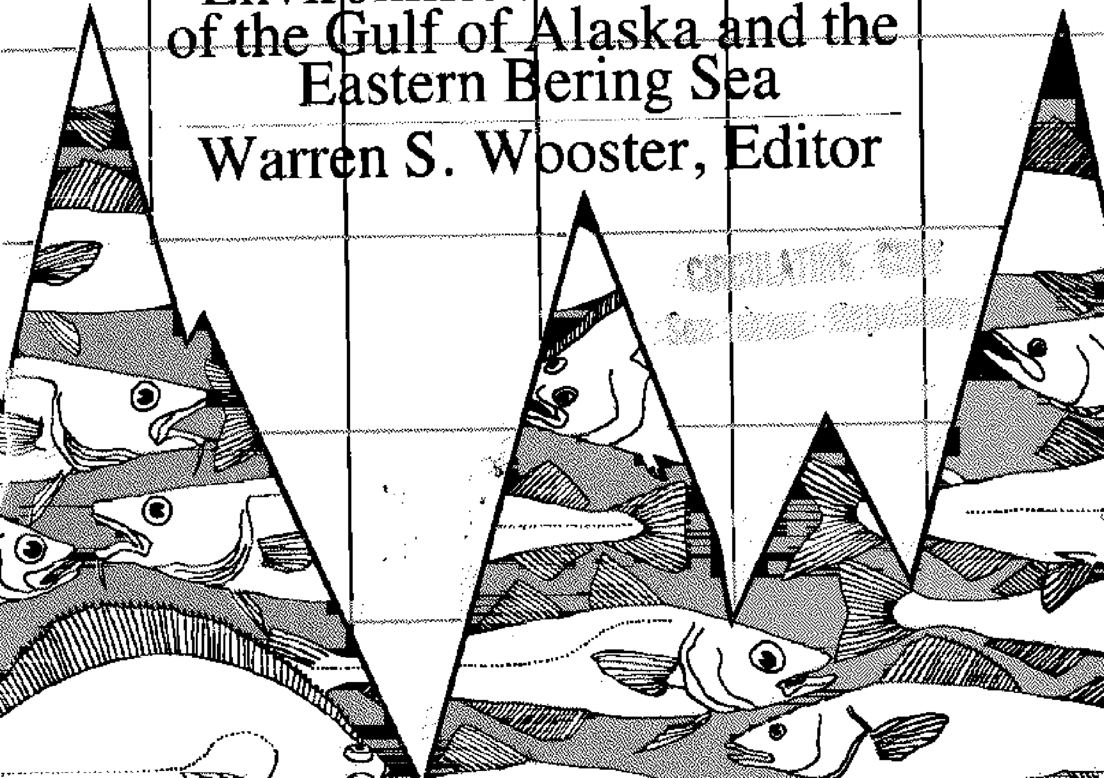
YEAR TO YEAR

Interannual Variability of the Environment and Fisheries of the Gulf of Alaska and the Eastern Bering Sea

Warren S. Wooster, Editor



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Preface

With the establishment of the College of Ocean and Fishery Sciences of the University of Washington in September 1981, there was initiated a new series of activities known as Select Programs. These programs are intended to focus the resources of the several disciplines of the College on issues in ocean and fishery sciences that hold great promise of yielding advances in knowledge. One of the first funded was entitled "Ocean Environment and Fisheries Resources." This program is studying the relation between variations in the ocean environment and those in the abundance of fish and shellfish stocks, especially in the northeast Pacific and the eastern Bering Sea.

In order to review existing knowledge on ocean and fish variability and to develop a strategy for the investigation of the interactions, a workshop was convened at Lake Wilderness, Washington, on 16-18 May 1983. The first half of the workshop was dedicated to a series of review papers with commentary and discussion; the papers and commentary were revised after the workshop and constitute the bulk of the present volume.

Following the reviews, remaining participants (listed at the end of the volume) were divided into three working groups and were asked to identify appropriate research strategies to pursue in light of the reviews, taking into consideration the current interests and capabilities of the institutions concerned with the region. A synthesis of the reports of these groups is the final paper of this volume.

The workshop was organized by Karl Banse, Donald Gunderson, and me. We express our gratitude to Washington Sea Grant Communications for their assistance in publishing this report.

Warren S. Wooster

On the Determinants of Stock Abundance

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That the abundance of a cohort of fish depends on more than the abundance of its parents is not a recent discovery. For example, useful hypotheses on possible environmental causes of variations in recruitment success were offered by Hjort in 1914. But it must be observed that the intervening years have not been marked by intensive research and steady progress in understanding the determinants of stock abundance. The reasons for this state of affairs cannot be analyzed in depth here; they relate to the pervasiveness of the prevailing population dynamics paradigm, the perceived priorities of fisheries science, and the apparent immiscibility of oceanography and fishery science and their practitioners. However, in the last few years there has been a renaissance in consideration of the nature of ocean-fish interactions. This has been marked by a series of "fish ecology" meetings in the United States, by workshops and symposia convened by international organizations, by designation of an international program on "ocean science and living resources" and by the present workshop on interannual variability of the environment and fisheries of the Gulf of Alaska and the eastern Bering Sea.

My task is to review current thinking about processes that might determine the abundance of stocks and ways in which those processes might be affected by variations in the ocean environment. Such a review has recently been undertaken in a set of papers prepared for Fish Ecology III (Rothschild and Rooth, 1982). My remarks will draw upon that material, especially on the summary of discussions, but will be more a reflection of my understanding of its significance than a systematic summary of its content.

Fishing as a Cause of Variable Abundance

In the absence of intervention by man, a stock of marine animals exists in equilibrium with other species in its environment. Its average abundance is established by that equilibrium and is subject to gradual change as the equilibrium changes. On a shorter time scale, for example that of interannual variation, abundance varies as a function of inherent variability within the stock and in the species with which it interacts, and variations in the abiotic environment.

This simple natural system can be perturbed by human activity which may affect the stock itself (through fishing) or may transform its environment (through pollution). I shall set pollution aside at this point, since until now, its effects have been largely localized and transient.

If the stock of interest, or any of the species with which it interacts, is subjected to a fishery, an important source of variability is introduced. Fishing pressure will be variable, and its effects will vary depending on the nature and condition of the target stock and on the abundance levels of the interacting species. But this variability of fishing pressure itself seems unlikely to be a major cause of the observed interannual variability in fish stock abundance.

For one thing, the frequency and amplitude of change in fishing pressure is quite different from that in the abundance of its victims. The immediate effect of fishing is, of course, to decrease the numbers and biomass of the stock. But we are interested in effects on future abundance. The population responds to the fishery in such a way that the fish that are removed are replaced in roughly comparable amounts unless the stock is heavily overfished. In that case, spawning biomass is reduced below the critical level where adequate recruitment will, on the average, be produced. I would argue that only then does fishing pressure become an important direct contributor to interannual variability of fish stocks. At that point, recruitment to the stock becomes much more vulnerable to environmental effects.

Experimental determination of this critical level can be expensive, and even dangerous to the health of a stock (e.g., the Peruvian anchovy). For management purposes, a value is sometimes arbitrarily assumed -- e.g., "keep the spawning biomass above 5 million tonnes" -- but the uncertainties in such numbers can cause the fishery either to forego valuable harvest or to flirt with disaster.

A fishery on one stock can contribute indirectly to variability in the abundance of another with which the target species interacts. This other species may appear as predator, prey, or competitor during the larval and later stages of development of the species of interest, and it is conceivable that the abundance of the latter could be affected by an increase (or decrease) in the abundance of the former, as might arise from the differential effects of fisheries. Of course, when species "A" is depleted by a fishery and species "B" increases, there is not necessarily a cause and effect relationship. In any case, these interactions can be regarded as a special case of the variability in abundance arising from fluctuations in the biotic environment.

The Environmental Variability Paradigm

Apart from these fishery effects, the principal cause of variability in the abundance of stocks appears to be environmental variability, both biotic and abiotic, with the former being driven by the latter. Some evidence for this belief in the importance of the environment includes the following. Where adequate pre-historic records exist, it can be shown that fluctuations in abundance, including the replacement of species, occurred long before commercial fisheries had been established on the stocks in question (Soutar and Isaacs 1974). Variations observed in modern fish stocks and in the environment both contain strong interannual signals. There exists a variety of plausible mechanisms and potentially testable hypotheses that link environmental variability with that of fish stocks.

Most studies of the effects of environmental variations have attempted correlations with rather simple indices of environmental conditions, for example mean monthly sea surface temperatures or salinities at a coastal location, without much regard for the extent to which the index represents the environment experienced by the species in question, and in particular by some critical stage in its development, or without exploring mechanisms by which the environmental linkage with abundance could be established.

Bakun and Parrish (1980) have discussed some physical characteristics of the environment that are likely to have important effects on recruitment, namely (1) the field of horizontal advection, (2) the field of vertical stability, (3) the field of temperature, and (4) the field of convergence/divergence of flow at the sea surface (linked with the field of vertical advection). These characteristics vary in three dimensions, at a variety of scales and frequencies. Unfortunately, data on such characteristics are seldom available at the appropriate scale and with a sufficient duration of record, although surrogate data can sometimes be found (e.g., sea level as an index of horizontal advection). But it is with environmental characteristics such as these that plausible mechanisms accounting for environmental influence over recruitment success are likely to be constructed.

While the abundance of fish stocks could presumably be established at any life history stage, for many stocks there is evidence that the early stages are most critical. Of course, as discussed earlier, conditions before spawning will determine whether there is a sufficient quantity of viable eggs. During the weeks following hatching, survival success is determined primarily by the coincidence in time and space of hungry larvae and a food supply of adequate concentration and quality. In the absence of such a supply, larval growth is retarded, and vulnerability to predation is enhanced. The coincidence in time of predator and prey is governed by the timing of events, of spawning and hatching on the one hand, and of primary and secondary productivity on the other. The coincidence in space is governed by the physical processes of advection and diffusion. In both cases, the coincidence is in large part a product of environmental variability.

These interactions take place for the most part while the developmental stages are part of the plankton when it is reasonable that they will be most affected by the surrounding environmental conditions. From the point of view of the stock, the plankton contains its eggs and larvae, food for its larvae, competitors for that food, predators of its eggs and larvae (other predators are in the nekton), and alternative prey for its predators. The abundance and distribution of each of these elements is subject to the vicissitudes of environmental change. The period of greatest mortality may not be at the time of first feeding, the "critical" period of Hjort, but the mortality curve is steep throughout the early weeks when slight differences in survivability can have large consequences in abundance at a later stage (Houde, 1982). It is the prediction of this survivability to the time when year class strength is established that can be regarded as a key goal of research on interannual variability in fish stocks.

Some of the determinants of year class size are shown in Table 1.

To look at potential environmental effects more closely, it is useful to divide the early life history into two stages. Stage A extends from spawning through egg development to hatching. It is presumably the stage most susceptible to disease, although the importance of disease as a source of mortality in the ocean is not known. In Stage A, environmental conditions (scalar and vector) affect the timing and location of spawning; rate of development; extent of aggregation (patchiness); and the relative location of eggs and their predators.

Stage B includes first feeding and subsequent larval development. Some larvae may feed well, grow quickly, and pass safely through the period of high vulnerability to predation. Most, however, feed poorly, grow slowly, and because of their impaired performance are eaten (some may also die of starvation or disease). In Stage B, environmental conditions affect the rate of development and the duration of vulnerability to predation; the extent of aggregation; the location of larvae relative to their predators and prey; and the abundance, concentration, and quality of food and the timing and location of its availability.

The relative importance of starvation and predation as causes of larval mortality continues to be a matter for debate. Fish larvae are rare organisms in the plankton, especially when compared with potential food, and death by starvation appears to be relatively uncommon. Of course, all prey organisms, even when of the same size, are not the same when it comes to meeting the nutritional requirements of larvae, nutrition being affected by the quality (species, size, biochemical composition), as well as the availability (concentration, catchability) of the food. So, despite the relative abundance of potential food, there may well be competition for specific kinds of food.

TABLE 1

DETERMINANTS OF YEAR CLASS SIZE

	Depend on			
	numbers of present stage	success as predator	success of predators on present stage	environment
Initial number and viability of eggs (1)	---	---	---	---
mortality of eggs	---	---	**(2)	*(3)
growth of larvae, juveniles	*(4)	**(5)	---	*(6)
mortality of larvae, juveniles	*(7)	**(8)	**(9)	*(10)

Notes: (1) depend on numbers and condition of spawning stock; (2) predators on eggs include later stages of same species, other vertebrates and invertebrates; (3) apart from extreme conditions, principal effect is on rate of development and on dispersion, affecting vulnerability to predation; (4) density dependent growth expressed through competition; (5) growth rate principally affected by availability of food; (6) growth also affected by temperature, by dispersion and its effects on availability of food, and by other abiotic environmental conditions; (7) density-dependent mortality expressed through vulnerability to predation; (8) larvae are especially vulnerable to starvation soon after hatching; starvation may cause mortality directly or enhance vulnerabilty to predation; (9) presumably the principal cause of mortality at these stages; (10) direct effect of environmental variability on mortality is usually less important than indirect effects through starvation and predation.

If it is uncommon to encounter larvae dead of starvation, what is the importance of variable success at feeding in determining year class strength? The answer is suggested by the attempts to relate recruitment success to upwelling and hence to the level of primary production, namely that larval growth is as important as larval mortality. Another way to put this is that a greater than normal growth rate improves the likelihood that a larva will escape predation by shortening the period when it is most vulnerable. It also seems likely that the performance of a larva in escaping predation depends upon its nutritional stage. Unfortunately, there is little quantitative information on performance impairment. It is not known, for example, to what extent the vulnerability to predation of well-fed larvae is reduced, or whether underfed larvae can regain peak performance when their nutritional state is improved.

Predation is not, of course, solely determined by characteristics of the victims, but also depends on the kinds, numbers, and performance of the predators. Since predation requires physical contact between predator and prey, their relative distributions must also be taken into account, a matter that involves knowledge of the fine and even micro physical structure. The rates of predation are influenced by the abundance of alternative prey; most predators are not specific for fish larvae, and their numbers are regulated independently. Hence, predatory mortality may not depend on the density of larvae, when a preferred prey is also available.

Clearly, recruitment is not just a simple function of spawning stock size. The relative size of a cohort is also determined by its function as predator and prey at one or more stages of development in a variable environment. To describe all of the interactions and to evaluate them quantitatively will be difficult; furthermore, the relationships will not always be deterministic. Factors that influence recruitment success are likely to differ significantly among taxa, and perhaps even within taxa (in different environmental regimes). For the problem to be solved in any practical way, it will be necessary to find some generalities in the responses of similar species in analogous environments and some simple indices of environmental variability.

On Scales and Sampling

A fundamental dilemma in the study of recruitment is that while interannual variability of year class strength is a mesoscale or larger event, the factors that determine the survival of the few successful larvae operate on much smaller scales. Dimensions of the ambit of an individual larva and of its interactions with food and predators are of the order of centimeters or less to a meter or so. The average abundance and availability of larval food is related to fine and microscale patchiness and to the congruence of patches of prey and larvae. The quality of the food might depend on mesoscale or larger events, but its availability is probably determined on much smaller scales.

The interannual environmental variations associated with recruitment variations are compounded of higher frequency (smaller scale events). For example, the environmental difference between two years may lie in the timing, frequency of occurrence, or duration of such small events. The aggregation of small causes into large consequences poses considerable difficulties in designing experimental approaches to recruitment research. While much of the work on scales of 10^{-2} to 10^{2} m can, or must, be done in the laboratory or in enclosures, field studies on similar scales are also required to tie these findings together with those at larger scales, since large scale variability determines the overall productivity of the stock.

Problems in sampling both the biota and the environment at the various necessary scales are formidable.

A major difficulty in attempting to determine the effect of environmental change on stock abundance is that abundance is so poorly measured. If there is a fishery, the conditions under which catch per unit effort is a useful measure of abundance are limited. If there is no fishery (e.g., for a collapsed stock), fishery-independent measures are essential, yet they are costly (hence unlikely to be used) and often inaccurate. Useful estimates of recruitment are also hard to obtain and time series of year class strength tend to be scarce, so it is not surprising that the dependence of recruitment on environment has not been established and that the stock-recruitment relationship is so uncertain.

There are, in fact, difficulties in measuring key variables at all scales. The usual sampling methods for plankton, which capture fish larvae and their food and predators, give little or no information on details of their distributions and aggregations. While structure at scales of meters down to centimeters may be critical, for example, in showing the probability of encounters between larvae and their prey, the usual integrating tow can at best only resolve hundreds of meters. To the extent that nets are avoided by fish larvae, estimates of larval abundance and mortality are inaccurate.

Not only are there serious methodological problems in sampling various elements of the biota, from picoplankton to nekton, at appropriate scales, but there are few good ways to process and analyze the mass of samples that can be collected, to transform the samples into data. Thus, there is an urgent need for physical (e.g., optical) techniques for mass analysis of samples, as well as for better methods for collecting them. However, with the best of foreseeable methods, it will not be possible to sample all scales with equal intensity, so it will be necessary to optimize sampling at selected scales based on available information on those and other scales.

Another important approach is to measure physical attributes of organisms of interest, for example, particle size and concentration with a Coulter Counter or by acoustic methods, or fluorescence with a towed fluorimeter. Such measurements can be combined with those of purely physical parameters (e.g., temperature and salinity) in a towed, porpoising body, to obtain a continuous, two-dimensional description of distributions in the upper layer of the ocean. While the biological variable so determined is seldom that which is really of interest for a given problem, the relationship to the latter can sometimes be established by separate sampling.

Of course, sampling problems are not confined to biological variables. Scales of interest in the abiotic environment extend from 10^{-3} to as much as 10^6 meters, and the same problems arise of determining small scale variabiliity in the context of that at larger scales.

On the Development of a Research Strategy

As Rothschild et al (1982) point out, four approaches have until now monopolized research on recruitment variability: (1) evaluation of its dependence on stock size variability; (2) determination of the amount of food that causes starvation of fish larvae: (3) correlation between environmental variability and year class strength; and (4) meso-scale surveys of fish larvae and eggs. As the preceding discussion has suggested, these approaches miss large areas of the problem, and indeed one must conclude that in recent years they have not led to greatly improved understanding. Rothschild et al. proposed as an alternative, a more holistic approach focused on the trophodynamics of the micro and fine scale ecosystem. Work at such scales must to a great extent be done in the laboratory or in enclosures.

In more general terms, Fish Ecology III participants considered the following recruitment hypotheses and ways in which they might be tested:

I. Wide variability in larval growth results when food is limiting. This would be tested in large volume systems with equal stocking densities and little or no predation, comparing high and low food levels.

II. Food-limited individuals are more susceptible to predators than are well-fed ones; for a given size, fast-growing individuals are less susceptible to predation than are slower growing individuals. This would be tested on aquarium or mesocosm scale, depending on predator size and stocking density. One would identify appropriate predators, determine the susceptibility of individuals to predation as a function of nutritional stress, estimate predation rates, and define behavioral interactions between prey and predator.

III. Food limited populations are more susceptible to predation than well fed ones. This would be tested in a large volume system with equal stocking densities and would require a matrix comparison of high and low food and predation levels.

IV. The effects of food and predation are modulated by physical variability at all scales. This could only be tested experimentally in an experimental system where physical structure could be introduced and its effects observed on food, fish larvae, and their predators.

Specific attention was paid to research on (1) patches, (2) event variability, (3) role of starvation, (4) role of advection, and (5) role of predation.

The patch study was seen as a free-form equivalent of an enclosure experiment that would avoid the unnatural features of enclosures such as boundary effects and the absence of stratification and mixing. The purpose would be to study predator-prey relationships and important rates from yolksac through metamorphosis (10 days or more) while at the same time measuring transport and mixing. It was generally agreed that there were large practical problems in carrying out such experiments.

The event variability study would be based on the hypothesis that the frequency and intensity of high energy events on the scales of days to weeks (e.g., storms) which affect nutrient fluxes to the euphotic zone and spatial relationships among plankton organisms are major sources of interannual variation in recruitment. Optimal conditions maximize food supply and minimize predation pressure, and the study would examine in detail the consequences of such events on both factors.

The starvation study would be based on the hypothesis that larval growth and survival depend on the energy available in food, and that food in the natural environment can be sufficiently limiting to cause recruitment variation. The study would require identifying food items at each developmental stage and determining their caloric values. Statistical information would be needed on the distribution of contacts between larvae and their food, with activity levels measured at different concentrations of preferred foods. This information would then be applied to evaluate observed field densities of food organisms.

The advective study would examine the relative magnitude of advective losses of larvae from salubrious habitats compared to other causes of mortality. It would require defining the boundaries of important domains, calculating the fluxes of eggs and larvae into (out of) the domains, and making a mortality budget that would include estimates of starvation and predation.

The predation study would be based on the hypothesis that interannual changes in predation on eggs and larvae cause variations in egg and larval mortality. The latter could arise from variations in the level and kind of predation or in the vulnerability of the prey. For a given stock at a given site, one would identify several candidate keystone predators (those that significantly alter community structure by removing large numbers of specific prey), determine the eggs and larvae in their stomachs, estimate consumption rates and compare them with observed natural mortality rates, develop functional relationships between predatory consumption and prey density and size, verify and calibrate the predation model against field data on distribution, growth, and mortality of the ichthyoplankton, and the distribution and density of the predators.

These propositions apply to research on recruitment variability in a general sense, but we are seeking a more species-specific strategy. For the stocks selected for investigation, an initial approach would be to develop a systematic catalog of essential information on each species that would identify critical information that is missing and would eventually provide the basis for hypothesis formulation.

Criteria for the selection of stocks were suggested at a meeting in October 1982 on cooperative research on ocean-fish interactions in the northeast Pacific. These were (1) that their recruitment exhibits large interannual variations, (2) that their life histories at all stages are reasonably well known, and (3) that a relevant data base is available. It is clear that stocks of greatest commercial importance and those whose abundance is in decline will be of particular interest. It also seems likely that variability in some stocks is more amenable to understanding than that in others.

For each selected stock, the required information includes (1) time and place of spawning and the duration of early stages of development, (2) food used by larvae and their rate of development as a function of food quantity and quality, as modified by temperature and other environmental conditions, and (3) predators of the larvae and juveniles and their rate of inducing prey mortality under various conditions. The status of knowledge will, of course, differ from stock to stock. Often critical information, such as rates of encounter, growth, or mortality, will be missing and can only be obtained in the laboratory or in enclosures. Thus, in one case, some very basic experiments may be essential, while in another enough will be known to warrant a full scale field operation.

Apart from the temperature regime, which influences the rates of processes mentioned above, two kinds of environmental questions are particularly relevant. First, what environmental factors control the timing and magnitude of production of the food organisms used by the larvae? Second, what are the processes that concentrate, disperse, and transport eggs and larvae and their predators and prey? Combining such biological and environmental information will permit the formulation of hypotheses concerning the abundance of a given stock that can be tested in experiments such as those proposed in Fish Ecology III.

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Commentary

On the Determinants of Stock Abundance

John R. Hunter
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In this commentary I focus on four issues discussed in Warren Wooster's report (Determinants of Stock Abundance) which I feel warrant additional discussion or amplification. In no manner should this commentary be considered an appraisal or review of Wooster's report on Fish Ecology III (Rothschild and Rooth, 1982). I use quotations from Wooster's report to identify each of the subject areas.

"The planktonic stages of the life history are most affected by environmental conditions"

The planktonic larvae of marine fishes are more directly affected by the environment than other life stages but it may be overlooked that not all larval stages are planktonic. The larval period, after the onset of feeding, is a transitional period between the planktonic embryonic stage (egg and yolk-sac stages) and the nektonic juvenile stage. This transition may occur early in the life history, and the truly planktonic stages may be a short segment of a long larval period. In northern anchovy, this transition occurs over about a 10-day period between the 20th and 30th day (10-15 mm, 16°C) of a 70-day larval period. The following events occur during transition: the larva breaks free from the hydrodynamic realm that is transitional between the viscous realm of the yolk-sac larva and the turbulent realm of the nektonic larva (Weihs, 1980); rods appear in the retina and the lens becomes focusable (O'Connell, 1981); the swim bladder becomes functional permitting greater body mass without loss of bouyancy; diel vertical movement to the water surface each night begins (Hunter and Sanchez, 1976); the transition between integumentary and gill respiration begins (O'Connell, 1981); and schooling begins (Hunter and Coyne, 1982).

These behavioral and structural changes have very important ecological and demographic implications. The change in hydrodynamic regime, and the changes in visual, respiratory and other systems set the stage for the onset of schooling and vertical migration. The onset of schooling reverses a trend of continuing dispersion and declining patchiness of larvae to one of increasing contagion (Hewitt, 1981; Hunter and Coyne, 1982). By the end of the planktonic phase mortality rates are much lower than during the highly vulnerable embryonic period. This fact plus the rapid increase in body weight reverses a trend of rapidly declining cohort biomass to one of increasing cohort biomass. The increase in the biomass of the cohort, and increased aggregation due to schooling imply that nektonic larvae occupy the habitat more intensively than planktonic larvae. More intensive occupation of the habitat may increase the likelihood of larval density dependent effects on growth.

Thus the planktonic larval phase is characterized by a pattern of declining contagion (increasing dispersion), high mortality rates, decreasing cohort biomass and a larval existence almost entirely dependent upon the immediate planktonic habitat. In the nektonic larval phase, the larvae become progressively more independent of the immediate planktonic habitat, are capable of extensive vertical movements in search of food, become more aggregated because of schooling, the biomass of the cohort begins to increase and the likelihood of density dependent effects on larval growth increase. Thus interpretation of the effects of the environment on larval survivorship depends upon a thorough knowledge of these developmental changes and the timing of transition from the planktonic to nektonic states. The timing of the transition depends, of course, on the availability of food, as well as temperature specific growth rates.

"The key goal of research on interannual variability of fish stocks is prediction of survivorship until the strength of the year class is identified"

It may never be practical to use the results of larval counts or extensive environmental measurements to provide timely and accurate estimates of year-class strength. In addition, methods already exist for early estimation of year class strength including commercial catches of small fish, trawl or acoustic surveys. I believe the key goal of research on year class variability is to establish how the abundance of the adult stock affects the strength of incoming year classes and to identify the conditions which cause the occasional and remarkable rises or falls in populations (Hunter et al., 1976.) Clearly, the effect of stock size on recruitment is a critical issue since the only option available to managers is regulation of catch.

"It is uncommon to encounter larvae dead of starvation"

I feel partially responsible for this quotation as it reflects perhaps an extreme position that I took in my report for Fish Ecology III. Consequently, I summarize below some of the more important evidence for the relative role played by starvation and predation of marine fish larvae.

Evidence for larval starvation

1. Most laboratory work indicates that marine larvae at the onset of feeding are highly vulnerable to starvation because they search such a small volume of water, have low feeding success, and are unable to withstand prolonged starvation (Hunter, 1981).

2. The food densities required for high survival in the laboratory are not found in the open sea, implying that larvae must depend on the patchiness of food and stable oceanographic conditions to survive (Hunter, 1981).

3. In inshore areas, the incidence of starving anchovy (4-10 mm) using histological criteria (in my mind the only reliable method) was 8% (O'Connell, 1980) and no larvae >10 mm long were starving. In offshore areas about 50% of first feeding jack mackerel larvae were starving but the fraction of starving larvae decreases rapidly with larval age, reaching zero in 2-week-old larvae (G. Theilacker, pers. comm.). These fractions were not adjusted for the duration of the larval stage and cannot be compared to daily mortality rates. On a daily basis the fraction of starving larvae may be lower as the first feeding stage of jack mackerel persists for 2-3 days.

Evidence for predation

1. The highest losses occur during the embryonic period (egg and yolk-sac stages) where starvation can be eliminated as a source of mortality.

2. A great variety of invertebrates and fishes are known to consume eggs and larvae (Hunter, 1981; Bailey and Yen, 1983) and high consumption rates of eggs or larvae have been documented in a few cases (Hunter and Kimbrell, 1981; Möller, 1980).

3. Our most accurate mortality estimates for post-embryonic anchovy (1980-1983) larvae give no sign of an increase in mortality at the onset of feeding. Inaccurate aging might mask the critical period; the first feeding period is the most difficult life stage to assign an age or duration because otoliths cannot be used to age larvae.

4. Growth rates of clupeoid larvae in the sea based on daily increments in otoliths seem to indicate that they grow at the same rates as they do at the laboratory when given abundant food (Blaxter and Hunter, 1982).

5. In large enclosures cod larvae have extremely high survival when predators are excluded and food densities are equivalent to those in the sea (Ellertsen et al., 1981).

These assertions are based on very few field studies and clearly the dominant mechanism may vary among species, habitats and years. What is certain is that the incidence of starvation or slow growth can be documented with greater ease and accuracy than rates of predation because of the existence of starvation-histology and otolith-ageing methodologies. No similar advances have been made that facilitate studies of predation.

> "One must conclude that in recent years meso-scale ichthyoplankton surveys have not greatly improved understanding and Rothschild et al. propose as an alternative, a more holistic approach on trophodynamics of micro- and fine-scale ecosystem"

This point of view reflects an interesting hypothesis which links survival of planktonic larvae to the environment in a novel and functional way (the stability hypothesis, Lasker, 1981). On the other hand, I believe that this is misleading advice for an overall program on recruitment mechanisms when the species spawn over a large geographic area and the localities from which the survivors originate vary unpredictably in space and time. Under these circumstances surveys which delimit the spawning habitat (meso-scale surveys) are essential for the following reasons:

1. Testing of the stability hypothesis or any other larval survival mechanism must be set in the context of the spawning distribution of the population and this information can only be provided by meso-scale surveys. Knowledge of events in a small segment of the population is not sufficient for estimating effects on the population as a whole.

2. Rates of mortality are powerful research tools but they require meso-scale surveys. Mortality rates cannot be measured over a segment of the population because of dispersion and advection of larvae.

3. The annual production of eggs and larvae over the season must be known in order to determine whether changes in year class size are a result of differences in larval mortality or due to differences in the annual or seasonal production of eggs. If the annual egg production is unknown one is unable to use a powerful tool, the birthdate distribution of the juveniles, for assaying the quality of the environment (Methot, 1981).

4. Many of the hypotheses of survivorship of larvae can only be studied on a meso-scale, for example, the larval drift hypothesis and the expansion of spawning range hypothesis of MacCall (1980) and Lasker and MacCall (1983).

5. Most of the significant advances that have been made in recent years on the ecology of northern anchovy were made chiefly as a result of meso-scale surveys.

These comments apply to most of the commercially important marine fish stocks that spawn over a broad geographic area. On the other hand, micro-scale, site intensive studies alone would be preferable under several special circumstances: when the young destined to perpetuate the population originate from a small area that is constant in location and time; or when they originate from an oceanographic feature which is predictable in space and time; or when they suffer the same fate over the entire spawning habitat. Most importantly, the answer to the question of whether or not these special circumstances apply to a given species probably requires spawning-habitat-scale (meso-scale) surveys. Perhaps the failure of many meso-scale surveys has been that they were not sufficiently extensive to delimit the spawning habitat in space and time nor sufficiently intensive to reveal biological processes.

In summary, to limit work on recruitment mechanisms to site intensive microscale studies is not advisable unless documentation exists that the site is truly representative or that it contains most of the potential survivors. If these conditions are not met then use of only site intensive work is to focus on only a few of the possible mortality processes without adequate geographic and temporal context, and to ignore some of the most powerful tools for understanding (birthdate distributions, juvenile abundance, life stage specific mortality rates and variation in spawn distribution). It is certainly important to do such work, not as an alternative to meso-scale research, but in conjunction with it.

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Review of the Biology and Abundance Trends of Pacific Herring (*Clupea harengus pallasi*)

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Introduction

Time series of abundance data for non-salmonid pelagic fishes in the northeastern Pacific Ocean are generally limited to commercial catch records. Marcy et al. (1978) reviewed information for 24 pelagic species or species groups in the Gulf of Alaska and Bering Sea. The most extensive data was that for Pacific herring (Clupea harengus pallasi) which had been recorded in commercial catches since the 1880's and which had been studied by scientists since the 1920's (e.g. Rounsefell, 1929). Therefore, we chose this species for a review of interannual abundance and an examination of factors which influence abundance fluctuations. We tried to limit our discussion to Pacific herring stocks off the coast of Alaska, but drew upon results of studies done in other locations to fill gaps in available data and to provide insight into possible causes of interannual variability.

Geographic Distribution

Pacific herring occur from southern California to Cape Bathurst along the North American coast, and from the east coast of Korea to the Lena River along the Asian coast (Hart, 1973; Kasahara, 1961). North American Pacific herring stocks of commercial importance occur in San Francisco Bay, Puget Sound, British Columbia, the Gulf of Alaska (including southeast Alaska, Prince William Sound and Kodiak Island) and the eastern Bering Sea (from Bristol Bay to Norton Sound). Asian stocks of commercial importance occur in the Japan Sea, Okhtosk Sea (Hokkaido-Sakhalin) and the western Bering Sea (including Korf-Karensky and the Gulf of Navarin).

Seasonal Distribution

Pacific herring stocks in Alaskan waters follow a common seasonal migration pattern (i.e. distinct spawning, feeding and wintering areas), but differ greatly in the distances traveled during each annual cycle. Pacific herring in the Gulf of Alaska remain within coastal waters the entire year (Powell, 1957). In southeast Alaska

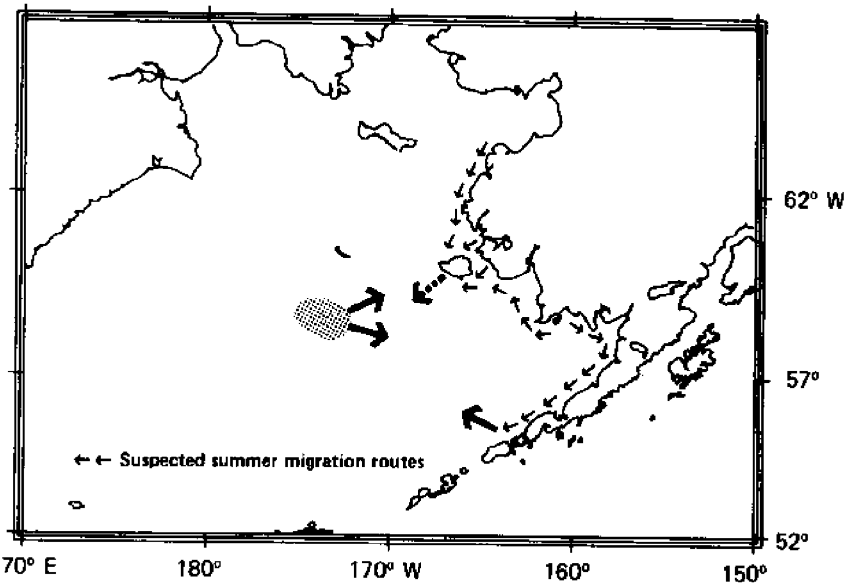

Fig. 1.--Herring migration routes to and from eastern Bering Sea winter grounds. Large solid arrow: direction of movement in offshore waters as determined by Soviet research and Japanese catches. Large dashed arrow: area of autumn reappearance in offshore waters reported from Soviet research. Small arrows: possible summer feeding routes and autumn migration routes (from Wespestad and Barton 1981).

feeding areas are located in open straits, but wintering areas are usually in sheltered, deep water close to spawning beaches (Carlson, 1980). In the eastern Bering Sea feeding areas are located in coastal waters (Bakkala and Wakabayashi, 1983; Rumyantsev and Darda, 1970), while wintering areas for most stocks are northwest of the Pribilof Islands, near the shelf break, more than 700 km from the major spawning area in northern Bristol Bay (Wespestad and Barton, 1981; Rumyantsev and Darda, 1970, Shaboneev, 1965) (Fig. 1). But not all eastern Bering Sea Pacific herring stocks undertake such extensive travels; some Norton Sound stocks may remain closer to their spawning areas during the winter (Wespestad and Barton, 1981). Chukchi Sea stocks may also winter under the sea ice, close to spawning areas (Whitmore and Bergstrom, 1983).

Spawning Requirements

Pacific herring are considered to be spring spawners, although stocks in the southern portion of their range (e.g. southern California) spawn during winter and early spring (December to mid-April) (Spratt, 1981). Peak spawning for the most abundant stocks (i.e. British Columbia through the eastern Bering Sea) occurs April to early June

(Wespestad and Barton, 1981; Kasahara, 1961). In the Chukchi Sea spawning does not begin until June and extends into at least July (Whitmore and Bergstom, 1983).

Most spawning occurs at water temperatures of 5°C or above. Alderdice and Velsen (1971) suggested that temperatures between 5.5 and 8.7°C may be optimal for egg development and survival. While some stocks may spawn in temperatures as low as 0°C and as high as 14°C, the most abundant stocks (i.e. British Columbia through the eastern Bering Sea) are found in areas where spawning temperatures fall between 5 and 9°C (Barton and Steinhoff, 1980; Alderdice and Velsen, 1971; Kasahara, 1961).

Egg Survival

During spawning eggs are deposited on aquatic vegetation (kelp, Laminaria sp.; rockweed, Fucus sp.; eel grass, Zostera sp.) in the intertidal and shallow subtidal zones. Eggs may also be deposited upon bare rock, cobbles and gravel. Egg survival has been found to vary with thickness of the deposited egg mass (Taylor, 1971). Best survival occurs at light to moderate substrate coverage (i.e. 1 to 6 egg layers). Increased mortality at higher egg densities may be due to suffocation of eggs in lower layers, increased concentrations of toxic metabolites and disease induced by stress. Eggs are also subject to other sources of mortality including wave action, predation and, within the intertidal zone, desiccation. Mortality within the intertidal zone may be high due to these factors; Taylor (1964) and Outram (1958) estimated egg loss due to wave action and bird predation to be 37% and 39%, respectively. Mortality within the subtidal zone is often assumed to be lower (Haegele et al., 1981). However, predation by fishes (e.g. yellowfin sole, Limanda aspera, in Bristol Bay; humpback whitefish, Coregonus pidschian, in the Chukchi Sea) and wave action from storms may take a considerable toll on Pacific herring eggs deposited in the subtidal zone (Whitmore and Bergstrom, 1983; Barton and Steinhoff, 1980). Unfortunately, no quantitative estimates are available.

Eggs hatch within 6 to 21 days after deposition at temperatures of 14 and 4°C, respectively (Alderdice and Velsen, 1971). Within Bristol Bay hatching has been documented to occur within about 14 days at temperatures of 8 to 11°C (Wespestad and Barton, 1981) and 18 days at temperatures of 5 to 9°C (Barton and Steinhoff, 1980).

Larval Survival

Pacific herring hatch as 8 mm larvae and metamorphose in 6 to 10 weeks at a size of about 30 mm (Taylor, 1964). Mortality is high during the larval stage and most investigators believe that future adult abundance is determined at this time (Blaxter and Hunter, 1982; Cushing, 1981). Predation and starvation both play major roles in determining larval survival. In British Columbia the direction and magnitude of wind induced surface stress affects larval survival; net offshore flow is associated with poor year classes (Outram and Humphreys, 1974; Stevenson, 1962). Such studies have not been done for Alaskan stocks, but storms or deviations in current patterns may affect survival of these stocks by transporting larvae away from nursery areas and into less productive offshore areas where they may starve or be subject to predation.

Growth, Natural Mortality, and Maturity

Pacific herring stocks inhabiting the central portion of their distributional range have larger age specific sizes (Fig. 2). Along the North American coast Pacific herring are largest in Bristol Bay; stocks both to the north and south are characterized by progressively smaller mean age specific lengths (Fried et al. 1982; Whitmore and Bergstrom, 1983; Wespestad and Barton, 1981).

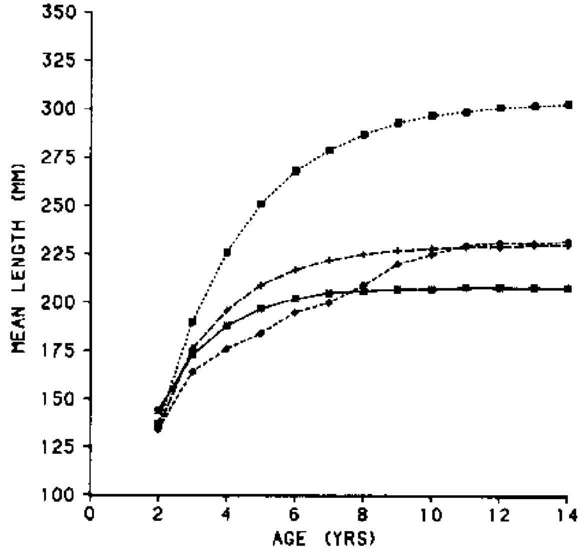

Fig. 2.--Growth in length of Pacific herring by area: San Francisco (*), Puget Sound (+), Bristol Bay (■), Kotzebuk Sound (◆).

Natural mortality rates follow a similar pattern, but estimates are not available for individual eastern Bering Sea stocks or for any Chukchi Sea populations. However, age specific instantaneous rates are generally lower for eastern Bering Sea Pacific herring (Wespestad, 1982) than for either southeast Alaska (Skud, 1963) or British Columbia (Tester, 1955) stocks (Table 1).

Age of sexual maturity also varies by geographic area. In California Pacific herring enter the spawning population at age 2 or 3 (Spratt, 1981). In British Columbia (Outram and Humphreys, 1974) and the Gulf of Alaska (Rounsefell, 1929) Pacific herring mature at age 3 or 4. In the eastern Bering Sea (Wespestad and Barton, 1981; Naumenko, 1979) and Chukchi Sea (Whitmore and Bergstrom, 1983) maturity is reached between the ages of 3 to 5.

Table 1. Age specific estimates of instantaneous natural mortality rates for Pacific herring from different areas in the northeastern Pacific Ocean. Data for British Columbia from Taylor (1964) and Tester (1955). Data for the Gulf of Alaska from Skud (1963). Data for the eastern Bering Sea from Wespestad (1982).

	Age									
Area	1	2	3	4	5	6	7	8	9	10
British Columbia	0.11	0.25	0.38	0.43	0.63	0.75	0.82	1.03	1.18	-
Gulf of Alaska	-	-	0.20	0.33	0.46	0.59	0.72	0.85	-	-
Bering Sea	0.25	0.25	0.25	0.15	0.18	0.23	0.29	0.36	0.45	0.57

Variations in Commercial Catches

Pacific herring stocks, like those of other clupeoid fishes, tend to undergo great fluctuations in abundance. These fluctuations are often reflected in commercial catch records. While the best index of abundance would be catch per unit of effort, this information is not presently available for most of the stocks in Alaskan waters. Therefore, total annual catches will be used to illustrate abundance fluctuations.

In Alaska Pacific herring fisheries for cured herring and reduction to oil and fertilizer began in the 1880's (Reid, 1972; Rounsefell, 1929). The southeast Alaska reduction fishery peaked in 1929 when over 70,000 t were harvested (Fig. 3). This fishery declined in the post-war years and finally ended in the 1960's due to economic causes rather than a decline in Pacific herring abundance. With development of a market for sac roe (egg skeins) in Japan the harvest gradually climbed through the 1970's, averaging about 5,500 t. In 1982 the sac roe and bait catch totaled about 8,000 t

Pacific herring fisheries in Prince William Sound, Cook Inlet and the Kodiak Island area began during the early twentieth century (1914 to 1920's) (Reid, 1972; Rounsefell, 1929). Earliest fisheries were for cured herring, but reduction fisheries developed and catches rose to a peak of over 100,000 t during the 1930's and then declined (Fig. 3). With the advent of sac roe fisheries catches from these central Alaska areas rose during the 1970's. In 1982 about 6,600 t of Pacific herring were taken in Prince William Sound, 180 t in Cook Inlet and 2,500 t in the Kodiak Island area.

In the eastern Bering Sea Pacific herring fisheries first developed in Norton Sound (Wespestad and Barton, 1981; Rounsefell, 1929; Marsh and Cobb, 1910). By 1928 a salt fishery developed at Dutch Harbor in the Aleutian Islands. Lack of demand kept harvests low (about 3,000 t during peak years), and these fisheries disappeared during the 1940's. In 1959 trawl vessels from the U.S.S.R. began harvesting Pacific herring near the Pribilof Islands during the winter. This fishery grew rapidly and peaked in 1970 when the U.S.S.R. and Japan havested over 140,000 t (Fig. 4). Catches dropped due to decreased Pacific herring abundance and were further curtailed by establishment of the U.S. Fishery Conservation Zone in the late 1970's. As the foreign offshore fishery was phased out a domestic fishery began to develop in coastal waters for sac roe. Catches in the domestic fishery have steadily increased. In 1982 over 27,000 t was harvested. Stocks appear to have recovered from the 1970's decline and seem to be fairly stable. British Columbia is the only area south of Alaska which supported larger Pacific herring fisheries (Fig. 2). During the height of the

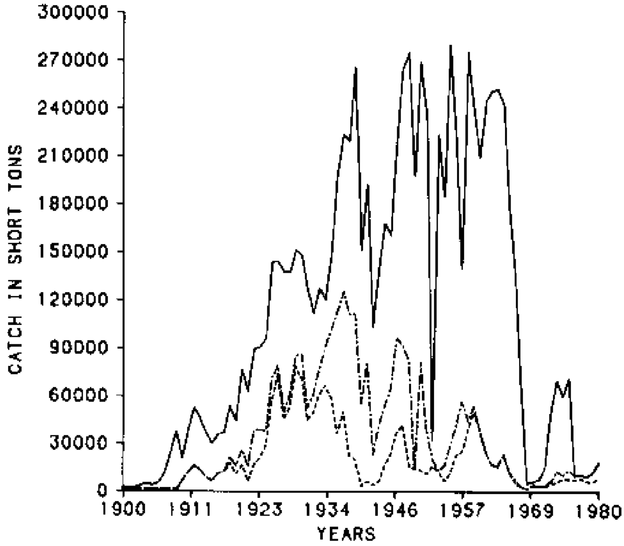

Fig. 3.--Catches of herring in the northeastern Pacific Ocean, 1900-1980. Southeastern Alaska (dashed line), central Alaska (dash-dot), and British Columbia (solid line).

reduction fishery (1935 to mid-1960's) annual catches as high as 250,000 were taken before the stocks declined in the late 1960's (Hourston, 1980). Recent catches for food, bait and roe total about 45,000 t annually (Webb, 1983).

Stock Size Fluctuations

Pacific herring populations lack strong density-dependent regulatory mechansims and thus are subject to large fluctuations in recruitment and population size due to environmental change and heavy fishing pressure (Blaxter and Hunter, 1982; Cushing, 1981). It is generally believed that most variation in year class strength is determined during the early life stages, but it has proven difficult to establish well defined relationships between abiotic and biotic variables and Pacific herring survival. Favorite and McLain (1973) found a close correlation between winter sea surface temperature anomolies in southeast Alaska and Pacific herring year class strength. Year classes spawned during warm years were usually more abundant than those spawned during cold years. Rounsefell (1930) reported a similar correlation between mean annual spring temperatures in

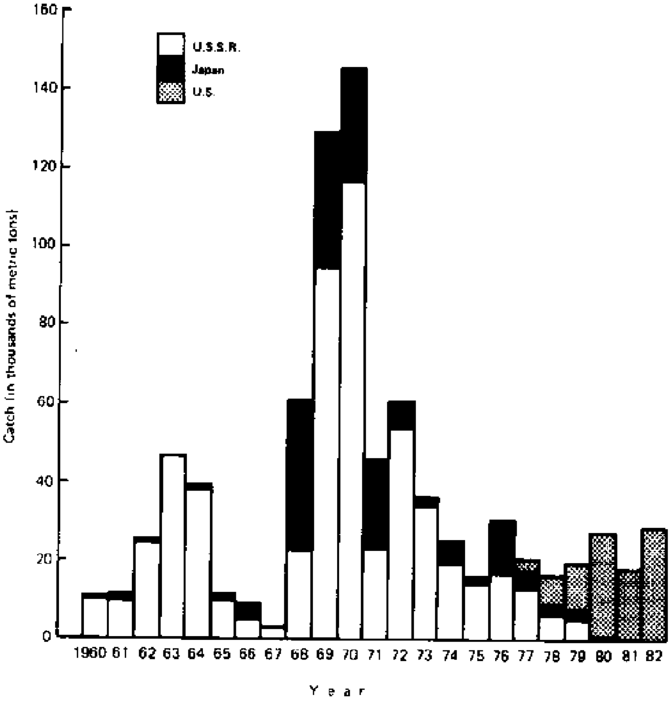

Fig. 4.--Catch of Pacific herring in the eastern Bering Sea by nation, 1960-1982.

Prince William Sound and Pacific herring year class strength. In the eastern Bering Sea Laevastu and Favorite (1978) hypothesized that variations in Pacific herring biomass could be explained by predation (walleye pollock, *Theragra chalcogramma*, and sperm whales, *Physeter macrocephalus*, being the most important predators) and winter water temperature anomolies (cold surface temperatures causing abundance declines). Finally, Wickett (1975) proposed a relationship between salinity and year class strength for British Columbia stocks. He used salinity as a measure of winter storm mixing of the water column which caused movement of nutrients into the euphotic zone and, thus, increased production. Changes in salinity accounted for about 85% of the variation which occured in stock size and year class strength.

Although we have not yet analysed other Alaskan Pacific herring data to examine causes of abundance fluctuations, we can offer some observations and make some hypotheses concerning eastern Bering Sea stocks. As has been noted for other clupeoid fishes, variation in recruitment is extreme. From 1958 to 1979 year class size at age 1 has varied from 53,000,000 to 10,600,000,000 individuals for all major eastern Bering Sea Pacific herring stocks combined (Wespestad, 1982) (Fig. 5). Mean recruitment was estimated to be 1,280,000,000 individuals with a coefficient of variation of 178% (Fried and Wespestad, in press). No year class since 1957 has approached the abundance of that apparently extraordinary cohort. Conditions which produced the 1957 year class are not known.

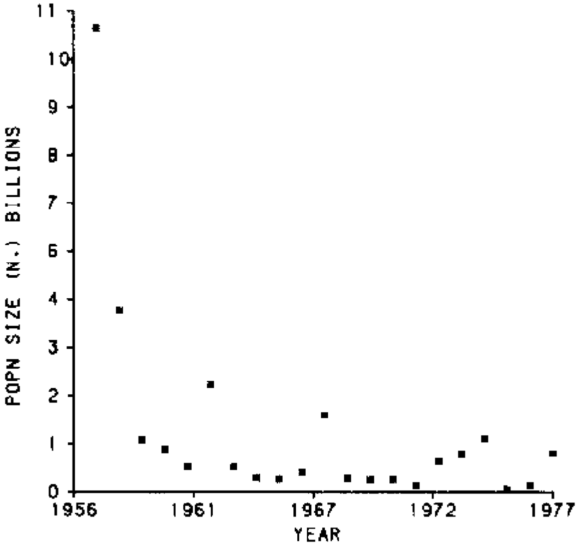

Fig. 5.--Estimated numbers of age 1 herring in the eastern Bering Sea by year-class, 1957-77.

Relative abundance of individual stocks within the eastern Bering Sea may largely be a function of extent of suitable spawning substrate (Fig. 6). However, estimates of spawning substrate are crude and do not fully account for density, type or subtidal extent of vegetation. Lack of large spawning concentrations of Pacific herring along the north side of the Alaska Peninsula cannot be explained by a paucity of aquatic vegetation, however. Izembeck Lagoon contains one of the largest known stands of eel grass in the world (McRoy, 1968). Yet, no major spawning concentration of Pacific herring has been reported from this area. Abundance of stocks may depend upon availability of a suitably large larval retention area as well as presence of large amounts of spawning substrate, as was found for Atlantic herring (C. harengus harengus) stocks (Iles and Sinclair, 1982).

Species interactions may also play a major role in determining eastern Bering Sea Pacific herring stock abundance. An inverse relationship appears to exist between walleye pollock and Pacific herring in this area (Fig. 7). This could be due to predation by walleye pollock on Pacific herring (Laevastu and Favorite, 1978) or to competition for food by both species

Whatever the factors are which affect recruitment in eastern Bering Sea Pacific herring populations, they must operate over a large area since relative year class strength is similar for all major spawning groups (Fried et al. 1982).

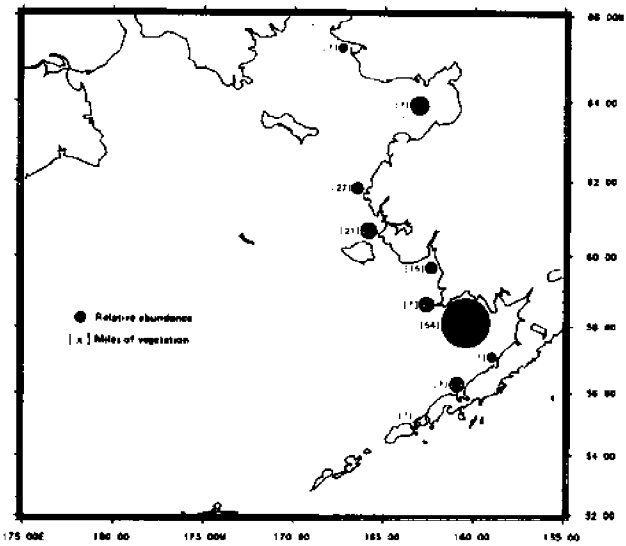

Fig. 6.--Distribution of Pacific herring spawning areas in the eastern Bering Sea, the relative abundance of herring in each area, and the estimated spawning habitat in each area. Relative abundance of 1 = 1% or less.

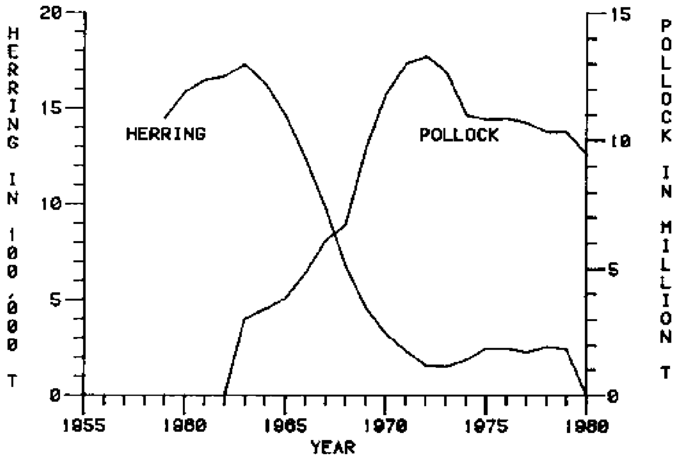

Fig. 7.--Relationship between pollock and herring abundance in the eastern Bering Sea.

