NORTHWEST & ALASKA FISHERIES CENTER PROCESSED REPORT

OCEANOGRAPHY
OF THE
NORTHEASTERN PACIFIC OCEAN
AND EASTERN BERING SEA,
AND RELATIONS TO
VARIOUS LIVING MARINE
RESOURCES

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I. INTRODUCTION

Environmental studies have been considered a part of fisheries re-
search since the formation of the first U.S. Fisheries Commission,
and there have been a number of investigations in the northeastern
Pacific Ocean and Bering Sea that have contributed significantly to
our present knowledge of oceanographic conditions and processes in
these areas. These studies have been widely spaced in time--com-
mencing with the coastal studies aboard the U.S. Fish Commission
steamer Albatross in the latter part of the 19th century and the
early part of this century, studies associated with the Pacific halibut
(Hippoglossus stenolepis) fishery by the International Fish Commission
(IFC) in the late 1920's and early 1930's; studies on sockeye salmon
(Oncorhynchus nerka) in the eastern Bering Sea by the U.S. Bureau of
Fisheries just prior to World War II, the post-war studies in relation
to Pacific sardine (Sardinops sagax) and tuna along the California
coast by the California Cooperative Fisheries Investigations (CALCOFI),
the transpacific tuna studies by the Pacific Oceanic Fisheries Investi-
gations (POFI) in the 1950's and 1960's, and the transpacific Pacific
salmon and northeast Pacific groundfish studies by the International
North Pacific Fisheries Commission (INPFC) from the early 1950's to
the present time.

It is not our intention to review individually these and all other marine
research activities, nor to provide specific environmental indices that
might lead to better fishing. Rather, the objectives of this report are
to synthesize in as direct and simple a format as possible oceanographic
conditions and processes in the Subarctic Pacific Region; to point out
those environmental factors that do and possibly could influence signif-
icantly the various life stages of living marine resources that are of
immediate concern to the newly formed North Pacific Fisheries Council;
and to suggest ways to accelerate resource-environment studies that can
add a new dimension to fisheries research by providing insight, if not
explanation, as to why fish are where they are and identifying indices
that permit establishing fishery forecasts. Implicit in this task is
the necessity of assessing: how complete is our understanding of environ-
mental conditions and processes as well as our understanding of relations
between the environment and living organisms, what are the major gaps in
our knowledge, what research can be pursued rewardingly with existing
techniques and equipment, and what additional knowledge is required that
will have to await further technology?

The three general environments on earth--air, land and water--are readily
identifiable by the layman in at least general terms, but in reality each
is infinitely complex in composition and dynamics. Many people think of
the water body--the ocean, as largely two-dimensional, that is, a rather
smooth water surface isolating land masses, islands and continents, and
providing omnidirectional movements of ships that provide transportation
of goods and people. Of course the ocean has another dimension, that
of depth, which is primarily the realm of the fisherman and the scientist
(except for depths related to the safety of surface vessels and the navi-
gation of submersibles). Usually the fisherman thinks of the water column

primarily as the space between the surface and bottom in which fish are found, either by acoustic devices or fortuitous positioning of nets and trawls; whereas, the marine scientist recognizes the water column as a dynamic and complex physical, chemical, biological and geological regime that is in constant motion yet composed of discrete layers, not only as a result of local phenomena, but as a result of forces that originate possibly in another hemisphere. Thus, time and space scales of seconds to centuries and centimeters to thousands of kilometers are involved. One must grasp the overwhelming significance of such vast scales as well as the myriad interactions in order to understand the immensity of the task confronting fishery oceanographers whose aims are to identify environmental factors that affect fisheries, and to forecast the incidence and intensity of these phenomena so that maximum exploitation can be obtained under proper conservation measures. Modern technology has provided the equipment and computers to process the vast amounts of data required, and there are numerous agencies and groups conducting marine studies. It behooves fishery groups to identify areas of interest that could provide a focus for many of the existing uncoordinated studies and to increase the scope of their own resource-environment studies.

A. BACKGROUND

The ocean environment is the life-support system for all marine organisms and the extant distributions of stocks are due to physiological, behavioral, and morphological adaptations to prevailing environmental conditions. Most people would agree that fluctuations in environmental conditions affect the distribution, abundance, and movements of fish, however, the complexity, variability, and interactions of physical, chemical, and biological processes in the ocean make it difficult to show or predict explicitly many specific cause and effect relations. There are many indications that this is primarily because of our limited knowledge of not only these processes, but also the physiological capabilities of the organisms, rather than because such relations do not exist. It would be reasonable for oceanographers and fishery biologists to continue to pursue independent studies until more knowledge in both fields is obtained before attempting to seek correlations. This would, however, reduce the benefits of interim although incomplete knowledge to commercial fisheries and to international commissions making long-term decisions. There is another important reason for accelerating the acquisition and integration of oceanographic and fisheries information as, in spite of attempts at international conservation measures, many stocks either have been or are being fished to very low levels before their niche in the ocean environment can be ascertained. This has happened to several species—Pacific cod (_Gadus macrocephalus_) in the Aleutian Island area, Pacific sardine in the California area, yellowfin sole (_Limanda aspera_) in the Bering Sea, and Pacific ocean perch (_Sebastes alutus_) in the Gulf of Alaska and off the coasts of Washington and Oregon. To further compound the problem, the spectre of ocean pollution has risen above the horizon. If we are unable to understand existing relations between living marine resources and the ocean environment, the burden of assessing the added effect of hydrocarbons, heavy metals, insecticides, and other pollutants makes the problem nearly overwhelming.

One dilemma is the formidable task of acquiring sufficient data to define existing environmental conditions. Although general knowledge of fish distributions and abundances is available from fish catches from thousands of fishing vessels, few or none of these vessels make or record even superficial environmental observations. Environmental data are obtained from only a handful of research vessels operating over a huge area. Data obtained from these vessels, obtained in conjunction with finite research studies, are aperiodic and widely spaced, useful primarily to define only gross climatic means. Although informative, these data are understandably of little use to specific problems of fishery management or to operational fishing vessels. In addition to defining existing conditions, it is also necessary to define mean conditions so that anomalous conditions and their effects on fish populations can be ascertained. This also implies a knowledge of natural variability, but once these factors are known, we can move toward a cause-effect understanding of environmental conditions and of variability of fish distribution and abundance.

Fish, particularly anadromous and pelagic species, move about in a three-dimensional continuum that is in constant motion and except for the possibility of magnetic fluxes, celestial orientation, instinct, or change or purposeful encounter with the sea floor (which can be several thousand meters below) or with the continental coasts (which are over several thousand kilometers apart) do they have any frame of reference for movement other than the air-sea interface and the physical-chemical properties of its environment. Although cold-blooded, a fish confined to a specific water mass can experience a temperature range as great as 15°C throughout a narrow range of the water column, or from season to season at the sea surface. However, with essentially a flip of the tail, it can seek out a constant temperature at depth and remain in that stratum with little effort for extended periods of time.

Although the ocean is basically a turbulent regime, the surface circulation is primarily wind-driven and has recognizable, although fluctuating, patterns. These currents,, which respond to day to day, season to season and year to year changes in surface weather patterns, affect changes in the ocean environment. There is an inherent order to all natural phenomena and as the increasing body of scientific evidence is sifted, there are recognizable relations between ocean conditions and processes, and fish distributions and movements. At the present time, these relations are admittedly general because of the paucity of both fish and environmental data, and of inadequacies in fish-catching and analytical environmental techniques. Understanding of the relations between fish and the environment requires an exact assessment of the abundance of fish at specific locations, not merely what is caught in a net. Further, the olfactory sense is highly developed in fish, yet we do not have the techniques to identify subtle odors trapped in water masses that, for example, could provide a homing mechanism for salmon. No one who lives 25 to 50 miles downwind from a pulp mill will deny the potential of olfactory sensing to ascertain a point source having a particular characteristic odor. With proper chemical techniques similar clues should be evident in the water samples seaward of a major river mouth where snowmelt and runoff from unique geological structures and organic surroundings having discrete chemical identities are discharged into the sea.

Our intent is not to provide an atlas of oceanographic conditions for to do so on a broad scale would permit showing only a general picture that would not be particularly informative, and to do so on a small scale, even if such information was available, would require more space than is available. Rather, some dominant, as well as some unique, aspects of the overall environment are presented as background for subsequent discussions of relations to specific fisheries. The abundant but still inadequate data base of environmental information, the accelerating contributions made by fishery oceanography programs, and the need for expanded and coordinated interdisciplinary studies involving the participation of research as well as commercial vessels, and inputs from satellite imagery are discussed.

II. PHYSIOLOGY OF FISH IN RELATION TO THE MARINE ENVIRONMENT

Some knowledge of the effects environmental parameters have upon the life
processes of fish is prerequisite to understanding how and why variability
in the ocean environment influences the distribution behavior of these
animals. Considerable experimental research on the influence that environ-
mental factors have on the physiology of aquatic animals has been conducted
in the laboratory and results have been used to explain occurrences in the
sea (Hela and Laevastu 1961; Harden Jones 1956; Hoar and Randall 1971;
Rounsefell 1975. Laevastu and Hela, 1970, International Commission for the
Northwest Atlantic Fisheries 1965).

Our intent is to draw upon segments of this knowledge to explain the
physiological effects of those particular parameters which biologists believe
to be major factors influencing the behavior, movement, and abundance of
fish and shell fish in the eastern North Pacific Ocean and Bering Sea.

As with terrestrial animals, the life processes of fish and shellfish are
controlled by the physical and chemical features of the environment in which
they live. For these animals the vital functions of feeding, digestion,
assimilation, growth, responses to stimuli, and reproduction are dependent
on the characteristics of the water. The most important of these water
characteristics are temperature, salinity, light penetration, oxygen
concentration, toxic substances, and disease organisms. Natural or purpose-
ful variation in these factors will result in corresponding variable
responses in the behavior of fish and shellfish which ultimately manifest
themselves in changes in stock abundance and distribution.

A. TEMPERATURE

Fish and shellfish are cold-blooded animals and, unlike terrestrial and marine
mammals and birds, their body temperature is not internally regulated but
approximates that of their surroundings. Therefore, because of the influence
heat has upon chemical reactions (metabolism) environmental temperature has
profound effects on the life processes of fish and shellfish.

Because of the nature of environmental temperature, the fundamental thermal
requirement of fishes is an external temperature most suitable to their internal
tissues (Brett 1956). That this temperature may not be limited to a matter
of a few degrees attests to the extent to which cold-blooded animals have
been able to evolve bodily functions which can maintain adequate roles
despite variations in body temperature.

Results of laboratory research on the influence of temperature on the life
processes of fish have shown that they have upper and lower limits within
which they can live. In addition, temperature sets limits to the animals'
metabolic rate within which they are free to perform, it governs the rate of
development and growth, and acts as a directive factor resulting in the
congregation of animals within thermal ranges or movements to new environ-
mental conditions (Brett 1956).

1. Thermoreception in Fish

Research has demonstrated that sensory receptors located in the skin are
primarily responsible for thermoreception in fish. The sensitivity
of fish to temperature changes has been well established experimentally.
Numerous marine fishes have been shown to perceive temperature changes
as low as $0.03^{o}C$ (Murray 1971). Thus fish are capable of perceiving fine
gradients of temperature enabling them to select thermal ranges most
conducive to their survival.

2. Optimum Temperature and Activity

The congregation of fish within a segment of a thermal range (optimum
temperatures) available to them has been repeatedly observed in nature.
This ability among fish to perceive and select a limited thermal range
is related to the temperatures which offer the animal an opportunity for
maximum expression of activity. Included within the scope of this activity
are feeding and swimming which must be sufficient to permit the animals
existence in the face of competition and predation. In addition, remaining
within an optimum temperature range is important for resistance to disease
and successful reproduction. Within a population of fish, inability to
maintain any one of these activities at moderately extreme temperatures
may be decisive to its continued survival. The temperature for optimum
activity is subject to change through acclimation and therefore may vary
for the same species in different parts of their geographic range.

The optimum thermal range for many species of fish (Table 1) changes
seasonally in connection with spawning and during various stages of growth;
thermal requirements are most exacting for survival in the very early stages
of development of an animal.

3. Lethal Temperatures

The upper and lower limits of temperature which an aquatic species can
withstand defines the extremes of its tolerable thermal environment.
Behavioral responses of cold-blooded animals to a temperature change depend
both on their thermal history and immediate thermal environment.

Lethal temperatures tend to be species specific for animals occurring in
areas with similar temperatures. However, lethal temperatures for a given
species are subject to change through the species' acclimation to a different
thermal range. For example, Pacific herring (Clupea harengus pallasi),
occurring in the warmer waters of Puget Sound, Washington, may have upper
and lower lethal temperatures quite different from herring residing in
the Bering Sea.

Fish vary in their ability to extend their temperature tolerance through
acclimation. The rate of increase in ability of fish to tolerate higher
temperatures appears to be a relatively rapid process requiring less than

Table 1.--Temperature ranges (^{O}C) for several species of commercial fish at three developmental stages.

Species	Location and season	Adult Range	Adult Optimum	Spawning Range	Spawning Optimum	Egg and larvae Range	Egg and larvae Optimum
Hippoglossus stenolepis (Pacific halibut)	Southeastern Bering Sea Winter and spring	>3-7[2/]	3.5-5.5[2/]	4.7-9.7[1/]	5.6-7.2[1/]		
	Summer and fall	-0.5-10[2/]	4.5-10[2/]				
	Northwest Central Bering Sea Summer	0-4[2/]	1.5-3[2/]				
	Gulf of Alaska Winter			• 3.5-6.0[3/]			
Limanda aspera (Yellowfin sole)	Southeastern Bering Sea Fall and winter	0.5-4.3[4/]					
	Spring and summer	0-12[4/]	2.0-6.0[4/]				
	Summer			6.4-11.4[*5/]		8.2-9.3[*5/]	
				4.4-11.4[†5/]		8.1-9.2[†6/]	
	Northeast Bering Sea Summer					6.6-10.7[*5/] 6.6-1c 0.8-6.9[†6/] 4.1-6.	
Clupea harengus pallasi (Pacific herring)	Southeastern Bering Sea Winter	2.0-3.5[2/]		-1.7-7[2/]			
	Fall	2-3.5[2/]		0.8-15.0[1/]	0.5-9.7[1/]		
	Auke Bay Winter	1.5-7.8[8/]					
	Spring	4.1-7.1[9/] 6.8-12.9[8/]					
	Summer	5.0-12.9[8/]					
Gadus macrocephalus (Pacific cod)	Bering Sea All seasons	0.10.0[9/]		3.0-5.0[9/]		3.0-5.0[*9/]	
	Spring					0.3-3.43[*10/] .04-1.45[†/10/] 7.2-8.6[*5/] 0.78-6.5[†/5/]	
Theragra chalcogramma (Walleye pollock)	East Bering Sea All seasons			-1.43.3[*11/] -0.3-3.38[†11/]	0.5-3.3[11/]		
	Southeastern Bering Sea Winter					-1.18-2.9[*5/] -1.34-4.55[†5/]	
	Summer					6.7-10.6[*5/] 1.94-11.3[†5/]	
	North Pacific	0-10.0[12/]	2.0-5.0[12/]				
Sebastes alutus (Pacific ocean perch)	Gulf of Alaska Summer					8.0-14.0[13/]	
	Spring and Summer					4.5-14.0[*14/]	
	All seasons	4.0-6.5[†13/]	2.5-3.5[13/]				
	Southeastern Gulf Summer	3.2-5.7[†15/]					
Anoplopoma fimbria (Sablefish)	Continental Slope Bering Sea All seasons		3.0-5.0[16/]				
	Gulf of Alaska Summer	5.1-10.0[c17/]				5.6-5.7[17/]	
	All seasons		5.0-6.0[17/]				

. [1/]Kuslenko (1970); [2/]Novikov (1964); [3/]Dunlop et al (1964); [4/]Fadeev (1965); [5/]Musienko (1963); [6/]Kashkina (1955; [7/]Dudnik and Usaltsev (1964); [8/]Auke Bay Fisheries Laboratory--Unpublished; [9/]Moiseev (1953); [10/]Rakhacheva and Zayayina (1960); [11/]Serobaba (1968); [12/]Kasahara (1961); [13/]Lyubimova (1963); [14/]Lisovenko (1964); [15/]Carlson and Haight (1976); [16/]Kuhkov (1965); [17/]Kodolov (1968); *surface temperature; †bottom temperature; 0-10 fathom temperature; 10 meter temperature; *3.0-5.0 and below; /larvae encountered; /sexually immature fish; /juvenile fish; ccaptured at 0-10 meters.

24 h. The loss in this increased tolerance and the gain in resistance
to low temperature are inherently slower processes requiring up to 20
days in some species to approach completion (Brett 1956). These rates
appear to be governed by the rate of metabolism which, if depressed by
low temperature, reduces the rate of acclimation. Sudden changes of
temperature are normally more dangerous to fish than slower changes during
which they have time to acclimate. Death of fishes at both upper and
lower lethal temperatures appears to be linked to failure of the central
nervous system.

The rate of acclimation to thermal changes and upper and lower lethal
temperatures of a species determines its geographic distribution, freedom
of movement, and successful existence in the sea.

4. Metabolism, Feeding, Growth, and Swimming Speed

Metabolic processes can be thought of as similar to the slow combustion
or chemical transformation where energy for activity (i.e. feeding and
swimming or growth and development) is derived from the carbohydrates,
fats, and proteins eaten by the animal. Because cold-blooded animals
cannot regulate their body temperature, it fluctuates with that of the
environment. Thus their rate of metabolism and feeding activity and
hence their nutritional requirements are dependent on the temperature
of the surrounding water. Since the waters of the North Pacific Ocean
and Bering Sea may have seasonal fluctuations of more than $15^{o}C$ a wide
range of metabolic rates and food consumption can occur in the same
individual animal throughout the year. These differences in metabolic
rate and feeding activity result in the observed seasonal differences
in the growth of fishes in temperate waters.

Metabolic processes and feeding activity are accelerated with rising
temperatures until an optimum is reached. There is a temperature level
at which the difference between active and resting metabolic rates is
maximal. This is the maximum activity level of fish with optimum energy
release. There are also optimum temperatures for rapid growth--those
at which the appetite is high and maintenance requirements low. Minimum
growth occurs when maintenance requirements are high because animals are
most active. The influence of temperature on metabolic rate (food con-
version in this instance) is illustrated for young sockeye salmon (Figure 1).

Growth increased with temperature up to a plateau followed by a rapid
decline with further increase in temperature. Donaldson and Foster (1940)
reported that when young sockeye salmon were placed in water in which the
temperature was gradually raised from $17.2^{o}-25.6^{o}C$ over a period of a week
they refused to eat and their respiration rate became excessive. By
lowering the temperature to $21.1^{o}C$ the fish began to eat and were able
to make a very slight increase in weight. Water temperatures in the range
of $4^{o}-7^{o}C$ produced poor growth. At approximately $10^{o}C$, growth and food
utilization were highest for the temperatures studied.
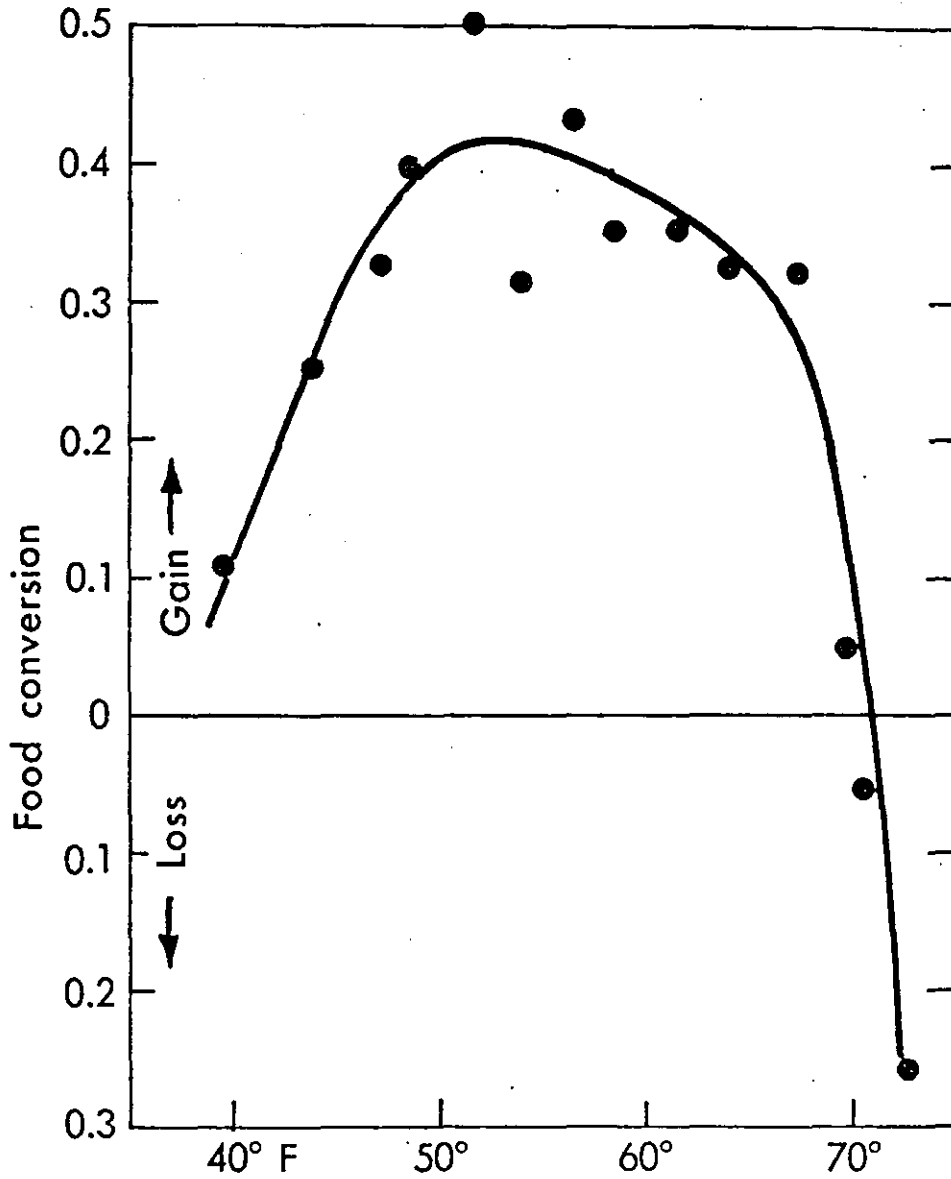
Figure 1. Growth of young sockeye salmon in 2-week periods as shown by food conversion at different water temperatures (from Rounsefell 1975).

Each species of fish tends to have its own range of favorable temperatures
for optimum growth and in many species found over wide areas, stocks in-
habiting different areas have developed genetic differences in physiologic
temperature accommodation. This is best illustrated by the size of Pacific
herring from a number of localities throughout their geographic range
(Figure 2).

Longevity as well as the growth of fish is affected by temperature. Many
fishes in southern warmer waters are generally smaller when compared with
the same species in the cooler northern waters, i.e. the Pacific herring.
This does not mean that southern stocks grow slower but that they usually
grow faster, mature earlier, and die younger.

Temperature not only influences metabolic and feeding rates but also the
rate of swimming of fishes. In laboratory experiments it has been demon-
strated with a number of species that swimming speed increases with
increasing temperature and that some species show a reduction in activity
as the lethal temperature is approached. This relationship is illustrated
(Figure 3) for under-yearling sockeye and coho (O. kisutch) salmon.

If the relation of swimming activity to temperature has survival value,
cases in which similar lethal temperatures exist accompanied by dissimilar
peaks for maximum activity--related species might be expected to have
different distributions according to temperature under otherwise similar
habitat conditions. In addition, environmental variability in temperature
can also be expected to result in corresponding variations of swimming
speed which may result in differences in the distribution of migratory
fish species.

The regulation of metabolic rate by environmental temperature also influences
fish and shellfish during the periods of rapid cellular change when gonads
are maturing and embryos and larvae are developing. Temperatures critical
to reproduction may vary with the reproductive stage. For example, many
marine fish require cool water for the maturation of the gonads. For
some invertebrates the critical temperatures for cleavage in eggs is lower
than the temperature required by the larvae. For animals in general the
developing embryo is particularly susceptible to thermal changes during
the period of gastrulation.

Studies of various fish species has shown that low or high water temperatures
during the spawning season may delay or hasten the onset of spawning due
to its influence on the maturation of sexual products. The temperature
at which fish spawn also varies with the species with each having its own
thermal range for spawning. Thus, among Pacific salmon (genus Oncorhynchus)
the five species indigenous to the west coast of the United States do not
all spawn at the same season; there is a regular progression in the runs
(Figure 4).
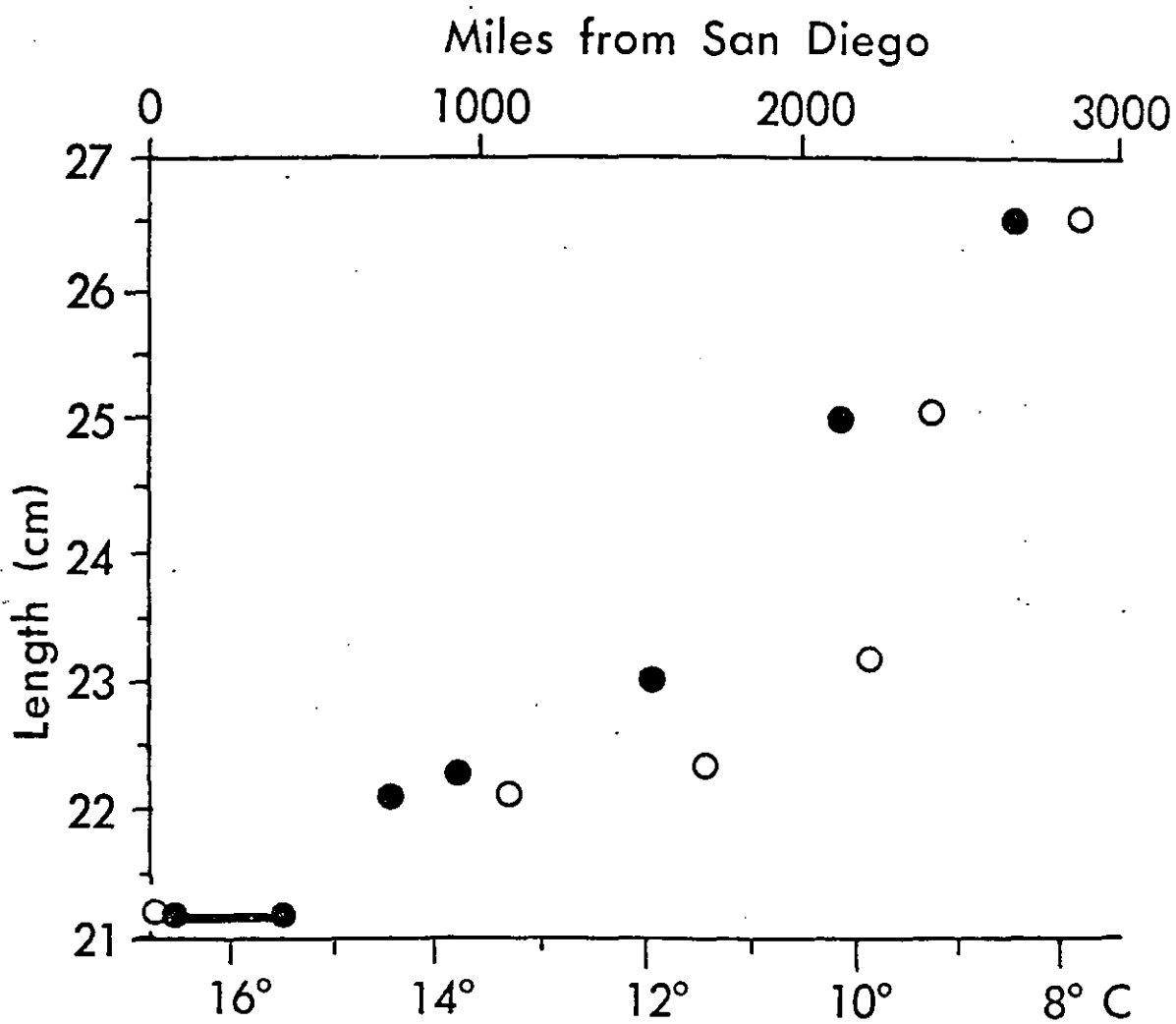
Figure 2.   Length of Pacific herring from "outside" waters at age
6 years in relation to temperature at 10 m (filled circles)
and to miles from San Diego following trend of coast
(open circles)--(from Rounsefell 1975).
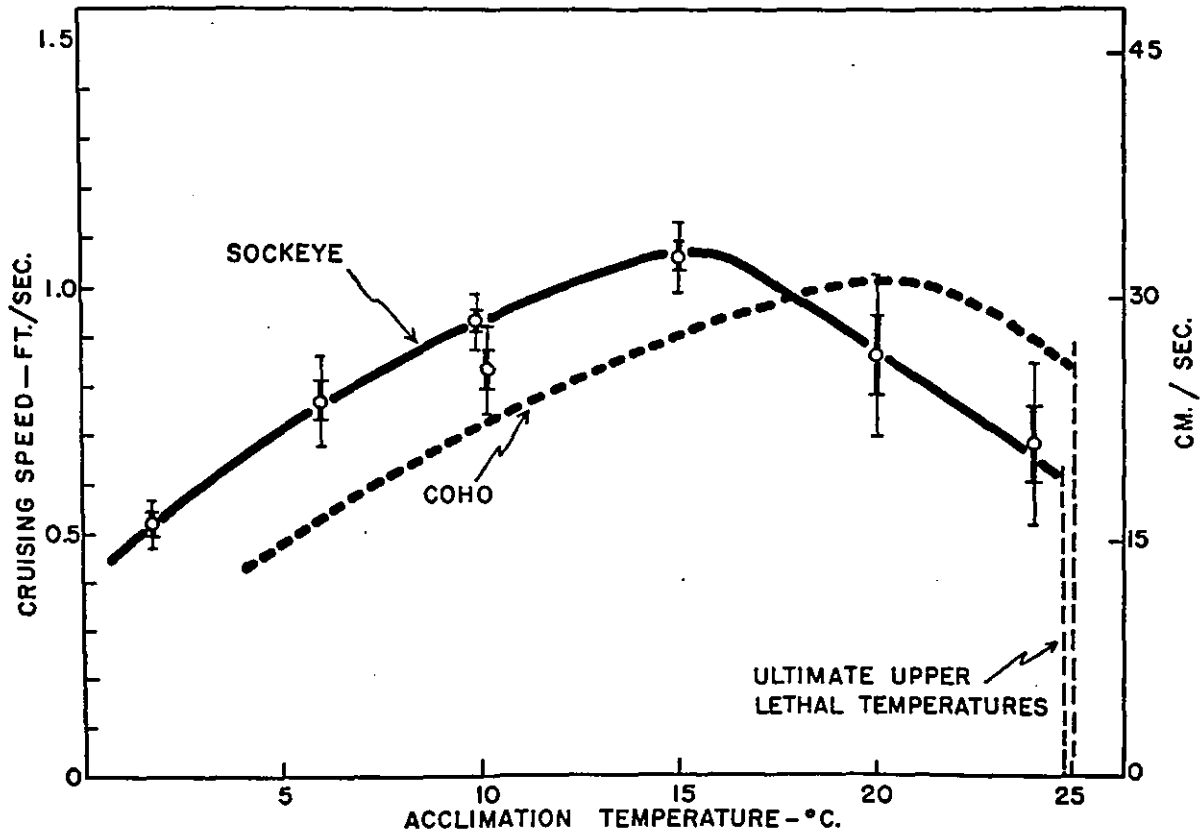
Figure 3. Variations in cruising speed for temperatures acclimated
underyearling sockeye and coho adjusted in each case to
common mean lengths of 6.9 cm and 5.4 cm respectively.
The samples were cultured under similar conditions and
are of comparable age, 4 to 6 months from hatching (from
Brett 1958).
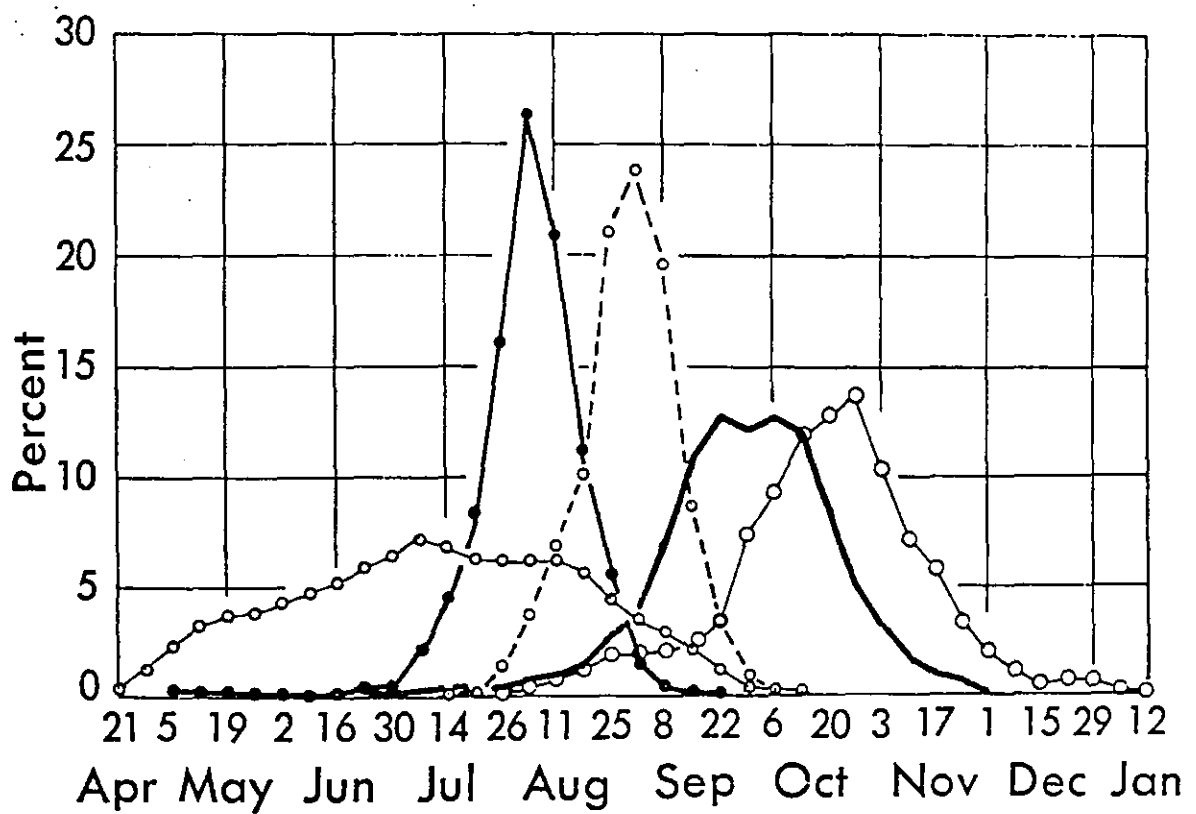
Figure 4. Seasonal occurrence by 7-day periods of five species of
Pacific salmon taken by traps as they migrated through
Puget Sound and San Juan Islands toward natal streams to
spawn. Modes from left to right are chinook (king) salmon
(Oncorhynchus tshawytscha), sockeye salmon (O. nerka),
pink salmon (O. gorbuscha), coho or silver salmon (O.
kisutch), and chum salmon (O. keta)--(from Rounsefell 1975).

The narrowness of the temperature range suitable for spawning may affect the geographic distribution of spawning of a species. Therefore, abnormal temperatures on the spawning grounds during the spawning season may force fish to spawn in other areas than those to which they normally return.

Environmental temperature because of its influence on the rate of metabolism and growth directly affects the rate of development of eggs and larvae. The length of time taken for the incubation of eggs as well as the length of larval life of fish and shellfish depends directly on temperature (Hela and Laevastu 1961). This relationship is illustrated (Figure 5) for three species of fish. Thus the prevailing temperature both before and after the time of hatching of eggs can significantly affect the proportion that survive. The developmental period for eggs and larvae is undoubtedly the most critical period in the life history of fish and shellfish because this is when they are most strongly influenced by physical conditions such as temperature. Therefore, annual variations in environmental temperature will affect the relative strength of brood years through its influence on the rate of development and growth.

In many species, cannibalism and predation are enhanced when young larvae or juveniles grow slowly. When the young grow fast, the fish reach a size large enough to avoid heavy predation in a much shorter period of time (Rounsefell 1975).

5. Directive Factor

As we have shown, the ability of fish to detect fine temperature gradients permits fish to respond behaviorally or physiologically to the environment. Temperature gradients may also serve as a directive function to fish providing signals of recognition of boundary regions such as between currents or areas of upwelling and divergence where food is usually more abundant. For fish stocks such as Pacific salmon, temperature gradients may mark the entrance to a pass or inlet along the migration route to their spawning ground.

B. SALINITY

Osmosis is defined as the flow of water (or other solvent) through a semi-permeable membrane. There is a tendency for solutions separated by such a membrane to become equal in molecular concentration; thus, water will flow from a weaker to a stronger solution, the solutions tending to become more nearly equal in concentration (isotonic).

The gill and oral membranes of fishes and other aquatic animals are permeable to both water and salts. Therefore, these animals are faced with the task of regulating the volume and electrolyte (salt) concentration of body fluids. When the concentration of the body fluids is similar to that of the external environment (isotonic) fluid movement is low.
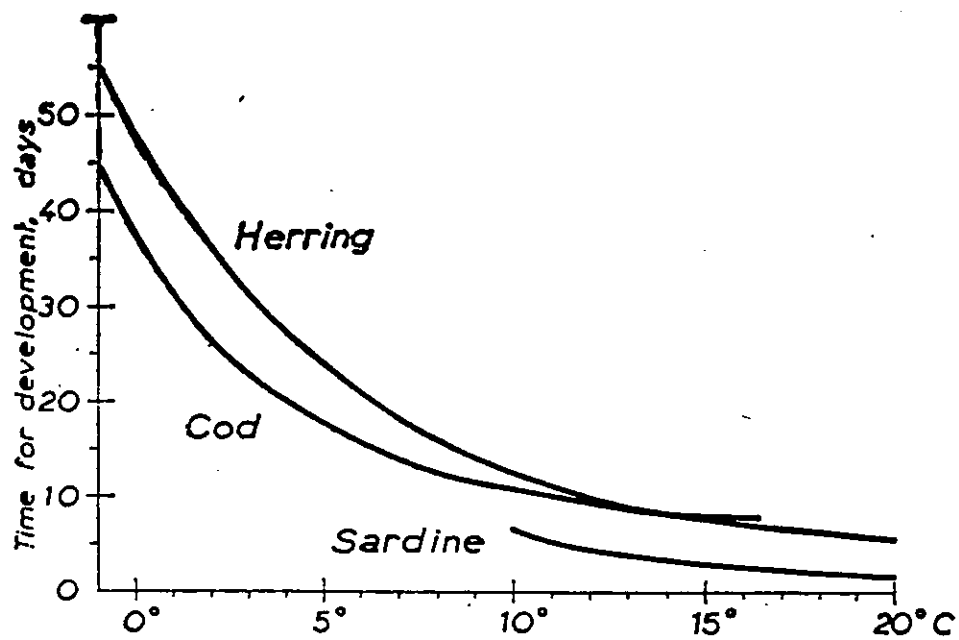
Figure 5.   Incubation periods of herring, cod, and sardine eggs (from
Hela and Laevastu 1961).

Aquatic animals faced with a diversity of environments have selectively evolved a regulatory system that can control both the volume of water and the concentration of salts of the internal body fluids to within very narrow limits. This control is known as osmoregulation and is treated in detail in many physiology texts (Brown 1957; Hoar and Randall 1969).

In fish the osmoregulatory process is shared by the gills and kidneys. Osmoregulation requires the expenditure of energy on the part of the organism. The amount of energy required depends upon the differences in salt concentration existing between the external environment and internal body fluids.

In the ocean, the salinity of the water is more concentrated than that of the body fluids, so water is drawn out, but salts tend to diffuse inward. Therefore, marine fish consume seawater and rid themselves of excess salts. By contrast, freshwater fish lose salt and take up water through the gills, because their internal salt concentration is greater than that of their surroundings.

1. Tolerance

The ability of organisms to tolerate changes in salinity, which influences their water-salt balance, is important to their seasonal and areal distribution (Rounsefell 1975). The ability to tolerate and/or compensate osmotically for salinity changes varies between species. Species which can tolerate only a narrow range of salinity cannot successfully invade estuaries. Animals that can tolerate wide changes in salinity and which attempt to maintain their own internal concentration expend a certain amount of energy in doing so. If the difference between internal and external concentrations becomes great, the animal may be under considerable stress. As a rule marine animals can tolerate lower salinities at higher temperatures (Rounsefell 1975). This may be responsible for the movement of the adult forms of many species out of the estuaries during the winter.

The young of many marine species are found in low salinity water. This is an established part of the life cycle of many marine fish. The adults spawn in water of high salinity and the young invade the estuaries (Rounsefell 1975). Apparently as they grow larger their tolerance for low salinity is diminished.

Despite the fact that anadromous fish such as salmon migrate between fresh and salt water, they are not very tolerant to wide ranges of salinity. They are able to migrate because of hormonal activity that results in physiological changes required for survival in the new environment (Black 1957). For example, salmon eggs cannot develop normally in saline solutions. Young chum salmon (O. keta) cannot enter the sea until salt-secreting cells have developed in their gills and other physiological changes have taken place. When returning to fresh water to spawn adult salmon undergo physiological change and exhibit a slight decrease in the osmotic concentration of the blood (Black 1957).

With respect to salinity tolerance in shellfish, Lough (1976) states that although the adults of various species of brachyuran crab inhabit waters with a wide range of salinities, specific larval stages have been shown to require restricted ranges of salinity and temperature to varying degrees for complete development. The larvae of Dungeness crab (Cancer magister) require salinities above 20°/oo for development and survival. In laboratory experiments mortality of Dungeness crab larvae increased greatly for larvae reared at 20°/oo. Early zoeal larvae were killed within a short period of time in salinities less than 20°/oo (Lough 1976).

2. Influence on Reproduction

The results of research on the physiological effects of salinity on the eggs and larvae of boney fish is excellently summarized by Holliday (1969). The discussion of this topic is based primarily on this work.

Salinity is an important factor in the survival of many fish. The eggs of some marine fish are often spawned close inshore near estuaries where fluctuations of salinity are likely to occur. The majority of fish of economic importance that spend any significant portion of their lives in the estuaries cannot reproduce at low salinities (Rounsefell 1975). So, they spawn either offshore or in the salt wedge in the mouth or deeper channels of estuaries.

Before spawning the eggs and sperm (gametes) of herring will remain fertile to some extent 12 h in full strength seawater and in 50% seawater for at least 24 h (Holliday 1969). The same relationship is shown in Figure 6 for the Atlantic herring (Clupea harengus harengus) and Atlantic plaice (Pleuronectes platessa).

Results of laboratory experiments have shown the existence of a wide salinity tolerance for eggs of the Pacific herring (McMynn and Hoar 1953). There appeared to be a trend toward higher survival of eggs at salinities which approximated those of the egg, i. e. were isotonic to the egg (11.55°/oo – 16.24°/oo). The explanation offered for this is that eggs spawned and developing within this range of salinity would have little or not osmoregulatory problems, and therefore be in a better position to survive (McMynn and Hoar 1953). Survival of eggs at very low salinities tends to be lower than at higher salinities.

The response to salinity of the most susceptible stage of egg development will determine the survival of the embryo upon hatching. High mortalities of eggs have been reported to occur at gastrulation and at hatching (Holliday 1969). Holliday describes some of the observed effects of salinity on the general rate of development and success of hatching of fish eggs. For Atlantic herring and Pacific cod the rate of development of eggs was reported to be greater at high salinities.
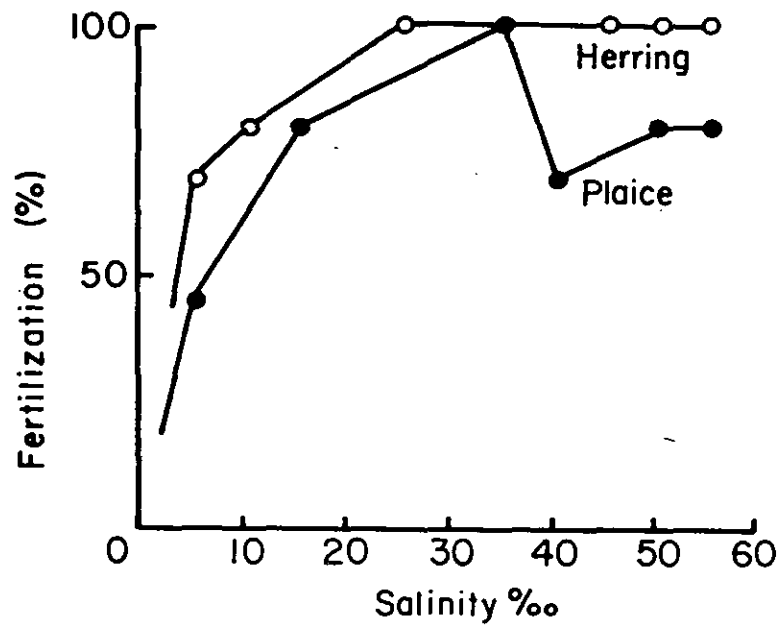
Figure 6. Percentage fertilization of herring, <u>Clupea</u> <u>harengus</u> <u>harengus</u>, and plaice (<u>Pleuronectes</u> <u>platessa</u>, eggs (from Holliday 1969; data for herring from Holliday and Blaxter 1960).

3. Influence on Larval Development and Survival

The skin of fish larvae at hatching is a thin two-layered epithelium through which the movement of salts and fluids takes place (Holliday 1969). The gills and kidney, which function is osmoregulation in adults, are not well developed in the larvae. Thus, the ability of the larvae to survive changes of salinity depends on the ability of the body fluids and tissues to function, at least for a short time, in an abnormal range of internal osmotic and salt concentrations and the ability of the larvae to regulate fluids to restore volume and concentrations to near normal.

Laboratory experiments have demonstrated that the yolk-sac larvae of some marine fish, e.g. herring and cod, can survive very wide ranges of salinity (Holliday 1969). The results of experiments conducted with herring and plaice showed that with increasing age there was a gradual change in tolerance to extremes of salinity so that at metamorphoses tolerance levels were the same as in the adult. In chum salmon the ability to tolerate high salinities begins soon after the yolk sac has been absorbed. This increased ability to survive high salinities precedes the seaward migration of the juvenile stages by about 6 months (Holliday 1969). A change with age in the salinity preferred by fry and under-yearling Pacific salmon has also been demonstrated.

As already discussed, survival of larvae is based on a combination of tissue tolerance and the ability to regulate body fluids and salt concentration. The survival benefit of equality in the internal and external salinities (isosmotic salinities) of larvae during development results from the conservation of energy required in osmoregulation. Activity levels are generally lower in low salinities near the isosmatic level and the ex-penditure of energy is therefore less and the ability to survive and achieve rapid growth rates may be increased.

