them to show that taking of the second species contributes indirectly to the first's gain or loss rate by altering the loss rate in the assemblage's herbivore population (as well as the rate of gain in fishing effort).

Isocline theory shows that fishery communities such as the assemblage production units proposed by Tyler and others exhibit a potential for multiple steady states of productivity. In effect, there may be an unlimited number of practicable carrying capacities for a population, depending on how that population interacts with its community and influences affecting the community. Liss, Thompson, and Warren have suggested that isocline analysis implies that multiple-species fisheries may be more prone to being overfished than single-species fisheries. In essence, fisheries such as Oregon's trawl fishery for pleuro-

nectids exploit not individual species populations but entire marine fish communities. Therefore, to obtain a desired yield, the resource manager needs to bring the entire community to the stage where it can support the desired level of exploitation. Effective management of such species groups requires consideration of demand for the catch, costs of fishing, and other factors which influence the community structure. (Ref. 3-44 through 3-47)





## APPENDIX

### References Cited

- 2-1. Ketchen, K.S. 1956. Factors influencing the survival of the lemon sole (Parophrys vetulus) in Hecate Strait, British Columbia. J. Fish. Res. Bd. Can. 13: 647-694.
- 2-2. Alderdice, D.F., and C.R. Forrester. 1965. Some effects of temperature and salinity on early development and survival of the English sole (Parophrys vetulus). J. Fish. Res. Bd. Can. 25: 495-521.
- 3-1. Hewitt, G.R. 1980. Seasonal changes in English sole distribution: An analysis of the inshore trawl fishery off Oregon. M.S. thesis. Oregon State University.
- 3-2. Richardson, S.L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: Abundance, distribution, and seasonality, January 1971 to August 1972. Sea Grant publication ORESU-T-77-003, Oregon State University.
- 3-3. Richardson, S.L., and W.G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.
- 3-4. Pearcy, W.G., M.J. Hosie, and S.L. Richardson. 1977. Distribution and duration of pelagic life of larvae of Dover sole, Microstomus pacificus; rex sole, Glyptocephalus zachirus; and petrale sole, Eopsetta jordani, in waters off Oregon. Fish. Bull., U.S. 75:173-183.
- 3-5. Laroche, J.L., and S.L. Richardson. 1979. Winter-spring abundance of larval English sole, Parophrys vetulus, between the Columbia River and Cape Blanco, Oregon during 1972-1975 with notes on occurrences of three other pleuronectids. Estuarine and Coastal Mar. Sci. 8:455-476.
- 3-6. Laroche, J.L., S.L. Richardson, and A.A. Rosenberg. In press. Age and growth

of a pleuronectid, Parophrys vetulus, during the pelagic larval period in Oregon coastal waters. Fish. Bull., U.S.

3-7. Richardson, S.L., J.R. Dunn, and N.A. Naplin. 1980. Eggs and larvae of butter sole, Isopsetta isolepis (pleuronectidae), off Oregon and Washington. Fish. Bull., U.S. 78:401-417.

3-8. Richardson, S.L., J.L. Laroche, and M.D. Richardson. 1980. Larval fish assemblages and associations in the northeast Pacific Ocean along the Oregon coast, winter-spring 1972-1975. Estuarine and Coastal Mar. Sci. 11:671-699.

3-9. Westerheim, S.J. 1955. Size composition, growth, and seasonal abundance of juvenile English sole in Yaquina Bay. Fish. Comm. Oregon Res. Briefs 6:4-9.

3-10. Laroche, W.A., and R.L. Holton. 1979. Occurrence of 0-age English sole, Parophrys vetulus, along the Oregon coast: an open coast nursery area? Northwest Sci. 53(2):94-96.

3-11. Percy, W.G., and E.E. Krygier. 1980. Ecology of 0-age group English sole. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.

3-12. Kruse, G.H. 1980. A simulation model of English sole (Parophrys vetulus) recruitment mechanisms. M.S. thesis. Oregon State University.

3-13. Kruse, G.H., and A. Huyer. 1980. The relationship between shelf temperatures, coastal sea level and the coastal upwelling index off Newport, Oregon. Limnology and Oceanography. In press.

3-14. Kruse, G.H., and A.V. Tyler. 1980. Influence of physical factors on English sole (Parophrys vetulus) spawning season. Oregon State University.

3-15. Kruse, G.H., and A.V. Tyler. 1980. Recruitment simulation of English sole. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.

3-16. Rosenberg, A.A. 1981. Growth of juvenile English sole, Parophrys vetulus, in estuarine and open coastal nursery grounds. M.S. thesis. Oregon State University.

3-17. Rosenberg, A.A., and W.G. Percy. The growth of English sole from two nursery

grounds. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.