Summary

Pacific herring is the only pelagic Alaskan marine fish that seems to provide an opportunity for examining interannual variation in abundance. Long time series of catch data are available for several areas in the northeastern Pacific Ocean. All Pacific herring stocks undergo large fluctuations in abundance. However, the resiliency of individual stocks is variable, and fishing may intensify or increase the possibility of stock declines. Many explanations and hypotheses have been offered concerning the causes of recruitment variability, but most recognize that environmental factors may be of most importance in controlling year class strength unless spawning stocks have fallen below a critical threshold level. Examination of data available for Alaskan Pacific herring stocks could yield valuable insights on responses of stocks to long term oceanographic trends and local abiotic and biotic variations.

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Commentary

Abiotic Variations In Regional Environments

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Introduction

Wespestad and Fried have given us an excellent review of the biology of herring and the status of stocks off Alaska. Although other pelagic animals (e.g., capelin, smelt, squids) are undoubtedly important in the ecosystem of subarctic waters, the Pacific herring is the most amenable of the pelagic, non-salmonid species to studies of interannual variations of year-class strength. This is because: (1) long time-series of catches and age compositions are available, (2) large fluctuations occur in year-class strengths and dominant year classes may sustain the fishery of an area for several years, and (3) many separate stocks of herring exist along the Pacific coast, each with a spawning area that is generally geographically isolated in nearshore, protected bays, estuaries and inlets. These many distinct and geographically widespread stocks permit analysis of the coherence of fluctuations of year-class strengths and hence the spatial scales of the environmental variables that are responsible for interannual fluctuations.

Since large variations in year-class success of Pacific herring have been recognized and studied since the 1920's, and since a cogent underlying cause for these fluctuations has not yet been found, we can conclude that the mechanisms are multiple and complex. I will mention several features of year-to-year variability that are hints of the spatial of temporal scales involved and that I believe merit further study.

Coherence Among Year-Classes

Some year-classes of herring appear to be strong in more than one region, suggesting that common, large-scale environmental events affect survival of several stocks in the same year. For example, Dahlgren and Kolloen (1943) noted that the 1926 and 1931 year classes were exceptionally strong in waters of southeastern Alaska, Prince William Sound and Kodiak, supporting the fisheries in these districts from 1929 to 1937. The 1957 and 1958 year classes were strong in southeastern Alaska (Favorite and McLain, 1973) as well as in the eastern Bering Sea (Wespestad and Fried, this volume).

Moreover, after the strong year classes of the late 1950's a series of weak year classes occurred through the 1960's in the Bering Sea, southeastern Alaska and off northern British Columbia. Wespestad and Fried found that year classes in the eastern Bering Sea were weak from 1956-77 compared to the strong 1957 and 1958 year classes. Mysak, Hsieh and Parsons (1982) show that herring recruitment for northern British Columbia was poor in the 1960's and 1970's following the strong 1957 and 1959 year classes and a moderate 1962 year class. Mysak et al.'s data for Vancouver Island, on the other hand, showed an opposite trend, with increasing year-class strengths from the 1940's to 1980, illustrating that different trends may prevail for stocks from different geographic regions.

Figure 1 shows the percentage of age III herring in the catches from southeastern Alaska, 1929-1966 (data from Reid, 1971), plotted as estimates of relative year-class strengths. These data also

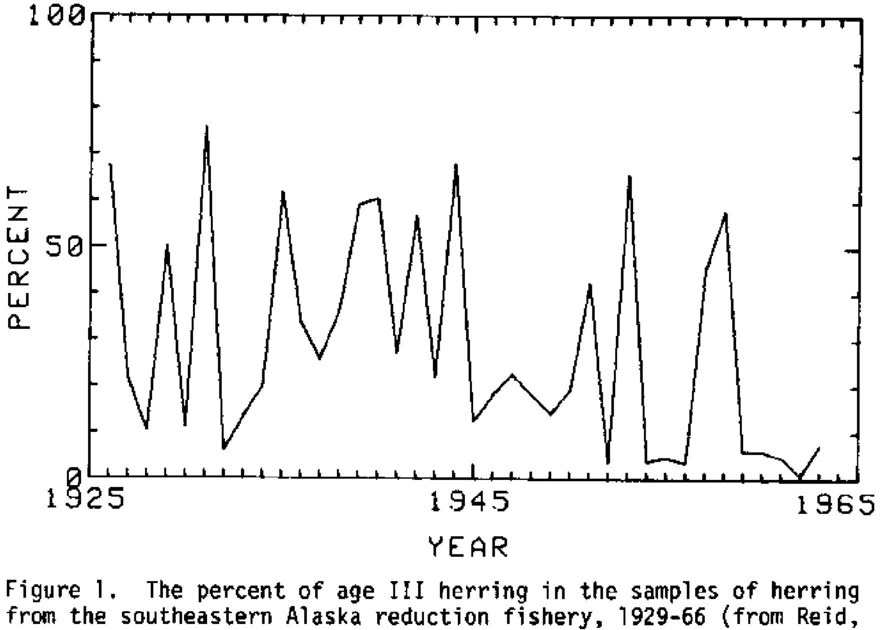

Figure 1. The percent of age III herring in the samples of herring from the southeastern Alaska reduction fishery, 1929-66 (from Reid, 1962) plotted as relative year-class strengths at age 0. Percent of age III for years lacking data (1940 and 1942) were estimated from the percent of age IV and the average differences between age III and IV.

suggest that the strong 1957-78 year classes were followed by a series of weak year classes. Strong year classes in the late 50's and weak year classes in the 1960's in these widely separated regions, northern British Columbia to the eastern Bering Sea, may be related to common environmental conditions during this period. Wickett (1973) found a positive correlation between year-class strengths of British Columbia herring and mean annual surface salinity at Station "P" between 1957 and 1966. Salinities at "P" were relatively high from 1958 through 1961 and were low from 1962 to 1968. Zooplankton biomass at "P" was also high from 1958-1961 and low 1962-1966 (Fulton, 1983 and unpublished). However, increased salinity and zooplankton in the late 60's and the 70's were not correlated with increased year-class success of herring in the northern regions.

The El Niño Connection

The strong 1953, 1957 and 1958 year-classes in southeastern Alaska (Favorite and McLain, 1973) and the strong 1957 and 1958 year-classes in the eastern Bering Sea (Wespestad and Fried, this volume) were all produced in El Niño years. Other El Niños of strong or medium intensity (see Quinn et al., 1978) coincided with years of strong year classes in southeastern Alaska during 1926, 1929, 1939-40 and 1951 and 1953 (Fig. 1).

Of the strong year classes indicated in Fig. 1, 1926 and 1931 were also noted as "phenomenally successful spawnings" by Dahlgren and Kolloen (1943) and 1926, 1931, 1935, 1942 and 1944 were identified as strong year classes by Hanamura (1961) for herring in southeastern Alaska. Of the eleven year classes with peaks of age III comprising 45% or more of the catches of a year, seven were from moderate or strong El Niño years and four were from anti-El Niño or weak El Niño years. Of the 27 year classes contributing less than 45% of the age III catches, one occurred during a moderate (1930) and one during a strong (1941) El Niño event; the rest occurred during anti-El Niños or weak El Niños. The chi-square resulting from a 2 x 2 contigency table of these data is significant, suggesting a correlation between El Niños events and strong year classes of herring.

Periodicity

Spectral analysis of the data of Fig. 1 shows a large peak at about 0.45 cycles per year, or two years. Relatively strong year classes are often found two years apart. Only twice in the series for southeastern Alaska did strong year classes occur in two consecutive years. This happened in 1939-40 and 1957-58. Interestingly, both these periods coincide with prolonged El Niño events. These trends suggest that high survival of two succeeding year classes is a rare event, probably because of density-dependent interactions among age groups.

From cross-spectral analyses, Mysak et al. (1982) reported high coherence between year-class strengths of herring and sea level in northern British Columbia at about 0.17 cycles per year, or 6 years. They also found high coherence between sea level at Victoria and temperature at Amphitrite Point, B.C. at a 5-year period. Favorite and Ingraham (1978) noted a 5- to 6-year periodicity in 12-month running mean sea level from Astoria, Oregon to Kodiak, Alaska, with peaks in sea level usually occurring in El Niño years (1953, 1958, 1963, 1968-69, 1972-73) and largely in phase with 5- to 6-year sea-surface temperature maxima reported by Favorite and McLain (1973). White (1975) identified a 6-year cycle in large-scale baroclinic transport across the North Pacific. Long-term periodicity and coherence in variations of year-class strengths among different herring stocks may be a fruitful subject for future research.

Conclusion

Environmental variables that affect year-class success of herring probably range from single, short-term events such as a storm or freshet that affect the survival of a cohorts in an isolated inlet to large-scale events that affect the productivity and circulation of large areas of the northeastern Pacific for a year or more. The synchrony of strong year classes in distance stocks during El Niños supports the idea that large-scale ocean events are important. But we lack information on interannual differences in oceanographic conditions in the northern North Pacific, as well as on specific mechanisms on how varying ocean conditions modify year-class success of herring. Are the warm temperatures and high sea levels accompanying strong El Niños due to a strong California Countercurrent (McLain and Thomas, in press), propagation of baroclinic waves (Mysak et al., 1982), or increased flow into the Gulf of Alaska from the south and west (e.g. as in 1958, Dodimead, 1963)? High sea levels are associated with onshore convergence and reduced offshore transport of water along the coast, a situation that may be conducive to high retention and good survival of herring larvae in inshore nursery grounds (Stevenson, 1962).

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Factors Affecting Recruitment Of Selected Gadoids in the Northeast Pacific and East Bering Sea

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Introduction

Marine fish production is a function of the population characteristics of growth, recruitment, and post-recruitment mortality. In some species, and possibly most, the pre-recuitment life stages are the most important in determining subsequent fishery production.

In this paper, we describe the fishery production of Pacific whiting (Merluccius productus) in the Washington-Oregon-California coastal region and Walleye pollock (Theragra chalcogramma) in the eastern Bering Sea (EBS). We then suggest hypotheses about causes of recruitment fluctuations in these two gadoid stocks, hypotheses which reflect some of the fundamental differences in the two ocean areas these stocks occupy. The dynamics of the pollock resource of the Gulf of Alaska are not discussed here, although the resource supports a significant and developing fishery, primarily on spawning fish in the Shelikof Strait region.

Fishery Production of Whiting and Pollock

The most recent synopses of the biology and fisheries of whiting and EBS pollock are those of Bailey et al. (1982) and Smith (1981), respectively. The coastal stock of Pacific whiting occupies the continental shelf and slope area of the California current system, ranging from a summer feeding area as far north as central Vancouver Island to a winter spawning area as far south as the southern tip of Baja California (Fig. 1). Juveniles remain off central and northern California during the northward feeding migration of adult fish. The feeding population tends to stratify on a north-south gradient by size. Between 1973 and 1981, the estimated numbers of age 3 recruits ranged between 0.1 billion and 3.0 billion individuals with a coefficient of variation of 124%.

A small, rather insignificant domestic fishery for whiting, used in the manufacture of pet food, has existed since at least 1879. Since 1966, whiting has been the target of a large foreign fishery off the west coast of the U.S. and Canada. Estimated catches have ranged

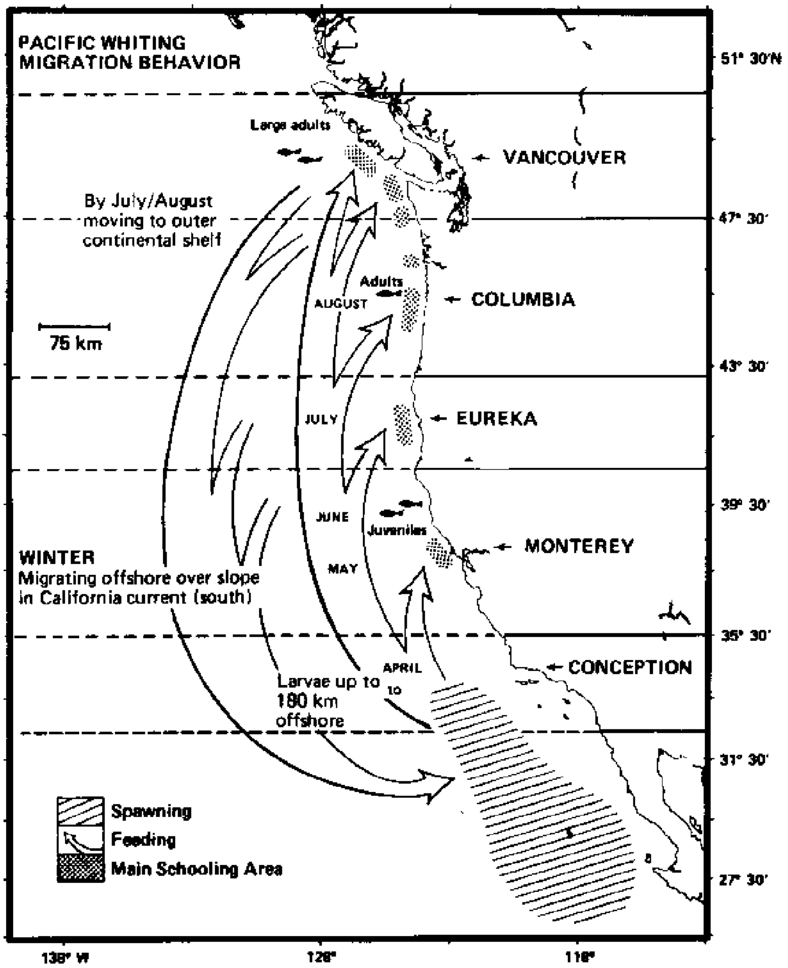

Figure 1. Migratory patterns of Pacific whiting.

from 91 to 236 thousand mt. The average all-nation reported catch for 1966-1982 was 154 thousand mt. In recent years, a domestic joint venture for whiting has begun to develop. The U.S. joint venture catch was estimated at 3, 13, 41, 45, and 67 thousand mt in 1978 through 1982, respectively. Figure 2 provides the estimated age structure of the whiting catch in U.S. waters for 1973-1981. The importance of strong year classes (1970, 1973, 1977) is clearly shown. Between 1973 and 1981, these three year classes accounted for 43% of the estimated whiting catch in numbers. Whiting has been found to represent a large fraction of the standing stock of west coast demersal fishes (Dark et al. 1980). Between 1973 and 1982, whiting constituted 66% of the total catch of groundfish along the west coast of the U.S. Comprehensive statistics on the whiting

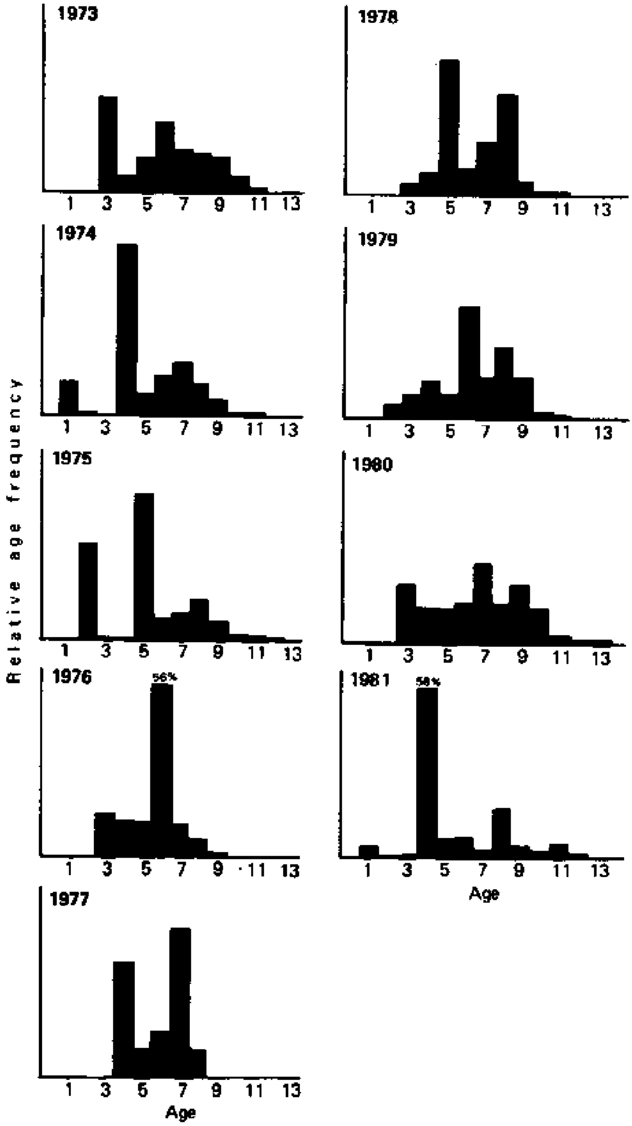

Figure 2. Relative age-frequency of Pacific whiting catch in U.S. waters, 1973-1981.

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fishery in U.S. waters have been collected since the expansion of the foreign fisheries observer program in 1977. Extensive trawl-hydroacoustic surveys of the stock are performed by NMFS on a triannual cycle. Reliable estimates of stock biomass and biological structure are currently available from the 1977 and 1980 surveys. A third comprehensive survey is planned for the summer of 1983.

EBS stock(s) of walleye pollock are widely distributed over the continental shelf, slope and Aleutian Basin but show highest densities along the shelf edge (Figs. 3 and 4). These pollock exhibit seasonal movement on and off shelf. During winter, the entire population tends to concentrate along the deep outer shelf area and extend pelagically into the Aleutian Basin. Over the Aleutian Basin, pollock are dispersed throughout the upper 40 m of the water column during the summer and fall and then form spawning aggregations during late winter and early spring. During and after spring spawning of adults along the outer shelf, onshore movements occur which result in a dispersal, primarily of juveniles (ages 1 and 2), into the central and inner shelf regions (Fig. 5).

There is some controversy over the stock structure of pollock in the EBS (see Fig. 6). There appear to be some fundamental differences between the outer continental shelf areas northwest and southeast of the Pribilof Islands (Smith 1981). Temperature conditions are colder in the northwest area and, as a result, the timing of pollock spawning and associated phenomena appear to lag behind the southeastern region. Studies by Lynde et. al (in prep.) indicate that both feeding and growth rates of pollock caught northwest of the Pribilofs are significantly lower than those caught southeast of the Pribilofs.

Many different estimates of the dynamics of E. Bering Sea pollock recruitment have been made. Bakkala and Wespestad (1982) estimated that recruitment at age 1 between 1973 and 1979 varied from a low of 20 billion to a high of 46 billion individuals with a coefficient of variation of 30%. Based on some of our ongoing work, we estimate that recruitment at age 1 between 1974 and 1980 varied between 5 billion and 35 billion individuals with a coefficient of variation of 44%. When separate cohort analyses are performed on the catch data from northwest (INPFC areas 52 and 53) and southeast (INPFC areas 51 and 54) of the Pribilofs for the years 1974 through 1981, the coefficient of variation of recruitment is estimated to be from 3 to 6 times as large in the southeast as in the northwest. Figure 7 gives some preliminary estimates of a normalized pollock year class index based upon estimates of recruitment at age two. Regional trends in pollock recruitment, although similar over much of the time period, diverge noticeably during 1972 and 1978. This is corroborated by the recent (1973-1982) distribution of pollock catch between the two areas (Fig. 8). Strong year classes in 1972 and 1973 appear to have supported the fishery in the northwest in the early and mid 70's (62% of the catch between 1973 and 1977 was taken in the northwest), whereas a strong 1978 year class appears to be supporting the recent fishery in the southeast (75% of the 1981-82 catch was taken in the southeast). This is further illustrated in Figure 9 by data on the age-frequency of catch by area. Later in the paper, we speculate on why regional differences in recruitment might occur.

Since 1964, pollock has been the target of a large foreign fishery in the EBS. Estimates of annual catch (Bakkala and Wespestad 1982) range from 0.175 to 1.874 million mt. In recent years, a domestic joint venture for pollock has developed. The U.S. joint venture catch was estimated at 10, 42, and 55 thousand mt in 1980

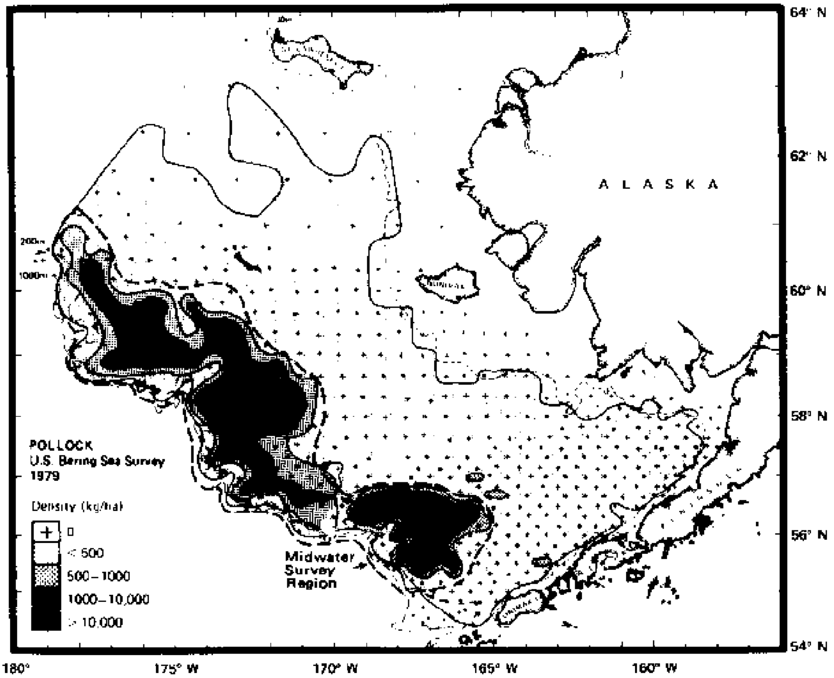


Figure 3. Distribution and abundance of pollock in the E. Bering Sea in 1979 based on combined results of the Japanese - U.S. demersal midwater trawl surveys (Source: Bakkala et al 1982)

through 1982. Figure 9 gives the estimated age structure of the pollock catch in the EBS for 1974 through 1981 separated by area. As with whiting, strong pollock year classes appear to play an important role in supporting the fishery. For example, between 1974 and 1981 the 1972, 1973, and 1978 year classes accounted for 51% of the estimated pollock catch in numbers. Surveys reveal that pollock represent a large fraction of the total standing stock of EBS demersal fishes (Pereyra et al. 1976, Bakkala and Wakabayashi in prep.). In 1982 pollock constituted 78% of the total foreign and joint venture groundfish catch from this region.

Statistics on the EBS pollock fishery are comprehensive since the full implementation of the foreign fisheries observer program in 1977. Limited observer coverage has existed since 1973. Comprehensive trawl-hydroacoustic surveys of the stock(s) are performed by NMFS on a triannual cycle (alternating with surveys of the Gulf of Alaska and U.S. west coast). Reliable survey estimates of stock biomass and biological structure were made in 1979 and 1982. Estimates of biomass and age-structure based only on bottom trawl surveys have been shown to be inadequate for stock assessment purposes (Bakkala and Wakabayashi in prep). For example, Fig. 10 compares estimates based on hydroacoustic and demersal components of the 1979 comprehensive Bering Sea survey for the shelf and slope area northwest of the Pribilofs.

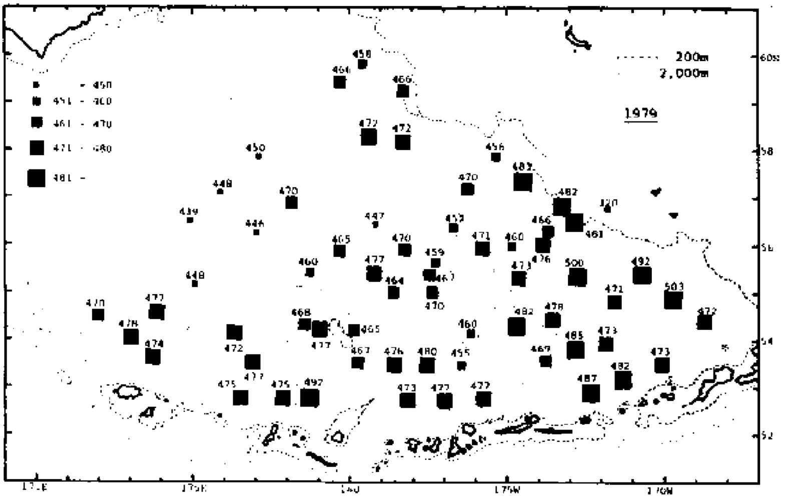


Figure 4. Relative abundance of pelagic pollock (number/60 min. of trawling) at each midwater station trawled during Japanese hydroacoustic surveys in the Aleutian Basin during 1979 (Source: Bakkala et al. 1982).

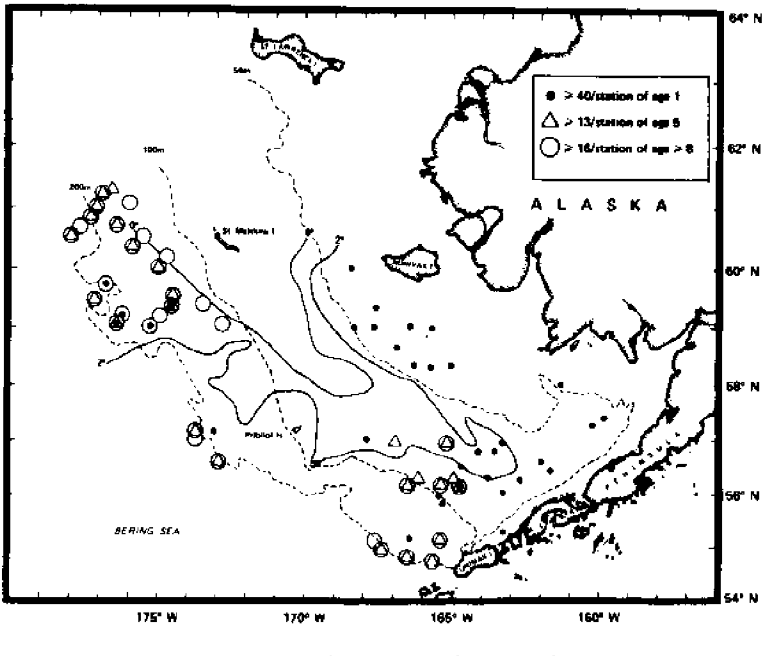
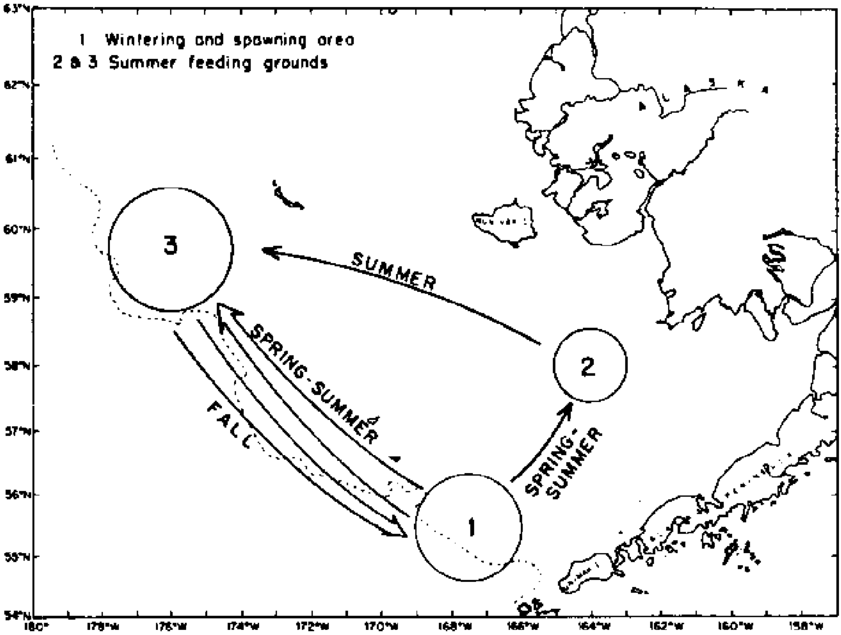


Figure 5. Stations with high (≥mean no/station) catches of ages 1, 5, ≥8 year old pollock in 1975 NWAFC bottom trawl survey (Aug-Oct) and location of 0° C and 2° C bottom temperature isotherms from survey.

ONE STOCK CONCEPT



TWO STOCKS CONCEPT

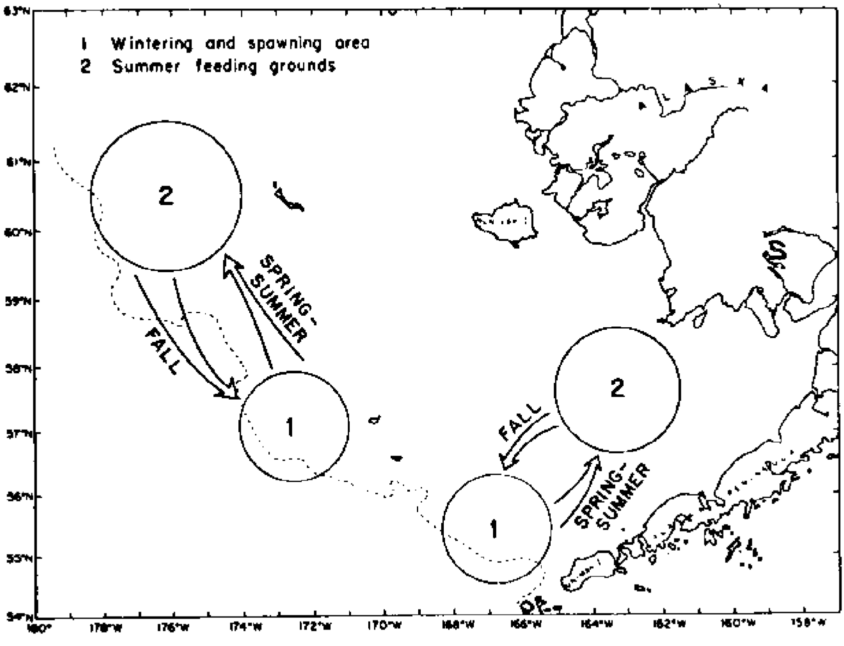
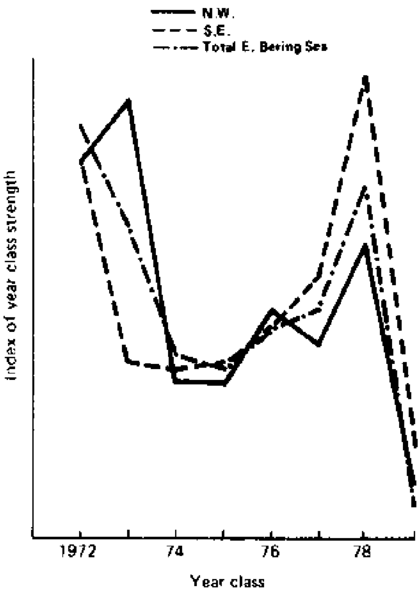


Figure 6. Hypothetical seasonal movements of pollock in the southeastern Bering Sea based on the concept of one stock (Adapted from Takahashi and Yamaguchi 1972) and two stocks (Adapted from Maeda 1972).

Figure 7. Normalized indices of pollock year class strength (recruitment at age 2) northwest of the Pribilofs, southeast of the Pribilofs, and for the two areas combined.



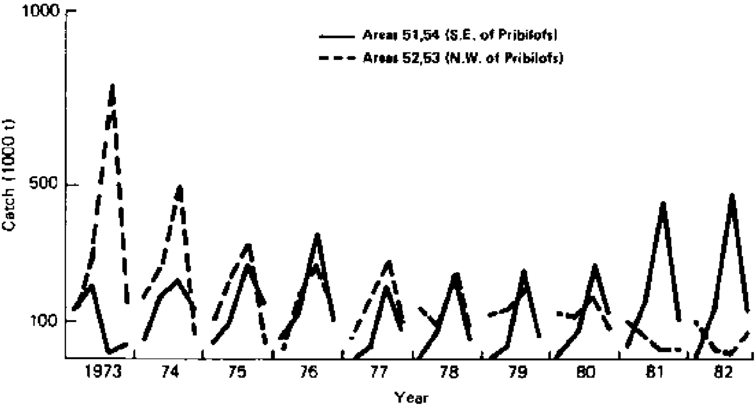


Figure 8. Estimates of quarterly catch (1000 t) of pollock in the E. Bering Sea northwest and southeast of the Pribilofs, 1973-1982.

Mechanisms Which Might Affect Recruitment of Whiting and Pollock

The chance of demonstrating a significant mathematical relationship between spawning biomass and recruitment is more difficult for most gadoids than, for example, herrings because variation in the spawning biomass of most assessed gadoid populations appears small compared with that of most assessed populations of herring. Figure 11 shows estimates of variation in recruitment and spawning biomass of selected stocks of gadoids and herrings, drawn primarily from cohort analyses reported in ICES documents as well as NWAFC reports. We argue that, even if an underlying stock-recruit relationship exists

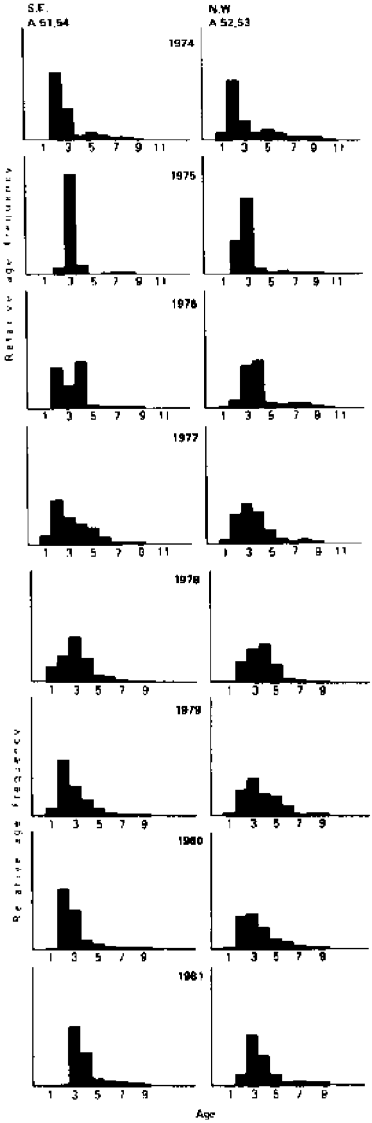


Figure 9. Relative age-frequency of pollock catch in the E. Bering Sea northwest and southeast of the Pribilofs, 1974-1981.

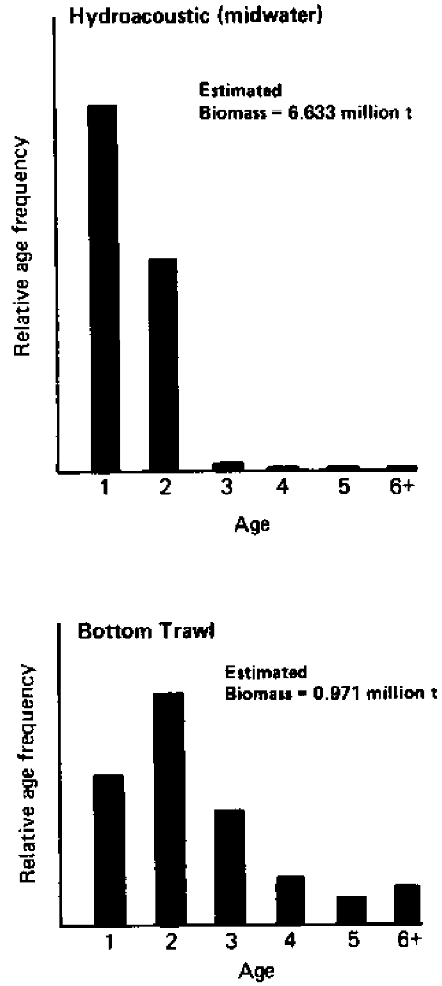


Figure 10. Estimates of biomass and age-structure for 1979 NWAFC survey in the shelf and slope area northwest of the Pribilofs.

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for whiting or pollock, the existing time series of reliable data is so short that it precludes a statistical, as opposed to a mechanistic, approach to determining the nature of this relationship. For example, the coefficient of variation of stock biomass of the southeastern Bering Sea pollock (INPFC Areas 51, 54) from 1974 through

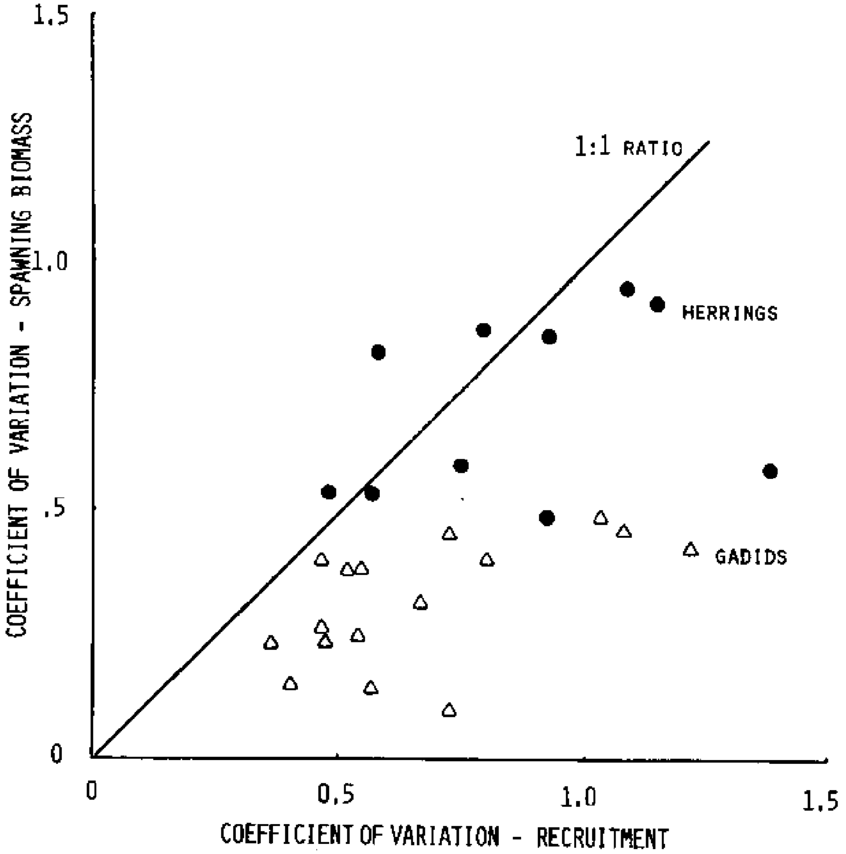


Figure 11. Coefficients of variation of spawning biomass and recruitment for selected gadids and herrings.

1981 is estimated to be around 20% whereas the coefficient of variation of annual recruitment could be well over 100% (Francis and Bailey, unpubl. data). Likewise, the coefficient of variation of estimated whiting biomass from 1973 through 1981 is around 30% whereas the coefficient for recruitment is well over 100%.

Pacific Whiting

Bailey (1981, 1982) documented the current state of knowledge of early life history and its effect on subsequent recruitment in Pacific whiting. His studies point to conditions during the first few months of life as being critical in determining year class strength.

The distribution of eggs and small larvae (2-3 mm) indicates that whiting spawn from Cape Mendocino to southern Baja California. Almost all eggs and larvae are located in waters over the continental slope, except in the Los Angeles Bight, where eggs and larvae are often found over very deep water and far out to sea (400 km). Over these depths, eggs are normally located at the base of the mixed

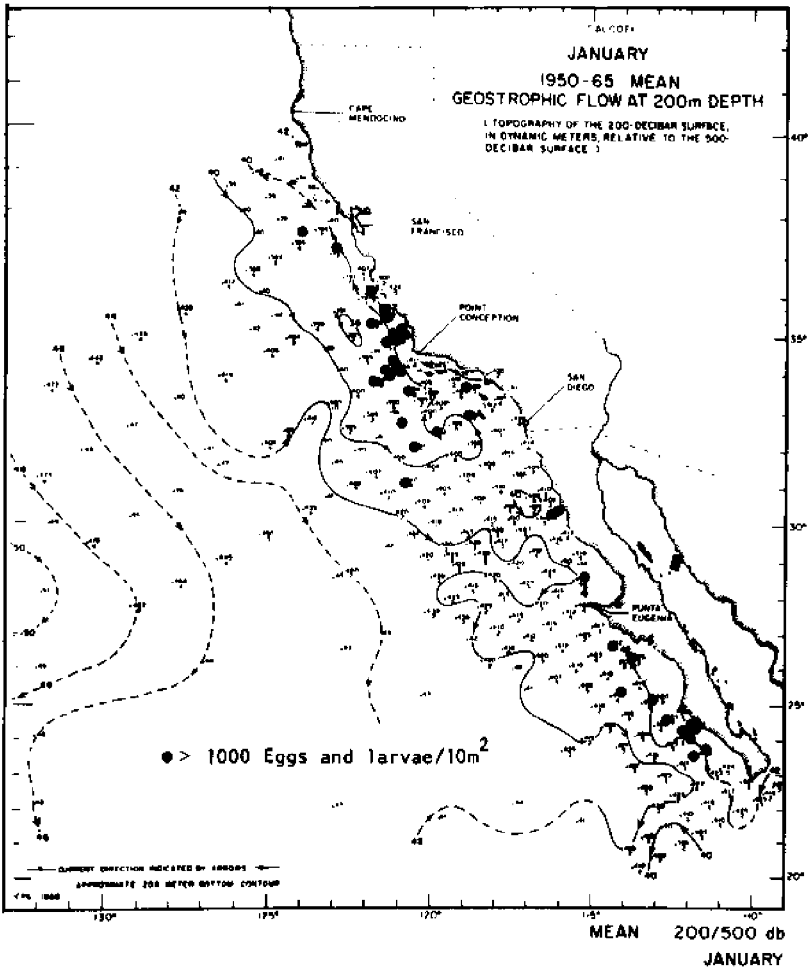


Figure 12. Large catches of Pacific whiting eggs and larvae (all size classes) in January surveys, 1950-1979, plotted on a chart showing geostropic flow at 200m depth (Source: Wyllie 1967).

layer, usually 40-60 m. Bailey (1981) postulated that whiting spawn in the California Undercurrent, which usually occurs over the continental slope at depths of 200-400 m, but spreads seaward some 200-400 km in the Los Angeles Bight and some other places where eddies occur. Large concentrations of eggs and larvae are found in areas overlying northward geostrophic flow at 200 m depth. Based on the northward distribution of larvae, spawning appears to commence when the southward migrating adults arrive in the warm and saline waters of the southern transitional water mass (Fig. 12). The location of the northern front of spawning has been correlated to water temperature;

in warm years the southern transitional water mass and spawning are both farther north.

Larvae of all size classes occur in significant numbers in the water from December to May but some 80% of eggs and small larvae are found in two months, January and February. This indicates a very sharp peak in spawning. Interannual variation in the time of spawning probably results from changes in environmental conditions and the age structure of the stock, assuming that old fish spawn earlier than young fish.

The factors most often considered to affect reproductive success of marine fishes are cannibalism, food supply, predation, and larval transport. Although cannibalism is sometimes observed, the majority of adult whiting spend a limited time in the spawning area (1-3 mo.) and the overall impact of cannibalism is probably fairly low. Sumida and Moser (1980) found instances where large larvae eat smaller larvae and speculate that this could be an important source of early larval mortality when patches of yolk-sac larvae coincide with larger larvae and juveniles. A few reports of adult predation on juveniles also exist, but spatial segregation of size classes must minimize this interaction.

Bailey (1982) found that the food requirements of whiting larvae are low because of relatively low growth and metabolic rates. Large mouth size enables first-feeding larvae to ingest a wide spectrum of food particles, including juvenile and adult copepods (Sumida and Moser 1980). Bailey (1982) calculated that a first-feeding whiting larva can satisfy growth and metabolic requirements by ingesting 25 copepod nauplii, 6 small calanoid adults or 1 Calanus adult per day. By contrast, both first feeding mackeral and anchovy require smaller food particles (Hunter 1980). Hunter (1977) calculated that a first feeding northern anchovy (Engraulis mordax) larva, with its small mouth, must capture at least 2000 Gymnodinium cells per day to satisfy metabolic requirements alone. A first feeding Pacific mackeral (Scomber japonicus) larva would have to capture 4000 Gymnodinium cells or 39 copepod nauplii to satisfy its daily ration requirements (Bailey, 1982). In addition, Bailey (1982) reported a relatively long starvation time for whiting larvae, i.e. 6-12 days after complete yolk utilization, whereas anchovy take only about 4 days. He concluded that starvation from first feeding failure is probably not as likely for whiting larvae as it appears to be for northern anchovy, and that whiting may not be as dependent on finding patches of prey as northern anchovy (Lasker 1975).

Whiting eggs and larvae are subject to predation by a wide variety of vertebrate as well as invertebrate organisms. However, the magnitude of predation is difficult to assess. Yolk-sac stages are most vulnerable to predation by invertebrates (Bailey and Yen, 1983), a factor which may be important in cold years when development through the yolk-sac stage is comparatively slow.

Oceanographic conditions appear to play a major role in the recruitment of Pacific whiting (Bailey 1981). The distance from shore of larvae was positively correlated with indices of wind-driven Ekman

Figure 13. The distribution of larvae offshore in January-February surveys versus the January upwelling index, 1959-1979 (linear correlation coefficient, r=0.70, P=0.001) (Source: Bailey 1981).

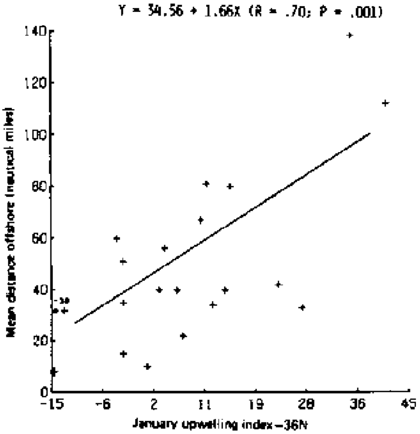


Figure 14. Logarithm of year class index against January upwelling index (Source: Bailey 1981).

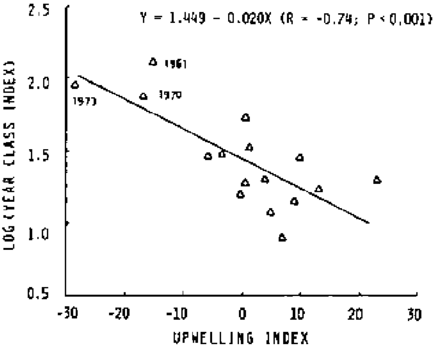
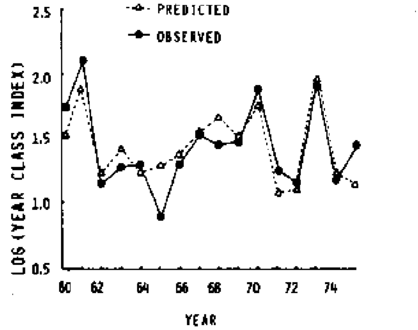


Figure 15. Observed index of year class strength compared to the predicted index from the multiple regression model (Source: Bailey 1981).



transport (Fig. 13). Although there is a good deal of variability in this relationship, it is statistically significant and indicates that larvae may be transported offshore during winter periods of high upwelling. (Alternatively, adults could be spawning further offshore in these years; nevertheless the result is the same). Since the juvenile nursery is inshore over the continental shelf, advection of larvae offshore is expected to be detrimental to survival and, in fact, Ekman transport during the spawning months is negatively correlated with year class strength (Fig. 14).

Recruitment is also related to sea surface temperature, possibly due to the predation-temperature interactions noted above and the previously described influence of temperature on the location of spawning. Together with Ekman transport these two factors account for 68% of the observed variation in an index of year class strength (Fig. 15).

While Bailey (1981) and Swartzman et al. (1983) point out that offshore transport of larvae tends to cause unfavorable conditions for the production of strong year classes, those conditions that ultimately result in strong year classes are not well understood. What is apparent is that in years of low upwelling (either little offshore transport or some onshore transport) at the time of spawning, there is a large amount of variability in year class strength and that the likelihood of a large year class is significantly greater than 0; whereas in years of high upwelling at the time of spawning there is little variability in year class strength and the likelihood of a large year class is very small.

Pollock

Compared with whiting, relatively little seems to be known about pre-recruitment dynamics of pollock in the EBS. Information presented in Smith (1981), Nishiyama and Haryu (1981), Waldron (1978, 1981), Serobaba (1975), and Moiseev and Bulatov (1979) as well as discussions at the recent NWAFC Pollock Ecosystem Review Workshop of May 2-4, 1983, provide the following picture of pollock spawning and early life history in the EBS. Spawning occurs from February to June in large midwater aggregations in the open ocean (>200m depth) to the west of the shelf break and over the outer (100-200 m depth) and, occasionally, middle shelf (50-100 m depth) domains from Unimak Pass as far west as 179° W. Relatively little is known about spawning and early life history northwest of the Pribilofs except that it appears to be delayed in timing when compared with the southeast (Smith 1981). Southeast of the Pribilofs, it appears that spawning commences in February west of the shelf break and progresses easterly over the outer shelf. Researchers hypothesize that the onshore extent of spawning is limited by the location and movement of the 2° C bottom isotherm. Accordingly in warm years (such as 1978), spawning should extend into the middle shelf, an area of limited net transport, whereas in cold years (such as 1972 and 1973), spawning should be limited to the open ocean and outer shelf where the net transport of eggs and larvae will be to the northwest. This interaction between water transport and the location of spawning would tend to support the relatively strong recruitment of the 1972 and 1973 year classes of pollock in the area northwest of the Pribilofs and the relatively strong recruitment of the 1978 year class in the area southeast of the Pribilofs (see Fig. 16).

There is much speculation as to whether pollock are multiple spawners and it is therefore unknown whether the distribution and timing of spawning represented in Fig. 16 is a result of migration of the spawning population or of different groups of fish spawning at different times and locations. Yoon (1982) shows evidence that pollock are definitely capable of batch spawning. M. E. Clarke (Scripps

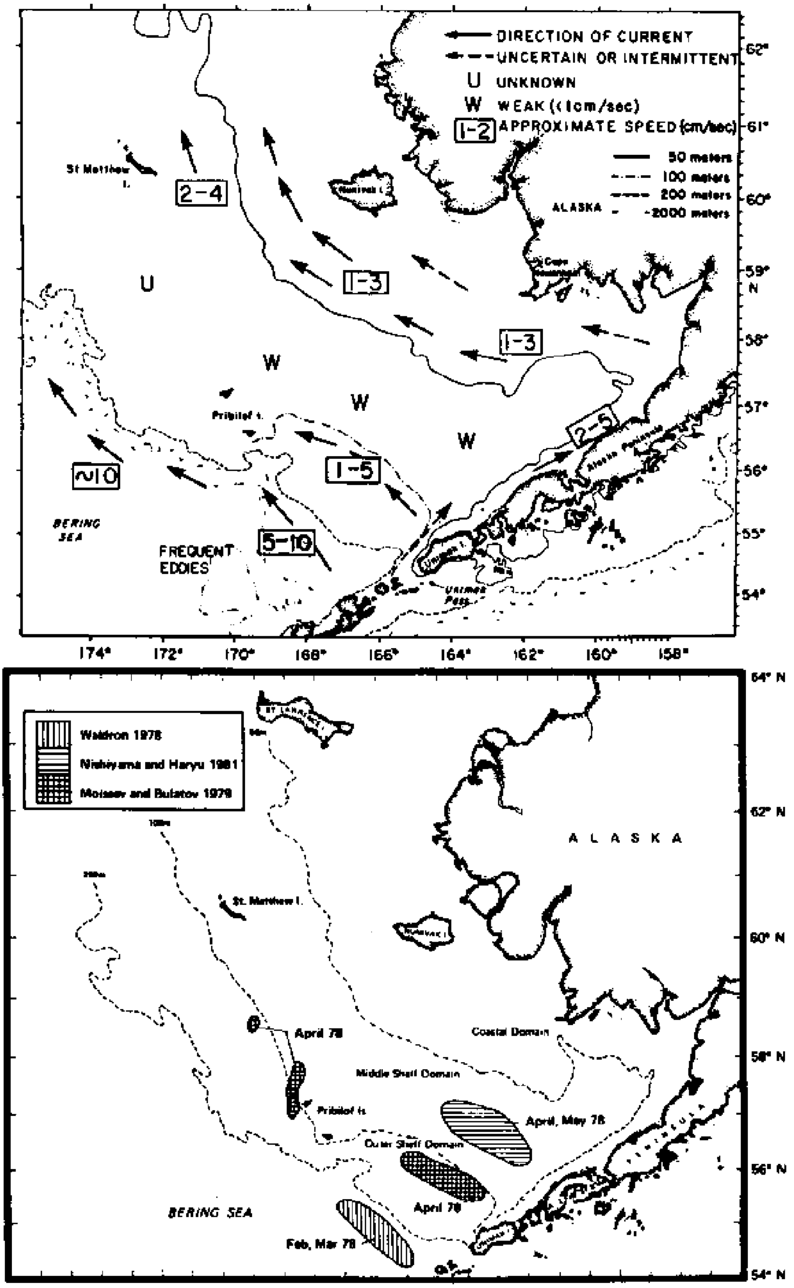


Figure 16. Estimated mean circulation in the E. Bering Sea (Source: Kinder and Schumacher 1981) and composite view of the major concentrations of pollock spawning in March-May 1978 (Sources: Waldron 1978, Nishiyama and Haryu 1981, Moiseev and Bulatov 1979).