4. Influence on Distribution

To recapitulate, salinity appears as an important factor which influences the survival of distribution of marine fish and shellfish at different stages in their life history. Many marine fish come near the coast and invade estuaries to spawn so that the development of the eggs and early larval stages occur in water of low salinity. Other fishes such as Pacific salmon, migrate to freshwater lakes and streams to spawn with the young undergoing physiological changes to cope with pending osmoregulatory problems before entering the sea.

The effect of salinity on distribution may be direct, e.g. may restrict the invasion of animals into regions not suited to their specific salinity requirements for succesful spawning and development. The effect of salinity on distribution may also be indirect, e.g. may affect the specific gravity of eggs and early larval stages of aquatic animals, and therefore their vertical distribution. During these early stages of development most marine fish and many shellfish species are at the mercy of the environment, either drifting in the plankton or being attached or buried in the substrate of the spawning bed.

The occurrence of anomalous salinity conditions during certain critical phases in the life cycles of aquatic species caused by heavy freshwater runoff for example may account for observed differences in their normal distribution and/or abundance. Correlations between salinity and the abundance of various species of marine fish and shellfish have been reported by numerous workers (Poulsen 1930; Walford 1946; Alander 1952; Jensen 1952; Lough 1976; and others).

Salinity may influence the distribution of fishes in another way. In laboratory experiments McInerney (1964) investigated the modal salinity preferences of juveniles of the five species of Pacific salmon. The sequence began with a preference for fresh water which changed gradually in the direction of increasing seawater concentration. The terminal preference was for open-ocean concentration. The temporal progression of salinity-preference changes was shown to parallel closely the salinity gradients typical of river outflows through which young salmon pass on their migration to the ocean. On the basis of this evidence, McInerney (1964) proposed the hypothesis "...that the salinity preference response of juvenile salmon reflects an ability to use estuarine salinity gradients as a means of orientation during their seaward migration." It is possible that adult salmon during spawning migration may also use estuarine salinity gradients and/or odor gradients in the location of their home river systems.

C. LIGHT

1. Perception and Fish Behavior

Light is an important environmental factor in the lives of aquatic animals. Light affects these animals directly through vision. Many fish rely on sight for capturing food, receiving signals that bring on or complete mating behavior, for locating shelter, and orientation. Light also affects fish indirectly through its influence on coloration. Light may also trigger and direct migrations and movements, have a timing role in reproduction, and influence the rate and pattern of growth.

Light perception in many fish occurs not only by way of the eyes but also the pineal region of the brain. The influence of light on fish is illustrated (Figure 7) which is reproduced from Blaxter (1965).

The function of the eye vision in aquatic animals is common knowledge. All fish do not have the same sensitivity to light, nor is their vision equally as good. The eyes of fish show many diverse modifications and adaptations to the mode of life of particular species. Aspects of vision and variations in the structure and physiology of the eye in different groups of fish is reviewed by a number of workers (Lagler et al 1962; Nicol 1963; Woodhead 1965; Munz 1971; Tomita 1971; and Ingle 1971). In general the fish eye is not dissimilar in structure to that of man. The retina contains both rods and cones, but accomodation is brought about by

Light

Eye   Pineal

(Vertical	(Horizontal	(Intensity	(Intensity)	(Object and	(Diurnal	(Seasonal	(Artificial	(Intensity)
direction)	direction)	colour)		movement	change)	changes)	light)	
				perception)				
Equilibri-	Naviga-	Colour	Activity	Feeding*	Vertical	Endocrine	Phototaxis	Colour
um (dorsal	tion	change		shoaling	migration	cycles		change
light re-		death		spawning				Phototaxis
action)				predation				
vertical				gear avoid-				
migration				ance				

Figure 7.   The influence of light on the physiology and behavior of
            fish (from Blaxter 1965).

movement of the whole lens towards or away from the retina. The arrangement of cones in the retina of marine fish has been reviewed by Engstrom (1963). Adaptations of the lense of the eye to the marine environment is discussed by Clarke and Denton (1962). There is little movement of the pupil and adaptation to light and dark results from migration of retinal pigment or of the visual cells. Vision in high light intensities is due to the cones and in low intensities to the rods. Most boney fishes have color vision.

Although the threshold of light sensitivity of the fish eye has not been measured, it is believed that in many fish it is equally or more sensitive than in man. The eyes of marine fish frequently have a number of properties tending to increase their sensitivity such as the size of the pupil, the density of pigment, and longer length of the cones in the retina (Woodhead 1965). It is likely that the absolute threshold of light perception in some marine fish may be much lower than in man. In clear oceanic waters, normal daylight can stimulate the human eye to a depth of 250 meters, and it is probable fish normally living at low light intensities can visually perceive light at deeper depths (Laevastu and Hela 1970).

In general visibility in water is restricted by light scattering and by heavy absorption which is much greater than in air and affects visual range (Woodhead 1965). The visibility of objects therefore depends not only upon the intensity of residual image-forming light reaching the eye but also upon the degree of diffusion of the image, and upon the radiance from the scattering of ambient light in the water along the line of vision. The relationship of the amount of image-forming light reaching the eye, to the ambient radiance, is dependent upon the scattering properties of the water and independent of light intensity, so that above a critical visual threshold underwater visibility would be expected to be constant over a wide range of intensities (Woodhead 1965). As the light intensity rises above the visual threshold, visual activity increases very quickly and fish can probably begin to discriminate surrounding objects at intensities only a few times greater than the threshold. This would be only short distances above the approximate depths of light penetration in various bodies of water (Table 2) given by Woodhead (1965).

The pineal region of the diencephalon portion of the fishes brain appears to have an influence on the behavior of color pigments in skin and on the reaction of these animals to light and dark (Healey 1957). The diencephalon seems to be an important correlation center for incoming and outgoing messages relating to the internal wellbeing of the animal and in affecting the endocrine system through the pituitary gland. The effect of day length on the pituitary gland brought about by the annual photoperiod is to elicit hormonal changes which prepare the organisms for future seasonal events such as temperature changes. Dermal reception of light has also been reported to occur in some fish (Harden Jones 1968).

Table 2. Calculated approximate depths of penetration of sunlight and moonlight into various seas in relation to minimum intensity for vision in fish (from Woodhead 1965).

Sea	Sunlight	Moonlight
Turbid harbours or estuaries	20 m	--
Southern North Sea (53^ON 2^OE)	120 m	65 m
Baltic Sea) English Channel)	200 m	100 m
Barents Sea	500 m	250 m
Clearest oceanic water	900 m	500 m

The reaction of fish to light (phototaxis) appears to be mainly under nervous control and is either positive or negative. Observations and experiments suggest that every species has a particular optimum light intensity where activity is at its maximum (Laevastu et al 1970). Light intensity in the sea is dynamic and it has been suggested that the observed movement in fish is an attempt to remain within the optimum range of intensity.

Fish are either positively or negatively phototactic. Phototaxis and a preference for different lights has been reviewed by Breder (1959). The use of lights to attract fish has been reviewed in general by Scharfe (1953) and Blaxter and Holliday (1963), and it has been suggested this may provide an artificial stimulus which cause abnormal behavior patterns in fish (Blaxter 1965). Various explanations have been offered to explain light attraction in fish--such as curiosity, feeding, positive phototaxis, following optimum light intensity, and hypnosis. The attraction of fish to light has been used to practical advantage in a number of commercial fisheries to improve catches; e.g. Pacific herring.

2. Induced Behavioral Rhythms

Like terrestrial animals, fish show a cyclic pattern in daily and seasonal activity, which results from physiological rhythms as adaptations to the daily and seasonally changing environment. The periodic change in the activities of fish are related to periodically changing physical character- istics such as light and temperature. Catch statistics, when correlated with time of day and observation of feeding activity, are indicative of the cyclic or periodic movements of fish.

Fish can be classified into diurnally active species which rely on vision and nocturnal species which rely on tactile, chemical, or electrical senses. One of the most striking features of the response of fish to changes in light intensity is often a vertical migration from deep water by day to shallow water by night. In general, most pelagic fish, e.g. herring and sardines, rise to the surface before sunset and move to deeper layers by sunrise (Hela et al 1961). Woodhead (1965) reviews the evidence for vertical migrations in demersal fish with respect to time of day. Laevastu and Hela (1970) have classified marine animals into six groups according to the nature of their vertical migrations and give examples of each. Five of these groups are illustrated in Figure 8 and described below.

— Pelagic species with daytime occurrence slightly above
the thermocline; migration to surface layer at sunset;
dispersion between surface and thermocline during the
night; descent to above the thermocline by sunrise.

— Pelagic species with daytime occurrence in layers below
the thermocline; migration through thermocline into surface
layers during sunset; dispersion between surface and bottom
during the night with bulk occurring above thermocline;
descent through thermocline into deeper layers during sunrise.
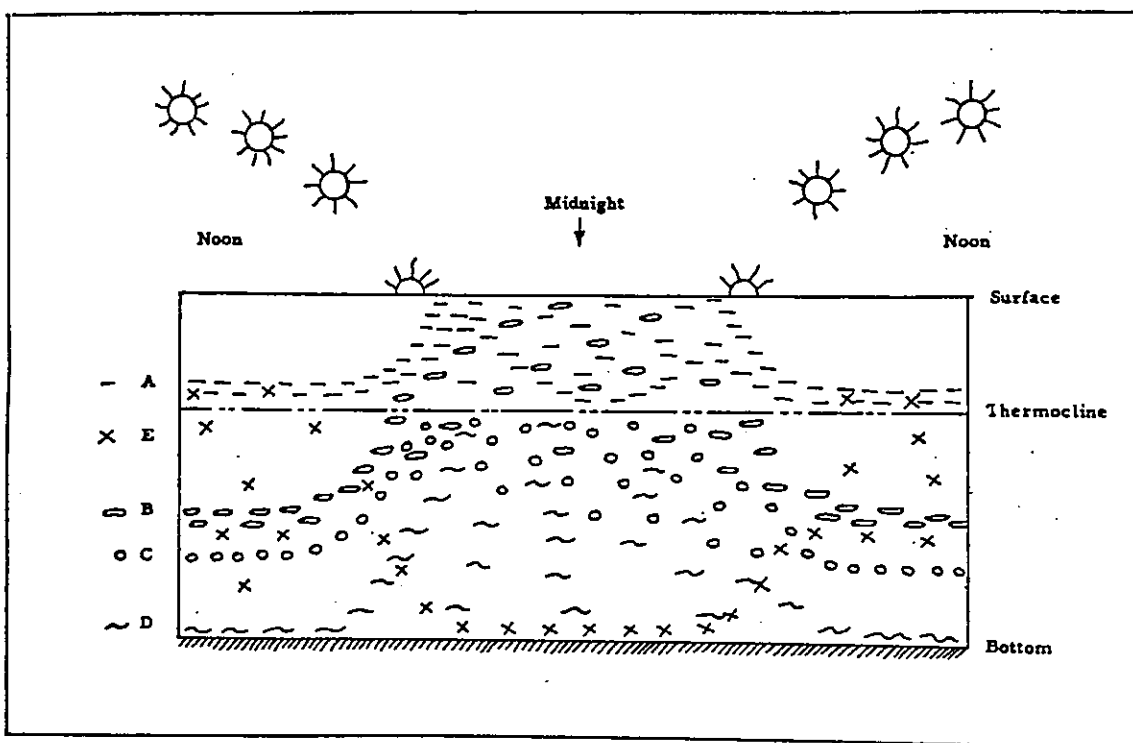
Figure 8. Schematic presentation of five different types of diurnal vertical migrations (from Laevastu and Hela 1970).

— Pelagic species with daytime occurrence in layers below
thermocline; migration to thermocline during sunset;
dispersion between thermocline and bottom during the night;
descent into deeper layers during sunrise.

— Demersal species with daytime occurrence on or close to the
bottom; migration and dispersal into the water mass below
(and occasionally also above) the thermocline during sunset;
descent to the bottom during sunrise.

— Species which are dispersed throughout the water column during
the day but which descend to the bottom during the night.

— Pelagic and demersal species without any distinct diurnal
migrations.

The adaptive value of vertical migration in marine fishes is related to
feeding and probably distribution. Diurnal vertical movements have often
been correlated with the need to follow food organisms towards the surface
at night. In many pelagic fish, e.g. herring, feeding generally occurs
at twilight near the surface. It has been suggested that daily vertical
migration is of advantage to the fish in changing their environment and
choice of food by scanning a range of depths twice daily (Woodhead 1965).
Laevastu and Hela (1970) suggested diurnal vertical migration with respect
to light may have adaptive value to fish in that they would avoid con-
centrations of toxic substance produced by phytoplankton during the day-
time photosynthetic period. Diurnal changes in vertical distribution of
demersal fish which take them away from sensory contact with the bottom
might be important in the distribution of fish. Vertical migrations may
take fish into different current systems from those which exist at the
seabed.

Light intensity is also important in the schooling behavior of many fish
which show a diurnal pattern (Schwassmann 1971). Schooling and the
dispersal of fish schools are greatly affected by changes in light intensity.
The minimum light intensities at which schools disperse differ widely for
different species (Laevastu et al 1970). Fish schools have been shown
to disperse during dark nights and no food is taken in darkness. The
threshold light value for dispersal was found to be relatively low so
that on moonlight nights some species of fish might not disperse and so
be capable of feeding near the surface. Although schools appear to
break up in the dark, they may remain as a group due to other stimuli as
well as a decrease in activity. The literature on the importance of light
in the schooling of fish has been reviewed by Loukashkin and Grant (1959)
and Shaw (1961).

The reproductive drives which motivate migratory behavior in many marine
fish may be in whole or in part induced by light. There have been a
relatively large number of laboratory experiments which demonstrate the
effects of light on the reproduction of fish. For many species the critical
levels and sequences of light and temperature necessary to control reproduction
have been established. Most experiments indicate that these factors
influence the production of pituitary hormones. As mentioned earlier,

Light can affect the pituitary-gonad system by means other than the eye, i.e. by way of the pineal organ. The predictable seasonal reproductive cycles and resulting migrations of marine fish provide the basis for many of the fisheries in the northeastern Pacific Ocean and Bering Sea; e.g. salmon and herring.

3. Orientation

Visual cues are an important factor to fish in the detection of and orientation to water currents (Rheotaxis). To receive visual cues it is assumed that fish must reamin in site of the bottom. Harden Jones (1968) proposed that fish may use visual cues such as moving debris or zooplankton to detect a velocity gradient when out of visual contact with the bottom. Using visual cues fish have been shown to swim against simulated water currents as slow as 2 to 5 cm/sec (Harden Jones 1968).

The detection of water currents will probably depend on the range at which fish can receive visual cues. Visual contact with the bottom or a velocity gradient is probably lost during darkness, and the overall movement of fish will then be the outcome of an interaction between orientated swimming utilizing other cues and passive drift. The loss of visual contact with the bottom in fish which undergo diurnal or seasonal vertical migrations could result in changes in distribution which are important in migration. Fish rising off the bottom could enter a body of water moving at a different speed and in a different direction to which they were swimming during the day or at a different time of year.

Since fish usually orientate to a moving field so that the image passes over the retina of the eye from anterior to posterior, with the background passing from tail to head, a fish receiving visual cues from the bottom will face upstream. In open water a fish below a velocity gradient and orientating to targets drifiting past above will head downstream, and those laying above the gradient and orientating to targets drifting past below will head upstream. Velocity gradients are often associated with temperature or salinity discontinuities (thermo- and haloclines). The position of the fish in relation to the thermocline or halocline may be the deciding factor in determining whether the fish faces with or against the current (Harden Jones 1968) and therefore the direction of its movement in the sea.

In addition to the importance of light with respect to orientation to currents is the utilization of its directional component by fish in open water navigation. Laboratory experiments with sunfish and juvenile salmon have shown that they have the ability to navigate by the sun and that they possess a clock system which allows them to compensate for changes in azimuth bearing depending on the time of day, longitude, and season (Hasler 1957; Brett and Groot 1963). Saila and Shappy (1963) analyzed the migration of Pacific salmon to the American coast and concluded that only a very rough ability to orientate by the sun is necessary. The directional properties provided by polarized light in the sea has also been proposed as a possible mechanism utilized by fish in open water navigation.

D. RESPIRATORY GASES—OXYGEN AND CARBON DIOXIDE

1. Aquatic Respiration

Fishes and marine invertebrates, like all terrestrial animals, must take
in oxygen and eliminate the waste carbon dioxide that results from internal
cellular respiration. Respiration in water as opposed to respiration in
air is conditioned greatly by two factors. These are density of the
medium and the greater dilution of oxygen in it. Water is approximately
800 times as dense as air at the same temperature. Depending on whether
it is fresh water or salt water, water at 20°C., for example, will contain
(at saturation) 9.4 mg or 7.6 mg of oxygen per liter respectively—as
compared to approximately 250 mg to be found at that temperature in a
liter of air at sea level.

The gills are typically the site where oxygen, dissolved in water, enters
a fish and where carbon dioxide leaves the blood stream. These structures
and associated organs are extremely efficient in supplying oxygen from
water of adequate oxygen content. In some fishes, gas exchange with the
water also takes place through the skin. The relative extent of the
respiratory surface in fish varies greatly from species to species and
appears correlated with the degree of activity of the species (Gray 1954).
The structures which maintain the flow of water over the respiratory surfaces
are the walls and floor of the oral cavity, the gill covers, and the gill
apparatus. Water is ordinarily taken in anterior to the gills through
the mouth or, in the case of those groups which possess them, through
spiracles as well and is passed laterally through the gills and out through
external openings. The intake and expulsion of water is usually an inter-
mittent process but in some instances water is propelled by peristaltic
waves of the gill cover and inflow may be continuous. When fish are active
some irrigation of the gills is obtained as a by-product of forward movement.

Oxygen diffuses very slowly from the water into the blood of fishes, which
functions in the transport of the respiratory gases essentially as it
does in terrestrial vertebrates. The red blood cells account for 99 percent
of the oxygen uptake and the plasma for 1 percent.

In developing embryos of fishes, various tissues serve as temporary breathing
structures. Among these structures, the yolk sac has (for a time) a
respiratory function. In most cases, a vascular network enveloping the
yolk greatly extends the respiratory surface (Fry 1957). Many embryos
develop threadlike external gills. The gross anatomy, development and
physiology of the gills and other structures used in oxygen-carbon
dioxide exchange in fishes may be found in numerous texts e.g. Brown (1957),
Lagler et al. (1962).

2. Oxygen Requirements

Ordinarily the rate of oxygen consumption by fish may be taken as a general
measure of the intensity of its metabolism (Fry 1957). Such measures have

been made to determine the ability of a given species to take up oxygen when under the influence of various external environmental factors including gradients of partial pressure of oxygen itself, such measurements of oxygen uptake must consider both the metabolic rate of fish at rest (standard rate) and when active (active rate). Fish are easily provoked to consume oxygen at a near maximum rate and are slow to reduce their metabolic rate after activity. Oxygen consumption at the active rate is restricted to only a few multiples of the standard rate. In contrast the oxygen uptake in man, with maximum work, may be 20 times that at the standard rate and in insects it may be of the order of a hundred times (Fry 1957). The resting metabolism of fishes is adequately handled by their respiratory system often down to a concentration of ambient oxygen in the order of 1 mg/l. The lowest level of oxygen at which the resting metabolism can be met in a given species depends as much on its oxygen demand as on the characteristics of its respiratory system. The active metabolism of fish is more strongly dependent on the oxygen content of the water. The degree of this dependence is related as much to its oxygen demand as to the character of its respiratory system. The activity of which the fish is capable is correlated with the difference between its standard and active rates of metabolism, thus, any partial pressure of oxygen which reduces the active rate of metabolism reduces the activity of the fish and places the species in question at a disadvantage. At a particular low partial pressure of oxygen, the active metabolic rate of the fish is reduced to bare maintenance requirements, and it is no longer able to perform external work. Below this level a further reduction in oxygen quickly leads to death.

The rate of oxygen consumption by fish is influenced by its size and the characteristics of the water. The standard rate has been shown to increase in certain species in response to an increase in the external concentration of carbon dioxide. The increase has been attributed to the increased cost of respiration (Fry 1957). The standard rate also increases continuously with increasing temperature up to the lethal temperature in fish allowed sufficient time for adjustment and not subject to other environmental stress. The active rate of metabolism, however, may level off or even decline at a temperature well below the upper lethal limit. The scope for activity in fish, which depends on the difference between the standard and active metabolic rates, varies with temperature but in a way that cannot be predicted from the standard rate. According to Fry (1957) it may be uniform over an extended range of temperature or may show a well defined optimum at a temperature not necessarily related to lethal temperature. The effect of a reduction in the oxygen content of the water will differ at different temperatures. The general effect will be to severely restrict the activity of fish at the highest temperature.

The metabolic rate of fish in relation to size gives a straight line when the logarithm of respiratory rate is plotted against the logarithm of the body weight. Most species of fish show a standard rate of oxygen consumption that is related to their weight raised to a power of 0.8. The relation of the standard rate of oxygen consumption to size is essentially

independent of temperature. According to Fry (1957) the relation of the active metabolic to size is of the same order as the standard rate in the one species where it has been investigated but was found to change some-what with temperature, with larger fish not quite keeping pace with smaller ones.

3. Effect of Carbon Dioxide on Oxygen Consumption

A number of investigators (Hall 1931) and (Meyer 1935) have shown that increasing the partial pressure of carbon dioxide in water leads to a decrease in the percentage of oxygen utilized. This is because at higher levels of carbon dioxide part of the hemoglobin is prevented from combining with oxygen. However, it is only under anaerobic conditions that free carbon dioxide ordinarily reaches such major levels that it will affect oxygen utilization. The major point of concern to fishery biologists with respect to the respiratory gases is that under natural conditions oxygen lack is a more likely limiting factor in fish behavior than carbon dioxide excess.

4. Oxygen as a Limiting Factor

Experimental information on the oxygen tolerance of marine fish is scant. Warm water fishes in general have a lower threshold of tolerance than colder water fishes. Above the lethal limit, the effects of varying concentrations of oxygen on fish is that imposed on their activity. Activity, in this respect, included development, growth, and movement. The limiting effect of oxygen supply may have special significance in the case of developing embryos. In the developing egg the metabolism required to organize the yolk into embryo provides a high oxygen demand. To satisfy this demand a high ambient level of oxygen is often required. A restriction on the oxygen supply for developing eggs results in a reduction in development. Eggs developed at reduced levels of oxygen have been observed to develop more slowly. Apparently the most dangerous time for developing eggs, as far as a lack of oxygen is concerned, comes just prior to hatching. (Lindroth 1942).

Fluctuating oxygen levels may also influence the growth of fish (Figure 9). Fish exposed to fluctuating oxygen levels showed no growth while those at a constant level increased their weight normally. The movement of fish is also influenced by oxygen levels in the water (Figure 10). Low oxygen concentrations reduce the swimming ability of fishes, the extent of which is influenced by temperature.

E. SOUND

Throughout fisheries literature, currents have been emphasized as an important environmental factor influencing the behavior, distribution, and abundance of fish. The detection of sound is briefly mentioned here because it is one of the several senses in fish which may be utilized in the identification of and orientation to currents.
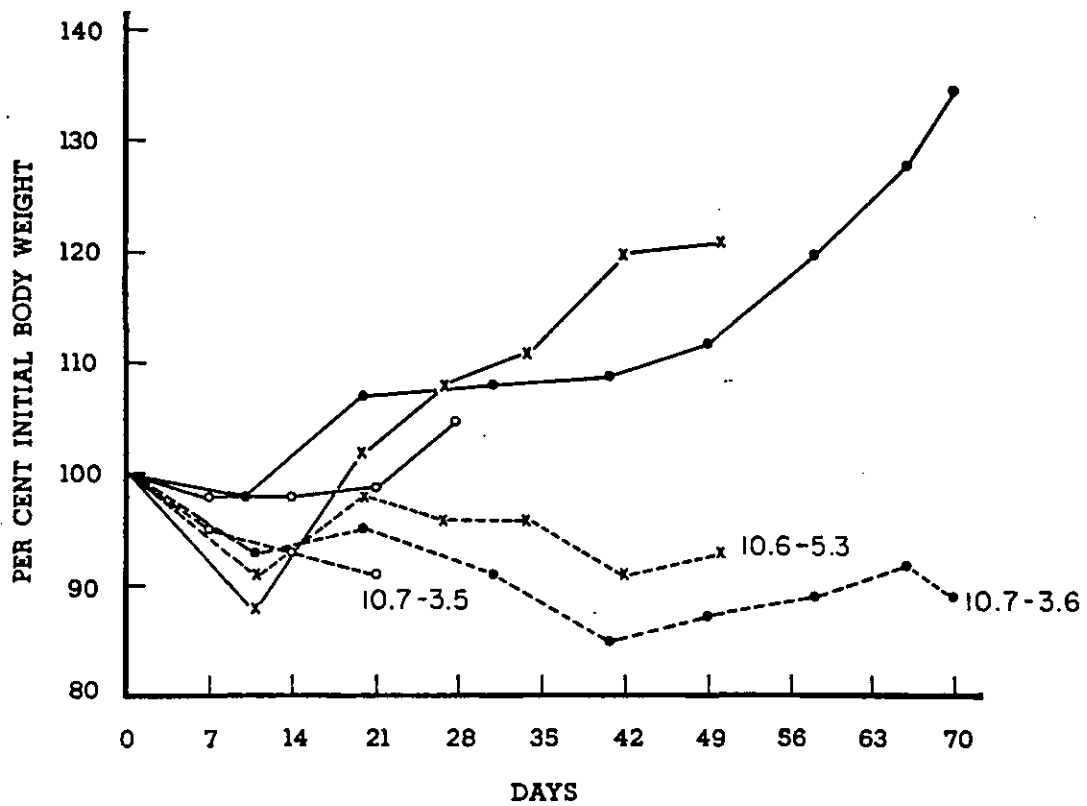
Figure 9. Growth of yearling eastern brook trout, _Salvelinus fontinalis_, at constant high (solid lines) and various daily fluctuating levels of oxygen (broken lines). Numbers indicate upper and lower levels of oxygen in mg/1 (from Whitworth 1968).
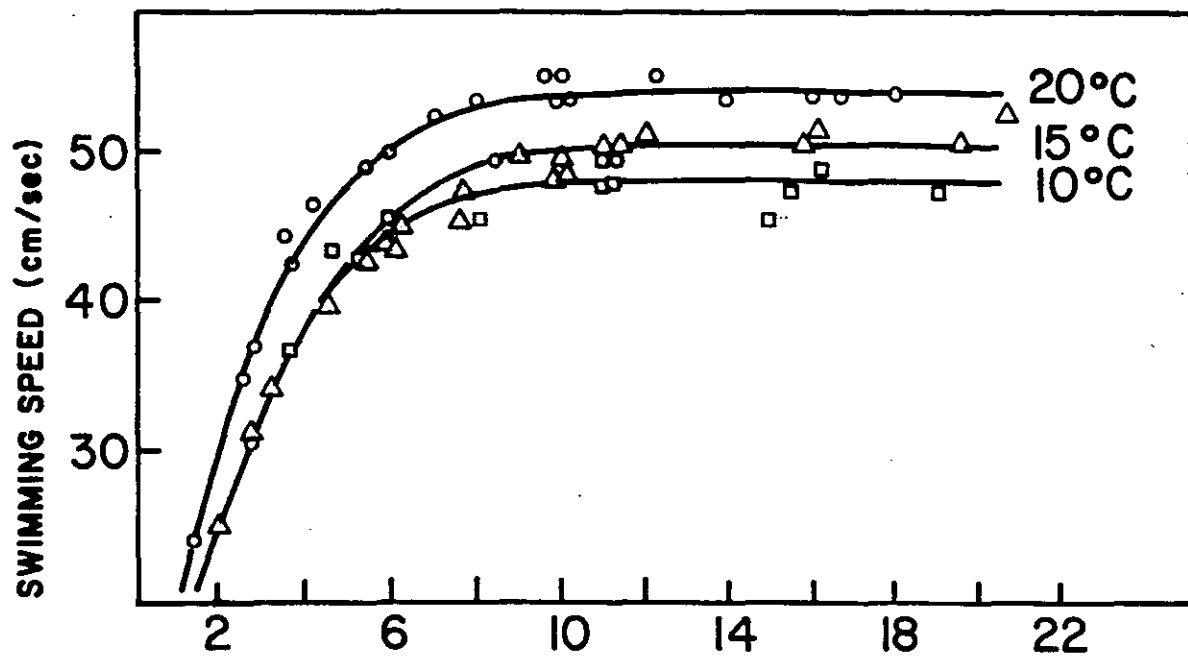
Figure 10. Swimming speed of underyearling coho salmon, Onchorhynchus
kisutch, in relation to oxygen concentration (from Davis
et al. 1963).

Three physiological mechanisms are employed by fish to discriminate sound: the inner ear, the swim bladder, and the lateral line system. The anatomy and physiology of these systems are covered in detail in such texts as Brown (1957) and Hoar and Randall (1971). Van Bergeijk (1964) has reviewed the available data with respect to the nature of the acoustic stimulus presented to fish and emphasized that the distinction between two forms of acoustic energy must be made: i.e., between the far-field (pressure) and the near-field (displacement). Fishes have, at best, only one pressure receptor, the swim bladder (a hydrostatic organ), which is coupled in certain groups to the inner ear. The acoustic discontinuity of a swim bladder in a fish enables it to respond to pressure waves (i.e., far-field sound), and the bladder transforms them into local near-field effects that excite the inner ear (Harris and Van Bergeijk 1962; Van Bergeijk 1964). Specializations such as the Weberian apparatus, a chain of bones coupling the swim bladder to the inner ear, enhance far-field hearing. Both the inner ear and the lateral line are essentially displacement sensitive; but, as mentioned above, the inner ear receives near-field displacements from the swim bladder. The lateral line functions primarily as a displacement detector and, as a result, a hydrodynamic motion detector. It is essentially a near-field hearing organ with the capabilities of localizing sound sources (Van Bergeijk 1964). It informs the fish of localized disturbances caused by small currents, mechanical vibrations below 100 cycles per second (Lagler et al 1962), or irregular non-violent displacement of the surrounding water. The lateral line system is also involved in "distant touch" location of moving objects such as prey, in the sensing of fixed objects which reflect water movements such as rocks and shoals or brought about by the swimming fish itself.

F. CHEMORECEPTION

Chemical reception in fishes is involved in the procurement of food, recognition of sex, discrimination between individuals of the same or different species, in defense against predators, avoidance of dissolved toxic substances, parental behavior and in orientation. Hasler (1957), Teichmann (1962) and Kleerekoper (1969) present an excellent review of chemoreception functions in fishes.

On the basis of location and structure—as well as innervation, chemical reception is divided into three categories: olfaction or smell, gustation or taste, and a general chemical sense. In terrestrial animals, those receptors which have high sensitivity and specificity, and which are "distance chemical receptors", are distinguished as olfactory, those receptors of moderate sensitivity and stimulated by dilute solutions are gustatory or "contact receptors", and those which are relatively insensitive and non-discriminating are considered common chemical sense. In fishes, smell and taste are both mediated by aqueous solutions so that the distinction is made anatomically and physiologically.

1. Odor Perception

Odor perception in fishes are those chemically induced sensations which
are relayed to the central nervous system from the olfactory sac. Among
fishes extreme variations are found in the morphology of olfactory organs.
Details on the anatomy and morphological variations of olfactory organs
among the various groups of fishes may be found in Hasler (1957) and
Hara (1971).

The acuity of odor perception in fishes matches any attainment in terrestrial
animals and defies comparable attainment by most sensitive instruments of
modern chemical analysis. For example Teichmann (1957) noted that young
eels conditioned by training were able to detect three parts of β-phenyl-
ethyl alcohol in 10^{18} parts of water. He calculated that at this dilution.
only two or three molecules would be in the eel's olfactory sac at one
time.

Odor perception is generally regarded as a distance perceptor as in the
case of emanations of a chemical in which a gradient of concentrations
exists to its source. The acuity of odor perception is considerably greater
than taste perception and is responsive to multifold substances, most of
which are organic in nature.

2. Taste Perception

Taste in fishes is mediated through the taste buds which are ennervated
by cranial nerves. Taste buds lie not only in the mouth and pharynx
but also in the gill cavity, on the gill arches, on appendages such as
barbels and fins and in some fishes, on all external surfaces of the body.
A discussion of the anatomy, morphological variations, and acuity of the
gustatory receptors in various groups of fishes may be found in Hasler
(1957) and Hara (1971).

The designation of taste as a different sensory function from olfaction is
based on the training of fish to discriminate certain taste substances
even after extirpation of the olfactory lobes, while conditioning for
odorous substances was only possible in intact fishes (Hara 1971). Krinner
(1935) provided data on thresholds of minnows for sucrose and salt, using
training techniques. These thresholds were 512 and 184 times lower,
respectively, than those of humans for sucrose and salt. Removal of olfactory
lobes caused no change in these thresholds, thus verifying that a true
gustatory sense was involved. As mentioned above, the acuity of taste
perception is much less than odor perception.

3. General Chemical Sense

There are numerous free nerve endings in the skin of fishes which are presumed
to have chemical sensory capabilities. Both external taste buds and free
nerve endings are sometimes regarded as taste receptors (Bardach 1967).

Electrophysiological evidence indicates that there are two types of nerve discharges (fast- and slow-adapting) following chemical stimulation of fin rays of red hake (<u>Urophycis</u> <u>chuss</u>) where chemical receptors are located. Slow-adapting discharges are apparently characteristic of taste buds while fast-adapting discharges may originate from the free nerve endings around taste buds (Bardach and Case 1965). Reactions following stimulation of the common chemical sense are usually negative or defense reactions.

4. Some Aspects of Chemoreception in Fishes

There are numerous observations reported in the literature which show that all senses; e.g., sight, acoustic, and chemical; are involved in the search for food. The importance of chemical sense, especially the sense of smell has been demonstrated by various investigators: e.g., Sheldon (1911), Parker (1914), Gilbert et al (1964), and Hasler (1957).

The sense of smell has been demonstrated by numerous workers to be involved also in the discrimination of body odors (Wrede 1932; Todd et al 1967), and maintaining the coherence of fish schools (Keenleyside 1955, Stevens 1959, and Hemmings 1966).

The olfactory sense is involved in the detection of alarm substances released from injured skin of a member of the same species (von Frisch 1938) and from the uninjured skin of certain predatory fish (Reed 1969).

Brett and MacKinnon (1952) found that a striking reduction in the upstream migration of three species of Pacific salmon occurred when human hands were rinsed in a fish ladder. Upon detecting the repellent odors from the hands, salmon swam excitedly, moving in a circle in the enclosed area, exhibiting an alarm reaction. Chemical analysis of the properties of a repellent from human skin indicate that only L-serine elicited a strong repellent action and at an extremely high dilution (8×10^{-10}).

Olfactory cues are important in the orientation of migrating fish such as salmon and eels and in the localization of spawning grounds. Many theories have been proposed to explain the mechanisms of migration of anadromous salmon to their spawning grounds (Hasler 1966; Harden Jones 1968). It has been suggested that the orientation to the home-stream or spawning grounds is mediated through olfactions, and reference has been made to a home-stream odorous substance. Considerable experimental evidence has been offered in support of this hypothesis (Hasler 1957; Hara et al 1965; Hasler 1966; Ueda et al 1967; Oshima et al 1969).

III. OCEAN ENVIRONMENT AND RELATIONS TO SELECTED FISHERIES

The known effects of environmental conditions on fish behavior enumerated
in Section II are either of a general nature or obtained under controlled
conditions; there have been few field studies in the North Pacific Ocean
and Bering Sea that permit observation or verification of these relations.
Although there have been instances where relations between surface temper-
atures and tuna distribution off the Washington-Oregon-California coast
appeared satisfying, subsequent appreciable differences in albacore
(Thunnus alalunga) catches by jig boats that fish at the surface, and
bait boats that attract tuna to the surface, have shown that even when
acceptable surface temperature regimes occur albacore may still be absent
at the surface but abundant at depth; this example indicates an instance
wherein an accepted fishing technique failed to denote the actual distri-
bution and abundance. Similar instances may occur when the presence or
absence of salmon is determined solely by shallow gill-nets or troll gear.
Although acoustic devices accurately denote the presence or absence of
pelagic or off-bottom fish, there are areas having variable bottom
conditions where demersal fish are not detected or their presence is
masked by bottom echoes, and areas where bottom conditions prevent
trawling. In addition, when viewing fisheries data, one must ask whether
learned-behavior in the longer-lived fishes eventually results in their
avoiding conventional fishing gear.

In view of the above, one should expect only general resource-environment
relations for adult fishes unless carefully planned experiments are con-
ducted. A number of very rewarding relations have been obtained primarily
with respect to the Pacific salmon, but there are also examples of relations
pertaining to pelagic and demersal fish as well as crustaceans. However,
in many respects, to search for specific relations in the limited data
available is tantamount to seeing the "trees" but not the "forest". Those
that believe the environment has no effect on a given species because of
extensive migration paths, for example from Baja California to the Bering
Sea, do not comprehend the "forest". Within any ecosystem there is an
established order that permits survival of those organisms that have
adapted to overall conditions, some organisms are far-ranging and some
limited to local areas, but all are subject to and react to varying
environmental conditions. Resource-environment relations based on limited
data obtained during fishing operations are well within the province of
the fisheries biologist, but the overall assessment of environmental
conditions, why they occur, the processes causing them to occur, and the
prediction of the future time and space occurrences of those conditions
are the province of the oceanographer or ecologist. Such assessments
considerably expand the horizons of the fisheries biologist and demonstrate
the value of interdisciplinary teams in marine studies.

The Subarctic Pacific Region is unique in that there is continuity of
surface circulation around the region that insures minimal loss of plank-
tonic larvae of pelagic, and some demersal, stocks and provides migration
paths for adult pelagic stocks. In addition, there is continuity of the
continental shelf and slope around the northern sector of the region that

insures successful dispersal of some demersal larvae and a path for adult
demersal stocks. It is the variations in the surface and subsurface
conditions that cause abrupt, and sometimes major, if not catastrophic
changes in fish movements and abundances, and any significant changes
are transmitted in one way or another throughout the ecosystem. In this
Section, the unique characteristics of the Subarctic Pacific Region are
summarized briefly and relations to salmon, Pacific saury (Cololabis
saira), albacore, and Pacific hake (Merluccius productus) are discussed.

A. SUBARCTIC PACIFIC REGION

Prior to the recent intense exploitation of fish stocks along the western
margin of the North American Continent by foreign fishing vessels, the
frequent recovery of Japanese fish nets and glass floats on local beaches
was considered evidence that the "Japan Current" (generally understood to
be the Kuroshio Current off the southeast coast of Japan) swept past local
shores. Only a few decades ago it was still believed that the source of
flow into the Gulf of Alaska was the Japan (Kuroshio) Current (Thompson
and Van Cleve, 1936) even though this implied that tropical waters were
the source of subarctic plankton and forage, rather than recirculation
in the Subarctic Pacific Region. This belief originated in the 19th
century when similarities in circulation between the North Atlantic and
North Pacific Oceans became evident; both were characterized by central
anticyclonic gyres with intense, warm, western boundary currents (Gulf
Stream and Kuroshio Current) which generally turned northeastward at
middle latitudes and thereby ameliorated the typical cold climate in
high latitudes at their eastern side (northern Europe and southern Alaska)
to the extent that sea ice was not present at or even in excess of
lat 60°N. However, the constraint imposed by the southern Alaska coast
and its westward extension, the Aleutian-Commander island arc system,
greatly restricts the northward flow in the eastern North Pacific Ocean
compared to that in the North Atlantic Ocean. As a result, surface
conditions in the Gulf of Alaska are only indirectly related to the
Kuroshio Current, and are primarily associated with the Subarctic Current,
a transpacific flow that forms east of the Kuril Islands and diverges off
the coast of the North American Continent. Drift bottle recoveries have
shown that objects released off Hokkaido and the Kuril Islands, north of
the Kuroshio Current, have been recovered along the coast of North America
from Oregon northward around the Gulf of Alaska (Favorite 1964), and the
transpacific distribution of water properties, as well as, computations
of geostrophic currents, support this conclusion.

As a result of oceanographic studies conducted for the INPFC by federal
fisheries agencies in Canada, Japan, and the United States in relation
to problems concerning the oceanic distribution and migration of Pacific
salmon, the Subarctic Pacific Region is one of the better known parts of
the world ocean (Favorite et al 1976). This transpacific region is
defined as bounded on the north by the land constriction at the entrance
to the Arctic Ocean, Bering Strait, and on the south by a change in
vertical water structure--generally the location where the marked
temperature inversions (characteristic of surface dilution and winter

cooling) end and marked salinity inversions (characteristic of net surface
evaporation) begin. The southern boundary, generally referred to as the
Subarctic-Subtropic boundary, is for convenience specifically denoted by
the 34°/oo isohaline in the surface layer. The region may be considered
a two-layer system: an upper layer in which insolation, precipitation,
evaporation, and river runoff cause marked changes in water properties;
and, a lower layer, where advective effects are masked by diffusion,
resulting in relatively steady-state conditions in water properties.

1. Circulation

It is convenient to consider surface circulation in the region as charac-
terized by a large cyclonic gyre existing just northward of the mid-Pacific
anticyclonic gyre. Western boundary currents in these two systems--
southward flow (Oyashio) along the northeast coast of Japan and northward
flow (Kuroshio) along the southeast coast of Japan--converge, mix, and
turn eastward across the Pacific Ocean forming a transition zone between
the cold, dilute subarctic waters and the warm, saline, subtropic waters
(Figure 11). The demarcation of these two flows is sharp and abrupt in
the western side of the ocean, but it gradually becomes more diffuse as
stirring, advective, and diffusion processes occur, and broad, weak,
boundary currents occur at the eastern side. Net inflow at the western
side of the ocean as a result of this confluence, as well as, other factors,
such as, subsurface flow, precipitation, and river runoff is balanced by
a net discharge southward at the eastern side of the ocean, where there is
also a northward flow into the Gulf of Alaska. This latter flow is largely
constrained by the coast to turn westward out along the Alaska Peninsula
and then northward through openings in the Aleutian-Commander island arc,
part discharging northward through Bering Strait, but most continuing
westward around the Bering Sea basin and southward along the east coast
of Kamchatka, completing the gyre. The time required for the passage of
a water particle around the periphery of this gyre would be at least 3-6
years. Drift bottle and current studies indicate that it requires only
about 2 years to traverse the southern boundary, several months to circuit
the Gulf of Alaska, less than a year to exit the Bering Sea, and only
several months to move southward along the Kuril Islands. Of particular
significance, because of their large size, relative permanence, and inherent
vertically upward transport, are the four cyclonic gyres: The Alaska,
Bering Sea, Western Subarctic, and Okhotsk Sea gyres. These gyres provide
numerous opportunities for water particles to circumvent movement around
the periphery of the larger system (Larson 1970).

Although at one time it was believed that flow in the subarctic Region
was driven largely by the momentum of the main Central Pacific Gyre, there
is adequate evidence that local winds are the primary cause (Fofonoff and
Tabata 1966; Favorite 1967). It is generally recognized that flow in the
surface layer of the ocean is largely caused by wind-stress, and because
wind observations are fragmentary it is convenient to derive wind fields
from sea level pressure distributions. Data at selected grid points are
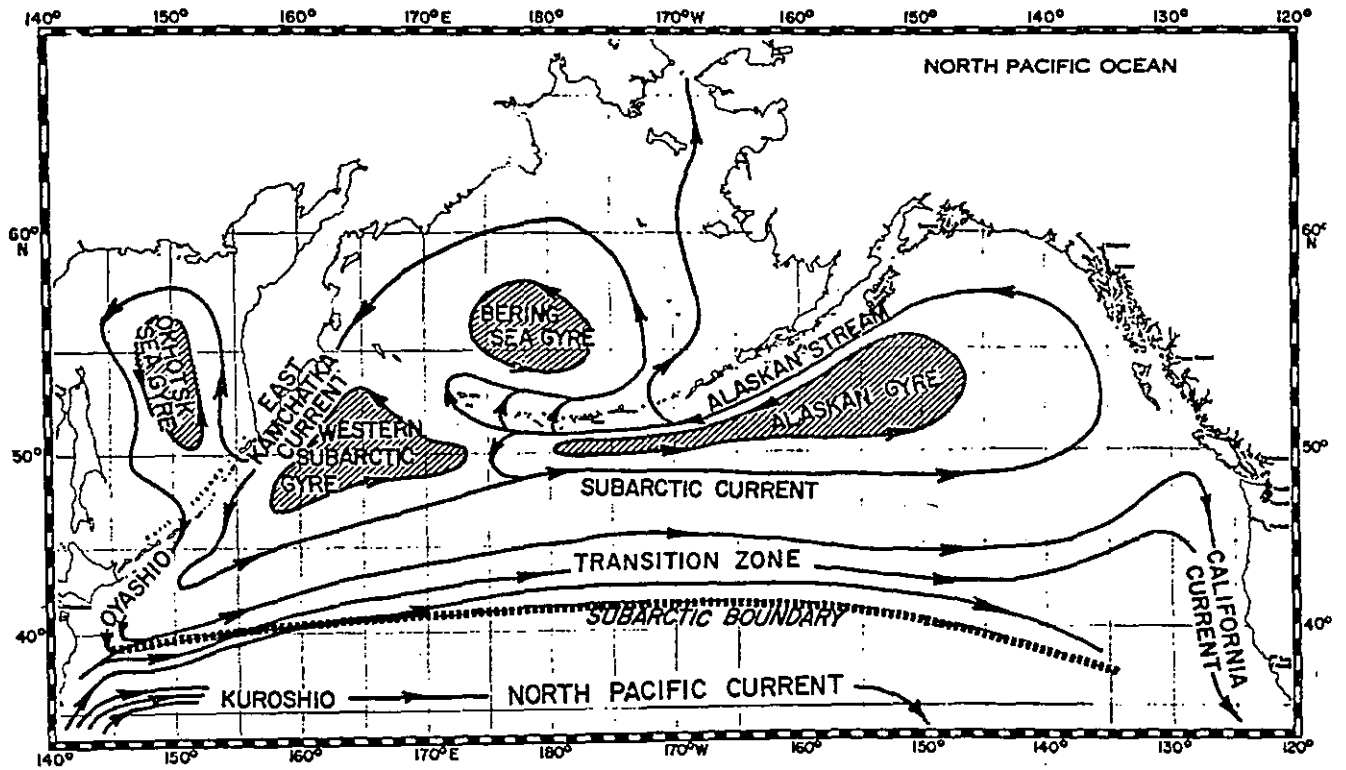
Figure 11. Schematic presentation of major oceanographic features of the northern North Pacific Ocean.

averaged over various periods (e.g., weekly, monthly, quarterly, semi-
annually) and wind stresses are translated into ocean transport. It has
been shown (Fofonoff 1962) that ocean transports derived in this manner
reflect flow fields estimated by other methods (geostrophic flow, distri-
butions of water properties, and drift floats) and such analyses are not
limited to the small areas covered by vessel cruises, or by problems
associated with non synoptic data. Even though obvious problems associated
with averaging of data and the lack of knowledge of the nature of the
coupling between air and water illustrate some of the inadequacies of
ascertaining flow using wind-stress data, the method provides insight into
the general flow regime.