3-18. Rosenberg, A.A., and J.L. Laroche. In press. Growth during metamorphosis of English sole, Parophrys vetulus. Accepted, Fish. Bull., U.S.

3-19. Kreuz, K.F., A.V. Tyler, G.H. Kruse, and R.L. Demory. 1981. Variation in growth of Dover sole and English sole as related to upwelling. Environmental Biology of Fishes. Trans. Am. Fish. Soc. In press.

3-20. Tyler, A.V. 1977. Evidence for the assumption of independence between gastric emptying rate and swimming activity using Atlantic cod, Gadus morhua. J. Fish. Res. Board Canada 34:2411-2413.

3-21. Tyler, A.V. 1979. Statistical analysis of diet differences related to body size. In: C.A. Simstad and S.J. Lipovsky (eds.). Fish Food Habit Studies. Proc. 2d Pacific Technical Workshop. U. Wash. Sea Grant, Seattle, 51-55.

3-22. Tyler, A.V. 1979. Apparent influence of fluctuations in physical factors on food resource partitioning, a speculative review. In: C.A. Simstad and S.J. Lipovsky, (eds.). Fish Food Habit Studies. Proc. 2d Pacific Technical Workshop. U. Wash. Sea Grant, Seattle, 164-169.

3-23. Carey, Jr., A.G., E.W. Hogue, and L. Kaskan. Intensive study of invertebrate prey of pleuronectids: availability and meiobenthic-juvenile English sole food web. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.

3-24. Bertrand, G.A., and A.G. Carey, Jr. 1980. Infaunal communities of the central Oregon continental shelf. Unpublished. Oregon State University.

3-25. Bertrand, G.A., and A.G. Carey, Jr. 1980. A comparative study of the infaunal biomass and numbers of the central Oregon continental shelf. Unpublished. Oregon State University.

3-26. Percy, W.G., and D. Hancock. 1978. Feeding habits of Dover sole, Microstomus pacificus; rex sole, Glyptocephalus zachirus; slender sole, Lyopsetta exilis; and Pacific sanddab; Citharichthys sordidus, in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 75:641-651.

- 3-27. Kravitz, M.J., W.G. Pearcy, and M.P. Guin. 1977. Food of five species of cooccurring flatfishes on Oregon's continental shelf. *Fish Bull.*, U.S. 74:984.
- 3-28. Wakefield, W.W., and W.G. Pearcy. 1980. Feeding relationships within an assemblage of demersal and nekto-benthic fishes on the Oregon shelf. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.
- 3-29. Gabriel, W.L., and W.G. Pearcy. 1981. Feeding selectivity of the Dover sole (*Microstomus pacificus* Lockington) off Oregon. *Fish. Bull.*, U.S. In press.
- 3-30. Gabriel, W.L. 1979. Statistics of selectivity. In: C.A. Simenstadd and S.J. Lipovsky (eds.). *Fish Food Habit Studies. Proc 2d Pacific Technical Workshop*. U. Wash. Sea Grant, Seattle, 62-66.
- 3-31. Gabriel, W.L. 1979. Feeding selectivity of Dover sole off Oregon. In: C.A. Simenstad and S.J. Lipovsky (eds.). *Fish Food Habit Studies. Proc. 2d Pacific Technical Workshop*. U. Wash. Sea Grant, Seattle, 129-130.
- 3-32. Peterson, W.T., R.D. Brodeur, and W.G. Pearcy. Unpublished. Feeding habits of juvenile salmonids in the Oregon coastal zone in June 1979.
- 3-33. W.W. Wakefield. 1980. Unpublished. Occurrence and food habits of pelagic *Anarrhichthys ocellatus* juveniles collected off the Oregon coast during 1979 and 1980.
- 3-34. Wakefield, W. 1980. Oregon shelf food web focusing on English sole. Unpublished. Oregon State University.
- 3-35. Tyler, A.V. 1977. Sea Grant annual report 1976-1977 for project R/OPF-1. Oregon State University.
- 3-36. Tyler, A.V. 1980. Multi-species fishery analysis. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.
- 3-37. Hayman, R.A., A.V. Tyler, and R.L. Demery. A comparison between cohort analysis and catch per unit effort for Dover sole (*Microstomus pacificus*) and English sole (*Parophrys vetulus*). *Trans. Am. Fish. Soc.* 109:35-53.
- 3-38. Tyler, A.V., and V.F. Gallucci. 1980. Dynamics of fished stocks. In: R.T. Lackey and L.A. Nielsen (eds.). *Fisheries Management*. Blackwell pp. 111-147.
- 3-39. Tyler, A.V. 1979. Environmental influences of fishery sustainability. Sea Grant annual report 1978-1979 for project R/OPF-1. Oregon State University.
- 3-40. Gabriel, W.L., and A.V. Tyler. 1980. Preliminary analysis of Pacific coast demersal fish assemblages. *Mar. Fish. Review* Mar.-Apr. 83-88.
- 3-41. Tyler, A.V., W.L. Gabriel, and W.J. Overholtz. 1981. An alternative assemblage management approach in a mixed groundfish fishery. *Can J. Fish. Aquat. Sci.* In press.
- 3-42. Tyler, A.V. 1980. Alternative assemblage management approaches. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.
- 3-43. Pearcy, W.G. 1978. Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. *Fish. Bull.*, U.S. 75:629-640.
- 3-44. Liss, W.J. 1977. Toward a general theory of exploitation of fish populations. Ph.D. thesis. Oregon State University.
- 3-45. Liss, W.J., G.C. Thompson, and C.E. Warren. 1980. Interpretative application to the benthic fisheries of a general theory of productivity and resource utilization. Sea Grant annual report 1979-1980 for project R/OPF-1. Oregon State University.
- 3-46. Warren, C.E., and W.J. Liss. 1980. Adaptation to aquatic environments. In: R.T. Lackey and L.A. Nielsen, (eds.). *Fisheries Management*. John Wiley and Sons, New York. pp. 15-40.
- 3-47. Liss, W.J., and C.E. Warren. 1980. Ecology of aquatic systems. In: R.T. Lackey and L.A. Nielsen, (eds.). *Fisheries Management*. John Wiley and Sons, New York. pp. 41-80.