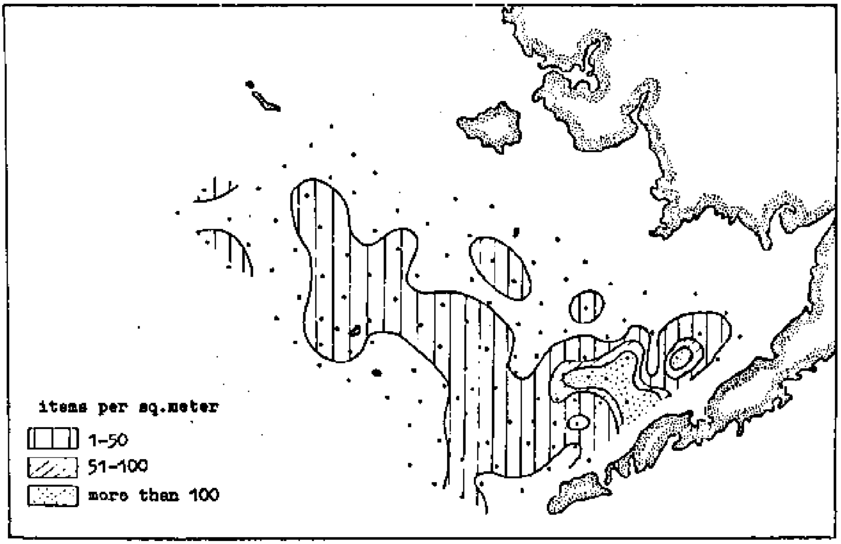
Institution of Oceanography) expressed the view at the recent Pollock Ecosystem Review Workshop, based on her nine years of observations of pollock spawning in the southeastern Bering Sea, that the multiple spawning/migration hypothesis is quite possible.

Nishiyama and Haryu (1981) report that pollock egg size appears to vary both by season and geographic location in the southeastern Bering Sea with a tendency for larger eggs to be produced in the north than in the south. More recently, Nishiyama (pers. comm.) indicates that spawning females tend to produce smaller eggs over the middle shelf later in the year than over the outer shelf and open ocean earlier in the year. There are several possible reasons for this. First, if EBS pollock are multiple spawners, one might expect a seasonal decline in egg size attributable to a reduction in energy reserves over the spawning season (Blaxter and Hunter 1982). Since spawning over the middle shelf tends to occur later than over the outer shelf and open ocean (presumably due to seasonal warming of middle shelf bottom water), this inshore migration of spawning females would tend to produce the observed seasonal and geographic distribution of egg size. On the other hand, if EBS pollock are not multiple spawners, then perhaps the smaller eggs found over the middle shelf reflect spawning of smaller younger females in the middle shelf domain.

Waldron (1981) presents a survey of the distribution of pollock larvae from 1955-1979. Figure 17 shows the distribution of pollock larvae from a Soviet survey in June 1982 (Fadeyev et al. 1983) and the distribution of 0-age pollock from a NMFS hydroacoustic survey of August 1982 (Jim Traynor, unpubl. data). From these figures it appears that there is a rapid dispersion of larvae (primarily in the surface layer) during the summer, over both the outer and middle shelf areas.

The state of knowledge of the dynamics of larval and juvenile pollock is quite limited and somewhat contradictory. If one looks at the timing and biomass of potential food (copepod eggs, nauplii, and copepodids: Cooney 1981) for larval pollock over the outer versus the middle shelf domain (Walsh 1983), one finds higher year to year variability in copepod production over the middle shelf than over the outer shelf, perhaps due to the higher interannual variability in temperature in the middle shelf region. One might speculate that if recruitment to the southeast component of the adult pollock stock is a result of successful spawning and larval/juvenile development over the middle shelf domain, then this might explain the greater variability in estimated recruitment in the southeast as compared with the northwest, as reported earlier.

Walline (1980) reports that potential food items for first feeding pollock tend to be smaller over the middle shelf domain (the eggs, and nauplii of small copepods, mainly _Oithona_ and _Pseudocalanus_) than over the outer shelf domain where large oceanic copepods, especially _Neocalanus_, are abundant. It is interesting to speculate on the adaptive advantage of producing larger eggs over the outer shelf and open ocean than over the middle shelf. Blaxter and Hunter (1982) indicate that for herring, larger eggs imply larger initial larval



Distribution of pollock larvae in vertical catches of IKS-80 - June 1982

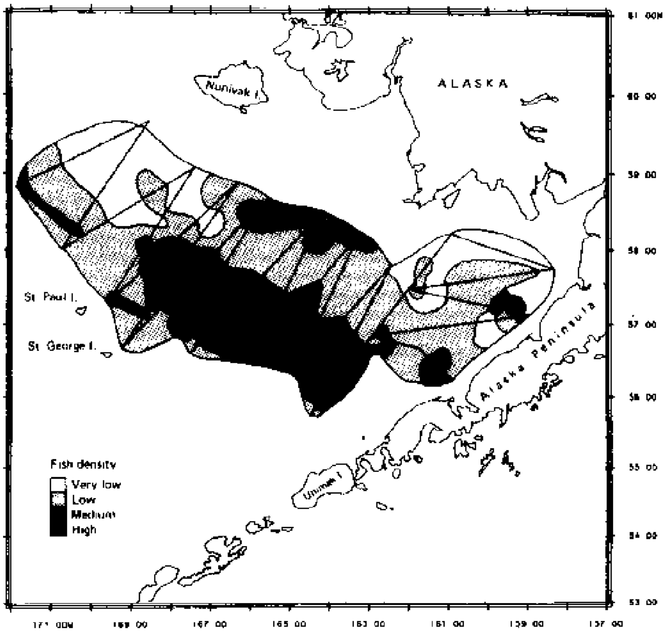
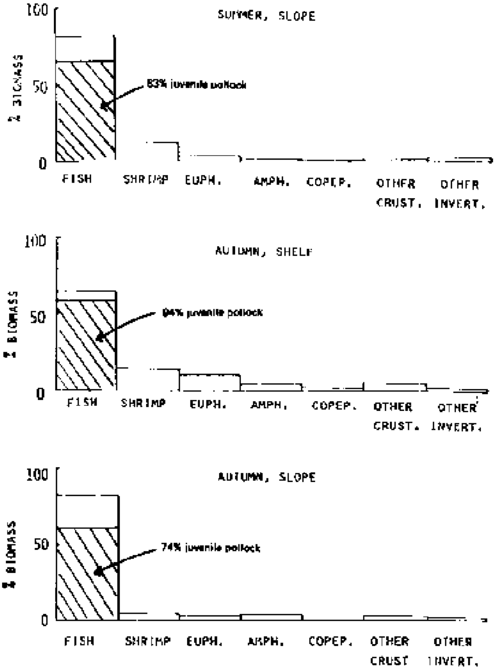


Figure 17. Distribution of pollock larvae in June 1982 (Source: Fadeyev et al. 1983) and juveniles in August 1982 (Source: J. Traynor, NWAFC).

Figure 18. The prey composition of pollock stomachs by percent biomass in two areas and two seasons, 1981.

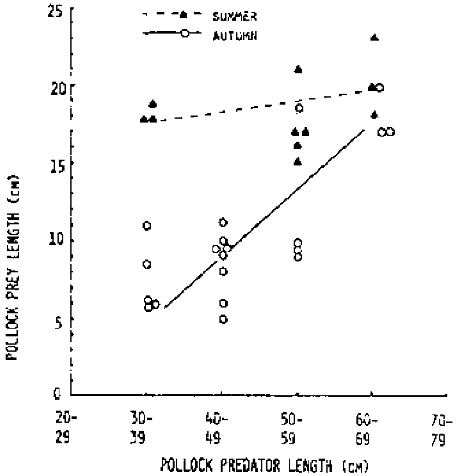


size and a longer duration of the initial survival period using the yolk reserves. If this is the case for pollock, then the larger larvae of the outer shelf might be more capable of a) surviving a period of northerly transport during the yolk-sac stage, and b) feeding on the larger potential prey items found in the outer shelf domain. However, the longer duration of the yolk-sac stage prolongs a period of life which may be more vulnerable to predation (Hunter 1981).

On the other hand, Walline (1982) and others have observed relatively uniform larval growth rates over a variety of environmental conditions as well as long periods of time during which pollock hatched and survived first feeding. A.J. Paul of the University of Alaska (1982 PROBES report in press) has found that larval pollock in laboratory conditions can satisfy their basal metabolic requirements at the time of first feeding even at low, environmentally realistic, food densities. These studies suggest that food supplies available to larval pollock in the EBS may not be limiting subsequent recruitment. This led Walline (1983) to speculate that predation must be responsible for the reduction in numbers of larvae or juveniles and must be the most important factor in controlling year class strength.

Although pollock are fed upon by a wide variety of species, cannibalism has been singled out by many (Laevastu and Favorite 1981, Smith 1981, Knechtel 1983) as being one of the most important mechanisms of predation on juvenile pollock. Beginning in the summer of 1981, we have been collecting stomachs of adult pollock using both the NWAFC Bering Sea surveys and the foreign fisheries observer

Figure 19. The cannabalistic relationship between prey pollock length and predator pollock length during two seasons, 1981.



program to test this hypothesis. In 1981 heavy cannibalism (on a percent weight basis) was found to occur in both summer and autumn (Fig. 18). However, distinct differences occurred in the size of pollock found as prey between summer and autumn 1981 (Fig. 19). In the summer, all juvenile pollock found in adult stomachs were in the size range of 14-23 cm, which corresponds to one year old fish, and no larvae were found. In the autumn, 5-10 cm pollock appeared in the stomachs; this is the size range of 0-age fish. This indicates that 0-age pollock may not be vulnerable to cannibalism while planktonic (during their first summer). However, when settling out of the plankton in late summer and early autumn (at 4-5 cm), they may become vulnerable to predation by adults. Because of the size difference between 0 and 1 year olds, the numerical impact of cannibalism on 0-age fish must be far greater.

It is our feeling that cannibalism could be a very important mechanism affecting the abundances of year classes of pollock in the EBS when juveniles and adults spatially overlap. Under certain environmental conditions (cold years), it appears that adults remain over the outer shelf and slope, whereas juveniles within the size range of potential prey for adults may not be so restricted in their distribution (Figs. 5 and 20). Examining the distribution of catches in the Japanese trawl fishery in June in relation to bottom temperature (Fig. 21), one sees that adult (exploitable) pollock apparently avoid the cold, middle shelf domain water mass in preference to the warmer water over the outer continental shelf and slope. Resource surveys show the same trends for adult pollock. In contrast, small fish less than 20 cm. (ages 0 and 1) are commonly found within and inshore of the cold water mass. (Fig. 5).

Even when adults and juveniles overlap spatially they have to overlap in their vertical distribution in the water column in order for cannibalism to occur. Figure 21 shows echograms of the vertical distribution of age-0 pollock along with the corresponding temperature profiles for two locations in the EBS in August 1982 (J. Traynor, unpublished data). In this case, when the water column was

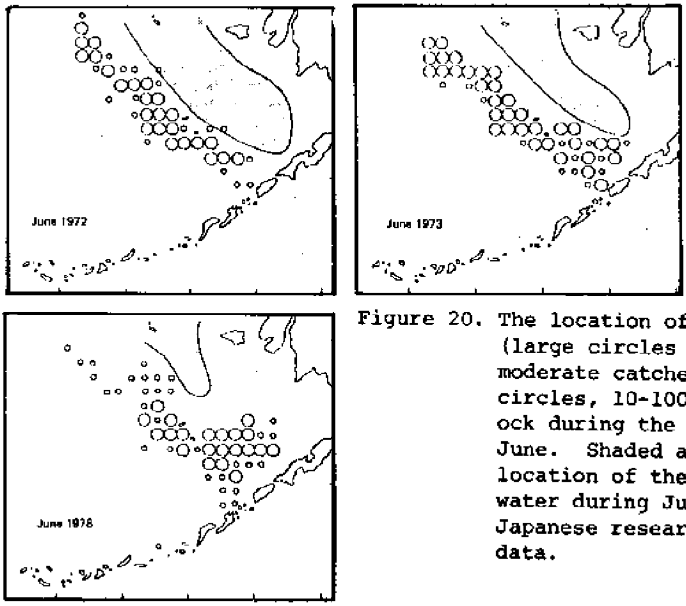


Figure 20. The location of large (large circles 1000t) and moderate catches (small circles, 10-1000t) of pollock during the month of June. Shaded area is the location of the 2°C bottom water during June from Japanese research survey data.

stratified, the juvenile pollock remained above the thermocline, whereas they were distributed throughout the water column when the latter showed no vertical density structure. We hypothesize that the longer the age 0 pollock occupy areas with stratified water, the longer they stay in the upper water column where they are less vulnerable to cannibalism and may grow into a size range less vulnerable to other forms of predation. So perhaps years when the middle shelf water column remains stratified into the autumn, and larvae are located there, large year classes of pollock are more likely to be produced. We throw this rash speculation out to our oceanographic colleagues for possible consideration.

Summary

This paper is an attempt to discuss the state of knowledge and provide some speculation on causes of fluctuations in recruitment of Pacific whiting off the coast of Washington, Oregon, and California and walleye pollock in the eastern Bering Sea. Naturally there is a heavy emphasis on our own work. If we have omitted the work and views of others, we hope that this will stimulate subsequent presentations and debate. Perhaps the most important concept that arises from this presentation is an awareness of different oceanic regimes and their potential impacts on the behavior of apparent analogues (i.e. the dominant gadoids) within each system. We believe we have demonstrated that the intuition one develops about the dynamics of fishery production in one system cannot necessarily be carried over into another system. The California Current and the EBS ecosystems are "oceans apart" in terms of environmental

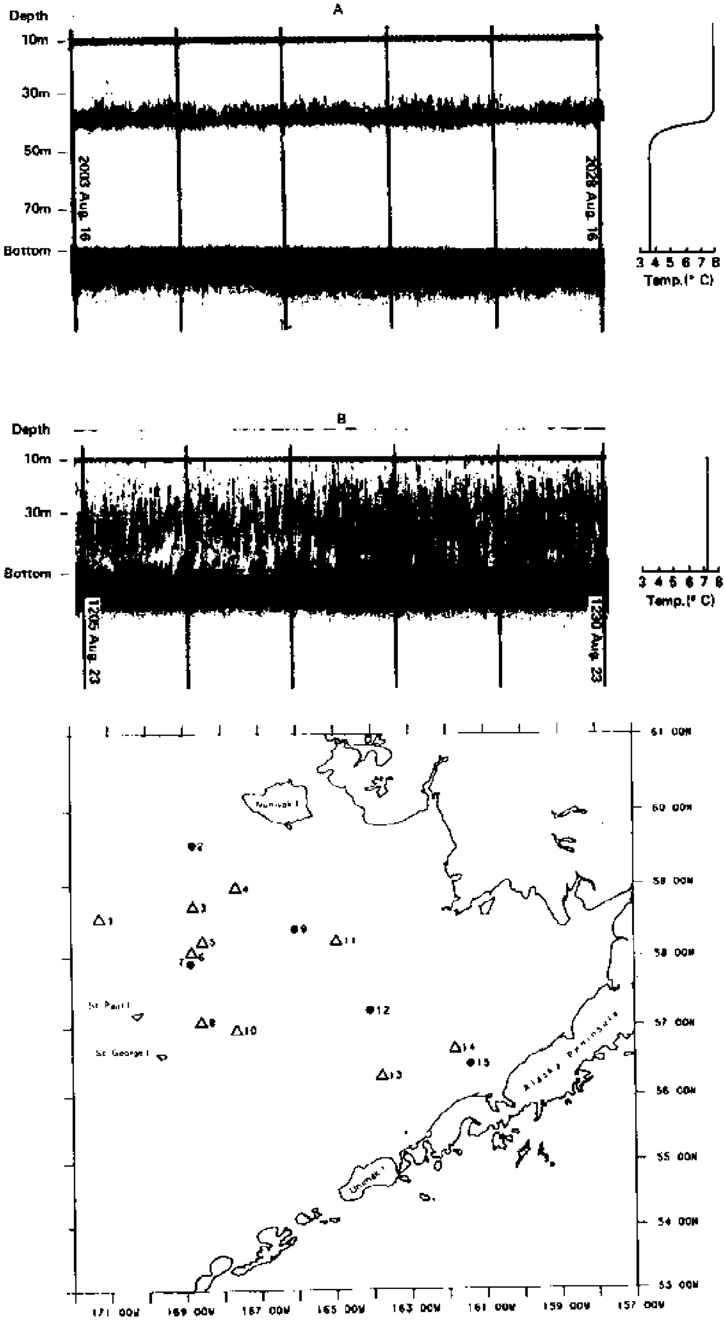


Figure 21. Echograms of juvenile fish sign, along with water temperature profiles, A) prior to Haul 10, and B) prior to Haul 11, Chapman Cruise 82-4, and location of trawl stations. (Source: J. Traynor, NWAFC)

effects on recruitment of fish. In fact, if one compares the reproductive and early life history dynamics of pollock in the EBS and Gulf of Alaska, one again finds great differences (Walline 1982). In all three areas (U.S. West Coast, Gulf of Alaska, eastern Bering Sea), these dominant gadoids have adapted their behavior to the dynamics of the physical system. It is, therefore, only through a thorough understanding of the physical dynamics that fisheries biologists and managers can hope to improve their ability to assess and manage these valuable fish resources. However, oceanography alone, for that matter fisheries biology alone or ecosystem modeling alone, cannot do the job. What is required is a synergy of research which produces an understanding far exceeding that gained by individual scientists operating independently.

Fishery management requires the expertise of a broad range of people: oceanographers, ecologists, economists, modelers and resource managers to name but a few. Identification of successful management systems is dependent on our ability to bind the inputs from all sources into a meaningful whole. Favorite and Laevastu (1981) make this case in their review of Bering Sea fisheries oceanography (by the way how many of the questions posed in their paper have been addressed?) when they say, "because this [understanding ecosystem conditions and processes] requires extensive accountability of species interactions and environmental effects, we are at a loss to handle the multiplicity of factors involved without formulation of some sort of modeling or simulation techniques." We agree. Mathematical models are perhaps the best way to summarize, synthesize, and integrate much of what we do know about ecosystem dynamics and to investigate, in terms of ecosystem behavior, the consequences of reasonable hypotheses about little known processes. By comparing results of models with real data, we are able to test our understanding of major processes, and to discover what we do and do not know. Models also provide a marvelous focus for communication between people from varied backgrounds. Bakun and Parrish (1980) put environmental inputs to fishery population models into a nice perspective:

> Dynamic modelling is undoubtedly useful in clarifying conceptual understanding. Mathematical models provide the necessary "bookkeeping" to test whether a given set of assumptions can lead to results which resemble reality. However they cannot generate, nor are they a substitute for, observational data. Their results can only reflect the information and assumptions which are put into their formulation. Mathematics cannot, for example, by itself inform us how far offshore larvae must be transported for their contribution to eventual recruitment to be seriously impaired.

Finally, what we find particularly challenging is the process of developing an understanding of the interaction between the basically deterministic physical system and what we believe to be a fundamentally stochastic biological system. Now, whether the stochastic nature of a biological system is due to our uncertainty about the behavior of a complex system or due to inherently uncertain responses of the system itself is a matter of speculation. We feel both are true. What we need to come to grips with is how to live with, and deal with, the resultant fundamental variability in fisheries oceanographic systems. Hilborn (1982) divides this into three steps. First, we must describe and classify the uncertainties we face. (Hilborn breaks the spectrum into three segments: frequently observed "noise", rarely observed "uncertain states of nature", and never before observed "surprises"). Second, we must identify those who are affected by uncertainty. And third, we must develop strategies and tactics for dealing with each type of uncertainty we face. As Hilborn (1982) quotes Ralph Yorgue, "Recognizing that surprise exists is only the first step, developing strategies to deal with it is the challenge."

Acknowledgments

We wish to acknowledge the special contribution of Dr. Lewis Incze, Northwest and Alaska Fisheries Center, to this paper. Not only has he reviewed drafts, but he has openly shared his ideas concerning the dynamics of the eastern Bering Sea ecosystem. We also wish to thank C. M. Lynde for his helpful review of the paper.

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Commentary

Interannual Variability of the Environment And Gadoid Fisheries of the Gulf of Alaska And Eastern Bering Sea

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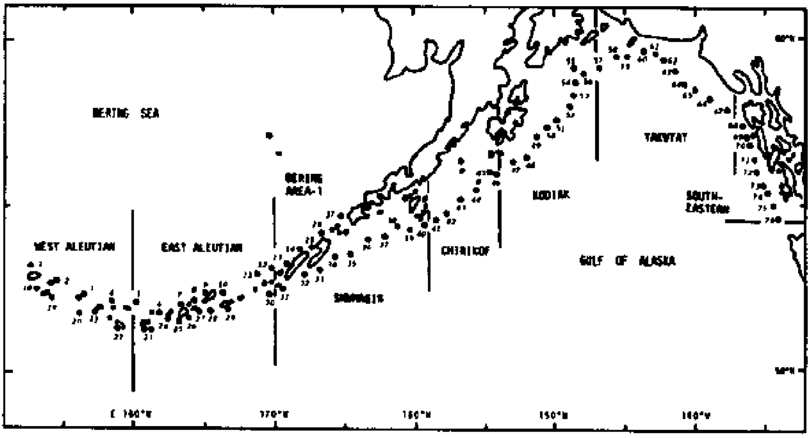
Since the previous review by Francis and Bailey has focused on Pacific hake and walleye pollock, the task that has befallen me is twofold: first, to supplement their excellent review with some information on interannual variability in Pacific cod (Gadus macrocephalus) stocks, and second, to comment on the status of research into the gadids as a whole. In addressing the latter point, we are interested primarily in that research that pertains to interannual variability in the environment, and its relation to fluctuations in recruitment.

An Overview of the Pacific Cod Resource and Its Biology

Although the geographic range of Pacific cod extends from Santa Monica Bay, California (about 34°N) to the northern Yellow Sea off Korea (about 39°N), it is only taken in commercial quantities from northern Washington to Korea. The magnitude of commercial catches in 1968-77 suggests that cod may be more abundant in the eastern Bering Sea than in other regions of its range (Bakkala et al. 1981). Catch rates from setline surveys (Fig. 1). substantiate this, but also suggest that stocks are plentiful throughout the northern Gulf of Alaska. Pacific cod landings (Fig. 2) show significant interannual variability, with 1970-1980 coefficients of variation of .24 in the eastern Bering Sea and Aleutians, .41 in Hecate Strait, .38 in Queen Charlotte Sound, and .48 off Vancouver Island. The Gulf of Alaska fishery has developed only recently, and interannual variability is difficult to assess.

Evidence from trawl surveys indicates that stock size in the eastern Bering Sea has fluctuated far more than the catch data suggest, and that a 7- to 10-fold increase in stock biomass occurred between 1975-77 and 1979 (Wespestad et al. 1982). This increase was primarily due to the recruitment of a single large cohort, the 1977 year class, to the stock.

Pacific cod undertake seasonal bathymetric migrations of about 50 m in some parts of their range (Fig. 3), but latitudinal migrations appear to be limited. Tagging studies carried out in



Depth (m)	Bering Area 1		West Aleutian		East Aleutian		Shumagin		Chirikof		Kodiak		Yakutat		South-eastern	
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
100-200	19.51	22.54	8.41	7.43	6.59	12.84	11.73	14.65	15.52	13.92	10.03	10.89	7.08	4.59	1.07	--
200-300	15.92	12.63	3.55	2.49	3.38	7.52	2.54	3.33	2.26	4.28	6.69	3.14	2.68	2.10	1.17	1.56
300-400	0.98	3.44	0.15	0.09	0.50	1.17	0.01	0.01	0.01	0.01	0.09	0.14	0.03	0.02	0.06	0.12
400-500	0.00	0.00	0.00	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
500-600	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10

Fig. 1. Survey positions of joint Japan-U.S. longline survey in 1981, and mean catch rates (number of fish caught per one hachi longline unit) for Pacific cod during 1981 and 1982 surveys (from Sasaki et al., 1982).

British Columbia and Washington have shown that most recaptures (88-99%) usually come from the same PMFC statistical area where they were originally tagged (Westrheim 1982).

Although cod grow rapidly and attain a relatively large size, few fish appear to live longer than 10 years in the eastern Bering Sea and Gulf of Alaska, or longer than 7 years in Hecate Strait. In 1980, commercial catches were dominated by 3- to 4-year-olds in the eastern Bering Sea and Gulf of Alaska (Foucher et al. 1981).

Pacific cod mature at an age of 2-3 years off Vancouver Island, and at 3-4 years in Hecate Strait (Westrheim 1977). Spawning occurs in January-March in the northern Bering Sea (Svetovidov 1949), March in Hecate Strait, and February-March off Vancouver Island (Westrheim 1977). The eggs are demersal, euryhaline, euryoxic and stenothermal, and the temperature range associated with reasonable egg viability and incubating success is estimated to extend from about 2.5°-8.5°C (Alderdice and Forrester 1970).

Larvae are only infrequently encountered during ichthyoplankton surveys in the Bering Sea and Gulf of Alaska, although

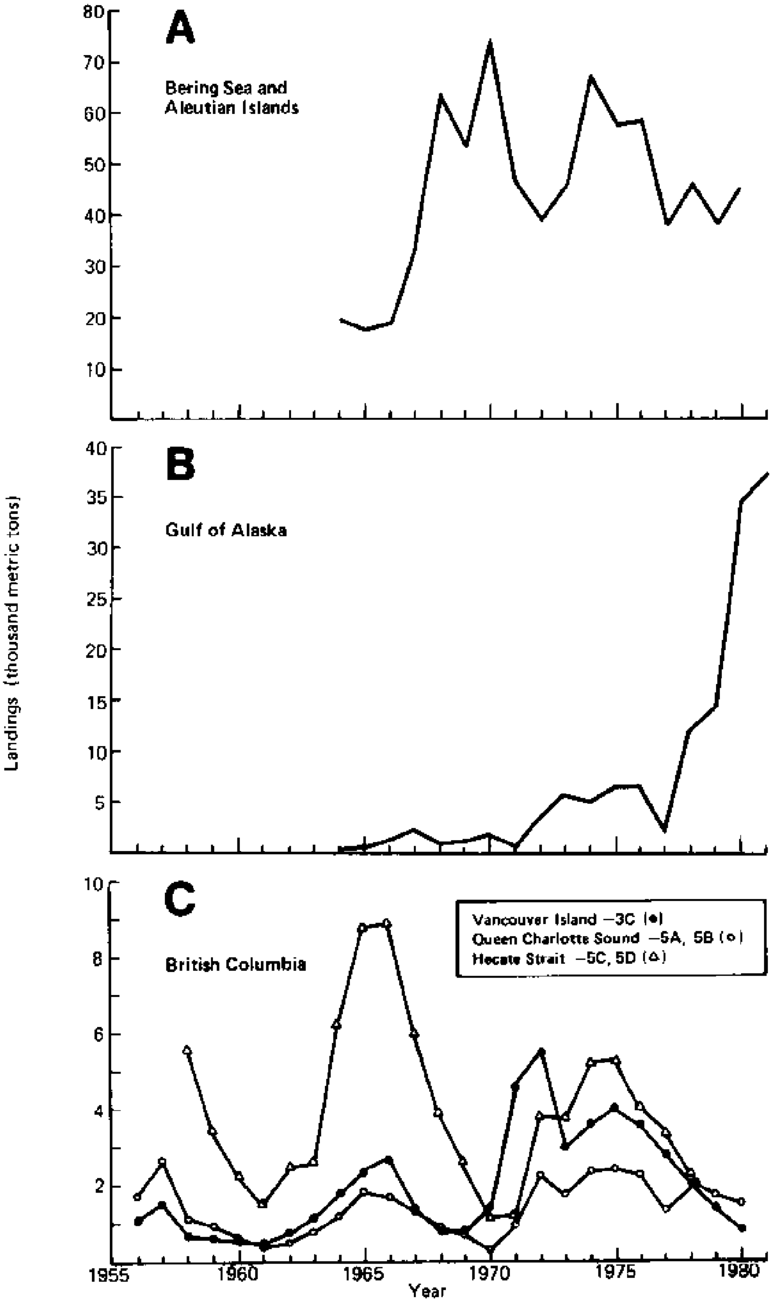


Fig. 2. Pacific cod landings from (A) the eastern Bering Sea and Aleutian Islands (West of 170°W), (B) the Gulf of Alaska (INPFC Shumagin-Southeastern areas) and (C) the British Columbia coast (N. Cummings, NMFS, unpublished).

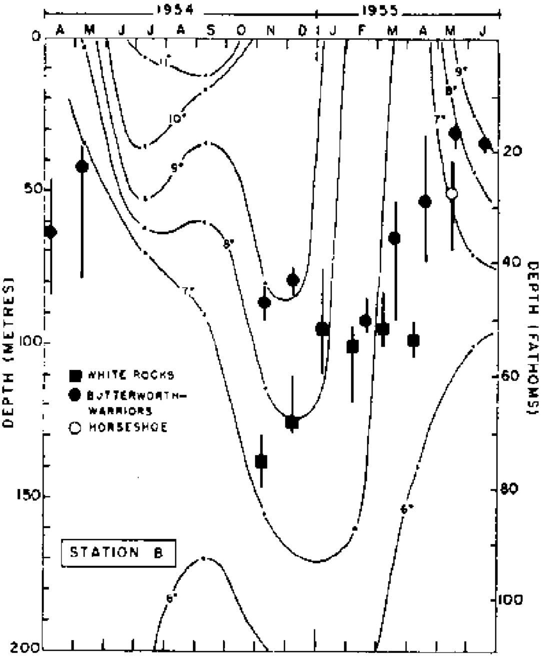


Fig. 3. The seasonal cycle of water temperature at Station B and its relation to the monthly depth distribution of Canadian commercial catches of cod from the Butterworth-Warriors, White Rocks, and Horseshoe grounds of Hecate Strait during 1954-55 (Ketchen 1961).

significant numbers of larvae have been captured with a demersal sled in Puget Sound (G. Walters, NMFS, pers. communication). Juveniles 6-10 cm long have been found in shallow bays (20 m and less) in the Gulf of Alaska and Puget Sound. Trawl survey data from the eastern Bering Sea suggest a gradual dispersal of juvenile cod offshore as the fish attain progressively larger sizes (A. Shimada, NMFS, pers. communication). Juveniles recruit to the adult stock by 12 months of age in Puget Sound (Fig. 4).

Environmental Variability and Its Relation to Gadoid Recruitment

Successful prediction of recruitment using environmental data generally entails research in three major areas: hypothesis development, experiment and correlation, and model development (Table 1). The process is not a linear one, and work in all three areas is usually carried out simultaneously, results from the different areas feeding into one another in a synergistic manner. How does research on northeast Pacific gadids fit into this scheme?

Evaluation of life history strategy is well advanced for the major gadid stocks, and the distribution of walleye pollock,

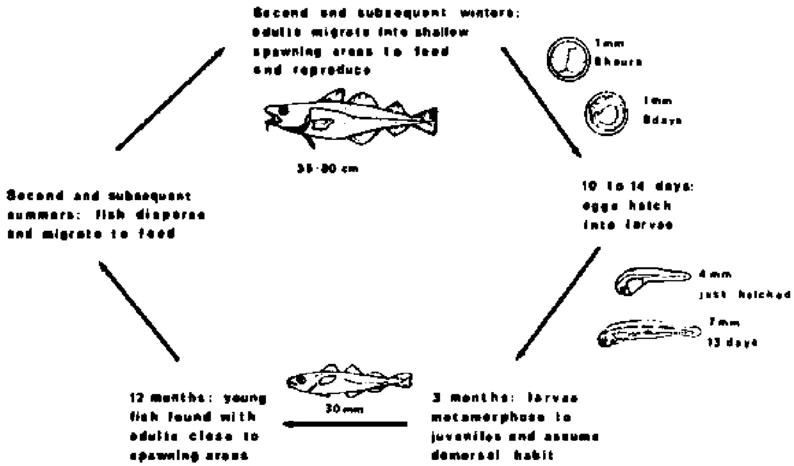


Fig. 4. Generalized life history of Pacific cod in the inside waters of Washington (Karp 1982).

Table 1. Major areas of research in assessing the relation between environmental variability and recruitment.

HYPOTHESIS DEVELOPMENT

- EVALUATION OF LIFE HISTORY STRATEGY AND BIOTIC/ABIOTIC MILIEU
  - Geographic Distribution of Eggs, Larvae, Juveniles, Adults
  - Reproductive Biology
  - Predators, Prey Items and Competitors
  - Oceanographic Environment in Relation to the Above
- DEVELOPMENT OF HYPOTHESES ON DETERMINANTS OF RECRUITMENT

EXPERIMENTATION AND CORRELATION

- LABORATORY, MICROCOSM AND MESOCOSM STUDIES OF PREDATION, STARVATION, COMPETITION, TEMPERATURE SENSITIVITIES
- STATISTICAL CORRELATION BETWEEN ABUNDANCE (OR RECRUITMENT) AND TIME SERIES REFLECTING CHANGES IN BIOTIC/ABIOTIC MILIEU
- CORRELATION BETWEEN GEOGRAPHIC TRENDS IN LIFE HISTORY STRATEGY (AGE AT MATURITY, FECUNDITY, GROWTH, LONGEVITY, ETC.) AND CHANGES IN BIOTIC/ABIOTIC MILIEU
- ATTEMPTS TO SEGREGATE THE "KEY FACTORS" IN CASES WHERE SEVERAL VARIABLES ARE INTERCORRELATED

MODEL DEVELOPMENT

- EXPLICIT FORMULATION OF APPROPRIATE RECRUITMENT MODEL
- PREDICTION

Pacific whiting and Pacific cod have been mapped out, at least in a general sense, for the entire life history. More work on the ecology of the juvenile stages of Pacific cod and walleye pollock would be desirable, however, particularly in the latter species where Francis and Bailey suggest that predation processes during the juvenile stage may play a major role in shaping year class strength. The importance of the juvenile stage was also noted by Lett et al. (1975), who concluded that the transition from the larval to the juvenile stage was the most important step in the recruitment process for Atlantic cod in the Gulf of St. Lawrence.

The demersal eggs of Pacific cod are unique, yet little exists in the literature in the way of documenting spawning ground selection or the location of newly hatched larvae in the water column. Demersal spawning by Pacific cod shows a distinct departure from the reproductive tactics employed by Atlantic cod, walleye pollock, or Pacific hake, and offers an intriguing area of research into the adaptive value of alternative life history strategies. Examination of differences in life history strategies across environmental gradients have proven useful in gaining insights into the relative importance of environmental variables in species such as American shad (Leggett and Carscadden 1978) and Atlantic salmon (Schaffer and Elson 1975), yet appear to have found little or no application in the case of the gadids.

Reproductive biology has not received much attention in the Pacific gadids, and surprisingly little fecundity work has been undertaken for either cod or pollock in the eastern Bering Sea and northern Gulf of Alaska, or for Pacific whiting in the California current region. No studies of interannual variability in fecundity or reproductive effort have ever been carried out for these species.

As summarized by Francis and Bailey, predators, prey items and competing species have been identified in a qualitative way for Pacific whiting and walleye pollock. The task of identifying the more important of these relationships, and quantifying them is far from complete, however. An extensive study into the food habits of Pacific cod in the eastern Bering Sea was initiated in 1981, stimulated in part by concern by king crab fishermen that the burgeoning stocks of cod could be adversely impacting their livelihood.

In the case of Pacific whiting, those oceanographic effects that are most important in influencing recruitment have been identified by Bailey (1981A), and his multiple regression model indicated that upwelling index at 36°N, sea surface temperature in the Los Angeles Bight and spawning biomass accounted for 72% of the variation observed in his recruitment index. While the process of hypothesis development and testing is in a far more advanced state for this species than it is in the other gadids, it is notable that the identification of the "key factors" involved is still far from complete. Bailey found recruitment to be negatively correlated with upwelling and positively correlated with surface temperature in the Los Angeles Bight. Bailey (1981B) provided additional data on larval distribution and growth rates which indicated that Ekman transport associated with upwelling carried whiting larvae into offshore regions where feeding conditions were poor, so that the underlying mechanisms are clear. The correlation between sea surface temperature and year class strength is more difficult to explain, however.

Pacific whiting spawn further north in years when sea surface temperatures are high, and the positive correlation obtained could be explained on the basis of either enhanced spawning or larval feeding conditions in these areas, or as Bailey and Francis suggest, by reduced losses to predation in warm years when development is more rapid. In addition, we would not expect sea surface temperature and upwelling to be independent of each other, but negatively correlated. The relationship between upwelling, sea surface temperature, spawning location, larval feeding conditions, and predation is clearly an area deserving of further study, using laboratory studies or microcosm studies and additional statistical analyses to identify the "key factors" that are operating.

Model development for walleye pollock has advanced to the hypothesis stage, where refugia from cannibalism have been proposed as a major factor in determining pollock recruitment. The testing of this intriguing hypothesis lies ahead, and should provide the basis for some exciting field and laboratory work in the future.

In the case of Pacific cod, a review of the literature failed to reveal any advances in model development beyond the early explorations of the relation between air temperatures and catch rates carried out by Ketchen (1956). This is remarkable in a species that undergoes the wide extremes in recruitment that have characterized the eastern Bering Sea stock in recent years.

Formulation of improved predictive models would seem to provide ample opportunities for research in the gadids, and should enhance both the quality of management advice and the viability of the fishing industry in general. The Pacific gadids are relatively short-lived, with commercial catches usually being based on eight age groups in the case of Pacific whiting, four for pollock, and three for cod. Interannual variability in gadid recruitment is substantial, with coefficients of variation on the order of 124% for Pacific whiting and 44% for pollock. Given the small number of age groups in the fishery, the impact of variability in recruitment rapidly cascades up the food chain to mankind, and can have a dramatic effect on fishing conditions, commercial landings, and markets for fishery products.

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Potential for the Study of Environmental Effects on Interannual Variability In Flatfish

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International Pacific Halibut Commission

There are approximately fifteen species of flatfish (family Pleuronectidae) in the Bering Sea and the Gulf of Alaska, but for most species data are insufficient to properly study environmental effects upon their life histories at the present time. Yellowfin sole (Limanda aspera) and Pacific halibut (Hippoglossus stenolepis) are two exceptions; these species have extensive data records and qualify as candidates for a preliminary investigation of the environmental effects on year-class strength and other natural history phenomena. Several other flatfish species have short time-series of data and have ongoing data collection programs that may qualify them for future research. For Greenland turbot (Reinhardtius hippoglossoides) and arrowtooth flounder (Atheresthes stomias) there is limited data on catches since 1960, survey data from the Bering Sea and the Aleutian Islands since 1970, and age structure data since 1979. Survey data and age structure data on rock sole (Lepidopsetta bilineata), flathead sole (Hippoglossoides elassodon) and Alaska plaice (Pleuronectes quadrituberculatus) are available from the Bering Sea and Aleutian Islands since the early 1970's and limited catch data are recorded from foreign fisheries back to 1963. While some indication of environmental affect may be present in these other flatfish species, analysis of the inadequate data bases will only increase the probability of finding spurious correlations. During the initial phase of this research, effort should be directed at only those species with long-term data series. Therefore, it is my opinion that only yellowfin sole and Pacific halibut should be examined at the present time.

This report describes the available data on yellowfin sole and Pacific halibut and discusses the potential for environmentally caused perturbations. Possible mechanisms are postulated and several analytic approaches are described.

Data Description

Yellowfin sole

Yellowfin sole is the dominant flounder species in the Bering Sea, but a minor component of the flounder group in the Gulf of Alaska

(Bakkala 1981). Intensive fishing on yellowfin sole by foreign fleets began in 1959 and continues to the present time. There is considerable catch-effort data from the fishery and survey data from the Japanese pair-trawl survey and the Northwest and Alaska Fisheries Center (NWAFC) surveys. These data are summarized by 1° longitude by ½° latitude statistical blocks and by months in which yellowfin sole made up 50% or more of the catch. There are year-class strength estimates from cohort analysis from 1959 to the present. Figure 1 shows the relative year-class strengths from 1973 to 1981. The apparent variability in year-class strength may well be related to environmental effects on early life survival.

Considerable mark-recapture data is available from which annual movements have been described. These data compliment the NWAFC trawl survey data to give an accurate assessment of seasonal movements. Figure 2 depicts the movements in the eastern Bering Sea from the mark-recapture data. Age-length data are available and growth rates have been estimated.

Pacific halibut

Data collection on Pacific halibut began in the mid-1920's and has continued without interruption to the present time. An extensive record of catch and effort data by 60-mile regions of the coastline from California to the Bering Sea is available. Age structure data from otoliths sampled from the commercial catch is complete from 1935 to the present. Approximately 300,000 halibut have been tagged and roughly 31,000 have been recovered over a 50-year period. Migration rates have been estimated for various time periods from 1930 to the present. Juvenile survey data in the eastern Bering Sea and Gulf of Alaska is complete from 1961 to the present. The data consists of number, age, and sex of halibut per standard haul.

These data have been used to estimate biomass, catchability coefficients, growth rates, and annual surplus production by year and region.

A gap exists in the biological knowledge of Pacific halibut in the early life stages, particularly between the pelagic larval stage and 0-age juveniles four or five months of age. The only data available are from an egg and larvae survey in the Gulf of Alaska conducted from 1928 to 1934. Spatial and depth distribution of eggs and larvae were recorded and a theory regarding egg and larvae drift was developed. The data are highly variable and short-term but are very important to the understanding of the life history of halibut. No data on the distribution and density of juveniles during the first four or five months of benthic existence have ever been collected. It may be that this is a very critical life stanza for Pacific halibut for determining year-class survival. If environmental effects on production of halibut are to be fully understood, research must include a study of the first six months of life.

Possible Environmental Relationships

Yellowfin sole

In the eastern Bering Sea large annual fluctuations in oceanogra-

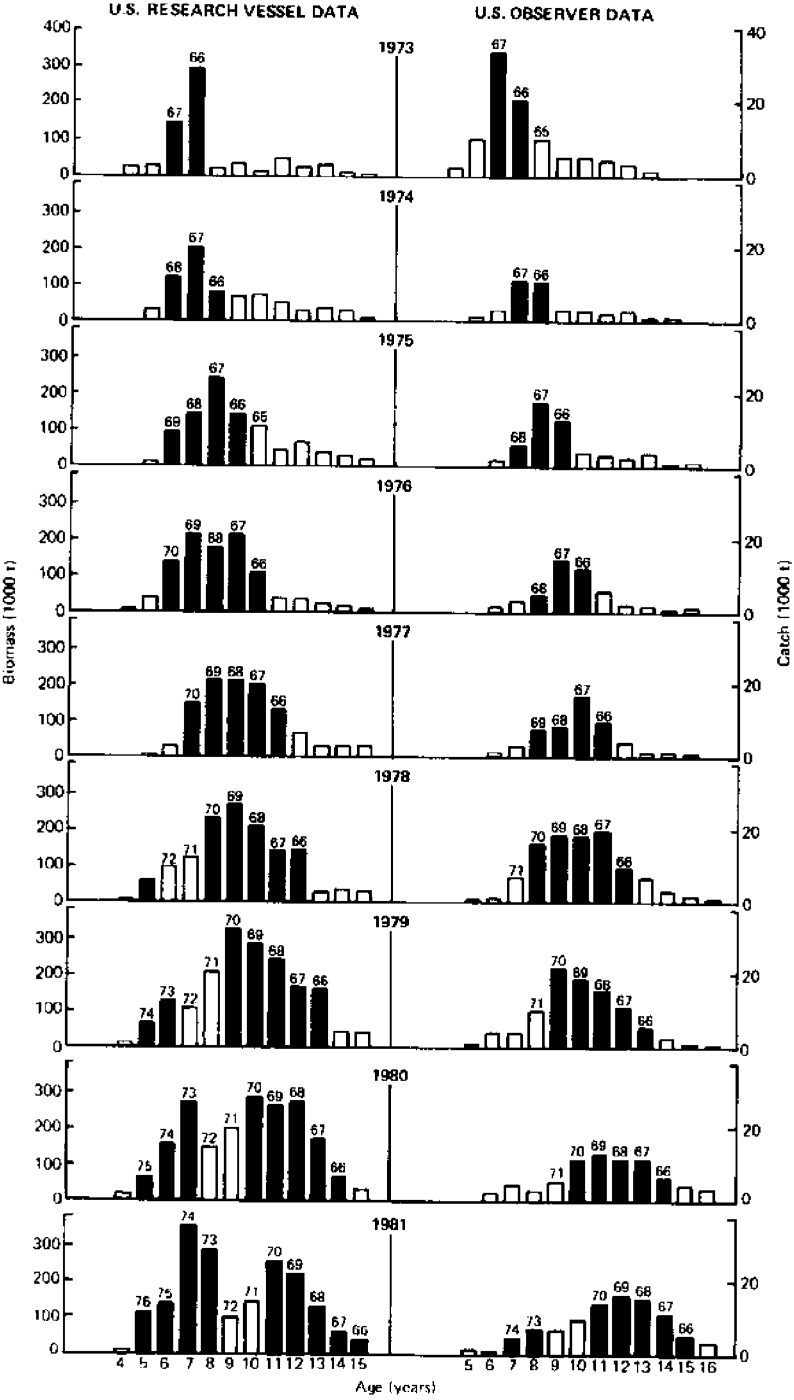

Figure 1. Estimated age distribution of yellowfin sole from the eastern Bering Sea (from Bakkala and Wepestad 1983).

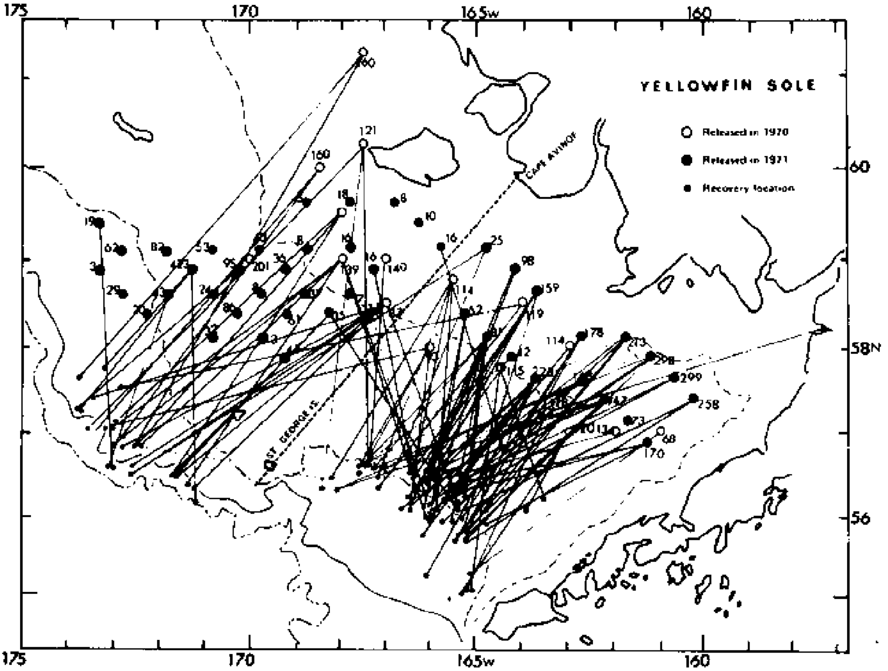

Figure 2. Release and recovery locations of yellowfin sole tagged by Japanese vessels in 1970 and 1971 and recovered by commercial fishing vessels (from Wakabayashi et al. 1977).

phic conditions occur. These fluctuations may have an effect on distribution, year-class strength, growth, and biomass. Climatic conditions in the Bering Sea seem to vary in multi-year cycles rather than individual year fluctuations. Typical of this cyclic phenomenon is temperature. It has been shown that temperature increased from 1961-1967, decreased from 1968-1976, and again increased from 1977-1982. Maeda (1977) has shown a correlation between predominant year-classes and years of relatively high temperature. There appears to be an opportunity here for considerable research.

Yellowfin sole migrate annually over considerable distances. They are concentrated along the Bering Sea edge in winter in relation to bottom temperature and the ice edge. They migrate onto the Bering Sea shelf as water temperatures increase. Figure 2 shows the movement of yellowfin sole as indicated by the release and recovery of tagged individuals. The timing and extent of migration appears to be strongly linked to the ice edge and bottom temperature.

After migration onto the shelf, yellowfin sole spawn from July to September. Environmental condition might affect the early life history stages during that time and varying mortality on eggs and larvae may determine to a considerable degree the resulting year-class strength. The data on yellowfin sole are not as extensive for the Gulf of Alaska (Rose and Brown 1982), and should not be considered at this time.

Pacific halibut
The long-time series of various kinds of fisheries and biological information make Pacific halibut a worthy candidate for the investigation of environmental effects. There is a history of controversy over the relative effects of the environment and overfishing on Pacific halibut. The Thompson-Burkenroad debate generated considerable interest in this problem. The more recent view of halibut population dynamics is that both fishing and environmental effects are expressed in a variety of ways. The staff of the International Pacific Halibut Commission is in the process of initiating research to attempt to explain how changes in the environment affect the many life history stages of halibut.

Pacific halibut spawn from December to February along the edge of the continental shelf over the whole range of the stock. Eggs and larvae drift in relatively deep water (100-900 meters) and are subject to the action of coastal currents (Thompson and VanCleve 1936). As the larvae develop they rise in the water column and drift inshore where they settle on the bottom as young adults 6-7 months after spawning. During the pelagic phase they drift north and westward in the Gulf of Alaska and are subjected to a variety of environmental conditions. The distribution of newly settled larvae is not known but may be a determining factor in year-class strength. If the currents transport larvae far offshore the larvae may be forced to settle on unsuitable habitat. Unfortunately, no biological information is available to investigate this phenomenon.

In response to this westward drift there is an eastward and southward migration of halibut in the Gulf in compensation for the egg and larval drift (Skud 1977). Fifty years of mark-recapture data have been analyzed by the Halibut Commission staff; migration rates have been estimated and an attempt will be made to determine if they are affected by environmental conditions such as cyclic changes in bottom temperature. In the past four years the relative density of halibut south of Frederick Sound in southeast Alaska has declined. At the same time, a warming trend in bottom temperature has occurred in the eastern Gulf of Alaska. Perhaps a change in migration rate due to changing oceanographic conditions is responsible for this unusual divergence in halibut distribution.

Growth rates of halibut have been recently estimated for each IPHC region and by five-year cohorts from 1920 to the present. Considerable differences in growth rate are observable over both area and time. A large increase in growth rate has occurred since the mid-1940's in all areas. An attempt to explain these differences is underway. The relationship with environmental change will be investigated, however, the situation is considerably confounded by migration. In addition, length-at-age data from the eastern Bering Sea is being analyzed to determine if bottom temperature is related to the growth during the first four years of life. It may be that temperature effects are indirect and affect halibut by changing the density of their prey species.

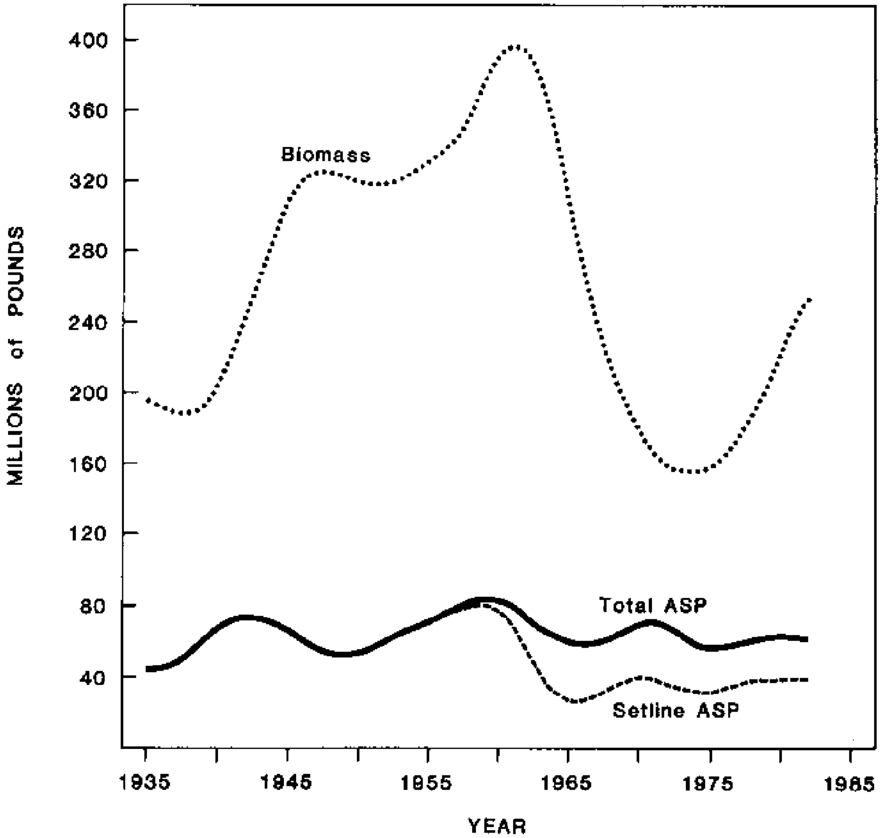

Figure 3. Smoothed estimates of total biomass and annual surplus production of Pacific halibut 1935-1982.

Estimates of numbers and biomass by age class are available from age structure models and from catch-per-unit-effort (CPUE) analysis from 1929 to the present. The total estimates are broken down by IPHC region. Total biomass and annual surplus production are presented in Fig. 3 and total biomass and numbers of 8-year-old recruits is presented in Fig. 4. Environmental effects on biomass and year-class strength are complicated by the wide variety of oceanographic situations occurring in different parts of the total range of Pacific halibut and by the substantial migration and large removals by commercial fishing.

Catchability coefficients have been estimated for each IPHC region from 1930 to the present using biomass estimates from age structure data and CPUE from the commercial fishery. Figure 5 shows a plot of catchability estimates over time. Environmental conditions may affect halibut directly or affect their prey species which results in changes in catchability. It is the opinion of the IPHC that catchability may be strongly affected by the ocean environment.

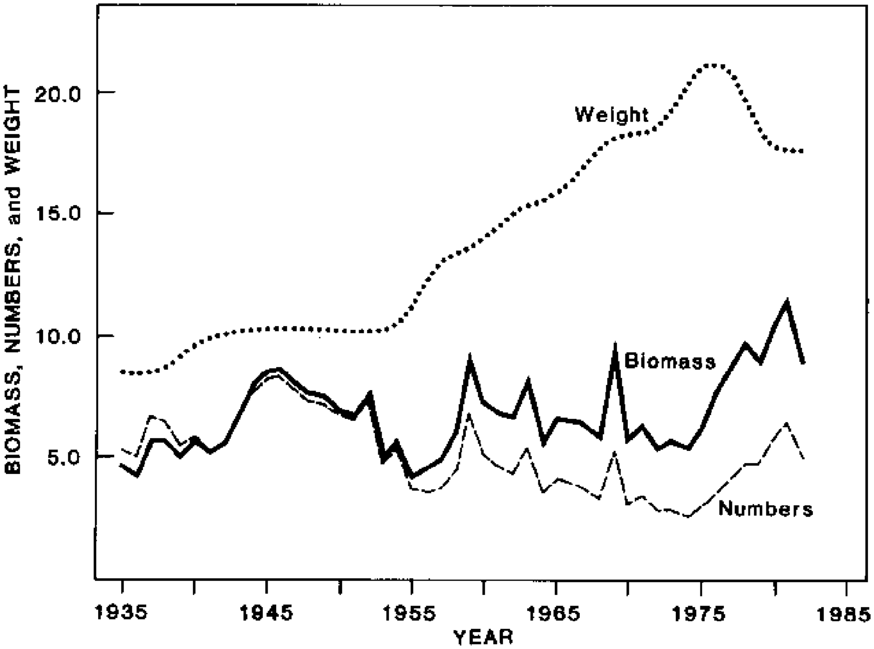

Figure 4. Estimated biomass, numbers, and average weight of 8-year old recruits 1935-1982. Weight in pounds; numbers in millions; and biomass in tens of millions of pounds.