The dominant feature of the sea level pressure distributions in the region
is the Aleutian low pressure system whose center is evident in the eastern
Bering Sea in September, moves southeastward into the Gulf of Alaska through
December, and westward to the western Aleutian area in January where it
remains through April; from May to August the Eastern Pacific high pressure
system expands into the Gulf of Alaska. The winter intensification of
cyclonic winds associated with the Aleutian low is evident in increased
water transport in winter compared to summer as derived by a numerical
wind-stress transport model developed at the Northwest and Alaska Fisheries
Center (Figure 12). Thus, we can conclude that the circulation in the
Subarctic Region is accelerated during winter, and relaxation occurs
during summer. Over a long time the distribution of mass in the ocean
has gradually adjusted to the effects of these winter pulses of energy
and a basic circulation pattern (steady-state condition) has resulted
that is in general in equilibrium with frictional and other forces. Although
anomalous winds can establish pressure forces that result in changes in
flow, these changes will be short-lived because rarely will the winds
persist for a long enough period (months) to alter the distribution of
mass much below the surface layer. Thus, the basic circulation remains
as long as the Aleutian low maintains its present nature and the config-
uration of the ocean basin remains unaltered.

2. Water Properties

There are a number of surface temperature atlases readily available, and
it is sufficient to show here monthly mean oceanic distribution represent-
ative of periods of maximum winter cooling (January) and summer warming
(August) (Figure 13). During winter, surface temperatures less than $0^{\circ}C$
occur over much of the northern Bering Sea and the western side of the
region--these temperatures reflecting ice cover; whereas, temperatures
of $3-5^{\circ}$ occur in the Gulf of Alaska, and temperatures of approximately
$10^{\circ}C$ prevail at the southern boundary of the region. By summer, temper-
atures throughout the region increase roughly $10C^{\circ}$, ranging from $10^{\circ}C$ at
the northern boundary to $20^{\circ}C$ at the southern boundary of the region.

Another distinctive feature of the surface layer is the low salinity
values. At no place in the region do surface values exceed $34^{\circ}/oo$ (by
definition); whereas, in offshore areas at comparable latitudes
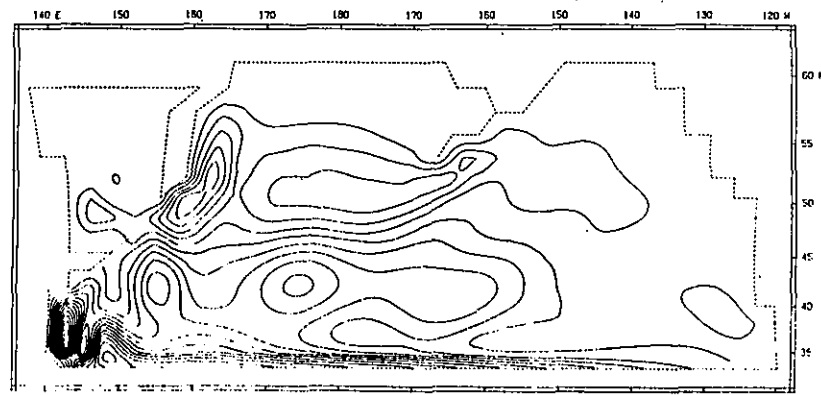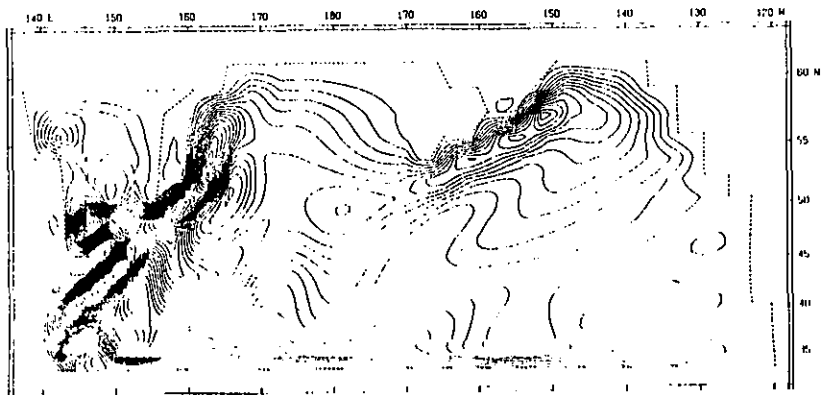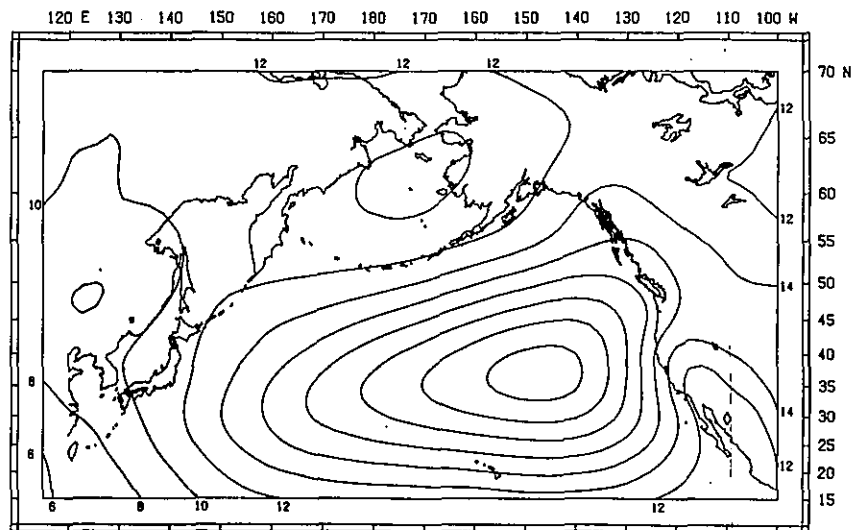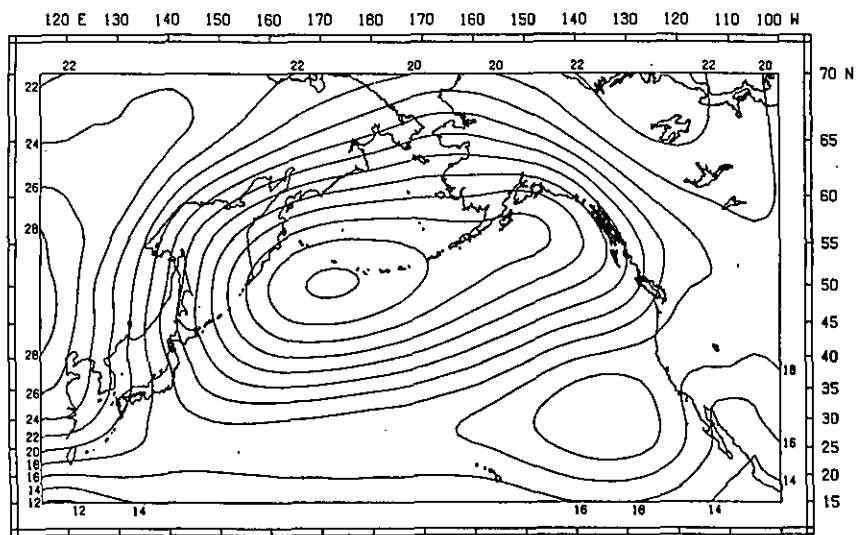
Figure 12. Transport in Sverdrups ($10^6 m^3$/sec) obtained from numerical
model assuming a transport of 50 Sv in the Kuroshio and
(A) winter mean wind-stress, and (B) summer mean wind-stress.
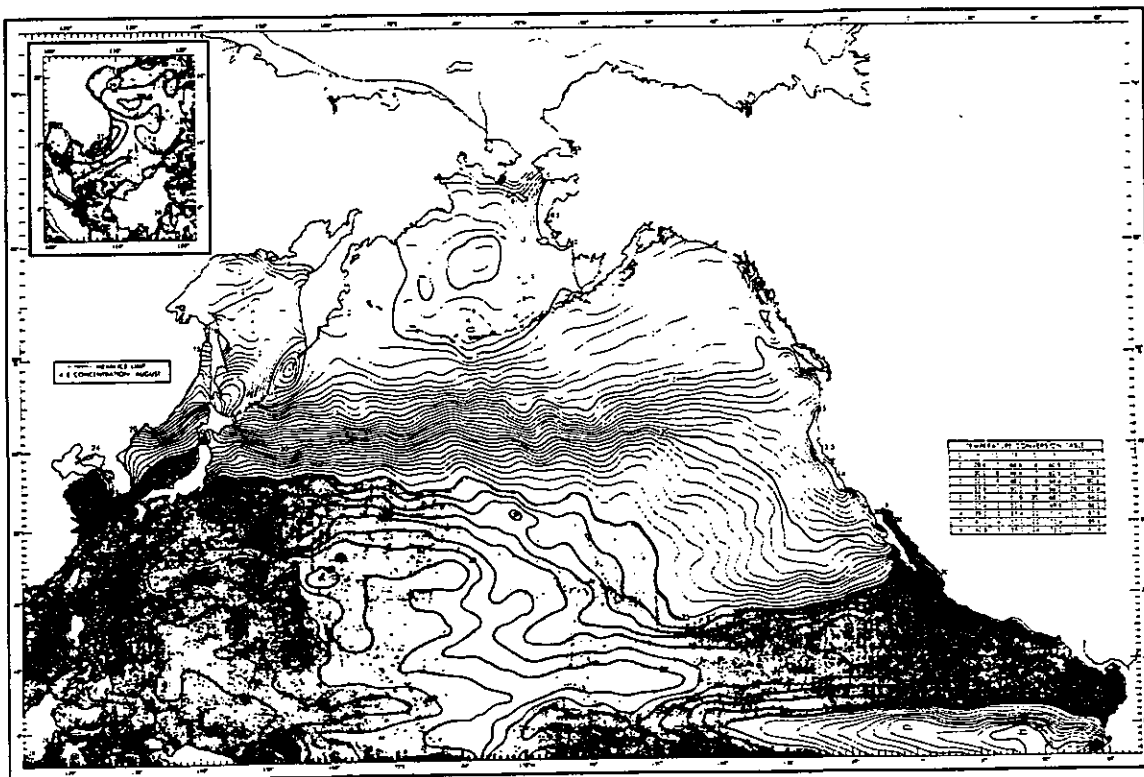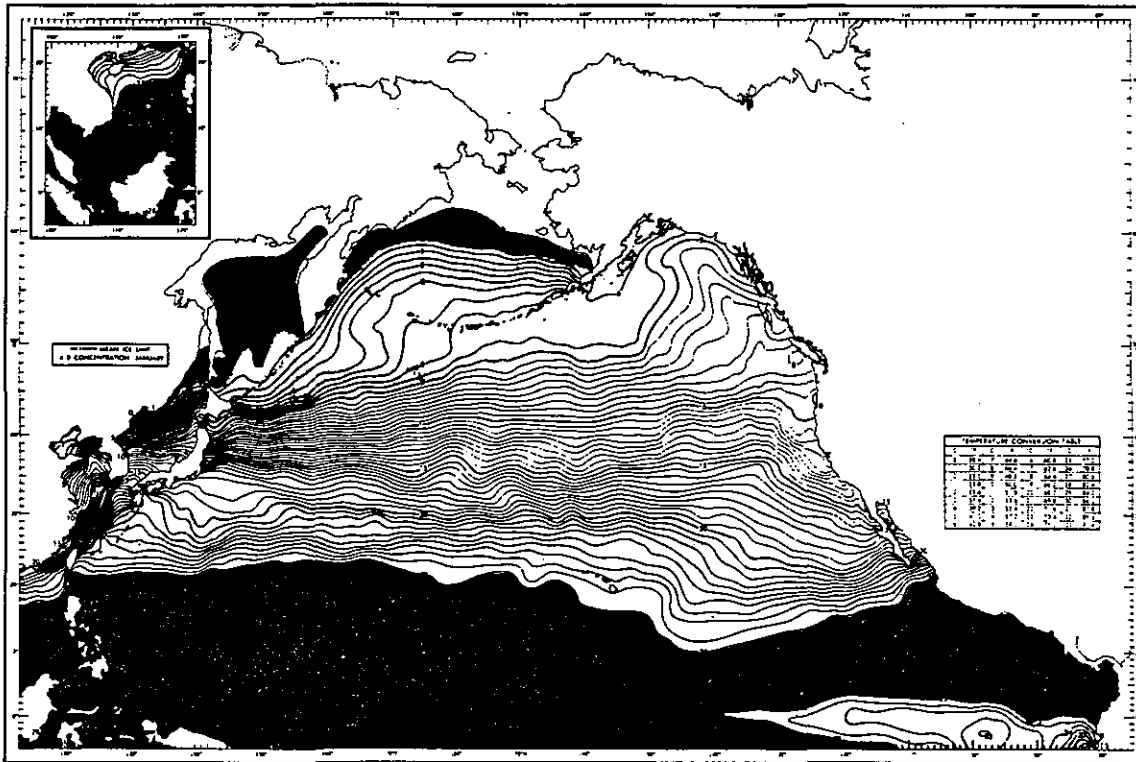
Figure 13. Mean surface temperatures for January and August (from
Robinson 1976).

in the Atlantic Ocean values of $36^{\circ}/oo$ occur. Winter and summer mean
surface salinity distributions (Figure 14) indicate the sharp salinity
gradients at the boundary of the Subarctic Region and the seaward ex-
tensions of dilute water in summer at both sides of the ocean caused by
various factors, largely river runoff and, where applicable, ice melt;
however, precipitation and reduced evaporation are also factors. Of
particular interest is the separation at long $170^{\circ}E$ of low salinities
(<$32.8^{\circ}/oo$) extending eastward from the Kuril Islands and Kamchatka
Peninsula from those extending westward along the south side of the
Aleutian Islands. Some of these features will be shown in greater
detail when relations to specific resources are discussed.

The effects of surface temperature on the temperature structure in the
water column provides a convenient and easily recognizable feature that
permits defining two layers in the vertical water structure. This feature
is temperature-minimum stratum caused by winter turnover, a process whereby
cooling and evaporative processes in winter result in water particles
at the sea surface becoming more dense than those in subsurface layers,
causing surface water to sink and be replaced by water from below. This
establishes a surface convection cell which, aided by winter storms,
increases in depth and results in a homogeneous surface layer, the depth
of which is dependent on stability within the water column. Surface
dilution, vertical divergence, and other processes result in the formation
of a halocline at 100-200 m depth that usually provides enough stability
to the water column to limit the effects of winter turnover to such depths.
In the northern and western parts of the region, where ice occurs at the
sea surface during winter (Figure 15), negative temperatures (0 to $-1.8^{\circ}C$)
occur in the isothermal surface layer, and these temperatures can persist
throughout the summer at the bottom of the layer (100-200 m). Thus,
water in this stratum is colder than that at any place in the water column,
even at the sea floor thousands of meters below. This feature is also
present in the northeastern Pacific, but because of the absence of ice,
temperatures in the stratum are higher, $2-3^{\circ}C$; however, equivalent temper-
atures do not occur in the water column until largely 1000 m depth.

Just as the land configurations have evolved over long periods of time,
so have oceanographic conditions in the lower layer. One is probably
aware of the eons of time required to establish the complex chemistry of
sea water and the variety of life in the sea, but perhaps doesn't realize
that the basic water structure is the result of a quasi-equilibrium
adjustment to conditions throughout the world ocean that has also required
a long time, typically some hundreds of years. Driven primarily by winds,
modified by the rotation of the earth and thermohaline processes (heating
and cooling, evaporation and precipitation), influenced by internal friction
and constrained to flow within land boundaries, the general circulation
and the accompanying distribution of properties represent long-term adjust-
ments to relatively constant and periodic forces, as well as the inevitable
diffusion processes that establish the basic distribution of mass in the
ocean. Although seasonal meteorological factors affect conditions in the
surface layer in the region, they are of too short a duration to markedly
alter water property relationships much below approximately 300 m, which
have remained largely relatively constant for as long as direct observations
are available.

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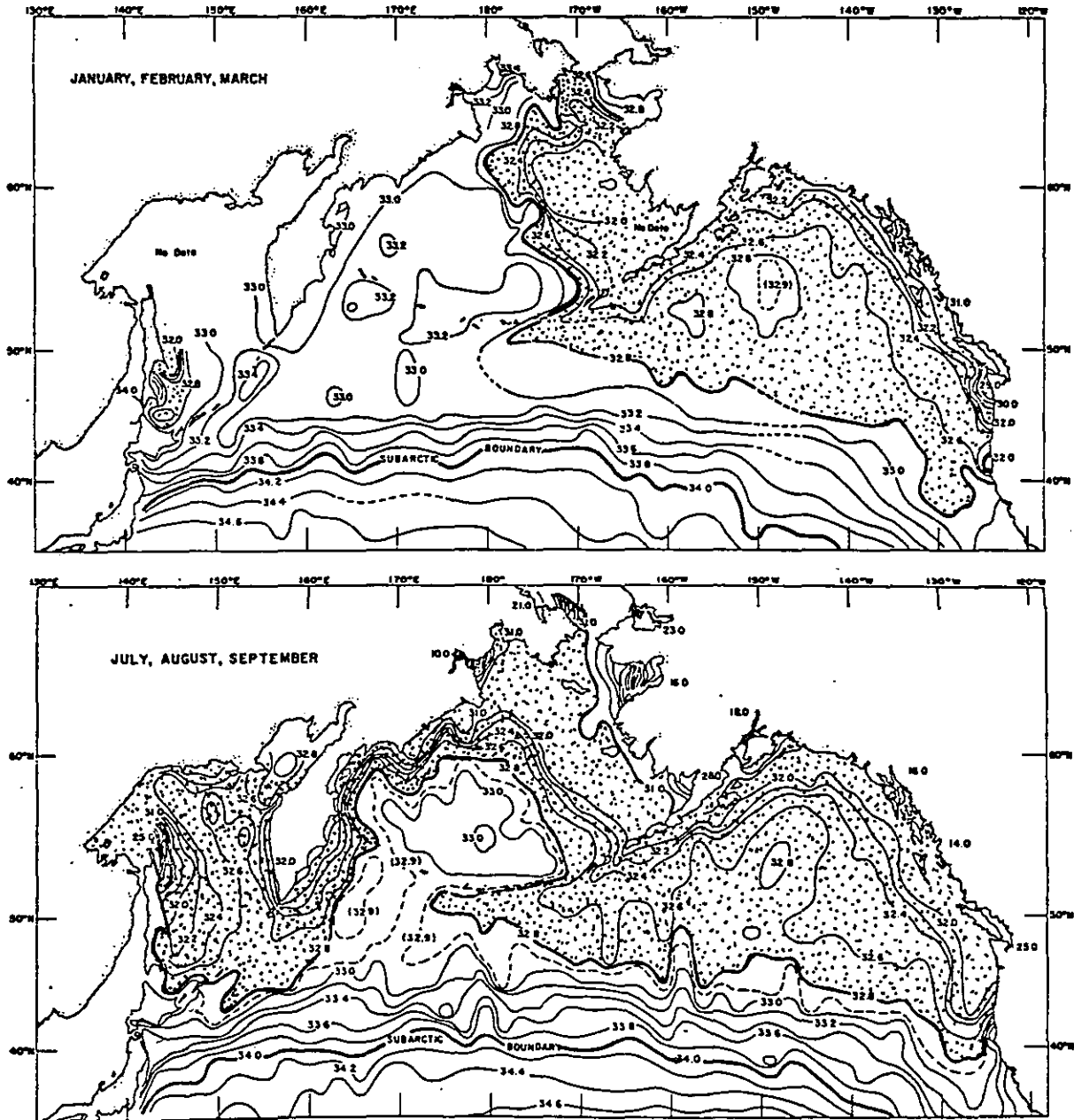
Figure 14. Winter and summer mean surface salinity (all station data averaged by 2x2° quadrangles), (from Favorite et al. 1976).
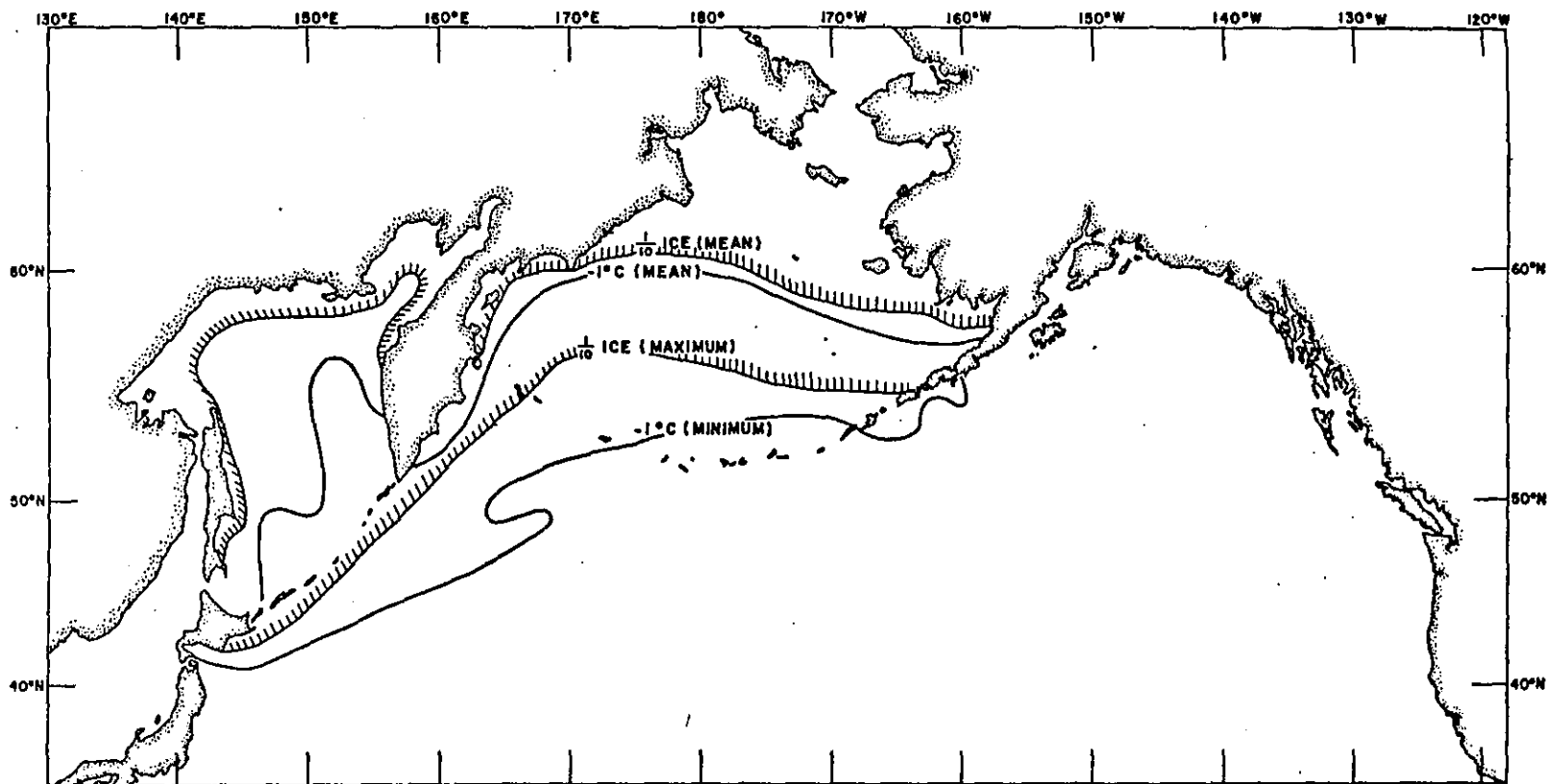
Figure 15. Mean and maximum southern extent of sea ice of 1/10 or greater concentration and of the -1°C isotherm during March (from Favorite et al. 1976).

The distribution of temperature at 300 m (Figure 16A) shows the broad central area, the Ridge Domain, having temperatures less than 4°C—bounded on the south by a marked temperature gradient, on the west by temperatures less than 3°C originating from the Okhotsk Sea, and on the east by temperatures greater than 4°C off the west coast of North America (it should be pointed out that much of the eastern Bering Sea has a depth of less than 300 m). Although it might be assumed that temperatures in the central area were due to atmospheric conditions in winter, this is not the case, these temperatures are associated with deep oceanic water that has been displaced hundreds of meters upward. There are several factors contributing to this phenomenon: first, it is a natural result of northward flow at great depth from the more southern latitudes that, upon impinging on the land barrier imposed by the Aleutian-Commander island arc and the edge of the Bering Sea basin, is forced upward; second, the presence of the Aleutian low pressure system during winter causes a surface transport (Ekman transport) at right angles to the wind (looking downwind) and results in the displaced surface water being replenished by vertical motion from below; and, third, the shear zone between the eastward flow south of approximately lat 50°N and the westward flow out of the Gulf of Alaska along the Alaska Peninsula and Aleutian-Commander island arc.

Major features of the salinity distribution at 300 m (Figure 16B) are associated with the 34.0°/oo isohalines. The nearly transpacific isohaline at approximately lat 40°N denotes the southern boundary of the Subarctic Region, and its isolation from the 34.0°/oo isohaline near the coast at long 125°W indicates the general location of southward discharge of subarctic water. The coastal band of saline water has a southern origin, different from that of the offshore water. The two closely but widely separated 34.0°/oo isohalines near lat 50°N indicate the general locations of the Western Subarctic and Alaskan Gyres, and reflect the vertical intrusion of deep water. These features are also evident in variations in the dissolved oxygen distributions (Figure 16C). Of particular significance is the presence of dissolved oxygen values less than 1.0 ml/l, which reflect about 20% saturation at depths of less than 300 m. Equivalent values occur at 400-500 m over the continental slope and these conditions are discussed in Section IV.

A schematic diagram of a mid-ocean north-south vertical section of water properties (Figure 17) clarifies the unique water structure from south of the Aleutian-Commander island arc to the southern boundary of the Subarctic Region: the depressions of isolines adjacent to the land caused by westward flow out of the Gulf of Alaska, the Alaska Current System; the broad plateau-like structure reflecting a vertical movement of cold, saline, oxygen-depleted water toward the surface layer, the Ridge Domain; the area of cold (3.5°C) water south of the Ridge Domain, the Subarctic Current system; and the area of warm water northward of the Subarctic Boundary indicative of eastward flow, the Transition Domain. These features, with modifications, are evident across the region. The transpacific extents of these and other current systems and domains in the Subarctic Pacific Region are also shown in a schematic diagram (Figure 18). These features are explained in some detail in Section IV, and a rather complete discussion can be found in Favorite et al 1976.
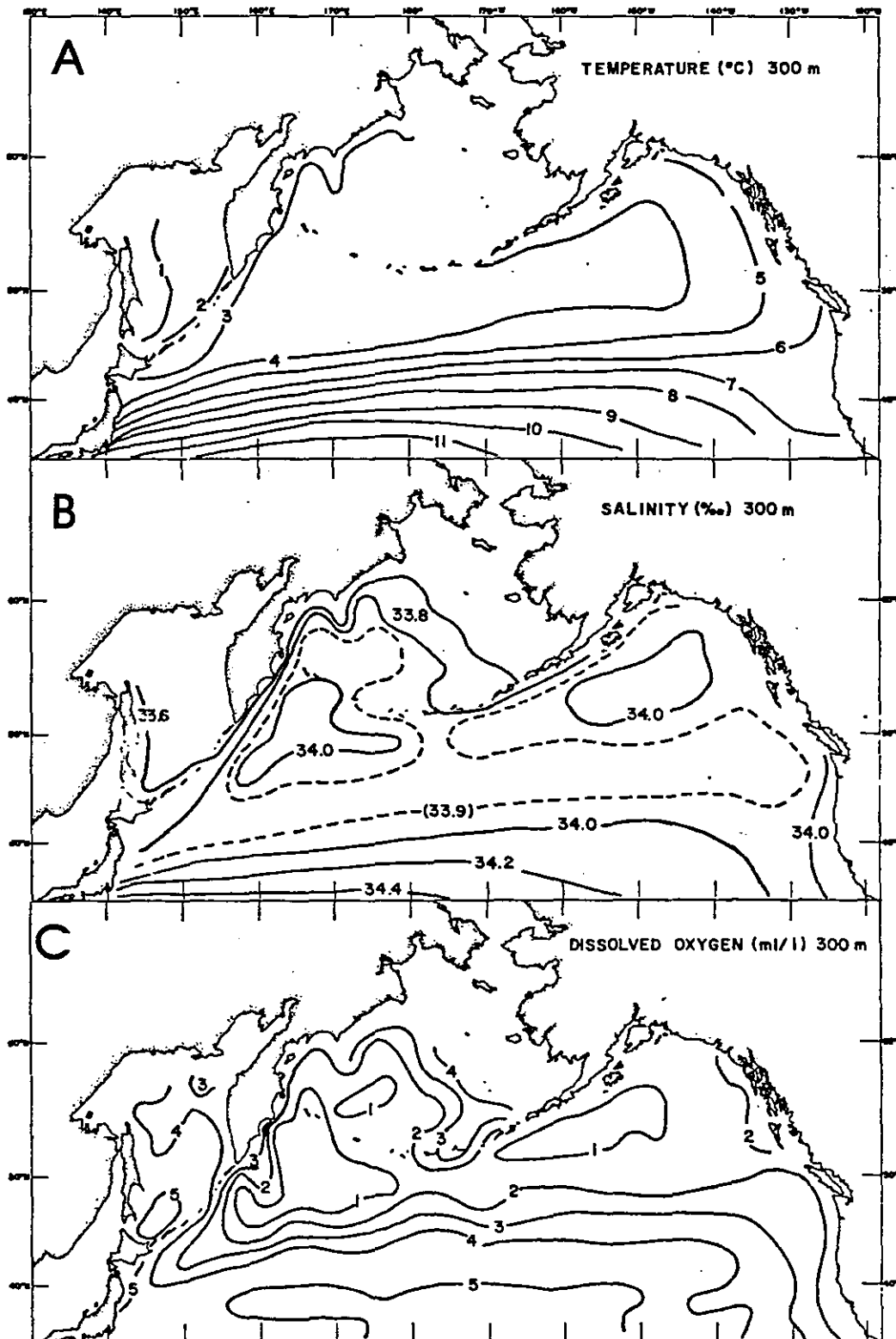
Figure 16. Distribution of mean (A) temperature ($^{\circ}$C), (B) salinity ($^{\circ}$/oo), and (C) dissolved oxygen (ml/l) at 300 m (all station data averaged by 2x2° quadrangles).
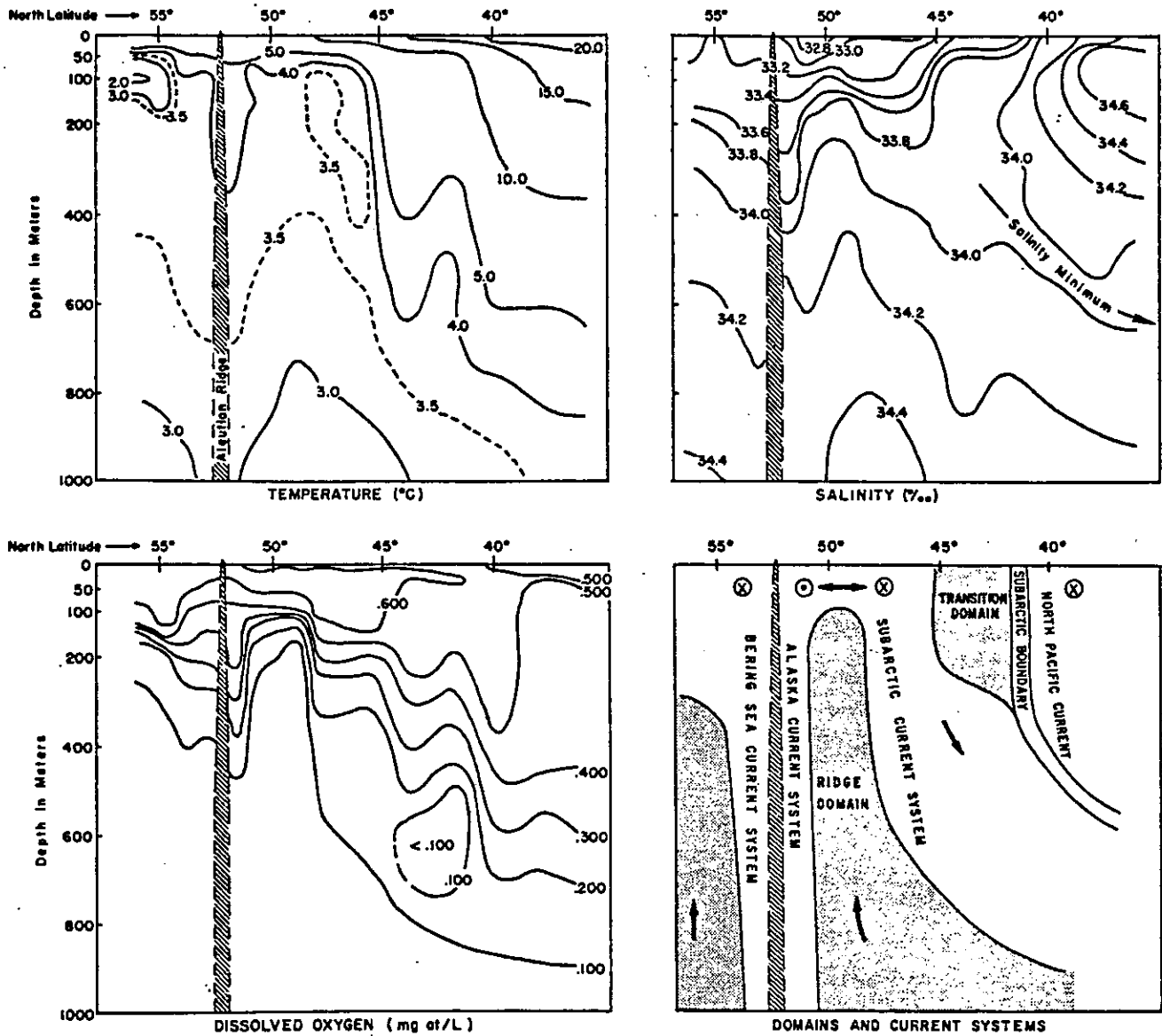
Figure 17. Schematic presentation of vertical distribution of (A)
temperature ($^{\circ}$C), (B) salinity ($^{\circ}$/oo), (C) dissolved
oxygen (ml/1), and (D) major features.
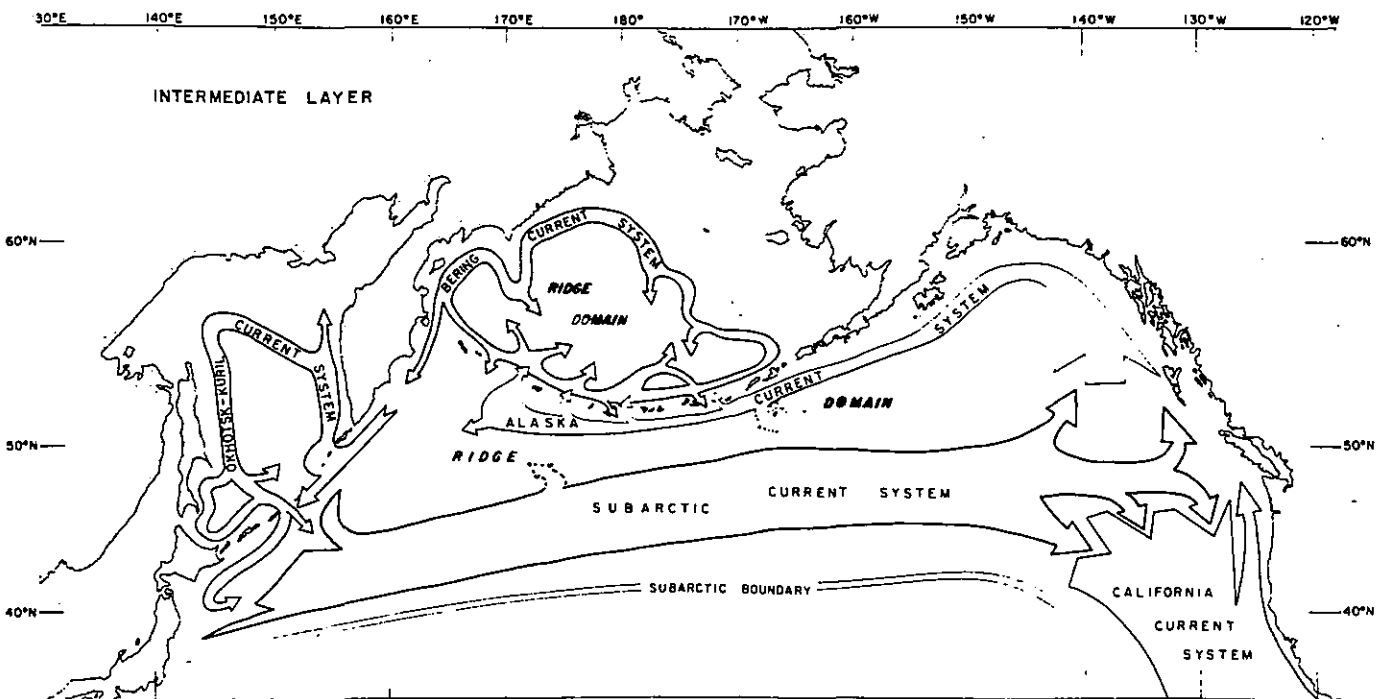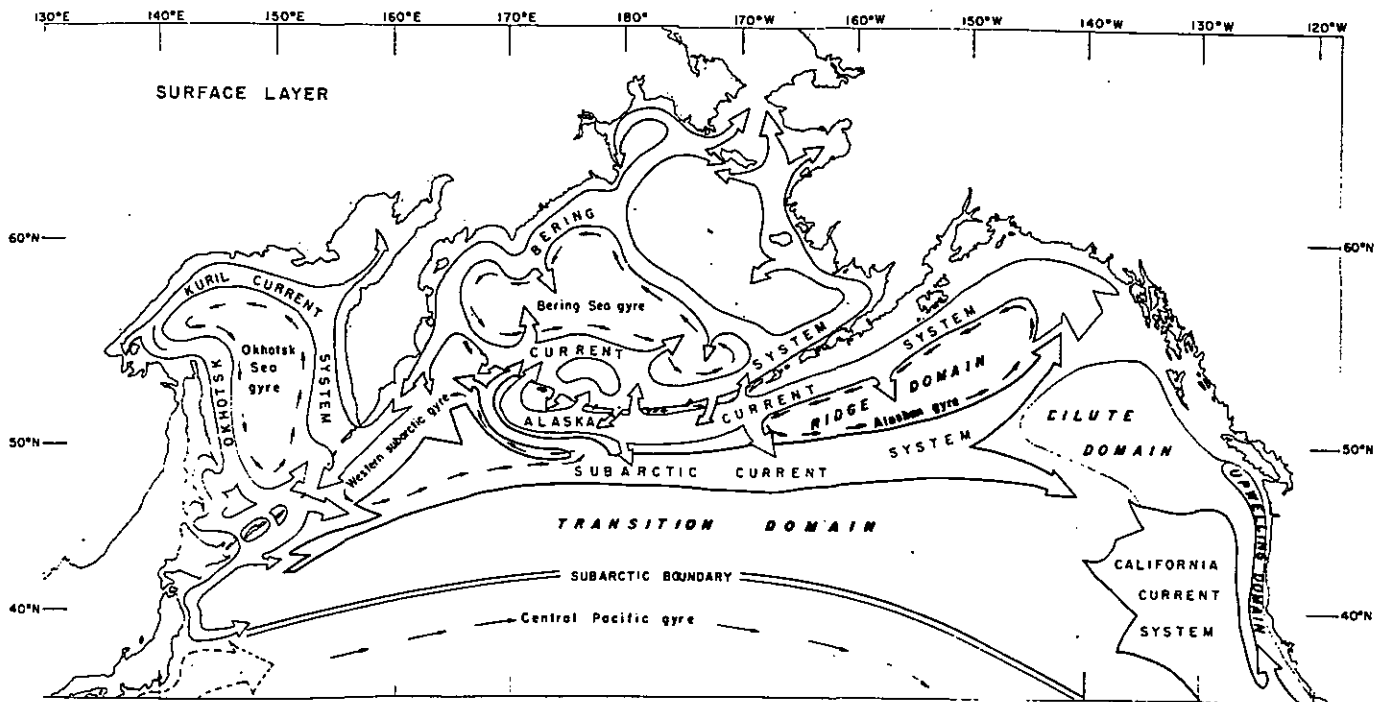
Figure 18. Schematic presentation of Subarctic Pacific Region domains and current system (from Favorite et al. 1976).

3. Biological Processes

Consider the fate of emersal and demersal eggs discharged, in quantities of several thousand to hundreds of thousands, from millions of individual fish, into the murky waters of the ocean and left to drift passively for various periods at the caprice of ocean currents. Vulnerable to predation through planktonic, or benthonic larval stages, each has to be literally surrounded at critical periods by food organisms of a size matched to unique individual capture and digestion capabilities, and must not be transported into a lethal environment before attaining mobility. Voracious appetites of adult stages are satisfied, not only by subsequent productions of eggs and larvae, but by plankton and other organisms of appropriate size. Thus, life in the sea contains myriads of various sized organisms, from microscopic to easily visible size, each with individual life cycles, each more or less filling a niche in the pyramidal structure of life in the ocean (Figure 19).

A characteristic feature of the region is the "spring bloom" in which resting plant spores overwintering in the water column become active at a critical period of increased insolation and stability in the water column and cell division occurs, in some instances almost daily, until arrested by grazing or depletion of nutrients. The term "nutrients" is a vaguely defined term encompassing those elements in the water column required for plant growth, and these are many and varied. In general, concentrations of phosphates, silicates, and nitrates can be used as indices of nutrient availability. Because of the vertical upward movement in the Ridge Domain, the vertical movement of deep water, in which the decomposition of organic matter settling in the water colum has run its course, large amounts of nutrients are furnished to the surface layer. Although surface replenishment is probably more complete in winter (because of turnover of the water column and cyclonic winds associated with the Aleutian low pressure system) than in other seasons, at no time are major nutrients completely consumed (as indicated by extant chemical techniques); whereas, in more southerly latitudes, near total absence of phosphates at the surface is common during summer and little, or marginal, primary production occurs. Thus, if the major nutrients are not exhausted (nitrite may be an exception) through the region, the total primary production is not attained. This condition can be caused by several factors, but two apparent ones are that one or more minor chemical constituents vital to plant growth and reproduction is exhausted, or that, after the initial bloom of phytoplankton, cropping by herbivores occurs faster than phytoplankton are reproducing; the latter condition is suspected to be the primary cause. Nutrient replenishment also occurs in the Upwelling Domain as well as in the general vicinity of the Aleutian passes and in the Coastal Domain, particularly over the Bering Sea Shelf, where mixing and stirring extend to the sea floor.

Primary production is dependent not only on nutrients, but also on sunlight, and varies between wide limits. Although primary production of algae takes place in three biomes, i.e., the water column, in and beneath sea ice, and by epibenthic algae on tide flats, hardly anything is known about production via the latter two modes. The organic matter produced by phytoplankton is
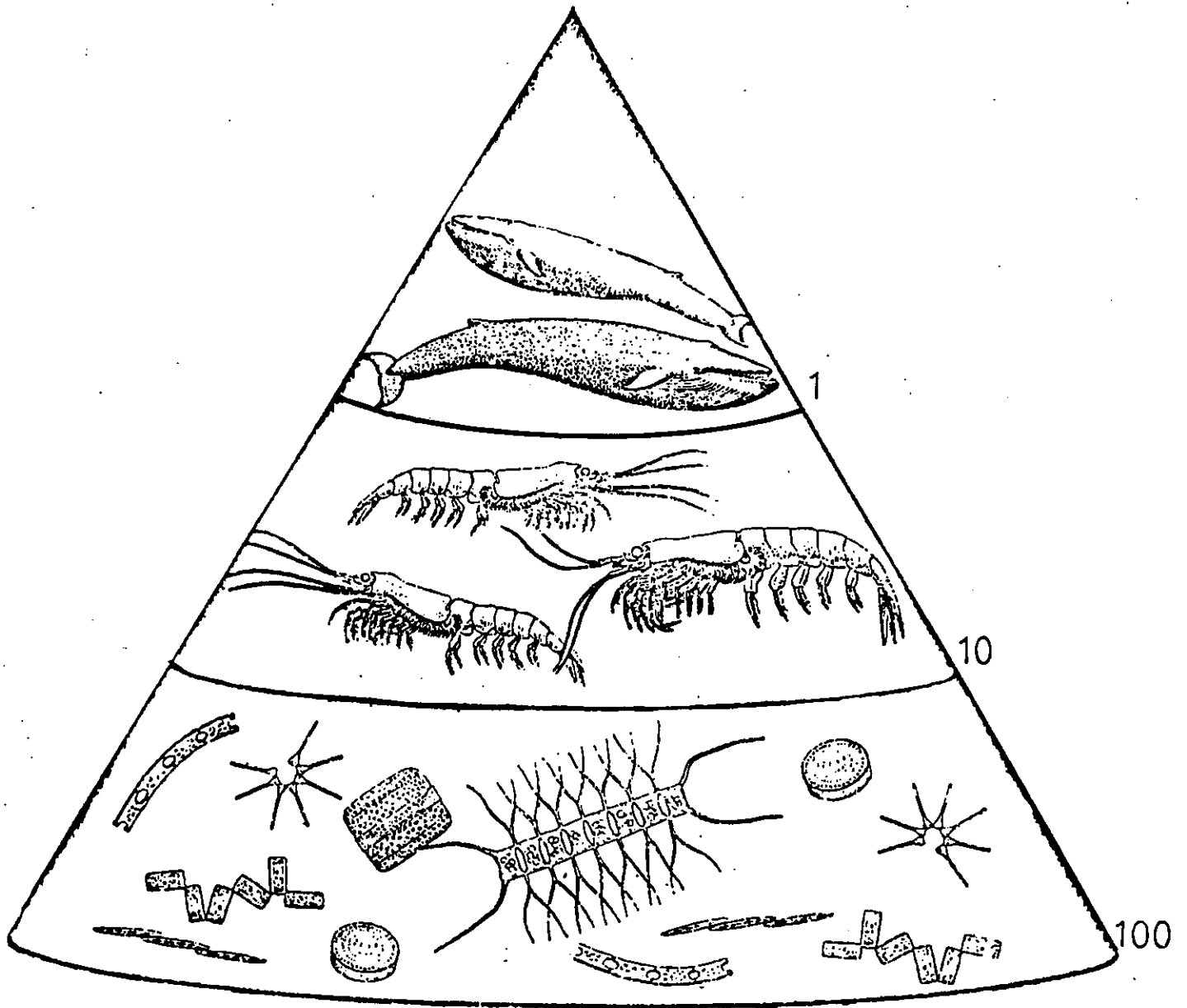
Figure 19. Schematic presentation of pyramidal structure of life
in the ocean.

transferred upward to more complex organisms as a result of consumption of these plants by micro- and macroscopic herbivores (secondary production) which are, in turn, consumed by carnivores (tertiary production), the zooplankton, which provide the bulk of forage for an extraordinary range of marine animals--ichthyoplankton, small and large fishes, and even huge mammals (e.g., whales). Thus, all life in the sea is basically dependent on the production of phytoplankton.