#### Related Publications Not Cited

- Bertrand, G.A., and A.G. Carey, Jr. In preparation. An analysis of infauna of the central Oregon continental shelf.
- Carey, A.G., Jr. In preparation. Macroinfaunal and mega-epifaunal species groups on the central Oregon continental shelf.
- Carey, A.G., Jr. and H.R. Jones. In preparation. The vertical distribution of central Oregon continental shelf infauna within the sediment.
- Gabriel, W.L., 1978. Feeding habits and feeding selectivity of the Dover sole (Microstomus pacificus). M.S. thesis. Oregon State University.
- Hayden, T.R., and A.V. Tyler. In preparation. A computer simulation for the population of English sole off the Oregon and Washington coast.
- Hayman, R.A. 1978. Environmental fluctuation and cohort strength of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus). M.S. thesis. Oregon State University.
- Hayman, R.A., and A.V. Tyler. 1980. Environment and cohort strength of Dover sole and English sole. Trans. Am. Fish. Soc. 109:54-68.
- Hewitt, G., W.G. Pearcy, and A.V. Tyler. In preparation. Movement of English sole (Parophrys vetulus): an analysis of the inshore trawl fishery off Oregon. Sea Grant publication series. Oregon State University.
- Kreuz, K.F. 1978. Long-term variation in growth of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus). M.S. thesis. Oregon State University.
- Kruse, G.H., and A.V. Tyler. In preparation. A simulation model of English sole (Parophrys vetulus) recruitment mechanisms.
- Mundy, B.C. In preparation. Yearly variation in the abundance and distribution of fish larvae in the coastal zone off Yaquina Head, Oregon, from June 1960 to August 1972. M.S. thesis. Oregon State University.
- Pearcy, W.G., and E.E. Krygier. In preparation. Distribution, abundance, and growth of 0-age English sole in estuaries and along the coast of Oregon: the importance of estuarine nursery grounds.
- Richardson, S.L. Pelagic eggs and larvae of the deepsea sole, Embassichthys bathybius (Pisces: Pleuronectidae), with comments on generic affinities. Fish. Bull., U.S. 79(1). In press.
- Richardson, S.L., and J.L. Laroche. In preparation. Early life history patterns of English sole, Parophrys vetulus (Pleuronectidae): distribution, transport, natural mortality.
- Richardson, S.L., and W. Stephenson. 1978. Larval fish data: a new approach to analysis. Sea Grant publ. ORESU-T-78-002. Oregon State University.
- TenEyck, N., and R.L. Demory. 1975. Utilization of flatfish caught by Oregon trawlers in 1974. Informational Report. Oregon Department of Fish and Wildlife.
- Tester, P.A., and A.G. Carey, Jr. In preparation. Molt classes, size at maturity and population size structure of Chionectes tanneri Rathbun (Brachyura: Majidae) off the southern Oregon coast.
- Thompson, G.G. 1979. A theoretical framework for understanding aspects of fisheries bioeconomic systems. M.S. thesis. Oregon State University.
- Tyler, A.V., and R.A. Hayman. In preparation. Estimation of stock-recruitment relationships from surplus production models, with application to Pacific halibut data.
- Tyler, A.V., and W. Stephenson. In preparation. Application of statistical cluster analysis methods to otter trawl data.