The long time-series of data on Pacific halibut make this species ideal for the initial study of possible environmentally-induced changes in life processes. Hopefully, these studies will lead to new theories of the population dynamics of halibut and stimulate new research leading toward greater predictability of population change and, hence, more efficient management.

Analysis of Flatfish—Environmental Information

There are several approaches to the problem of determining relationships between biological and oceanographic information. One common approach may be termed "exploratory data analysis", and another entails proposing hypotheses based on biological knowledge and testing these hypotheses with previously collected information.

The first approach involves searching for correlations between environmental parameters and biological phenomena. The literature is fairly extensive in examples of this approach. Ketchen (1956) found a linear correlation between temperature and year-class strength in English sole off British Columbia. Kreuz et al. (1982) showed a correlation between growth and temperature for 2-year-old Dover sole and one-year-old English sole off the Oregon Coast. Whether there is cause and effect between these variables cannot be determined from their analyses. They have generated hypotheses for further scientific examination. Ketchen (1956)

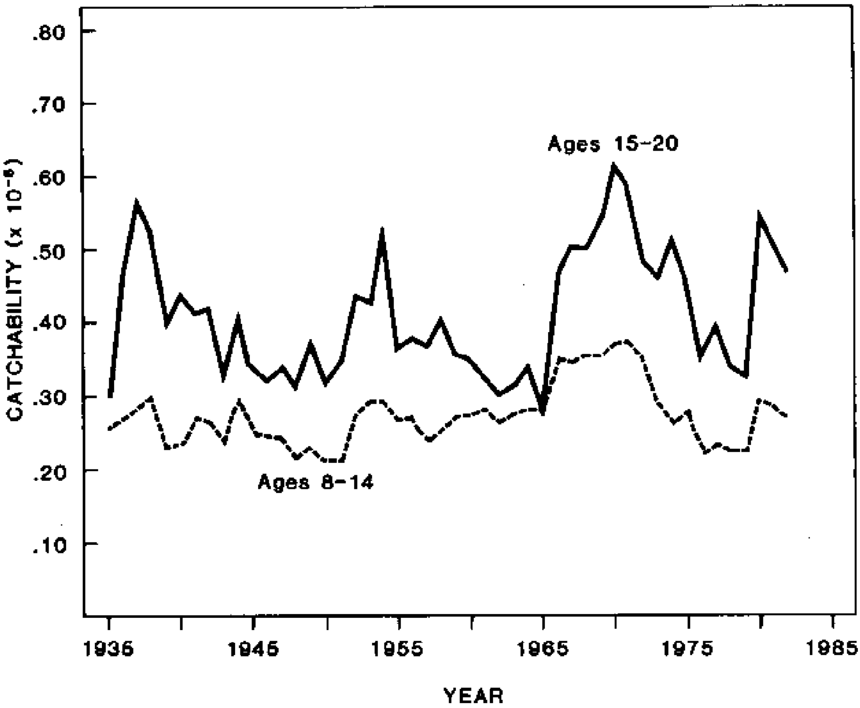

Figure 5. Estimated catchability coefficient for ages 8-14 and ages 15-20 for Pacific halibut 1935-1982.

states the problem succinctly, "The real test of the interdependence of two variables (brood strength and environmental factor) lies in the success with which the relationship enables prediction of future events." One of the major difficulties with the exploratory data analysis approach lies in the selection of data. For example, halibut caught for age-size determination in British Columbia may have migrated from the Bering Sea. It is not clear, therefore, what temperature data to use in trying to determine whether temperature and growth of Pacific halibut are correlated. A lot of "trial and error" in data selection is usually necessary and the probability of spurious correlation is very high. A good example of a spurious correlation can be seen in a report by Wickett (1975). Wickett regresses the halibut catch in IPHC Area 2 with surface salinity lagged 10 years at Langara Island. The analysis uses catches from 1950-1974. During that period of time the catches were constant from 1950-1962 and then declined from 1963-1974. Over the same time period salinity declined approximately 0.20°/₀₀. A negative slope of catch regressed on salinity was estimated (R^2=0.56). The claim is made that the Halibut Commission blamed the decline on early overfishing, but that the simple analysis in the report indicates about 50% of the variance was associated with a period of decline in environmental quality. Since 1975, however, the catches have declined slightly but the salinity increased back to 1950 levels. The important point is that catches are under con-

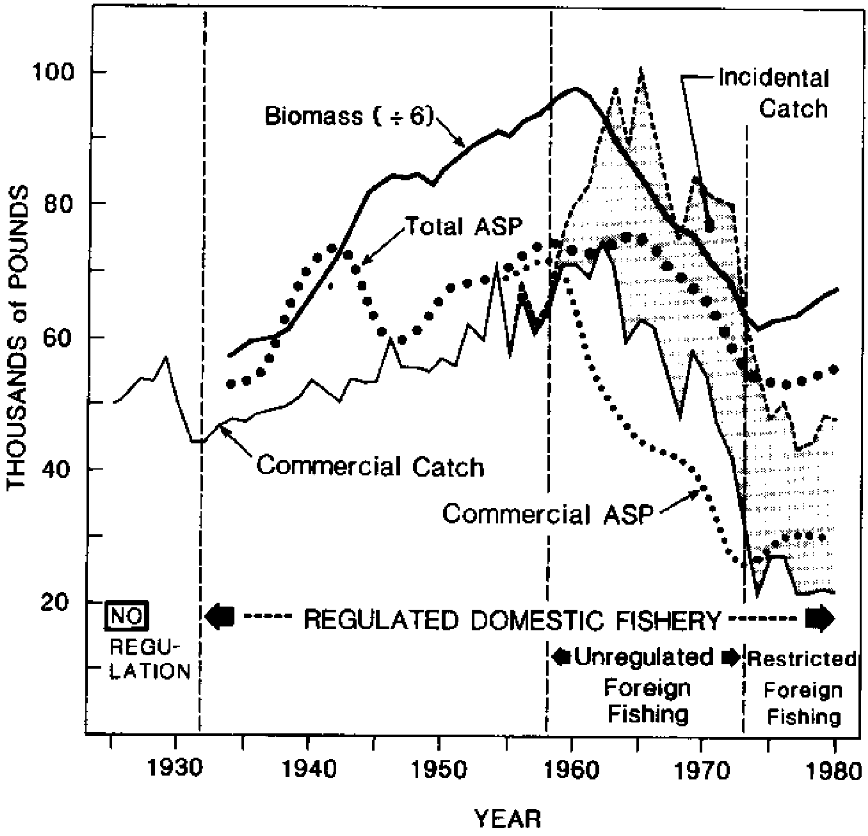

Figure 6. Estimated biomass, annual surplus production, and incidental catch of Pacific halibut 1925-1982.

trol of IPHC and were reduced by regulation and are not necessarily proportional to stock size. CPUE would have been a much better measure of stock density. In addition, salinity was measured at Langara Island, but most Area 2 fish spend their pre-recruit life in the Gulf of Alaska and the Bering Sea. It is also quite unclear what effect a reduction in surface salinity of 0.20°/∞ has on the environment of a major predator like halibut. A more reasonable hypothesis (Fig. 6) is that the huge incidental catches of juveniles in the Bering Sea and Gulf of Alaska by foreign fleets in the 1960's was the major cause of the decline in the stocks. Environmental fluctuations may also have affected stock abundance, but it is doubtful that they were of the magnitude which could account for the observed reduction in Area 2 stocks and even more doubtful that the minute change in surface salinity at Langara Island reflected environmental changes that affected Area 2 abundance.

A large number of authors place a great deal of emphasis on a "statistically significant" correlation coefficient (r) and on the proportion of the total sum of squares attributed to the model

(R^2) in linear model analysis. A significant r means there is a high probability the correlation coefficient ρ, for which r is an estimate, is not zero. Whether ρ is zero or not has little bearing on whether two variables are related. Values of r close to 1.0 mean there is a high degree of linearity between the variables. Small sample sizes and high variability may result in small r values with linearly-related random variables, and a zero value of ρ occurs with random variables that have a second degree relationship. With R^2 small values may occur with perfect models and larger values with incorrect models, depending on the variance. The literature is filled with incorrect interpretation and misunderstandings of these two statistics. Researchers often attempt to persuade the reader there is an important relationship between variables when the correlation coefficient is significantly different from zero. In most cases a good graph is a much more useful analysis of the data.

Perhaps the most important effort in the initial phase of work on the environmental effects on fish is to summarize what is known about the life history of each species and to speculate on the effect of the environmental conditions that prevail at each particular life history stanza. In some cases there is considerable information from laboratory research, particularly on temperature and salinity effects. Some of the theory developed may be testable with existing data, some theory may stimulate new data collection programs.

Whatever approach is used, the goal is to develop models of population turnover which incorporate environmental as well as fishing effects. This will bring us one step closer to the level of understanding necessary for effective management of our fisheries resources.

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Commentary

The Study of Environmental Effects On Interannual Variability in Flatfish

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To begin this commentary I would like to review a few other time series on flatfish not mentioned by Dr. McCaughran. Landings and effort records have been kept by scientists at the Pacific Biological Station, Canada Department of Fisheries and Oceans, since 1945 for English sole (Parophrys vetulus) and since 1954 for rock sole (Lepidopsetta bilineata), (Ketchen 1980). Catch (landings) per unit effort statistics for Hecate Strait, off British Columbia, have been calculated for these fishes. Stochastic stock reconstructions (Stocker 1981) and cohort analyses (J. Fargo, unpublished) have been carried out. Both species show similar fluctuations in year-class strength for a period extending from 1950 to 1975 for rock sole, and 1952 to 1975 for English sole. Coincident strong year-classes occurred for both species in 1953-1955 inclusive, 1961-1962 inclusive, and 1969-1970 inclusive. Rock sole had a strong year-class in 1975, but English sole had an average size year-class that year. El Niños in the eastern tropical Pacific are sometimes associated with warm water anomalies along the west coast of North America. For this time series, El Niño occurred in 1957, 1965, and 1972. The coincidence between El Niño years and poor survival is notable. Years 1957 and 1958 produced weak cohorts for rock sole and about average cohorts for English sole; 1964 through 1966 were poor years for both species, as was 1971 through 1973. These observations are consistent with published negative correlations for both species between temperature and cohort strength in Hecate Strait (Ketchen 1956a,b). The data are being examined further for possible relationships between physical environmental factors and year-class strength by researchers at the Pacific Biological Station.

Other substantial time series have been compiled by the Oregon Department of Fish and Wildlife at Newport, Oregon. One of these is for Dover sole (Microstomus pacificus) from the Astoria Canyon region off the Columbia River. Cohort analyses have been carried out from 1946 through 1962 year-classes. Another series is for English sole off northern Oregon and Washington. Cohort analyses have been carried out for year-classes from 1955 to 1966 (Hayman et al. 1980).

Year-class strength in Oregon Dover sole seems to be related to interannual variation in water-mass transport. Hayman and Tyler (1980) reviewed information on early life history of Dover sole, and proposed several hypotheses on possible influences of physical factors at particular life history stages. Both curvilinear and linear relationships were sought. A multiple linear regression with two independent variables accounted for 65% of the variance. Year-class strength was inversely related to off-shelf divergence of water in January when young fish were at the egg stage and when, in January a year later, they were settling. Dover sole are unusual in that they have a very long larval stage (Pearcy et al. 1977). The second variable was northerly wind speed in June. This is the wind that generates coastal up-welling off Oregon. Many larvae complete yolk-sac absorption in June. Upwelling was negatively correlated with survival, which is consistent with observations that low and intermediate levels of upwelling produce greater primary productivity (Cushing 1974, Small and Menzies 1981), which should result in better feeding conditions for larval Dover sole.

Year-class strengths have also been interpreted for English sole of the shelf off Oregon. The year-class strengths of Dover and English sole were not significantly correlated with each other. There are life history differences between the two stemming from the generally more shallow distribution of English sole as compared to Dover sole. Cohort analysis showed that English sole produced an enormously successful year-class in 1961 for Oregon and Washington. The size of this year-class was far beyond the sizes normally produced (Hayman et al. 1981). Statistical work with physical variables could not account for this banner year, although variance through the normal years was partially accounted for. Apparently the circumstances in 1961 involved factors not prevalent in other years. The factors seemed to affect several species over large areas of the Pacific coast of North America. Other species showing particularly strong year-classes were Pacific hake (Merluccius productus) (Dark 1975), Pacific halibut (Hippoglossus stenolepis) (Hoag and McNaughton 1978), and Pacific ocean perch (Gunderson et al. 1977). For the period 1955 to 1966, excluding 1961, 73% of the annual variation could be explained by Bakun's upwelling index off central Oregon for October. The hypothesis that extension of upwelling into fall could influence spawning time was originally made by Dr. Sally Richardson when she was at Oregon State University. Hayman and Tyler (1980) proposed that a match/mis-match phenomenon was occurring (Cushing 1982). Possibly when upwelling is prolonged in fall, spawning is delayed, giving rise to stronger cohorts because larvae-at-first-feeding were better matched with the onset of spring productivity. More recently, the mechanisms of spawning timing were explored in a simulation model that could largely reconstruct peak spawning for a 13-year period (Kruse and Tyler 1983).

Dr. McCaughran has been critical of Wickett's work with halibut year-class strength as related to salinity change. I quite agree that catch is a poor indication of year-class strength. In fairness to Mr. Percy Wickett, recently retired from the Pacific Biological Station, I believe his work deserves more attention, however. I have seen an updated, unpublished manuscript in which Mr. Wickett relates cohort analysis data of the International Pacific Halibut Commission (Hoag and McNaughton 1978) to spawning stock and salinity changes at Langara Light using curvilinear fitting techniques. His halibut survival hypothesis runs as follows: 1. there is evidence for upwelling in the winter in the central part of the Gulf of Alaska due to storm winds; 2. the upwelled water is often propagated to the eastern rim of the Gulf, as evidenced by small salinity changes witnessed at Station P and Langara Light; 3. the advection of upwelled water takes nine months to pass to the rim; 4. this upwelled water carries biologically fixed nutrients, and, 5. the interannual variation of the nutrients is related to varying survival of larval halibut.

There is at times a tendency for biologists working with demersal fishes to ignore pelagic processes. For example, flatfishes seem to be among the most benthic of fishes. Usually they derive their food energy from benthic amphipods and polychaetes. They dig in the substrate and often hide themselves with mud and gravel. They are taken commercially in bottom trawls with relatively low headropes. However, many species release floating eggs that move upward through the water column. It has become fairly clear that the numbers of fishes, including flatfish, are largely determined in the pelagic region of the ocean by changes in water-mass advection, temperature, food availability, and perhaps predation by hordes of denizens such as chaetognaths and euphausiids. In this way, demersal fishes often have a dual life. They are both pelagic and benthic in terms of their life history and the processes that determine their numbers. There are some demersal fishes that deposit adhesive eggs and are catchable as eggs and larvae near bottom (Dr. John Mason, personal communication). Rock sole and Pacific cod are examples of adhesive egg producers in the North Pacific. These species might not be strongly influenced by pelagic processes. For purposes of recruitment studies, it might be useful to classify demersal fishes into <u>pelagic-demersal</u> and <u>benthic-demersal</u> forms, depending on their early life history. Which species are pelagic-demersal is fairly well known because of abundance of pelagic ichthyofaunistic work. However, much less work has been carried out with on-bottom plankton gear because of technical difficulties. I suggest that more on-bottom work should be done.

Finally, I would like to point out that students of cohort-strength formation have largely overlooked the influence of interannual variation in spawning timing on egg and larval survival. A good number of fishes, of course, have quite fixed times for egg release (Cushing 1982, p. 302). However, some, such as English sole and Pacific halibut, have quite variable spawning timing. A bit of evidence has been reviewed here that changes in spawning timing may influence subsequent brood strength. It would be interesting to make a list of species that seem to be rather variable in spawning timing. Evidence would largely come from ichthyoplankton surveys. One would try to match spawning timing changes with subsequent changes in year-class strength. A notable point is that spawning time is probably influenced by processes and factors acting on the adult fish. More broadly speaking, strategies of adult reproductive biology may prove an influence on interannual variation in year-class strength in many cases.

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Variation in the Abundance of Crab and Shrimp with some Hypotheses on Its Relationship to Environmental Causes

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Life History and Survival

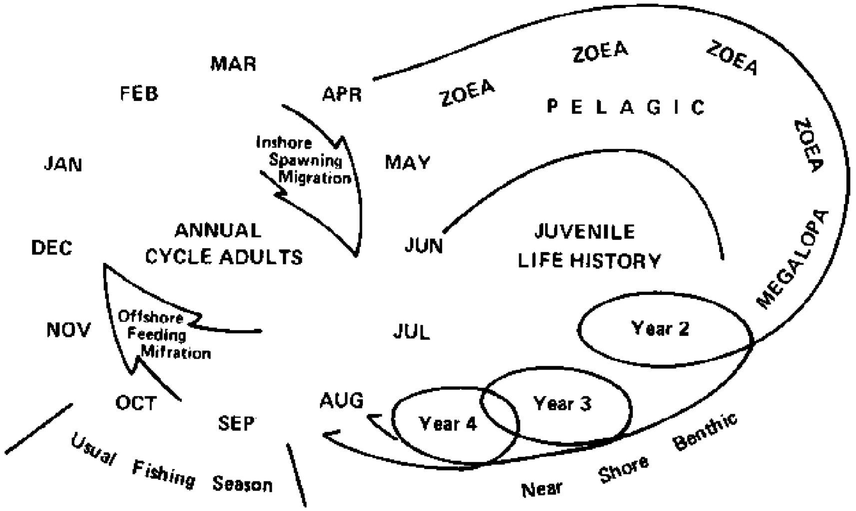
Crabs and shrimps comprise a large group of crustaceans that are important both commercially and as food chain organisms. This paper considers only a few of the important species and stock units in the western part of the Gulf of Alaska and in the eastern Bering Sea for which the best data sets exist. These will include the king crabs, Paralithodes camtschatica, P. platypus, Lithodes aequispina; the Tanner (snow) crabs, Chionoecetes bairdi, C. Opilio; and the pink shrimp, Pandalus borealis. A number of other commercial and food chain species occur in the areas, but information on their life history and time series data is less complete. The biology of important crabs and shrimps is fairly well known. I will use king crab as an example and describe the biology in terms of life stages and processes that may be vulnerable to environmental influences. Later, as interannual variation and possible environmental causes are considered, we will refer back to these stages and processes.

Biology of King Crabs

Three species of king crabs are harvested in the eastern north Pacific Ocean. The most important species is Paralithodes camtschatica, but P. Platypus and Lithodes aequispina also enter catches. In Alaska, these species are known respectively as red, blue, and brown king crabs. The king crab, Paralithodes camtschatica, is found from the littoral zone to the edge of the continental shelf in certain waters of the eastern Bering Sea, the Aleutian Islands, and eastward along the edge of the Gulf of Alaska to southeastern Alaska and northern British Columbia. Juveniles are generally found in the littoral zone and shallow water, whereas adults display annual inshore-offshore migrations associated with spawning and feeding.

Reproduction of king crabs has been studied in Alaska (Powell, et al 1974). Adult king crabs migrate to relatively shallow waters, from approximately 10 to 50 meters in depth, in late winter and early spring for molting and spawning (Figure 1). Males molt first,

Figure 1. LIFE HISTORY KING CRAB (*Paralithodes camtschatica*)



usually in March and April, whereas females molt just before spawning, usually in April and May. Although male king crabs attain sexual maturity at somewhat smaller sizes than females, competition on the spawning grounds apparently limits success to the larger males present.

King crabs mate in solitary pairs in shallow waters. Somehow the male is able to determine when a female is approaching her molt and will grasp her for a short period. Apparently, the male assists the female during the molting process and shifts his grasp to the new shell as the female emerges. Mating occurs within a day or two after the female molt. In king crabs, the female has no storage receptacle for the sperm which are deposited in a band around the female's egg pore. It has been demonstrated with caged king crabs that males can successfully mate with three to six females. Apparently, females first molting to maturity mate earlier in the year than animals which have previously carried eggs. Eggs are laid soon after mating and most females complete mating and egg laying in one or two days.

The eggs are attached to fine filaments on the appendages of the females' abdomens. The number varies with size of the female and ranges from about 50,000 to 400,000. Eggs develop for about 11 months and normally hatch in April and May. Interannual timing of the hatch can vary over more than a month (Armstrong et al, 1981). There are five larval stages, four zoea and the megalopa, which live in the water column and are subject to the mixing action and transport in the water moss. After about six weeks, the larvae settle to begin their life on the sea bottom.

During their first year of life juveniles assume a solitary, benthic existence in relatively shallow water. They are commonly found among the encrusting organisms on dock pilings and among rocks and seaweed in the littoral zone. During the second, third, and fourth years of life, king crabs often occur in shallow water in dense aggregations called pods (Powell, 1965). These "piles" of crabs usually contain only one year-class and have been observed near Kodiak in all months of the year. One such pod was studied over a period of 57 days. Another was estimated to contain over 500,000 animals which were about 70 millimeters in carapace length (probably their fourth year).

Fishermen commonly find adult king crabs concentrated in schools and, indeed, segregated by size, sex, and molt condition. In the eastern Bering Sea, tagging studies in the 1950's (Weber, 1974) demonstrated that large crabs which have skipped an annual molt move selectively to certain known spawning grounds during the spring months, whereas many crabs of similar size which do molt remain in deeper offshore waters. Such observations suggest that some modified form of the podding or schooling behavior persists in adults.

Growth of king crab, like that of other crabs, progresses in step fashion at time of molt. No way is known to age crabs directly, such as the growth rings in trees or the annual growth marks on fish scales. Instead, crab biologists study growth by determining the frequency of molts and the increment of growth per molt. Using this information, a growth curve is constructed.

In their first year of life, king crabs molt about 7 times and reach about 12 millimeters in shell length. King crabs molt several times per year as juveniles, and crabs of different year-classes are easily separated by size. King crabs reach about 34 millimeters in two years, 62 millimeters in three years, and 78 millimeters in four years (Weber, 1965). Larger king crabs can be tagged by a method that allows the tag to be retained by the animal when it molts. Tagging studies provide most of the growth data available for larger crabs.

After maturity, at about 90-100 millimeters in shell length, females molt annually just before spawning. They grow four to six millimeters per year. Adult males continue to molt annually for a few years after maturity. Growth increase at each molt is about 20 millimeters per molt near Kodiak and about 17 millimeters per molt in the eastern Bering Sea. Large male king crabs begin to skip molts when they reach about 145 millimeters in length. The proportion of large male king crabs which molt in a given year varies both with size and among years--probably in response to environmental conditions. Therefore, average growth decreases with age and varies among years.

In the eastern Bering Sea, Weber and Miyahara (1962), included the average proportion of crabs molting each year in their growth model. Using average growth determined from tag returns for the years 1956-59, king crabs would reach 110 millimeters in shell length in 6 years, 142 millimeters in 8 years, and 190 millimeters in 11 years. Newer studies by Balsiger (1976) have refined but not significantly changed the earlier findings. Based on data from areas near Kodiak, McCaughran and Powell (1977) demonstrated that king crabs could reach

118 millimeters in shell length in 6 years, 158 millimeters in 8 years, 203 millimeters in 11 years, and 224 in 13 years. These growth figures would be for crabs that did not skip molts.

King crabs are bottom-foraging omnivores. It is doubtful that they are scavengers under natural conditions since most foods from stomachs examined appeared to be 'fresh'. Food studies of crabs taken in the eastern Bering Sea (McLaughlin and Hebard, 1959) indicate that there are no significant differences in diets between the sexes or sizes for adult crabs. Major food items were starfish and their relatives, clams, and other mollusks. Other items eaten frequently include small crabs, shrimps, and other small crustaceans; marine worms; fish; and algae. Recent feeding studies for juveniles have quantified food taken in terms of energy and attempted to define food required (Pearson, 1983).

Other species of commercial crustaceans have similar life histories; but, of course, with variations characteristic of those species. Pandalus borealis has 6 larval stages. Pink shrimp are protandric hermaphrodites - that is they first mature as males and then transform sex to become female. In Alaskan waters, they mature as males in their 2nd or 3rd year of life and then transform to females in their 4th or 5th year. Large shrimp are all females, molt annually after sexual maturity, and live 7 or 8 years. The Tanner crabs, Chionoecetes spp., have three larval stages, each lasting for about one month in the eastern Bering Sea (Armstrong et al, 1981). Tanner crab females reach sexual maturity at about 4 or 5 years. They do not molt after sexual maturity but continue to produce fertile egg clutches for several successive years. Males continue to molt and grow after sexual maturity and reach sizes much larger than females, resulting in large differences in size of mature males and females. Distinct feeding and spawning migrations have not been identified for these other species - but there is inferential evidence that suggests some life history separations.

Harvest Variation, Stock Structure, and Fishery Independent Stock Assessments

Our focus here at Lake Wilderness is to look at interannual changes in the abundance of marine fish and shellfish as they may be influenced by variations in the environment; and, in particular, the degree to which such change can be related to variations in year-class strength. Sources of data include the harvest statistics and research data collected during fisheries surveys and oceanographic studies. We recognize at the onset that the annual time resolution represents a level of abstraction that confounds the short-term environmental events which may be critical to survival with year-class success. The second dimension to the problem - the geographic distribution of crabs and shrimps is equally confounded with the species composition and stock units.

The king crab population of Alaska consists of many relatively independent stock units. These can be identified from distribution, tagging, morphology, biochemical genetics, and other data sets that bear on stock differences. While fisheries statistics and assessment surveys usually address the full extent of the commercial stocks, environmental studies might best be focused on mechanisms and processes in smaller areas containing single stock units. The size of these relatively self-contained stock units also provide one estimate of the geographic size of "events" which might influence crab and shrimp populations. At Kodiak, Blau and his Alaska Department of Fish and Game (ADF&G) colleagues, 1983, have identified a number of king crab stocks which have been further divided into 20 ocean schools for harvest management. We currently recognize two red king crab and three blue king crab stocks in the eastern Bering Sea. Stock fluctuations and regional differences in composition suggest the existence of relatively small stock units for shrimp - often confined to one bay or offshore canyon area.

When we seek breakdown of statewide harvest totals, we find time series that are more or less complete for smaller administrative subdivisions, usually geographic areas, regions, and districts that have sometimes changed their boundaries. For example, many of the earlier records divide fisheries statistics into southeast, central and western Alaska. More recently, fisheries statistics have been available for Alaska Department of Fish and Game districts. The "districts" vary in geographic extent for each species or species group. For example, the state waters are divided into 5 statistical districts for shrimp (several species), 4 districts for Dungeness crab, 9 districts for king crab (3 species) and 4 districts for Tanner crab (2 species). While time series of harvest data for "districts" are sometimes available in state statistical publications, they again are of little use for environmental analysis because they often include more than one species and geographic stock unit. For example, the red king crab catch for area K - Kodiak Island - probably includes at least six stock units and small amounts of two other species.

Harvest variations.--With regard to time series data, the longest time series we can find easily would be statewide harvest totals for shrimp, Dungeness crab; and more recently, king crab, Tanner crab and horsehair crab (*Erimacrus isenbeckii*). These may be useful to indicate the history of harvest and relative commercial importance of the component species or species groups but they are of little value in environmental analysis. Otto (1981) has described the eastern Bering Sea crab fisheries (Figure 2).

The foregoing suggests that while conventional fishery statistics can be used to describe the fisheries, they are of very limited value for environmental studies because they are generally comprised of several stock units and sometimes of more than one species. Further, at times the harvest is more dependent upon the economics and market conditions in the fishery than on resource condition. These problems require that the researcher work closely with local experts (usually ADF&G) to identify stock units for environmental analyses. Since ADF&G statistics are collected by small statistical areas that are sometimes delineated to define ecological zones (nearshore, shallow, offshore, deep, etc.), it is possible to obtain data sets on a relatively fine scale for special purposes. In general, the best

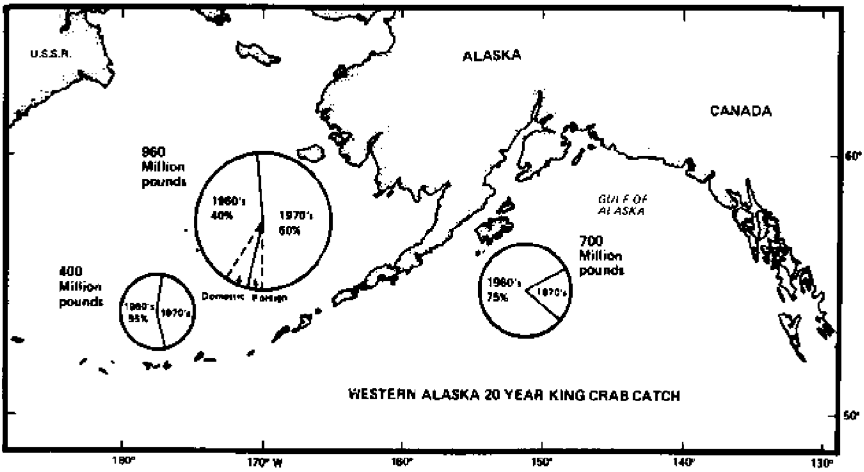


Figure 2.--Western Alaska 20 year king crab catch.

definitions of stocks of crabs and shrimps and the corresponding time series of catch data appear in the annual ADF&G staff reports to the Board of Fish and Game. However, these time series are short.

In addition to harvest data, state biologists collect logbook, interview, and catch composition data in ports of landing. These data sets are primary sources of data to give fine detail on geographic origin of catch, catch per unit effort, composition (species, size and sex) of catch, proportion of juveniles, and unusual conditions on the fishing grounds. Such contacts with fishermen are especially important to encourage and collect information on tagged crabs.

These data sets are maintained by the local ADF&G offices and vary in completeness by area and species. Their value, as time series for comparison with environmental data, must be determined on an ad hoc basis. The crab data on size composition of commercial catches is used in management to determine the proportion of 'recruit' crabs in the catch and these figures may be a rough approximation of year-class strength (more precisely size composition). Variation in the proportion of shell age categories by size may indicate the availability of and degree of competition for food.

Stock Assessments.--Because fisheries statistics provide limited information on interannual variation among stock units and provide a very limited basis for prediction of future stock condition, fisheries scientists have conducted independent stock assessments and surveys. Regular systematic trawl surveys for king crab began in the eastern Bering Sea in 1955 and, except for a 5-year hiatus from 1962 through 1966, have continued to date. This data set is the longest and most consistent time series of survey data available for north Pacific crabs. Assessment surveys for crabs using pots have also been conducted by ADF&G at Kodiak since 1971. This survey methodology has been extended by ADF&G to other major crab stocks in western

Alaska - south of Alaska Peninsula, Dutch Harbor, Norton Sound and Adak - but the respective series are short. For shrimp, trawl assessment surveys by the National Marine Fisheries Service (NMFS) were conducted from 1971-74 in the Kodiak area and in the Shumagin Island area from 1972-82. The ADF&G began trawl assessment surveys for shrimp in the early 1970's at Kodiak and has since expanded coverage to most important stock units.

The state surveys gradually replaced the NMFS surveys which are now limited to continuation of the Pavlov Bay time series to obtain data on shrimp growth and natural mortality. These four sets of surveys represent the principal time series of research data on fishery independent assessments of crabs and shrimps in the Gulf of Alaska and eastern Bering Sea.

The Bering Sea crab surveys began in 1955 when the chartered F/V Tordenskjold made 104 trawl hauls at 26 stations north of the Alaska Peninsula between False Pass and Black Hill (INPFC, 1955). These 26 stations were arranged in a 20-mile grid pattern over the area of known crab concentration in which the commercial fisheries occurred. At that time, the fishery targeted upon nearshore spawning concentrations in April, May, and June that contained predominately skip molt males. The fact that crabs were in high abundance in 1955 was indicated by the fact that every single trawl haul (104) contained crabs. The early survey objectives were oriented to collecting biological data on crabs with emphasis on tagging to determine migrations and growth. The survey was repeated in 1957 with essentially the same station pattern and objectives.

In 1958, the survey was expanded in an effort to cover the full range of this king crab stock in the eastern Bering Sea. The general strategy was to extend the station pattern in each direction until crabs were no longer taken (77 stations in 1957). This station pattern has continued to date; and, in fact, has been extended over the entire Bering Sea shelf from Bristol Bay to the Gulf of Anadyr and north to the Chuckchi Sea (Figure 3). Over the period 1957-61, a number of population estimates for king crab were made using the area-swept method. Comparison with estimates of population size determined from tag returns were not statistically different, and represent one of the first confirmations of the area-swept method in the literature (Miyahara et al, 1962):

	Area Swept Estimate ($x10^6$)	Tag Return Estimate ($x10^6$)
1958 (1)	22.2	20.8
(2)	17.4	
1959	25.2	33.5

From 1962-66, no trawl survey was conducted, but work continued to recover tags and analyze data from both survey and commercial fisheries sources. In 1967, field studies resumed and a new series of population estimates began which have continued to date. These

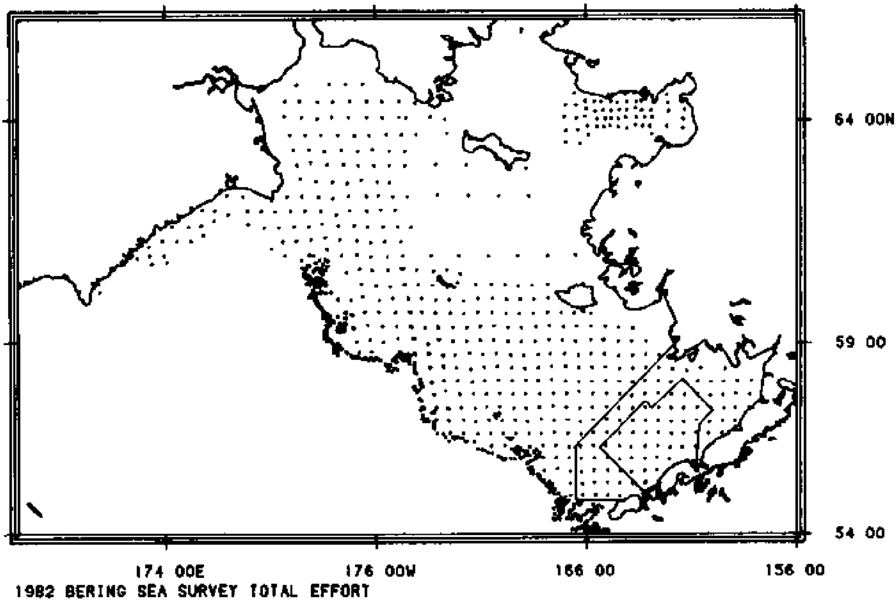


Figure 3.--Trawl survey stations in the eastern Bering Sea occupied in 1982 triennial survey. King crab surveys in 1955-57 illustrated by two smaller areas in the right side of this figure.

population estimates are made by 5-mm size groupings of males and females for each station and may be recombined in population estimates for different size categories and areas. Results are usually presented by size category useful to management: legal males, recruit males, immature males, and immature females. Figure 4 illustrates this data set with a graph of abundance estimates for males over 135 mm in carapace length which is approximate legal size. In this figure, I have suggested trends in abundance for periods when population estimates were not available from trawl surveys based on the catch per unit effort (CPUE) of Japanese and Soviet commercial fisheries and CPUE of Japanese scouting vessels performance.

Beginning in 1971, the station pattern was expanded to include king crab stocks (P. platypus) near the Pribilof Islands and Tanner (snow) crabs (Chionoecetes bairdi, C. opilio) over the entire area. In 1975-76, the area was further expanded to include more northern stocks of Tanner crabs. Annual surveys now include about 350 stations and triennial surveys (76, 79, 81) include about 1000 stations on the Bering Sea shelf extending from Unimak Pass to the US-USSR convention line. Similar data sets by species, sex, and size are available for these other species in these years (Otto et al, 1982).

The pot surveys for king crab at Kodiak began in 1971. In these surveys, stations are selected from predetermined grids of each major fishery. Standard 7 x 7-foot king crab pots with 3-1/2" mesh are fished 1/3 mile apart. Offshore stations are sampled with 10-13 pots and nearshore or bay stations with 3 or 4 pots. After a 24-hour soak, each pot is lifted and the catch examined for species composition, sex, carapace size, and shell age. A proportion of all commercial-sized crabs are tagged and released. The return of these tagged crabs in the commercial fishery is used to estimate population size at the beginning of the fishing season. This data set then provides an annual estimate of the exploitable population and its size composition. With additional information on the occurrence of the pre-recruits in the planning and growth, estimates of fishery yield for each of the succeeding 1-3 years can be made (Figure 5).

The shrimp trawl surveys have been conducted in a number of locations at Kodiak and along the Alaska Peninsula since 1971. These surveys provide area-swept estimates of populations and provide samples for species, size and sex, determination. One of the best time series is that for Pavlov Bay which extends from 1972 to date. The occurrence of very strong modes in the size distribution of Pandalus borealis, pink shrimp, has provided an opportunity to study growth and mortality (Anderson, 1981) and, of course, demonstrates the occurrence of strong year-classes (Figure 6).

Stock Variations and their Relationship to Environmental Causes.--Interannual variations in abundance of the exploited portion of king crab stocks have ranged over an order of magnitude in both the eastern Bering Sea and at Kodiak. These fluctuations result from the occurrence of particularly successful size cohorts that can be ob-

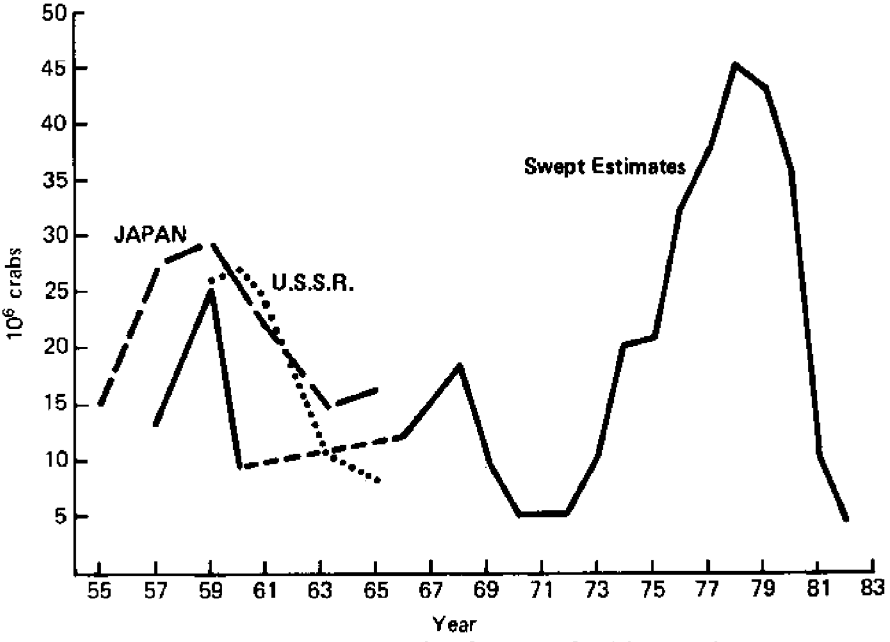


Figure 4.--Abundance estimates for large male king crabs, Paralithodes camtschatica, from NMFS trawl surveys in the Eastern Bering Sea (Solid lines are area swept estimates, dotted line is an index based on Japanese CPUE, dashed line an index based on USSR CPUE).

served to grow and progress through successive samples and represent classic year-class phenomena. At this conference, we are attempting to examine such variations and to develop hypotheses that may link these changes to environmental conditions in order to understand and predict abundance. In this section, I will select a few samples of interannual variation that may suggest some directions in environmental research.

First, I would like to suggest that we can learn a great deal about the environment through understanding the requirements of the species which occur in it. A living organism integrates its environmental experience over its life history. For example, the stock structure of king crabs, as defined by tagging studies at Kodiak, suggests that an environmental mechanism exists that maintains the separation observed in the data. We might hypothesize that such stock structure results from current patterns on the Kodiak Island shelf that retain crab larvae within these areas - low energy systems or gyres, perhaps. Other indicators of environmental units come from analyses of the distribution of species. The latitudinal replacement of species in the eastern Bering Sea, for example, might be used to represent environmental clines. Somerton (1981) has documented the fact that mature female C. bairdi are larger from east to west and that mature female C. opilio are larger from south to north. Also, large populations of juvenile C. opilio occur in the northern portions of the Bering Sea where mature crabs are absent. Do these juveniles migrate to areas where mature crabs occur or do they represent animals that have been transported to an area where environmental factors prevent reproduction? While these are not interannual variations, they may suggest the types of environmental variation that may be important in shaping a year-class.

Life history also suggests that crabs are vulnerable to different environmental effects depending upon the life history stage. For example, larval forms are found in the water column and are subject to a very different set of conditions than in the later benthic life. The conventional wisdom is that year-class strength is determined during the period of larval development. Incze (1983) studied the larval life history of Tanner crabs and relationships to regional oceanography. The data base is exceedingly short. Incze examined data from 1419 plankton samples over 6 years, and he suggests his results are more in the form of hypotheses than conclusions. He hypothesized that year-class strength for C. opilio may depend upon the thickness and stability of the mixed layer during April over the middle shelf zone - relatively strong larval year-classes were observed in years of shallow mixed layer depth in April.

At the time of molting, crabs undergo major physiological stress and are particularly vulnerable to physical damage and predation. Juvenile king crabs occupy different habitats than adults and their schooling or podding behavior concentrates large numbers in small areas. One must be cautious, however, in identifying size cohorts with year-classes. Growth in size of crabs occurs at the time of molt and modern growth models are based on frequency of molt and growth increments. Since there is no known way to determine the absolute age of crabs, associating adult abundance with past environ-

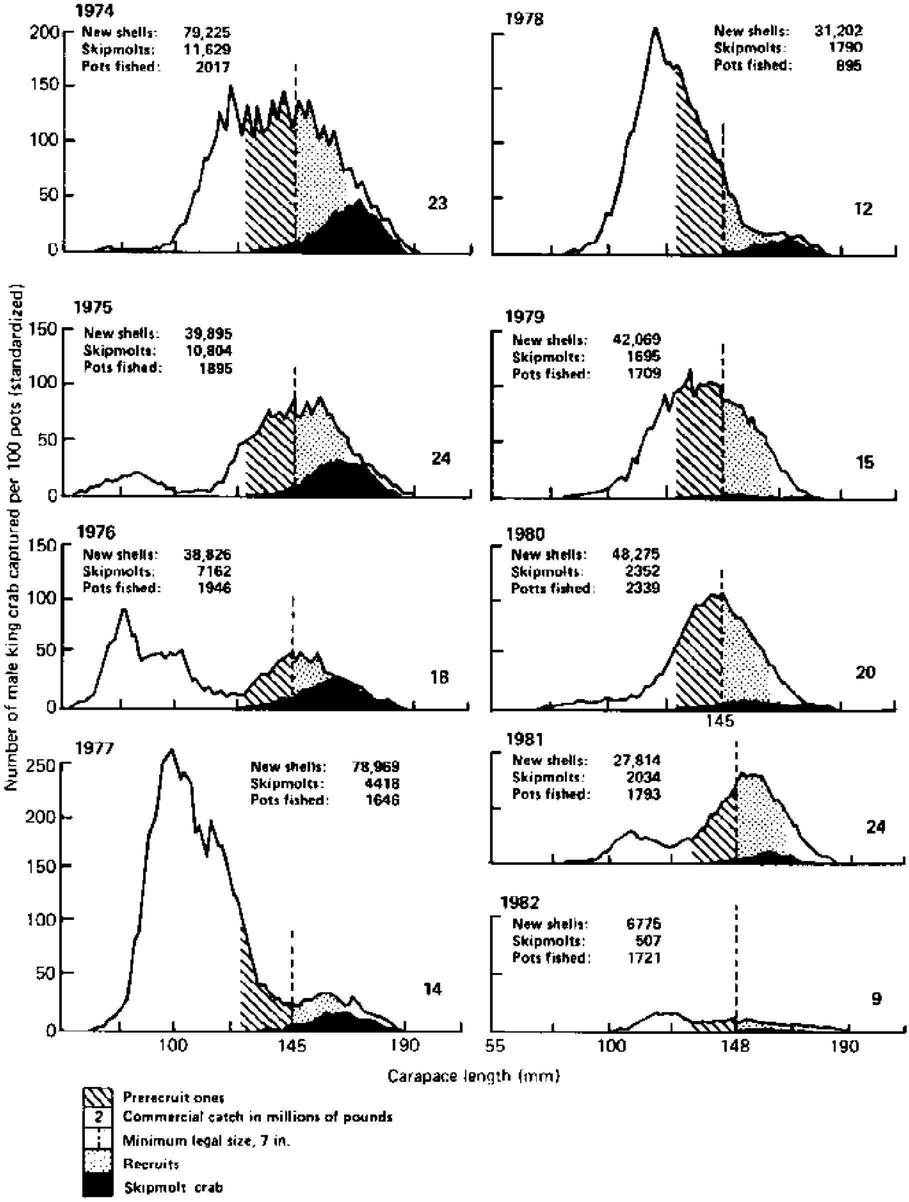


Figure 5.--Kodiak male red king crab size distribution, for each year 1974-82, as determined by research pot sampling. Note: Skipmolt crab (the black area) masks new shell crab (From ADF&G 1983)

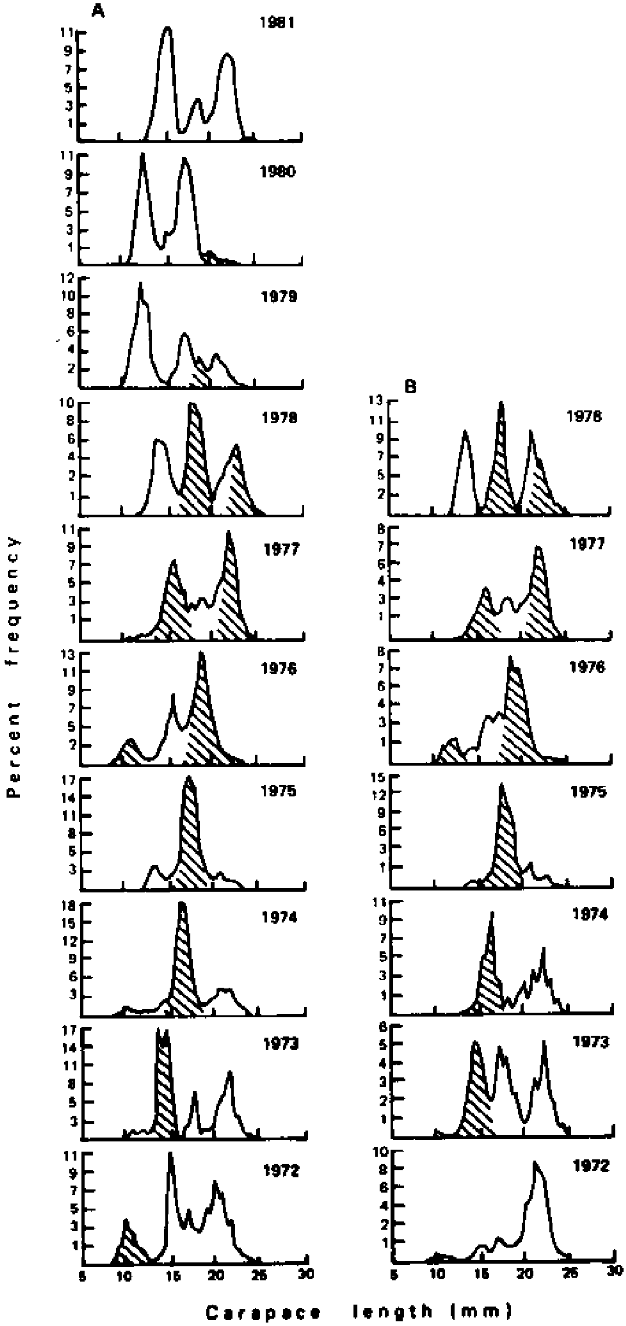


Figure 6.--Size composition for Pandalus borealis from Pavlov Bay, Alaska, from standard research hauls (left) and of samples from the commercial fishery (right).

mental events is inexact. For example, consider Weber's model of crab growth that indicates crabs at a given size may come from a number of year-classes (Figure 7).

With regard to interannual variation, we can measure wide variation in abundance in all of the time series available. In king crab in the Bering Sea, we note that population levels of exploitable males have varied more than an order of magnitude (Figure 4). We have good population estimates for 1957-60 that indicate the population of exploitable males was over 20 million crabs, in 1970-72 the population was at a low level of about 5 million, in 1978-79 at a high level near 50 million, and in 1981-82 at a low level of 4-5 million crabs. These changes were undoubtedly influenced by the harvest, but population estimates of females, which are protected, also show wide variations.

At Kodiak, stocks of king crabs have also shown variation in abundance (Figure 5). In these data, the sporadic appearance of strong size cohorts and their progress through the fishery suggests wide variation in recruitment. Also, examination of this data suggests that certain abundant size cohorts have simply disappeared. For example, the difference in abundance between 1981 and 1982 (Figure 5) cannot be accounted for by the fishery alone. Where did these crabs go?

Somerton (1981), using the NMFS trawl survey data base, has shown that the two species of Tanner crabs in the eastern Bering Sea have somewhat different patterns of year-class success. Since females molt to maturity and do not molt thereafter, year-class strength can be measured by the relative number of primiparous females taken in trawl surveys. His data showed that for C. opilio larval and juvenile survival was high enough to produce a cohort that was large enough to be identified in the size histograms in only 3 of 11 years. In contrast, C. bairdi juvenile modes were prominent in most years. From this information, Somerton proceeded to develop the hypotheses that strong C. opilio year-classes are associated with the amount of ice in the study area. Somerton also presented data to support the hypotheses that average size of mature females decreases in areas of lower mean bottom temperatures.

The shrimp data for Pavlov Bay also demonstrate wide differences in the strength of year-classes. In this case, the progress of a large mode could be followed for 6 years providing new data on the life span and natural mortality of Pandalus borealis. Why did this year-class occur?

Finally, we usually assume that year-class strength is determined in larval or early juvenile periods of the life history. But there is some evidence in these data sets that suggests that mass mortality may occur in later parts of the life history. On several occasions in the ADF&G pot surveys, strong size modes of king crabs have been followed for several years and then simply disappear. In the eastern Bering Sea trawl surveys in 1981 and 1982, the number of male king crab over 135 mm carapace length was about one-half the number projected from the earlier year survey after allowance for the fishery, natural mortality, and growth. Further, in 1982, a large proportion

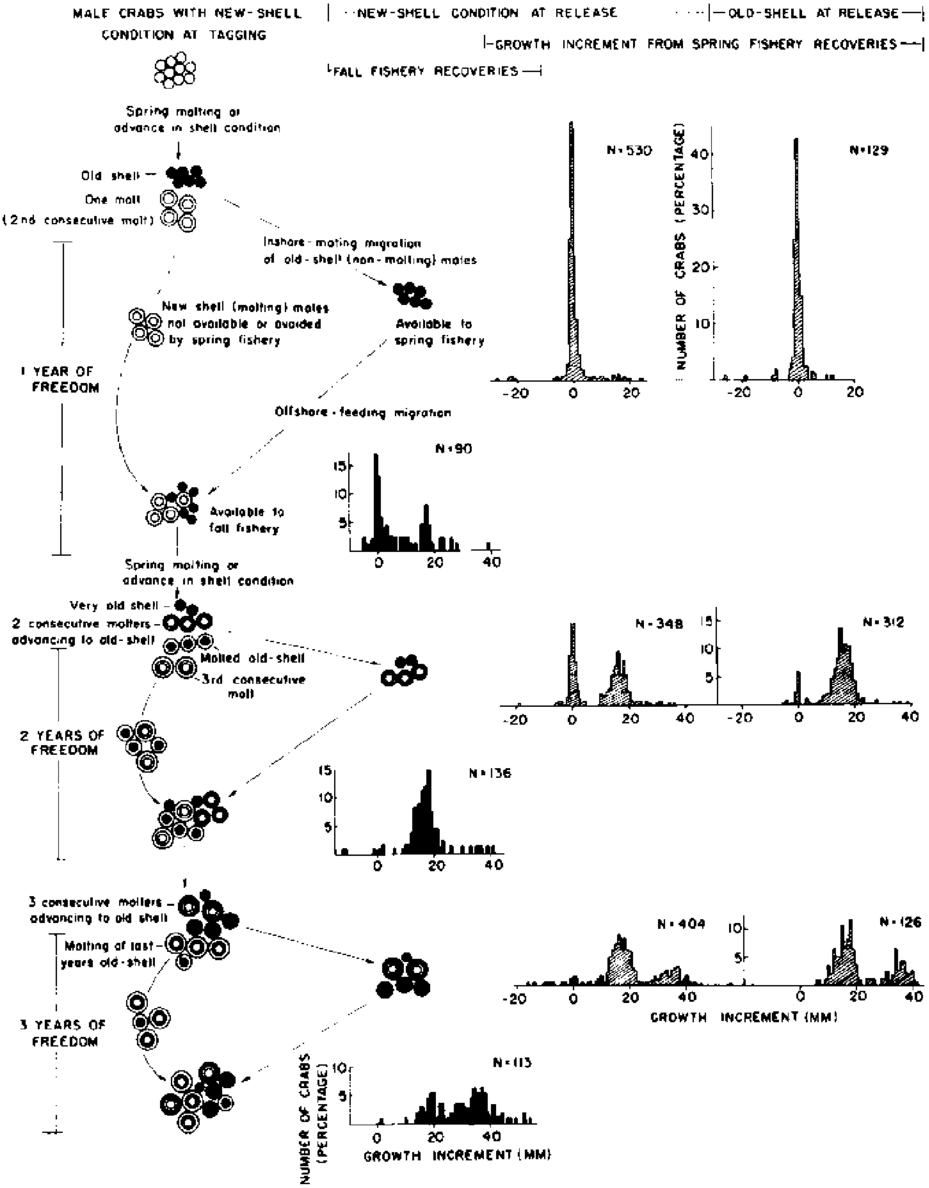


Figure 7.--Relation between stage in molting cycle at release, time and area of recovery, and effect on growth observed from tag recoveries. Refer to text for discussion. (From Weber, 1974)

of the larger mature females did not molt before the annual survey. Special surveys conducted in September and March suggest these crabs did not molt in 1982 and were not present in the March 1983 survey. These observations, while not definitive, suggest that mass mortality of adults may occur under some conditions - perhaps predation pressures or because of epizootics.