The passage, or transfer of organic matter from plants (primary producers) to grazing animals to predators is often termed a "food web". Short, simple, food webs rarely exist in the sea. The usual case in the ocean finds many links in a food web, with some animals feeding on more than one link, and "feedback" mechanisms operating wherein the organic matter in animals at one link is recirculated back to phytoplankton through death and the release of nutrients via microbial action before the animals have a chance to be eaten. The concept of the various food organisms existing as food energy available at specific locations in the web has given rise to the term "trophic level". The trophic level concept simplifies illustration of the food web by lumping organisms with similar food habits, or having similar predators, at the same trophic level regardless of size. A major problem inherent in estimating production at the different trophic levels is the lack of knowledge of how efficient each trophic level is at assimilating energy from the lower trophic levels. Another problem inherent in food web studies is the uncertainty of the number of trophic levels in a community. In an exceedingly complex environment (such as the eastern Bering Sea shelf) food organisms and detritus, which is important to benthic infauna such as clams, exist in sizes ranging from the smallest detrital particles and phytoplankton up to the largest baleen whales; thus, in reality, there are numerous trophic levels. Further complications arise because as most planktonic and nektonic animals grow they ascend to higher and higher trophic levels until fully grown. Food web estimates are further complicated by the fact that primary production is measured and expressed in terms of organic carbon produced. To be related to stocks or organisms, estimates of organic carbon must be converted to biomass and the data on the organic carbon content of planktonic organisms are incomplete.

Although the food webs and energy exchanges are difficult to structure or quantify, there is a distributional order to the biological components of the oceanic regime that, although more general in scope, is closely related to the physical-chemical domains presented earlier. McGowan (1974) has outlined the maximum areal ranges of a variety of planktonic and nektonic species in the Pacific Ocean and presented percentage levels of the Subarctic, Transition Zone, and Central fauna (Figure 20). Of particular interest is the sharp division of Subarctic and Central fauna near 40°N, and the northward and southward overlap of the Transition fauna, particularly off the west coast of the United States (see Figure 18 for environmental boundaries).
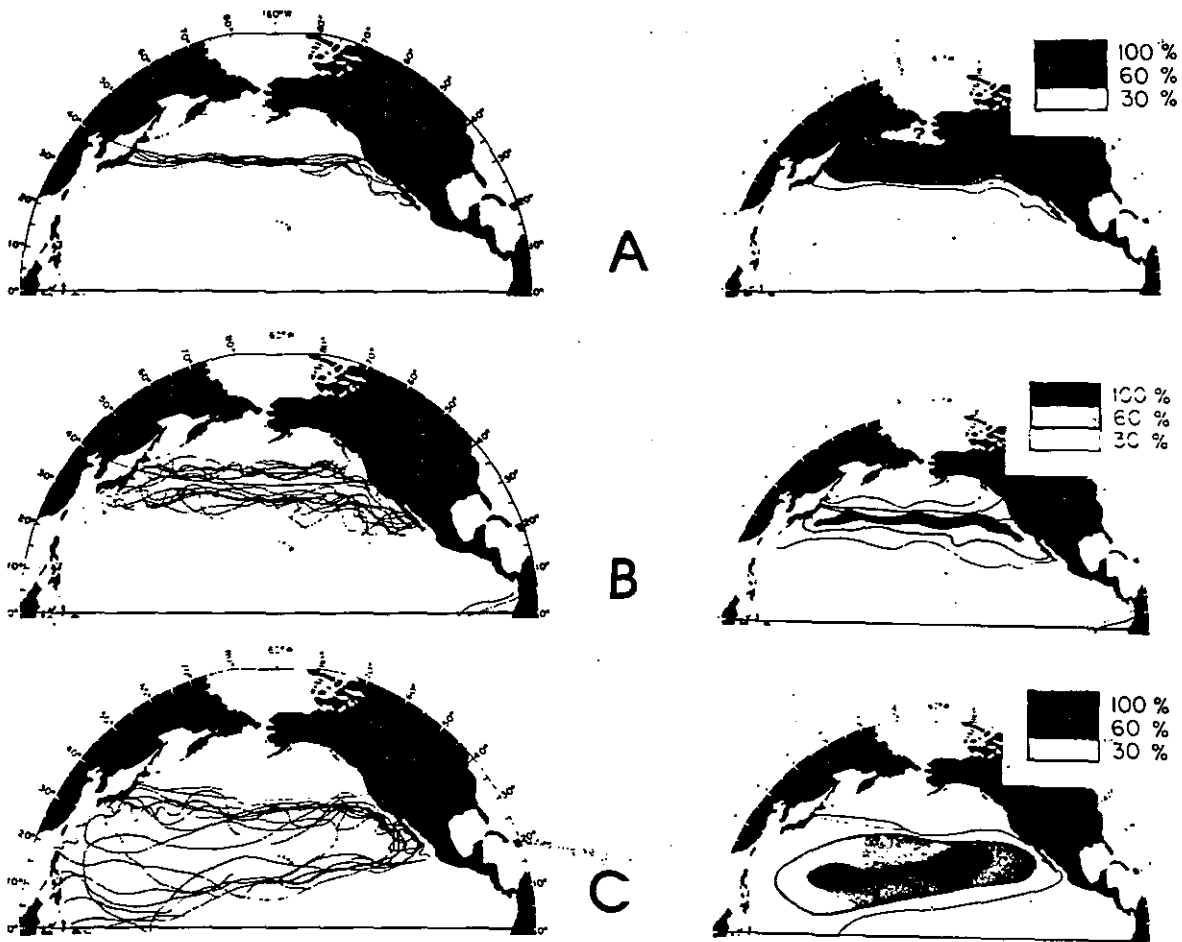
Figure 20. Distributional boundaries of (A) subarctic, (B) Transition Zone, and (C) central species and percent levels (from McGowan 1974).

An interesting survey to evaluate faunal distributions in the Subarctic Pacific Region (north of 40°N) was conducted by the Northwest and Alaska Fisheries Center in the area south of the Aleutian-Commander island arc in 1966-68. Physical processes greatly compressed the longitudinal extent of the Ridge Domain between westward flow in the Alaska Current System to the north, and eastward flow in the Subarctic Current System to the south (Figure 21). Zooplankton, primarily euphausids, copepods and chaetognaths were 2-7 times more abundant at stations in the Ridge Domain than in the current systems to the north and south. Further, with respect to species composition of euphausids, Thysanoessa longipes constituted nearly 80% of the forms on the north side of the Ridge Domain and Euphausia pacifica constituted nearly 80% of the forms on the south, suggesting a distinct affinity or environmental selection by these two species with respect to the two current systems (Favorite et al 1967). This survey provided some indication as to the potential significance of forage areas to resident or migrating fish. It was well known that salmon migrated to the Aleutian Islands area to feed and mature, but it was believed that this movement was related to forage in the immediate vicinity of the islands. These and other results (Favorite 1970) suggested that this oceanic migration may be primarily related to an environment well offshore from the islands, the Ridge Domain.

B. ANADROMOUS FISH

The most abundant and valuable species of anadromous fish in the region are Pacific salmon. Moulton (1939), in the foreword of a symposium concerning the migration and conservation of salmon that was held nearly 4 decades ago, summarized the state of knowledge and the challenges inherent in a study of the Pacific salmon:

> "....In the problem of accounting for the migration of salmon one enters a field in which science and romance appear to meet. At least it has often been maintained that the mature fish moved by some strange super-human instinct, return after several years at sea to precisely the stream of their birth and there, in their first home, deposit and fertilize their eggs to begin a new generation. The method of science, however, is to look for explanations of phenomena in the general properties of the world about us, even though at first this seems to us almost or quite supernatural. During the past two or three decades these methods have been extensively used in attempts to account for the migration of salmon. Not only have the currents and the temperatures and the chemical constitutions of the waters in which they live been extensively surveyed, but salmon of various ages in numbers running into tens of thousands have been marked. In spite of the fact that large numbers of these tagged or marked salmon have been recovered, as reported in this symposium, the story of what takes place in their migrations is yet far from being complete, and the explanations of them are as much open to question...."
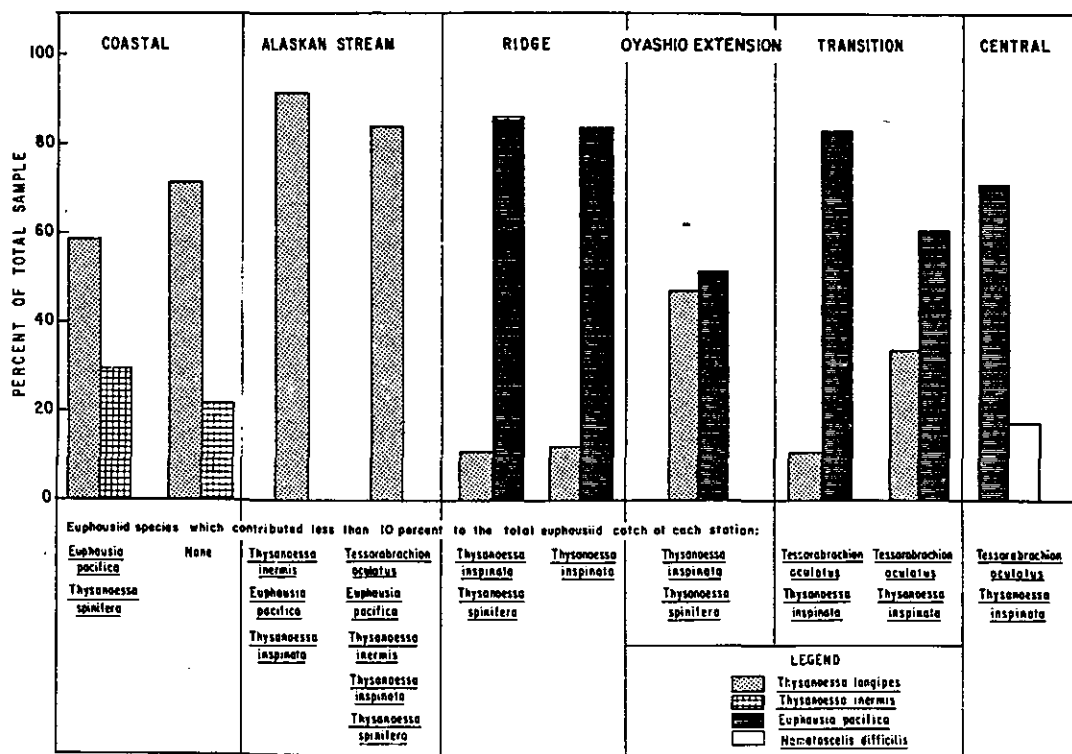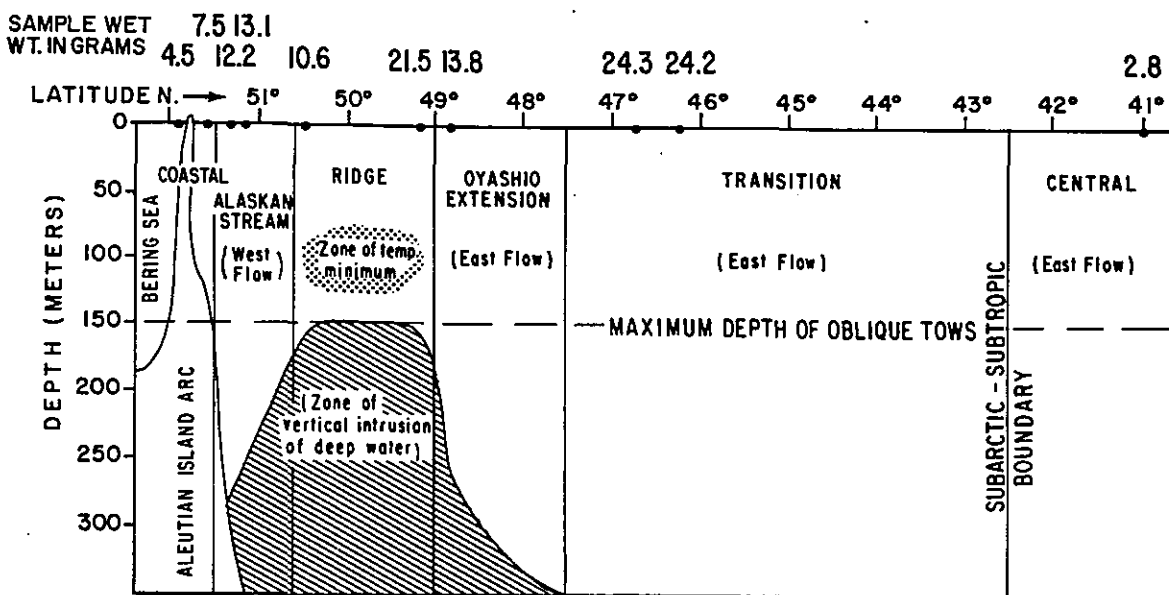
Figure 21. Composition of zooplankton samples along long 175°25'W during March 1966 in relation to subarctic domains and flow.

Even 4 decades later, including over 2 decades (1953-present) of trans-
pacific studies by the International North Pacific Fisheries Commission,
the question of how salmon find their way back to natal streams after
one or more years in the ocean is still unanswered, but much clearer and
more logical explanations have evolved.

1. Background

According to a summary by Davidson and Hutchinson (1938), Pacific salmon
were present historically along the North American coast from Monterey
Bay (California) northward to Kotzebue Sound (Alaska); along the Asian
coast from the Anadyr River (Siberia) southward to the Tumen River (Korea)
and Cape Inuboye (Japan); as well as in isolated streams along the Arctic
Ocean coast. Although transplants of this genus had been attempted in
various parts of the eastern coast of North America, east and west
coasts of South America, western Europe, Australia, New Zealand and
Hawaii, only limited successes were attained.

Prior to the INPFC studies there were two opposing theories as to the
effect of the marine environment on the movements of salmon: (1) on
entering the ocean, salmon remained throughout their lives at sea close
to the influence of their natal stream; and (2) they ranged widely, far
beyond any conceivable influence of the natal stream to feed and mature,
but eventually returned in large numbers to spawn. Which theory was
correct was really indeterminate because most of the early marine
tagging and environmental studies, which commenced in the 1920's, were
limited to coastal waters, however, this did not deter speculative
opinions and conclusions related to both theories.

In the eastern North Pacific Ocean, tagging studies by Gilbert (1924)
and Gilbert and Rich (1927), showed that sockeye salmon returning to
streams in Bristol Bay moved westward in great numbers over the continental
shelf on the southern side of the Alaska Peninsula and northward into
the Bering Sea at the first opportunity, through False Pass and also
through Unimak Pass. Dall (1882) had noted the presence of a southward
flow in the eastern Bering Sea, referred to as the Bering Current, and
it was perhaps convenient to assume that such a current could advect
odors or other chemical traces—perhaps even a detectable salinity
gradient from Bristol Bay streams extended southward through Unimak Pass
and along the south side of the Alaska Peninsula. However, recent
oceanographic studies do not indicate a persistent, dominant flow that
could justify such a conclusion or serve such a purpose. A chum salmon
tagged during these experiments was recovered from the Kamchatka Peninsula,
indicating an extensive oceanic migration of at least that species, and—
although, in subsequent years a sockeye salmon was reported caught in
the middle of the Gulf of Alaska and a school of sockeye salmon was
reported several hundred miles offshore (Moulton, 1939)—the movements
of salmon during the marine phase of their life cycle were relatively
unknown.

Davidson and Hutchinson (1938) believed that salmon frequented waters
of the open sea as well as those of the immediate coast and proposed
that salmon were limited to waters with temperatures of 0° to 20°C.,
salinities of 30 to 35 °/oo and depths of 0 to 200 m. These temperature
thresholds would limit the southern distribution of salmon largely to
lat 40°N across the entire Pacific Ocean in summer, except for the area
of southward flow (California Current) off the west coast of the United
States; however, they would also permit during winter a mid-Pacific
distribution as far south as lat 30°N and an eastern Pacific distribution
as far south as lat 20°N. In spite of extensive fishing, no salmon have
been caught in either of these areas. As recently as 1952, a report on
an extensive tagging program in coastal waters of southeastern Alaska
indicated that there was no evidence that pink salmon came from the open
sea when they first appeared in coastal waters, and it was hypothesized
that they might simply rise from deep water.

The Japanese conducted tagging studies in the western North Pacific
Ocean during the 1920's near the Kuril Islands and Kamchatka Peninsula
and reported that the marine phase of the salmon life cycle was spent
in a then unknown area of the North Pacific Ocean (Taguchi, 1956).
This assumption was given further credence by Japanese tagging studies
conducted during the periods 1936-38 and 1941, which showed extensive
oceanic migrations of sockeye salmon in the Bering Sea and western North
Pacific Ocean. Hartt (1962; 1966) has summarized the results of other
early and more recent salmon tagging investigations in the eastern and
western North Pacific Ocean.

The Japanese commenced a commercial salmon-fishing operation in the western
North Pacific Ocean in 1952, and Fukuhara (1953) reported sizable catches
were made in the open ocean and in the vicinity of the Aleutian Islands.
These commercial operations continued, but no additional information
concerning the distribution of salmon in the eastern North Pacific Ocean
was forthcoming because the Japanese were prevented by Treaty from fishing
east of long 175°W and conservation principles prevented Canadian and
American commercial interests from fishing in oceanic areas. However,
salmon and oceanographic research programs were established, under the
aegis of the INPFC, by research teams in Japan, Canada and the United
States in 1955 and extensive information on the transpacific salmon
environment began to be accumulated and pieced together. These analyses,
when combined with the extensive inshore studies conducted by the Fisheries
Research Institute of the University of Washington in the Bristol Bay
and Kodiak areas, the International Pacific Salmon Commission in the
Vancouver Island area, and the various State and Federal programs
along the west coasts of Canada and the United States, provide considerable
knowledge concerning the life history of Pacific salmon. Several years
ago, Favorite (1969c) compiled a bibliography of nearly 200 papers
pertaining to relations between Pacific salmon and the marine environment,
and a current list would contain several times that amount; thus, discussion
in this section has been limited largely to sockeye salmon.

2. Oceanic Sockeye Migrations

The Pacific salmon, in particular sockeye salmon, provide an excellent
example of not only the fragmentary nature of environmental studies usually
associated with living marine resources, but also the extensive knowledge
that can be obtained when such studies are conducted. Sockeye salmon
are an important commercial resource, and extensive stream and lake studies
relating to this species have been conducted for many decades. There
is a firm basis for such studies, in that man can assist the spawning
process by removing obstacles blocking spawning migration paths and, in
some instances, enhance conditions in the spawning area. However,
perhaps most important is the fact that spawning and/or escapement
assessments provide indices of the numbers of mature salmon that will
return to natal streams usually 2 to 4 years later.

Although the sockeye salmon fishery has been exploited since the 1880's,
there have been only three periods during which concerted efforts have
been made to investigate the marine phase of their life history--the mid
1920's in the western Gulf of Alaska and the late 1930's in the eastern
Bering Sea by the U.S. Bureau of Fisheries, and from the mid-1950's to
the late 1960's by the INPFC throughout the entire oceanic regime salmon
inhabit.

Studies conducted by the Northwest and Alaska Fisheries Center of the
National Marine Fisheries Service (NMFS) for the American Section of the
INPFC point out not only the oceanic distribution of sockeye salmon, but
also the value of opportunistic oceanographic observations made in
conjunction with fishery operations. Initially, the primary objective
of INPFC studies was to ascertain a line or lines that would permit an
equitable division of Asian and North American salmon stocks, while an
interim line (long 175°W in the Aleutian Islands area) served as an
abstention line east of which no nation could conduct oceanic commercial
salmon fishing as long as other conditions were met (i.e. the stock was
fully utilized and under research, etc.). This line was originally
selected as sufficiently westward of any oceanic migrations of North
American salmon to protect the entire stocks from high seas exploitation.
Subsequent oceanographic studies revealed 4 instances in which environ-
mental observations contributed significantly to our knowledge of the
distribution and migration patterns of sockeye salmon, even though limited
studies were conducted.

First, certainly there were little or no fisheries data to indicate
that long 175°W was not a wise choice for an abstention line, but there
were oceanographic data which suggested that westward flow out of the
Gulf of Alaska, where sockeye salmon of Bristol Bay origin were known
to occur prior to homing migrations, along the south side of the Aleutian
Islands extended beyond long 175°W (Barnes 1936). Oceanographic studies
conducted under the supervision of the American section of the INPFC that
were concentrated in the Aleutian area from long 155°W to long 175°E, not
only confirmed that this westward flow extended to at least long 165°E and

was present year round, but also it was a major current of the Pacific Ocean--the Alaskan Stream (Favorite 1967). The westward flow diverges near long 170°E sending one branch northward into the Bering Sea and the other eastward to lat 50°N, long 165°E before losing its identity, as traced by water property characteristics at depth, as a result of impinging on water flow eastward from the Asian coast (Dodimead et al 1963; Favorite et al 1976). Subsequent U.S. salmon tagging studies and racial analysis studies showed that Bristol Bay salmon occurred as far west as the western terminus of this flow; Japanese studies (Kondo et al 1965) showed this general area (lat 49-53°N, long 168-173°E) to be a zone in which both Asian and Bristol Bay sockeye salmon stocks met--the eastern extent of the former and the western extent of the latter (Figure 22). It was soon apparent that the Japanese high seas commercial salmon fleet generally commenced oceanic fishing each year in the area lat 48-50°W, long 165-170°E and based subsequent fleet movements on conditions encountered. Thus, it was obvious early in the INPFC studies that the abstention line did not protect completely the sockeye salmon stocks of the Bristol Bay area from exploitation by Japanese vessels west of long 175°W, and that oceanic flow patterns were clearly related to mature stock distributions during the shoreward migration period.

Second, there were two types of fishing operations designed by U.S. scientists to ascertain the distribution and migrations of salmon, and each was based on different concepts of sampling. The broad area sampling was accomplished through widely spaced stations at which typical salmon-mothership fishing gear (gill nets) was used and, in order to obtain catches adequate for statistical analyses, up to several miles of gill nets were used. The nets were set in the evening and hauled early in the morning. The long time required to retrieve the nets (in most cases 3-6 hours depending on catch) prevented any nearshore fishing, because of possible loss or damage to the expensive nets, in the early phases of the study; thus, initially, little or no sampling was accomplished in the Alaskan Stream, which, in the central and eastern Aleutian areas, occurred from the islands to 50-100 km offshore on the south side of the island arc. An alternate fishing plan was to retain the same area of coverage but considerably reduce the number of stations so that repetitive sampling at key stations could be obtained. This design called for sampling at 3 locations, three degrees of latitude apart (324 km), along meridians 10° apart (lat 50°, 53° and 56°N at long 175°E, 175°W and 165°W) and provided the opportunity to make two fishing sets (by remaining on station an additional night) if the initial catch was inadequate. Of course these locations had no specific relation to known flow patterns and proposed migration routes; and for these and other reasons, this design was only used one season, in 1957.

The alternate mode of fishing was by purse seine in order to obtain salmon for tagging purposes. Early studies were planned in the vicinity of the eastern Aleutian passes because of results of tagging studies in this area in the 1920's. This type of fishing was particularly conducive to inshore sampling because the net could be retrieved quickly (in minutes rather than hours as in the case of a long gill net); in addition, because
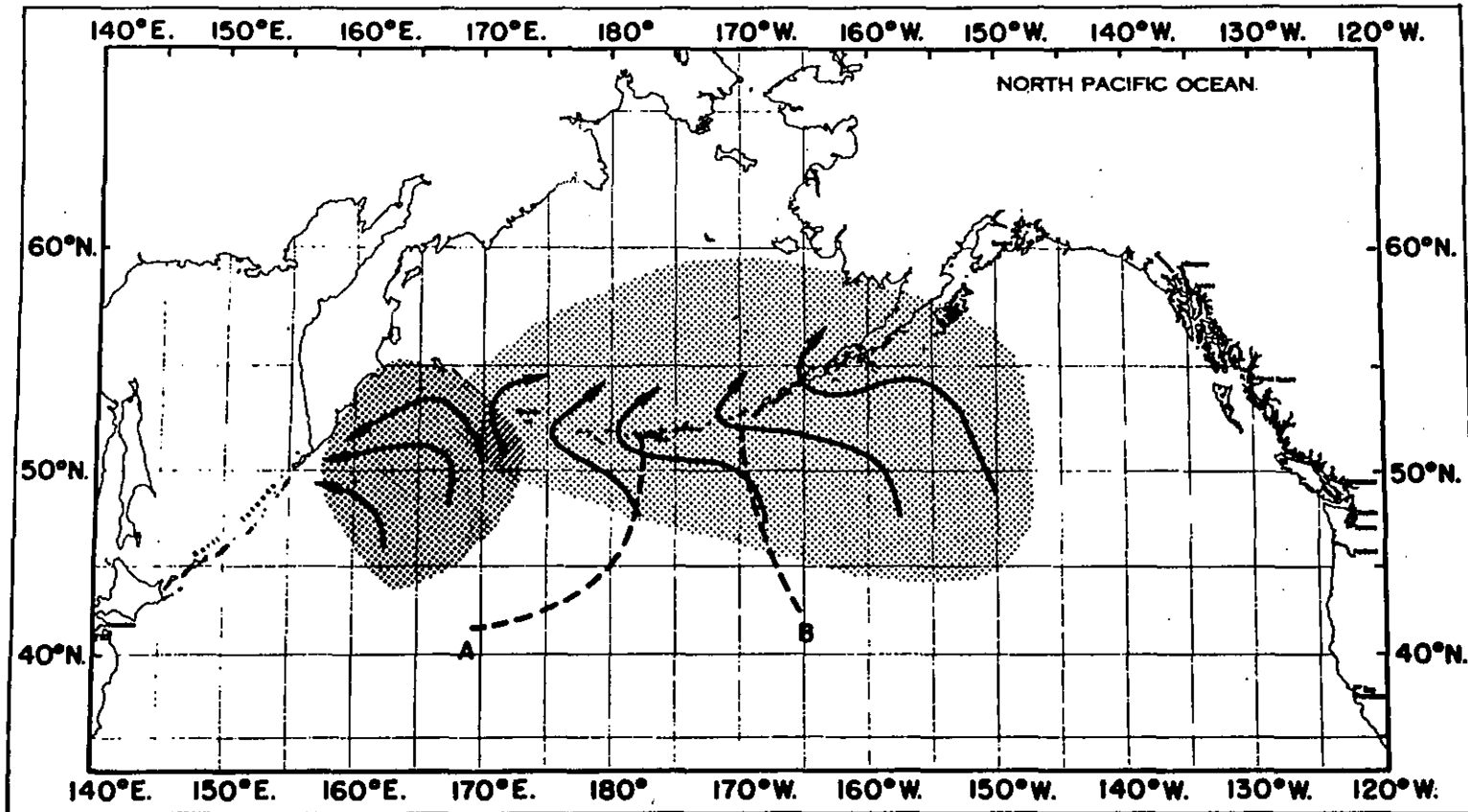
Figure 22. Migration routes and distribution of sockeye salmon of Asian and Bristol Bay origin during spring (after Kondo et al. 1965).

this operation could not be conducted in rough weather, which occurred frequently, it was convenient to venture forth short distances from protected island anchorages when good weather occurred. It subsequently became apparent that salmon returning to Bristol Bay streams were present in high numbers all along the south side of the Aleutian Islands in waters of the Alaskan Stream and--as catches dropped off sharply with distance from shore--broad oceanic tagging studies were curtailed in favor of studies in the area of the Alaskan Stream. Eventually purse-seine fishing at stations south of Adak Island within 100 km of the shore became an indexing site for short- (1-2 months) and long-range (1 year) forecasts of Bristol Bay sockeye salmon. The interesting point here is that mature salmon caught in this area and due to arrive in Bristol Bay streams (over 1500 km away) within a month or so are moving westward, away from their destination, in the direction of the westward flowing Alaskan Stream. It was also discovered that, although mature salmon were caught in large numbers in spring south of the Aleutian-Commander island arc and in the passes, invariably very poor catches were made along the north side of the island arc east of long 180°. This was also puzzling from an environmental standpoint because, although data were sparse, it was generally recognized that flow along the north side of the island arc was largely eastward toward Bristol Bay. However, subsequent studies (Favorite and Ingraham 1972) showed that flow through Amchitka Pass (long 180°) trends northeastward across eastern Bering Sea impinging on the continental shelf in the general vicinity of the Pribilof Islands (Figure 23). Large catches of mature sockeye salmon have been made in the general vicinity of this trajectory, catches that first appeared anomalous until this flow was ascertained. There is also evidence that in years of extensive ice cover over the shelf low water temperatures (<2°C) delay the trans-shelf shoreward migration and also speculation that trans-shelf eddies carry river runoff westward to the shelf edge, possibly providing a triggering mechanism or guidepost to maturing salmon (Favorite et al 1976; Fujii 1975).

Third, environmental studies have provided a basis for determining the southern boundary of salmon in the central part of the ocean. Although such a boundary can be determined by experimental fishing, this is a time consuming and costly procedure that provides information only for that location and instant of time. General surface environmental characteristics such as those given by Davidson and Hutchinson (1938) would imply that salmon could be found as far south as lat 30°N. However, it has been shown that water structure and associated biota provide rather precise boundaries that are readily identifiable and relatively constant (Favorite and Hanavan 1960). Sockeye salmon were found in summer in surface layers in the central part of the region northward of the sub-surface temperature front (Figure 24). This front was subsequently shown to extend from approximately lat 42°N in the western Pacific Ocean to lat 48°N in the eastern Pacific Ocean. Further, no salmon species occurred south of the transpacific salinity front near lat 42°N that denotes the presence of the Pacific Central Water Mass and the southern boundary of the Subarctic Pacific Region (Figure 25). This concept of a southern boundary of salmon distribution being related to an environmental feature was successfully tested in mid-winter (Favorite et al 1964),
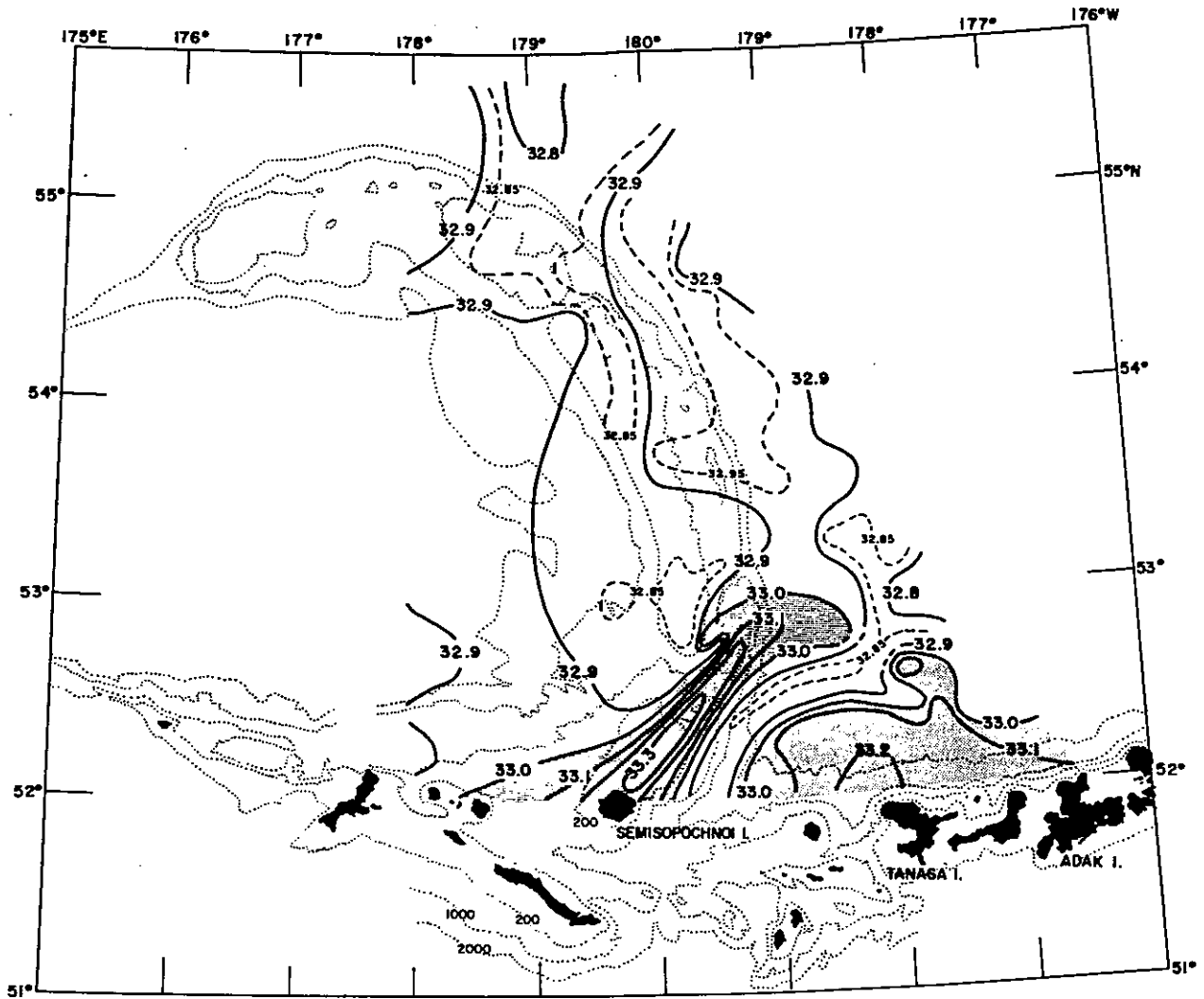
Figure 23. Surface salinity distribution reflecting northward flow
of dilute Alaska Stream water through Amchitka Pass
(summer 1970), and selected recoveries from drift bottles
released at indicated locations (from Favorite and
Ingraham 1972).
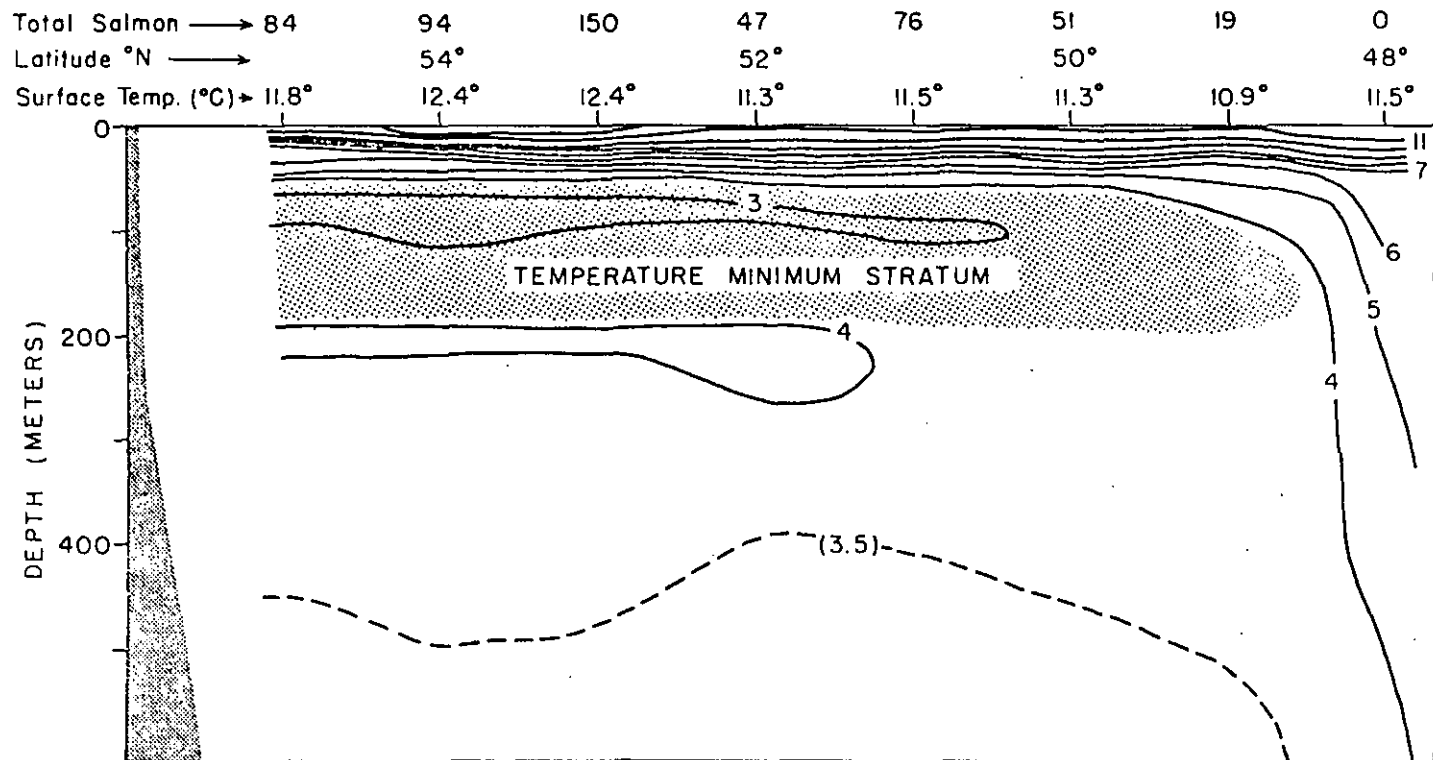
Figure 24. Vertical section of temperature ($^{\circ}$C) structure along
long 155°W in summer 1956 indicating the absence of
salmon in gill net catches south of the subsurface
temperature front at lat 48°N (from Favorite 1969b).
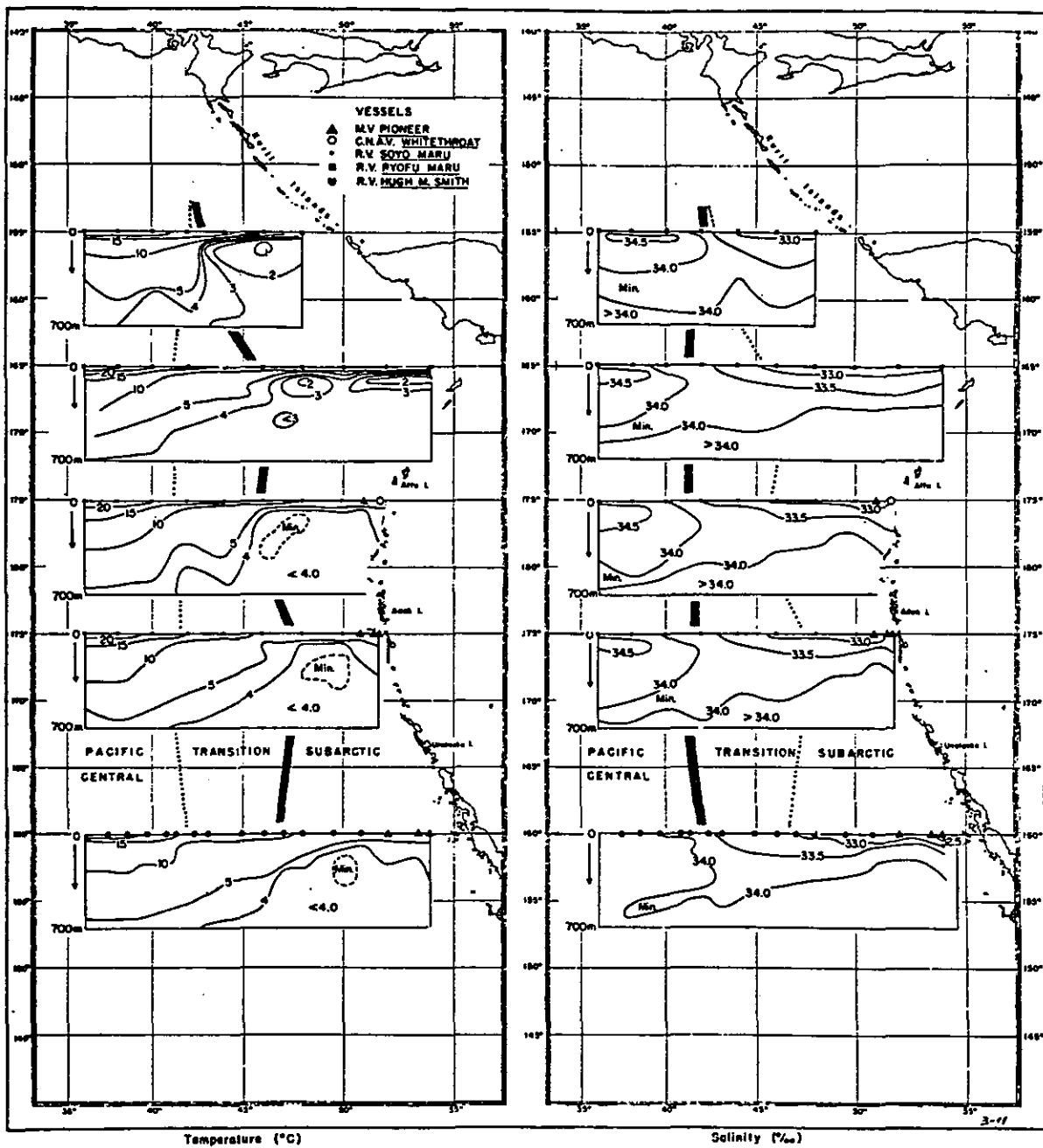
Figure 25. Vertical sections of temperature (°C) and salinity
structure in the central part of the Subarctic Pacific
Region (1958). The former indicating the northern
boundary of the Transition Zone and the latter the
southern boundary of the Transition Zone or southern
extent of the Subarctic Pacific Region (from Favorite
and Hanavan 1960).

a period of supposed southernmost distribution of salmon; and, this knowledge provided part of the rationale for subsequent curtailing of salmon research gillnet fishing well to the south of the Aleutian Islands. However, we still do not know if salmon occur in winter well below the surface layer south of the Subarctic Boundary where Subarctic Pacific Water sinks under water associated with the central Pacific gyre (the zone of the salinity-minimum stratum in Figure 25).

Fourth, the central portion of the Alaskan Gyre provides environmental conditions favorable for sockeye salmon during winter; in fact, spring conditions indicate a separation of sockeye and pink salmon (O. gorbuscha) stocks in this area (Favorite 1975) with the latter to the south of the area of the temperature-minimum stratum (Figure 26). The reason for this distribution of sockeye salmon is still unclear, possibly winter upwelling provides concentrations of forage, but the distribution is consistent with the general summer distributions. Of course, during late spring and summer, mature sockeye salmon must move shoreward to complete spawning migrations. This association between sockeye salmon and the Alaskan Gyre permitted assessments of the relative size of populations of mature sockeye 3-6 months prior to their arrival in lake systems and provided useful indices not only for fishery management plans, but also to commercial cannery operations. Here again one might assume that such forecasts could be based on salmon distributional data alone, but it is argued that because this phenomenon is associated with recognizable environmental features, better and more controlled sampling can be obtained, and one doesn't have to wonder whether or not the forecast relationship will suddenly collapse. What - is never a substitute for why.

In summary, it has been shown that as a result of limited environmental studies a number of oceanic features were discovered which are associated with sockeye salmon; they are as follows: (1) the separation of stocks from two continents, (2) the location of migration paths, (3) the limits of geographical distribution, and (4) differences in oceanic and coastal distributions at certain times of the year. It should be pointed out that although environmental studies explained, in part, salmon distributions, at no time were U.S. salmon fishing locations actually based on forehand knowledge of ocean conditions, nor were the pre-scheduled locations ever modified as a result of known environmental conditions. Numerous other examples of resource-environment relations could be cited. For example, Japanese data indicate the concentration of coho salmon in late spring 1966 and 1967 at the northern edge of the Transition Domain in the central Subarctic Pacific Region (Figure 27). Although the general distributional salmon studies have been terminated by Canada and the United States, some specific research study areas are suggested in Section VII-B-3.