Conclusions

Crabs and shrimps have interannual variations in abundance that range over an order of magnitude at the exploited phase. The fact that many of these variations can be detected early in the life history is evident from the progress of size modes (age classes) in successive annual samples. The time series are short, however, and we may not have seen the full range of variation to be expected. Density dependent factors influencing abundance have not been studied but such effects are complex and probably related to the community and ecosystem rather than being single species effects. Knowledge of environmental interactions are rudimentary. Analyses of environmental and biological time series data have produced several hypotheses as to the relationships between year-class strength and the environment. Incze (1982) hypothesized that mixed layer depth in April and Somerton (1981) suggested that ice extent during hatching and early larval life were significant influences in year-class survival. "Scattered" studies of physiological processes and feeding energetics suggest the need for additional experimental evidence on which to base environmental investigations.

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Commentary

Cyclic Crab Abundance and Relationship To Environmental Causes

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The biological sketches of S.E. Bering Sea and Gulf of Alaska crab and shrimp provide interesting species contrast in life history and reproductive strategies that are important considerations in management formulas. Murray Hayes has highlighted germane biological information to the extent known for each group, and has focused on factors that may influence population dynamics vis-a-vis year-class strength. Vagaries in abundance severely impact the fisheries, most notably in the case of red king crab to date, and this problem assails other U.S. crustacean fisheries as well.

My comments on the material presented by Murray Hayes will first reference one other fishery, that for Dungeness crab (Cancer magister), as an example of persistent, high amplitude cycles of abundance; a pattern that is apparently emerging for red king crab as well. Hypotheses will be discussed that promote both biotic and abiotic factors that bear on year-class strength and, ultimately, the magnitude of the fisheries. Last, I will reiterate hypotheses outlined by Dr. Hayes on factors controlling abundance (susceptible weak links in the life history) and suggest research pertinent to a better understanding of the species' biology.

Dungeness Crab, *Cancer magister*: The Fishery

Cancer magister is regulated as a males-only pot fishery that opens and peaks about December 15 thorugh February to March. Legal males are recruited to the fishery at 3.5 - 4.0 years (Botsford and Wickham 1978). The fishery is largely supported by the newly recruited year class and mortality has been estimated at 80-84% (Jow 1965). More recently Methot and Botsford (1982) calculated preseason abundance and derived exploitation rates from 54% to 84%. Such shifts were seen as a lagged response of fishing effort to cyclic changes in crab abundance.

The most striking feature of the Dungeness crab fishery is the cyclic trend in landings and apparent population abundance since 1950 (Fig. 1), and for Washington state again in 1981-82 (lowest state catch in 30 years; Fig. 2). An interesting feature of the

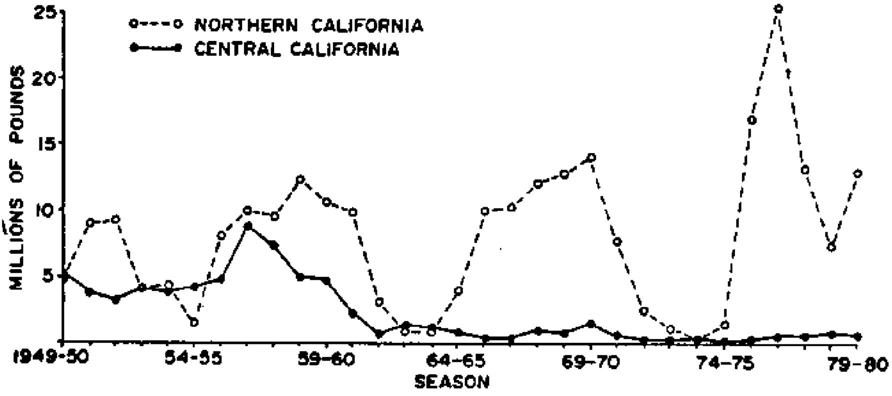

Fig. 1. Dungeness crab commercial fishery landings for northern and central California by season since 1949.

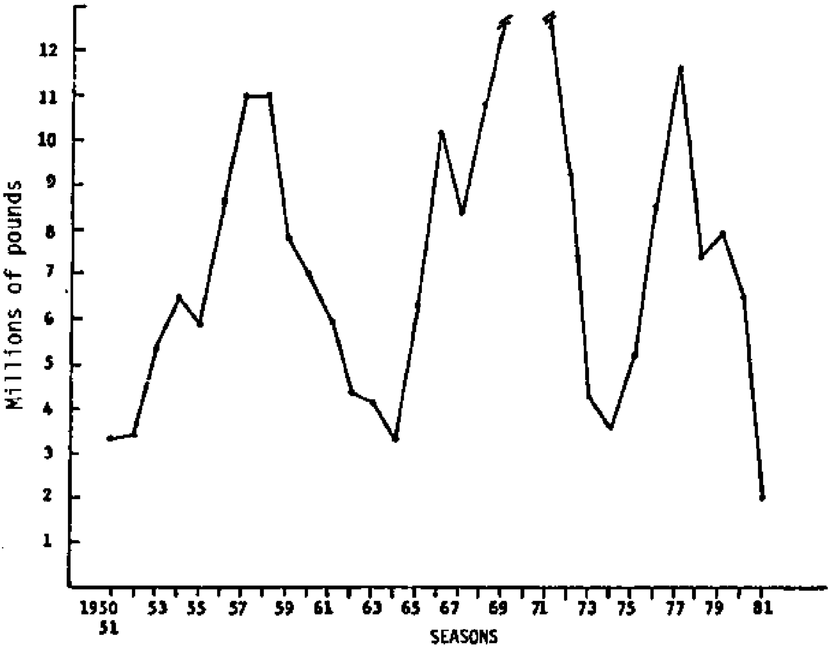

Fig. 2. Annual landings for Washington coast ports: Grays Harbor, Willapa Bay, and Columbia River (from PMFC, 1979). Data for 1981 is preliminary (Steve Barry, Washington Dept. Fisheries, personal communication).

California crab fishery has been the cyclic nature of northern populations, but a decline and long-term collapse of the central (San Francisco) fishery (Fig. 1).

Hypotheses for the Cycles

The pronounced fluctuations in coastal landings (considered California through Washington; excludes British Columbia and Alaska) that went from 7.8 million lb in 1973-74 to 53.0 million lb in 1977 has prompted several causal hypotheses. They generally fall within categories of biotic and abiotic factors that impact egg/larval production and survival, or that influence survival of early benthic stages.

Abiotic

1. Peterson (1973) investigated correlations between upwelling indices along the west coast of the United States and annual catches of Dungeness crab. He found fairly good agreement between years of strong upwelling and good commercial landings 1.5 yr later in California-Oregon, and 0.5 yr later in Washington. He hypothesized from this result that nutrient availability increased with upwelling, which ultimately increased benthic food supplies for crab via greater phytoplankton/zooplankton productivity in the water column. After appropriate time lags, this material settles, is used by epibenthic and infaunal consumers and thereby creates a more plentiful food reserve for crab which reduces competition. Older year classes, 0.5 to 1.5 yr from entering the fishery, are the primary beneficiaries of strong upwelling years in Peterson's model.

2. Botsford and Wickham (1975) followed Peterson's lead and used different correlation procedures to study upwelling and crab catch relationships. From auto-correlation they concluded that crab landings are definitely cyclic but upwelling is not. While upwelling may contribute to crab abundance, as a noncyclic, abiotic factor it is probaly not primarily responsible for year-class strength. Rather, Botsford and Wickham suggest that biotic, density-dependent interactions may drive the cycles.

In accord with this conclusion on upwelling, Chelton (1981) found poor statistical correlation between local coastal upwelling indices and zooplankton biomass along CALCOFI transects. Rather, he concluded that large-scale advection in the California current plays a dominant role; notably that advection of northernly, colder, nutrient-rich water increases zooplankton biomass.

3. Lough (1976) studied larval Dungeness crab population dynamics off Oregon in 1970-71, and reported a catastrophic reduction in larval abundance during 1971, suggesting a mass mortality had occurred. He considered several hypotheses to explain the failure of 1971 larvae, including below-normal water temperatures, reduced food availability, and greater offshore transport of larvae beyond shelf areas of probable recruitment back to the fishery. Lough did not conclude that any single factor was most responsible for larval

mortality, only that larvae are very sensitive to environmental perturbations which need only be of relatively brief duration to severely affect the population.

4. Analyses of long-period physical oceanographic fluctuations in the California Current, while not applied to crab larvae per se, have been correlated to zooplankton biomass (Bernal 1981; Chelton 1981). In neither study was upwelling a good indicator of zooplankton biomass, but Bernal found peak biomass in association with maximum gradients of average flow where water masses converge (Davidson and California Currents), suggesting nutrient introduction via turbulent mixing. Both found that an index of advection was as good a predictor of zooplankton biomass as sea surface temperature. They suggest that the ecosystem may be under permanent nonequilibrium conditions, which portends that resident animal populations (e.g., pelagic crab larvae) are not so much regulated by forces of competition and predation as by disruptive effects of the physical conditions.

Biotic factors

Some researchers point out that abiotic factors such as upwelling or anomalously low temperatures will not occur at regular intervals and cannot, therefore, account for the periodicity of crab abundance. Hypotheses of biological forces driving cycles include:

1. Density-dependent mechanisms based on compensatory influences such as competition for food between young and older crabs, and cannibalism. Botsford and Wickham (1978) concluded that the extent of survival of early benthic young-of-the-year crabs (first few instars) largely explains later abundance reflected by commercial landings. During a time of very large adult populations (e.g., Figs. 1 and 2 show large populations in 1977), newly metamorphosed first instars will settle out from pelagic existence to face tremendous populations of adult and older juvenile crabs. Direct cannibalism (Stevens et al. 1982) or competition for food will result in poor survival of the year-class, and a poor fishery 3 to 4 years later (e.g., mortality of the 1977 year-class should have been high, and in 1980-81 a decline in the fishery is the consequence - Fig. 2).

2. Larval and egg natality and subsequent survival to metamorphosis. McKelvey et al. (1980) used mathematical models to describe possible causes underlying cycles in crab landings and highlight the most sensitive life history stages. They concluded that survival of eggs and larval stages is most crucial for the species and can best account for cycles. Density-dependent cannibalism of young-of-the-year by older crabs was discounted as an important variable (although they base this on the poor assumption that only mature crabs, 2+ years old, prey on young-of-the-year).

3. Predation on crab eggs by a species of nemertean worm, Carcinonemertes errans, represents a significant source of mortality that might be linked to cycles of abundance. In a series of papers, Wickham (1979a, b; 1980) documents predation by this worm on Dun-

geness crab eggs, and resultant direct mortality as high as 55% of eggs borne by females off California. With mortality rates this high and predator densities up to 100,000 worms per female crab, Wickham suggests that C. errans may be the most significant predator of Dungeness crab. The interaction of worms and crabs would partially explain cycles of commercial landings and also the long-term suppression of the San Francisco fishery (Wickham 1979b).

4. Salmon predation on crab larvae has been observed for years. Botsford et al. (manuscript submitted) studied cylic covariation between catches of king salmon and Dungeness crab but found them to be of different phases, and therefore did not consider such predation a plausible mechanism to explain crab abundance.

Hypotheses for the Demise of the San Francisco Crab Fishery

Abiotic factors

1. Oceanographic conditions off central California changed in the late 1950's and have persisted at least 20 years with a detrimental effect on crab life cycles. Wild (1980) showed an increase in mean October-Decmeber (period of C. magister egg brooding and hatch) ocean temperatures off San Francisco from 13.2 to 14.1°C with several years exceeding 15°C. In laboratory studies of rates of egg development, time-to-hatch at elevated temperatures were 64 days at 16.7°C and 123 days at 9.4°C. However, there was a strong negative correlation between temperature and hatching success. At 10°C an average of 685,000 eggs per experimental female hatched while at 16.7°C an average of only 14,000 (2% of former) developed to hatching. Wild speculates that even a long-term increase of only 1°C toward higher temperatures may severely reduce the reproductive success of Dungeness crab off the Central California coast.

2. Pesticides and other pollutants, and substantial alteration of the estuary have long been considered likely stresses affecting the San Francisco-based fishery. A study of pollutants done as one aspect of a five-year California Fish and Game crab program (Orcutt et al. 1978) has given no evidence that pollutants are detrimentally affecting crab (California Fish and Game 1981). Researchers have found, however, that from 50-80% of any year-class hatched offshore uses the San Francisco estuarine complex in their first year (Orcutt et al. 1978). Extensive dredging and filling may have dangerously diminished critical juvenile habitat in the estuary causing reduced survival.

Biotic factors

1. Nemertean egg predators of Dungeness crab have been at much higher population levels in the San Francisco region than elsewhere on the coast during the last 20 years. Wickham (1979a, b) has estimated annual egg mortality rates around San Francisco to be 45-63%. He hypothesizes a direct predator-prey balance between worms and crabs has suppressed crab to a low-point equilibrium that is reflected in the 20-year reduction in fishing stocks (Wickham 1979b).

2. Silver salmon (Oncorhynchus kisutch) production by Columbia River hatcheries has escalated tremendously since the early 1960's. Salmon are major predators of Dungeness megalopae (Orcutt et al. 1977), and the return of megalopae from offshore to nearshore water coincides with the arrival of the hatchery-reared fish off San Francisco. Evidence of cause-and-effect impact is circumstantial but this historic change in a predatory fish population might have reduced crab recruitment off central California.

Population Fluctuations of Red King Crab: Research Needs

Based on commercial fishery landings and NMFS groundfish surveys, red king crab abundance appears to fluctuate on the same order as Dungeness crab. Dr. Hayes has summarized such data and suggested hypotheses that might explain relative abundance of king crab as well as Tanner crab and shrimp. Red king crab, P. camtschatica, is the most noteworthy of Alaskan crustacean fisheries since the present demise of commercial stocks has been ruinous for many fisherman. Thorough understanding of the general biology and ecology of all life history stages is needed to better pinpoint causal mechanisms of year-class strength, which might enable earlier forecasts of abundance than the 3-4 year pre-recruit gauge currently provided by NMFS.

As suggested for Dungeness crab, year-class strength is probably determined by some combination of: 1) reproductive success of the mature female population; 2) survivorship of larvae and; 3) survivorship of young benthic juveniles for one to two years after metamorphosis. A suite of biotic and abiotic factors act in optimal or perturbational combinations on these three life history links to produce changes in abundance. Even the fishery itself may exacerbate the effects of suboptimal conditions influencing reproductive effort and survivorship of environmentally sensitive life history stages.

This very short discussion will not allow thorough consideration of the biotic and abiotic factors that might drive cycles of abundance (e.g., spawner and larval-recruit relationships, thermal limits and food requirements of larvae, currents and larval drift, settlement areas, predators and refuge habitat). Rather a list of informational gaps and research needs might direct thought to future programs. While NMFS has provided the most thorough data base for any U.S. commercial crustacean in the case of red king crab, there is still a great deal of information unknown for the species. The following lists pertain to crab biology in the S.E. Bering Sea.

Female stocks and reproductive biology

1. Examination of NMFS survey data to detect interannual change in female abundance relative to areas of larval hatch and development in the S.E. Bering Sea. Since larvae of red king are found over a more restricted range than adult females (Armstrong et al. 1981), a variable percentage of the females may be superfluous to the annual reproductive effort because they spawn in areas un-

suitable for larval and/or early juvenile survival. Otto et al. (1982) show a decrease from 150 million mature females in 1977 to 55 million in 1982. This decline might be more severe if based on regional contrasts (e.g., nearshore vs. offshore of the 70 m isobath, east vs. west of Port Moller, north vs. south Bristol Bay).

2. Reexamine spawner-recruit relationships developed by Reeves and Marasco (1980) in light of Item 1 and results of juvenile surveys suggested under Juvenile Biology. This effort would enable a better gauge of minimum numbers of spawners required for high recruitment based on abundance in "optimal spawning habitat," and estimates of progeny younger than the five year lag currrently required of NMFS data (gear does not adequately catch juveniles until five years after settlement; Reeves and Marasco 1980).

3. Study interannual variation in peak egg hatch based on NMFS "clutch" data. Annual shifts of 1.0 to 1.5 months might reflect winter-spring temperatures and influence larval development time, settlement, and first-year summer growth of 0+ juvenile crab.

4. Investigate timing of the oogenic cycle to partially determine if adverse temperature would sometimes delay reproductive events (e.g., molting and copulation, egg extrusion) with detrimental effects on larval growth and survival.

5. Examine NMFS data to determine major annual shifts in the percentage of the mature female population that are primiparous (newly recruited year-class) or multiparous in regions suggested under Item 1. Incorporate data on clutch size and relate both factors to fecundity to derive potential larval hatch. Correlate annual reproductive effort lagged to population abundance of juveniles.

Larval biology and ecology

1. Better determine major areas of larval hatch along the North Aleutian Shelf (NAS) and in Bristol Bay (Armstrong et al. 1981, present preliminary data on this), and gauge the magnitude of interannual variation (e.g., larval density in 1983 is at least 10x less than in 1982; Armstrong unpublished data).

2. Conduct several consecutive years of larval surveys to compare initial abundance at hatch and survivorship at metamorphosis to later abundance of specific juvenile year-classes.

3. Incorporate physical oceanographic events (notably current patterns and rates, and storm events) to examine the annual direction and extent of larval transport. Use information to gauge the extent of settlement onto optimal "refuge" habitat (see Juvenile biology), as a prediction of 0+ survivorship.

4. Determine lower lethal thermal limits of zoeae and their energetic-growth responses to very low temperatures as an indication of potential survival in years of below average cold (e.g., 1976).

5. Study food preferences of larvae and also feeding rates as a function of temperature and prey density to address requirements for adequate growth and the possibility of starvation.

Juvenile biology

Annual NMFS groundfish surveys do not catch juvenile red king crabs until about five years of age (Reeve and Marasco 1980), probably because of gear type and low effort in areas of initial settlement from the plankton.

1. Determine areas along the NAS and in Bristol Bay where major populations of young juveniles occur (0+ through 4+ age-classes).

2. Characterize the substrate and plant-animal assemblages associated with juveniles to define "refuge" habitat. Estimate the extent of such habitat in different regions of the S.E. Bering Sea.

3. Determine interannual differences in location of year-class settlement and relate to annual distribution of female stocks, areas of larval hatch, and predictions of larval transport as previously noted.

4. Synthesize such data into a qualitative prediction of annual 0+ survivorship based on the extent of settlement into appropriate refuge habitat. Incorporate information on the magnitude of potential prey populations (e.g., yellowfin and rock sole, Pacific cod) as an indication of the importance of such habitat.

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Interannual Variability in the Abiotic Environment of the Bering Sea And the Gulf of Alaska

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Introduction

Recent studies of relationships between ocean/climate variability and that of fish stocks indicate that the key abiotic parameters are turbulence (patchiness and stability), transport, and temperature (e.g., Bakun, Beyer, Pauly, Pope and Sharp, 1982; Sullivan, 1982) and that variations in these features are most critical at early life stages of marine organisms. The oceanographic parameters are related to the atmosphere, a source of momentum, heat, and moisture. Further, transport and turbulence influence nutrient concentrations and primary production.

Some connections between the abiotic and biotic environments are hypothesized for the Bering Sea and Gulf of Alaska. Nishiyama, Hirano, and Haryu (1982) used the term "nursery layer" for "that portion of the water column in which physiological and ecological conditions are advantageous for the survival and growth of pollock at the early life stages in the eastern Bering Sea." The existence of this layer depends on an influx of buoyancy and mixing. Ice melt is the early spring source of buoyancy, and momentum transferred from the atmosphere provides mixing energy. Further, the presence of ice depends on its generation by a loss of heat to the atmosphere and then advection by wind. The stability resulting from these processes is conducive to phytoplankton production and thus is important for the success of other species (e.g., larvae of Tanner crabs; Incze, 1983). Other connections between physical and biological realms are less complex. Along the northern coast of the Alaska Peninsula survival of King crab early life stages may be enhanced by remaining in the nearshore environment (Otto, personal communication, 1983). They are, however, subject to offshore transport which would remove them from their nursery grounds and increase mortality. Similarly, coastal divergence along the southern shore of the Alaska Peninsula may remove larvae (especially pollock) from the Kenai Current and transport them across the shelf where they could be lost to recruitment into the fishery. Temperature itself can affect biota, and McLain and Favorite (1976) have noted the impact of anomalously cold winters on fisheries in the Bering

Sea. Similar relationships between abiotic and biotic components of the environment are demonstrated elsewhere (for example, Parrish, Nelson, and Bakun, 1981; Mysak, Hsieh, and Parsons, 1982; Murray, Leduc, and Ingram, 1983).

It is our intent here to describe some key features of the abiotic environment which are relevant to the biota. Our presentation is based on numerous studies of atmospheric conditions, circulation, and water properties of the Bering Sea and Gulf of Alaska. Comprehensive reviews of the physical environment were recently completed and provide more complete references to regional oceanography (Royer, 1983; Schumacher, Kinder, and Coachman, 1983). After establishing mean or typical conditions, we emphasize interannual signals which may dictate year-to-year survival of organisms. We then suggest further research and strategies which will enhance our understanding of the abiotic environment and its relation to biota.

The Eastern Bering Sea

A major influence on the general atmospheric circulation over the Bering Sea is the region of low pressure, normally located in the vicinity of the Aleutian Islands, and generally referred to as the Aleutian Low. This feature is a manifestation of the passage of storms, which dominate climatology of the Bering Sea (Brower, Searby, Wise, Diaz, and Prechtel, 1977; Overland, 1981). During winter there are typically two storm tracks, one parallel to the Aleutian Islands and one curving northward along the Siberian coast. However, there is always a decrease in the number of storms with increasing latitude (Overland and Pease, 1982). Because of the juxtaposition of the Aleutian Low and the Siberian High, mean winter winds are from the northeast. Outbreaks of cold polar air are a common winter phenomenon and often last for one to two weeks. Mean winds are stronger in winter than during summer and have an interannual signal which affects both sea surface temperature (McLain and Favorite, 1976) and ice extent (Niebauer, 1980, 1981, 1983; Overland and Pease, 1982). During summer, storms tend to migrate northward into the Bering Sea, and mean winds are from the south. Because the meteorology is dominated by storms, vector-mean winds tend to be weak. Direct observations on St. Paul Island indicate the strongest monthly mean wind was only ~3.4m/sec from the northeast (Brower, Searby, Wise, Diaz, and Prechtel, 1977). Further, since most shelf waters are farther than a Rossby radius (~150 km) from the coast, they respond by following the rotating winds. Thus, while winds affect mixing and ice transport and generate current pulses, they contribute little directly to generation of mean current.

There is little or no information showing interannual variations in forcing mechanisms (pressure gradient and tidal current rectification, Schumacher and Kinder, 1983) for the mean coastal circulation. Figure 1 presents a composite of circulation from previous studies (Arsenev, 1967; Takenouti and Ohtani, 1974; Favorite, Dodimead, and Nasu, 1976; Kinder and Schumacher, 1981; Ingraham, 1981a; Salo, Schumacher, and Coachman, 1983; Schumacher, Kinder, and Coachman, 1983). Coastal waters from the Gulf of Alaska flow into the Bering Sea through Unimak Pass and continue northeastward along the Alaska Peninsula. This transport affects water properties, mass balance, and nutrients (Schumacher, Pearson, and Overland, 1982). The strongest baroclinic gradient is in the vicinity of the 50-m isobath (or associated with the inner front). The current flows counter-clockwise around Bristol Bay and then northwest past Nunivak Island. As tidal current magnitude decreases to the north (Pearson, Mofjeld, and Tripp, 1981), both the inner front and coastal current appear to be focused near the 30-m isobath. Flow exits the system through Shpanberg Strait and Bering Strait. Current speeds averaged over periods greater than one month are statistically significant and vary from ∿5 to 25cm/sec in Unimak Pass, ∿1 to 6cm/sec along most of the path, and ∿5 to 10cm/sec in Shpanberg Strait; the higher values are typically present in winter. Although we expect little interannual variation in the mean along-isobath current, pulses of offshore transport occur along the Alaska Peninsula (Schumacher and Moen, 1983).

Between the 50- to 100-m isobaths all data from the southeastern sub-region show statistically insignificant (<1cm/sec) mean flow and sluggish transport here is a year-to-year feature. Similar conditions appear to obtain for the more sparsely studied region between St. Lawrence Island and St. Matthew Island. In the vicinity of the middle front (or the 100-m isobath) and over the outer shelf, current speeds are statistically significant with alongshelf means between 1 and 10cm/sec and cross-shelf means of 1 to 5cm/sec. The former current appears to be continuous over the outer shelf, flowing northwestward to the vicinity of Cape Navarin. Here, some portion of the flow follows the 80-m isobath toward the northeast, exiting the region through Anadyr Strait at mean speeds of 10 to 20cm/sec. Although forcing for the along-isobath flow is the same as that for the coastal current and likely does not vary greatly from year to year, the cross-shelf flow is related to other forcing mechanisms (probably fluctuations in the Bering Slope Current) and likely varies.

Changes in flow towards the northeast along the Aleutian Islands were inferred by Kihara (1982) and correlate with mean bottom water temperature over the outer portion ($z>100$ m) of the shelf. This suggests an interannual signal in Bering Slope current transport. Off the southeastern shelf, the Bering Slope current is rich in baroclinic structure and eddies and flows northwestward along the continental slope at 5 to 15cm/sec (Kinder, Schumacher, and Hansen, 1980). It is not clear where the Bering Slope Current originates, although water mass analysis suggests the presence of Alaskan Stream water. These waters likely entered the Bering Sea through the deeper passes in the western Aleutian Islands. All evidence suggests that slope transport is highly variable over time scales of months to years.

While observations of interannual signals in circulation are not definitive or do not exist, such signals clearly exist in water properties, with those in temperature and ice extent being most dramatic (Niebauer, 1980, 1983). Typically, waters over the south-

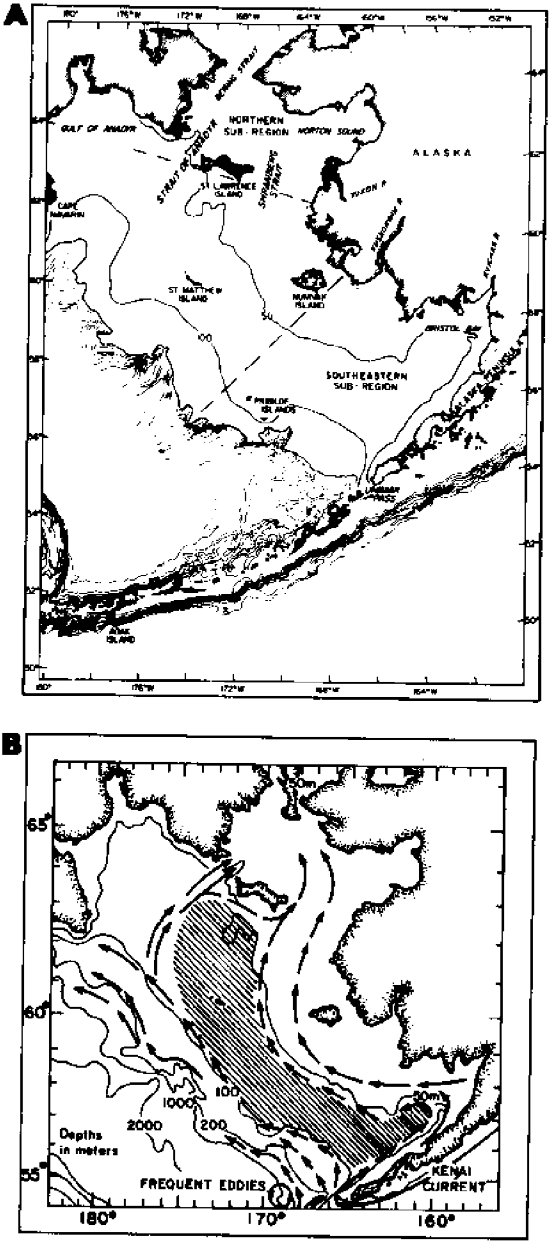

Figure 1. A) Geographic names and prominent bathymetric contours, and B) schematic of long-term mean circulation based on direct measurements, inferred baroclinic flow, water mass analysis and model results.

eastern shelf can be classified by water column structure and depth, with domains separated by fronts (Fig. 2). During winter, the middle shelf domain becomes uniformly mixed as a result of heat flux and wind mixing; with melting ice present, however, two-layered structure is rapidly reestablished (Kinder and Schumacher, 1981). Observations presented by Kitani and Kawasaki (1978) and Salo, Pease, and Lindsay (1980) suggest that the three hydrographic domains present over the southeastern shelf extend northward to the vicinity of St. Lawrence Island. Shoreward of the 100-m isobath (away from the influence of advection of slope water onto the shelf) heat content is dominated by net radiation and air/sea exchange rather than advection (Reed, 1978). Coachman and Charnell (1979), for example, found a high correlation (-0.96, between mean lower-layer temperatures in June over the middle shelf and degree days of frost for the preceding winters. Year-to-year, monthly mean ice extent has been shown to vary by up to 500km (Walsh and Johnson, 1979; Overland and Pease, 1982).

Analysis of ice extent, sea surface temperatures (SST), degree days (DD), surface and upper-air (700-mb) winds, and storm tracks has lead to a conceptual model in which upper-air pressure fields are the primary mechanism causing interannual variations in the first four parameters (McLain and Favorite, 1976; Niebauer, 1983). For example, in Fig. 3 the anomalous winds from the north over the winter of 1975/1976 are correlated with extremes of ice cover, ~2°C below normal SST and ~400 DD above normal conditions. While the linkage seems straightforward, note that from October 1980 to February 1981 mean monthly winds from the north were stronger than in 1975/76; however, DD's and SST were above normal, and ice cover was far below (~30%) normal. The seeming paradox of strong winds from the north not causing much cooling or ice production in 1980-81 was explained by the nature of upper air patterns which resulted in warmer air being pumped into the Siberian high (Niebauer, 1983). Overland and Pease (1982) also conclude that upper-air pressure patterns steer storms and were the primary factor in determining year-to-year variations in ice cover. Rogers (1981) suggests that steering is determined primarily external to the Bering Sea (that is, on a global scale).

Studies also have related ice to biota (Alexander and Niebauer, 1981, Niebauer, Alexander, and Cooney, 1981, and Niebauer, 1982). Ice can affect nutrient concentrations and phytoplankton populations in several ways: ice melt creates local stability and fronts, which promote plankton booms, and under certain conditions nutrients are upwelled at the ice edge. Alexander and Niebauer (1981) note that the location of the marginal ice zone may be critical: when ice cover is extensive, it approaches the shelf break in the proximity of nutrient rich waters. If such waters are made available through upwelling, then the phytoplankton bloom can be of longer duration. Cross-shelf transport of the Bering Slope waters could also provide a mechanism for a richer nutrient supply near the ice edge even without extreme ice cover.

Clearly, interannual variations exist in the abiotic environment, and there are suggested relationships to biota. There are, however,

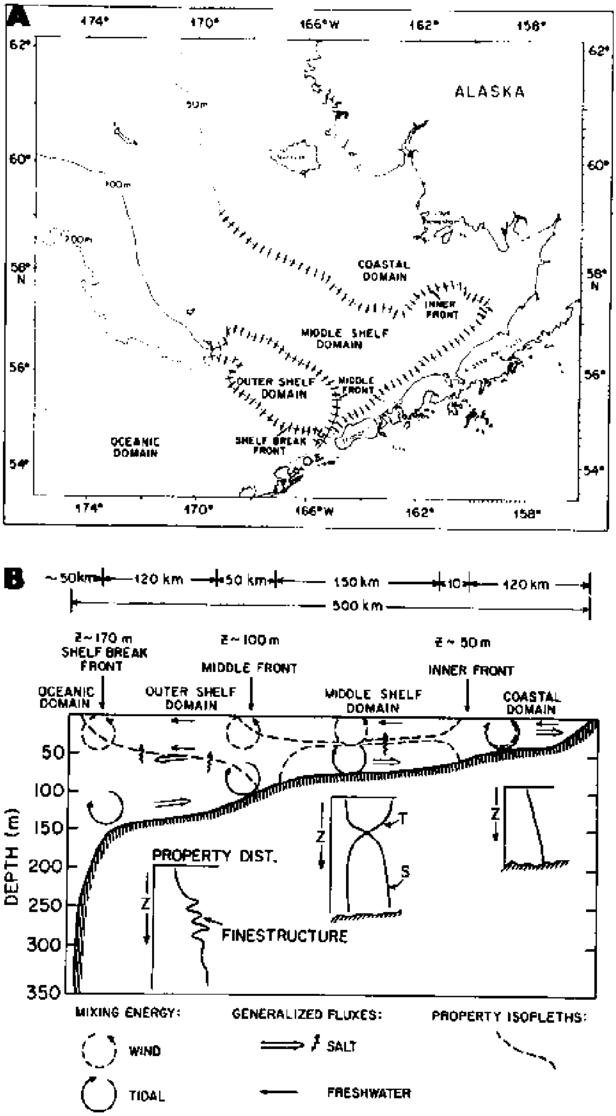

Figure 2. A) Approximate locations of hydrographic domains and fronts over the southeastern Bering Sea shelf, and B) a schematic interpretation on the cross-shelf plane of energy balance, fresh and salt water fluxes, and vertical structure. Note that the middle shelf domain becomes mixed either during periods of surface cooling (winter) or during extreme storms (from Schumacher, Kinder and Coachman, 1983).

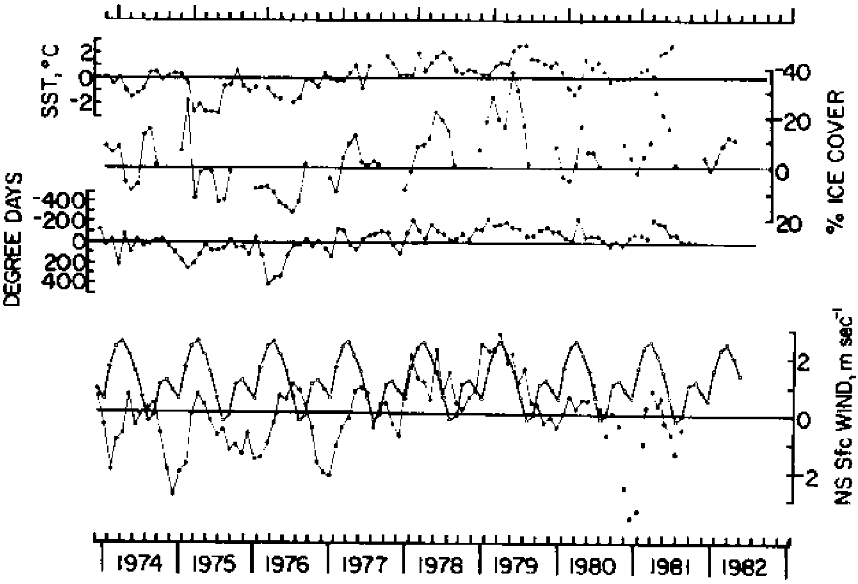

Figure 3. Departures from monthly mean % ice cover, sea surface temperature (SST), degree-days (DD), and north-south component of the surface wind (solid line with solid circles) from the eastern Bering Sea. In the wind panel, open circles with solid lines are seasonal mean winds plotted such that, for a given month, when wind anomalies (solid dot) fall below the seasonal mean (open dot), the wind is actually from the north regardless of the sign of the anomaly. When the anomaly rises above, the wind is from the south. Wind data have been smoothed by a 3-month running mean (from Niebauer, 1983).

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many gaps in our knowledge of the abiotic environment. Among the features of the Bering Sea which need further investigation are the Bering Slope Current, the nature of "melt-back", and the frontal systems. It is clear that the Bering Slope Current is a source for heat, salt, momentum, and nutrient-rich water which bathes the outer shelf. These properties are important to transport across the outer shelf, the thermodynamic limit of ice, and biota. Yet, very little is known about the current itself. Although ice melt and biota are related, we do not have a definitive understanding of the melt-back process nor of the longevity of the induced stability. Enhanced vertical fluxes occur at the inner and middle fronts (Coachman, Kinder, Schumacher, and Tripp, 1980). Other studies show that plankton communities are organized by the system of fronts and domains (Iverson, Whitledge, and Goering, 1980; Goering and Iverson, 1981) and that the distribution of feeding sea birds around the Pribilof Islands correlates with the location of the local inner front (Kinder, Hunt, Schneider, and Schumacher, 1983). The physics that generates such fluxes and the relation of cross-shelf currents to the the middle front are not known.

The Gulf of Alaska

Meteorology in the Gulf of Alaska is dominated by strong cyclonic systems. These include the Aleutian Low, a low over the Gulf, a low over central Alaska, and a stagnating low off the Queen Charlotte Islands, where these four weather types occur more than 70% of the time (Overland and Hiester, 1980). Low-pressure systems can be enhanced by cyclogenesis (Winston, 1955). Adiabatic ascent of moist marine air over the coastal mountains leads to extremely high precipitation rates (some greater than 8m/yr) in the coastal drainage areas and hence to a baroclinic component in the coastal circulation (Royer, 1982). The general nature of the cyclonic systems is such that wind stress tends to augment the baroclinic component by confining it against the shore (favoring downwelling) and by generating a barotropic pressure gradient which induces flow in the same direction. These conditions generally occur from the southeast coast around the perimeter of the Gulf to Kodiak Island. Somewhere along the Alaska Peninsula a transition occurs, and wind stress here usually favors upwelling between April and December (Ingraham, Bakun, and Favorite, 1976) and generates a barotropic pressure field in opposition to the baroclinic field (Schumacher, Pearson, and Overland, 1982). From Brower, Searby, Wise, Diaz, and Prechtel (1977), the maximum monthly mean alongshore wind is ∿3.1, 3.2, and -4.1m/sec off Sitka, Middleton Island, and Unimak Pass respectively (where positive values imply coastal convergence or downwelling). During summer, about 30% of the time the weather types are either a high pressure over interior Alaska or a Pacific anticyclone (Overland and Hiester, 1980). These conditions tend to result in eastward wind stress (relaxation of downwelling) and can weaken or reverse the coastal current (Schumacher and Reed, 1980).

Studies of coastal meteorology indicate that isobars are packed against the coastal mountains with winds increasing significantly nearshore. Katabatic winds and pressure gradient winds (associated with glaciers and valleys respectively) also have a profound impact on coastal winds (Reynolds, Macklin, and Hiester, 1981). Most oceanographic studies, however, use winds generated by surface atmospheric pressure data (Bakun, 1973). When compared to actual winds on Middleton Island, Bakun's winds were reasonably accurate in displaying seasonal trends but missed high-frequency changes (Royer, 1983). In contrast to the Bering Sea winds in the Gulf of Alaska are more persistent in direction, for example (Schumacher and Reed, 1980) show a three-month period of wind-stress favoring coastal convergence , and data from most meteorological stations are of limited use for oceanographic interpretations.

Unlike the sluggish coastal current in the Bering Sea, coastal flow around the Gulf of Alaska (from southeast Alaska to Unimak Pass) is often vigorous. Results from recent studies (Royer, Hansen, and Pashinski, 1979; Royer, 1979, 1981, 1982; Hayes and Schumacher, 1976; Hayes, 1979; Schumacher and Reed, 1980; Mysak, Muench, and Schumacher, 1981; Niebauer, Alexander, and Cooney, 1981; Reed and Schumacher, 1981; Reed, Schumacher, and Wright, 1981; Schumacher, Pearson, and Overland, 1982) are compiled as a general circulation scheme in Fig. 4. The coastal current is distinguished by its low-salinity signal, a consequence of accumulation of runoff beginning along the British Columbia coast. The strongest baroclinic gradients are found west of Kayak Island along the Kenai Peninsula. The portion of the Alaska Coastal Current from Kayak Island west to Unimak Pass is known as the Kenai Current.

Mean speeds along the southeast coast are not well known, but likely vary between 10 and 30cm/sec. Between Icy Bay and Kayak Island observed mean currents speeds are somewhat stronger (10 to 60cm/sec). Several authors note that the presence of Kayak Island causes some portion of the Coastal Current to become incorporated with the shoreward edge of the oceanic circulation. West of Kayak Island, circulation over the shelf is complex and is typified by two quasi-permanent gyres (Feely, Baker, Schumacher, Massoth, and Landing, 1979). Along the Kenai Peninsula, flow in the Coastal Current is best documented: mean speeds vary from 20 to over 100cm/sec, the current is usually confined to within 25km of the coast, and baroclinic structure is substantial over the upper 100m. Baroclinic transport here can be greater than $1\times10^6 m^3$/sec during the one-month duration fall maximum. The Kenai Current flows westward into Shelikof Strait (primarily through Kennedy Entrance) and results in mean speeds of 10 to 70cm/sec toward the southwest (Mysak, Muench, and Schumacher, 1981). Data from the western Gulf of Alaska shelf indicate that some fraction of the Kenai Current flows along the Peninsula and exits this shelf via Unimak Pass (Schumacher, Pearson, and Overland, 1982).

Forcing for the Alaska Coastal Current is primarily a combination of cross-shelf pressure gradients resulting from freshwater addition and wind-induced sea level changes: along most of the Gulf of Alaska coast, both mechanisms are additive in effect, yielding a counterclockwise flow. The coastal current, particularly west of Kayak Island, is not related to oceanic forcing. Off the southeast coast, however, hydrographic data (Ingraham, 1979) and adjusted sea level measurements (Reed and Schumacher, 1981) suggest that some freshwater discharge is lost from the coastal current either by wind effects or interactions with oceanic features. Along the Alaska Peninsula winds tend to act in opposition to the Kenai Current and induce upwelling. Throughout the Gulf of Alaska, nutrient concentrations below the halocline (~200 to 300 m) are quite high (Reid, 1965). Enhanced concentrations of nitrate and chlorophyll-a have been observed in Unimak Pass (Hattori and Goering, 1981) and may be a manifestation of upwelling along the Alaska Peninsula and subsequent transport by the Kenai Current.

While both primary forcing mechanisms for the Coastal Current vary annually, they also contain longer period variations. For example, as shown in Fig. 5, anomalies of upwelling index and freshwater discharge have an impact on transport. The strongest correlation (0.74) was between in-phase transport (station 1-2) and freshwater discharge, while that for wind and transport (station 1-7) was weaker (0.42). As Royer (1981) noted, however, the transport data for the months December through March are very sparse. From an analysis of fifty years of air temperature and precipitation data, interannual variations in discharge were as large as a factor of

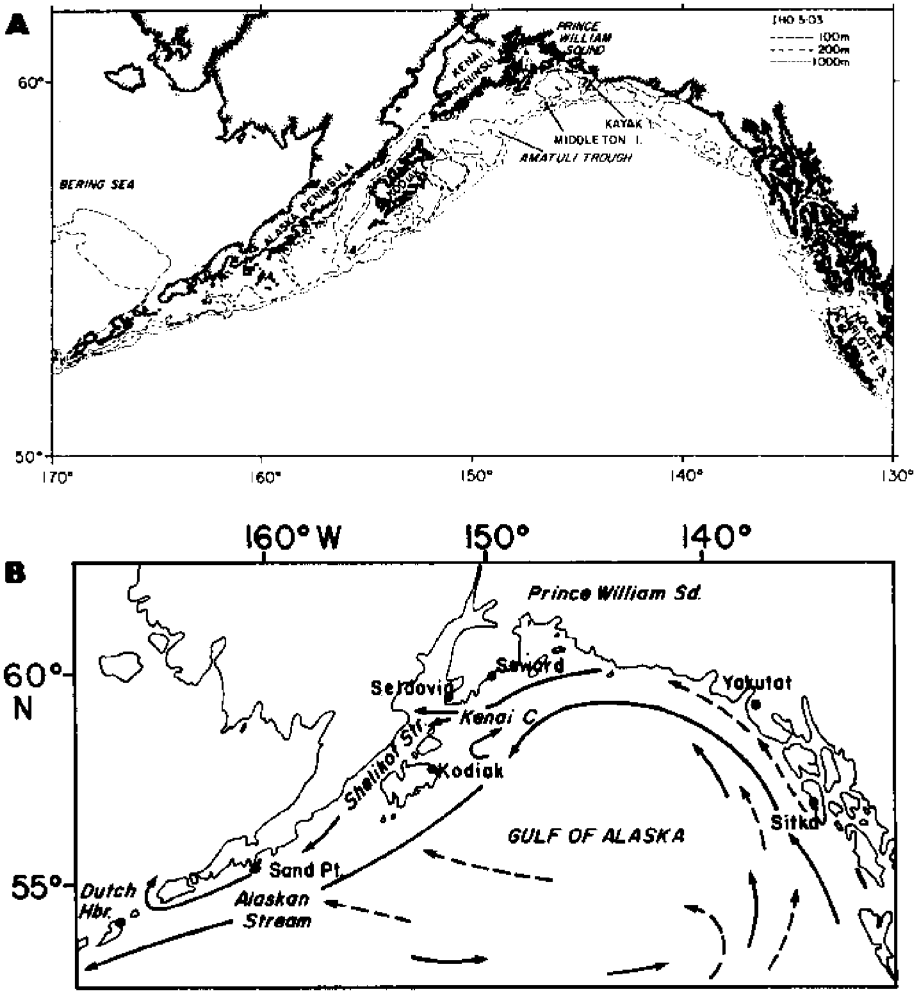

Figure 4. A) Bathymetric features of the Gulf of Alaska and B) schematic of long-term mean circulation based on direct current measurements, inferred baroclinic flow, and model results. Note that the dashed arrows on the Coastal Current indicate regions where baroclinic flow is less vigorous while those in the Gulf of Alaska represent anomalous behavior in the Alaskan Stream.

two (Royer, 1982). As the transport increased, observations indicate that deeper waters are "drawn up" or entrained into the flow. This is clearly shown in CTD time-series off Seward as an annual signal (see Muench and Schumacher, 1980, their Fig. 4 after Royer, 1975). While the mechanism is not defined, it is likely that as transport increases, more bottom waters are drawn across the shelf (or along

Amatuli Trough). This could occur during either the peak baroclinic flow (October) or the peak barotropic flow (December-March).

Interactions between oceanic circulation and the shelf may be important at times in some regions. Measurements along the shelf break (~200m) from Icy Bay to Unimak Pass show a counterclockwise flow with alongshelf mean speeds of 10 to 30cm/sec, with the higher values generally occurring during winter (Lagerloef, Muench, and Schumacher, 1981; Muench and Schumacher, 1980; Hayes, 1979). Over the northeast Gulf shelf, Hayes (1979) showed that the alongshore flow was consistent with barotropic, quasi-geostrophic dynamics (i.e., wind-induced changes in sea level); currents off the shelf (~250m), however, were much more variable and indicated the influence

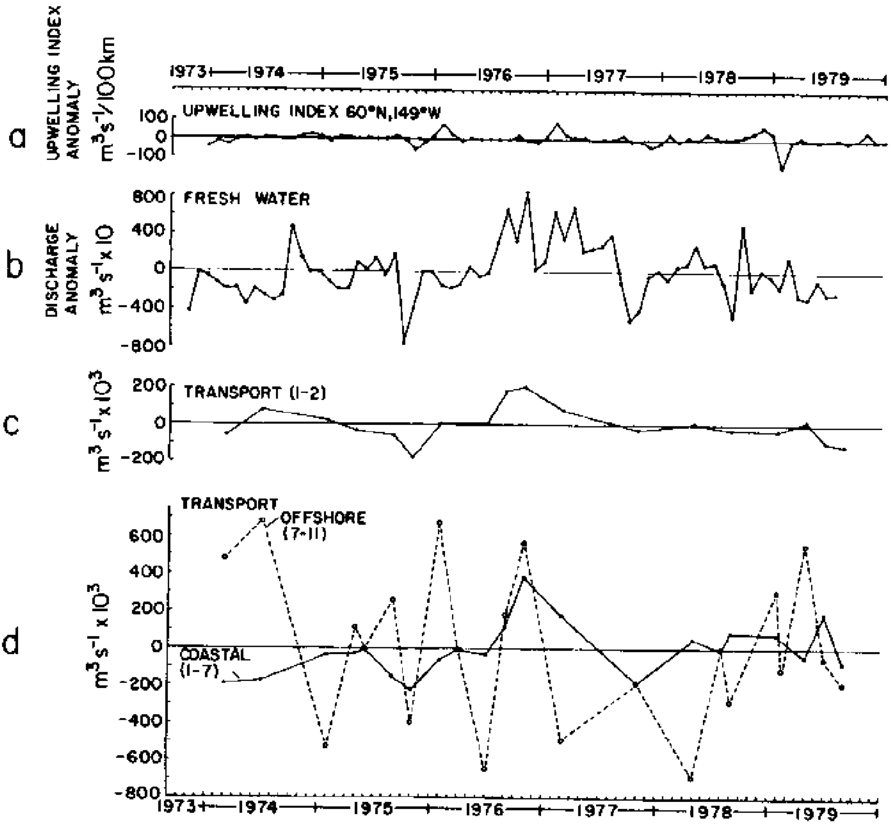

Figure 5. Anomalies of a) upwelling index, b) freshwater discharge. c) baroclinic transport between stations 1 and 2 of Seward section, and d) baroclinic transport for the coastal (solid) and offshore (dashed) segments of the Seward section from 1973 to 1979 (from Royer, 1981).

of oceanic forcing. Lagerloef, Muench, and Schumacher (1981) also attributed the very low-frequency (<0.1cpd) fluctuations to oceanic-scale, aperiodic features such as eddies or meanders. West of Kayak Island, the current over the slope (or Alaska Current) can be clearly identified by a low-salinity surface layer (Ingraham, 1979), by anomalously warm sea surface temperatures (Royer and Muench, 1977), and sometimes by clouds of suspended particulate matter concentrations (Feely, Baker, Schumacher, and Landing, 1979). Direct observations of currents seaward of Amatuli Trough indicate that in addition to the along-isobath mean flow, high levels of fluctuating or eddy kinetic energy exist, which suggests the influence of the Alaska Current (Niebauer, Roberts, and Royer, 1981). Reed, Muench, and Schumacher (1980) showed an eddy in the vicinity of Stevenson Trough, and satellite-tracked drifters deployed in this feature moved northward across the shelf into Shelikof Strait at speeds of about 50cm/sec. These examples of ocean/shelf interactions are all likely to vary from year to year.

Tabata (1982) discussed the existence of intense baroclinic, clockwise-rotating eddies offshore from Sitka. These features may be evidence for an interannual signal in the source waters of the Alaskan Stream. The Sitka eddy seems to be a feature which is intermittent in time, but nearly always occurs near the same site. Its volume transport is appreciable ($\sim 10 \times 10^6 m^3$/sec referred to 2000db), but much of its baroclinic structure seems to result from an entrainment of coastal water into the eddy. The overall effect of such eddies on water properties over the mid- and inner-shelf is not known. Another mechanism which links shelf flow and properties to oceanic features has been elucidated in the Kodiak bank-trough region by Lagerloef (1983). He showed that the relatively weak ($\sim$5cm/sec) southwesterly mean flow over the banks, which is likely a result of forcing by the Alaskan Stream (50-100cm/sec), conserves potential vorticity by following isobaths. Even over the relatively narrow ($\sim$20km) troughs there is a shoreward flow on the upstream side and seaward flow on the downstream side. This mechanism may also be important for transport in other cross-shelf features such as Amatuli Trough or the Yakutat Canyon.

We next consider variations of the Alaskan Stream. This deep, intense offshore flow (see Fig. 4) is the poleward boundary of the cyclonic subarctic gyre. As the slow, eastward-flowing West Wind Drift approaches the Washington-British Columbia coast, the flow diverges with the southern branch forming the California Current and the northern one the source waters for the Alaskan Stream (Dodimead, Hirano, and Favorite, 1963). The stream source waters carry a warm-water signature into the Gulf of Alaska, and they are also diluted along their path. After leaving the head of the Gulf, the flow narrows appreciably and through vorticity conservation attains characteristics similar to western boundary currents. The stream continues along the Aleutian Islands and eventually enters the western Bering Sea.

Along the Aleutian Islands, the Alaskan Stream is a narrow, high-velocity flow with a total transport of perhaps $20 \times 10^6 m^3$/sec, referred to a deep reference level such as 3000m (Reed, 1983).

Although time variations in flow here do occur, it is not clear what form they take or what induces them. From the data in Favorite, Dodimead, and Nasu (1976), Reed, Muench, and Schumacher (1980) concluded that the suggestion of a seasonal signal may be an artifact from failure to adjust the transport with near-bottom isopycnal slopes in water depths less than 1500m. A possible cause of temporal variation is quite localized changes in wind-stress curl near some of the Aleutian Islands; wind data are not available on a scale small enough to test this, however.

We have recently obtained data and performed analyses that show large coherent changes in flow in the eastern part of the Alaskan Stream and suggest a mechanism that may cause them. The variations to be discussed appear to be largely interannual. Fig. 6 shows the geopotential topography of the sea surface, referred to 1500db, from the data obtained on cruises of the NOAA ship *DISCOVERER* in winter 1980 and summer 1981.

Along the Aleutians, flow was similar during the two periods, although there was recirculation and inflow of western subarctic water in winter 1980 that was absent in summer 1981. To the east, however, the differences are striking. In winter 1980, inflow had all occurred on the east side of the Gulf to produce a very typical flow structure (Dodimead, Favorite, and Hirano, 1963) with normal transports of $12\text{x}10^6\text{m}^3$/sec and peak speeds of 100cm/sec. In summer 1981, inflow on the east side of the Gulf was apparently disrupted; only about half the normal transports and peak speeds were present between 145 and 155°W. Also, between 155 and 165°W there was an appreciable inflow across the southern stream boundary. The situation suggests a split in the subarctic gyre; part of the source water flowed into the head of the Gulf, but the rest turned much farther west than normal before joining the stream.