C. PELAGIC FISH

Perhaps the only true, transpacific, pelagic fishery is limited to tuna. There are a number of species of tuna, but the one most closely associated
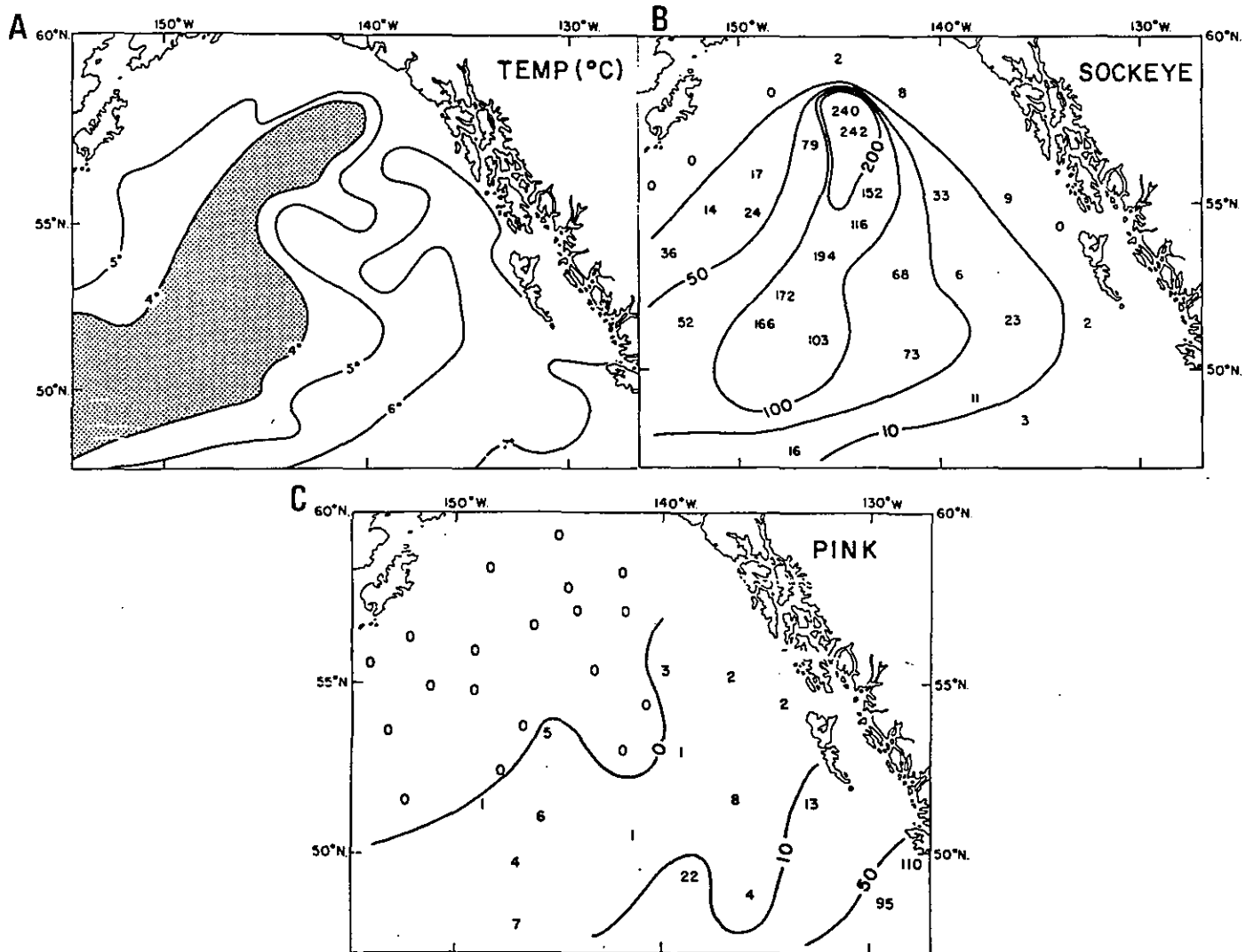
Figure 26.   Comparison of (A) temperature distribution (^{o}C) in the temperature-minimum stratum in spring 1962, (B) numbers of sockeye and of pink salmon in longline catches (per 1000 hooks) April 9 to May 6, 1962 (catch data from INPFC 1964).
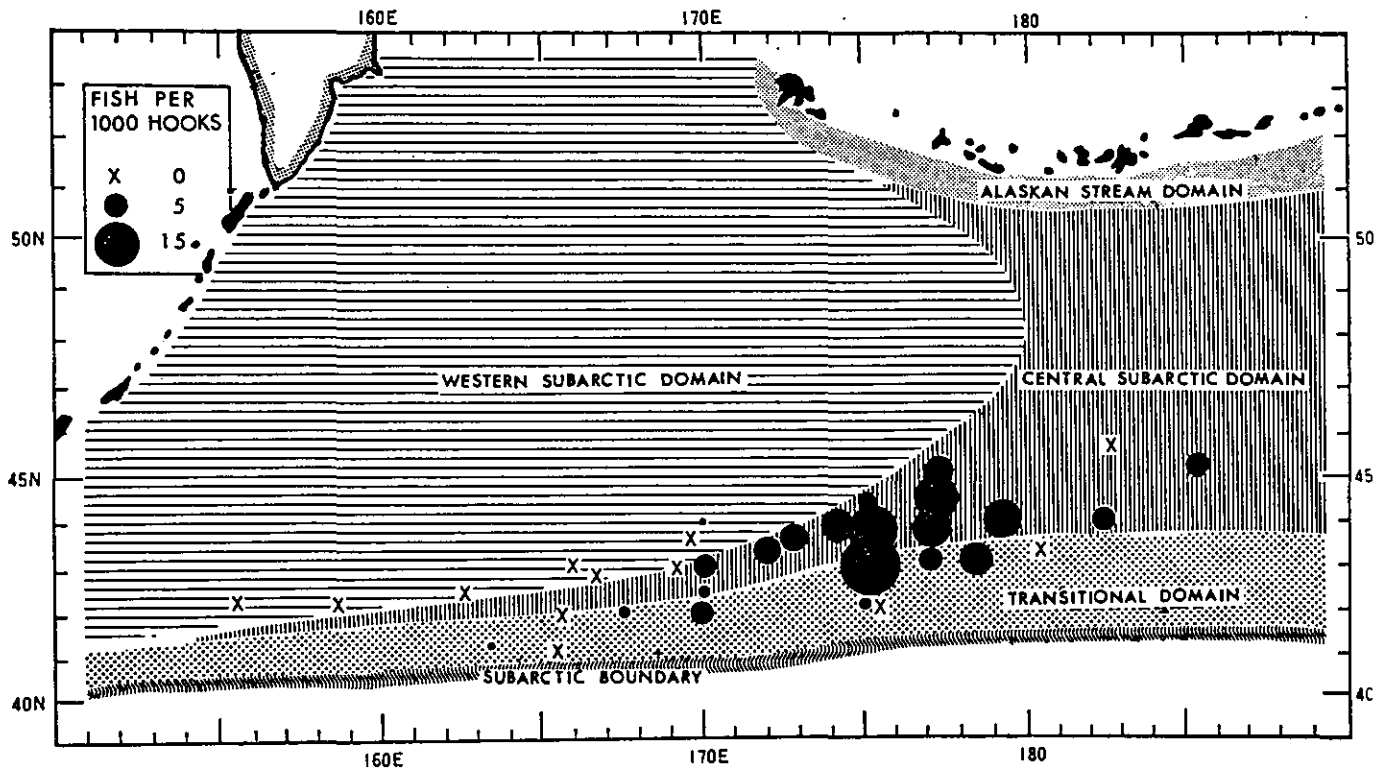
Figure 27. Relative abundance of coho salmon in longline catches
(per 1000 hooks) with schematic diagram of upper zone
domains (from Dodimead et al. 1963) in the northwestern
North Pacific Ocean June 7 - July 5, 1966 and June 5-13,
1967 (from Fishery Agency of Japan 1973).

with the Subarctic Pacific Region is the albacore which has been caught
in the southern part of the region in late summer. Commercial exploitation
of albacore occurs largely at the eastern and western extremity of the
Pacific Ocean, and their transpacific migration patterns are based largely
on fragmentary data from tagging studies. Some information on the Pacific
saury is also available, again largely at both sides of the ocean. The
Pacific hake is usually considered a demersal fish, but its movements
to and from various spawning grounds are so poorly known, it is considered
in this grouping. Other fish could have been considered, for example
Pacific pomfret (Brama japonica) in the eastern part of the region and
Atka mackerel (Pleurogrammus monopterygius) in the northern; however,
except for the tuna, our knowledge is so fragmentary that little is to
be gained from any discussion. What we have attempted to do here is
suggest that there is an order to the distribution and movements of the
fish that is not only interesting from a scientific or ecosystem point
of view, but also important from a management one—an aspect often
overlooked when individual stocks are studied or managed by separate
groups.

1. Albacore

As in the previous section on salmon, resource-environment relations are
discussed largely with respect to only one species, albacore. This is
because tuna studies have been conducted largely by the NMFS Southwest
Fisheries Center. The albacore have been selected because there are
interactions between the species and other fish groups discussed in this
report.

Studies on the arrival, distribution, and departure of albacore off the
west coast of the United States have been conducted for decades and for
a number of years albacore forecasts have been made largely on the basis
of sea surface temperature data. Temeratures of 14.4 to 16.1°C (58-61°F)
were generally considered to indicate "albacore water" even though Alverson
(1961) reported that exploratory fishing activities, conducted in August
and September in excess of 322 km (200 mi) seaward of the coast, failed
to take commercial concentrations of albacore even though these favorable
sea surface temperatures prevailed. Nevertheless, these temperature
guidelines were considered better than no information at all and fore-
casts persisted.

Pearcy (1973) showed that albacore resource-environment relations off the
Columbia River involved more than surface water properties. He noted that,
although the first albacore catches of the 1970 seasons were probably
from an area characterized by Columbia River plume water, the record catches
by jig boats in July declined abruptly and continued poor throughout the
remainder of the season; whereas, bait boats had good fishing off Oregon
during the latter period. Because favorable surface temperatures prevailed,
this shift in availability was attributed to a descent by the albacore into
subsurface water to feed on Pacific saury, their preferred prey. Certainly
this also challenges the validity of surface temperatures as absolute

indicators of albacore distribution and abundance, but the paucity of
environmental observations at depth do not permit attributing this
behavior entirely to a feeding response, particularly in view of the
fact that Pacific saury are usually found at the surface at night and
have been found in abundance at the surface during the day (Inoue and
Hughes 1971). Perhaps more significant to this behavior is the difference
in surface and subsurface conditions in this area. It is apparent from
the surface salinity distribution presented in Figure 14 that a surface
lens of dilute water moving seaward from the coast and the offshore
component from upwelling, overrides the more basic oceanic circulation
at depth, which is onshore and southward along the coast. Since tuna
are a tropical species it is likely that they respond more directly to
subsurface features.

Laurs and Lynn (In press), as a result of an excellent albacore study
conducted during the last few years over 1000 km from the California coast,
have reported that during June 1973 large concentrations of albacore
suddenly appeared in the area lat 33–35°N, long 139–143°W (Figure 28).
Temperatures of 19 to 20°C (66–68°F) prevailed at that location, but in
July, when the albacore appeared off Cape Mendicino, surface temperatures
were largely 15–16°C (59–61°F). Obviously temperature criteria denoting
the presence of albacore apply only to discrete areas and times. Those
not disposed to search for environmental relations would perhaps argue
that this is additional evidence that environmental conditions do not
directly influence albacore movements, but the June distribution of
albacore was clearly shown to be related to the Transition Zone (Domain).
What is not known is the stimulus that causes the albacore to cross the
California Current System at this location and at this time. Arguments
that they are awaiting higher temperatures will not withstand scrutiny
because good troll catches have been made in temperatures of 11.1 to
11.7°C (52–53°F) (Alverson 1961). In fact, we know that as a result of
high-seas salmon studies conducted by the NMFS Northwest and Alaska
Fisheries Center, albacore occurred in August and September 1956 at the
northern boundary of the Transition Domain where temperatures of 12°C
prevail (Figure 29). Obviously the surface temperature distribution
during this period (largely August-September, 1956) does not provide
specific criteria for the selection of fishing stations, but the subsurface
temperature distribution at the northern boundary of the Transition Domain
(which is also the southern boundary of the sockeye salmon distribution
(see Figure 24)) is quite distinct, as is the southern boundary of the
transition zone (see Figure 25); both apparently influence the distribution
of albacore. Thus, we see albacore entering areas wherein the surface
temperatures change progressively from 20° to 12°C. However, the important
point to remember is that they have remained within a well-defined oceanic
regime, the Transition Domain.

Perhaps more significant from an ecological viewpoint is the fact that there
appears to be a sharp boundary between the southern limit of salmon and the
northern limit of albacore. This is not necessarily a temperature phenomenon
because albacore have been caught in surface temperatures of 10.8°C and thus
might be found as far north as the Aleutian Islands. However, there has
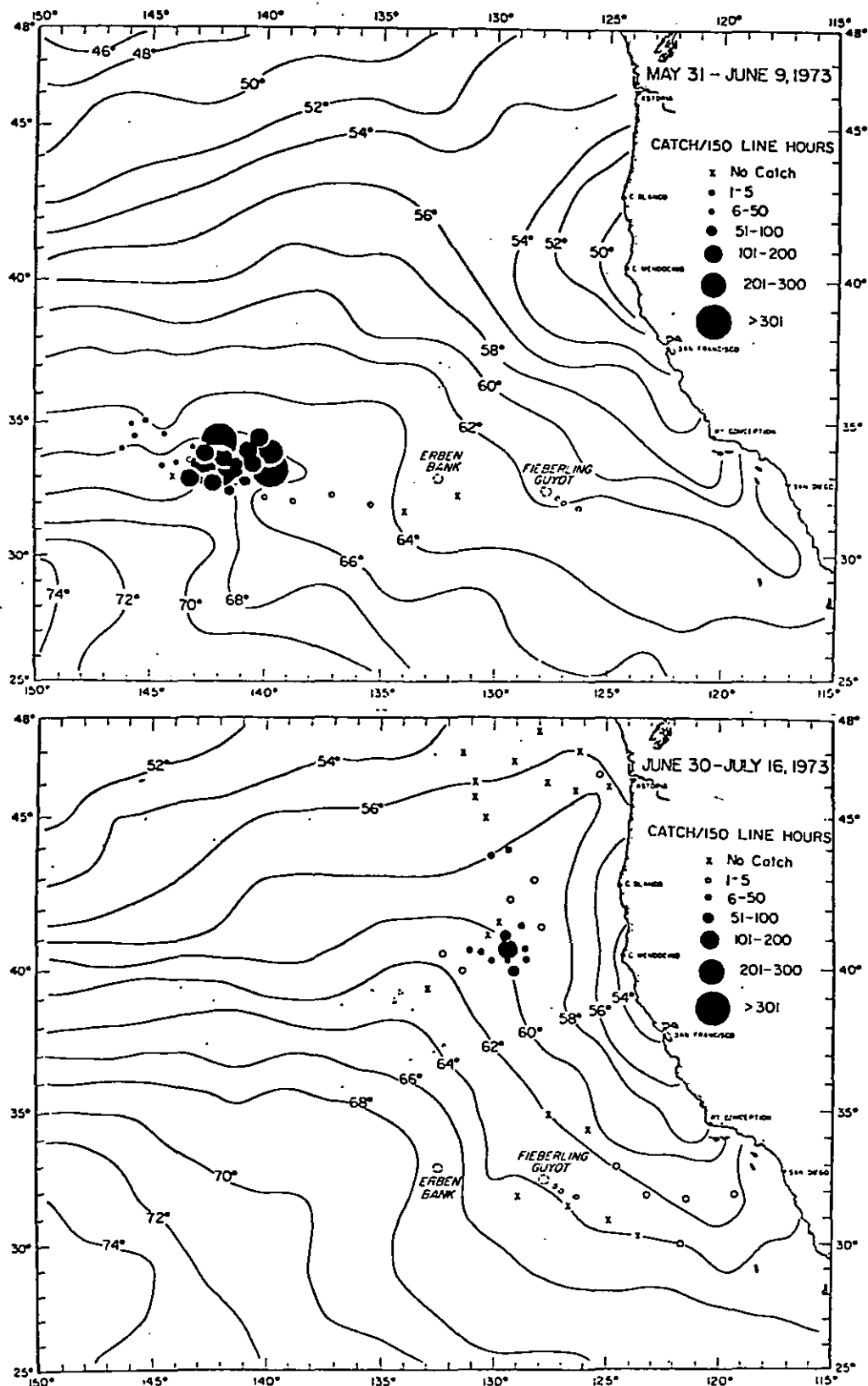
Figure 28. Albacore catches and sea surface temperatures (°C) during
early June and July 1973 indicating the onshore movement
into areas of lower temperatures.
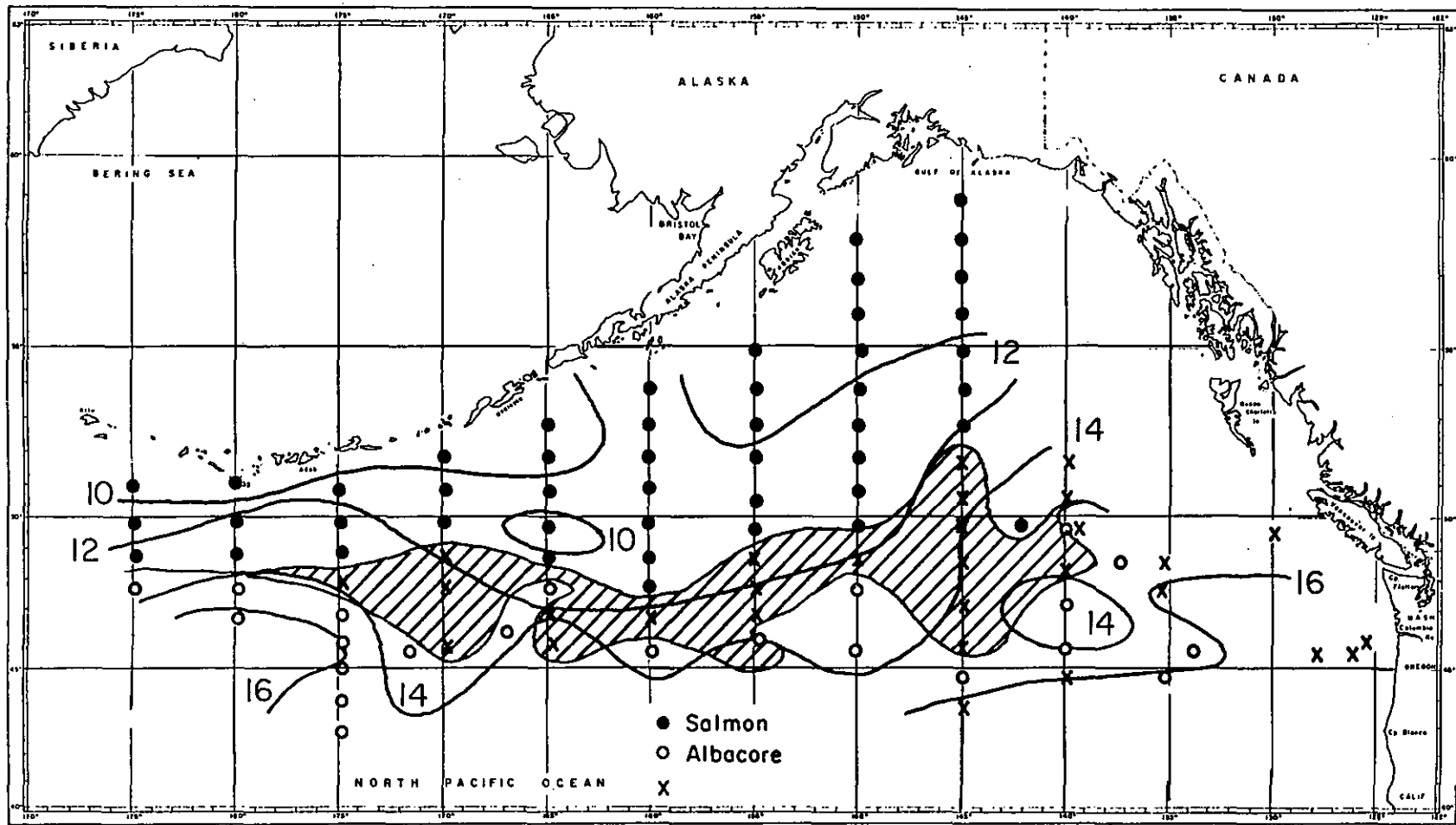
Figure 29. Distributions of salmon and albacore gill net catches and sea
surface temperatures (July 27 to September 16, 1956) indicating
the sharp separation between the two stocks and the presence
of albacore in water of near and below 12°C. The separation
of stocks is more clearly associated with subsurface environmental
features — see text (data from INPFC, 1957).

been extensive gillnet fishing throughout the Aleutian area and none
have been caught. Certainly, one factor (other than the fact that water
north of the Transition Domain is a true subarctic type with a character-
istically different planktonic flora and fauna) is the low dissolved
oxygen concentrations (1 ml/l or about 20% saturation) as shallow as
200-300 m north of the Transition Domain (Figure 30) because there are
estimates that tuna metabolism requires water of at least 50% saturation.
But, it should be noted that 100-200 m depth in this area is well below
the thermocline (and temperatures at 3-4°C, lower than any reported values
that tuna have been found in), and there is a prevalent acceptance that
tuna, even in southern areas, do not sound through the thermocline. How-
ever, such a behavior even in southern areas may also be related to low
dissolved oxygen values as much as the thermal structure. Thus, we see
that the albacore distributions may be closely related to well defined
environmental features that exist at depth, even though we do not know
precisely how they respond to these features at this time.

2. Pacific Saury

Pacific saury occur along the west coast of North America from Baja
California to the Alaska Peninsula, and there is a suggestion of trans-
pacific continuity of an Asian stock in the vicinity of Japan to lat 50°N
in the eastern Pacific Ocean. They appear to be a surface fish usually
found at depths less than 70 m during the day and at the surface at night.
Dense concentrations of adult saury have been reported between lats
42°18'N and 44°22'W off the west coast of North America in August, October,
and November at water temperatures of 12.5 to 13.5°C during Soviet surveys
(Novikov and Kulikov 1966). Kramer and Smith (1970) noted that spawning
probably occurs completely across the Pacific Ocean, and Inoue and Hughes
(1971) indicated evidence of spawning between lats 32-43°N from long 135°W
eastward to the coast from May through August.

With such scant data it is difficult to assess any resource-environment
relations. However, the apparent discontinuous transpacific distribution
is closely associated with the southern boundary of the Subarctic Current
(Figure 31A); and even though the life span of saury is only 2-3 years,
it is possible that transpacific continuity and even transpacific movement
could occur along the southern boundary of the Subarctic Current System
(Favorite et al 1976). This relation has a further significance in that
it is known that albacore feed heavily on saury, and the northern extent
of transpacific albacore distribution and movement also occurs at the
southern boundary of the Subarctic Current System. One can further
speculate that the distribution of saury in the eastern Pacific Ocean
is related to the movement of cold, dilute surface water from the Subarctic
Pacific Region into the California Current and Extension. Drift bottle
studies indicate that surface drift in this area has continuity to the
Hawaii area (Dodimead and Hollister 1962--see Figure 106). It is also
interesting to note that saury, although just one of numerous stocks present
off the Washington-Oregon coast in summer, spawns near the surface, the
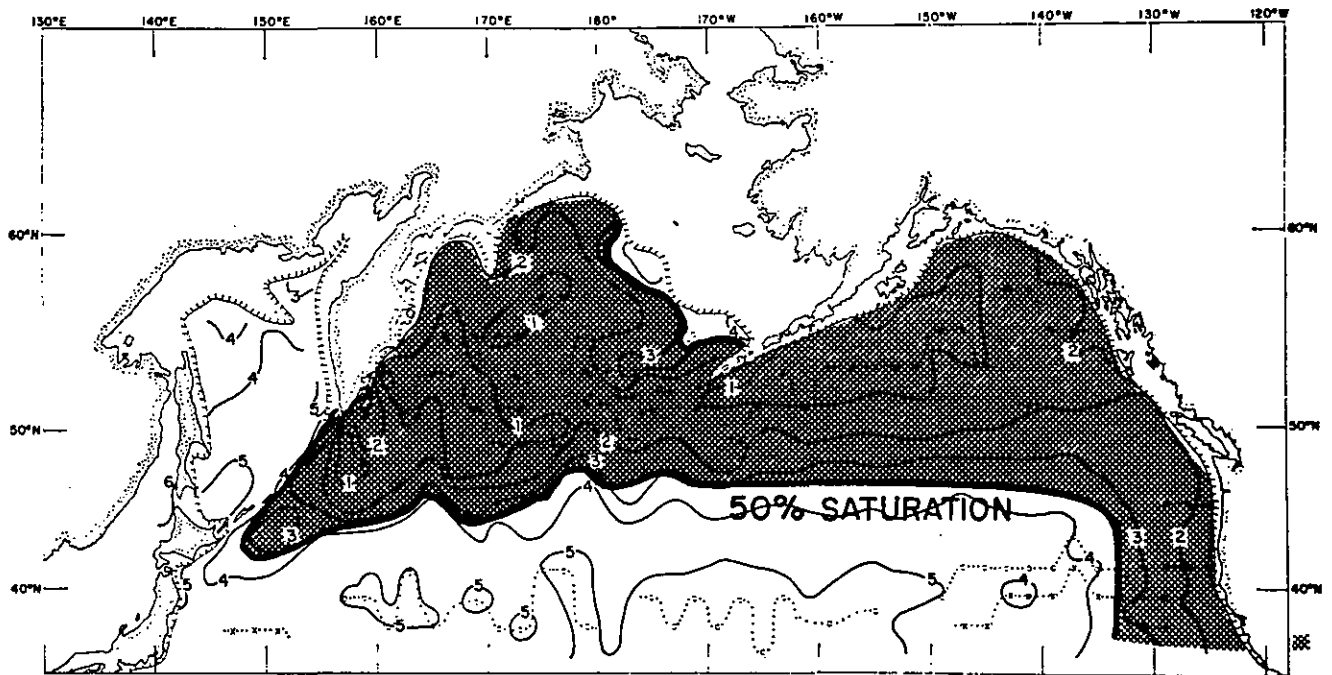
Figure 30. Horizontal distribution of dissolved oxygen (ml/1) at 300 m (all station data averaged by 2x2° quadrangles-- from Favorite et al. 1976).
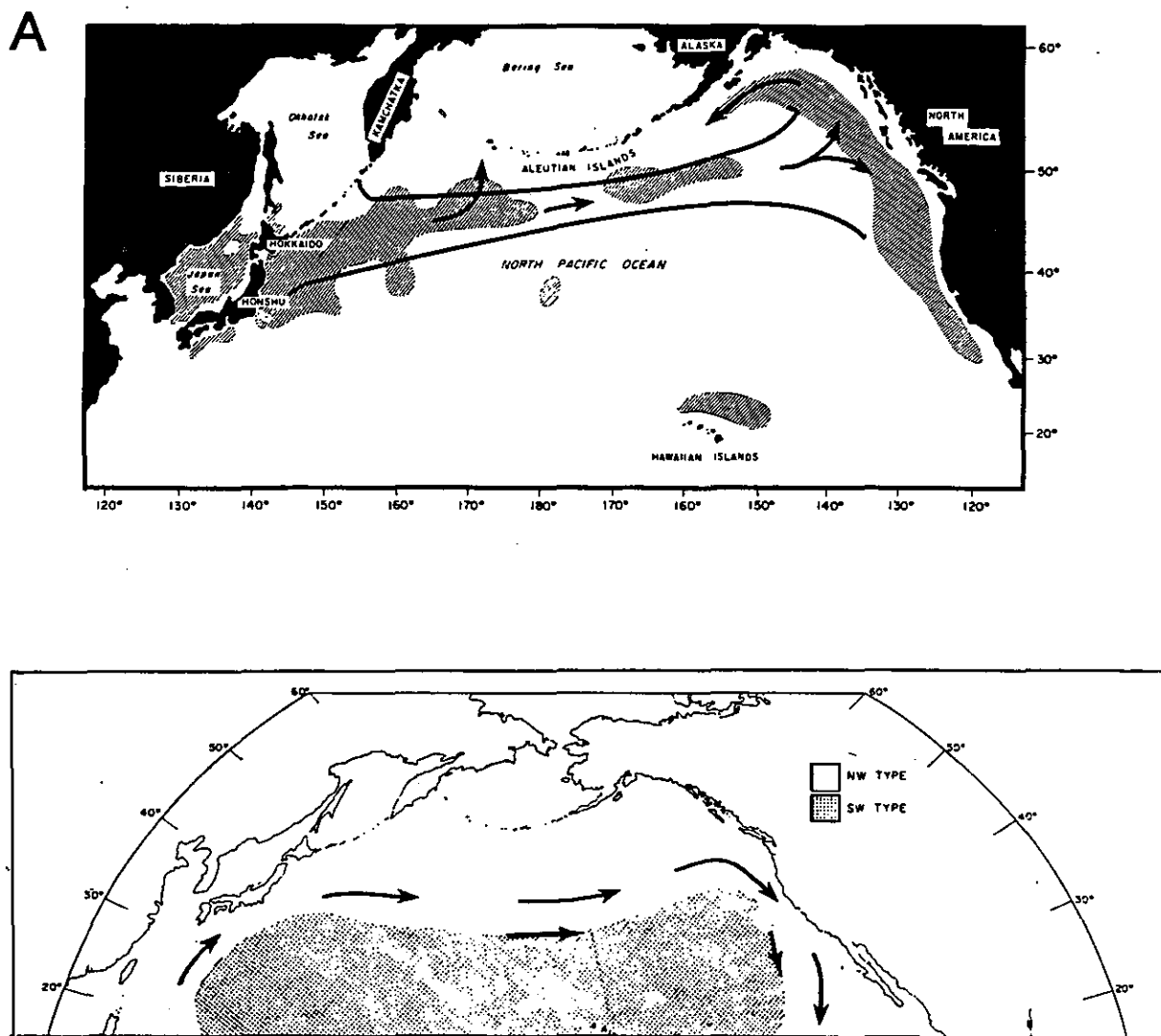
Figure 31. The general oceanic extent of (A) the influence of the Subarctic Current System superimposed on the distribution of Pacific saury as reported by Kobayashi et al. (1968) and presented in Inoue and Hughes (1971); and (B) the general oceanic distribution of Velella (as presented in Favorite 1972).

eggs attaching to floating flora. This makes them vulnerable to predation by myriads of <u>Vellela</u> that occur off the British Columbia-Washington-Oregon coast, at times as dense as one per m^2 over areas of 50,000 km^2 (Favorite 1972). The distribution of the "NW" type is closely associated with the area encompassed by the Transition Domain (Figure 31B).

3. Pacific Hake

Although primarily a demersal fish, Pacific hake spawn in oceanic areas and are largely associated with the California Current System; thus they are discussed in this section. Annual Pacific hake catches ($\sim$ 200,00 mt) are an order of magnitude larger than any one of the other trawl groups (flounders, rockfishes, sablefish (<u>Anaplopoma fimbria</u>), and jack mackerel (<u>Trachurus symmetricus</u>)) or of the incidental catch of other species in this area. The hake are highly migratory (Alverson and Larkins 1969) along the west coast of the United States but the southern boundary of the oceanic distribution occurs where the relatively cold and dilute surface waters of the California Current System are no longer readily identifiable and the subsurface values of dissolved oxygen are extremely low (Figure 32). This is also roughly the northern boundary of the Panamanian hake (<u>Merluccius angustimanus</u>), suggesting a marked preference by these two species for specific ocean environments. Although attempts to locate spawning Pacific hake in commercial quantities have met with little success (Nelson and Larkins 1970), the Pacific hake are believed to spawn near the southern edge of their oceanic distribution. This is unusual because eggs and larvae would be subsequently carried out of the geographical range and environment of the adult populations. Although this could reduce cannibalism and thereby enhance survival of early life stages, there may be another answer because only eggs and larvae released or carried into the surface layer would be transported farther southward; whereas, spawning at depth in the California Undercurrent would permit the larvae to be passively carried northward under the southward surface flow (Figure 33). Current speeds in the Undercurrent are not known, but are apparently low. A net flow of 2-5 cm/sec would result in an annual northward advance of 500-1500 km or roughly from lat 25° to lat 30°, or lat 40°N. Since juveniles spend 1-2 years in oceanic waters before approaching coastal waters off the California coast, it appears that the opposing flows in the surface and subsurface flows could play an important role in keeping these juvenile hake localized. Adult hake move northward in spring along the continental shelf and slope arriving off the Oregon, Washington, and Vancouver Island coasts in summer and in great abundance. They appear to be uninfluenced by the southerly surface flow, coastal upwelling, or river runoff that occurs at this time. The largest catches have been made off Vancouver Island and the availability decreases markedly northward of this point, which is also the southern limit of the Alaska Current System. Since the California Undercurrent flows northward into the head of the Gulf of Alaska before merging completely with the Alaska Current System, it would appear reasonable to find low abundances of Pacific hake at depth in this area. Thus, it would appear that: (1) the southerly distribution of hake is influenced by the highly variable frontal zone at the southern edge of the California Current, (2) the survival of eggs and larvae are affected by the presence and strength of the Undercurrent, and (3) the northern distribution of adults is influenced by the Undercurrent.
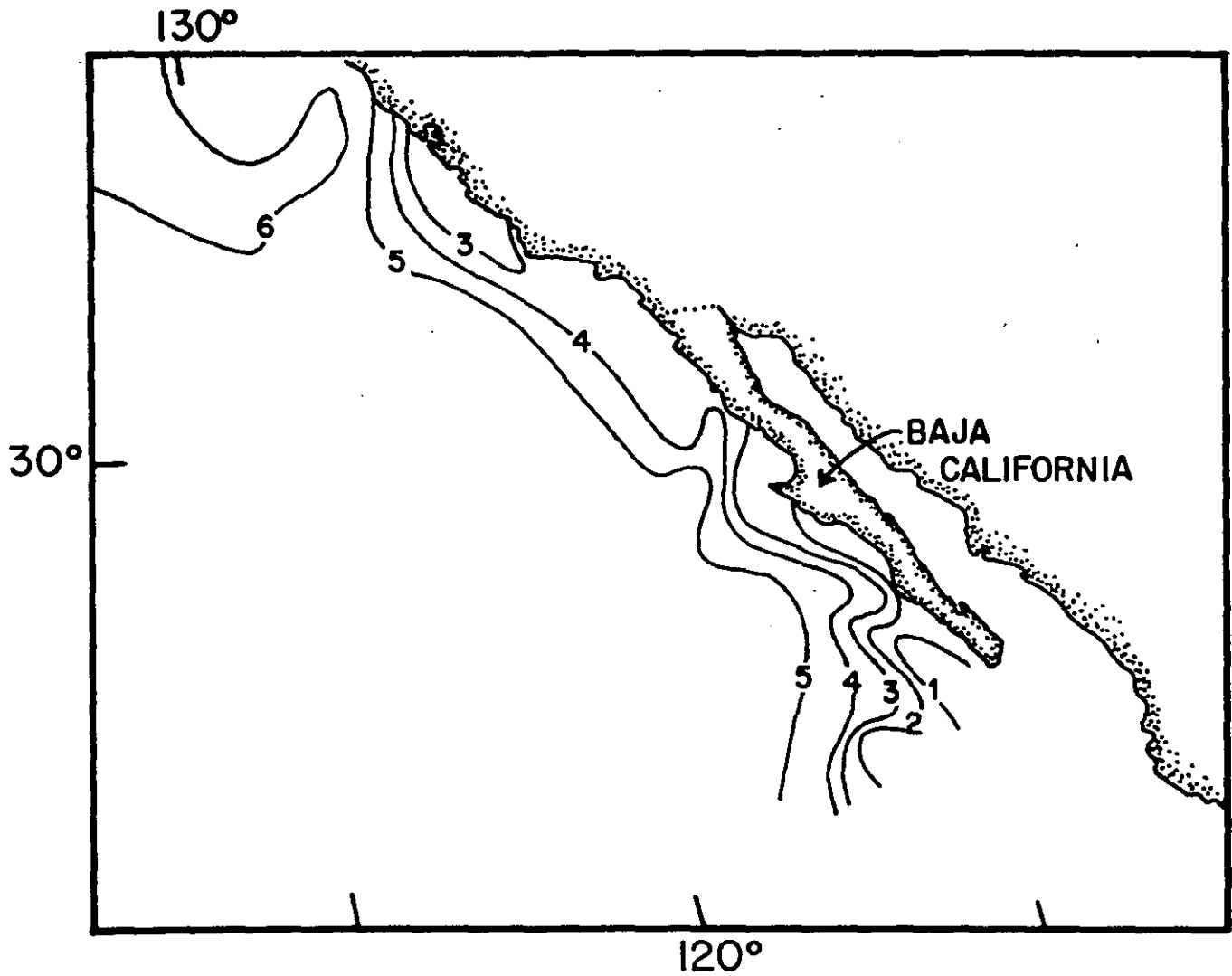
Figure 32. Horizontal distributions of dissolved oxygen (ml/l) at
100 m in summer 1955 indicating the low values occurring
off Baja California.
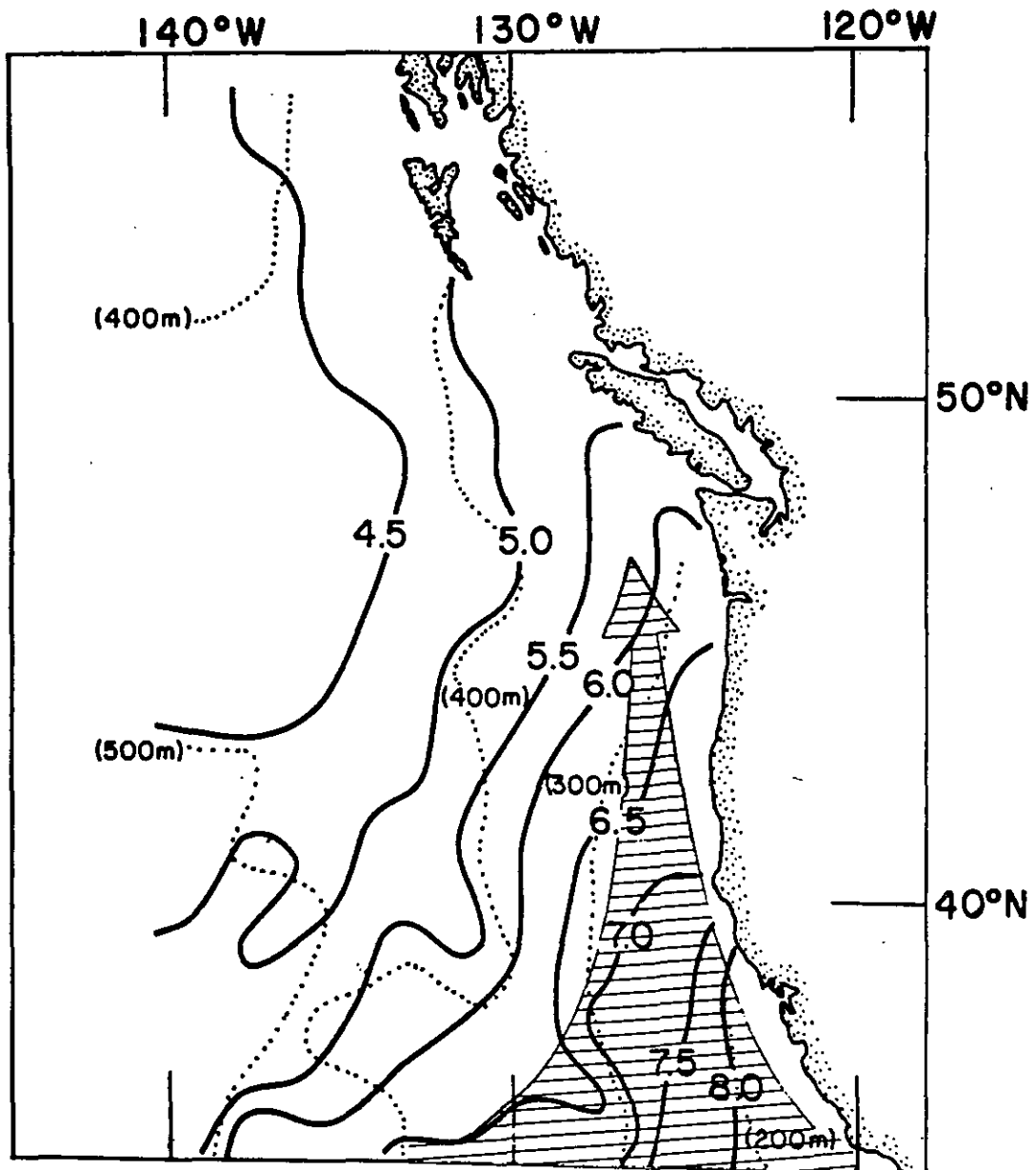
Figure 33. Distribution of mean temperature on, and depth of, salinity surface = 34 °/oo in the California Undercurrent Domain suggesting a broad, northward subsurface flow along the west coast of the United States (all station data averaged by 2x2° quadrangles--from Favorite et al. 1976).

In summary, the recent suggestion that two discrete albacore stocks occur off the Washington-Oregon-California coast clearly demonstrates the temporal nature of the present state of scientific knowledge of this resource. However, there is an extensive tuna fishery, and intensive studies have been and are being carried out by the NMFS Southwest Fisheries Center. Perhaps it is sufficient here to point out that of particular importance is the nature and location of transpacific albacore migrations, and their effect on resources in the southern part of the Subarctic Pacific Region. The sharp division between the southern extent of sockeye salmon and the northern extent of albacore in late summer provokes ecological considerations that may contribute to the successful niche of the former. It is generally accepted that sockeye salmon move northward in spring from the Transition Domain and are generally found in summer and autumn in waters associated with the remainder of the Subarctic Pacific Region, an area albacore apparently avoid. Thus, one can postulate that if a westward migration of albacore occurs along the southern edge of the Subarctic Current System in autumn, the oceanic distribution of salmon may not expand southward into the Transition Domain until after this migration is completed. Of course, the migration paths would be a function of perturbations in the north-south extent of the boundary. One can also speculate that the eastward transpacific migration of albacore in spring would be at the southern boundary of the Transition Domain because of the cold conditions at this time at the boundary of the northern edge of this domain (see Figure 25) which occurs at the southern boundary of the Subarctic Current System (Figure 34). Further, the concentration of albacore in the complex ecosystem off the west coast of the United States may be related to feeding behavior on saury, and the return of albacore to the western side of the Pacific Ocean may also involve saury abundance enroute--as well as at the western side of the ocean; however, it is not known what triggers these migration patterns or guides the albacore along their migration routes. Finally, the extensive foreign fishery and continued studies by the NMFS Northwest and Alaska Fisheries Center and the NMFS Southwest Fisheries Center provides considerable knowledge on the general distribution and abundance of Pacific hake. However, attempts to establish hake reduction plants (for fish protein concentrate) on the Washington-Oregon coast in the 1960's was unsuccessful because of the inability of the fishery during a test period to provide the amounts required for a successful operation. Thus, more precise knowledge on the movements of hake would be beneficial, and it is believed that resource-environmental relations with respect to adult movements, particularly immediately prior to and after the spawning period, and the nature of juvenile movements during the several years of pelagic existence would be instrumental in providing safeguards for this species.
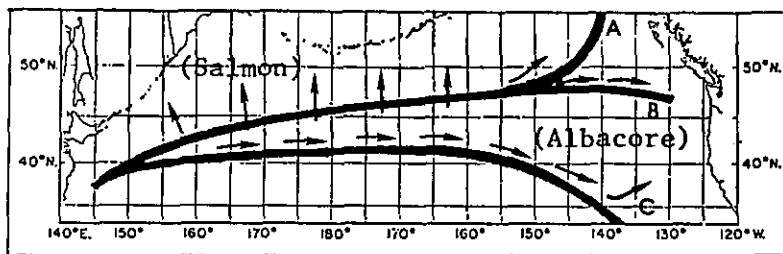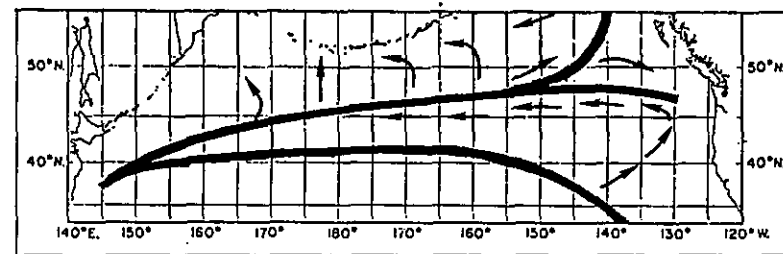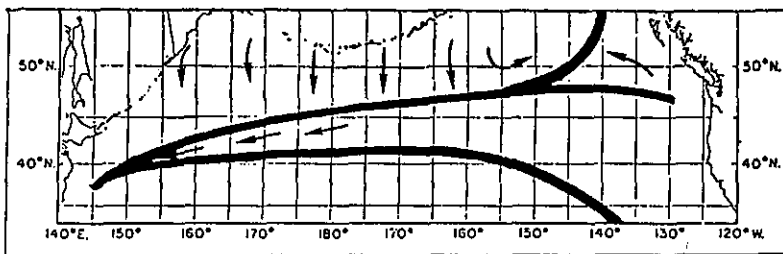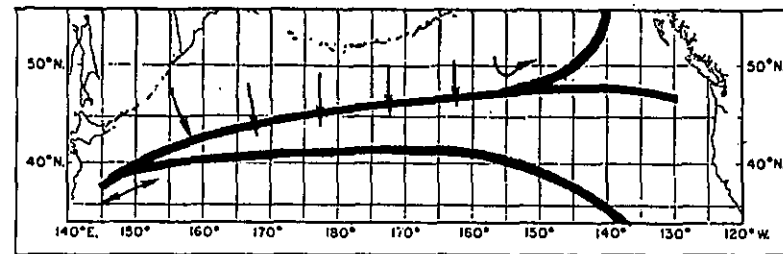
Figure 34.   Schematic diagram of salmon and albacore interactions.

IV. COASTAL ENVIRONMENT AND RELATIONS TO SELECTED FISHERIES

When considering resource-environment relations of commercially important marine fish in coastal areas of the northwest coast of North America, one has to include not only anadromous, pelagic, and demersal fish, but also crustaceans. In this section some comments are made in relation to juvenile salmon, herring, groundfish, crab, and shrimp. Because the coastal regime is of major importance to problems related to extended jurisdiction, additional information on environmental conditions is presented. Certainly greater temporal and spatial detail will be required to deal with definitive relations but in most instances neither the fisheries, nor the environmental data are adequate at this time.

The coastal fisheries (with the exception of Pacific hake discussed in Section III) are considered to be those present over the continental shelf and slope, features that impose physical constraints to oceanic circulations. The continental slope represents the edge of the ocean basin and flow is largely along the isobaths. Complex flows, such as undercurrents, flows contrary to surface flows and even to flows at great depths, are common. The extent to which oceanic circulations affect conditions on the shelf are dependent on areas of convergent and divergent slope flows, the number and extent of submarine canyons, the width of the shelf, and the degree of isolation of the shelf. Conditions along the coast are influenced by tidal currents, river discharges, and upwelling.

A. EASTERN SUBARCTIC PACIFIC REGION

The diversity of surface and subsurface geographical features, the extreme ranges of climatic conditions, and the variability in water properties and oceanic circulation make the eastern Subarctic Pacific environment from California to northern Alaska one of the most interesting marine areas of the world. Submarine canyons and seamounts, as well as, the Aleutian-Commander island arc, and its associated trench are conspicuous bathymetric features, but the most dominant one with respect to fisheries is the continental shelf. Although narrow off the California coast, it progressively broadens to the northward encompassing the fjord-like Puget Sound basin and approaches; the wide, exposed Queen Charlotte Sound; the winding island passages of southeastern Alaska's Alexander Archipelago; and, the shallow, enclosed Prince William Sound and Cook Inlet, before reaching the eastern Bering Sea where it reaches a width unsurpassed anywhere in the world, over 500 km.

Coastal mountain ranges, which in some areas drop precipitously to the sea, ring the shore and form large watersheds; snow trapped at high elevations in winter melts in spring, drains into river systems, and eventually dis-charges into the ocean, usually, as dilute, tongue-like plumes. In shallow coastal areas, such as the eastern Bering Sea, river discharges results in extensive areas of dilute coastal water; whereas, in areas where the sea floor drops off sharply, such as off the Columbia River, this results in surface lenses of dilute water that, depending on coastal current, may

turn northward or southward along the coast, or extend seaward over several
hundred kilometers. The high coastal mountain ranges affect the local winds,
which in turn affect the surface currents and other water movements in the
oceans.

Sea surface temperatures are largely a function of latitude and normally
follow seasonal climatic cycles ranging from subtropical conditions off
the southern California coast to arctic conditions off the coast of northern
Alaska, where ice is present from November to April. A marked departure
from normal seasonal temperature cycles occurs along the coast from southern
California to British Columbia where coastal upwelling occurs in late spring
and early summer bringing cold water at depth to the surface during the
period of maximum insolation; the resulting equilibrium temperatures reduce
the annual range of temperatures in this area to that of more subtropic
regions, and temperatures are much lower than mid-ocean conditions at the
same latitude. Furthermore, the circulation in the Gulf of Alaska changes
markedly the general latitudinal temperature distributions. Thus, general
surface conditions in the area under study are due to a number of factors:
inshore coastal dilution caused largely by runoff and associated with the
continental shelf; the extension of coastal dilution seaward beyond the
shelf; the presence in northern areas of ice, which not only affects surface
but subsurface temperatures; seasonal surface heating and cooling due to
isolation; the balance of evaporation and precipitation; and, the presence,
in the southern part of the area, of upwelling, as well as prevailing and/or
day to day varying ocean and tidal current conditions.

Tides are of small amplitude in the open ocean, but may sometimes show a
range of 10-12 meters in certain areas of the coastline, and, especially,
in sounds, narrow straits, and inlets. Although modified in amplitude and
nature of progression by reflection, friction, and Coriolis force, there
are two basic types in the North Pacific. The dominant type is the mixed
tide, with predominantly two high and two low waters per day, and there
are several areas which exhibit a mixed tide with predominantly one high
and one low water per day; irregularities in the two types also occur. Along
the coast there is an interesting northward progression of specific tidal
phases from California to Bering Strait. Tidal currents exhibit most of
the same irregularities that are associated with tidal heights, in that
they do not repeat themselves exactly at any one given place; further, speed
and direction of the tidal currents depend upon local features, as well as,
the range of tide. In the near-shore regime, the tidal currents are of
the reversing type, setting in one direction during half the tidal cycle
and in the opposite direction during the other half of the cycle; but
offshore, away from the influences of the coastal boundaries, the tidal
current progressively changes direction through all directions of the
compass. These rotary currents do not exhibit periods of slack water, but
periods of maximum and minimum currents associated with high and low tide.