It seems unlikely that integrated Sverdrup transport induces time changes in flow (Blaha and Reed, 1982), at least without some very long lag (Lighthill, 1969), but evidence is mounting that the ocean responds rapidly to differential Ekman pumping in the form (Meyers, 1975):

$$W=\mathrm{div}_h \vec{M} = \mathrm{curl}_z \frac{\vec{\tau}}{\rho f} \quad ,$$

where $\vec{M}$ is horizontal Ekman transport, $\vec{\tau}$ is the wind stress, ρ is density, and f is the Coriolis parameter. Time integration of the vertical velocity W yields the isopycnal displacement, and the horizontal difference in displacement is proportional to baroclinic flow. After examining wind-stress maps prepared by A. Bakun, it appeared that the southern boundary of the stream near the Alaska Peninsula (approximated by 52.5°N) was a region with large changes that might be crucial to the inflow of stream source waters. The concept adopted is that anomalously weak or negative local wind-stress curl between the coast (134°W) and the center of the Gulf (approximated by 146°W) may reduce the normal isopycnal slope (and the flow) of source waters into the Gulf and that a strong westward increase in local curl along the south side of the stream may enhance northward flow there. The results of computations of the effects of differential Ekman pumping, by time integration of W for three months prior to the cruises, for this zone is shown in Table 1.

Table 1. Estimates of the horizontal differences in isopycnal displacement integrated over the periods shown from eq.(1). The estimates were made along 52.5°N for two zones: (1) 146 to 134°W; and (2) 161 to 146°W.

Period	Displacement (m) (146-134°W)	Displacement (m) (161-146°W)
Nov. 79 - Feb. 80	9	-5
May - Aug. 81	0	4

Prior to the winter cruise there was a relatively large isopycnal displacement, which should enhance inflow, on the east side of the Gulf, and the negative wind distribution to the west would further tend to funnel flow into the Gulf. Before the summer 1981 cruise though wind stress over the east side of the Gulf collapsed, and the increase in curl to the west created a tendency to divert the inflow westward as observed. The total difference in differential displacement is 18m; although these are not absolute slopes, the displacements are in the right sense to suggest that differential Ekman pumping may induce significant changes to the flow into the Gulf. In an effort to extend the time scales discussed and to provide information that is easy to visualize, we show time-series plots of the difference in wind-stress transports over the zones 146-134°W and 161-146°W for the five-year period 1978-1982 in Fig. 7. Since the increase or decrease of local wind-stress curl is usually approximately linear with longitude, presentation in this form (as differences in integrated transport) allows one to envision large positive differences as inducing northward geostrophic flow through differential Ekman pumping and vice versa. There are five periods of two months or longer duration with clear divergence of the two plots that might lead to a split inflow. The periods of expected weak flow are early summer 1978, fall 1978, early summer 1979, summer 1980, and summer 1981. During 1978-79 a few hydrocast sections were taken off Kodiak Island (Reed, Muench, and Schumacher, 1980). The transport in early June 1978 was only $8.0 \times 10^6 m^3/sec$, in agreement with expectations, two values in October 1978 were 10 and $11 \times 10^6 m^3/sec$, and a normal transport of $12 \times 10^6 m^3/sec$ was present in February 1979. Values were not available during the possible periods of weak transport in early summer 1979 and summer 1980, and the values for summer 1981 averaged about $7 \times 10^6 m^3/sec$. The periods of reduced transport do appear to occur mainly in summer; they probably do not occur every summer though, and values as low as those in summer 1981 may be rare. These variations only appear to occur in the eastern part of the stream and not along the Aleutian Islands.

What are the easily discernible effects during these periods of weak flow in a region such as off Kodiak Island? It is not easy to derive volume transport from simple observations, but peak speeds also appear to be reduced, as measured at our current moorings off Kodiak Island (Reed, Schumacher, and Blaha, 1981, and data in preparation) during the periods of low transport. Furthermore, the subsurface waters were abnormally warm and dilute to depths as great as 1000m. At first this situation seems curious because the

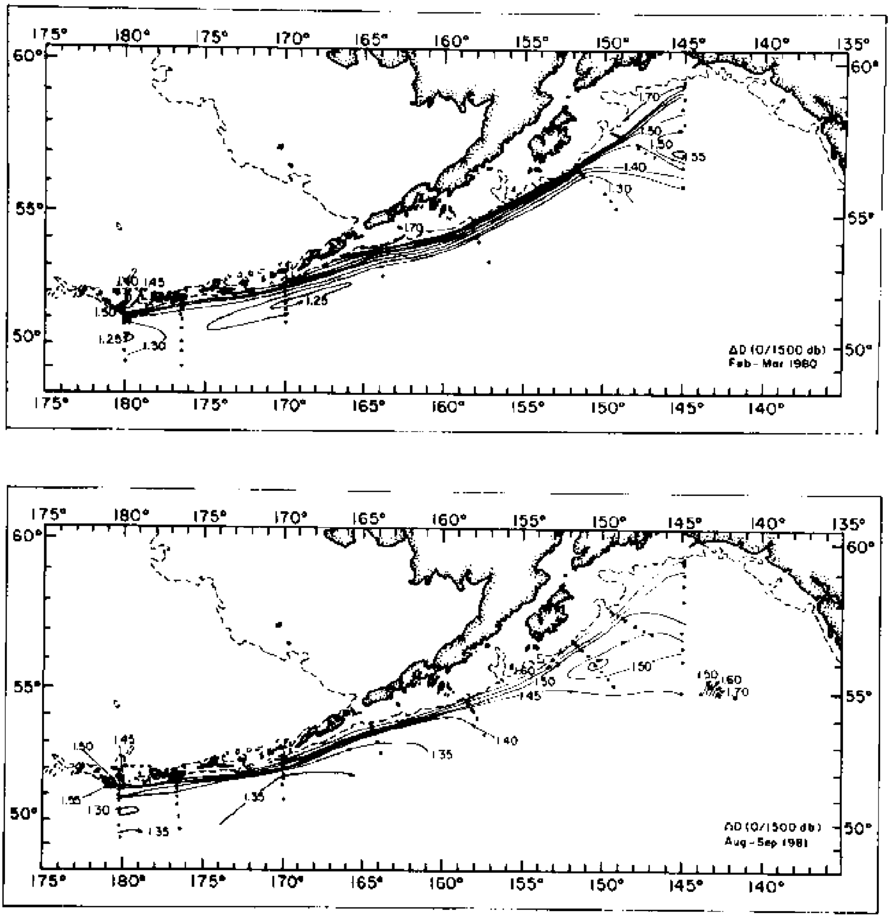

Figure 6. Geopotential topography (ΔD, dyn m) of the sea surface, referred to 1500db, 11 February - 3 March 1980 (upper panel) and 25 August - 16 September 1981 (lower panel).

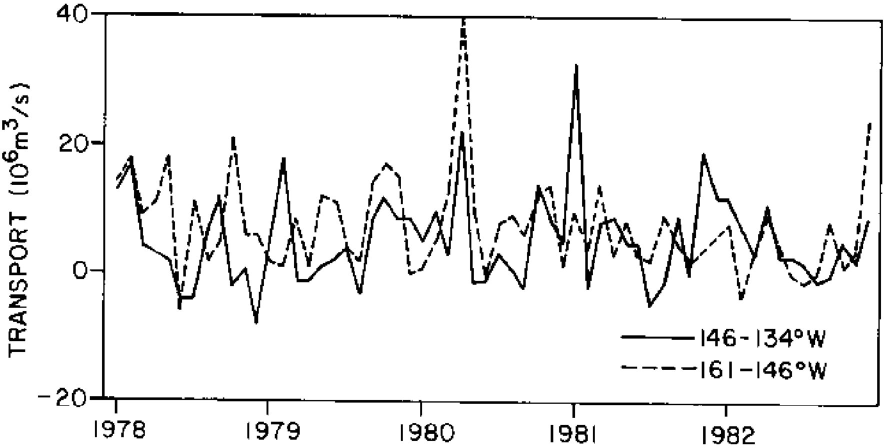

Figure 7. Plots of the difference in integrated wind-stress transport along 52.5°N between 146 and 134°W and between 161 and 146°W, 1978-1982 (from Reed, 1983).

stream is the source of the warm, dilute water, and it was weak. During the periods of weak flow though the cold, saline subarctic water which normally adjoins the stream is displaced, and loss of heat and gain of salt by lateral mixing between these water masses is impeded. The duration of these periods of weak inflow is not exactly known, but 3-4 months may be typical.

It is clear that interannual variations occur in the abiotic environment of the Gulf of Alaska, with those in transport of both the Alaskan Stream and the Coastal Current being marked. The Alaskan Stream is a source of momentum, heat, salt, and nutrients. It is not certain, however, how these properties are fluxed onto the shelf nor what the nutrient concentrations are. We have provided evidence for shelf/slope exchange due to eddies and flow up trough-like features, but details of how often eddies occur and what volume is exchanged are not known. While the troughs provide access of deeper water to the vicinity of the coast, the mechanisms by which these waters are incorporated into the coastal flow are not known. Although our knowledge of the Alaska Coastal or Kenai Current has grown in the past five years, there is little information regarding this feature west of Shelikof Strait.

Future Fisheries Oceanography Cooperative Research

In order to elucidate relations between the abiotic and biotic environments and their interannual variations, we suggest the following plan. First, we believe that existing environmental data have not been exhaustively examined for interannual variations. For example, Enfield and Allen (1980) examined sea-level and SST anomalies, with Yakutat as their northern-most station. Such analyses could be extended to Dutch Harbor. Kruse and Parker (1983) have assembled a bibliography of fisheries-related oceanography in the Gulf of Alaska; this could also be done for the Bering Sea. While such bibliographies are useful, to make further advances in our understanding, a comprehensive environmental data base should be established. Ingraham (1981b) has assembled temperature and salinity data from the eastern Bering Sea shelf. A similar product for the Gulf of Alaska is not yet available, but an environmental data base is being assembled at PMEL for both regions. Once the historical data are readily accessible, they can be analyzed both separate from biotic data using existing systems such as R2D2 (Pearson, 1981) and in conjunction with fishery data as proposed by the PMEL/NWAFC Fishery Oceanography Cooperative User System (FOCUS). In this manner, we would enhance our knowledge of physical processes and then examine linkages between abiotic and biotic components of the ecosystem. With respect to the former goal, it is extremely important to elucidate time-scales of events. Much emphasis has been placed on monthly means and anomalies, yet one extreme storm can critically alter stratification, water properties, and transport. Averaged over a month, such an event might be obscured, but its impact on biota could be devastating.

The co-analyses should lead to reasonable hypotheses; one cannot test a hypothesis, however, with the data used to establish it. Further, very few historical studies were conducted with interdisciplinary analyses in mind; hence new results will occur only in a serendipitous manner. Thus the second stage should be integrated field observations, such as those conducted by PROBES. Such work must be continued for an adequate period of time (order years), taking advantage of ongoing analysis and results to redirect field studies. We also recommend that models that mirror observed processes be developed in parallel with field studies so that various interactions among parameters can be tested.

As the second stage evolves, we believe that it will become clear what the primary physical factors are and thus how they could be monitored. For example, if increased transport in the Kenai Current results in more slope water being drawn across the shelf, providing transport for heat, nutrients, salt, and larvae to the coastal embayments, and if the correlation between transport and changes of sea-level is strong, then continued monitoring of tidal heights at Seward may enable one to predict recruitment of such larvae as halibut. Admittedly this is a simplistic example, and it may be more realistic to think that differences in adjusted sea level (say between Seward and a tide station established on Middleton Island) would be a better index. McLain and Parish (1982) have noted the importance of routine monitoring of coastal currents for climate and fisheries, and they suggested the following measurement programs: 1) observations of sea surface slopes between tide gages, 2) frequent sections of closely spaced XBT drops, and 3) measurement of surface currents by automatic ship drift computations. Other remote sensing techniques will also be useful, particularly those which are not affected by cloud cover. In all aspects of this scheme, a key requirement is that scientists from many disciplines must work together to understand the complexities of our ecosystem.

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Commentary

Interannual Variability in the Abiotic Environment of the Bering Sea And the Gulf of Alaska

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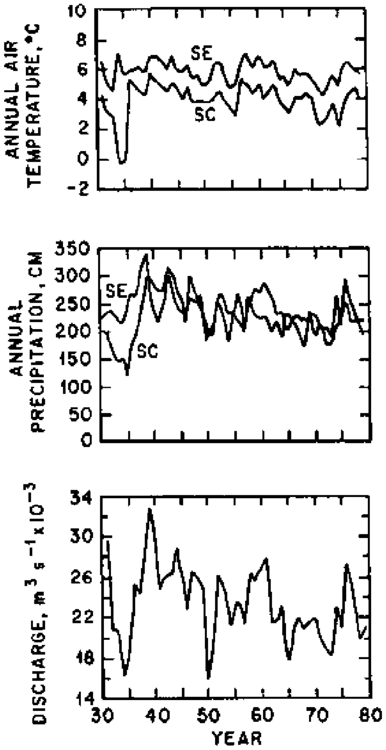
This summary by Schumacher and Reed of North Pacific environmental conditions tends to concentrate on the seasonal variability as observed since 1974, which is reasonable since there has been extensive field work in this region since 1974. However, these data should be evaluated in the proper context using all available data. The argument that little other comprehensive data are available is not necessarily valid. Questions should be addressed about how the circulation system here operates, that is, what forces influence the system and are long term measurements of these forces available?

Some water property data exist for the Gulf of Alaska for the period 1954-1960 and can be compared with the 1974+ data to determine whether this latter period is typical. In addition to these hydrographic data, a fairly comprehensive suite of meteorological data exist for this region. A necessary step in any analysis is to determine those parameters which significantly influence the ocean circulation. Possible candidates for these vital parameters are wind stress and precipitation over both the open ocean and coastal regions (Royer, 1981a & b). The data for these parameters are available for at least 35 years (Royer, 1982). [Schumacher and Reed also indicate that long time histories of sea level measurements are available for various locations around the Gulf of Alaska, however, these sea levels primarily contain the local fresh water discharge signal (Royer, 1979).] For example, as can be seen in the time series in Figure 1, the calculated fresh water discharge for Southcoast Alaska has quite low mean values (<20,000 m^3/s) in the mid-1930's raising rapidly to greater than 30,000 m^3/s) in 1940 with a general decline through the early 1970's when it increased again. These changes are caused by fluctuations in the annual coastal air temperature and precipitation (Fig. 1). This fresh water discharge modified by the wind stress is responsible for the fluctuations found in the Alaska Coastal Current. It is within this coastal current that a large portion of the marine mammals are found. Fluctuations in this flow might have significant impact on the water balance for the entire shelf.

Figure 1. Annual mean air temperature (top) for southeast Alaska (SE) and southcoast Alaska (SC), precipitation (middle), and fresh water discharge (bottom). (From Royer, 1982)



We also have evidence of some recent changes in the large scale ocean circulation. Satellite tracked drifters released in 1976-77 along about 160°W north of 45°N tended to move northward and become involved in the Alaskan Gyre. Drifters released north of 45°N since 1981 have described different trajectories. Instead of entering the Alaskan Gyre they have entered the California Current system. Even drifters released as far north as 52° have followed this pattern.

The Sverdrup transport across the Gulf of Alaska had northward anomalies in 1976-80 whereas in the 1950's and after 1981 the anomalies have been zero or slightly southward. The cause-effect relation between the wind system and ocean circulation, is beyond our capabilities to determine presently. However, it would be useful to assemble the sea level pressure and calculated winds along with their anomalies since 1947 and to make these available to fisheries oceanographers in order to determine if any major shifts in the fisheries can be seen to coincide with anomalies in the wind field. There is now an ongoing study to evaluate how well these 3° x 3° pressure fields can be used to determine local winds over the northern Gulf of Alaska.

The longest time series of hydrographic data in the Gulf of Alaska, other than Ocean Station PAPA data, has been gathered at the mouth of Resurrection Bay near Seward, Alaska. This time series began in December 1970 and continues at the present time. Temperature and salinity versus profiles have been obtained on 56 occasions during this series, (Fig. 2), however, they are irregularly spaced in time. Anomalies in temperature and salinity are determined by subtracting the monthly mean values, (Fig. 3). Based on these data 1971, 1975 and 1982 were cold years with 1973 and 1976-77 being warm years. The 1976-77 period also displayed negative salinity anomalies (freshening). In the short term, the abnormally cold water found in November 1982 has been replaced by warm water in April and June 1983. Whether or not this is a consequence of this year's El Niño is purely speculative at this time.

Most regions of the ocean which support important fisheries are also upwelling areas. However, in the Gulf of Alaska the dominate feature of the wind driven circulation is downwelling. This downwelling is most pronounced in winter and virtually disappears in summer. It is possible that the high production in the Gulf of Alaska in summer is a result of this diminished wind, allowing nutrient enriched water to move onto the shelf and mix upward, especially in the coastal region. This high production is caused by the absence of wind and high light levels. Such a system is quite different from an active upwelling region.

Future studies should include routine hydrographic sections especially including the long time serial station at Seward, wind field calculations from pressure grids, coastal meteorology, Lagrangian drifter studies (which the Canadians are carrying out presently as their replacement for Ocean Station PAPA), and an investigation of the impact of hydrology and glaciology on the interannual variability in the Northeast Pacific.

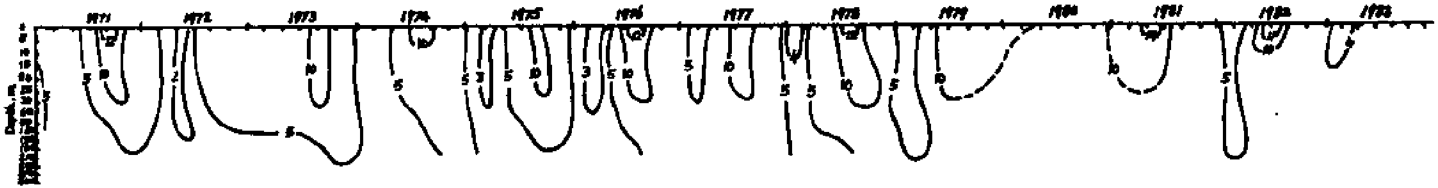


Fig. 2a. Time series of temperature at Seward.

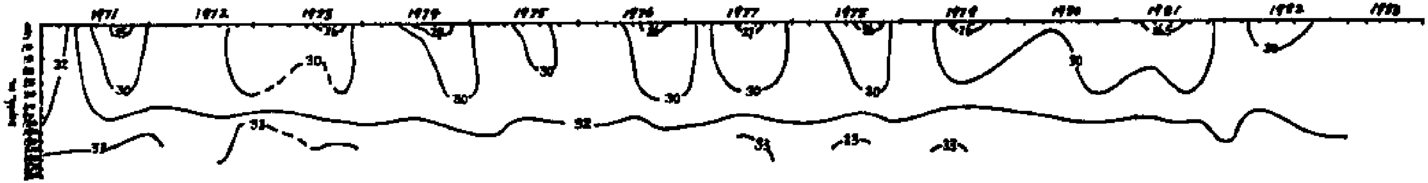


Fig. 2b. Time series of salinity at Seward.

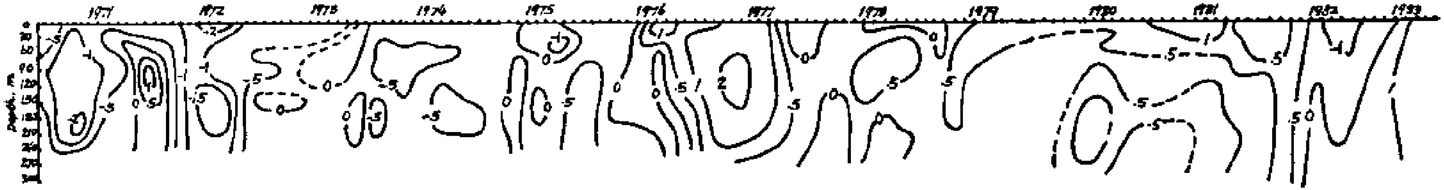


Fig. 3a. Time series of anomalies of temperature at Seward.

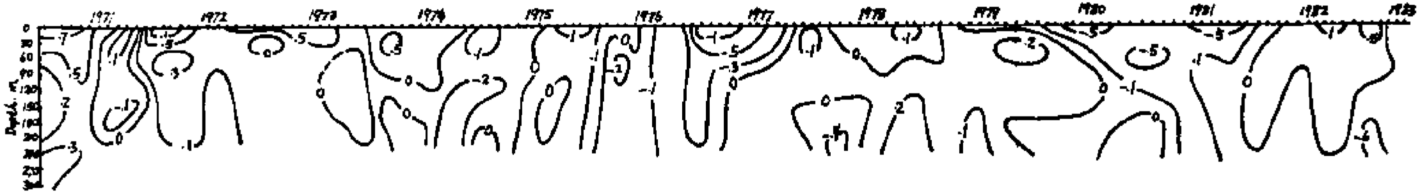


Fig. 3b. Time series of anomalies of salinity at Seward.

Commentary

Interannual Variability in the Abiotic Environment of the Bering Sea And the Gulf of Alaska

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Introduction

Schumacher and Reed have presented a good up-to-date review of the physical oceanography of the Bering Sea and the Gulf of Alaska, particularly the former. They have established the mean oceanographic conditions in the two regions and have briefly discussed the interannual variability of the abiotic environment therein.

However, the paper deals very little with the interannual variability in the abiotic environment of the Gulf of Alaska. In a way this is understandable as there is only a limited number of ocean time-series measurements of sufficient length that are available for examining the interannual variability of the ocean conditions therein. Except for the relatively long series of sea surface temperatures, salinities and densities observed from coastal stations and sea level heights measured from tide stations along the coast, there is no comparable data available from the offshore region that can be used to determine the interannual oceanic changes properly.

The longest time-series measurements available from the open ocean of the north eastern Pacific are the 3-hourly sea surface temperatures from Station P (50° 00'N/145° 00'W) for over 30 years (1950-1981). Data based on twice-daily bathythermograph casts and those based on twice-weekly hydrographic/salinity-temperature-depth (STD) casts are available for the 29 years (1952-1981) and 25 years (1956-1981), respectively. Along Line P (section between Station P and southern coast of British Columbia) bathythermograph observations have been made since 1952 (29 years), and hydrographic/STD observations, since 1959 (22 years) as well. Although these time-series data are of only moderate length and there are gaps in the series, they are of sufficient length to comment upon the interannual ocean variability that has occurred. For the remainder of this paper a few examples of variability based on these data will be presented.

Sea Surface Temperature

A comparison of the anomalies of sea surface temperature of the open-ocean waters of the eastern Pacific represented by Station P data and those of the coastal waters represented Pine Island (50° 58'N/127° 44'W) data indicates that the interannual variability of the temperature of the oceanic waters and that of the coastal waters at about the same latitude is generally similar (Fig. 1). For example, the major positive anomalies (1957-1958, 1962-1963 and 1979) and the negative anomalies (1950, 1955 and 1975) at the two locations are correlated. However, significant differences do occur, as in 1951, 1961 and 1972).

Temperature at Greater Depths at Station P

In the open ocean of the north eastern Pacific there is very little or no annual variation in the water properties at depths greater than 150 meters (Tabata, 1965). Accordingly, any large changes at depths greater than 150 meters represent interannual variability. As is evident from Fig. 2 an appreciable change of temperature does occur at depths and although the magnitude of changes at depth of 1000 meters is small, in terms of the standard deviation of the overall mean the changes are significant. The most conspicuous feature of the variability is the presence of the two pronounced peaks in 1960 and 1974. These peaks and other lesser ones are generally in phase throughout the entire water column, from 200 to 1000 decibars. Most of the troughs are also in phase; however, the minimum temperature at 700 and 1000 decibars occurred in 1968 while that at the 200-400 decibars occurred earlier, during 1965-1966.

Large interannual changes are also represented in the salinity and oxyty (concentration of dissolved oxygen) data from greater depths. However, only the oxyty has pronounced peaks that are similar in extent to those of the temperature. The two large temperature peaks (Fig. 2) are associated with the two oxyty troughs and therefore suggests that during 1960 and 1974 waters of coastal origin intruded into the area.

Baroclinic Transport across Line P

The interannual variability of the circulation in the ocean probably has more relevance to the variability of the biota than that of other oceanic processes. Changes in currents could bring in undesirable cool or warm water, affect the availability of nutrients for phytoplankton growth, transport egg or larvae away from nursery grounds, etc. Chelton et al (1982), for example, has shown that the zooplankton abundance off California is primarily determined by the large-scale variations in the flow of the California Current.

From the Line P oceanographic data it is possible to deduce, at least, the long-term interannual variability of the baroclinic transports. Those shown in Fig. 3a represent transports across the entire Line (126° 40' - 145° 00'W); those shown in Fig. 3b. and Fig. 3c are transports across the western and eastern half of the

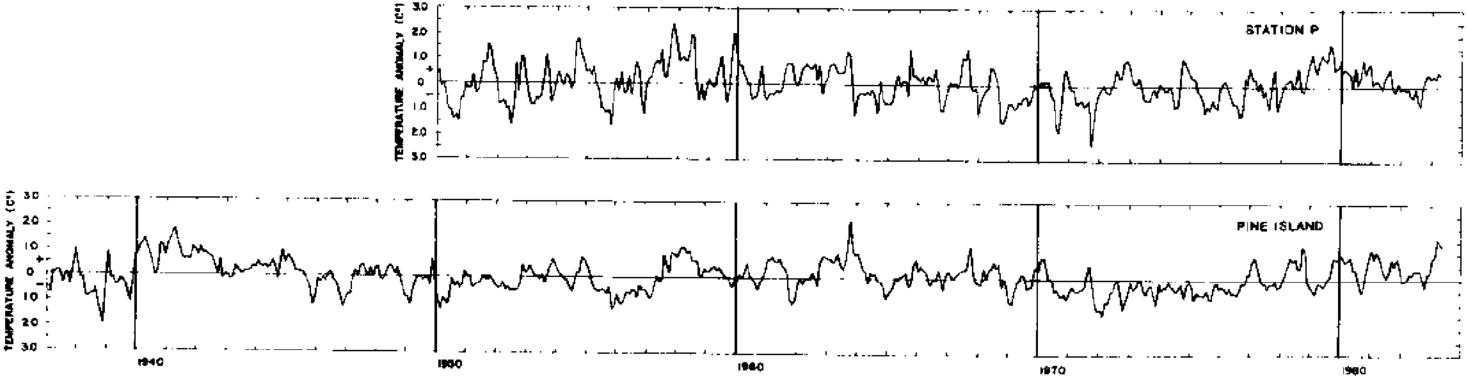

Figure 1. Anomaly of monthly mean sea surface temperature (^{o}C) based on 33-year averages (1950-1982).

(a) Station P (50^{o} 00'N/145^{o} 00'W) (1950-1983) Data from June 1981 are based on values listed in Oceanographic Monthly Summary (U.S. Dept. of Commerce, 1981; 1982; 1983).

(b) Pine Island (50^{o} 58'N/127^{o} 44'W) - Northern tip of Vancouver Island, B.C. (1937-1983).

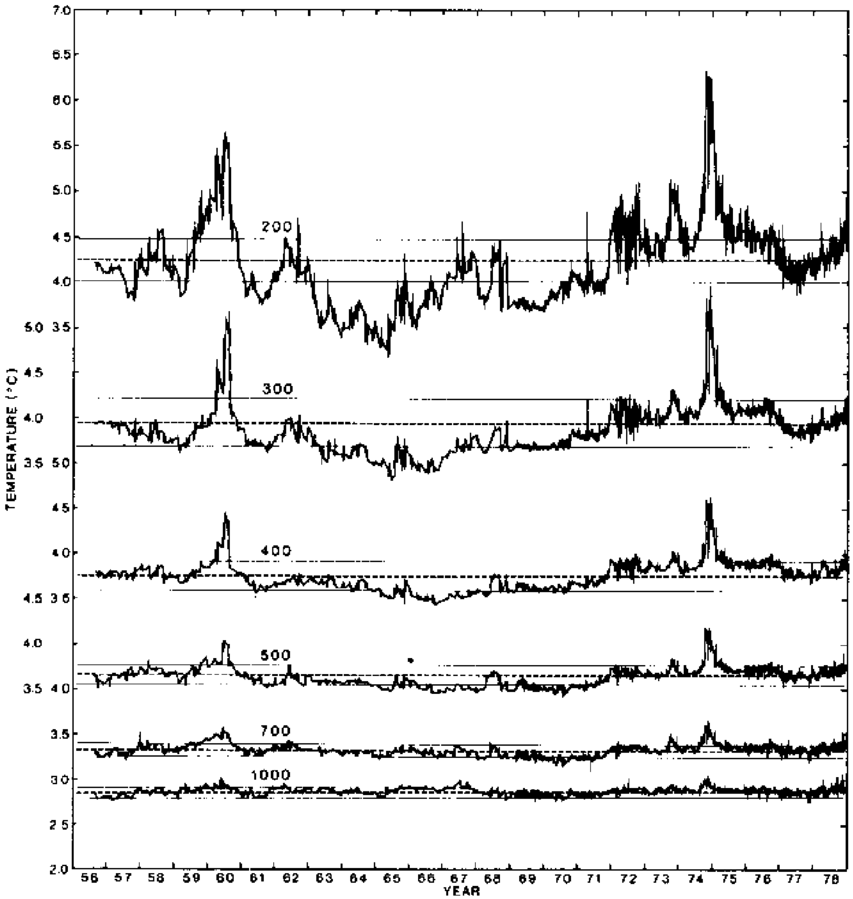

Figure 2. Temperature (°C) at isobaric surfaces (200-1000 decibars) (1956-1978). The dashed lines represent mean values (1956-1976) while the thin lines about the mean denote one standard deviation. Pressures in decibars are numerically equivalent to depth in meters approximately.

line, respectively (transports for the western and eastern half of the Line are calculated independently; consequently the two do not necessarily equal the transport for the entire Line).

It will be noted from Fig. 3a that along Line P there were four major periods during which relatively strong northward flow occurred (mid 1960-1961, 1963-mid 1965, 1968-1970 and 1977-1978). Only during the two periods (mid 1974-mid 1976 and late 1978-early 1980) were there any persistent weak transports. There was one period lasting approximately seven years (1969-1976) when the transports gradually, though with some irregularity, decreased with time.

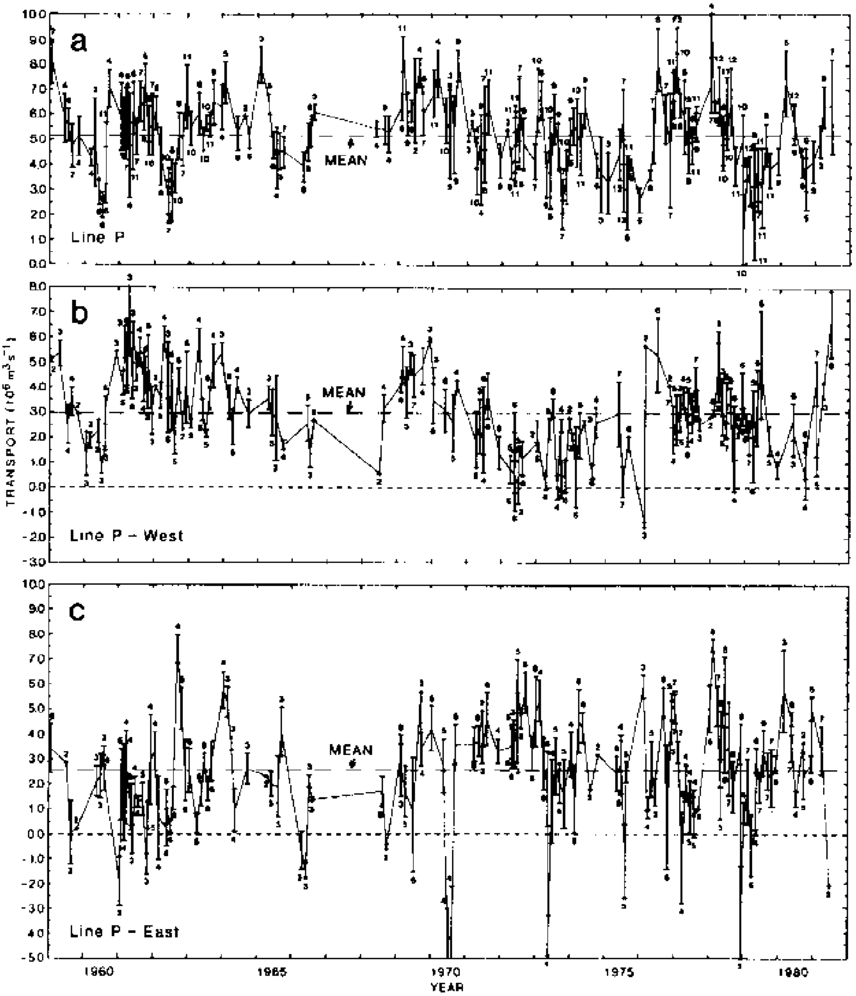

Figure 3. Baroclinic transports (10^6 m^3 s^{-1}) across Line P. (1959-1981).

a. Line P (entire line between 126° 40' and 145° 00'W)
b. Western half of Line.
c. Eastern half of Line.

Numerals denote the number of stations used to estimate transports. The dashed lines represent the mean value of the transports.

As Line P cuts across the path of the Alaska Current the variability of transports across Line P can be considered to be that of this Current.

In many respects the interannual variability of the transports across the western half of the Line (Fig. 3b) is in phase with that across Line P (Fig. 3a), for example during the early sixties, late sixties and mid seventies. However, differences are present. During 1962 and 1979 while the northward transports along the western half of the Line were strong they were weak for the entire Line. There is also a tendency for the transports along the western side to be more persistent than along the entire Line. For instance, stronger persistent northward flow occurred for 5 years (1960-1965) while weaker flow persisted for 5 years (1971-1975), approximately five years later. An interesting feature of the variability along this part of the Line is the decreasing trend of the transports over approximately 7 years, during 1961-1968 and 1969-1980. Another point of interest is the rapidity in which the flow can change within a short interval (e.g. 1960 and 1976).

The transports across the eastern half of the Line (Fig. 3c) are characterized by more irregular fluctuations than across the western half (Fig. 3b). This irregularity is probably due to the greater variations of water properties that occur in the area of the continental slope. There were only two periods during which persistent transport occurred, weak northward transport or southward transport for 3 years during 1959-1962 and strong northward transport for 3 years during 1970-1973. Though irregular, a trend of increasing northward transport is evident during 1960-1964 and 1968-1972. This trend is opposite to that along the western side.

Comparison of Transports of Alaska and California Current

A comparison of the variability of the Alaska Current (Line P transports) and that of California Current estimated by Chelton et al (1982) indicates that there is no clear relationship between the two, although during some period there appears to be some correlation. During 1961-1965 the California Current was persistently stronger; during the same period the Alaska Current was also strong (Fig. 3a). During 1966-1967 both Currents were weak. If it can be assumed that the Subarctic Current apportions equal amount of transports to each of the two Currents, then the above two correlations are to be expected. However, if it does not divide the amount equally, then an inverse relationship should hold. For the periods 1959-1961, 1975 and 1977, an inverse relationship is evident which would imply, in this case, that strong Alaska Current is associated with weak California Current.

Conclusion

A few of the interannual variabilities in the abiotic environment of the Gulf of Alaska, based mainly on data from Station P and Line P have been presented. It is clear that the results show that appreciable interannual variability of oceanographic properties and water movements in the Gulf of Alaska occur. They also suggest that there are low-frequency events with time scales of several years. Such events are difficult to interpret from known geophysical principles.

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Interannual Variation of Zooplankton Standing Stock in the Open Gulf of Alaska

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Introduction

This report inquires into the causes of interannual variability of zooplankton standing stock in the open waters of the Gulf of Alaska. The analysis is based on biological samples and other oceanographic data obtained from Canadian weatherships at Ocean Station P (50°N 145°W) during the period June, 1956, to December, 1980 (see Fulton, 1983). These data provide one of the longest and most comprehensive time series of observations at an oceanic locality. As noted by others (Wickett, 1967; Longhurst et al., 1972; Fulton, 1978), there is substantial year-to-year variation in the abundance of zooplankton at Station P. To the extent that this variation is representative of events occurring over a larger area (e.g., the entire open Gulf of Alaska), there should be some interest in its origin.

Material and Methods

The data of primary concern are net zooplankton standing stocks tabulated recently by Fulton (1983). About 2500 zooplankton samples were collected at Station P by standard methods, i.e., daytime vertical hauls, 150 m to the surface, using a net (351 µm mesh aperture) of 0.42 m mouth diameter (1956-1966) or 0.57 m mouth diameter (1967-1980). Unfortunately, the filtering areas of the two nets differed, contributing to an appreciable, but apparently variable, difference in their catching efficiency. There were other inherent biases in the sampling program (e.g., daytime sampling only, which missed deep diel vertical migrators and species which avoid the net by visual cues) which could strongly affect the pattern of seasonal variation but may not have influenced the pattern of interannual variation. Zooplankton standing stock was measured as displacement volume, and Fulton (1983) also reports abundances of major taxonomic groups. Some idea of spatial variability of zooplankton standing stock in the Gulf of Alaska can be gained by consulting LeBrasseur (1965).

The data on zooplankton standing stocks at Station P were treated in various ways to summarize the seasonal and interannual patterns. The number of samples per month ranged from 0 to 29. A simple average standing stock was calculated for each month, giving, after 1956, 8 to 12 monthly values for each year. The 24.5-year mean seasonal cycle of zooplankton standing stock was obtained as twelve weighted average monthly means (N = 16 to 25 years). Other manipulations of the data are explained below.

Additional data on concentrations of chlorophyll *a*, phytoplankton production rates, nutrients, temperature, and salinity were obtained from technical reports or other documents.

Results

Seasonal variation

The analysis and interpretation of interannual variation of zooplankton standing stock is best set in context by reviewing the average seasonal cycle and the major determinants of the cycle. Phytoplankton standing stock, measured as chlorophyll *a*, shows no discernible seasonal cycle despite considerable seasonal variation in phytoplankton production rate (Fig. 1). More recent observations are consistent with the data for the 7-year period represented in Fig. 1.

Parsons and LeBrasseur (1968) noted that net phytoplankton production may be possible even before the formation of the seasonal thermocline in late April or early May because the shallow halocline restricts winter mixing to the upper 100 to 130 m. Thus spring phytoplankton production could vary from year to year depending on interannual variation in insolation, which would be affected chiefly by cloud cover. From May or June to September the mixed layer depth is much less than the critical depth (see Fig. 1 in Parsons and LeBrasseur, 1968) and nutrient concentrations are continuously very high (Fig. 2A). The lack of change in phytoplankton standing stock in summer, despite apparently favorable environmental conditions (light, nutients) for phytoplankton growth, has led to the notion that phytoplankton net production is continuously removed by planktonic grazers, thus maintaining a steady standing stock of phytoplankton (for a brief review see Frost et al., 1983). The seasonal variation of zooplankton standing stock (Fig. 2B) is certainly consistent with this interpretation, at least in a qualitative sense. Should this turn out to be the explanation of the seasonal cycle of phytoplankton standing stock, then local processes which could cause interannual variation in zooplankton stock are those affecting phytoplankton production rate. Some likely candidates for investigation are insolation, both seasonal and interannual variation, time of formation of the seasonal thermocline, and depth of the mixed layer, both its seasonal variation and interannual variation. On the other hand, local processes which enhance nutrient supply to surface waters may not be so important, since concentrations of nutrients, at least those routinely measured, never decline to very low levels in summer.

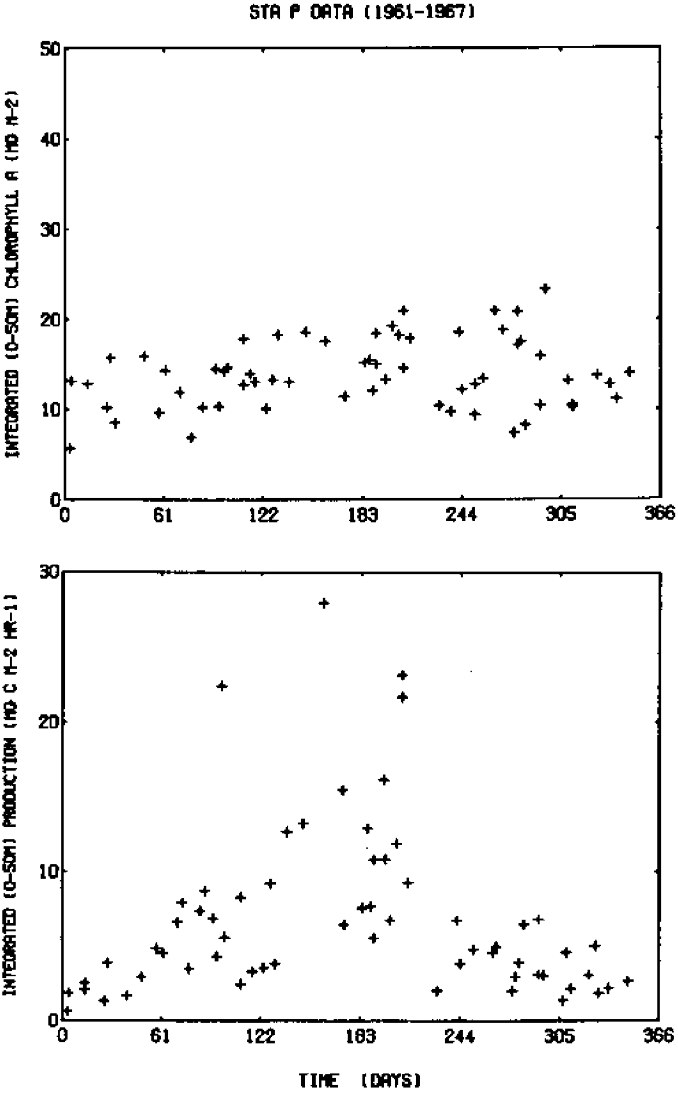


Figure 1. Standing stock of phytoplankton, measured as chlorophyll a, and phytoplankton production rate at Station P. Both are integrated over the upper 50 m. Sources of data are cited in Frost et al. (1983).

Interannual variation

Figure 3 gives mean monthly values of zooplankton standing stock for the 24.5-year period of observation at Station P. Clearly there is considerable year-to-year variation of zooplankton standing stock, and the variation may not be random. To look for interannual trends in the data, annual average values of zoo-

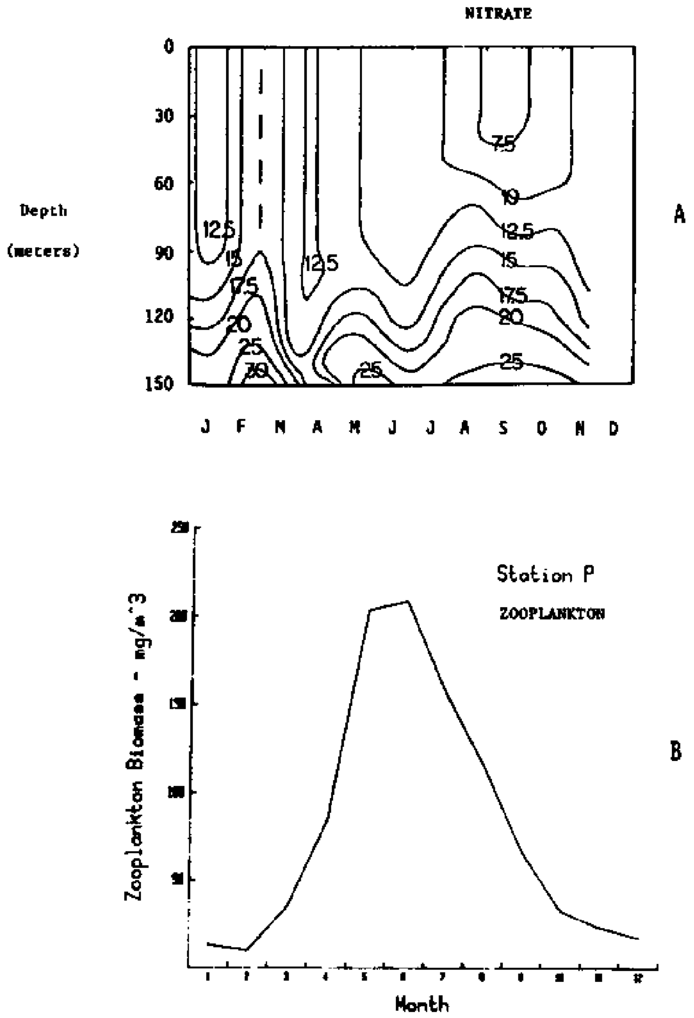


Figure 2. A, average concentration of nitrate (μg-at liter^{-1}) versus depth; monthly averages for the years 1965 to 1970 (data from Anderson et al., 1977). B, seasonal cycle of net zooplankton standing stock at Station P. The curve connects monthly values averaged over the 24.5-yr set of observations presented in Fig. 3.

plankton standing stock were calculated and from these the proportional deviations of average annual values from the long term (24-yr) mean were obtained (Fig. 4). Consecutive years of negative deviations occurred during 1961-65 and perhaps 1973-75, while strings of years with positive deviations included the periods 1958-60 and 1966-74 (interrupted by the strong negative deviation in 1969). During 1976-79 the zooplankton standing

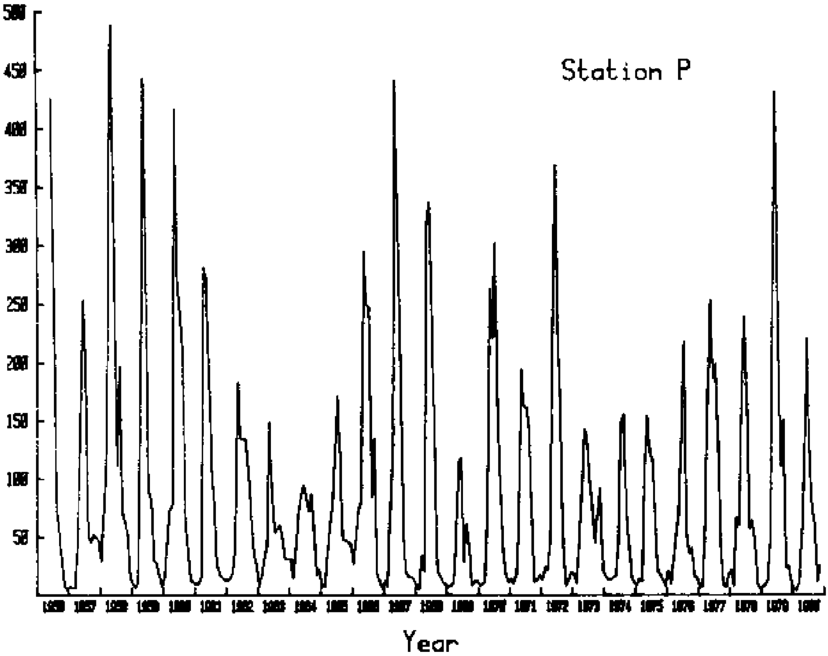


Figure 3. Seasonal and interannual variation of net zooplankton standing stock (displacement volume, mg m^{-3}) at Station P. Curve connects the mean values for each month of the 24.5-yr period of observation. Based on data reported by Fulton (1983), N and S4 nets only, N net data adjusted for lower catching efficiency (S4 = 1.74N). Missing data plotted by linear interpolation.

stocks were average, but in 1980 there was a strong negative deviation. Inspection of the pattern of deviations in Fig. 4 shows that there is no obvious cyclical trend in the data, nor can the sequence of positive and negative deviations be distinguished from a random sequence (runs test, $P > 0.05$; Sokal and Rohlf, 1969). Nevertheless, it is still of interest to determine if the interannual variation in zooplankton standing stock is caused by randomly varying characteristics or processes in the environment of the zooplankton.

Interpretation of interannual variation of zooplankton standing stock

Parslow (1981) evaluated the evidence for year-to-year variation in phytoplanton standing stock and production rate at Station P. Of the five years during which one or more anomalously high concentrations of chlorophyll *a* (1 to 4 mg m^{-3}) were observed at the surface, only one (1975) corresponded with a year of anomalously high zooplankton standing stock. Thus, small, short-lived surface blooms of phytoplankton apparently are not the cause of high concentrations of zooplankton observed in some years.

For reasons given by Parslow (1981), there is not a long time series of reliable data for phytoplankton production rate at Station P. In lieu of data, we use a time series of simulated phytoplankton production rate obtained by Parslow (1981) with a model incorporating the effects of light, mixed layer depth, and temperature on phytoplankton growth. Phytoplankton standing stock was maintained constant at the long term observed mean concentration of 0.4 mg chlorophyll *a* m^{-3}. However, since observed values of environmental variables were used in the model, any interannual variation (e.g., temperature; Bryan and Ripa, 1978) was represented. The simulated annual primary production rate varied within the very narrow range of 17.9 to 21.6 gC m^{-2} for the years 1964 to 1976. There was no correlation ($r = -0.09$, $0.90 > P > 0.70$) between average annual zooplankton standing stock (Fig. 4, upper panel) and Parslow's (1981) estimates of annual net primary production for those years (Fig. 5). Thus, assuming that Parslow's (1981) model gives reasonable estimates of annual phytoplankton production at Station P, the interannual variation of zooplankton standing stock does not appear to be driven by interannual variation of phytoplankton production.

Perhaps a more meaningful indicator of the processes responsible for year-to-year variation in zooplankton standing stock is zooplankton growth rate. For example, Parsons and LeBrasseur (1968) found an inverse relationship between a measure of zooplankton growth rate and depth of the mixed layer in April at Station P. The implication of this relationship is that a shallower mixed layer in April permits higher phytoplankton growth, which in turn supports higher zooplankton growth. Considerable year-to-year variation in late winter-spring phytoplankton production was evident in the simulations done by Parslow (1981, his Fig. 33). This must have been caused by interannual variations in the time of formation and depth of the seasonal thermocline. Unfortunately, tabulated data on depth of the mixed layer are not available. To explore the possible relationship between phytoplankton growth rate and zooplankton growth rate in spring, zooplankton growth rate (GR) was calculated

$$GR = \frac{Z_{May} - Z_{Mar}}{2}$$

where Z_{May} and Z_{Mar} are the average values of zooplankton standing stock for May and March. Calculations for the years 1964 to 1976 were made, then ranked. A ranking of late winter-spring phytoplankton production rate for the same years was obtained by inspection of an enlargement of Parslow's (1981) Fig. 33. The paired rankings are given in Table 1 below. Clearly there is no relationship between growth rate of phytoplankton and zooplankton according to these data (Spearman's rank-difference correlation coefficient, $r_s = 0.044$).

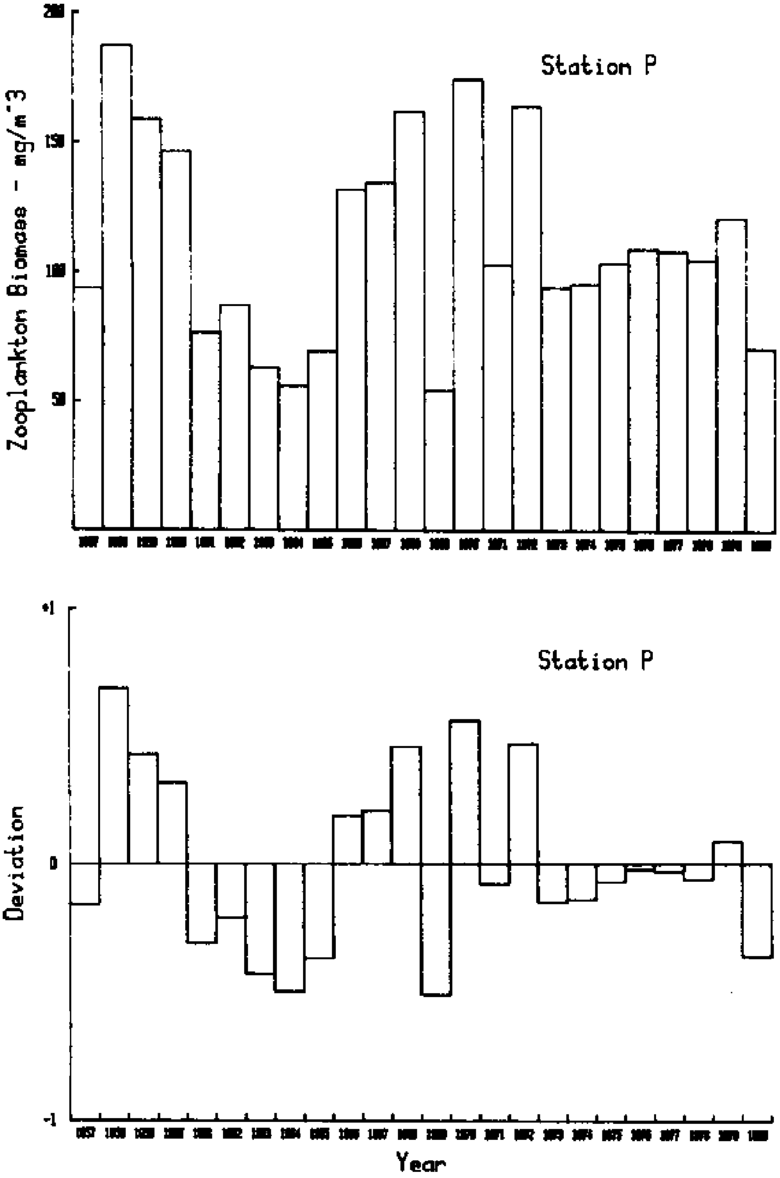


Figure 4. Time series of mean annual zooplankton standing stock (above) and deviation from the 24-yr mean (below). Deviation was calculated as the departure of the annual average value from the long term (24-yr) mean, expressed as a fraction of the long term mean.

Figure 5. Scattergram of annual net phytoplankton production (P, gC m^{-2}) and average zooplankton standing stock (Z, mg m^{-3}) for the years 1964 to 1976 at Station P. Phytoplankton data from Parslow (1981); zooplankton data from Fig. 4.

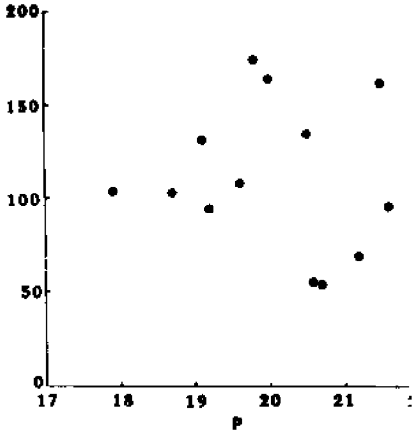
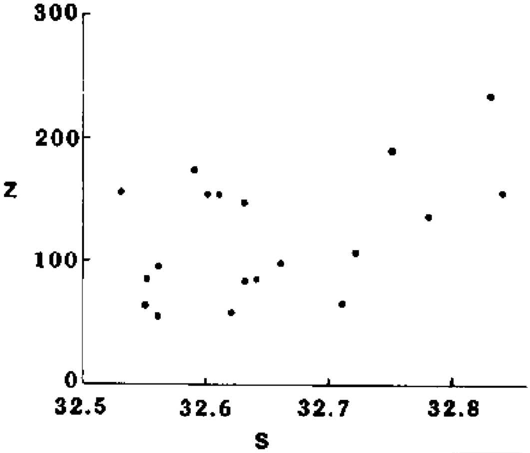


Table 1. Interannual variation in phytoplankton production rate (P) in late winter-spring and zooplankton growth rate (G) during March to May at Station P. Data for phytoplankton are ranks based on Fig. 33 in Parslow (1981); zooplankton data are ranks of calculated growth rates derived from the data illustrated in Fig. 3.

Year	P	G
1964	8	12
1965	4	11
1966	11	8
1967	9	7
1968	7	6
1969	6	3
1970	2	1
1971	10	5
1972	12	4
1973	5	9
1974	1	13
1975	3	2
1976	13	10

Wickett (1967) observed a positive corrrelation between zooplankton standing stock at Station P and surface salinity, both averaged over February to August, for the years 1957 to 1964. With 11 additional years of data the correlation coefficient is smaller, but still significant ($r = 0.48$, $0.05 > P > 0.02$; Fig. 6). Wickett (1967; 1973) suggested that surface salinity is indicative of intensity of vertical mixing, with higher salinity corresponding to more intense vertical mixing. In years with high average surface salinity, therefore, vertical mixing is unusually intense and the supply of nutrients to the surface layer is enhanced. According to Wickett (1973, p. 1), "The addition of nutrients leads to the growth of zooplankton populations around the [eastern subarctic] gyre...." It seems unlikely that enhanced vertical flux of nutrients will have a significant effect on a

Figure 6. Scattergram of zooplankton standing stock (Z mg m^{-3}) and surface salinity (S, °/₀₀), both averaged over February to August, for the years 1957 to 1975 at Station P. Zooplankton data derived from those illustrated in Fig. 3; salinity data from Wickett (1967), Favorite et al. (1976), and several technical reports from Institute of Ocean Sciences, Victoria, B.C.



phytoplankton assemblage whose growth is apparently never nutrient limited (Fig. 2A), unless that limiting nutrient is something not routinely measured such as some micronutrient (Parslow, 1981). For the years 1966 to 1975 there is indeed a strong correlation between average surface salinity and average nitrate in the upper 20 m (Parslow, 1981, Fig. 30a). However in the absence of a relationship between phytoplankton production rate and zooplankton standing stock (Fig. 5), the specific effect of enhanced vertical mixing remains obscure.

Wickett (1967) also noted correlations between zooplankton standing stock at Station P and zonal and meridional components of Ekman transport in the eastern subarctic Pacific. Wickett implied that zooplankton was affected indirectly by advection of nutrients to Station P. As noted above, however, the effect of nutrient additions to the surface layer is not clear. Moreover, recent calculations of zonal transport (Tabata 1976) indicate a substantially different circulation pattern than that depicted by Wickett (1967).

A possible effect of advection on zooplankton standing stock is the northward encroachment of transition water at Station P. The appearance of transition water is detected by characteristic species (Fulton, 1978) and is usually accompanied by low standing stocks of zooplankton. However, the occurrences of transition species, summarized in Fulton (1983), are as frequent in years of positive deviation of zooplankton standing stock as in years of negative deviation.

In conclusion, the interannual variation of zooplankton standing stock at Station P remains unexplained. An expected effect of year-to-year variation in phytoplankton production rate cannot be detected on seasonal or annual time scales. Deficiency in the method for modeling phytoplankton production rate cannot be ruled out, however. The correlation between zooplankton standing stock and surface salinity, first noted by Wickett (1967), has no obvious interpretation, although it could be indicative of interannual variation in the supply of a micronutrient essential for phytoplankton growth. Throughout the analysis the zooplankton data set was taken at face value, but other interpretations of Figs. 3 and 4 are possible. The apparent interannual variation may have no ecological significance, for the maximum annual mean zooplankton standing stock (187.4 mg m^{-3} in 1958) is only 3.46 times the minimum annual mean (54.2 in 1969). Alternatively, the variations in zooplankton standing stock may be significant but reflect as yet undocumented changes in species composition which have little effect on the dynamics of planktonic primary and secondary production. A more extensive study of these alternatives, involving both data analysis and modeling techniques, is in progress.

Interannual Variation in Other Oceanic Regions of the North Pacific Ocean

Elsewhere in the North Pacific Ocean interannual variation of zooplankton standing stock has been documented in the California Current (1950 to 1980; Chelton et al., 1982) and over the deep basin in the Bering Sea (1956 to 1968; Motoda and Minoda, 1974). The latter region harbors a zooplankton fauna virtually identical to that at Station P. Nevertheless, the interannual variation appears much reduced (possibly due to more restricted seasonal coverage) and of considerably higher frequency. In the California Current interannual variation in zooplankton standing stock has occurred almost exactly out of phase to that at Station P. Anomalously high zooplankton standing stock in the California Current is correlated with low salinity (10 m depth) in contrast to the pattern at Station P. According to Chelton et al. (1982) the variation in zooplankton stock in the California Current may reflect enhanced biological production due to horizontal and vertical advection of nutrients.

The general conclusion from comparison of interannual variations in zooplankton standing stock in various regions of the open North Pacific is that there is not strong coherence between the data sets. Therefore it is unlikely that causal mechanisms will be found which are common to all regions.

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Commentary

Interannual Variation of Zooplankton Standing Stock in the Open Gulf of Alaska

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In his submission to this workshop Dr. Frost has used the zooplankton biomass data from Ocean Station P to characterize 1) the annual cycle of standing stock in the oceanic sector of the Gulf of Alaska, and 2) the interannual variability of that stock. My comments are all directed to the details of the variations in particular species which must produce most of the variation in the stock overall. The annual cycle is not entirely due to changes in total water column stock, but is partly attributable to animal migrations between the upper 150 m represented in the long-term weathership samples and deeper layers. For example, most of the mid-summer decline in stock is due to the departure from the layer above the halocline of the large populations of several copepod species: Neocalanus plumchrus and Neocalanus cristatus. During the spring peak in standing stock those species make up a very large fraction of the biomass, particularly in samples like those taken from the weatherships with 0.35 mm mesh. Figure 1 illustrates the extent of that dominance, well over half of the plankton. For samples collected with fine mesh the dominance of Neocalanus appears to be less pronounced because the sizeable populations of Oithona similis and other small copepods are represented in them. It seems probable that the interannual variability of the total plankton is mostly interannual variability of the two Neocalanus species.

Frost and I utilized the weatherships during their last 1.3 years of service to obtain detailed information about life histories of Neocalanus spp. and other subarctic plankton animals. We were aided in that effort by excellent cooperation from the Institute of Ocean Sciences (particularly Dr. Tabata) and the Canadian Coast Guard. Both Neocalanus species have life histories that include a deep ontogenetic, vertical migration. The downward migration of fattened fifth copepodites (the last larval stage) produces a stock in diapause at depths below 400 m. This stock begins to mature in summer, immediately after it is established, and the adults are present and reproducing at depth throughout the year. Most successful growth back to the diapause phase occurs in April, May and June. The reproductive phase in particular is much more prolonged

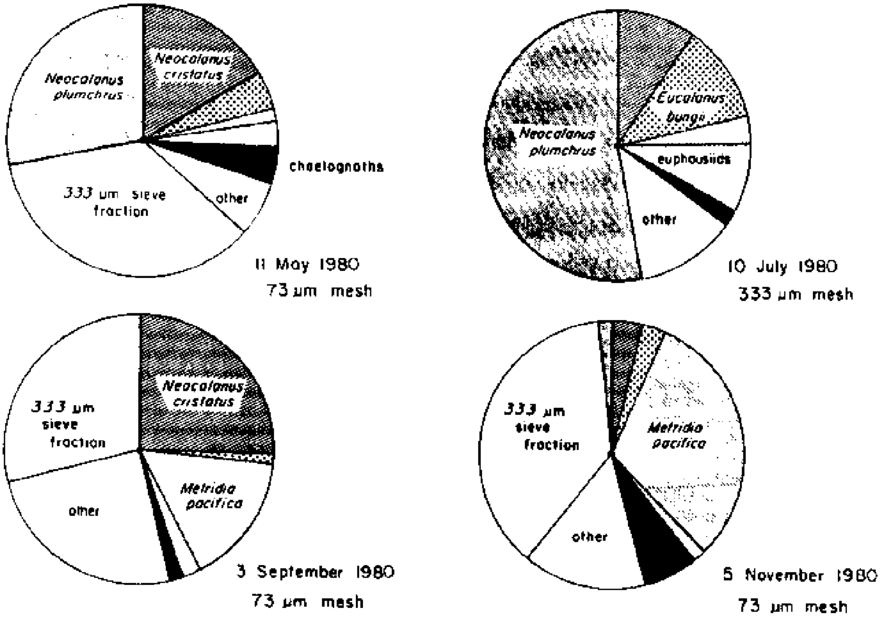

Figure 1. Proportional contributions of various categories to total dry weight to net plankton in the upper 100 m at Ocean Station P. Samples were sorted, rinsed, dried at 60°C and weighed.

in the oceanic population than had been previously observed in the coastal fjords of British Columbia (Fulton, 1973). Schematic representations of the oceanic life cycles of both species are presented in Figure 2. Some details of the data set and analyses were presented at the workshop. The entire story is told in a forthcoming paper, Miller et al. (in review). The complexities of the life histories suggest that while interannual variability may well derive from interannual variations in the habitat, some of the obvious autocorrelation in the year-by-year series may derive from the internal dynamics of the Neocalanus populations. For example, the size of the stocks in diapause from early summer on could affect the potential scale of recruitment in the year following, or large stocks might well be temporarily self-sustaining through cannibalism.

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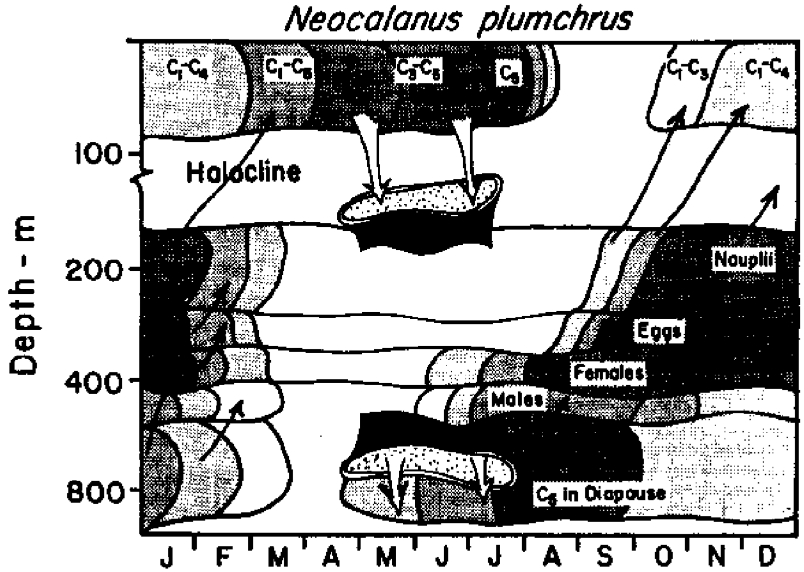

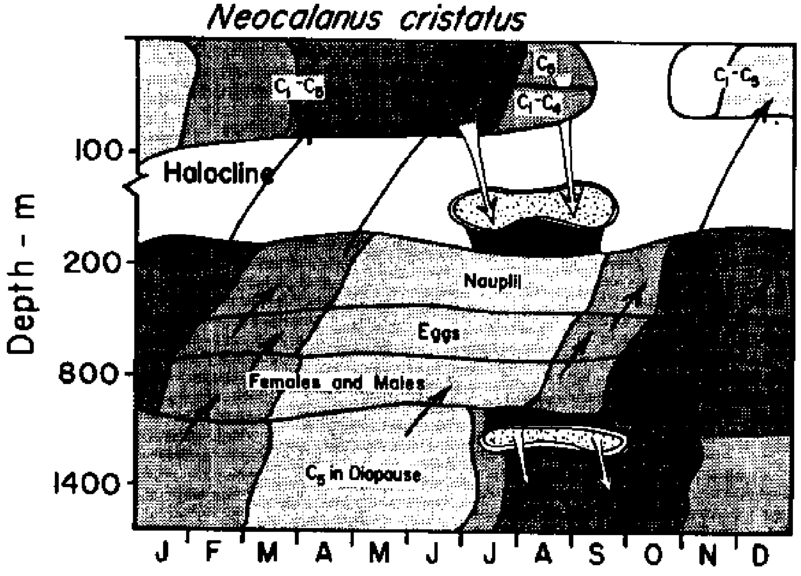

Figure 2. Above: Schematic diagram of the life history of Neocalanus plumchrus with respect to season and depth in the oceanic subarctic Pacific. Darker shading implies greater abundance. Designations C_1 to C_5 refer to successive, immature copepodite stages.
Below: Similar diagram for Neocalanus cristatus.

Interannual Variability of Phytoplankton And Zooplankton Production On the Southeast Bering Sea Shelf

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Introduction

Continental shelf waters contribute most of the higher trophic level productivity of the world oceans used by man (Ryther, 1969). Much of the yearly phytoplankton production on high-latitude shelves is associated with brief but intense periods of growth during the spring phytoplankton bloom. Marked seasonal and spatial variations in phytoplankton stocks have been reported in waters of several temperate and high latitude shelves (Riley, 1956, Holligan and Harbour, 1977), and the identification and quantification of the environmental variables controlling the observed patterns of phytoplankton growth in the sea has been an area of active research for several decades.

Interannual differences in phytoplankton and zooplankton abundance and growth have been noted for some areas of the sea, but in general, our knowledge of the biotic and abiotic variables regulating these differences is quite limited. In this communication we describe the observed interannual differences in phytoplankton and zooplankton abundance, distribution and growth on the highly productive southeastern Bering Sea shelf and discuss the climatological variables which appear to play an important role in regulating interannual differences.

<u>The study setting: The southeastern Bering Sea shelf</u>. The eastern Bering Sea has long been a biologically productive region for man. This shelf covers only 0.33% of the world's ocean area yet provides approximately 5% of the total world fishery catch (Goering and McRoy, 1981). In comparison with estimates for other ocean regions (Ryther, 1969), this catch per unit area is approximately 3 orders of magnitude greater than that of the open ocean but approximately one order of magnitude less than that of the world's ocean upwelling areas. However, it is approximately 3 times greater than the mean fish catch per unit area of the world's non-upwelling coastal zones, of which this shelf is a part. In addition, in comparing the Bering Sea shelf with those off Nova Scotia and in the northern North Sea, Coachman and Walsh (1981) suggest that the fish yields from all

three of these broad, high latitude shelf systems may be about the same.

During the last five years the National Science Foundation sponsored PROBES (Processes and Resources of the Bering Sea Shelf) project has collected oceanographic data in the southeast Bering Sea. These data document the development of intense diatom-dominated spring blooms on this subarctic shelf (Iverson *et al.*, 1979). These authors report observations supporting the hypothesis that major food webs leading to large stocks of pelagic and benthic fauna on the eastern Bering Sea shelf are separated in space by their relationships to a complex physical system of oceanic/shelf fronts separated by interfront regions. Further information on the physical oceanography and general meteorology of this shelf area are given by Schumacher and Reed in this volume.

Grazing studies suggest that copepod feeding activities have a significantly greater impact on outer shelf and oceanic areas than on the middle shelf of the Bering Sea (Dagg *et al.*, 1982). Shoreward of the middle front, a food web is observed in which less of the spring bloom production is consumed by the pelagic fauna and much of this production reaches the bottom intact where it supports a high benthic biomass. In the middle shelf domain the phytoplankton community is geographically isolated from the large and effective grazers of the outer shelf region (Cooney and Coyle, 1982). Due to its small horizontal advection and its reduced grazing stress, the middle shelf domain is an ideal site to examine the relationship between physical properties of the environment (e.g. vertical mixing) and phytoplankton bloom development.

Results and Discussion

The interaction of wind mixing and phytoplankton productivity: A mechanism for interannual variation. Interannual variability in phytoplankton production has been documented in coastal areas where high productivity depends on specific physical phenomena such as the upwelling of nutrient rich sub-surface water (Cowles *et al.*, 1977, Peterson and Miller, 1975). Meteorological influences are usually important in such low frequency biological variability. In the very productive Peru coastal area, for example, phytoplankton productivity decreases sharply during periods of warm equatorial water intrusion, and can impact the anchoveta fishery (Cushing, 1981). The intense El Niño currents are associated with large scale (hemispheric) meteorological changes (Wyrtki, 1975). On the broad, high latitude southeast Bering Sea shelf, such coastal upwelling is not the dominant factor supplying surface nutrients for plant growth. Instead, nutrients move horizontally onto shallower shelf areas as a diffusive flux from offshore Bering Sea-Slope water and are then dependent on vertical mixing due to local wind activity to reach surface waters (Coachman and Walsh, 1982).

Much of the progress made in analyzing the physical/biological relationships in the southeast Bering Sea are based on data from Station 12 (depth 77 m) located ca. 25 km inshore from the middle front on the main PROBES line. This station was occupied frequently during the 1979, 80 and 81 R/V *T.G. Thompson* field seasons (17 April - 13 June 1979; cruise 138; 25 March - 2 June 1980; cruise 149; and 14 April - 17 July 1981; cruise 159). Extensive time series of physical, biological and chemical measurements have been compiled at this station, some of which are shown in Figures 1, 2 and 3, and these data form the basis of our interpretation of the interaction between water column stability and the spring bloom production cycle.

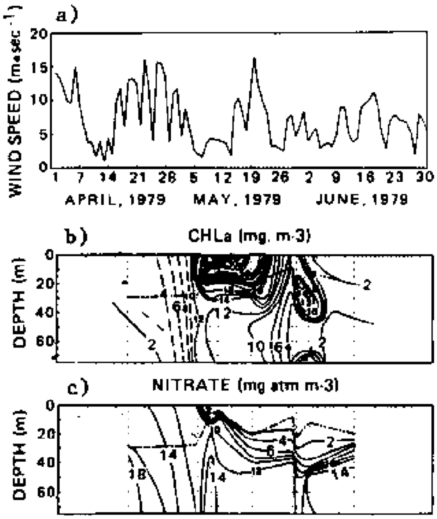
Mean storm tracks historically pass over the middle shelf domain of the southeastern Bering Sea from February through April (Brower *et al.*, 1977). In an average year, about 14 storms pass over the region during this period with 25-36% of the associated winds greater than 22 knots (Figures 1-3a). Since winter and early spring water column temperatures and salinities are vertically homogeneous the water column lacks vertical stratification and can be easily mixed. This winter end-pre-bloom period is characterized by the deep wind mixed layers, low and vertically homogeneous Chl *a* distributions and high NO_3^- concentrations of April (Figures 1-3b and c).

Sambrotto *et al.* (in prep) show that wind induced mixing controls not only the nutrients available for phytoplankton growth in this shelf sea but also strongly influences water column light conditions. Turbulence in the wind mixed layer, therefore, is very important for both the timing and intensity of phytoplankton growth on this and presumably other shelves. The temporal development of the spring diatom bloom in the lightly grazed, low flow regime of the middle shelf area for three consecutive ice free years was analyzed by Sambrotto *et al.* and divided into a winter-end pre-bloom, light limited phase and a post-bloom nutrient-limited phase separated by peak-bloom conditions which exhibit the greatest standing crop and productivity during the year. Net phytoplankton growth on the middle shelf begins during March, when the critical depth (Zc) as defined by Sverdrup (1953) first exceeds the mixed layer depth (MLZ). In ice free years at Station 12 (77 m) this first occurs in the latter part of March when the daily incoming PAR first exceeds about 7.0 Einsteins m^{-2} day^{-1}.

Among the variables comprising the ratio MLZ:Zc (the light index), mixed layer depth shoaling was found to be most important in improving light conditions. The timing of the spring phytoplankton bloom maximum therefore closely follows a hiatus in wind mixing events associated with low pressure systems moving through the area, and peak spring phytoplankton bloom conditions during 1979, 1980 and 1981 occurred consistently during late April-early May in the middle shelf domain (Figures 1-3a and b; 7 May 1979, 2 May and 16 May 1980, and 8 May 1981). After the exhaustion of surface nitrate (Figures 1-3c) and the concomitant species changes, however, the critical depth concept is of less use in interpreting physical-biological interactions.

The most sensitive indicator of changing growth conditions throughout the bloom development was found to be NO_3^- uptake since nitrogen is generally in shortest supply relative to its utilization in the

Figure 1 - 1979



Time series of selected parameters at PROBES middle shelf Station 12 during April, May and June of three years. a) Six hour calculated geostrophic surface wind speed (m/sec), b) Chl *a* (mg · m^{-3}), c) nitrate (mg-at · m^{-3}). Broken lines in b and c connect mixed layer depths.

Figure 2 - 1980

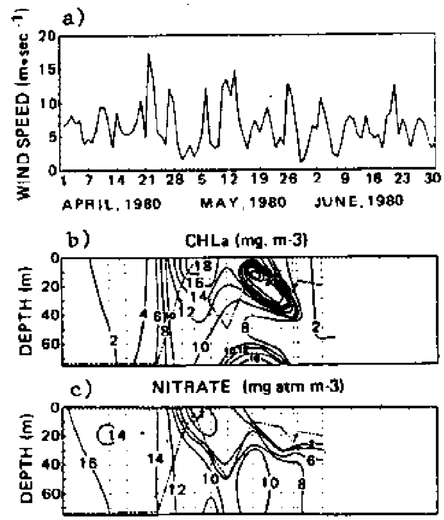
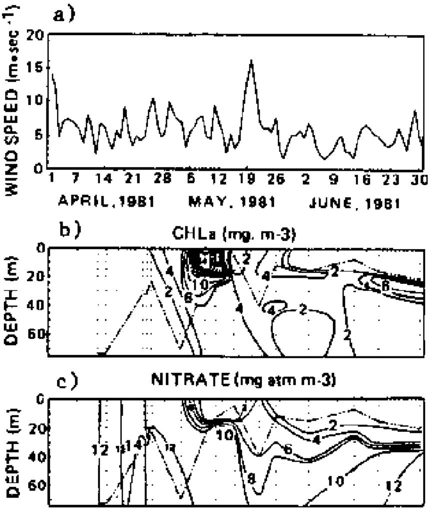


Figure 3 - 1981



marine environment (Ryther and Dunston, 1971). The most oxidized form of combined inorganic nitrogen (nitrate) is available only from deeper waters in stratified water columns, and after the exhaustion of mixed layer nitrate, water column productivity enters a nutrient-limited phase in which further euphotic zone production is dependent on the vertical diffusive supply of nutrients (Dugdale and Goering, 1967).

Although measurements of carbon productivity are more commonly used in the study of marine trophodynamics, nitrogen productivity is a useful parameter in several respects. As Dugdale and Goering (1967) point out nitrate uptake can be thought of as new productivity and is an indication of the plant production available for export or consumption under steady state conditions. Recent microbiological studies indicate that most of the nitrogen in marine microorganisms is in protein (Cuhel *et al.*, 1981). Also, in phytoplankton protein production is conserved under a variety of growth conditions (Morris *et al.*, 1979). The present measurements of nitrogen utilization by spring bloom phytoplankton then can be regarded as indicative of "primary protein production". It may therefore be a more conservative and reliable indicator of food availability than carbon productivity due to the more ubiquitous role of carbon in cellular chemistry. High nitrate uptake rates are associated with high carbon productivity (Eppley and Peterson, 1979) and this equivalence facilitates the transition between the two.

Finally and most important here, since the supply of nitrate to the surface water is mediated by the mixing in this layer, nitrate uptake is a sensitive indicator of the physical changes effecting phytoplankton growth during the spring bloom. The highest nitrate productivity associated with the bloom occurs during the transition between the light and nutrient limited phases and coincides with the periods of highest biomass recorded in the surface waters (Figures 1-3b). A vertical advection-diffusion model based on such nitrate uptake measurements indicated that a combined advective and eddy diffusive mixing rate of 2.0 m · day^{-1} was optimum for peak Bering Sea bloom conditions and high diatom growth rates. Greater mixing than this was associated with the pre-bloom, light limited conditions of April. Lower mixing rates allowed the establishment of a strong pycnocline and restricted the nitrate supply to the mixed layer in late May.

Steele (1962) observed that optimal primary production results from a very specific combination of hydrographic conditions. Some balance between the stability necessary for favorable light conditions, and that necessary to allow for a supply of nutrients for growth, must be present for maximum productivity, a point developed from critical depth considerations by Yentsch, (1981). The concept of an "optimum light and nutrient diffusion rate" for spring bloom diatom growth was identified at least as long ago as Riley, Stommel, and Bumpus, (1949) and the 2.0 m · day^{-1} mixing rate apparently defines these conditions for NO_3^- uptake on the basis of upper water column stability during the Bering Sea spring bloom development.

This mixing rate estimate facilitates the analysis of the variability in production associated with interannual differences in mixing conditions, since during the post bloom phase, continued new productivity depends on wind mixing to sustain the optimum 2.0 m . day^{-1} upper water mixing rate. Historically, by May storm tracks move out of the eastern Bering Sea and the mean wind speeds drop to 13-14 knots, although the region is still sporadically impacted by storms (Brower *et al.*, 1977). The sensitivity of post bloom phytoplankton growth to wind mixing is apparent in the observed biological response to May storms.

The advective supply of NO_3^- to the nutrient-depleted mixed layer can be restored by storm events which deepen the pycnocline to the depth of the NO_3^- nutricline and its associated settled pioneer diatoms. Such an entrainment of nutrients and plant cells into the upper water after the initial bloom had settled was observed during a 24 hour station occupation on 16-17 May 1979 (Figure 1b). The measured decreases in NO_3^- and NH_4^+ content of the upper 25 m correspond to the ^{15}N measured rates of uptake of these nitrogen species (ΔNO_3^- = 38.3 mg-atoms $m^{-2}day^{-1}$, ρ NO_3^- = 36.4 mg-at $m^{-2}day^{-1}$, ΔNH_4^+ = 27.9 mg-at $m^{-2}day^{-1}$, ρ NH_4^+ = 44.3 mg-at $m^{-2}day^{-1}$), and the total ^{15}N measured transport rates approach the observed 24 hour change in particulate nitrogen (90.0 mg-at m^{-2}). During this period the mixed layer deepened from 21 to 23 m under the influence of 25-30 knot winds (Figure 1a).

In May of 1980 a storm occurred which also functioned to prolong and increase productivity although the sequence of events was significantly different than that of the May 1979 storm. Winds of 6-10 May of approximately 30 knots destroyed the tenuous stability present and the mixed layer deepened to almost 50 m, which was several times deeper than the 0.1% euphotic zone. By 13 May, the low pressure system had stagnated and began to dissipate with winds reaching 5-10 knots on 14-16 May (Figure 2a). The mixed layer depth again shoaled to approximately 10 m marking the return of favorable water column light conditions in the presence of increased NO_3^- recently brought into the mixed layer by the storm. The main spring phytoplankton bloom of 1980 then commenced with chlorophyll concentrations of >25 mg m^{-3} found at 10-15 m on 15-17 May (Figure 2b). During 1980, this early May storm apparently "reset" the hydrographic conditions on the middle shelf to pre-bloom conditions (e.g. high nutrients, poor light, low NO_3^- uptake and growth) which were followed by bloom conditions when the upper water column again stabilized.

In late May, 1981 a storm which deepened the mixed layer arrived in the area on the 19th (Figure 3a). The mixing increased mixed layer NO_3^- concentrations to >4 mg-at m^{-3} (Figure 3c), and an increase in standing crop followed (Figure 3b) but was not as immediate as during the 1979 storm, nor was it as intense as during the 1980 storm. Importantly, however, in all these cases it is apparent that wind mixing in these post bloom water columns stimulates nitrate uptake by increasing upper water column mixing rates. Since these short time scale (2-5 day) storm events are capable of dramatically influencing the production cycle their occurrence during the spring bloom period is an important factor in regulating annual phytoplankton production.

Interannual variability of phytoplankton on the middle shelf. Post-stratification wind mixing events have been shown to be an important factor in the yearly production cycle of both embayments (Iverson *et al.*, 1974) and other shelf areas (Walsh *et al.*, 1978). In the New York bight, for example, wind mixing was estimated to account for a third of the yearly production. In the Bering Sea middle shelf the contribution of wind mixing events to the yearly production cycle is similarly high and the variability of these post-bloom storm events is largely responsible for the interannual differences in NO_3^- uptake observed during the spring bloom (Table 1). The excellent correspondence between the ^{15}N and mass balance methods of estimating NO_3^- uptake supports the hypothesis that the differences in NO_3^- uptake among years is real and beyond the "noise level" of these measurements.

Table 1. Station 12 comparison of estimates of phytoplankton nitrate uptake by the ^{15}N method in the 0.1% euphotic zone and the net change in integrated nitrate content of the water column for three years. Estimates based on period from 25 April to 2 June. In no case was the difference between the two estimates more than 11%.

	mg-at/m²	
	$\int_{Z=100\%}^{Z=0.1\%} \int_{25\ \text{April}}^{2\ \text{June}} \rho^{15}NO_3^-$	$\Delta \int_{Z=0}^{Z=77} NO_3^-$
1979	920	830
1980	670	710
1981	484	500

The measurements of NO_3^- uptake at Station 12 (Table 1) suggest an average 1979, 1980 and 1981 uptake of ∿700 mg-at NO_3^- m^{-2} over a 38 day spring bloom period. In each year, the initial bloom was largely deterministic, in that upon the initial attainment of suitable upper water column stability, and a favorable MLZ:Zc ratio, a strong response in growth was always observed. On average this initial high growth period, which lead to the exhaustion of NO_3^- from the mixed layer, accounted for ∿320 mg-at m^{-2} of NO_3^- uptake. NO_3^- uptake before water column stabilization accounts for 30-60 mg-at NO_3 m^{-2}, while post bloom diffusive flux can account for an additional 50-70 mg-at NO_3^- m^{-2}. The enhancement of new production by wind mixing, therefore, is on average responsible for the remaining ∿260 mg-at m^{-2} of NO_3^- uptake, about 37% of the yearly spring bloom total. It was the variation in this category which contributed most of the observed interannual variability in nitrate uptake.

The contribution of wind mixing to yearly NO_3^- uptake varied from negligible importance in 1981 (∿10%) to a very significant portion in 1979 (∿50%). On this basis, the low NO_3^- utilization observed in the middle shelf domain in 1981 relative to 1979 and 1980 resulted from a lack of post-bloom wind mixing, which restricted optimum mixing conditions and high NO_3^- uptake to the short time period immediately surrounding the initial 1981 bloom.

Inspection of the yearly weather patterns, including the position of the May-June storm tracks and maximum 700 mb flow, suggests that the mean position of the maximum upper air winds (which tend to guide or "steer" the surface lows) is approximately parallel to 40° north latitude, some 1500 km south of the eastern Bering Sea shelf. In May-June of 1981, the observed maximum upper air wind coincided with the mean 40° latitude position, keeping the lows out of the Bering Sea. This resulted in the calm ocean conditions and lack of mixing observed during 1981. In June 1979 the observed maximum upper air flow was approximately 1000 km farther north than the mean, driving some storms over the southeast Bering Sea. In June 1980, one branch of maximum upper air flow was directly over the shelf resulting in above normal storminess and in both 1979 and 1980 frequent storms continued throughout May (compare Figures 1, 2 and 3a). By their influence on the frequency of post bloom wind mixing, these large scale climatological factors may play an important role in bringing about the interannual variability observed in the southeast Bering Sea production cycle.

The two layered density structure of the middle shelf which develops in spring is dependent primarily on changes in upper water temperature. These temperatures vary seasonally from below 0°C in winter to 10°C in summer. Short term climatic fluctuations play a large role in conditioning the water in the middle shelf domain (Niebauer, 1980). In cold years it is ice covered (e.g., 1976), in warm years it is not (e.g., 1978-1982). Niebauer (1980, 1982) has suggested that the mean winter atmospheric circulation is the driving force behind large year-to-year temperature variations. Niebauer has also shown that this region has been under the influence of a warming trend since 1976, apparently peaking in 1979 and 1981 with a slight dip in 1980. Monthly mean sea surface temperatures for a 300 km square centered on the Pribilof Islands for May 1979, 1980 and 1981 were 4.66°C, 2.89°C and 4.13°C respectively, or 2.41°C, 0.64°C and 1.88°C above normal respectively. With essentially no advection through this region, the bottom water temperature distribution reflects the severity of the previous winter or winters which produce early spring temperatures ranging between 1 and 4.6°C (Coachman and Charnell, 1979). In any one year, however, its temperature varies little from spring to fall. Thus the formation of a stable upper layer in spring may first be initiated by ice melt in cold years, whereas in warm years changes in salinity play a small but significant role in controlling density.

During cold years, the retreat of sea ice across the middle shelf in early spring, for example, would stabilize the upper water due to ice melt. This stabilization in the presence of sufficient light would create a favorable light index and is probably responsible for the phytoplankton production associated with retreating ice edges (Schandelmeier and Alexander, 1981; Alexander and Niebauer, 1982). If the ice retreated before mid-April, wind mixing would eventually mix the water column to the bottom and terminate this initial ice edge bloom. The bloom sequence described here would then follow.

Since late May and early June wind mixing was less in 1981 than in 1979 and 1980 nitrate persisted at shallower depths in the euphotic zone in early June of 1981. For example, the 2 mg-at · m^{-3} isopleth in early June 1981 was at 18 m while in 1979 and 1980 it was at 25 and 26 m respectively (Figures 1-3c). In the more stormy years (1979 and 1980) the entrainment and subsequent consumption of deeper nitrate pushed this nutricline deeper into the water column. Since a typical photosynthetically active radiation extinction coefficient in late May is ∿0.17 m^{-1}, relatively high nitrate concentrations existed at the 5% light depth in 1981 while in 1979 and 1980 the early June nutricline was at approximately the 1.4% light level. In post-bloom or low-latitude oligotrophic water columns Chl *a* maxima are frequently associated with such conditions at the interface between a nutrient limited mixed layer and light limited lower layer (Goering *et al.*, 1970). The more favorable light levels prevailing at the top of the nutricline in 1981 may account for the more distinct and persistent Chl *a* maxima found throughout June. This maximum was also associated with higher June nitrogen productivity relative to the other years.

Interannual variability in cross shelf patterns of phytoplankton production with special reference to the outer shelf. The relationships between upper water stability and nitrate productivity observed in the detailed middle shelf time series are also useful in interpreting cross shelf patterns of production. Figure 4 depicts the average mixed layer nitrate concentrations across the shelf based on more than 500 hydrographic stations over the three sampling years (1979, 1980 and 1981). In the middle shelf domain and deeper (Stations #'s less than 16) the nitrate concentration decreases only when the water column is stable and favorable light conditions prevail, and increases when wind mixing deepens the pycnocline to nitrate rich depths. At inshore depths <50 m such as at Station 20 favorable light conditions do not depend on stratification and nitrate concentrations in this area are among the first to decrease (e.g. early April 1981, Figure 4c).

The mid-May 1979 storm, which dramatically increased phytoplankton growth at Station 12 of the middle shelf domain (Figure 1b), also had an impact on mixed layer nitrate at other stations across the shelf (Figure 4a). On about 16 May substantial amounts of nitrate were returned by storm activity to all of the middle shelf mixed layer and probably also to outer shelf upper waters. The mid-May to early June 1979 mixing was most likely responsible for keeping 1979 outer shelf mixed layer NO_3^- concentrations relatively high well into June.

In 1980 outer shelf mixed layer nitrate concentrations also reflect the mixing observed in the middle shelf time series. An important feature present in the outer shelf area in 1980 was the observed replenishment of mixed layer nitrate (Figure 4b) by the 10 May 1980 winds (Figure 2a). From late April to 6 May 1980, a consistent decrease in outer shelf surface nitrate was observed, and at Station 5, for example, the nitrate concentration decreased from over 20 to approximately 6 mg-at m^{-3}. The early May wind mixing returned nitrate concentrations to over 13 mg-at m^{-3} which set the stage for a second period of rapid nitrate uptake during the second part of May. This corresponds to the bimodal character of growth observed at Station 12 during 1980 (Figure 2b).

Figure 4

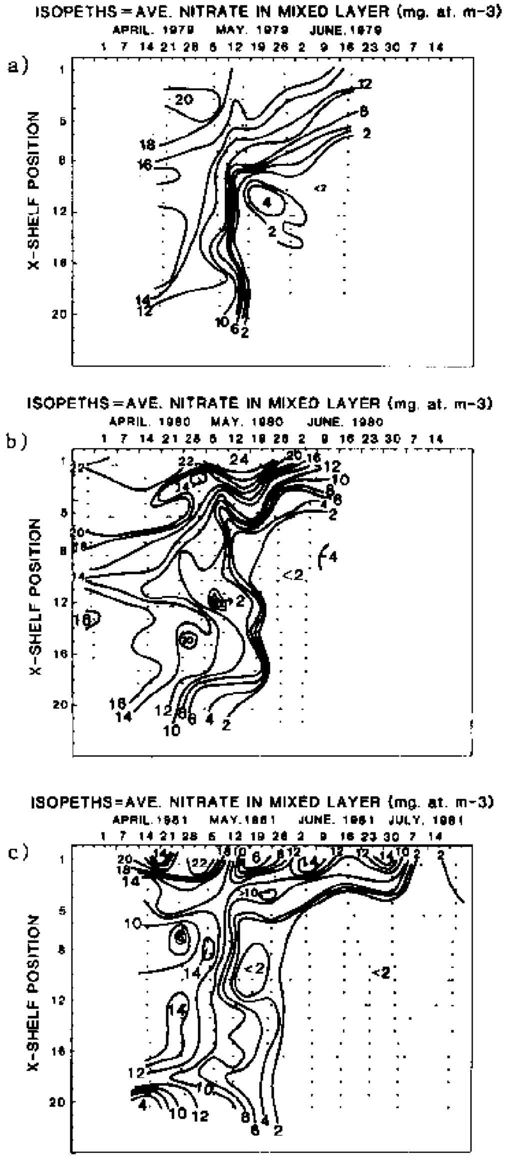


Figure 5

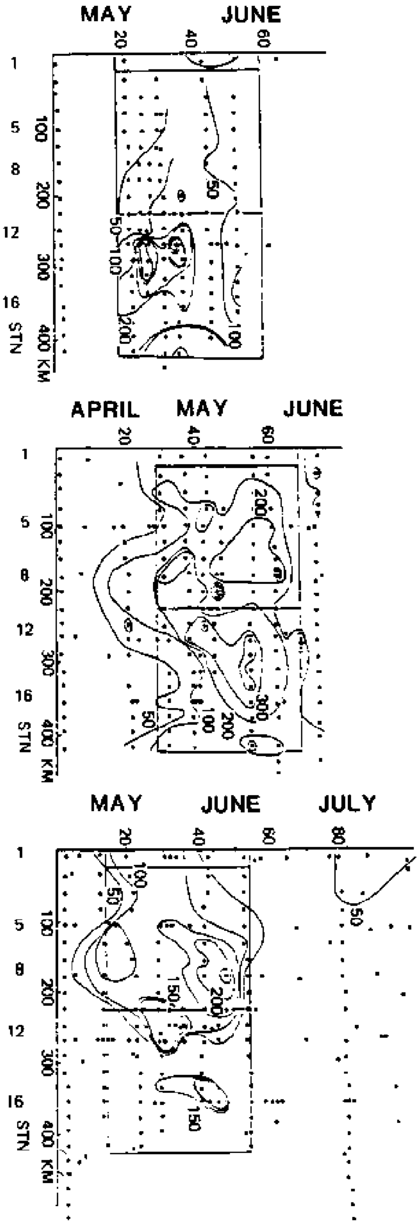


Figure 4: Time-space diagrams of the average NO_3^- concentration in the surface mixed layer along the PROBES station line (a) 1979, (b) 1980, (c) 1981.

Figure 5: Time-space diagrams of the Chl *a* content of the upper 20 m along the PROBES station line (a) 1979, (b) 1980, (c) 1981.

During 1981 nitrate depletion in the upper mixed layer occurred earlier than it had in the previous two years, this early depletion being particularly evident between Stations 12 and 5 (Figure 4c). There is apparently little nitrate replenishment with time since the 2 mg-at m^{-3} isopleth in early June, 1981 encompasses more of the shelf than it did in the previous two years. The cross shelf time series of Chl *a* (Figure 5c) suggests, however, that the 19 May 1981 storm did stimulate increased productivity near Station 8.

Although a reliable time series of $^{15}NO_3^-$ uptake measurements is not available for an outer shelf station a minimum estimate of nitrate uptake can be made from the observed disappearance of nitrate from the mixed layer and the known mixed layer depths. These estimates are compared to the water column nitrate changes in 1980 and 1981 for Station 5 (Table 2). In both years the estimate based on nitrate depletion from the mixed layer is lower since it does not account for uptake taking place during mixing events. Both estimates indicate, however, that nitrate uptake in 1981 was far less than during May 1980 in the outer shelf area near Station 5. A similar discrepancy between 1980 and 1981 exists in the intensity and persistence of the phytoplankton standing crop (Figures 5b and c). In 1980 Chl *a* levels were higher all across the shelf in comparison to 1981 and outer shelf levels of Chl *a* in 1980 persisted at higher concentrations throughout May.

Table 2. Station 5 comparison of 1980 and 1981 phytoplankton nitrate uptake from 25 April to 2 June in each year. The net change in the integrated nitrate content of the water column was computed as in Table 1.

	mg-at m^2	
	$\Delta \int NO_3$	Mixed Layer Depletion Rate Estimate
1980	990	550
1981	390	250

It appears that the wind mixing mechanism responsible for the interannual variability of middle shelf productivity can be extended to the outer shelf. May storm activity in 1980 prolonged optimum mixing rates on the outer shelf and kept the stability mediated nitrate uptake rates high. In 1981, as was observed on the middle shelf, the much calmer meteorological conditions hastened the development of a strong density discontinuity which restricted high nitrate uptake to a much shorter time period and thereby curtailed outer shelf phytoplankton production during the bloom period.

Interestingly, the only shelf area in 1981 which exhibited higher nitrate uptake (as observed from mixed layer nitrate values at Station 1, Figure 4c) during the bloom period than in previous years was the oceanic area. The oceanic region during 1981 exhibited a consistent pattern of nitrate utilization and replenishment over a three month period. Station 1 nitrate increases corresponded to storm events which were recorded on 4 May 1981 and 26 May 1981 at inshore stations. However, it is also possible that oceanic yearly nitrate patterns are regulated by interannual differences in the amount of lateral advection. Unlike much of the rest of the study area the shelf break region is an area of strong advection. If advection is responsible, the intrusion of new water into the oceanic area had a periodicity of approximately 21 days. Regardless of which circumstances were responsible, this pattern of mixed layer NO_3^- changes in the oceanic regime was not observed during the stormier 1979 and 1980 field seasons.

Interannual variability of zooplankton abundance and growth. The PROBES program has collected information relative to the abundance, seasonal distribution and growth of herbivorous zooplankton during the spring and summer of 1980 and 1981. Significant differences in temporal and spatial species distributions, biomass, growth rates, and population development were observed between the two years. A few of the major features of these interannual differences will be summarized. More thorough treatments of the seasonal and interannual distribution, abundance and growth of zooplankton on the southeastern Bering Sea shelf can be found in the papers and reports by Dagg *et al.* (1982), Cooney and Coyle (1982), Smith and Vidal (1982), Smith and Vidal (submitted), and Vidal and Smith (submitted).

Smith and Vidal (1982) have used frequency plots of 1980 and 1981 zooplankton data collected along the PROBES station line to assess interannual variability in the abundance and development of populations of herbivorous zooplankton during spring on the shelf of the southeastern Bering Sea. Although the main features of population structure in 1980 and 1981 were similar, the patterns of abundance and distribution for some species across the shelf differed substantially between the two years. For example, *Oithona* spp. was rather evenly distributed across the shelf in April through June 1980 and was much more abundant in the outer shelf during this period in 1981. During some years certain species exhibited a bimodal distribution. Chaetognathas for example were observed in maximum numbers at outer shelf station 1 and middle shelf station 16 in 1980, followed by outer shelf station 5 and middle station 12; in 1981 they were observed at high concentrations primarily at Stations 1 and 12 and occurred less frequently at 5, 8 and 16.

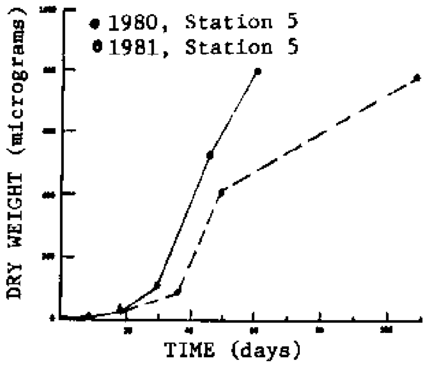
Selected zooplankton distributions presented by Smith and Vidal (1982) appear to be closely associated with the bio-physical relationships observed in the cross-shelf patterns of primary production. For example, the mean abundance of the larger outer shelf taxa were in general much greater in 1980 than in 1981. The abundance of *Neocalanus plumchrus* and *Neocalanus cristatus* stage CV's was greater by a factor of two or more in 1980 than 1981. However, the abundance of *Eucalanus bungii* copepodids at all outer domain stations was greater in 1981 than 1980, the reverse of the interannual trends in *N. plumchru* and *N. cristatus*. *Metridia pacifica* copepodids were much more abundant than were copepodids of *N. plumchrus*, *N. cristatus* and *E. bungii*, and were somewhat more abundant in spring and early summer of 1980 than in this period of 1981.

Importantly, the growth rates of *N. plumchrus* and *N. cristatus* in the outer shelf domain of the southeastern Bering Sea shelf in 1980 and 1981 have been shown by Smith and Vidal (1982) to differ (Figure 6). Both these species were somewhat more abundant in the outer shelf domain and grew faster in 1980 than 1981. The precise reasons for these interannual differences in distribution and growth rate are now known. However, food abundance and/or food quality may have played an important role in regulating population size and growth. Interannual temperature variations probably are not responsible since water temperatures were actually slightly cooler in 1980 and this would slow growth rates.

As noted previously the standing crop of chlorophyll *a* in the outer shelf domain was substantially greater during April-June of 1980 than 1981. Thus a greater abundance of food for the large-bodied outer shelf herbivores may explain the observed higher 1980 growth rates. Higher concentrations of phaeophytin were also observed in outer domain waters during May of 1980 than in 1981 suggesting an interannual difference in zooplankton food processing. Phaeopigments have been shown to be a useful index of zooplankton grazing activity (Therriault and Platt, 1978). In addition, Iverson (personal communication) found distinct diatom species differences in the outer shelf domain during May of 1980 than in May 1981. During mid-May of 1980 *Thalassosira aestivalis* and *T. nordenskoldii* dominated the diatom population, while in 1981 *Chaetoceros curvisetus* and *C. debilis* were most abundant. *T. aestivalis* and *T. nordenskoldii* compose the early successional stages of the spring bloom and flourish in water with high nitrate and relatively high mixing conditions. This also suggests that there was more prolonged wind mixing in 1980 than in 1981 on the outer shelf.

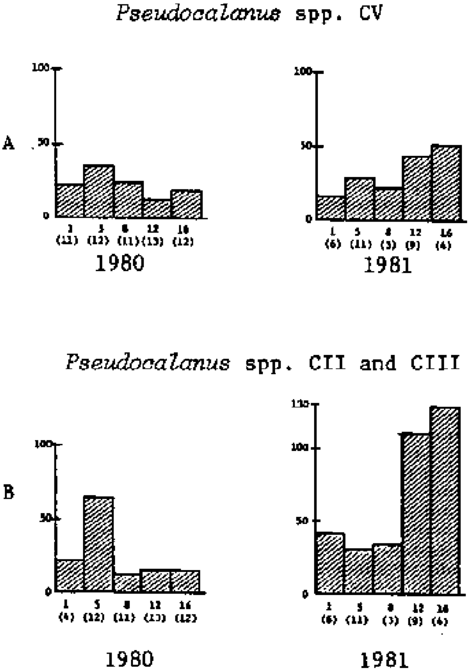
The amount of primary production reaching the benthos would similarly be dependent on prolonged mixing. In any year much of the primary production on this shelf reaches the bottom, but as observed the total annual production is dependent on post bloom mixing conditions (Table 1). It follows then, that the amount of organic matter reaching the benthos varies among years in direct proportion to surface production.

Figure 6



Growth rate of *Neocalanus plumchrus* at Station 5 in 1980 and 1981. (From Smith and Vidal, 1982)

Figure 7 A, B



Mean abundance (number/m^{-3}) over the upper 120 m of selected zooplankton taxa on the shelf of the southeastern Bering Sea in 1980 and 1981 (20 April - 7 June). Data from Smith and Vidal (1982).

Pseudocalanus spp. CV

Pseudocalanus spp. CII and CIII

Caution, however, must be used in the generalization of the above relationships. For example, the mean abundance of *Pseudocalanus* spp. in the upper 120 m during spring and summer was on average much greater over the middle shelf domain stations 12 and 16 in 1981 than 1980 (Figure 7). The difference in abundance was particularly large for copepodid stages II + III which were present in much higher numbers during the calm 1981 conditions. This relationship may be due to the association of *Pseudocalanus* spp. with the subsurface Chl *a* layers which were much more extensive during 1981. Such Chl *a* layers are the basis for an extremely active layer of pelagic trophic transfer which includes the larvae of the walleye pollock (Nishiyama and Hirano, 1982).

Interannual differences in wind mixing, therefore, may impact selected food chains in quite different ways. Years in which frequent storms pass over the southeast Bering Sea in May and June, such as in 1980, generate relatively high production and may increase the total organic matter flux to the benthos and the growth rates of water column grazers such as *N. plumchrus*. In the absence of these storms, as in 1981, calm conditions promote the development of sub-surface Chl *a* maxima and their associated food chains as typified by *Pseudocalanus* spp. and may play an important role in interannual differences in pollock·year classes. These results suggest that biological production on such a high latitude shelf responds to large scale (e.g. North Pacific) climatic variations, and that these interannual variations may effect food chains of interest to man.

Acknowledgments

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Commentary

Year-to-Year Biological Variability In the Bering Sea

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Sambrotto and Goering have reviewed the present knowledge of year-to year variability of phytoplankton production and the distribution, abundance, and growth of herbivorous zooplankton on the Southeast Bering Sea Shelf. They identify and discuss abiotic factors in the ocean environment which appear to be critical in regulating those year-to-year biological differences. Atmospheric variability is shown to correlate with biological differences, providing an increase in our understanding of the Bering Sea ecosystem and improving the possibility of monitoring meaningful year-to-year changes.

PROBES was an intensive series of observations by a large number of investigators spending relatively long periods at sea. The results for phytoplankton are discussed for three years (1979, 1980, and 1981) and the results for zooplankton are discussed for only two years (1980 and 1981). Process studies were emphasized at the expense of broad geographic coverage and extensive replication of observations. The considerable costs of obtaining long time series over wide areas are obvious.

Physical oceanographic observations by PROBES and other Bering Sea programs has provided a comprehensive description of oceanographic fronts on the shelf. The fronts are maintained by the conditions of tidal and wind energy. Observations on temperature, salinity, ice cover, wind speed, and water transport were also available to assist in interpretations of biological differences.

The investigations into the environmental factors controlling phytoplankton production identified mixing in the water column to be important to light conditions and nutrient supplies which in turn determined the timing and intensity of phytoplankton production. Marked seasonal and spatial variations in phytoplankton production were observed. The effects on species composition were not reported in detail. The observed differences in the timing and amount of phytoplankton production among the years were explained by differences in storm patterns among those years.

Storm frequencies and intensities were related to geostrophic wind speeds calculated from surface pressure weather charts. The authors provide models to relate storms and mixing to nitrate uptake. The models suggest intuitively reasonable qualitative relationships, but also demonstrate that useful quantitative results will require considerably more observations and more sophisticated models incorporating more environmental and biological factors.

The relationships suggested between phytoplankton production and the distribution, abundance, and growth of herbivorous zooplankton were highly speculative and inconclusive. The possible effects of sampling errors on the estimates for zooplankton are unknown; no confidence interval estimates are provided. A consideration of the effects of phytoplankton and herbivorous zooplankton on the distribution and abundance of fields of pollock prey or predators, or the year class strength of pollock, is necessarily even more speculative.

One can conclude that PROBES has demonstrated that year-to-year variations in phytoplankton production in the Bering Sea can be usefully monitored. The identification and quantification of controlling environmental variables can suggest how to monitor more effectively. Above all, Sambrotto and Goering have demonstrated that brief aperiodic storms have large effects in controlling the amount of phytoplankton production. The effects of storms upon phytoplankton species composition and the instantaneous and short-term effects on zooplankton and fishes are unknown. We can be relatively certain that storms affect the year class strength of fishes, but the causal relationships remain to be learned. The PROBES results are a necessary and realistic first step in what must be a long and complex investigation of the determinants of year class strength in fish populations.

Numerical Simulation in Fisheries Oceanography with Reference to the Northeast Pacific and the Bering Sea

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The Essence of Fisheries Oceanography and Its Past In the Northeast Pacific

This brief review pertains to two interdisciplinary areas - fisheries oceanography and numerical simulation (modeling) with reference to the Bering Sea and NE Pacific. It appears that both subject matters are nebulous in many minds, as some published literature as well as numerous recent "administrative" documents pertaining to future projects indicate. According to Henry Poincaré, clarity cannot be achieved in discussions before it is introduced into definitions; thus, I will briefly discuss the definitions of both subjects.

Fisheries oceanography (or fisheries hydrography, as it was called in Europe) was first defined in the first report of ICES in 1902. In fact, ICES was established mainly on the premise that the environment was in some manner responsible for the disappearance of the herring from the Bohus coast of Sweden, and the detailed causes for this disappearance could be established only through cooperative study of the ocean environment.