Non-tidal ocean currents are driven through the action of local as well as
large scale wind stress on the sea surface. The presence of the Aleutian
low pressure system in conjunction with the physical restraint imposed by
land boundaries establishes in the Subarctic Pacific Region, generally north

of lat 40°N, a cyclonic circulation northward of the Kuroshio system. It
is the transpacific eastward flow at the southern boundary of this cyclonic
circulation, the Subarctic Current System, that is the major source of the
surface flow in the northeastern Pacific Ocean. And it is the divergence
of this current, off the Washington, British Columbia, and southeastern
Alaska coasts, as it impinges on the western margin of the North American
continent, that is the main influence on environmental conditions in the
area we are concerned with here. The northward extension of this flow
along and through the Aleutian-Commander island arc, the Alaska Current
System, has a modifying effect on conditions in the western Pacific Ocean
and eastern Bering Sea. The southward extension of this flow along the
Oregon and California coasts, the California Current, interacts with not
only local upwelling, but an underlying countercurrent, the California
Undercurrent, and high variable conditions occur.

The diversity of planktonic forms and their diel migrations, patchy distri-
butions, and variability in abundance make plankton studies difficult and
costly. However, such studies are basic to any investigation of living
marine organisms. Dominant phytoplankton and zooplankton forms in the
region have been identified and a general transregion homogeneity exists
in oceanic areas, but little is known of the transport of forms around the
region and the large gyres may be effective in maintaining discrete pelagic
plankton stocks. Plankton in coastal areas may vary considerably. There
is a possibility that quasi-permanent resident populations may exist along
the Washington-Oregon-California coast where seasonal north-south surface
flows may result in little net horizontal transport and the California
Undercurrent may serve to restore populations carried too far south by
surface flow in summer. Further, there are indications that confinement
of zooplankton as well as planktonic stages of marine fish and shellfish
occurs in local eddies or gyres such as in the Aleutian Islands and Bering
Sea shelf areas, thereby perpetuating species. Although such comments are
subjective, there is evidence that large abundances of zooplankton occur
at the coast-oceanic interface, generally indicated by the 32 °/oo isohaline,
which may have differential effects on pelagic and neritic forms. This
is especially true off the Washington-Vancouver Island coast (Favorite 1969a).

It is largely through knowledge of oceanic conditions that we will be able
to understand and predict coastal conditions. At the present time, a great
deal of emphasis is being devoted to coastal zone management and monitoring
of coastal conditions; this work is necessary and should continue, however,
the primary objectives of such studies should be to predict conditions--not
merely to observe them. Obviously, not only the gradual, but the sudden and
often catstrophic changes in coastal conditions are the result of changes
and fluctuations in the onshore flow and the associated changes in physical,
chemical, biological, and geological oceanographic conditions.

1. Geology

The continental margin may be separated into three geographical regions
(Figure 35), each with distinctly shaped continental terraces, and trending
at approximately right angles to each other: 1) southeast, 2) southwest,
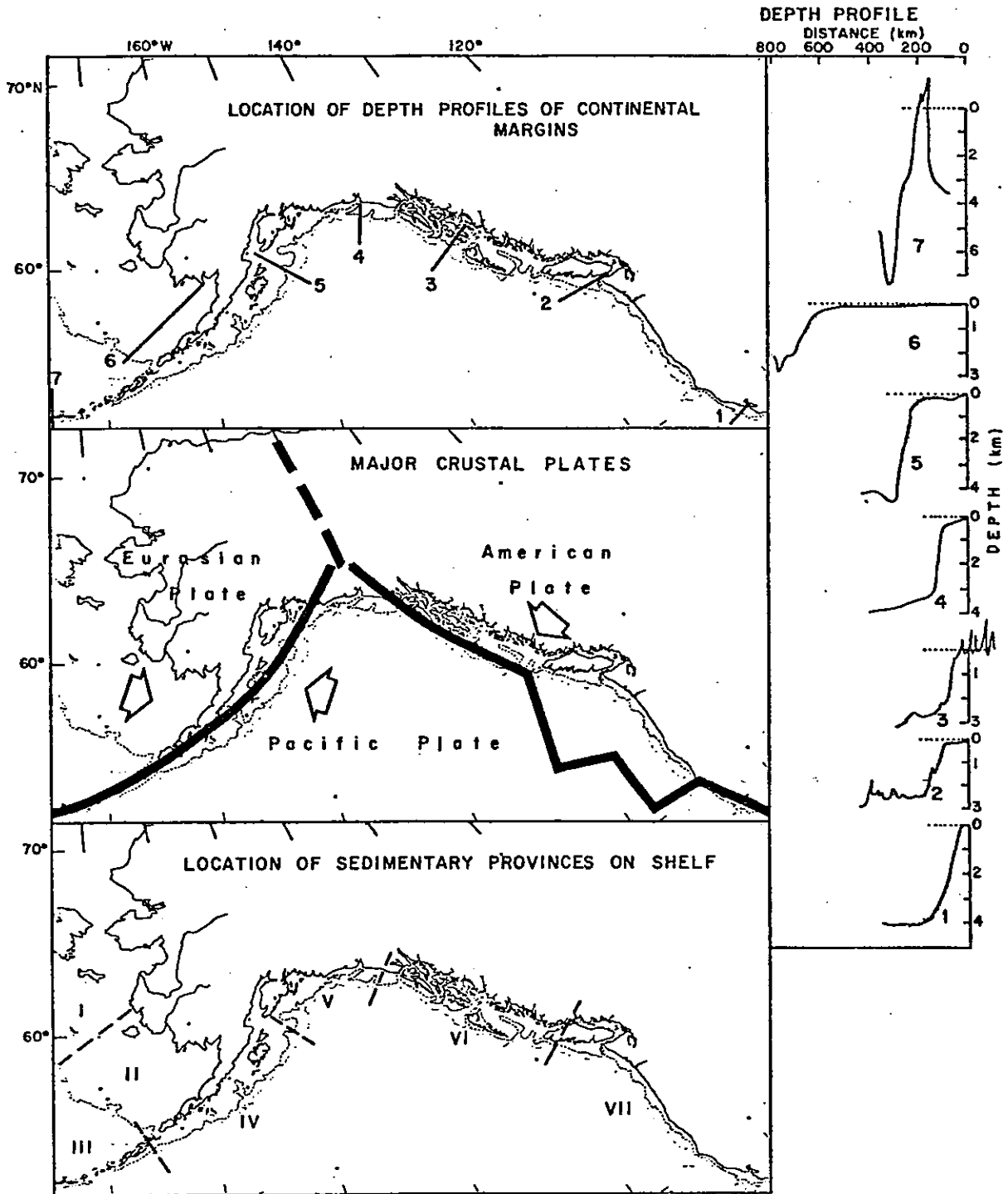
Figure 35. Profiles of the continental shelf and slope and the general extent of the Eurasian, Pacific and American plates.

and 3) northwest. Profiles 1 and 4 on the right-hand side of Figure 35
indicate transition zones where the slope extends downward directly to
the deep sea floor in the absence of continental rise. The southeast region
extends from Cape Mendocino, California, northward to Cape St. Elias,
Alaska (profiles 2 and 3). Its continental shelf has a characteristically
narrow to average width, the continental slope descends to about 2,500 m,
and the relatively large continental rise extends offshore down to a nearly
flat, volcanic-peaked, abyssal plain at 4,000 m whose only significant
relief is the northwesterly trending chains of volcanic seamounts.

The main structural trend changes direction at nearly right angles near
Cape St. Elias, and from there the southwest region (profile 5) extends
along the Aleutian island arc system. The width of the continental shelf
increases moderately off Cook Inlet, but gradually becomes narrowest along
the volcanic Aleutian Islands (profile 7). The significant change in the
shape of the continental terrace of this region is the great depression of
the Aleutian Trench which extends about twice as far below (to 7,300 m) the
main sea floor (4,200 m) as the continental rise of the southeast region
rises above (to 2,500 m depth). Both these regions are rimmed with a series
of parallel coastal mountain ranges whose trend is also offset at right
angles north of Cape St. Elias.

The northwest region is considerably different. The general terrace structure
is present, but the shelf is extremely broad, one of the widest in the world,
and the continental slope meets the flat floor of the Bering Sea with very
little evidence of a significant continental rise. Differences are also
apparent landward, because the series of mountain ranges that approach
normal to the eastern Bering Sea coast appear to terminate at the shore
without extending onto the shelf. Thus, the major topographic differences
in continental terraces among the three regions is the presence or absence
of a rise or trench at the base of the continental slope.

The two principal types of diverse topography--the stable, large, smooth,
shelf of the Bering Sea formed on Mesozoic formations; and, the active,
narrow, steep, valley-cut shelf of the Gulf of Alaska of Cenozoic age--will
have a variety of different sedimentary provinces. Distribution of bottom
sediments according to grain size (boulder to clay) is determined largely
by physical winnowing processes (wave action and currents) which are mainly
a function of topographic relief and distance from shore. Additional
differences in composition will be determined by the distribution of local
source materials from local shoreline bedrock, rivers, glaciers, volcanoes,
and benthic and pelagic calcareous shelled organisms. The abundance of
these components is determined by local rates of supply.

Seven provinces may be identified along the continental shelves from Bering
Strait to San Francisco that show similar sequences of grain size and
composition on similar topographic features but differ slightly from one
location to the next along the coast. The number of definable provinces
decreases offshore as does the grain size of sediments, because the coarser
fractions of the shelf have many more easily measurable and recognizable
differences. The deep sea sediments range from fine silts on the continental

slope to red or brown clay on the deep ocean floors and are differentiated
mainly by their minor biogenic components. In the Bering Sea, diatoms and
silicious sponge spicules in sediments increase to about 30% in the deep
basin, but in the northern and western Gulf of Alaska abyssal plain, sedi-
ments are largely brown clay. The continental rise in the eastern Gulf of
Alaska is differentiated by a slightly silicious (10 to 30%) component, and
continental slope sediments are typically muddy sand and sandy mud down to
about 500 m, sandy mud and mud down to 2,000 m, clayey mud deeper than
2,000 m. The rate of sedimentation in the Bering Sea is from 2 to 30 cm/1000
yr on the shelf, reaches a maximum on the lower slope of 40 cm/1000 yr, then
decreases to 6-10 cm/1000 years on the deep sea floor.

The part of the continental terrace that has the most diverse variety of
bottom sediments is the continental shelf. Since grain size is determined
by the amount of energy in the oceanic regime, grain size is largest near
shore in the breaker zone usually varying from boulders to coarse sand.
Beyond the breaker zone in the near shore environment at depths of 30 to
50 m fine sands or silty and muddy sands are present. On the outer shelf
on plateau elevations, generally coarse sediments are present; and an abrupt
transition occurs on the flanks of adjacent sea valleys--for troughs contain
sandy mud, mud, and clayey mud. Much of the middle and outer shelf contain
relic sediments of coarser nature that were deposited as the sea level rose
and the breaker zone migrated across the shelf toward the present shoreline.

Two of the seven shelf provinces are found in the Bering Sea. All sediments
are strictly terrigenous but this large shelf may be subdivided by grain-size
differences. The northern half of the shelf north of St. Matthew Island
contains a large oval region of fine silt. Some old Soviet charts suggest
a topographic depression here, but later U.S. charts do not. Thus, the
fine grain deposit appears to be a result of very weak near bottom currents.
Farther south between St. Matthew Island and the Alaska Peninsula in the
second province, the typical grain size is coarse silt over the large mid-
shelf expanse. This coarser silt extends northward around the fine silt
province, making it quite a distinct feature. A relatively higher concen-
tration of manganese, silica, and iron in the norther province tends to
support the existence of a more quiescent depositional environment. The
third province of the Aleutian Islands shelf is the narrowest and deepest,
therefore coarser sediments prevail which are also uniquely different by
their volcanic composition. Three more provinces are found in the western,
northern, and eastern Gulf of Alaska. The western province has an average
to moderate width shelf and extends from Unimak Island eastward to the
Kenai Peninsula including Kodiak Island. Pebbly, gravelly sand is found
on banks, but additional components are shell fragments and volcanic
material from nearby islands. Near the shelf edge, intermittent concen-
trations of calcareous foraminifera are found and volcanic ash is common
in the silt fractions being borne by prevailing northwest winds from
primarily Mount Katmai. Sand, silt, and clay are found on depressions
from 80-150 m deep such as in Shelikof Strait, but Cook Inlet is much sandier
because of its relatively swift tidal currents. Local hydrogen sulfide
points to a high supply rate of organic material in some depressions south

of Kodiak Island.. The northern province runs from the Kenai Peninsula to
Cape Spencer and has an average shelf width, and a number of valley
depressions similar to its western neighbor. This area is characterized
by the absence of coarse material due to the large supply of glacial fines,
particularly from the Copper River. Gray mud and clayey mud is present on
all relief. In the eastern or sixth province the outer continental shelf
is narrow because of the islands of the Alexander Archipelago. Coarse
clastics occur, similar to those of the narrow Aleutian Island shelf, but
volcanics are absent and fines are few. Muddy sediments are present in
deep narrow channels between islands and over the extensive inland shelf
of Queen Charlotte Sound. The shelf once again broadens south of Cape
Cook on Vancouver Island to an average width, demarking the seventh province.
This is a fairly typical shelf area with sands and silts, and even a
slightly coarser relic zone of gravel occurs near its edge.

2. Circulation

Even though the continental shelf and slope has continuity throughout
the Subarctic Region, it is convenient to discuss flow in relation to three
areas: Washington-Oregon-California coast, Gulf of Alaska, and Aleutian
Islands-Bering Shelf. Conditions in the first two areas differ as a
result of the onshore divergence of the Subarctic Current and all flow out
of the Gulf of Alaska does not move through eastern island passes into the
eastern Bering Sea.

The limitations of the following discussions can be pointed out at the
outset. As indicated earlier, onshore surface flow in the northeastern
Pacific Ocean diverges near lat 50°N sending one branch, the Alaska Current
System, northward and the other, the California Current System, southward
along the coast. The nature of this divergence and its exact location is
not known, nor has the phenomenon per se been studied. There is evidence
that the divergence actually occurs at the coast rather than well offshore,
as typically illustrated in schematics and atlases. The best evidence of
this is the lack of any indication in the distribution of properties in
the offshore areas of any vertically upward displacement of colder water
from depth, downstream of the divergence area required by continuity of
mass.

For over a half century, there has been speculation that this divergence
zone shifts southward to lat 45°N during winter as a result of the expansion
of the Aleutian low pressure center in the Gulf of Alaska from November to
January. Calculations of wind-stress transport also suggest this southward
shift, but there is little tangible evidence of drastic shifts in flow
characteristics. There is increasing evidence that short-term changes in
wind-stress can significantly alter basic oceanic flow patterns; but,
because the winter increase in wind-stress in this area does not occur for
a sufficient duration to alter the field of mass to any great depth in the
ocean, the actual changes in surface flow are difficult to assess without
direct observations--and none are available. To our knowledge, there have
been no attempts to resolve this dilemma. Favorite (1964b) showed that

drift bottles released in midocean from lats 41-50°N were recovered along
the Washington-Oregon coast (Figure 36); a proposal to release in this
area during one summer and one winter period, drifting, telemetry buoys
tracked by satellite (Buoy Experiment in the Eastern Pacific - BEEP) was
made by the NMFS Standing Committee on Oceanography in 1972, but the study
remains unfunded. Thus, we are only generally aware of the nature of flow
impinging on the west coast of North America, and there are numerous other
local features that we understand in less detail.

   a   Washington-Oregon-California Coast

The dominant non-tidal flows in the area are associated with upwelling,
river discharge, and the California Current System--including the Undercurrent.
Comparison of a typical summer sea surface temperature plot derived from
observed data with typical satellite imagery (Figure 37) indicates the
complexity of the actual temperature regime and the difficulty of deriving
specific resource-environment relations from fragmentary in-situ observations.
Upwelling occurs from late spring to fall when northerly winds along the
coast, associated with the Eastern Pacific high pressure system, cause a
net offshore transport of surface water which is replaced by upwelled sub-
surface water, not only colder, but higher in nutrient content; this re-
distribution in mass also reinforces southward flow in the coastal regime.
In winter, southerly winds, associated with the Aleutian low pressure system,
result in an onshore transport; and water piling up along the coast results
in a northward coastal surface current, generally referred to as the
Davidson Current which may be merely a surface penetration of the California
Undercurrent. This flow is fairly well documented by drift bottle studies
(Figure 38) (Burt and Wyatt 1964; Ingraham and Hastings 1976) and is apparent
in distributions of surface salinity. Although river discharges flowing
seaward through the Strait of Juan de Fuca lose much of their identity as
a result of tidal and turbulent mixing in the deep strait, dilute waters
from coastal rivers such as the Columbia and Sacramento are easily discernable
and clearly alter conditions in the coastal regime (Figure 39). In spring,
the Columbia River plume is marked by a sharp color interface as it protrudes
seaward, aided by the upwelling process, in a tongue-like configuration. As
indicated by salinity measurements, it can be detected several hundred
kilometers from the coast. In winter, the usual summer distribution of
dilution (caused by runoff) normal to the coast, is swept northward toward
the Strait of Juan de Fuca (Figure 40).

The California Current System consists of the California Current, the cold,
dilute surface flow out of the Subarctic Pacific Region off the west coast
of the United States, and the California Undercurrent, which flows northward
along the coast at depth. The former is largely a continuation of the
southern component of the Subarctic Current and the latter, a continuation
of northward flow along the western margin of the North American Continent,
sometimes referred to as the Davidson Current when it extends to the surface.
Even though there are a number of papers in which the presence of the
California Undercurrent has been reported (Dodimead et al 1963; Wooster and
Reed 1963; Ingraham 1968; Cannon et al 1975; and Favorite et al 1976) and
geostrophic currents of 5-15 cm/sec indicated, there are no current measure-
ments that permit ascertaining a net flow.
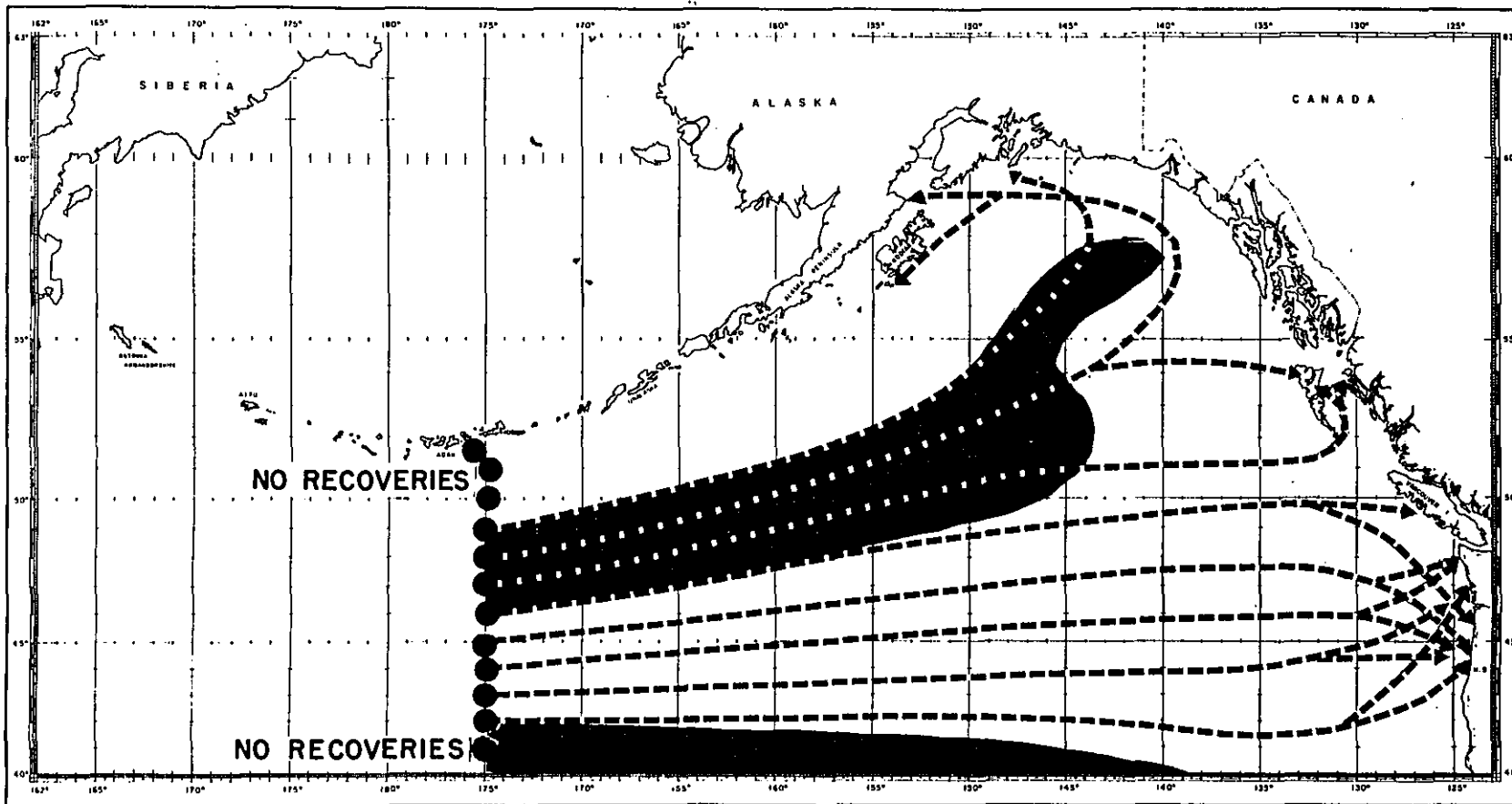
Figure 36. Drift bottle experiment showing the broad north-south
release zone along long 175°W from which recoveries were
made along the Washington-Oregon coast. Dark area
originating at 175°W between 45-50°N indicates area of
subsurface temperature-minimum stratum and the dark area
south of 42°N indicates water of Central Pacific Region
(from Favorite 1975).

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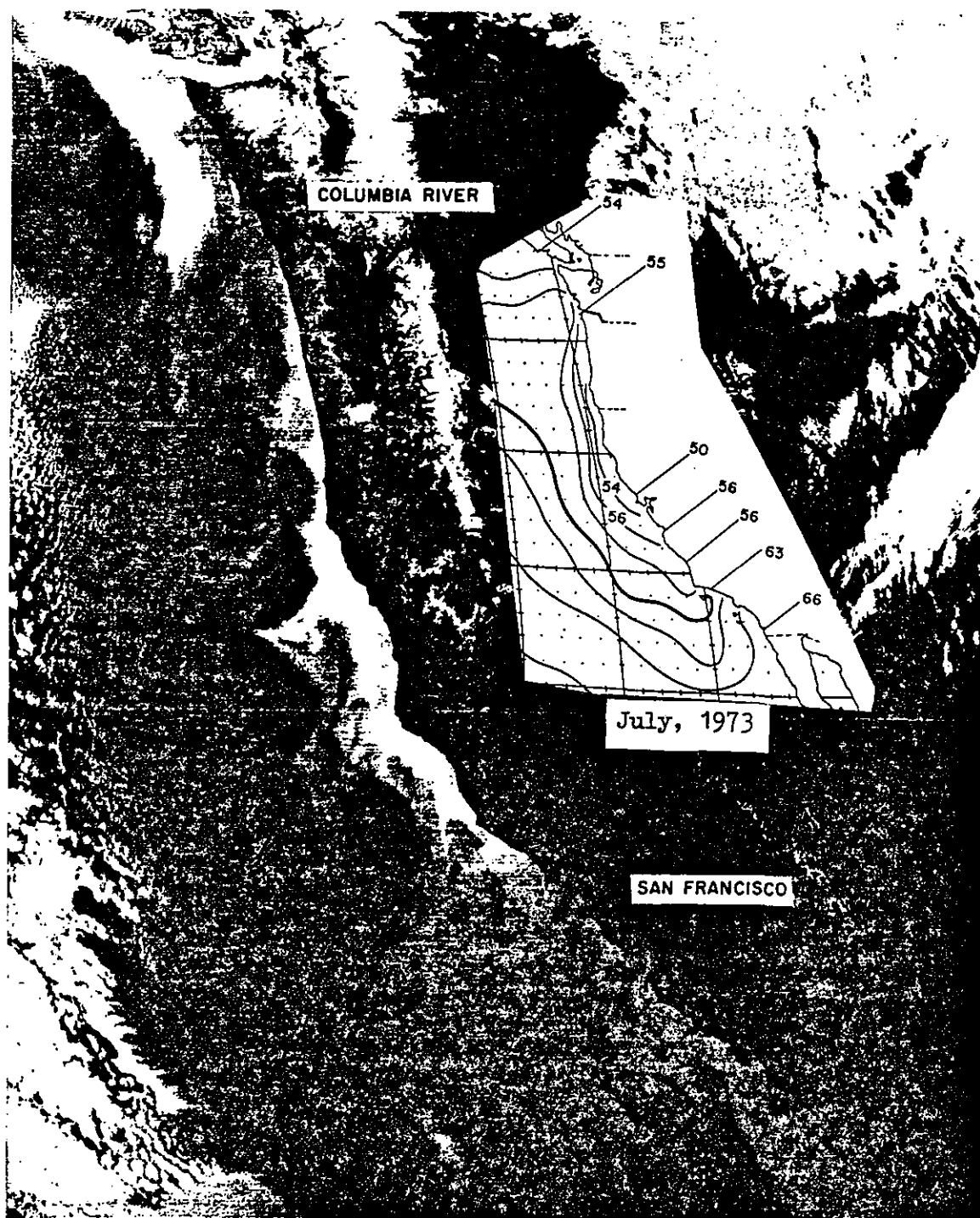
Figure 37. Comparison of typical summer sea surface temperature plot
derived from shipboard data with a non-synoptic example of
satellite imagery (white areas reflect cold temperatures)
indicating inadequacy of the former to denote precise
conditions or optimum fishing locations based on empirical
resource-temperature relations.
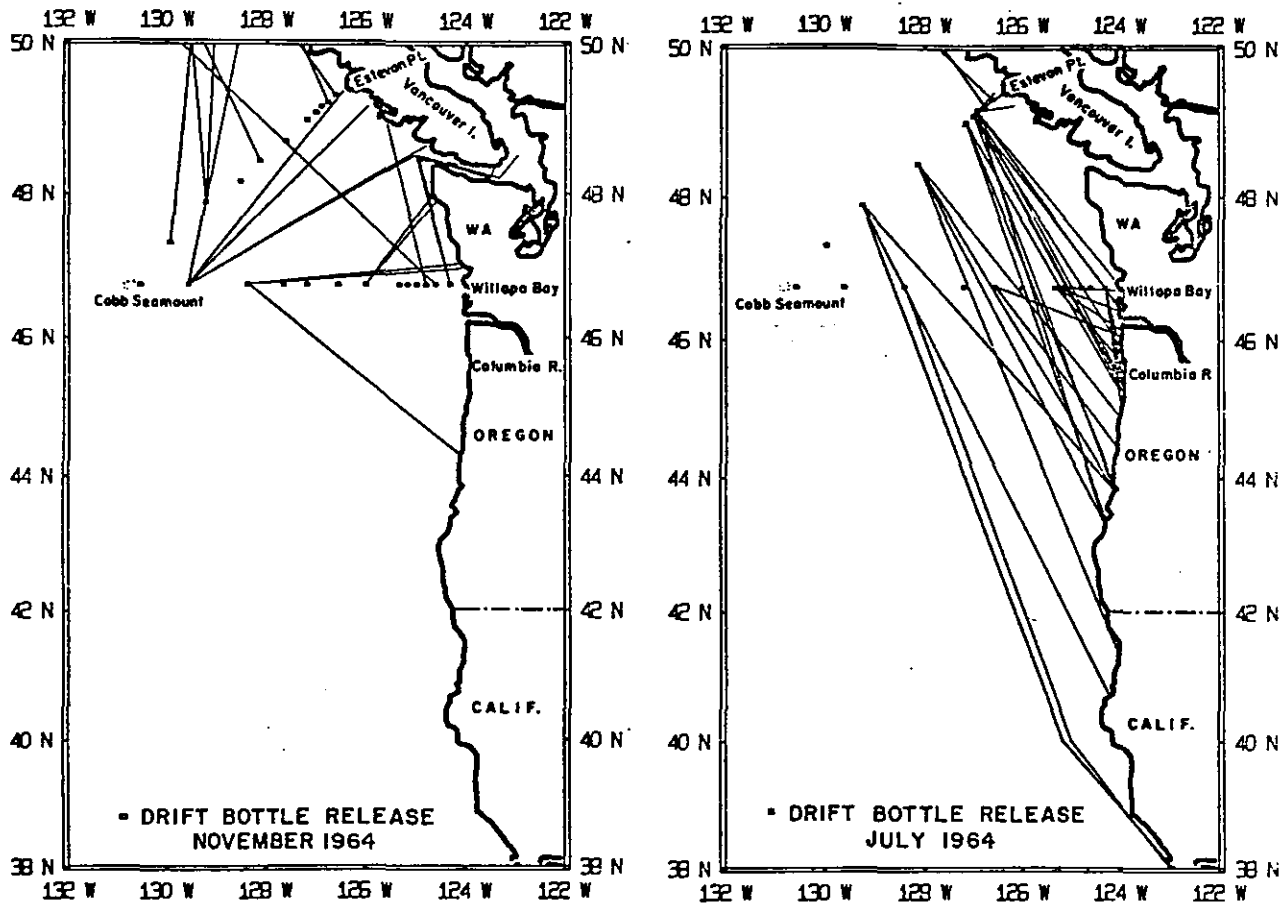
Figure 38.   Drift bottle experiment indicating northward surface flow
along the west coast of North America during winter and
southward flow during summer (from Ingraham and Hastings
1976).
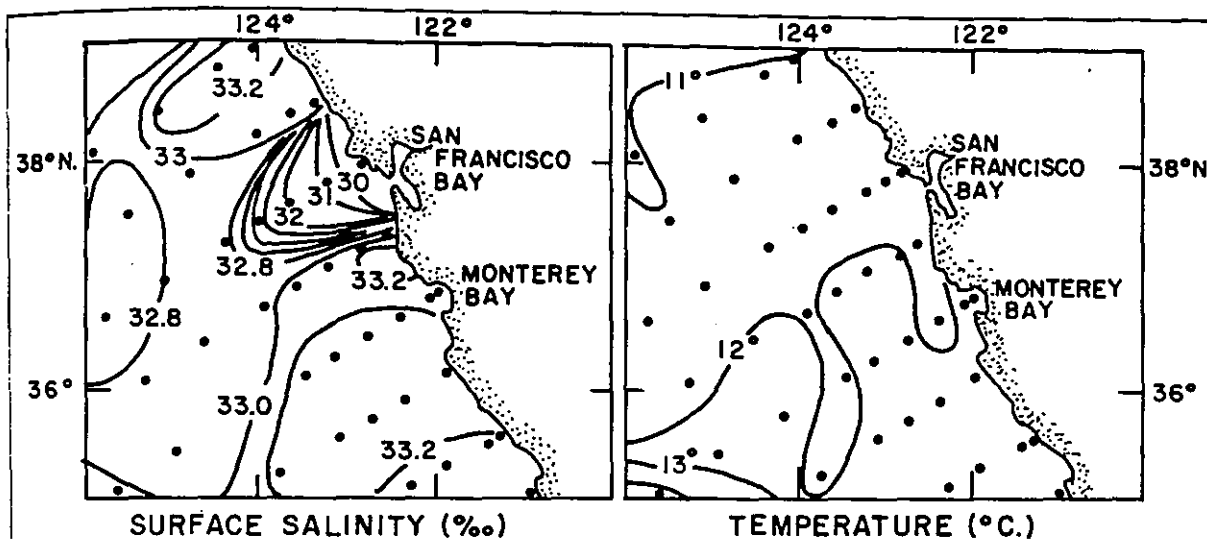
Figure 39. Horizontal distribution of surface salinity (°/oo) off
San Francisco indicating the seaward extent of dilution
from runoff originating largely from the Sacramento River
and the absence of any definition of the dilute plume in
the surface temperature distribution (from Favorite 1969a).
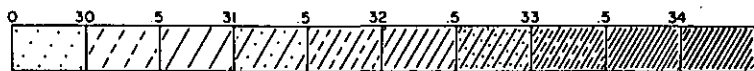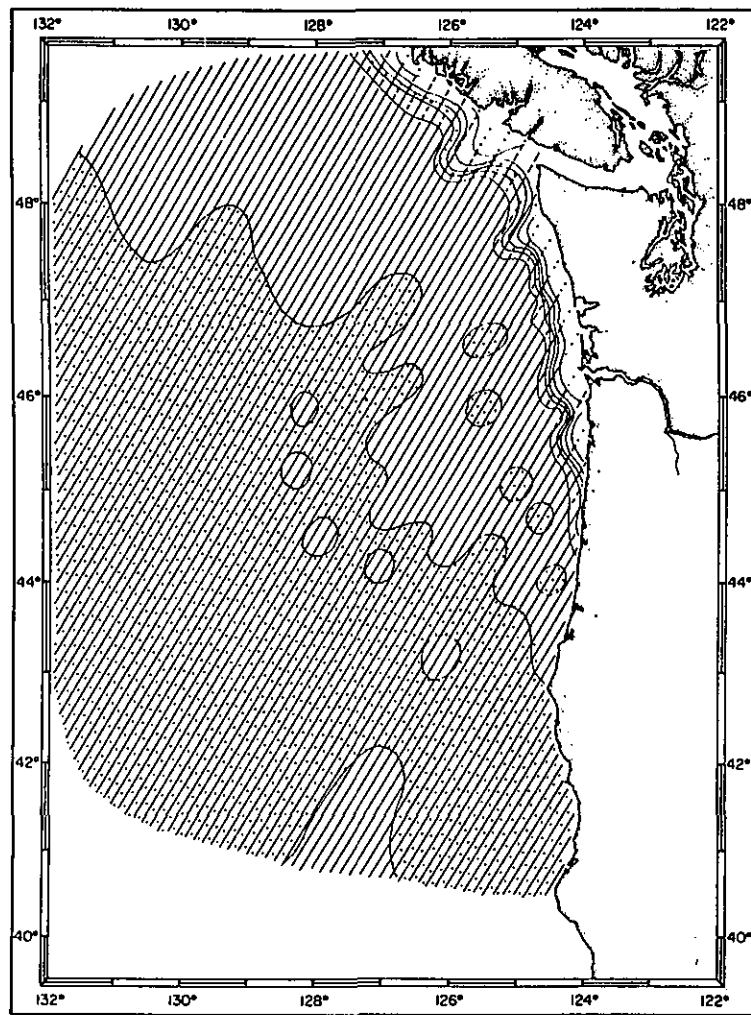
SALINITY % WINTER 0 m
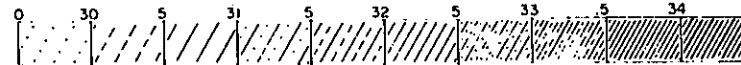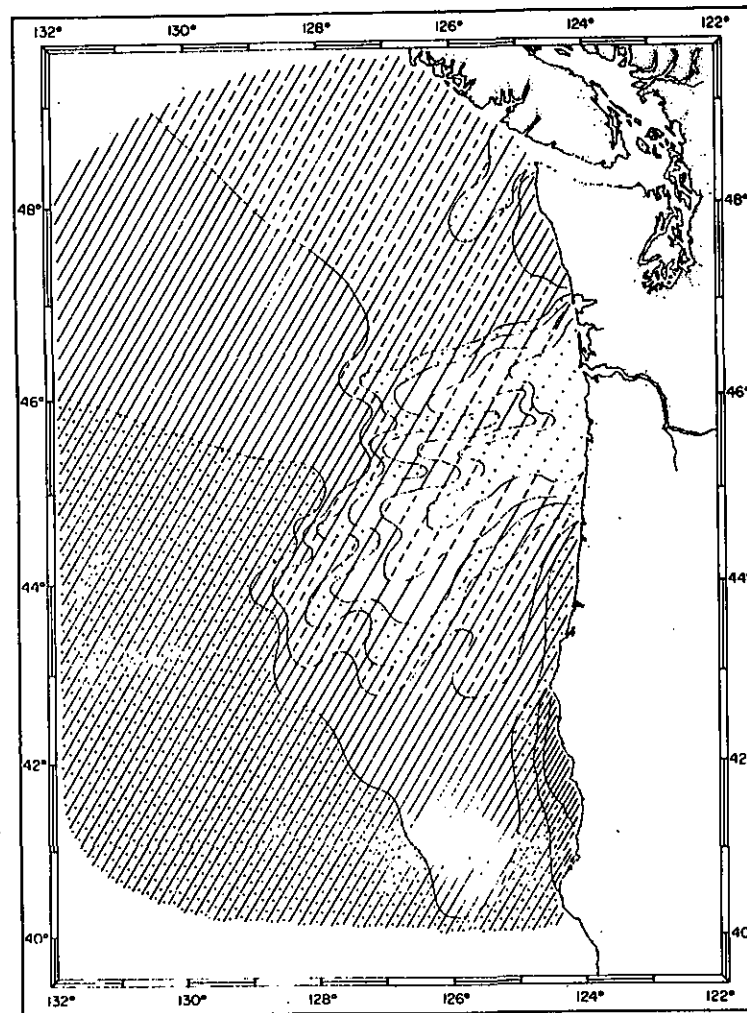
SALINITY %₀ SUMMER 0 m

Figure 40. Horizontal distributions of surface salinity (°/oo) indicating
a northward flow of dilute water along the Washington-Oregon
coast in winter and an offshore discharge normal to the coast
in summer (from McGary 1971).

Drift bottle studies have clearly shown that a northward flow approximately 100-200 km in width extends along the coast from off southern California northward into the Gulf of Alaska during winter. This flow, which extends to over 1,000 m depth, effectively confines southward flow in the California Current to offshore areas. Coastal dilution is restricted to inshore waters and advected northward along the coast; this is particularly noticeable off the Washington coast where the isohalines in the Columbia River plume trend northward and are confined close inshore in winter. This flow merges with the northern component of the Subarctic Current near the Queen Charlotte Islands and, perhaps in part, is aspirated northward by requirement of this flow. In addition, the southerly winds along the coast associated with the Aleutian low pressure system serve to pile up water along the coast, thereby altering the distribution of mass in the surface layer in such a manner to favor increased northward flow.

In summer, variable northerly winds associated with the eastern Pacific high pressure system drive surface water at the coast seaward causing intermittent upwelling in most areas from Vancouver Island southward. This alters the distribution of mass in the surface layer so as to favor southward flow along the coast, and this process, operating in conjunction with a northward shift in the offshore divergence indicated by wind-stress data, results in a general southerly to southwesterly flow along the coast which is markedly evident in the trend of isohalines in the Columbia River plume. Although these conditions suppress the northerly surface flow extant along the coast in winter, only surface conditions are affected; and the northward flowing California Undercurrent still exists below the surface layer (<300 m), contributing to the complexity of flow in this area. Thus, although there is a seasonal reversal of surface flow along the coast, there is a constant northward flow along the continental slope.

b. Gulf of Alaska

The dominant environmental features in this area are the Alaskan Gyre, a region of vertically upward divergence denoted as the Ridge Domain and the cyclonic peripheral flow, the Alaska Current system, that is manifested at the western side of the gulf as a boundary flow over the continental slope with speeds up to 100 cm/sec. Although the temperature regime in the surface layer is marked by seasonal heating and cooling there is a remarkably constant temperature regime of 4-5°C at the shelf break that is several degrees higher than surface conditions in the winter. Salinity conditions are affected by seasonal runoff and an excess of precipitation over evaporation, resulting in a wide-spread dilute surface layer.

There are five sources of water in the area: (1) water from the coastal watershed--snowmelt or runoff, (2) water from the west coast of North America advected northward in the California Undercurrent, (3) water from the Transition Domain, the surface layer representing a mixture and subsequent alteration of the Kuroshio and Oyashio Water Masses, (4) water from the Okhotsk Sea-Kuril Island-Kamchatka area carried across the Pacific by the Subarctic Current, and (5) water from the intermediate and deep layers moving upward in the Ridge Domain (Figure 41).
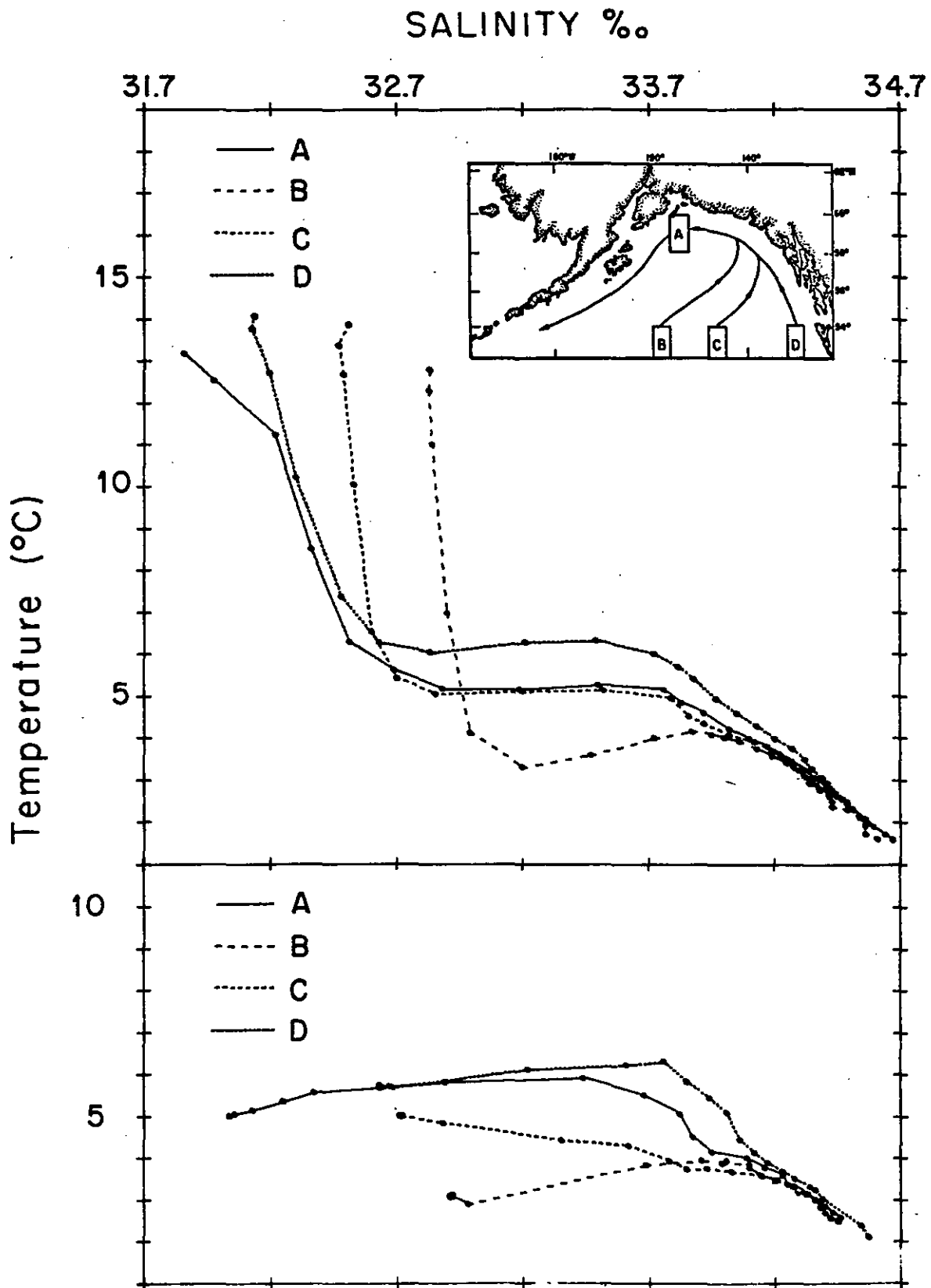
Figure 41. Mean summer and winter temperature-salinity (T-S) relations
at standard depths showing characteristics of the various
water masses funneling into the Gulf of Alaska (all station
data averaged in indicated 2x2° quadrangles—from Ingraham
et al. 1976).

here is evidence in the western Gulf of Alaska that westerly flow over
the continental slope is subject to pulses of seaward discharges (Favorite
1975) that could carry eggs and larvae from the shelf area into the central
part of the Gulf of Alaska and, thus, away from a shallow substrate required
for development of groundfish. The vertical temperature structure in this
area indicates a discrete offshore flow of warm water between 150 and 200 m
that could also affect larval drift (Figure 42). There is also evidence
of a major divergence of this flow southward of the eastern Aleutian
Islands (Figure 43). As much as a third of the flow in the upper 1000 m
of the water column (Favorite, 1967) turns southward as the Aleutian Current
and recirculates around the Alaskan Gyre; the remainder flows westward
along the south side of the Aleutian Islands.