Fisheries oceanography proper has been mainly pursued by oceanographers working in various fisheries services. On the other hand, the biologists have been dealing with a gamut of biological problems relating to the environment, such as plankton and benthos studies. The true interdisciplinary cooperation between physical oceanographers and fisheries biologists has never been perfect, despite considerable efforts, especially by ICES, to promote this cooperation. Furthermore, progress in obtaining undisputable results in fisheries oceanography has been slow in the last 80 years. Some reasons and difficulties for this slow progress are ventilated in this report.

Fisheries oceanography includes several scientific disiplines and its successful pursuit requires that the practitioners have considerable knowledge in most of these disciplines. This requirement is rarely met in present times of individual specialization. Essentials of fisheries oceanography are summarized by Laevastu and Hayes, 1981.

The other discipline of concern here - numerical simulation, is another highly diverse activity; many different approaches are called modeling - for example, the study of the behavior of a given mathematical expression which is postulated to represent the behavior of a given natural phenomenon, numerical rendering of available data sets, and numerical (quantitative) simulation of the behavior of a phenomenon, either as part of the environment alone or of an ecosystem. Consequently, many "models" are in existence; their number seemingly increasing at an exponential rate. To define numerical modeling would be futile, as few would accept any strict definition. Therefore, I will deal in a descriptive manner with the problems of numerical approaches to the study of fish-environment interactions.

The main reasons and incentives for the study of fisheries oceanography arise from the understanding that the ocean environment exercises some influence on the abundance and behavior of fish stocks. It is hoped that if this influence can be properly quantified, the fluctuations in the abundance and availability of fish stocks could be predicted from observations of the environment. I must emphasize that this was largely a pipedream, and has remained so.

Fisheries oceanography proper attempts to: 1) find quantitative relations between the fluctuations of environment and the availability of fish (i.e., effects of environment on the "behavior" of fish stocks); 2) find cause-effect relations between environmental changes and changes in the abundance of fish (i.e., recruitment throughout the early life history and to the exploitable stock); 3) provided some results from 1 and 2 above are available, to apply this knowledge to predict the fish availability and abundance in space and time.

Fisheries oceanography studies require environmental studies in all space and time scales, partly because the fishery resources are mobile over large areas, and partly because the effects of the environment and its anomalies on stocks are not instantaneous, but can at times be years delayed.

Felix Favorite used to point out that scientists involved in fisheries oceanography have always encountered two dilemmas; first, other Federal agencies have always received a larger share of the oceanography funds than fisheries agencies; and, second, fisheries groups have been required to spend their limited funds on small scale, short-term, fisheries related problems.

Attempts to conduct broad spectrum fisheries oceanography studies have been made in the past in the United States. The Bureau of Commerical Fisheries TRIDENT program in the 1960's and the National Marine Fisheries Service's MARMAP program in the 1970's were attempts to focus attention on the multidisciplinary studies needed to present the rationale for conducting such studies, and to justify the funds, vessel-time, and manpower needed.

In the late 1950's and early 1960's, the Bureau of Commercial Fisheries, Seattle Biological Laboratory, under the supervision of the American Section of the International North Pacific Fisheries Commission, was studying the oceanography of the entire Subarctic Pacific Region aboard fishing vessels 20-30 m in length. Then, the Environmental Science Services Administration (ESSA) received a mandate to conduct oceanographic studies in the Pacific Ocean; and, for several years conducted oceanographic observations along basically 2 meridians between the Hawaiian and Aleutian Islands from vessels in excess of 100 m in length. These multi-million dollar studies resulted in a single research paper that was of minor relevance to INPFC studies.

Although the main thrust of oceanographic studies, especially the studies of ocean processes, has been in the universities in Northwest USA, these institutions have contributed very little to the fisheries oceanography proper. The reasons for the lack of marine fisheries oriented studies in the universities might be manifold: interdisciplinary subjects are seldom popular in universities; fisheries oceanography studies have to be conducted hand in hand with fisheries survey works, but there is often no suitable fishing gear and no perannual sampling programs in the universities; and, there is a lack of persistency for long-lasting studies in the universities and a corresponding lack of common data systems required for such studies.

Empirical Correlations in Past Fisheries Oceanography Studies And the Need for Causal Mechanisms

In many interdisciplinary studies it is common to attempt to find correlation between phenomena and resulting conditions in the two (or more) different disciplines. Correlation studies are especially numerous in fisheries oceanography; for example, possible relations between the surface temperature at a coastal station and landings of fish along the coast. Seldom, if ever, has thought been given to possible mechanisms of these correlations. Indeed the field of fisheries oceanography has been simplified and banalized with these such often meaningless correlation "studies".

Radovich (1982) analyzed what we have learned from the collapse of the California sardine fishery and showed that many simplified generalizations were presented, e.g., that climate (temperature) changes were responsible for the replacement of the sardine by the anchovy. In reality, the circumstances were more complex and more variable. For example, considerable north-south migrations and shifts of populations occurred which had no relation to temperature. In fact, there were population shifts between different years quite opposite of those which might have been deduced from temperature anomalies. There were variable but independent spawning successes in different areas. Furthermore, there were considerable changes in the predator populations.

Although various correlation studies in fisheries oceanography will undoubtedly continue, it seems to be necessary to emphasize the importance of selecting variables in these studies which could be meaningfully related through cause and effect. Surface temperature and demersal fish are rarely related, unless surfiace temperature can be considered as an index for bottom temperature or for changes in currents.

The scale of ocean variability is another factor requiring serious consideration. Little value can be given to monthly and/or seasonal anomalies if short term (days or weeks) fluctuations have considerably greater magnitude than those monthly anomalies.

Progress in fisheries oceanography studies can be made when we base these studies on known cause-effect principles and create continuity in space and time. This can be done with numerical simulation studies which consider the total environment and total biocoenosis together - i.e., total (or holistic) ecosystem simulations.

Additional reasons for the sluggish activity in the past of fisheries oceanography studies and the absence of diagnostic/prognostic services for fisheries are: First, the fisheries biologists have been mainly engaged in a descriptive phase (survey and species specific studies); and second, modeling efforts in the past have emphasized single species models, which are no longer adequate. However, these two phases (descriptive and simple modeling) must precede a complex and comprehensive ecosystem approach. A third reason is that the environment-resource interaction studies have been lagging in fisheries research; the funds for oceanographic research have been funneled to other bodies who have not cared to consider fisheries problems or needs. Fisheries oceanography has specific objectives and approaches and must be pursued concurrently with other fisheries research objectives.

In order to pursue fisheries diagnostic/prognostic service developments, the National Marine Fisheries Service needs a clear mandate for this approach. This is at present lacking. In addition, some funds, proper scientific-technical personnel, and research/survey vessel time is required. Cooperation with other organizations in the basic data gathering is imperative. Above all, fisheries oceanography must take a holistic approach in which ecosystem simulation is a central part.

Ecosystem simulations must include all pertinent environment and biological data and knowledge. Present limitations in respect to data are severe, but there are some ways to derive the necessary data indirectly (e.g., some oceanographic data are simulated from meteorological driving forces). These ecosystem simulations guide our future research and prioritize data collections. Before discussing the present state of art in numerical simulation and numerical rendering, we need to review the present situation with regard to data availability.

Nature and Availability of Data And Methodology of Numerical Rendering

The physical oceanographic data collected in the past are available in NODC, provided all institutions have followed the requirements of data submission levied upon them at the time of funding. These data are inadequate for construction of any synoptic or quasi-synoptic picture, due to their sparsity and the short-term variability of the ocean. Any conclusion about the anomalies over larger areas would be uncertain, as the anomalies have relatively small space and time scales. An attempt to analyze the anomalies in two areas in the Bering Sea are shown in Fig. 1 (Ingraham, pers. comm.).

The available physical oceanographic data from hydrographic casts, mechanical and expendable bathythermographs have recently been analyzed into atlases of monthly values (Robinson and Bauer, 1976). The original, error-checked data and space and time averaged values are also available in numerical form.

The oceanographic data from the Bering Sea is sparse indeed and very unevenly distributed in space and time (Table 1). Surface and bottom temperatures from this area have recently been analyzed into monthly means, with the number of observations also indicated (Ingraham, 1981) (Fig. 2).

Sea surface temperature (SST) is the only parameter which can be analyzed in synoptic time scale (Wolff, Carstensen, and Laevastu, 1967) (Fig. 3). However, in some areas (e.g., in the Bering Sea and northern Gulf of Alaska) these analyses are unreliable due to lack of synoptic data. Sea surface temperature is of little use directly in fisheries oceanography, as it does not indicate conditions in the water mass nor on the bottom (except during winter in high latitudes). Although SST anomalies have often been used in "correlation studies" in fisheries, it is very questionable that in the case of a 2°C anomaly (which is about an average anomaly) a fish would make a 200 km migration to find an optimum temperature, when it can find the same optimum temperature by moving a few meters in the vertical.

Other oceanographic parameters of possible interest to fisheries oceanography include mixed layer depth and surface currents which can be computed using data from surface meteorological analysis (mainly surface wind) (Fig. 4). These ocean properties vary considerably over short periods, and meaningful values cannot be computed with monthly means of surface wind data. Twice daily analyses of these parameters must be made from which monthly means can be computed. At present this work is not done in any numerical meteorological center, mainly because little or no need has been expressed for these products.

Surface meteorological analysis (including surface wave analysis) is conducted in a few meteorological centers and the data archived. In the last fifteen years no daily surface meteorological analyses have been published in the USA. However, their publication has been taken up by the European Center for Medium Range Weather Forecasting (Fig. 5). Some northern hemisphere surface wind data have been worked up by Larson (1975), but most of it is unpublished (Fig. 6).

The state and availability of fisheries data for fisheries ocean-

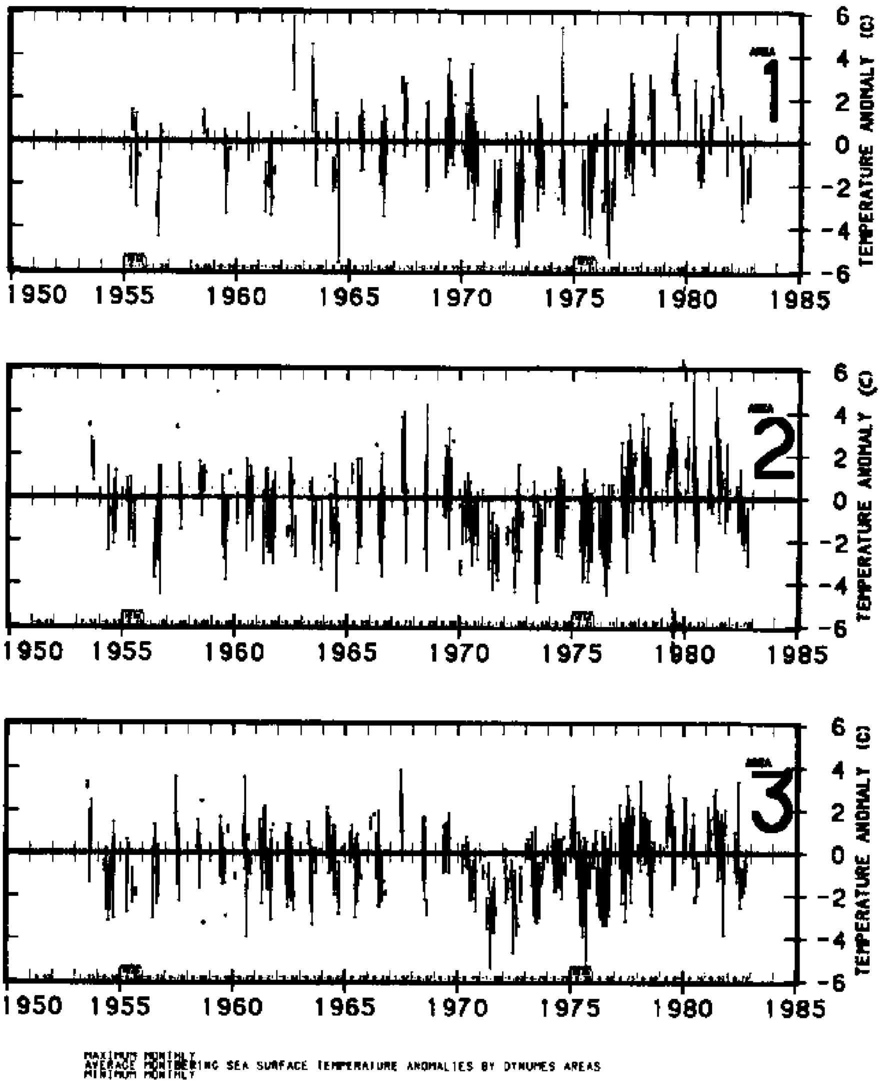

Figure 1. Maximum, average, and minimum monthly bottom temperature anomalies in three areas in the Bering Sea from 1950 to 1982 (Area 1, eastern Bristol Bay; Area 2, south-central Bering Sea; Area 3, continental slope region). (Ingraham, pers. comm.)

ography studies is as, if not more, complicated than for environmental data, especially in the Bering Sea and Gulf of Alaska. The only reasonably reliable data in respect to resource abundance are those from a few extensive resource surveys after 1975. Even these data need to be interpreted in the light of survey conditions and the gear used.

Table I. Number of near bottom temperature values in the Bering Sea by year and month with totals (Ingraham, 1981).

MONTH=	1	2	3	4	5	6	7	8	9	10	11	12	
YEAR													TOTAL
1932	0	0	0	0	0	0	6	106	12	0	0	0	124
1933	0	0	0	0	0	0	16	78	0	0	0	0	94
1934	0	0	0	0	0	0	19	65	0	0	0	0	84
1935	0	0	0	0	0	0	0	20	0	0	0	0	20
1936	0	0	0	0	0	0	0	0	0	0	0	0	0
1937	0	0	0	0	0	74	52	12	27	0	0	0	165
1938	0	0	0	0	0	0	0	116	75	0	0	0	191
1939	0	0	0	0	14	91	134	93	6	0	0	0	338
1940	0	0	0	0	0	0	70	69	0	0	0	0	139
1941	0	0	0	0	22	11	23	0	0	0	0	0	56
1942	0	0	0	0	0	0	0	0	0	0	0	0	0
1943	0	0	0	0	0	0	0	0	0	0	0	0	0
1944	0	0	0	0	0	0	0	0	0	0	0	0	0
1945	0	0	0	0	0	0	0	0	0	0	0	0	0
1946	0	0	0	0	0	0	0	0	0	0	0	0	0
1947	0	0	0	0	0	0	9	4	0	0	0	0	13
1948	0	0	0	0	0	0	11	6	0	0	0	0	17
1949	0	0	0	0	0	0	10	70	0	0	0	0	80
1950	0	0	0	0	0	0	0	0	0	0	0	0	0
1951	4	22	0	0	0	0	0	0	0	0	0	0	26
1952	0	0	0	0	0	0	0	0	0	0	0	0	0
1953	0	0	0	0	0	0	14	40	9	0	0	0	63
1954	0	0	0	0	25	2	26	5	27	0	0	0	89
1955	0	0	24	27	15	40	8	2	2	0	0	0	118
1956	0	0	0	0	0	0	4	14	8	0	0	0	26
1957	0	0	0	0	0	9	15	29	0	0	0	0	53
1958	0	0	0	0	1	13	50	16	7	0	0	0	87
1959	0	0	0	0	0	33	55	33	29	1	0	0	151
1960	3	15	0	0	0	1	150	81	14	23	0	0	287
1961	0	0	5	47	1	33	80	41	122	3	0	0	332
1962	0	0	0	0	1	20	36	3	151	21	0	0	232
1963	0	0	0	0	0	15	44	11	2	0	1	0	73
1964	0	0	9	15	6	30	41	43	1	1	1	0	147
1965	0	0	3	2	1	28	58	1	0	0	0	0	93
1966	0	3	0	0	1	100	127	31	0	0	0	0	262
1967	0	0	0	0	3	74	93	93	0	0	0	0	263
1968	0	39	0	0	0	28	228	13	0	0	0	0	306
1969	0	15	4	111	67	152	112	60	1	0	0	0	522
1970	1	12	21	35	43	61	13	95	42	11	0	0	334
1971	0	0	8	7	0	85	16	46	52	0	0	0	214
1972	0	1	3	0	24	50	103	51	12	7	0	0	247
1973	0	0	0	25	3	31	80	22	1	0	0	0	162
1974	0	0	1	13	1	5	73	27	0	4	0	0	128
1975	2	1	5	1	29	75	62	141	190	78	22	0	606
1976	0	0	47	60	135	179	39	199	236	111	0	0	1006
1977	0	26	11	48	213	73	114	150	177	10	0	0	822
1978	0	6	0	145	165	170	9	1	0	0	0	0	496
1979	0	0	0	103	139	120	0	0	0	0	0	0	362
TOTAL	10	140	141	639	909	1605	2000	1891	1203	266	24	0	8828

The lack of fisheries data from the NE Pacific is caused by too few research and survey vessels, dictated by the unavailability of funds. If there are about 15 to 20 vessel years spent in fisheries research in the North Sea, then the corresponding number for an area of concern four times larger in the NE Pacific is about 2 vessel years.

Any fish catch and/or landing statistics which exist do not necessarily reflect the abundance and availability of most of the resources for a number of reasons: First, the changing capacities of fleets and changing market conditions affect the catches and

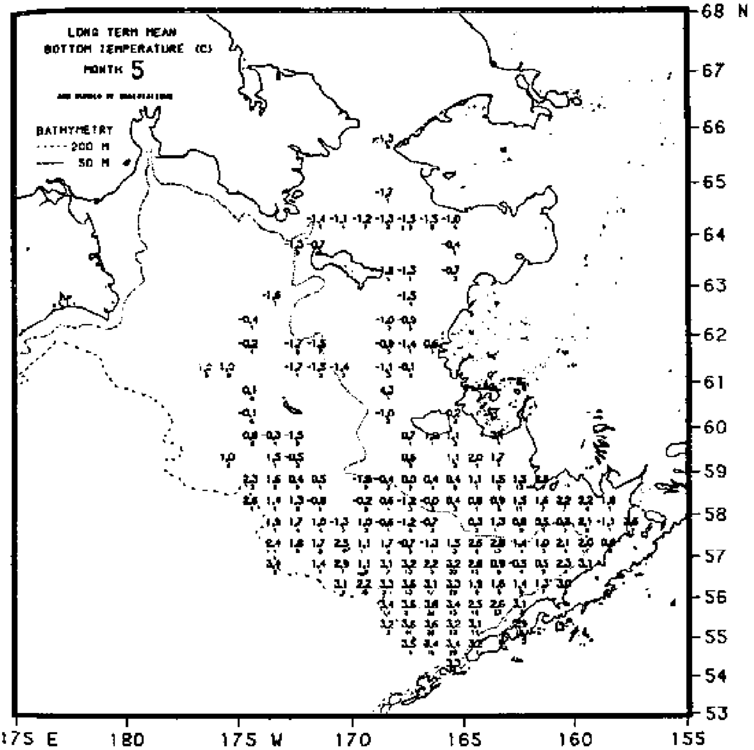

Figure 2. Long term May near-bottom temperature (°C). (Ingraham, 1981)

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landings. Second, catches are affected by weather conditions during the main fishing seasons. Third, the fleets frequent known fishing grounds and catch (and sample) thus only particular parts of the stocks. There have also been changes in gear. Fourth, the reports of foreign catches in earlier years are highly suspect and in recent years they have been controlled by quotas rather than by fish abundance.

Some Open Avenues for Numerical Simulation In Fisheries Oceanography

In the past a great number of single purpose models have been used in fisheries population studies. Although some believe that a model must be useful but not necessarily truthful, the present author does not share this view. Single purpose models ignore crucial complexes and present bogus answers. Small models do not capture the real world.

Rationalistic, holistic simulations on the other hand, should reproduce the total ecosystem realistically and the computers are used to process the complexities. Methods in these simulations are selected to fit the problems. The organism, its behavior and physiological needs prevail in the ecosystem; the most important being the interactions between organisms. The organisms are

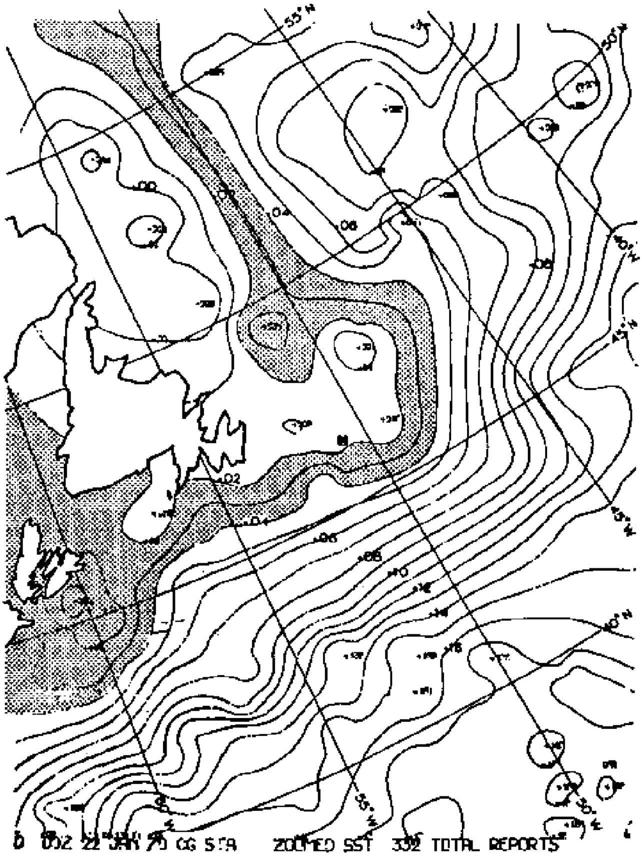

Figure 3.--Sea surface temperature analysis off Newfoundland-Grand Banks area on 22 January 1970. (The areas with temperatures from 2 to 4°C are hatched. Best cod catches during winter are made from this temperature range.) (Laevastu and Johnson, 1971).

controlled by the quantity (and quality) of materials (mainly as food) present in the system - a minimum requirement applies with the recognition that most organisms are mobile and can search for food. The organisms are also controlled by their tolerance to environmental factors but limits to their tolerance are wide.

The marine ecosystem contains a complex web of interactions among species (e.g., one species preying upon the other) and between the species and the environment. As there is an intense competition for living space and food in the marine ecosystem, the removal of part of one component of this ecosystem by a fishery alters the balance (or imbalance) in the ecosystem and can result in an increase and/or decrease in other components.

The only known dynamic marine ecosystem model that includes environmental processes in it and that permits simulation of the steady

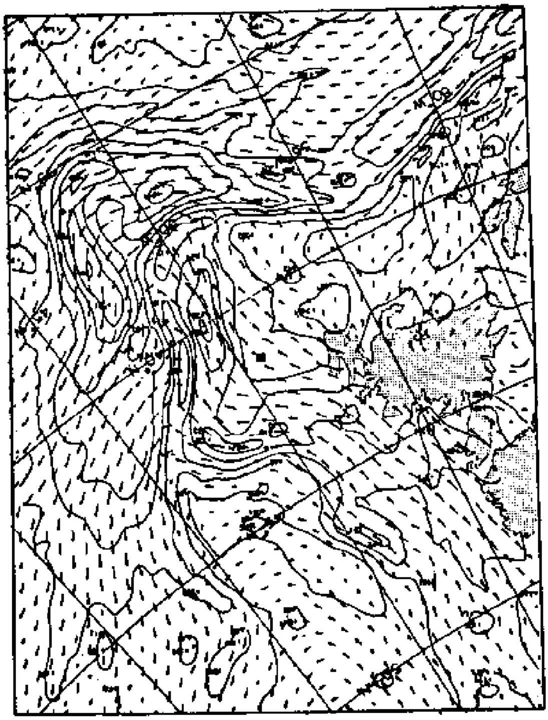

Figure 4. Surface current analyses in the area of Grand Banks, 3 October 1970. (Isolines indicate current speeds.) (Larson and Laevastu, 1972).

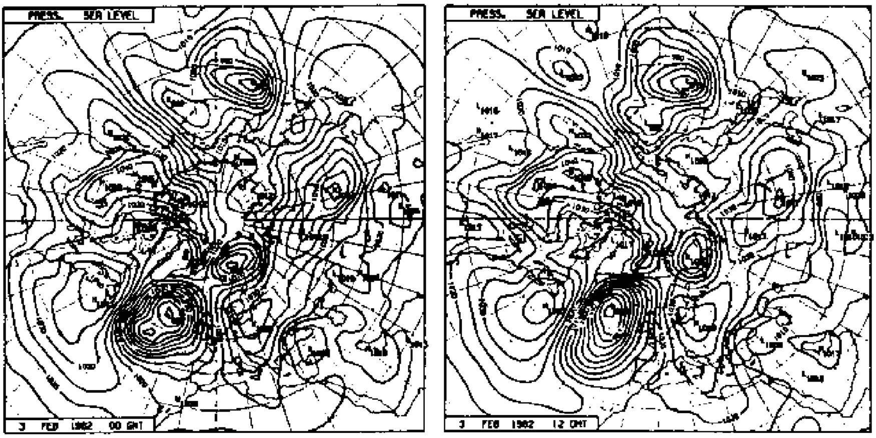

Figure 5. Surface pressure analyses on 3 February 1982 (00 and 12 GMT) (European Centre for Medium Range Weather Forecasts, 1983).

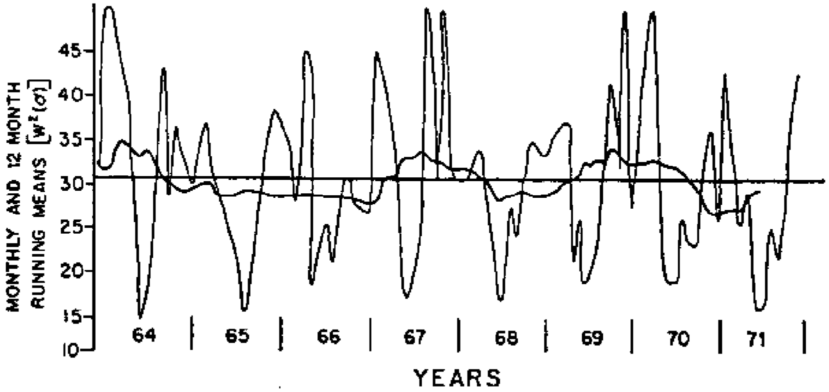

Figure 6. Monthly mean standard deviation of surface wind speed square and 12-month running means off the Washington-Oregon coast from 1964 to 1971, indicating the variations in winter wind speeds (Larson, 1975; Favorite, Laevastu, and Straty, 1977).

state as well as the dynamics of the standing stocks of species in space and time as affected by inter-specific interactions (e.g., predation), environmental factors (e.g., temperature, currents), and the activities of man (e.g., fishing), has been formulated at the NWAFC (Laevastu and Larkins, 1981).

This simulation has relatively small space and time resolution and has been used for a variety of environment-fish interaction studies based on known cause-effect principles. This model can also be coupled to atmospheric models. Furthermore, meaningful short-term fisheries prognoses (which are the only meaningful prognoses - Zemskaya, 1980) can be made with this simulation.

The "defined oceanographic features", such as fronts, are emphasized in fisheries oceanography, but they fail to influence effectively the aggregation, distribution, feeding differences, etc. of the species. There are no "fronts" in bottom layers, except where a thermocline intercepts the bottom. There are, however, a great number of processes on short term to interannual time scales, which can be studied with simulations. Climatological variations can explain some variations in e.g., larval recruitment; although, these climatological studies do lead to sea-air interaction problems which are at present largely excluded from ecosystem simulation.

The environment-fish interaction problems in relation to fishery research are listed in Figures 7 to 11. Figures 7 and 8 display the need for knowledge of environment-fish relations and study by conventional subject matter of fisheries research. Figure 9 shows the possible effects of temperature on the single species as well as on stocks.

Figure 10 shows the effect of temperature anomalies on two species in the eastern Bering Sea (pollock and herring), as computed with ecosystem simulation, mediated through the well-known temperature

- REPRODUCTION, LARVAL SURVIVAL
  - Reproductive potential
    - Number of spawners, maturation
      - Temperature anomalies (effect on maturation, displacement of spawning)
      - Food availability (starvation)(effect on maturation)
    - Survival of eggs, larvae
      - Predation on eggs, larvae (abundance, distribution of predators)
      - Dispersal, (transport, mixing)
      - (Availability of proper food)

- PREFISHERY JUVENILES, RECRUITMENT
  - Abundance, distrubution survival
    - Transport, migrations
      - Currents
    - Predation, survival (including recruitment from larvae)
      - Presence of predators
      - (Availability of other food for predators)
    - Growth
      - Temperature (especially winter season)
      - Availability of food (for larvae)

- EXPLOITABLE STOCK, FISHABILITY
  - Recruitment from juveniles
  - Distribution, abundance
    - Predation by mammals
    - Availability to fishery
      - Environmental anomalies (affecting seasonal migration)
  - Fishability of grounds
    - Types and roughness of bottom
    - Weather and sea conditions
  - Behavior in respect to gear
    - Diurnal behavior
    - Visibility of gear
    - Interspecies interactions with respect to gear
    - Temperature effects on gear avoidance

Figure 7. Processes and conditions in fish stocks potentially affected by the environment.

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effect on growth as the causal factor. Although temperature affects the abundance of pollock directly, its influence on herring as a forage species is mainly through changed predation pressure. Figure 11 illustrates the complexities of environment-fish interactions caused by migrations.

To summarize: Fisheries oceanography presents complex problems, the solutions of which require more data through continuous, planned monitoring and application of holistic ecosystem simulations. Simple models lead only to a "superabundance of speculative models

PAST THERMAL HISTORY (ANOMALIES)
    Time of maturation (delay of spawning)
    Growth, including effects of food availability

THERMAL ANOMALIES (PRESENT)
    Displacement of spawning
    Growth of biomass
    (Availability of food for larvae)

THERMAL STRUCTURE WITHIN DEPTH
    Availability, diurnal behavior (re. thermocline)
    Distribution and abundance of demersal fish

CURRENTS (WIND CURRENT ANOMALIES)
    Transport (eggs, larvae)
    Mixing, transport of food (e.g., plankton)
    Effects of currents on migrations
    Advection of ice

Figure 8. Environmental effects on fishery resources and their exploitation.

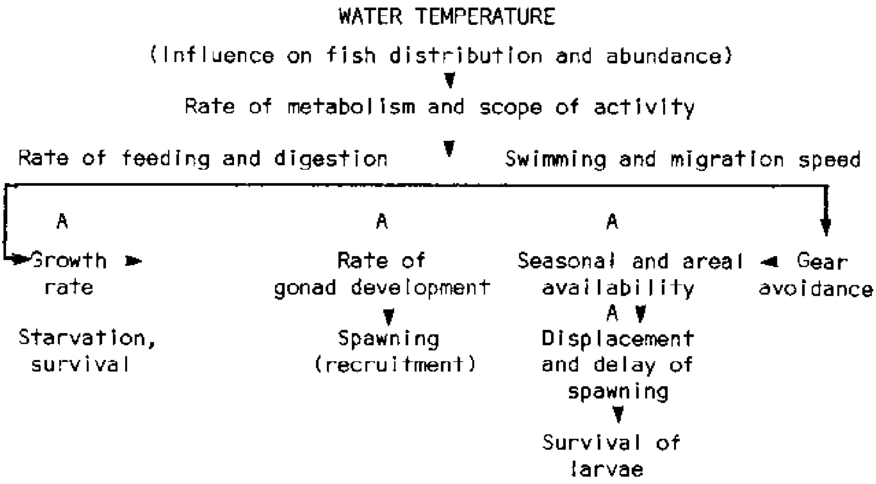

Figure 9. Schematic presentation of the effects of water temperature on the abundance, availability, and distribution of fish. Subjects marked with A are those where year to year anomalies occur which could be monitored for fisheries prediction purposes.

of doubtful reliability". Holistic simulations, though using mathematical statements, should not be based on assumptions that a given mathematical formula represents the behavior of nature, but rather on empirical knowledge and its quantitative reproduction - it should never enter the "dark age of barren formalism" (Skellam, 1972).

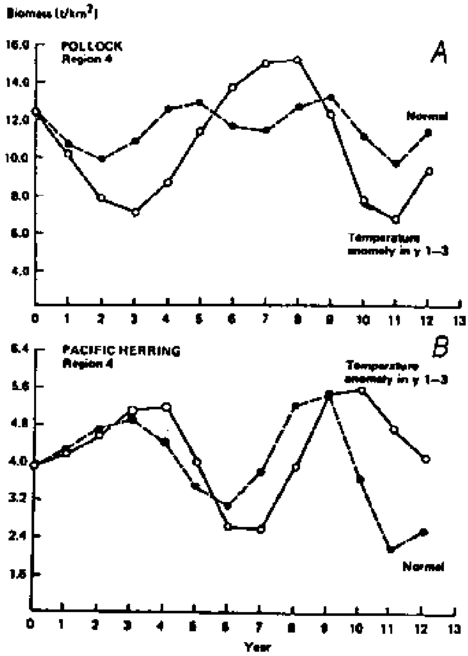

Figure 10. A. Changes of pollock biomass (in t/km^2) with time in Region 4 in normal conditions and with temperature anomaly in years 1 to 3.
B. Changes of Pacific herring biomass in (t/km^2) with time in Region 4 in normal conditions and with temperature anomaly in years 1 to 3. (Temperature anomalies: -1.5; -2.5; -1.5°C, respectively.)

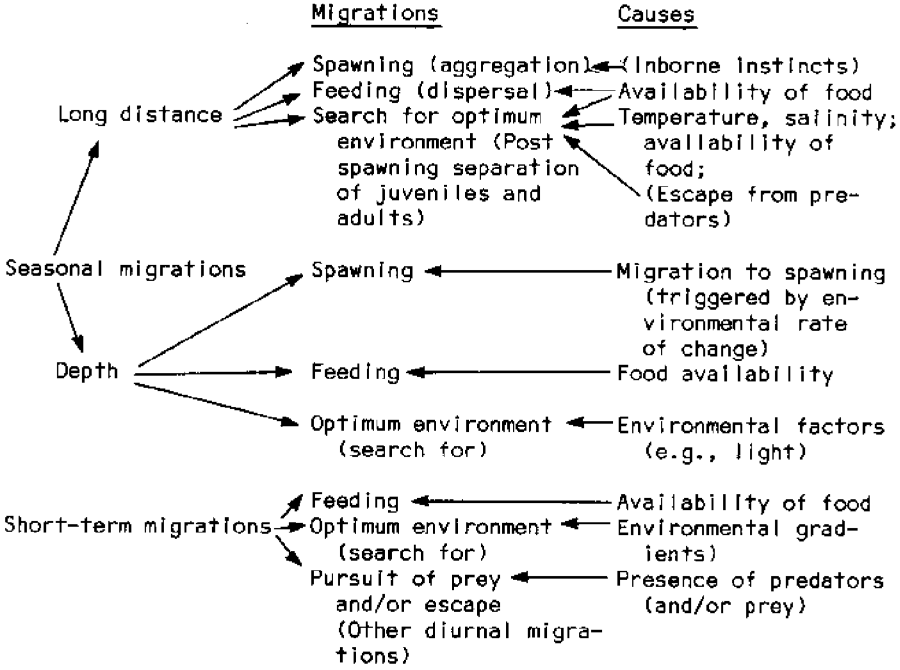

Figure 11. Scheme of environmental causes of migrations.

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Commentary

Numerical Simulation In Fisheries Oceanography

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This workshop has emphasized the problems of understanding the processes that control the environments of the Gulf of Alaska and the eastern Bering Sea, and the commercial fisheries therein. This brief commentary begins with the question, "what does the existence of various interfaces imply for management?" Oceanographers often address the atmosphere-sea interface via the physics of the interactions. Our interest here is in the biophysics of the animal-sea interface and in the biophysics of animal-animal interactions. Amazingly little is known, however, about the two biophysical interfaces. Therefore, the main question we address is the extent to which simulation/systems modeling contributes to the management of harvests, given our lack of knowledge of the interfaces. First, however, the topic of uncertainty is of considerable importance, and needs to be addressed.

The statement attributed to Einstein implying it was unlikely that God played dice, is as good a place to start as any because he was addressing a form of uncertainty linked to the very foundations of the physical theory of the universe. On the other hand, Einstein made significant contributions to the stochastic foundations of Brownian motion. There, the probabilistic aspect is present despite the ability to describe exactly (viz., with equations) the dynamics of particles. The probabilistic formulation circumvents the inability to parameterize the equations and the practical inability of solving many, many differential equations simultaneously. In otherwords, probability statements are used to describe deterministic processes as a matter of operational necessity. In neither case, however, is probability introduced to compensate for ignorance of the <u>processes</u> involved.

Another type of uncertainty concerns natural variability and the consequent inability to interpolate and extrapolate without making statistical statements. In some senses this uncertainty is analogous to that inherent in the formulation of Brownian motion because here, <u>even</u> if one could write the equations for the interactions, natural variability appears to be present and thus would imply uncertainty in the final answer to a question.

How does all this help in the formulation of a response to the presentation of Dr. Laevastu? Well, first of all, my interpretation of the approach he advocates is that it does not have the development of new theory as an objective. Further, it approaches the obstacle of inadequate or nonexistent theory by the collection of data of a sufficiently fine grain so that they can be used to construct a composite picture of the ecosystem. When theory is available, I infer that it may be used, or may not, depending upon its nature. Now consider a "data set" consisting, e.g., of the predicted abundance of some stock, based on other stocks' abundances, temperature data, etc., where all measurements were subject to at least some of the above types of uncertainty. Question: what can one infer of the type(s) of uncertainty in effect? One cannot distinguish between: a causal (cause-and-effect) relationship (viz., based on equations such as functional response or predator/prey) subject to natural variability, an inherently stochastic (random) situation, well-described by a stochastic function, and finally the situation in which no real insights into the processes exist (equals ignorance) but correlation relationships of various strengths are assumed valid. How are such models validated or evaluated? If error bounds are placed around estimates how are they interpreted? This overly brief discourse is, in effect, an elaboration of the often heard criticism that a problem with large models is that cause-and-effect is not preserved. The situation is worse: the different types of uncertainty present in truly large models, make it difficult or impossible(I suggest) to determine realistic error bounds on predictions.

Why then, do large models have such prominence today? The answer is, in part, that we reflect the values of a society currently enamored with technology, with home computers, with a faith in big machines that can absorb lots of data, can rearrange data, and can, at the turn of a handle, generate predictions. Whether or not simulation/systems advocates in fisheries ever claimed to do more than can be done is not the issue. Our own tendency to trust technology to improve on our logical processes plays a big role. Furthermore, the fact that large system/simulation models have been successful in modeling other phenomena and operations (e.g., manufacturing, where much more is known of the processes involved) appears to be a big factor in their favor.

But, what does Dr. Laevastu's presentation (if it is the same one I saw and heard at the workshop) say on this point. He says he is pessimistic about ever being able to predict fish population fluctuations from environmental data, but he is optimistic about being able to do so, if certain biological data is also available in the future. Actually, it is a rather modest statement.

Then we must ask whether there are any successes, at this time, that we can attribute to simulation/systems models. I have cast the question entirely in terms of predictions and not in terms of peripheral matters such as: these types of models assist in designing research programs, structure our thinking, etc. Dr. Laevastu answers that in the above paragraph.

What are the consequences if these matters are not fully addressed? I see two unfavorable consequences. One is that if the situation is as I have appraised it, a disenchantment may arise and this very important activity (simulation modeling) in fisheries may fall into disrepute. The area is in need of some perspective, which is not always provided. The 1982 publication, "Multispecies Approaches to Fisheries Management Advice" edited by M.C. Mercer, is an example of an unbalanced treatment that will be construed by some to indicate that such modeling efforts are more advanced than they are.

I am also concerned that Dr. Laevastu and others place the blame for simulation/systems models' inability to predict most heavily on a lack of a time series of data, rather than upon ignorance of how the marine ecosystem functions, viz., ignorance of the biophysical mechanisms and processes that define the interfaces noted in the first paragraph. As a consequence, research (money) will be diverted toward grand data collection efforts ultimately using high technology satellites, buoys, aircraft, etc., where communication is between computers. This means that research into the biophysics whether it be predator-prey, thermodynamic, physiological, etc., that generates testable hypotheses is neglected.

In particular, I advocate significantly increasing the research effort devoted to the coordinated use of experimental field studies, large tank experiments and manipulative experiments, and the use of "simple" single or multispecies models that focus upon the central processes thought to dominate the interactions. Such "simple" models have the advantage that they often preserve the relationship between the manager's knowledge of the fishery and his intuition about the outcome of a particular strategy. Since we all hope to present, via cold analytical reasoning, a (correct) counter-intuitive result, "simple" models allow uncomplicated explorations of the origin of an unexpected result in the model. "Simple" models also have the virtue of more well-defined uncertainty and allow for a more straight forward computation of error bounds around predictions.

The objective here is not to focus upon shortcomings (at least not exclusively), but to try to place simulation models within a philosophical context. Research, in the broad sense, in the field of simulation/systems models is an important aspect of modern ecology and will make, I suspect, important contributions. The field, however, will not reach its potential if the focus is upon data collection and correlation instead of upon the biophysics, represented by relatively simple mathematical formulations, that describe the biological interfaces.

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On The Development of Strategies For the Study of Ocean Fish Interactions

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The Lake Wilderness workshop had two major purposes, the review of present knowledge of interannual variability in the Gulf of Alaska and the eastern Bering Sea, and the development of strategies for investigating the linkages between environmental and fish stock variability in the region. To examine the latter question, participants were divided into three groups, chaired by J. Hunter, C. Miller, and A. Tyler, each of which was asked to address the following:

> The problem is to identify appropriate research strategies to pursue in the light of the reviews presented and discussed and taking into consideration the current interests and capabilities of the institutions concerned with the region. Of course, relevant research is in progress, and a minimum strategy would be to develop a conceptual framework for the overall question -- what needs to be known to predict the abundance of selected stocks? -- and to promote the identification and exchange of research findings to fill in the gaps. More aggressive strategies intended to accelerate the process (and requiring additional funds) would involve identification of specific approaches to be taken, hypotheses to be tested, species (stocks) and regions to be emphasized, priorities to be assigned, and so forth.

These groups met for several hours on each of two days, and their discussion were summarized by rapporteurs (D. Gunderson, K. Banse, W. Wooster). What follows is a synthesis of these reports prepared after conclusion of the workshop; it has not been reviewed and approved by participants.

General Comments

The discussions reflected the current paradigm that, except at low levels of stock abundance, year class strength is primarily determined by interactions with predators and larval food during the time between spawning and the time when year class strength has been established. The variability in these interactions is a function of fluctuations in the abiotic ocean environment which are in turn driven by atmospheric variability. Probably each stock responds differently to environmental variations, but it seems reasonable to seek general patterns of response among similar stocks in similar environmental regimes.

Some of the most important processes of interaction between factors of the abiotic environment and of the mortality of fish eggs, larvae, and juveniles are listed in the following table:

Abiotic factor	Mortality factor		
	Starvation	Predation	Other mortality (incl. disease)
Temperature	Timing and location of hatch. Zooplankton abundance. Timing of water column stability.	Growth of larvae. Isolation from predators by thermal barriers.	Thermal stress. Impact on parasitism, disease.
Turbulence	Timing of water column stability. Patchiness of prey items.	Reduced predation resulting from patch distruption.	Destruction by wave action.
Advection	Transport away from retention, nursery areas.		
Ice cover/ light	Timing and magnitude of food production.	Timing and magnitude of predation by marine mammals.	
Salinity			Osmotic stress. Impact on parasitism, disease.

It should be noted that spawning success is another possible source of variability in recruitment and that it is determined by conditions and events prior to those discussed above. Factors contributing to spawning production include the number and age structure of the spawners; their condition and energy storage; the batch fecundity, number of spawnings, and egg size; the location, timing, and "patchiness" of the spawning and the habitat available for it. Some of these factors, such as the number and age structure of spawners, are influenced by fishing mortality, while others are largely determined by environmental conditions. Energy storage preceding spawning occupies a protracted period, and the feeding conditions and abiotic factors operating as much as a year before the spawning period could be important in determining reproductive output.

For a given stock, required research will depend on its peculiar life history and on the knowledge of the species that is already available. But rather than considering species-specific investigations in any detail, the Workshop chose to work at a more general level. It identified criteria by which species could be selected for special attention, it developed a conceptual framework within which information on a stock could be compiled and hypotheses generated, and it looked at alternative approaches to the design of investigations. Thus, it cannot be said that the deliberations led to the selection of a research strategy, but only that they identified some of the ingredients that should enter into the formulation of such a strategy.

Selection of Species

There are several kinds of criteria for the selection of species or stocks. Perhaps the most powerful is the degree of commercial interest and economic importance. It is highly likely that programs of government fishery agencies will be directed toward certain species for this reason.

From the scientific point of view, the principal criterion is that the species exhibit significant variability in recruitment. If the variability is small, e.g., of a magnitude comparable to the uncertainty of its estimation, it will be very difficult to demonstrate a causal mechanism linked to environmental variability. All other things being equal, a species with large recruitment variability, including unusually strong year classes and conspicuous failures, may be most fruitful to study.

There are other criteria that relate to the feasibility of investigations:

1. Abundance: unless a species is abundant and subject to a substantial fishery, information on stock characteristics will be difficult to obtain.

2. Data base: an extensive data base on stock size and distribution, catch, age structure and recruitment is needed for a study of recruitment variability.

3. Survey logistics: the stock should be distributed within a reasonably limited geographical area that is feasible to survey and monitor. Migrations should be confined to this area, and it should be possible to sample all developmental stages without depending on the commercial fleet.

4. Stock structure: where there is a rich stock structure, with several well-defined substocks (as with herring and shrimp) with different spawning times and locations, each substock makes possible a separate "experiment" on environmental effects. In some cases, comparisons can be made with similar populations elsewhere.

5. Life span: species that experience recruitment at an early age and have a relatively brief life span will yield results in a shorter time than will longer lived species.

6. Experimental tractability: to obtain necessary information on feeding requirements and ecology and on associated growth and mortality will require experimental work in the laboratory or in enclosures. Success in this work will depend on the species being experimentally tractable under these conditions.

No one species or stock will meet all these criteria, and as noted earlier, the selection will often be determined by other factors. From that point of view, the feasibility criteria listed above are as much an indication of the difficulties of investigation as a basis for selection. The interests and motivations of the scientists and laboratories concerned are ultimately the determining considerations.

Species Schemata

A logic is required for identifying information needs and for organizing information about a stock and its environment in a way that suggests testable hypotheses. Such a conceptual framework was developed within which information on life history, on the influence at any development stage of the survival factors of food, predation, and physiology, and on the effects of abiotic phenomena on these survival factors could be compiled.

It was proposed that for each species of interest, and where possible for each stock, a table be developed containing information as follows:

ABSCISSA	Time, starting with month or longer prior to spawning, extending at least to metamorphosis; depends on life stage at which year class appears to be established.
ORDINATE	
Stage	Include both discrete events (marked *) and intervening periods: pre-spawning, spawning,* period to hatching, hatching,* period to first feeding, first feeding,* period to metamorphosis, metamorphosis.* For events, both average date and variance in timing are needed.
Habitat	For each stage, average depth and distance from shore (with their variances) and type of bottom where appropriate.
Survival Factors	
Food	Kind, quantity, associated growth, starvation mortality

Predation	Identity of predators, incidence, predation mortality
Physiology	Effect of temperature, salinity, dissolved oxygen, etc., on growth and mortality.

There will be few stocks for which it will be possible to provide all of this information; often the missing information will be of sufficient importance to justify a research effort.

To this point, the schema constitutes an annotated survival table, since it summarizes survival as a function of stage/time. In order to obviate stock size effects, it was proposed to normalize the information to a "survival per spawner" basis. Another simplification would be to consider "individual" rather than "local" changes, that is to follow mortality with reference to the moving stock rather than with reference to some fixed location.

In the next step, for each stage where the controlling survival factors have been identified, the abiotic phenomena, both scalar and vector, that govern variability in that factor would be identified. For example, the kind and quantity of food and the timing of its availability for first feeding larvae might be determined by the timing of the development of a surface mixed layer which depends on wind stirring, temperature, and insolation (a function of time of year and cloud cover).

With such tabulations, hypotheses of interaction and control would be constructed and tested with available time series and with simulation and analytical models; field observations would be planned to investigate clues revealed by the analysis. Laboratory and enclosure experiments would also be required to determine rates and fluxes; at each stage, the cost-effectiveness of obtaining the desired information would be evaluated.

Design of Investigation

In considering the actual design of investigations, there is a dichotomy between looking in detail at each developmental stage and all the variability it experiences, and selecting specific stages and phenomena which there is reason to believe are critical. While there are obvious dangers in the latter approach, the Workshop recognized the need for simplification.

For example, it was observed that while predation and starvation are the two most important biotic processes driving variability in recruitment, starvation is much more amenable to intensive evaluation. Predation experiments require analysis of gut contents for all predators, and they present significant problems in identifying larval stages (which rapidly become unrecognizable in the gut) and quantifying their rates of ingestion. Furthermore, the results of stomach analyses are difficult to extrapolate to the field without knowing the distribution of predator fields and their response to changes in temperature, turbulence, and transport.

In contrast, there are several criteria for establishing starvation, including the fraction of larvae showing histological signs of starvation; under some circumstances, the shape of the mortality curve; daily growth rates of larvae (obtained from analysis of daily growth rings on otoliths); stomach contents of larvae; and availability and quality of food items.

It was therefore proposed that initial attention be focussed on the starvation process with the view that if starvation were not thereby implicated as a major causal factor in recruitment variations, the alternative explanation of predation would be strengthened by default. A specific question was posed: Does transport influence starvation mortality for the species under consideration? To answer this question, the following information is needed:

1. The normal trajectory of eggs and larvae from the spawning area to the larval retention (or nursery) area.

2. Physical characteristics of the larval retention (or nursery) area.

3. Size-age structure and nutritional condition of the larvae over time and space gradients (to demonstrate that larvae have been transported out of favorable areas).

Transport may vary over a wide range of scales. While we are concerned with interannual variability, higher frequencies are also of interest. For example, the seasonal change in offshore transport on the Oregon coast has been well documented. The event frequency may be of particular importance, since storms at critical times may carry large number of larvae out to sea as well as destroying those near the surface in wave turbulence.

To examine the items listed above, a series of simultaneous field and laboratory experiments should be considered, in which several species of substocks would be examined to detect their different responses to the environment. The field surveys would be broad scale and descriptive and would require perhaps five or more years to complete; they would be coordinated with site-specific, process-oriented investigations. The surveys would attempt to define the space-time distributions of eggs and larvae of principal species and substocks, thus delineating spawning and larval drift periods, and would determine the physical characteristics of the habitat, field growth and mortality rates of larvae, the location of larval retention areas and juvenile nursery grounds, and the structure of ichthyoplankton assemblages, as well as permitting evaluation of sampling and other methodologies. From analysis of the birthdate distribution of prerecruits, survival rates for different segments of the spawning period could be determined. Site-specific experiments would be included, for example an intensive study of physical processes, larval size composition, and incidence of starvation along an offshore-onshore gradient.

It would be necessary to determine experimentally the direct physiological effects (e.g., thermal and osmotic stress) on egg hatching rates, larval viability and growth. Other laboratory studies would provide calibration of histological criteria for starvation, establish the validity of daily growth increments on otoliths, determine rates, limits, and other effects, and develop innovative technology and improved methods.

This proposal for broad-scale surveys contrasts with the wide-spread feeling that efforts should be concentrated on testable hypotheses. For example, one group argued that it was important to avoid large-scale ventures such as extensive studies of the Bering Sea. In order to estimate the mortality (or loss to the population) from diffusion or advection, it should suffice to work within a limited area that could be heavily instrumented and frequently resurveyed. A pilot survey would indicate the number of samples needed to provide useful confidence limits for mortality estimates.

The question is whether enough is known about the life histories and other vital statistics of species of interest to be able to formulate and test hypotheses, or whether the background information must first be strengthened, presumably by a broad-scale survey. The answer should become apparent in the completion of the species schemata described earlier. If a general survey appears necessary, serious thought must be given to defining its objectives carefully and to selecting the most effective way to achieve these objectives. An analysis of the CalCOFI surveys with determination of the minimum sampling that would have yielded a significant part of the information would be most instructive.

Apart from the question of a general survey, a matter that requires joint consideration by the participating institutions, it appears desirable now to move beyond the general level that marked the discussions at Lake Wilderness. The next step should develop from the specific proposals of scientists who intend to undertake the research and who would welcome the cooperation and participation of other scientists and research groups.

Monitoring

An ultimate result of a successful research strategy would be a realistic recruitment model. To develop and apply such a model requires that data on both stock abundance and environmental conditions be regularly available as products of monitoring systems.

Monitoring of the fish stocks is currently undertaken by government fishery agencies using catch data and the findings of direct stock assessment surveys. For many of the more commercially important species, the record of abundance and year class strength is reasonably good. For other species, the data are far from adequate, and the investigation of the determinants of their abundance will be correspondingly limited.

For the environment, there exist some reasonably long-time series of information on some atmospheric (e.g., surface pressure) and oceanic (e.g., sea surface temperature, sea level) variables, and repeated observations with broad coverage are being made by remote sensing from satellites. Future satellites are expected to give better information on surface wind stress and ocean circulation. Research may indicate that environmental variables not now monitored will be critical for predicting year class strength. Improvement and extension of environmental monitoring in the Gulf of Alaska and the eastern Bering Sea will undoubtedly be difficult and expensive. Thus careful study will be needed to determine the most economical ways to obtain the necessary information, and the joint efforts of all concerned will be necessary to carry out the observational program in the most effective and least burdensome way.

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Acronyms and Addresses:

IOS	Institute of Ocean Sciences, P.O. Box 6000, Sidney, British Columbia V8L 4B2
IPHC	International Pacific Halibut Commission, P.O. Box 95009, University Station, Seattle, WA 98105
NWAFC	Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard E., Seattle, WA 98112
OSU	Oregon State University, School of Oceanography, Corvallis, OR 97331
PBS	Pacific Biological Station, Nanaimo, British Columbia V9R 5K6
PEG	Pacific Environmental Group, P.O. Box 831, Montery, CA 93942

PMEL	Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Postal Bin C-15700, Seattle, WA 98115
SWFC	Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038
UAK	University of Alaska, Institute of Marine Science, Fairbanks, AK 99701
UW	University of Washington, College of Ocean and Fishery Sciences, Seattle, WA 98195