c. Aleutian Islands-Bering Shelf

The broad continental shelf at the western edge of the Gulf of Alaska tapers
markedly along the western end of the Alaska Peninsula but extends across
Unimak and other local Aleutian Island passes as far west as Samalga Pass,
the first pass in the Aleutian Islands having a sill depth of 200 m or more.
The Aleutian Islands are surface manifestations of a portion of the Aleutian-
Commander island arc, which extends westward from the Alaska Peninsula
almost to the east coast of the Kamchatka Peninsula. Surface environmental
conditions in this general area have been discussed in the section on
salmon (III, B). Except for surface exchanges through island passes, the
land barrier imposed by the island arc serves as the northern edge of west-
ward flow out of the Gulf of Alaska. Of the 39 passes (Favorite 1967),
only 14 have an area greater than 1 km^2 and a sill depth of at least 200 m
(Table 3). Only 5 of these openings (Amukta, Amchitka, Buldir, Near, and
Kamchatka) are large enough to have a significant influence on flow, and
only 2 (Near and Kamchatka) extend to 2000 m or more. Amutka Pass (also
Yunaska) is important because this is the first major interruption in
westerly flow below 200 m, however, only a small portion of westerly flow
(less than 5%) escapes northward into the Bering Sea. The maximum depth
of Amchitka Pass is in excess of 1000 m (although only a small width
attains this depth) and roughly 25% of the flow turns northward here. Except
for the shallow bottom topography at the southeastern side of the pass, which
diverts westerly flow southward around Amchitka Island, and a southeastward
component of flow usually present at the northwest side of the pass, a
considerably greater northward flow would occur here. However, the existing
flow is significant because it extends northward for a considerable distance
along the east side of Bowers Ridge (Favorite and Ingraham 1972). Buldir
Pass is wide but the deep portions have a limited area and opposing flows
restrict the northward loss to less than 5%. However, Near Pass is not
only wide but deep, and over 50% of the westward flow turns northward into
Bering Sea at the eastern side of this pass. The remainder of the westward
flow (less than 10%) is turned southwestward and loses its identity after
impinging on the Western Subarctic gyre near 50°N, 165°E (Favorite 1974).
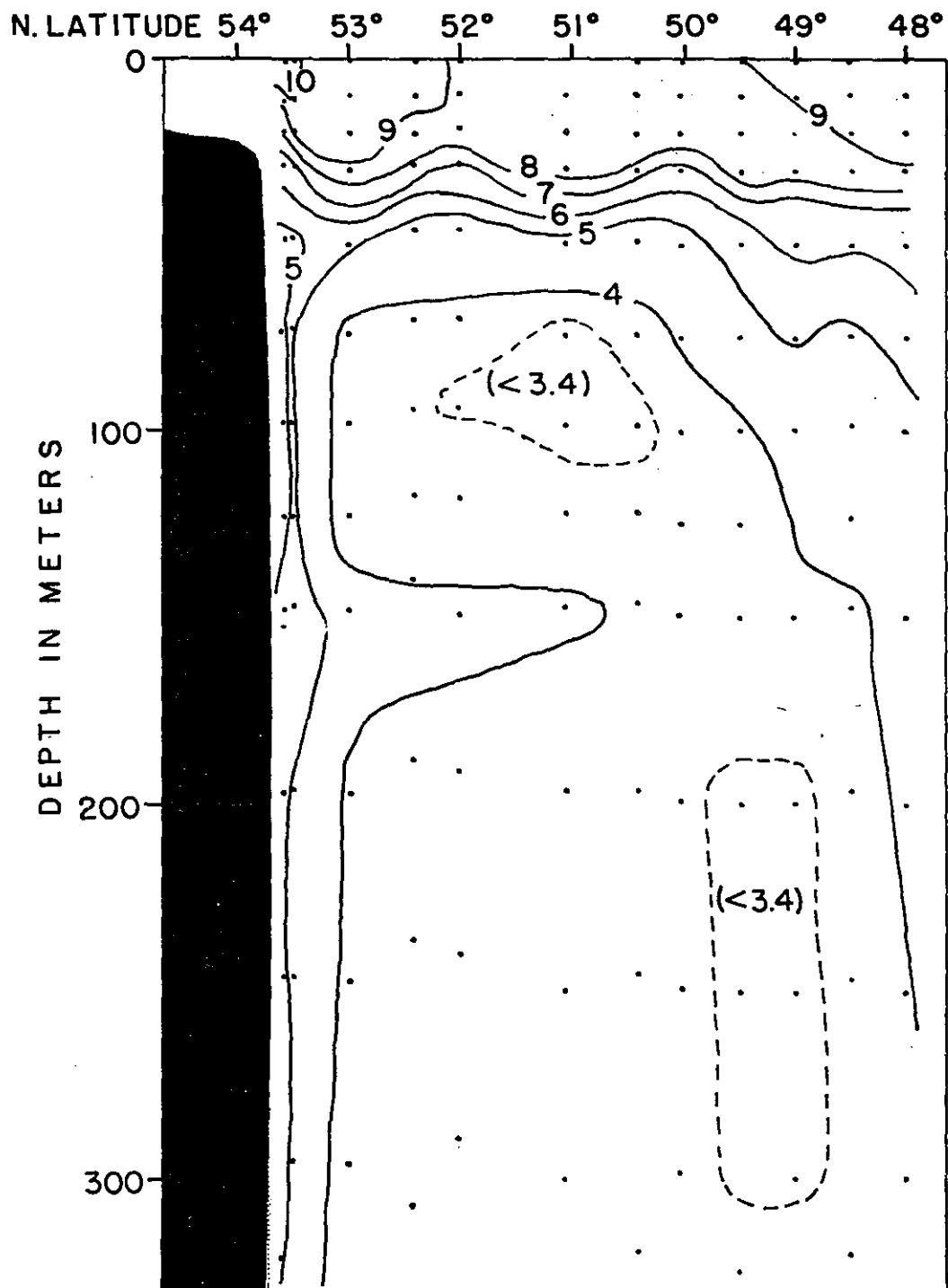
Figure 42. Vertical section of temperature (°C) structure at long
165°W (July 1959) indicating seaward protrusion of 4°C
isotherm at 150-200 m that could affect the distribution
of coastal demersal ichthyoplankton (from Favorite 1967).
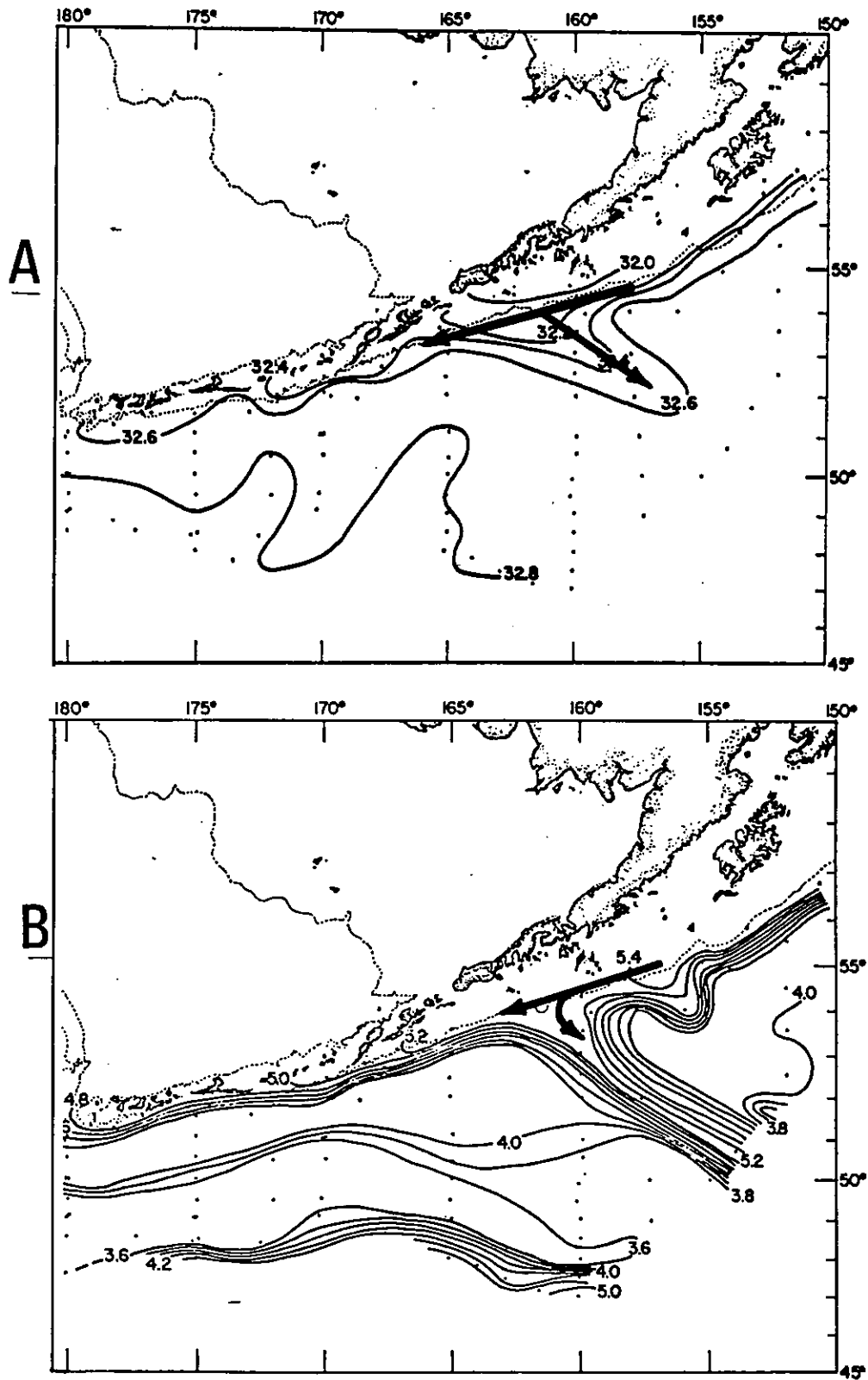
Figure 43. Horizontal distribution of (A) surface salinity and (B) distribution of temperature (°C) in the temperature-maximum stratum (approx. 200 m) in summer 1959 indicating recirculation of coastal flow eastward around the Alaskan Gyre; arrows simulate flow (from Favorite 1964a).

Table 3. Cross-sectional areas and sill depths of major passes or straits through the Aleutian Islands (from Favorite 1967).

Location	Pass or Strait[1]	Area $(m^2 \times 10^6)$	Max. sill depth (m)
163°W–165°W			
Alaska Peninsula to	1 False	0.1	35
Krenitzin Islands	2 Unimak	0.9	60
	3 Ugamak	0.2	45
165°W–170°W			
Tigalda Island to	4 Derbin	0.1	50
Herbert Island	5 Avatanak	0.4	80
	6 Akun	0.1	10
	7 Akutan	0.2	70
	8 Unalga	0.1	45
	9 Umnak	0.2	50
	10 Samalga	3.9	200
	11 Chuginadak	1.0	210
170°W–175°W			
Herbert Island to	12 (Herbert)	4.8	275
Atka Island	13 (Yunaska)	6.6	457
	14 Chagulak	0.3	65
	15 Amukta	19.3	430
	16 Seguam	2.1	165
	17 Amlia	0.1	25
175°W–180°			
Atka Island to	18 Atka	0.2	35
Amchitka Island	19 (Oglodak)	0.1	5
	20 Fenimore	0.2	35
	21 Tagalak	0.1	35
	22 Chugul	0.6	85
	23 Umak	0.1	20
	24 Little Tanaga	0.1	30
	25 Kagalaska	0.1	25
	26 Adak	0.5	60
	27 Kanaga	0.1	30
	28 Tanaga	3.6	235
	29 (Ogliuga)	0.1	10
	30 (Kavalga)	0.3	55
	31 Amchitka	45.7	1155
180°–173°E			
Amchitka Island to	32 Oglala	0.8	25
Attu Island	33 (Rat)	0.6	15
	34 (Kiska)	6.8	110
	35 Buldir	28.0	640
	36 Semichi	1.7	105
173°E–163°E			
Attu Island to Kam-	37 (Near)	239	2000[2]
chatka Peninsula	38 Komandorski	3.5	105[2]
	39 Kamchatka	335.3	4420[2]

The significance of westward flow south of the Aleutian Islands (i.e.,
the Alaskan Stream) confined along the south side of the island arc, is
that it provides a uniform environment as well as a transport for demersal
eggs and larvae, exiting the Gulf of Alaska at depths below the continental
shelf (>200 m) and eventually requiring a substrate, to the eastern
Aleutian Islands and Bering Sea shelf through Amukta Pass, to the central
Aleutian Islands and Bowers Ridge (and possibly the eastern Bering Sea)
through Amchitka Pass, and to the western Aleutian Islands through Buldir
and Near Passes. The extensions of the various components of these flows
may also serve as transport for eggs and larvae of populations to the
Aleutian Island area. For example, drift bottles released north of
Amchitka Pass at the eastern edge of Bowers Ridge not only were recovered
on the Pribilof Islands but also on eastern Aleutian Islands (Figure 44),
suggesting an anticyclonic gyre that could return plankton back to central
Aleutian areas. Similar gyres appear to be associated with all major
passes. There is also a complex flow pattern in the vicinity of Attu
Island that has been revealed by drift bottle studies which also suggest
that planktonic eggs and larvae released from this area and subsequently
requiring a shallow substrate for development are not all necessarily
carried into an oceanic regime where they are either consumed or die
(Figure 45).

There are several dominant oceanographic features in the eastern Bering Sea.
The so-called Golden Triangle area at the southeastern corner of the Bering
Sea basin--generally considered to be the area between Amutka Pass, the
Pribilof Islands and Unimak Pass--historically has been a productive Pacific
halibut area and within the last decade a highly productive walleye (Alaska)
pollock (Theragra chalcogramma) area. Although False and Unimak Passes
permit exchange of water from the North Pacific Ocean and Bering Sea, these
are shallow areas (<75 m) with limited net flow and similar water properties.
However, northward flow in Samalga and Amukta Passes carries the warmer,
more dilute, nutrient-rich slope water (below 200 m) of the Gulf of Alaska
into contact with the Bering Sea slope water moving eastward along the
north side of the Aleutian island arc. Mixing and stirring at the eastern
side of the passes--where a net northward flow is assumed to occur (net
southward at the western sides), and a subsequent marked reduction in speed
(from over 50 cm/sec to roughly 5-10 cm/sec) occurs after leaving the
influence of the momentum in the Alaskan Stream--result in a nutrient-rich,
ocean environment that gradually attains vertical stability north of the
passes. The stability of the water column permits normal biological
processes to become reestablished and a markedly high production to occur.
The general eastward flow along the continental slope of the Aleutian island
arc in the Bering Sea is also enriched by vertical movement of deep water
as a result of shoaling in the southeastern Bering Sea near Unimak Pass.
Although most of the slope water in this area is constrained by the land
mass below the continental shelf to turn northwestward, there is no restriction
other than frictional forces at and shoreward of the shelf break to restrict
flow in the surface layer. Various drift bottle studies verify this surface
flow (Favorite and Fisk 1971).
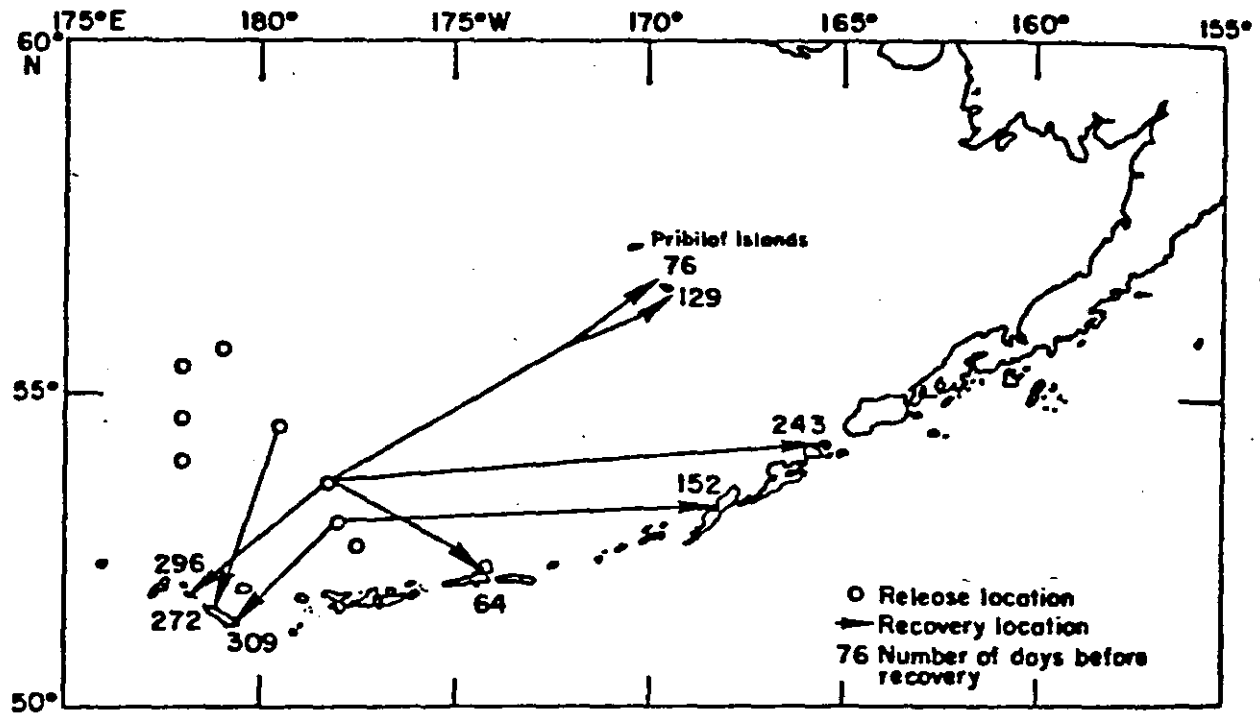
Figure 44. Drift bottle experiment north of Amchitka Pass (long 180°)
indicating northeast drift to the Pribilof Islands and
southerly drift to eastern Aleutian Islands.
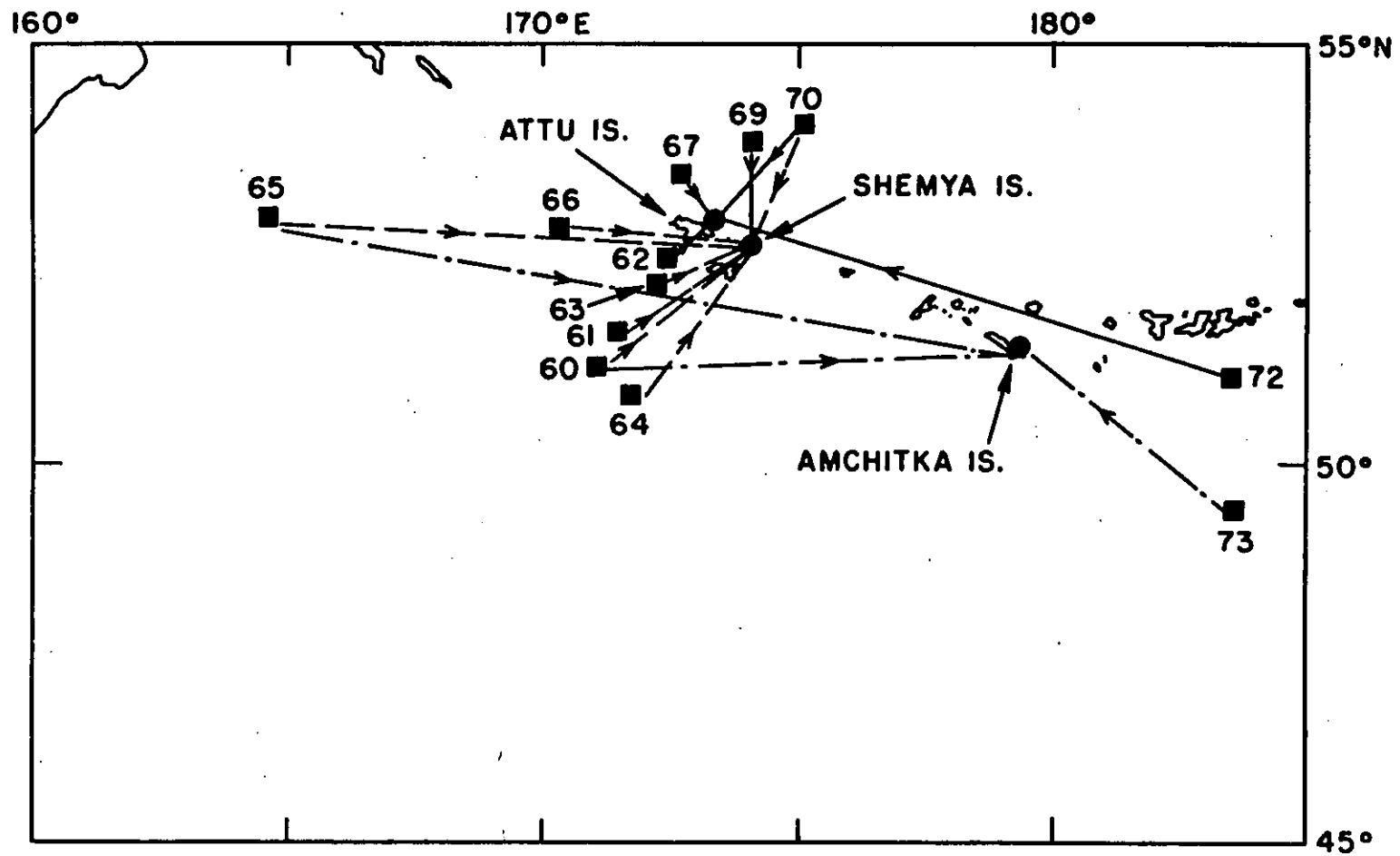
Figure 45. Selected drift bottle releases indicating drifts toward
Attu Island (from Favorite and Fisk 1971).

3. Current Systems

Sea maps of geostrophic current usually differ somewhat from actual flow because geostrophic currents, calculated from the distribution of mass, are subject to many conditions that are rarely fulfilled in typical usage--and, thus, are only generally representative of the actual flow. Flow relative to a reference level, assumed to be motionless, is obtained and calculations are usually based on properties in water columns of up to 1,000 m depth, or more. Major differences occur in the upper 300 m of the water column, but seasonal fluctuations occur only in the upper 100 m; thus, results primarily reflect the basic relatively permanent water structure of the lower layer rather than transient surface flows. The southward shift of zonal flow with depth complicates the task of accurately ascertaining actual surface flow. Geostrophic currents reflect relatively steady-state conditions and have characteristically low speeds (5-10 cm/sec) except near the shelf edge where closely spaced observations indicate speeds of 50 cm/sec. Calculations of volume transport around the Gulf of Alaska indicate a flow of 10 Sv* (referenced to 1,000 db) and 20 Sv (referenced to 2,000 db) indicating that significant flow extends to and below 2,000 m.

Perhaps a more representative indication of actual flow is afforded by calculations of wind-stress transports. This technique requires no information from the water column (i.e., station data), but only gross distributions of sea level pressure from which winds are estimated, and wind-stress at the sea surface is translated into water transport. Integrated total transports derived from mean sea level pressure (1951-1970) indicate marked changes in circulation in the northeastern Pacific Ocean (Figure 46). In summer, the eastern Pacific atmospheric high pressure system expands into the Gulf of Alaska and establishes a pattern of anticyclonic winds that results in zonal divergence near lat 50°N and a weak (<5 Sv) circulation in the Alaskan Gyre. In winter, the Aleutian low pressure system intrudes and the associated pattern of intense cyclonic winds results not only in a general reversal of wind direction but also an increased circulation. During winter, the Alaskan Gyre transport increases almost an order of magnitude, and the zone of meridional divergence shifts to near lat 40°N. The magnitude of wind-stress transport in winter is approximately one-third higher than generally accepted geostrophic transport but, on the other hand, the wind-stress transport in summer is considerably less than the geostrophic transport. Because it would require more than a few months, perhaps up to a year or more, for the distribution of mass to adjust to such surface stresses, these conditions suggest that an equilibrium or steady-state exists between the two extremes, and that marked differences in winter and summer surface flow occur that are not obvious in geostrophic current patterns. The above conclusion is supported by anomalous patterns of surface properties in relation to geostrophic flow, as well as by data on sea level during different seasons. An indication of the equilibrium conditions in this area is evident in a vertical section across the Gulf of Alaska (Figure 47) in which temperatures are plotted on density surfaces (sigma-t) and the vertical flow is indicated.

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* Sverdrup = 1 x 10^6 m^3/sec
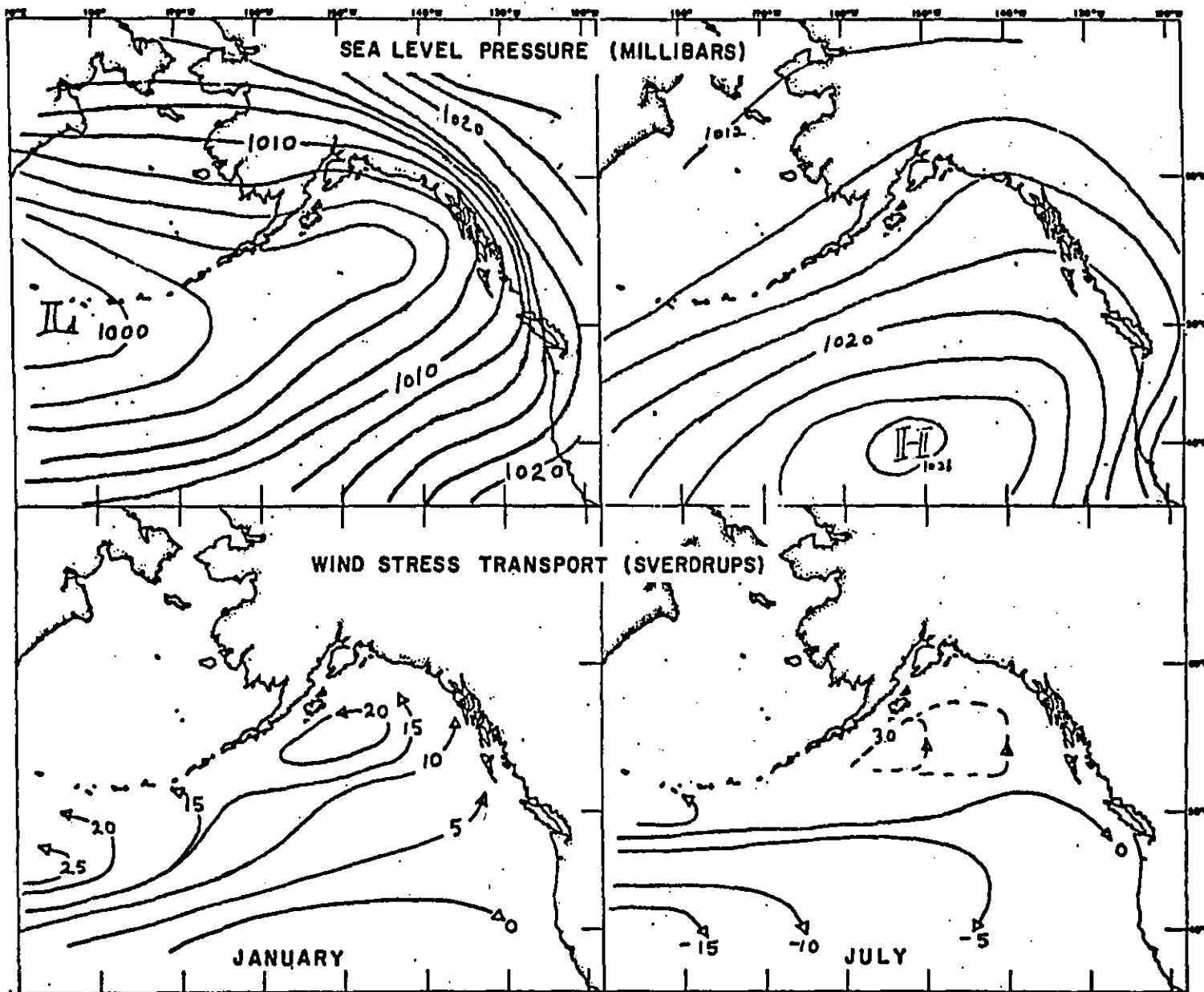
Figure 46. January and July mean (1950-71) sea level pressures (mb) and resultant wind-stress transports (Sv) indicating increase in transport in winter.

TEMPERATURE (°C) VS SIGMA-T AND SALINITY(‰) VS DEPTH (M).
OSHAWA-WHITETHROAT STATIONS, SPRING 1962
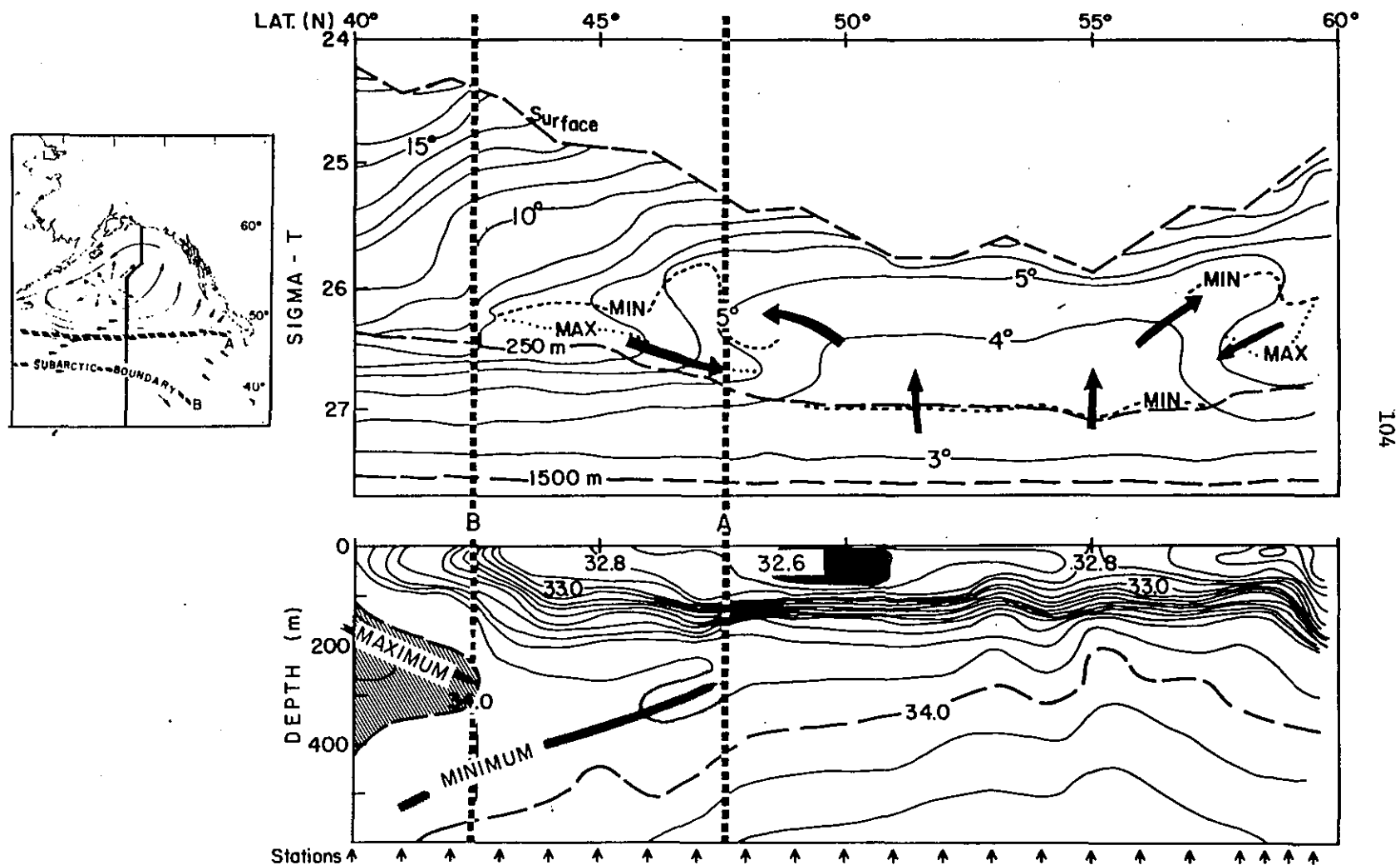
Figure 47. Vertical section of temperature (°C) on density (sigma-t)
surfaces and salinity (°/oo) versus depth across the Gulf
of Alaska, arrows indicate flow in both regimes. Line A
shows northern boundary of the salinity-minimum stratum
and line B the northern boundary of the salinity-maximum
stratum (Subarctic Boundary).

South of the center of the Alaskan Gyre there is a complex salinity structure (line A of Figure 47 indicating the northern extent of the salinity-minimum stratum and line B the northern extent of the salinity-maximum stratum). The area between lines A and B is considered the Transition Domain. Fluctuations in the boundaries of these two phenomena are indicated later (see Figure 80).

Normally, mean sea level decreases in winter because of reduced effects of heat and dilution on the specific volume of sea water; however, in the Gulf of Alaska, sea level data indicate anomalous increases in winter, even after adjustment for various factors (e.g., sea level pressure, heat, dilution) that can only be attributed to an increased slope of the sea surface caused by a proportional increase in cyclonic flow. The winter intensification of winds occurs primarily from November to February, and the marked reductions in wind-stress in early spring relaxes forces that have piled up water along the coast, and this should result in an offshore flow of water. The reversal of winds along the coast in early summer accelerates this process of transporting dilute coastal water out into the offshore areas. This process should be evident in surface conditions, and distributions of surface salinity discussed in a subsequent section clearly show extensive seaward penetrations of dilute coastal water. This offshore wedge of coastal dilution is evident only to depths of 200-250 m and, in order to exist, must cause a separation in the eastward surface flow of the Subarctic Current; the offshore flow apparently fulfills mass requirements for divergence normally provided by a vertical upward movement downstream because such an adjustment would result in higher salinities rather than lower ones. It's apparent that if an active onshore flow occurred near the surface, it would be impossible for the zone of coastal dilution to exist offshore. From 300 to 600 m the eastward flow in the Subarctic Current is relatively unaffected by this surface phenomenon, and divergence occurs right off the coast in the Queen Charlotte Island – Vancouver Island area. This new concept, suggesting a markedly different onshore flow at depth in the Subarctic Current in this area indicates a great complexity and inherent variability of conditions, and should provide the basis for the discovery of new resource-environment relations.

The California Current System consists of the California Current, the cold, dilute surface flow out of the Subarctic Pacific Region off the west coast of the United States, and the California Undercurrent, which flows northward along the coast at depth. The former is largely a continuation of the southern component of the Subarctic Current and the latter, a continuation of northward flow along the western margin of the North American Continent, sometimes referred to as the Davidson Current. Drift bottle studies have clearly shown that a northward flow of approximately 100-200 km width extends along the coast from southern California northward into the Gulf of Alaska during winter. This flow, which extends to over 1,000 m depth, effectively confines southward flow in the California Current to offshore areas. Coastal dilution is restricted to inshore waters and advected northward along the coast; this is particularly noticeable along the Washington coast where the isohalines in the Columbia River plume extend northward and are confined close inshore. This flow merges with the northern component of the Subarctic Current near the Queen Charlotte Island and, perhaps in part, is aspirated

northward by requirement of this flow. In addition, the southerly winds along the coast associated with the Aleutian low pressure system serve to pile up water along the coast altering the distribution of mass in the surface layer in such a manner to favor increased northward flow. In summer, variable northerly winds associated with the eastern Pacific high pressure system drive surface water at the coast seaward causing inter-mittent upwelling in most areas from Vancouver Island southward. This alters the distribution of mass in the surface layer so as to favor south-ward flow along the coast, and this process, operating in conjunction with a northward shift in the offshore divergence indicated by wind-stress data, results in a general southerly to southwesterly flow along the coast markedly evident in the trend of isohalines in the Columbia River plume. Although these conditions suppress the northerly surface flow extant along the coast in winter, only surface conditions are affected and the northward flowing California Undercurrent still exists below the surface layer (<300 m) con-tributing to the complexity of flow in this area. Thus, although there is a seasonal reversal of surface flow along the coast, there is a constant northward flow along the continental slope.

The Alaska Current System originates in the eastern Gulf of Alaska where the California Undercurrent and the northern component of the Subarctic Current merge. The large area of generally homogenous conditions at equivalent depth levels that are sufficiently different from conditions in either current justify denoting the origin of a new system. Northward flow in this system moves westward around the periphery of the coast and isolates the Alaskan Gyre, part of the flow continuing westward out along the Aleutian Islands-Commander island arc, part flowing northward through the shallow passes and ameloriating conditions in the southeastern Bering Sea.

The Bering Current System is characterized by the cyclonic flow around the Bering Sea basin. Northward flow through the major passes in the Aleutian-Commander island arc is swept eastward north of the island arc to the precipitous shelf edge in the eastern Bering Sea. Here a small surface component protrudes northeastward over the shelf edge toward the coast, but the main flow is diverted northwestward along the continental slope to the vicinity of Cape Navarin; there, another small surface component turns northeastward toward Bering Strait, but the main flow turns southwestward along the Siberian coast.

4. Domains

Because of the complexity of flow and the difficulty of defining the boundaries of the somewhat continuous although merging flow, the concept of denoting areas having rather distinctive characteristics as specific domains is helpful in describing environmental conditions. The eastern Subarctic Pacific Region can be characterized by four offshore domains; Transition, Upwelling-California Undercurrent, Dilute, and Ridge Domains. The general extent of these domains can be shown in relation to the salinity distribution at 100 m (Figure 48); of course other properties and other depths could also be used.
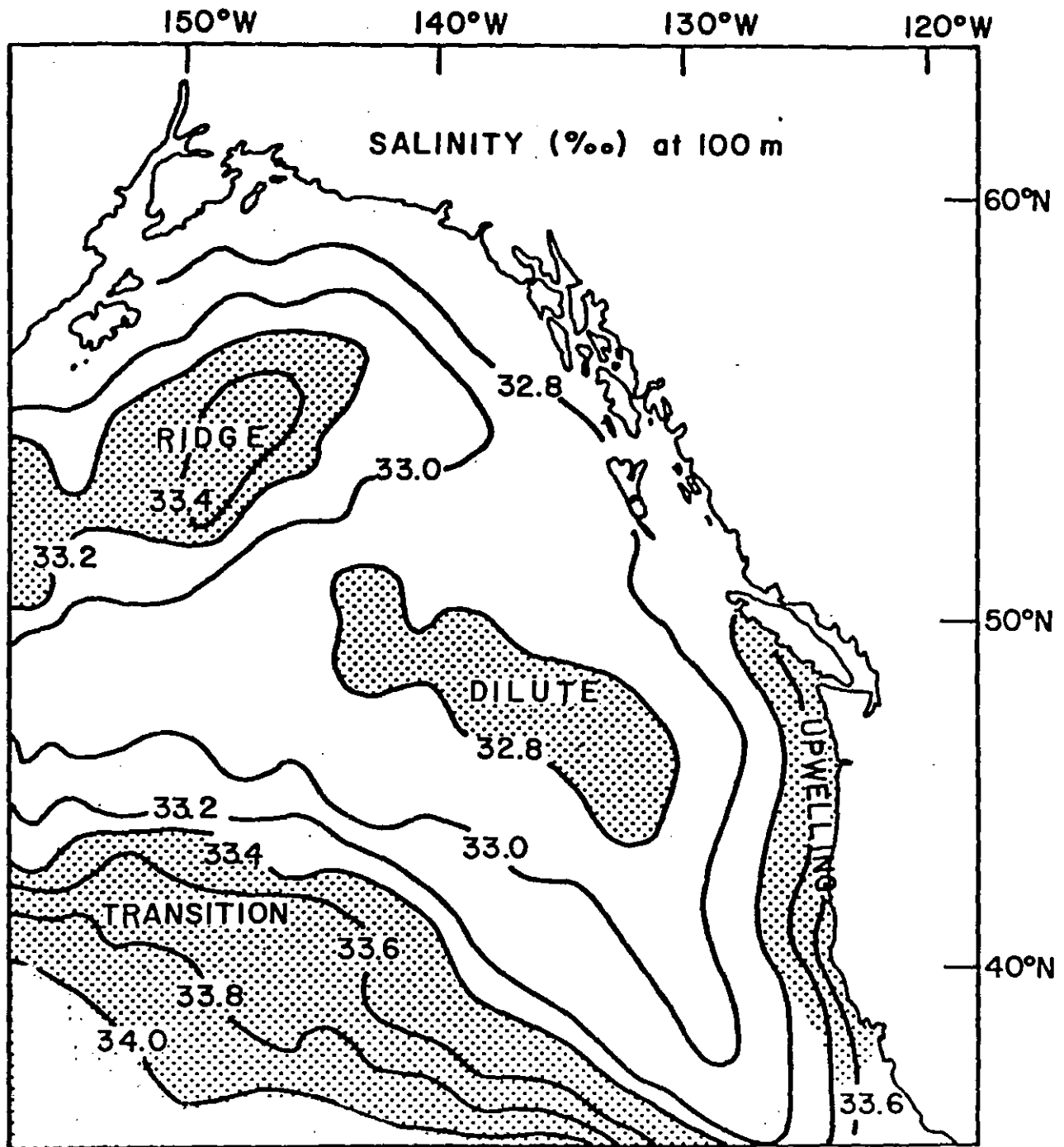
Figure 48. Eastern Subarctic Pacific Domains as indicated by mean salinity distribution at 100 m (all station data averaged by 2x2° quadrangles).

The Transition Domain represents the transition zone between subarctic and subtropic water as a result of mixing of Oyashio and Kuroshio waters and subsequent modification by conditions in the Subarctic Current and North Pacific Drift. The high salinities are associated with high temperature and high dissolved oxygen values.

The Upwelling and California Undercurrent Domains, whose individual character- istics at this depth level are difficult to separate and whose geographic location are somewhat similar, have lower temperatures and dissolved oxygen values than in the Transition Domain. Water properties in the California Undercurrent Domain are derived from conditions in sub-tropical areas.

The characteristic surface dilution and its apparent deep penetration permits easy isolation of the Dilute Domain from the surrounding domains. Although the dilution has a coastal origin, there is considerable lateral mixing in this domain along the offshore boundaries.

The vertical upward divergence of deep water, discussed previously, results in the Ridge Domain being characterized by deep or bottom water of high salinity but low temperature and dissolved oxygen values.

5. Water Properties

There is little question that a coastal domain exists, but its boundaries are difficult to define because of the variable nature of the coastline and the extensive runoff. One might select the edge of the continental shelf, but this boundary is not only seaward of the areas of complex tidal currents characteristic of inshore waters, but also not seaward enough to contain the vast plumes of dilute water extending seaward from rivers, straits, and sounds. Nevertheless, there is a coast-oceanic boundary--and it is a highly variable one; the gradients of its properties are largely poorly defined because of lack of observations and the various complex forces that control onshore and offshore flow.

Because of the complexity and variability of conditions as well as the paucity of data in time and space, it is necessary to revert to mean data in 1x1° quadrangles and to show only gross features of temperature and salinity at the surface.

One of the best documented oceanographic conditions is sea surface temperature. There are numerous stations along the coast at which these temperatures are recorded--usually daily, and annual cycles of heating and cooling are evident; but, because most stations are in shallow, protected waters, the effects of local air temperatures are more noticeable than the secular changes in ocean temperatures which usually signal marked changes in distributions and ranges of neritic marine organisms. Turbulent mixing and stirring by tidal currents in narrow or shallow passages also disturb the homogenity of inshore surface temperatures, and rarely do coastal and inland sea maps of mean sea surface temperature show any details of temperature structure that might influence the location of recreational or commercial fishing. Rather, only gross monthly average temperatures over large areas are depicted.

There have been two documented surveys of coastal sea surface temperatures
using infrared techniques from aircraft. Monthly observations along flight
lines extending up to 100 km off the west coast of the United States from
Washington southward to California were obtained from U.S. Coast Guard
aircraft by U.S. Bureau of Sport Fisheries and Wildlife personnel from
1963-68. These clearly show gross areas and times of upwelling, but do not
afford the detail and continuity of inshore features obtained by flights
within 30 km of the coast in summer 1969 conducted by Oregon State University's
Albacore Central Project. The latter shows that interesting and anomalous
temperature conditions occur within linear distances of 10 km or less and
these features are most likely related to other oceanographic conditions
and processes--such as areas of convergence and divergence that could con-
centrate plankton or restore nutrients to the surface. Thus, as ocean
conditions are documented in greater detail it will become easier to relate
specific conditions to fishery problems. Satellite data also reflect complex
temperature patterns.

There are numerous oceanographic atlases that provide general ocean temperature
distributions. In addition, 10-day maps of sea surface temperature are
produced by the Canadian Weather Service (Esquimalt) and monthly maps are
produced by the NMFS Southwest Fisheries Center; both products are based
on near real-time reports from ships at sea, but do not provide the detail
that might be useful to inshore fishing operations. Data are woefully
inadequate along the west coasts of Canada and southeastern Alaska where
high runoff, deep embayments, inland sounds, and passages provide highly
variable coastal conditions not encountered along the relatively linear
southern coast with its limited rainfall.

Typical mean surface temperature conditions along the coast during winter and
summer (based on mean data averaged by 1x1° quadrangles) provide an indication
of the extremes encountered and to some extent the variability; only gross
features, however, are evident (Figure 49). Commencing from the California
coast where winter temperatures of 10°C occur near Cape Blanco and then
proceeding northward, temperatures decrease gradually along the open coast
to 5°C at the head of the Gulf of Alaska. The rather uniform progression
is not evident in inshore waters. In the Strait of Juan de Fuca and eastward
of Vancouver Island, temperatures of <6°C (2°C lower than offshore temper-
atures) occur, and temperatures near 0°C--associated with the formation of
ice along the shore, occur near Cape Spencer, and in Prince William Sound
and Cook Inlet. Cold water (<3°C) discharges out of Cook Inlet to the
north and south of Kodiak Island terminate the westward extent of the 5°C
isotherm. Westward along the south side of the Alaskan Peninsula, temper-
atures decrease to 2-3°C along the Aleutian Islands and the edge of the
continental shelf in the Bering Sea. However, over most of the continental
shelf in the Bering Sea, temperatures of -1°C or lower occur in the ice
fields.

In summer, surface temperatures along the coast increase from 5-10C$^{\circ}$. Up-
welling off Cape Blanco restricts summer temperatures to 14°C, although
farther offshore, temperatures of 18°C occur. Temperatures in the Strait
of Juan de Fuca are 4-5C$^{\circ}$ lower (11°C) than those seaward of, or inside,
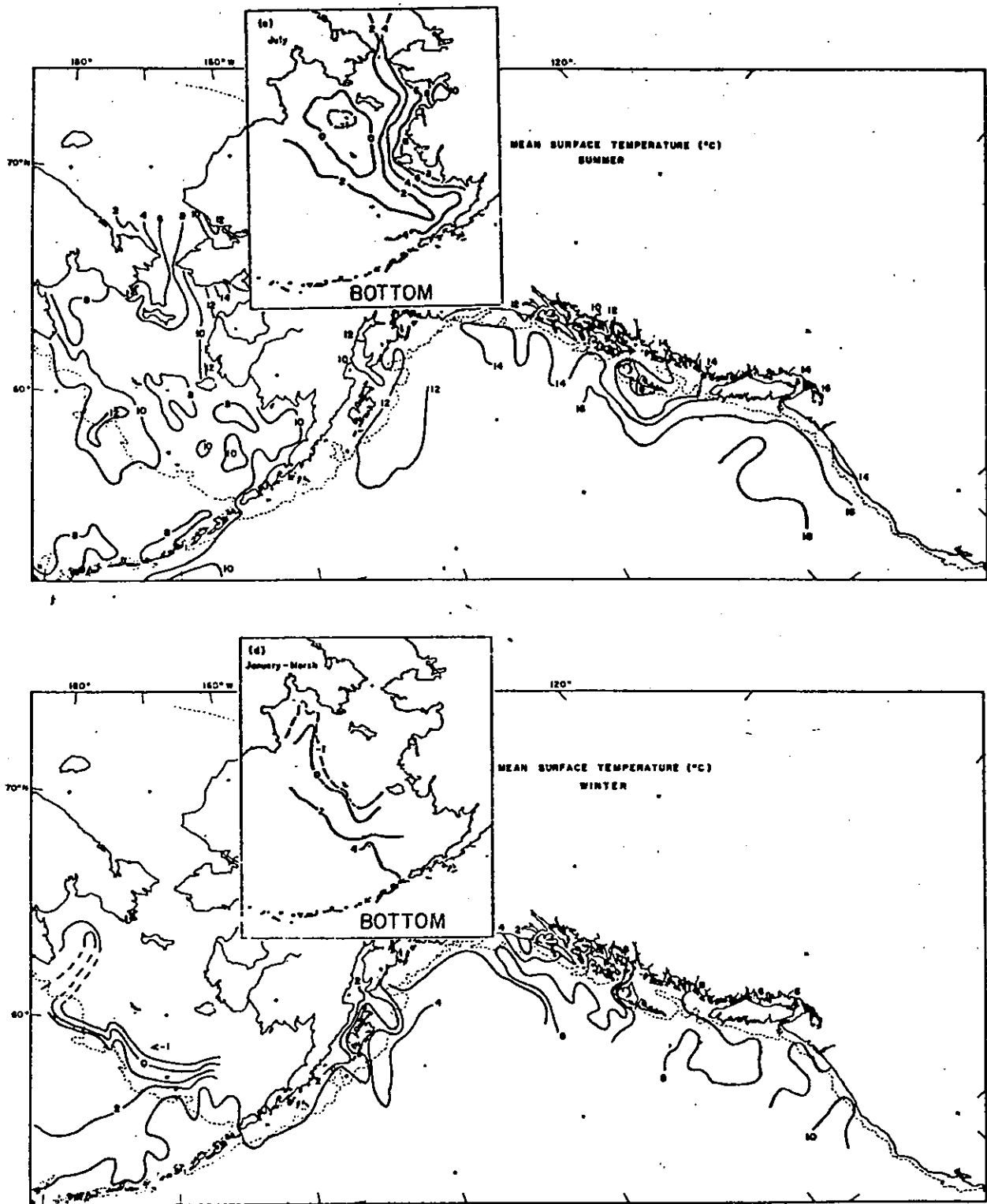
Figure 49. Horizontal distributions of winter and summer mean surface
temperature along the coast and winter and summer mean
bottom temperatures in eastern Bering Sea (all station
data averaged by 1x1^o quadrangles).

Puget Sound; and maximum coastal temperatures, 16°C, occur seaward of the
Queen Charlotte Islands where little or no upwelling is evident. The
band of low temperature, 14°C, offshore of the Queen Charlotte Islands is
unexplained, but appears to be associated with the discharge of cold water
from Dixon Entrance and southeastern Alaska's Alexander Archipelago. The
sinusoidal configuration of isotherms along the northeastern coast of the
Gulf of Alaska belies the uniform alongshore conditions usually depicted
in atlases in this area and indicates extensive offshore penetration of
coastal water. Conditions along the northwestern coast of the Gulf of
Alaska are dominated by the southwestward discharge north and south of
Kodiak Island of cold runoff out of Cook Inlet. The absence of ice and
the shallow depths over the eastern Bering Sea shelf permits a large annual
range of temperature, particularly in Norton Sound where seasonal temperatures
range from about -1.8 to 16°C.

One of the unique features of the Subarctic Pacific Region is the transpacific
distribution of low salinity water. Although there is a net surplus of
precipitation over evaporation throughout the region there is also an ex-
tensive discharge of runoff from coastal mountain ranges. A general salt
balance is maintained by vertically upward transports of saline water from
depth, largely in the Ridge Domain and in the central Bering Sea.

There are a number of rivers along the coast from Baja California to the
Chukchi Sea, and the five largest in terms of discharge are the Yukon,
Columbia, Fraser, Kuskokwim and Copper Rivers (Figure 50). Latitudinal
differences notwithstanding, maximum flows occur in June--except in the
Copper River where maximum occurs in July; and minimum flows occur in March--
except in the Columbia River where the minimum occurs in January. It is
interesting to note that mean flow in the Columbia River in June is five
times that in January, whereas, mean flow in the Yukon River in June is
20 times that in March; the abrupt change in the latter flow is due to ice
conditions.

Although many coastal stations that record sea surface temperature also record
surface salinity, this property is far more difficult and costly to measure
than temperature--and observations are proportionately fewer. Dilution
in spring, as a result of runoff and local precipitation, is readily apparent,
but salinity data are representative of only general local conditions and
change considerably with tidal and other local flow phenomena.

Up to the present time, salinity data were obtained almost exclusively through
monitoring or research programs; and, although sufficient to define general
distributional patterns, they are grossly inadequate to ascertain conditions
that could influence fishing operations. This is unfortunate because many
frontal zones in the region are more easily detected by salinity distributions
than by temperature data because the seaward discharge of dilute coastal
water can only be dissipated by mixing and stirring with more saline oceanic
water; whereas, anomalous coastal surface temperatures caused by fresh water
runoff are constantly equilibrating with air temperatures and reach homo-
genity over large areas much more rapidly. For example, distinct seaward
plumes extending as far as several hundred kilometers seaward of San Francisco,
California; Astoria, Oregon; Neah Bay, Washington; Queen Charlotte Sound,
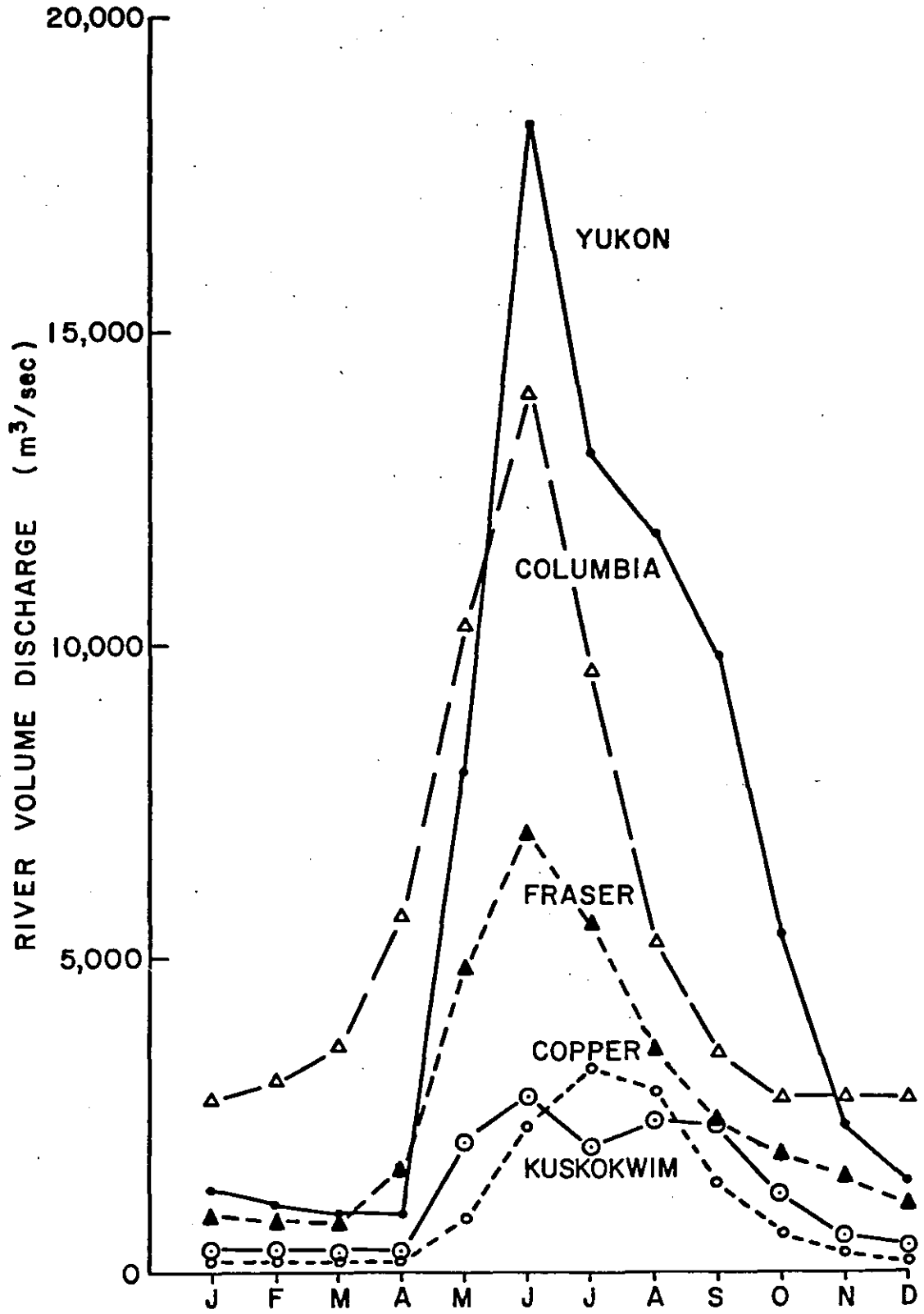
Figure 50. Monthly mean runoff of the 5 largest (volume discharge) river systems on the northwestern coast of North America.

British Columbia; and Icy Strait, Alaska, are evident in salinity distributions when adequate salinity data are available. The plumes intrude into oceanic areas and carry distinctive characteristics of river systems. Analyses of water samples for characteristic odors or other distinguishing chemical constituents are limited, but it has been shown that particulate aluminum and iron (Joyner 1964) as well as ratios of concentrations of specific elements are nearly as effective as salinity in determining the presence of the Columbia River plume in offshore areas (Figure 51).

General surface salinity distributions for winter and summer (Figure 52) indicate marked seasonal changes. Although river runoff peaks in June, the salinity distribution in summer adequately indicates the seaward extent of local runoff. One feature immediately obvious is the expanded area of a general coastal-oceanic interface represented by the 32.0 °/oo isohaline. Particularly significant is the seaward extension of the 32.6 °/oo isohaline westward from the Canadian coast in relation to the Dilute Domain. Also apparent is the extensive dilution over the Bering Sea shelf in summer as a consequence of runoff from Bristol Bay, Kuskokwim, and Anadyr Rivers, as well as ice melt. Because of the uniqueness of conditions and the importance of fisheries resources in this area, selected monthly salinity distributions are also presented (Figure 53). Subsurface conditions are discussed in Section III-D in relation to demersal fish.

B. JUVENILE SALMON

The majority of sockeye salmon produced in the lake and river systems that enter the northeastern Pacific Ocean, Gulf of Alaska, and Bering Sea migrate to the ocean after spending from one to three years in fresh water.

1. Sockeye

The seaward migration of sockeye salmon smolts begins in late April from river systems entering the southern Gulf of Alaska and in May and June in the northern Gulf of Alaska and Bering Sea rivers (Figure 54).

Initiation of the seaward migration of sockeye salmon smolts appears to be related to the ice breakup and warming of water temperatures of the lakes and major river system rearing areas which occur progressively later from south to north. The usual period of seaward migration for a given stock of sockeye salmon appears to be timed to coincide with the period when environmental conditions (i.e., sea temperature and food abundance) are most conducive to the stock's survival. Increasing solar radiation and warming of water result in increased food production, increased feeding activity, and rapid growth at a critical time when salmon are entering the marine environment. Rapid growth and larger size result in increased ability of salmon to avoid predators and secure food which are beneficial to stock survival.

Juvenile sockeye salmon occur in small numbers in the coastal regions off southeastern Alaska, southwestern Vancouver Island, and in the Straits of Juan de Fuca in June (Figure 55, Hartt and Dell 1977). By July, they begin
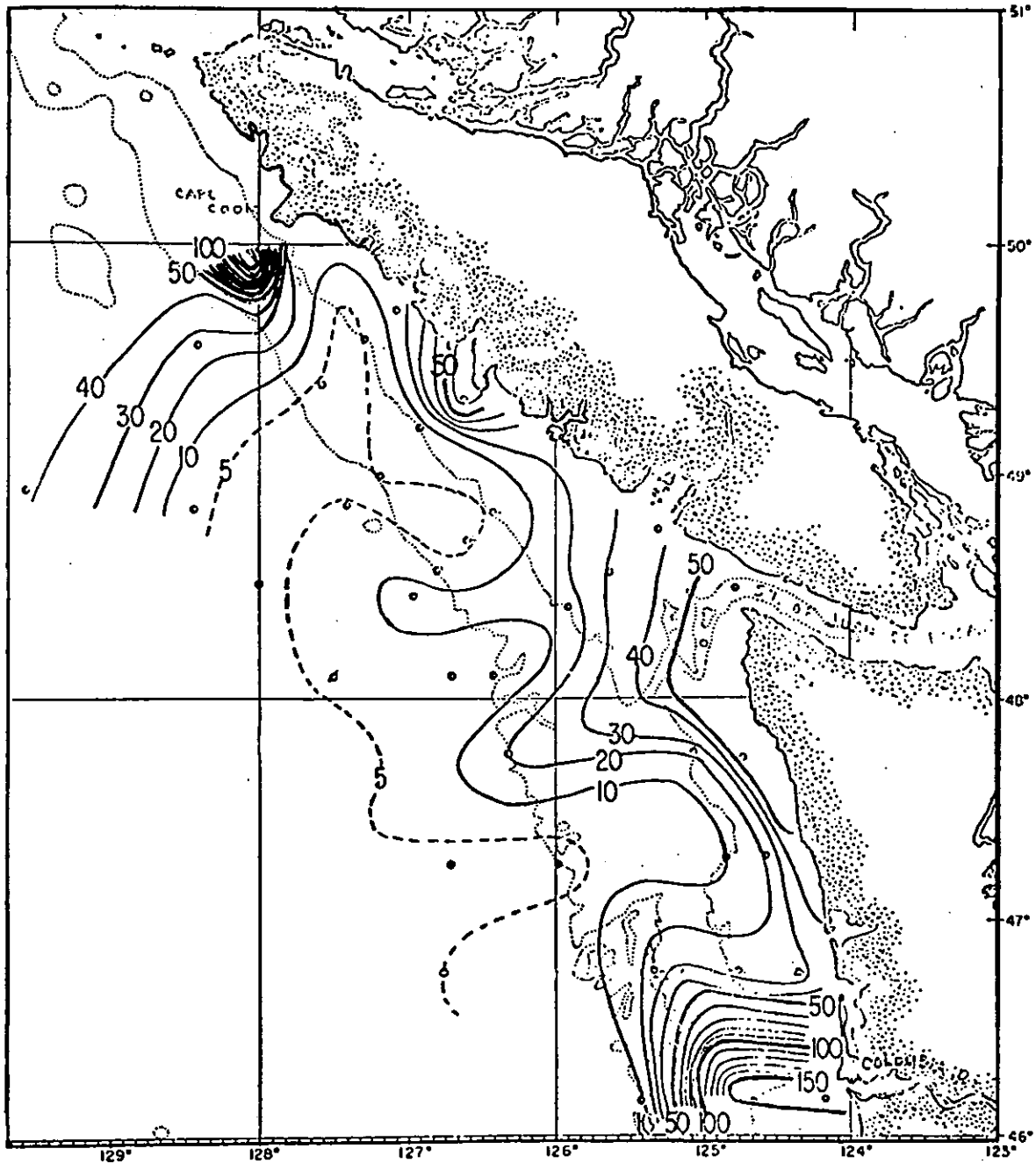
Figure 51. Horizontal distribution of particulate aluminum (μg at
Al/l x 10^{-2}) off the Washington-British Columbia coast,
spring 1963, indicating the variability in coastal waters
and particularly the delineation of the Columbia River
plume (from Favorite 1966).
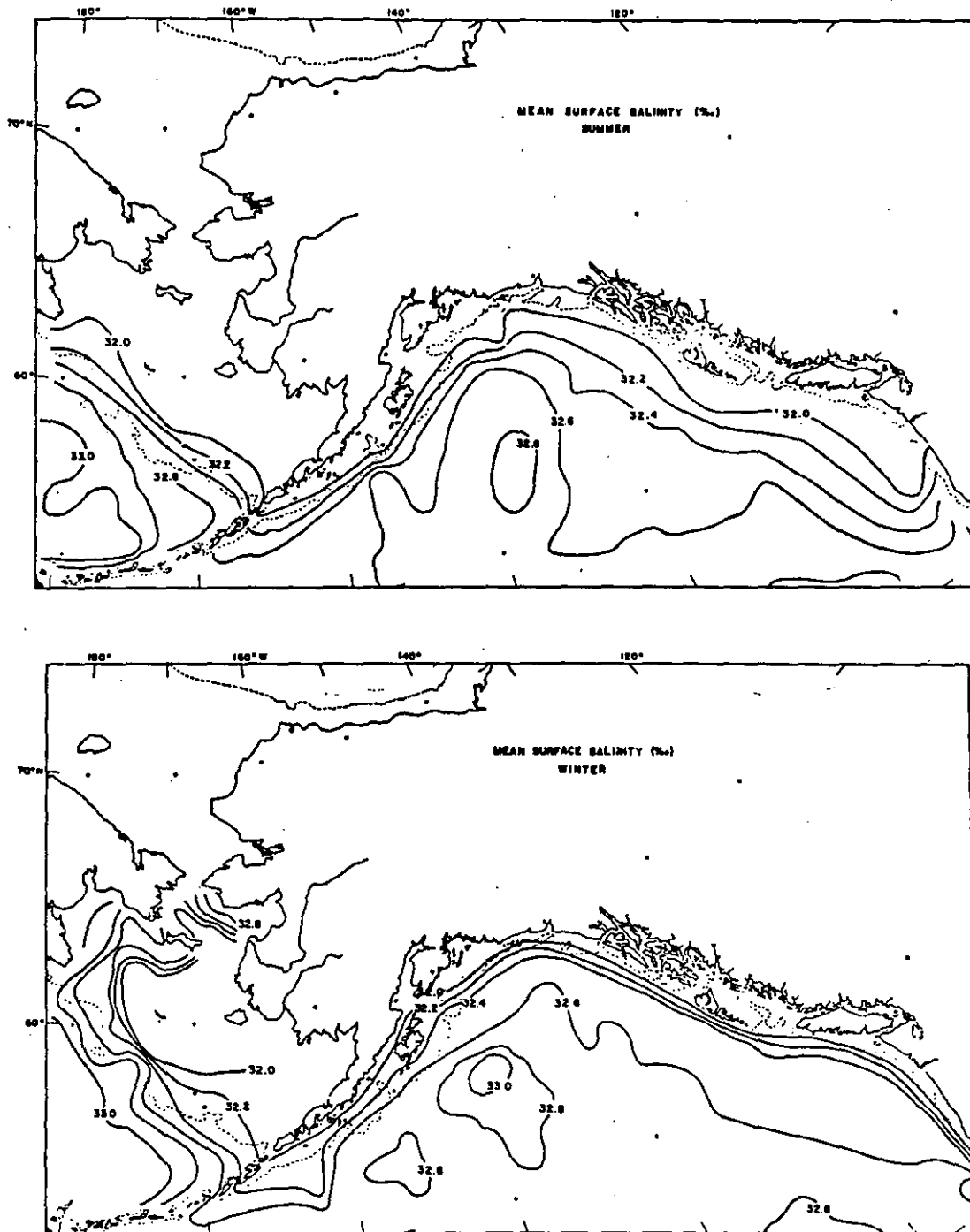
Figure 52. Horizontal distributions of winter and summer mean surface salinity (all station data averaged by 1x1° quadranges) indicating the marked seaward shift in isohalines during summer (note 32.6% isohaline in Gulf of Alaska) and increased salinity in Gulf of Alaska gyre in winter indicating upward displacement of deeper water.
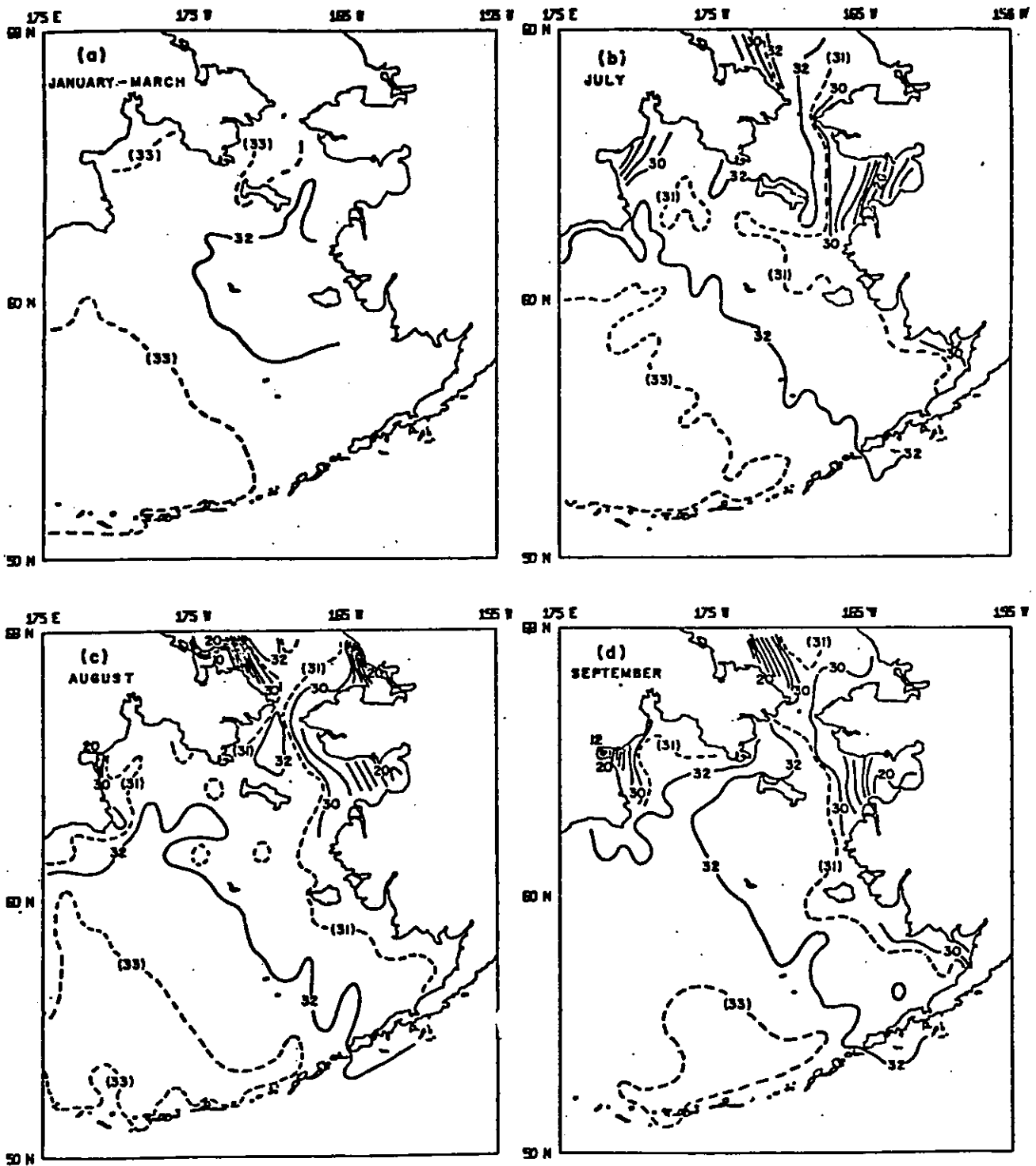
Figure 53. Horizontal distributions of selected monthly mean surface salinity (all station data averaged by 1x1° quadrangles) indicating the inshore dilution during summer particularly in Norton Sound and the Chukchi Sea.
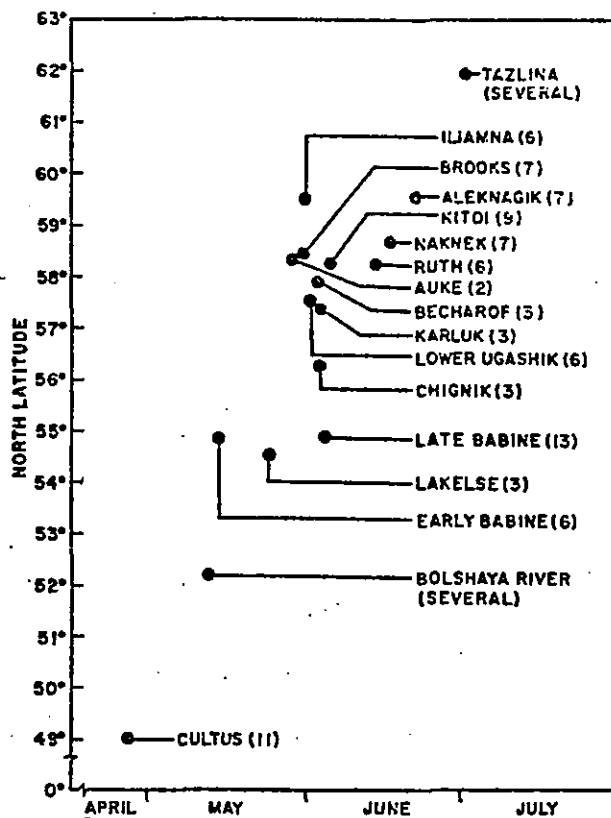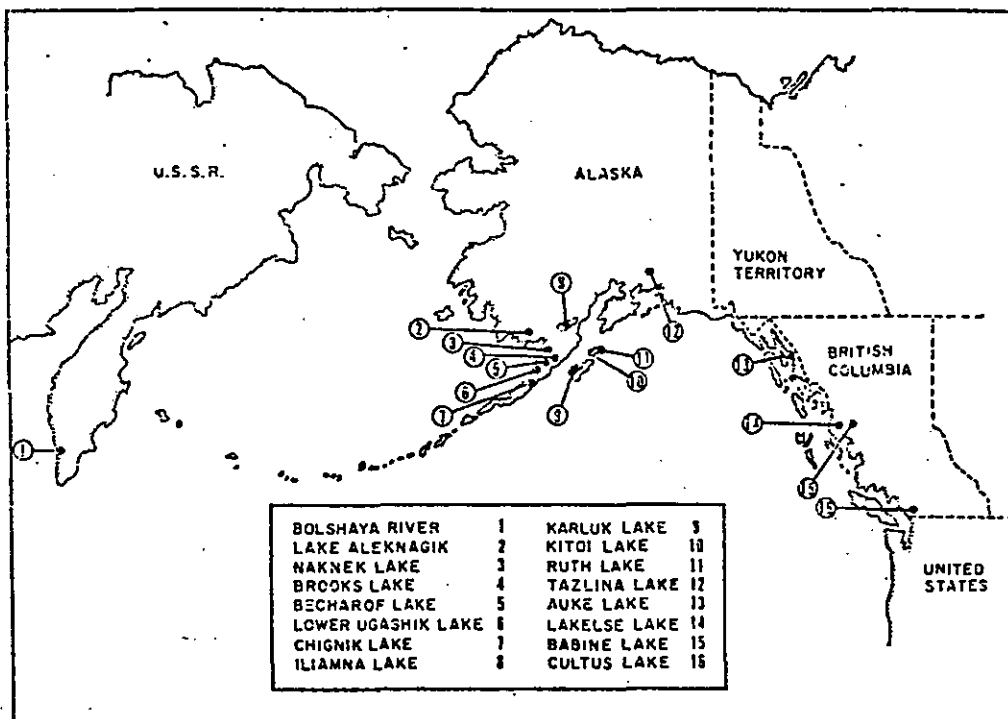
Figure 54. Locations of some of the major sockeye salmon-producing
systems and the average date 50% of the spring sockeye
salmon smolts had migrated from lake systems located at
different latitudes. Numbers in parentheses indicate the
number of years of observation (from Hartman et al. 1967).
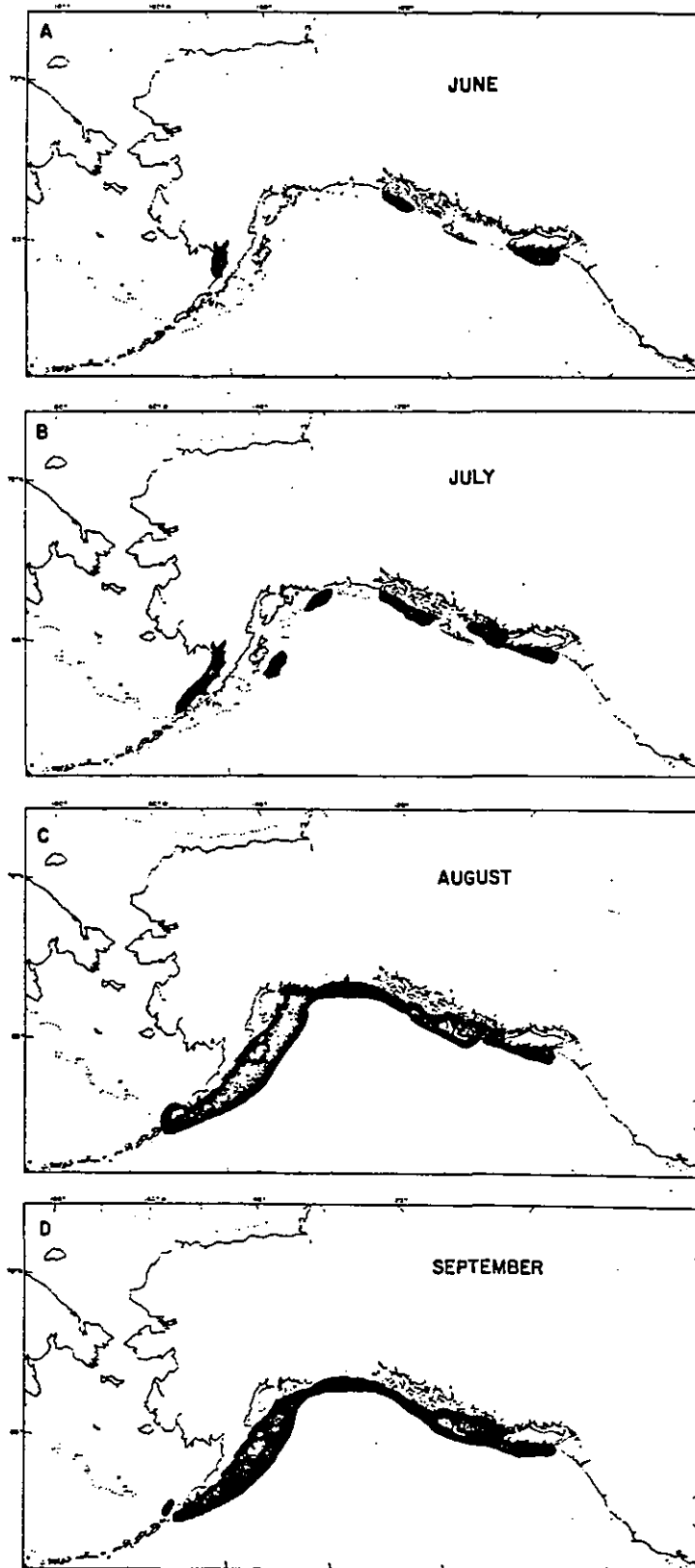
Figure 55. General distribution of juvenile salmon in the Gulf of Alaska and eastern Bering Sea (from Straty and Jaenicke 1971; Straty 1974; and Hartt and Dell 1977).

to become abundant in the coastal waters along the east and northeast coast of the Gulf of Alaska, but they are scarce or absent in the northwestern Gulf and south of the Alaska Peninsula and eastern Aleutian Islands. By August, juvenile sockeye salmon are more or less distributed in a continuous band along the coast from Cape Flattery to the eastern Aleutian Islands. This distribution is probably the result of the contribution of juvenile sockeye salmon from additional adjacent river systems and the counterclockwise movement along the coast of salmon from Washington, British Columbia, southeastern Alaska, and central Alaska which entered the ocean in June and July.

The distribution of juvenile sockeye salmon during September is similar to that described for August except for a decline in abundance along the eastern and northern coast of the Gulf of Alaska and an increase south of the Alaska Peninsula and eastern Aleutians (Hartt and Dell 1977). This distribution probably reflects the continued counterclockwise movement of sockeye salmon which entered the sea earlier in the summer.

Little can be said about the distribution and movement of juvenile sockeye salmon through the Gulf of Alaska and Bering Sea beyond September because of the lack of exploratory fishing after this time. Straty (1974) cited evidence which suggests that Bristol Bay stocks of juvenile sockeye salmon in the Bering Sea move to more offshore waters seaward of Port Moller after mid-August. This hypothesis is based on a decrease in the abundance of juvenile sockeye salmon in the nearshore waters seaward of Port Moller after mid-August and the winter (i.e., February and March) offshore distribution of age 0.1* sockeye (age 0.0 prior to January 1) in the central Bering Sea (Bakkala 1969). Age 0.1 sockeye were captured as far as 241 km north of the Aleutian Islands in the central Bering Sea at this time. If these age 0.1 fish were of Bristol Bay origin, then a gradual and continued offshore movement occurred during seaward migration until southward movement into the north Pacific Ocean, which is most probably through the passes east of long 175°C, primarily in the central Aleutian Islands area.

Hartt (pers. commun.) has also suggested that juvenile sockeye salmon in the Gulf of Alaska may move from the coastal waters to more offshore waters. Evidence for verification of such movement, however, is limited.

2. Environmental Factors in Eastern Bering Sea

The results of tagging experiments and purse seining in the north Pacific Ocean and Bering Sea (Hartt 1962, 1966) indicate that after entering the Bering Sea via the central Aleutian Island passes adult sockeye salmon move north a considerable distance before moving east into Bristol Bay. During their eastward migration into Bristol Bay and its adjacent major river systems, adult sockeye salmon remain well offshore until within 32 to 80 km of their home river systems (Straty 1975).

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*The use of this method (European Method) for designating the age of adult Pacific salmon in reference to marine life only was proposed by Koo (1962). An age 0.1 sockeye is thus considered to have spent only one winter of marine life.

The spawning migration of adult sockeye salmon occurs during June and July
in the Bering Sea at a time when juvenile sockeye salmon are migrating seaward
in the coastal waters. There appears to be little overlap of the migration
paths of the juveniles and adults at this time except in the vicinity of
some adjacent bays and river mouths. This difference in the migration routes
of juvenile and adult fish during the spawning migration has significant
survival benefits to the juvenile fish. They would avoid competition for
food with adult salmon while still in outer Bristol Bay and predation by
marine mammals and sharks which are prevalent among adult salmon offshore.
Adult salmon appear to feed actively while still in outer Bristol Bay but
feeding ceases when they approach the vicinity of their home-river systems.
Thus, in the area in which both juvenile and adults do occur at the same
time, competition for food between them may be reduced.

The implied movement of juvenile sockeye salmon into the offshore waters
seaward of Port Moller after mid-August would be at a time when most species
of adult salmon would have entered their home-river systems to spawn. Juvenile
sockeye salmon would then be entering the more productive offshore waters
of outer Bristol Bay (Straty 1974) and the eastern Bering Sea at a time when
a large source of competition and predation had been removed. The extent
to which food in the offshore waters is reduced during the passage of millions
of adult salmon has not been investigated. The offshore waters, which are
more productive than coastal waters, may in fact be poor in food abundance
for a time because of heavy grazing by the adult salmon.

If juvenile sockeye salmon follow the implied migration route offshore and
then south through Aleutian Island passes into the North Pacific, it would
be very similar to that followed by the adults during spawning migration.
Such movement would support the logical hypothesis that both the juveniles
and adults are responding to similar environmental cues in a manner which
leads them from and back to their home-river system.

As mentioned in the section on the physiology of fishes, there has been
considerable laboratory research conducted with respect to the influence of
various environmental factors on the behavior of fish. The application of
the results of this research to explain the movements, distribution, and
fluctuations in the abundance of salmon is quite limited and often speculative
for lack of supporting evidence. In the following sections we discuss the
behavior of juvenile sockeye salmon in the Bering Sea with respect to several
environmental factors which appear to support laboratory results. In some
cases, behavioral responses resulting from anomalous environmental conditions
may account for observed changes in distribution and abundance of a stock.
Since all species of salmon will respond to changes in environmental conditions
in varying degress but in a similar fashion, the discussion of juvenile
sockeye salmon behavior may apply to other species as well.

The hypothesis of McInerney (1964)--discussed in Section II--proposes that
juvenile salmon are able to use estuarial salinity gradients as one directive
cue in seaward migration. Straty (1974) has shown that the direction of
seaward movement of all major stocks of juvenile sockeye entering Bristol Bay

is through the region of the most pronounced salinity gradients (Figure 56). This is most pronounced in the movement of Wood River sockeye salmon which enter the bay on the northwest side and migrate to and seaward on the southeast side. Seaward migration by this route is the most direct route to the clearer waters of higher salinity in outer Bristol Bay.

During their homing migration, all stocks of sockeye salmon again encounter pronounced salinity gradients after leaving the offshore waters. At this time they are again becoming physiologically adapted to life in fresh water. The water of decreasing salinity resulting from fresh water discharge may include recognizable olfactory and physiochemical features of the salmons' home river system. Decreasing salinity would reduce energy required in osmoregulation. Decreasing salinity plus gradients in recognizable olfactory cues from home-river systems would seem more than adequate to guide returning stocks of salmon to the mouths of their rivers of origin. If true, the distribution of river water and climatic factors influencing this distribution may well determine the distribution of individual sockeye salmon stocks in the major fishing areas of Bristol Bay (Straty 1969).

Surface temperatures in Bristol Bay display great annual variability during the seaward migration period of sockeye salmon (Figure 57). Because of the influence of temperature on the metabolism, activity, and growth of fish, we can expect large annual differences in sea temperature to affect the juvenile sockeye salmon's size, distribution, and indirectly its survival.

Sockeye salmon have undoubtedly evolved behavioral characteristics with respect to temperature which serve to keep them in a thermal range most conducive to their survival during seaward migration. Extremely low sea temperatures, such as those which occurred in Bristol Bay in 1971, will inhibit feeding and, therefore, growth and may be avoided if warmer waters are available. The existence of cold water offshore and warmer waters nearer the coast affords the juvenile sockeye salmon a range of temperatures which may include those best suited to its thermal requirements at the time. Avoidance of colder offshore water has been offered as one possible explanation for the more coastal migration route of juvenile sockeye salmon through Bristol Bay and as far seaward as Port Moller (Straty 1974). Juvenile sockeye salmon were particularly close to shore during the summer of 1971 when extremely cold sea temperatures prevailed.

The swimming speed of juvenile sockeye salmon, and therefore the rate of seaward migration, is also affected by temperature because of its influence on growth and activity. Anomalous sea temperature such as observed in Bristol Bay in 1971 resulted in a difference in the seaward concentration of juvenile sockeye salmon over that observed in 1967, 1969, and 1970 (Straty 1974). In these years juvenile sockeye salmon were found in the Port Moller area by mid-June but were no farther seaward than Port Heiden in 1971, a difference of 160 km. Since cold sea temperatures prevailed through the remainder of 1971 and into 1972 the slower speed of migration would have continued well through the sockeye salmon's first year at sea.
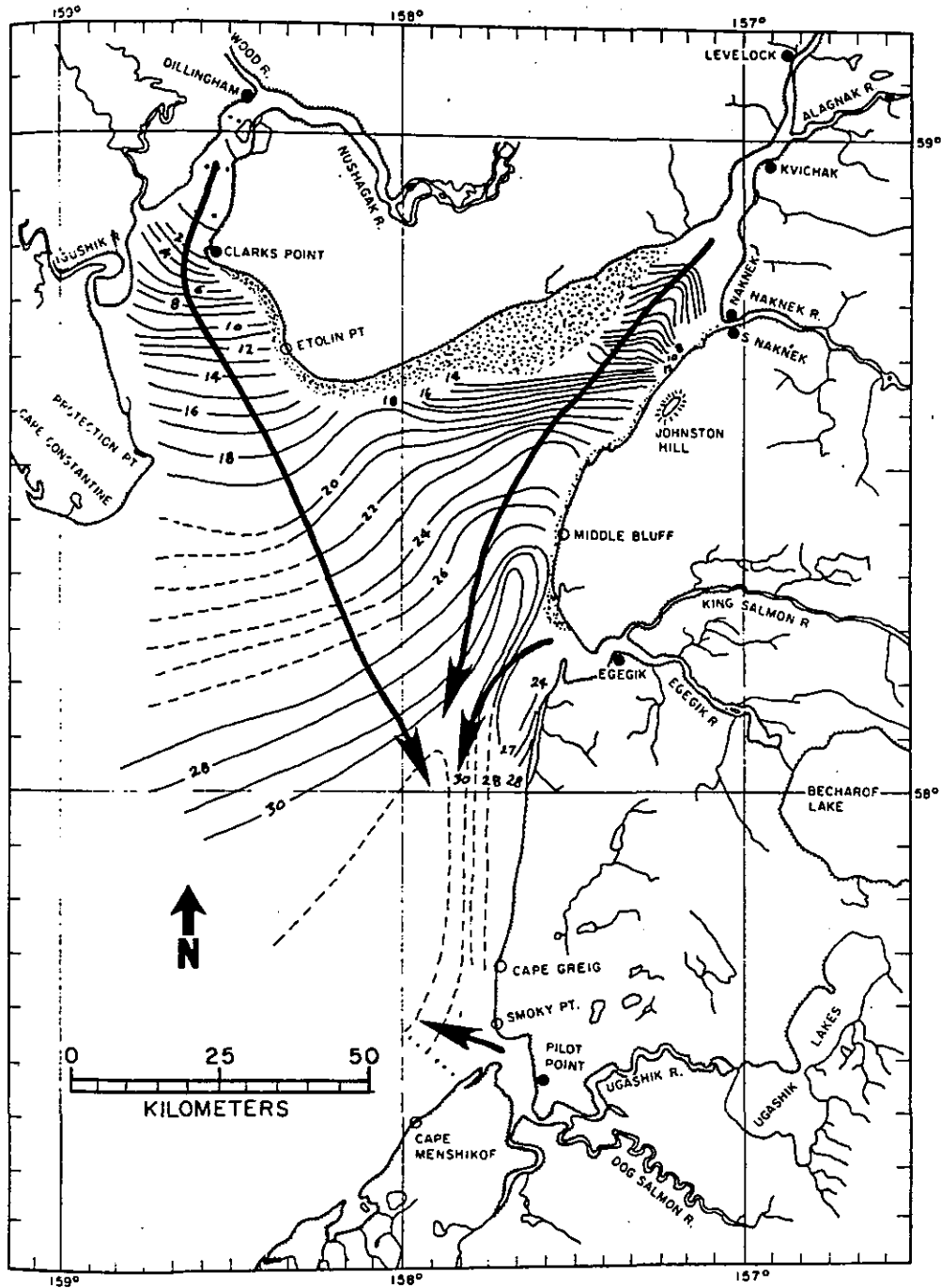
Figure 56. Horizontal distribution of surface salinity ($^\circ$/oo) at low
tide, Bristol Bay, during July and August 1966. Arrows
indicate direction of major river stocks of juvenile
sockeye salmon (adapted from Straty 1974).
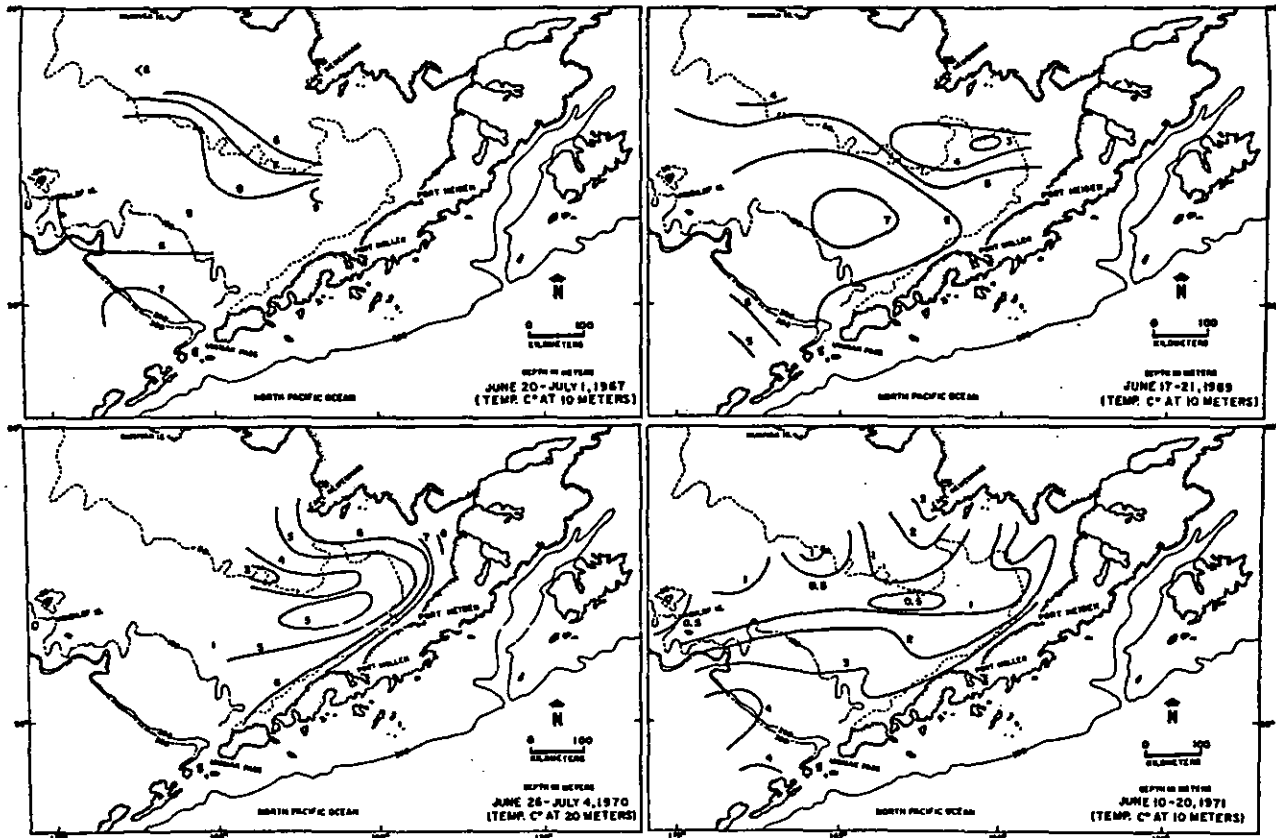
Figure 57. Horizontal distributions of surface temperature (°C) in
Bristol Bay and southeastern Bering Sea in mid-June and
early July of 1967, 1969, 1970, and 1971 (from Straty 1974).

This should have resulted in longer than usual residence in the Bering Sea and later than usual entrance into the North Pacific Ocean. With our present state of knowledge we can only speculate on the assets or liabilities of such an occurrence.

The prolonged cold sea temperatures prevailing in Bristol Bay and the Bering Sea in 1971 apparently reduced the growth rate and therefore size of juvenile sockeye salmon compared to those captured in other years of investigation (Northwest and Alaska Fisheries Center, Auke Bay Laboratory, Auke Bay, Alaska. Unpubl. data). As mentioned, this smaller size coupled with reduced swimming activity apparently resulted in a slower rate of seaward migration. A smaller size coupled with a reduction in swimming speed would also decrease the sockeye salmon's ability to avoid potential predation. If this situation is prolonged over a longer than usual portion of the sockeye salmon's ocean residence, as seems to have occurred in 1971-72, it would result in above average marine mortality. This increased mortality could have arisen not only from a reduced ability to avoid predators but also because the young sockeye salmon remained for a longer period of time at a size they could be eaten by potential predators, i.e., fish and marine birds (Straty and Haight In press). The extremely poor survival of those juvenile sockeye salmon which migrated seaward in 1971 is now a matter of record.

The abundance of distribution of zooplankton, the principal food of juvenile sockeye salmon (Dell 1963; Straty and Jaenicke 1971; Jaenicke and Bonnett 1977; Carlson 1976) may be a critical factor in their early marine growth, distribution, and period of residence in various regions of Bristol Bay (Straty 1974). Zooplankton was found to be more abundant in the clearer waters of outer Bristol Bay (i.e., seaward of Port Heiden) than in the more turbid inner bay waters (Straty 1974). Juvenile sockeye salmon captured in outer Bristol Bay were also found to contain more food in their stomachs than those captured in the inner bay. Marine growth of juvenile sockeye salmon was not apparent in salmon captured in the inner bay and did not occur until the fish had been at sea at least a month and had reached the outer bay. Straty (1974) proposed that the combination of a large population of sockeye salmon in the inner bay coupled with apparent low food abundance would account for the lack of growth of juvenile sockeye salmon during this period. Thus, food abundance at the time that juvenile sockeye salmon enter Bristol Bay and throughout their residence in the inner bay may be a critical factor in the rate of early marine growth and therefore the salmon's survival. The influence of food abundance on survival remains speculative at the present time for lack of additional information but will depend on such things as the size and age structure of the entering juvenile sockeye salmon population, the extent of grazing by the incoming adult salmon population, and the dynamics of the zooplankton population. The low abundance of food in the inner bay also appears to have an influence on the sockeye salmon's rate of movement through this region. Juvenile sockeye salmon were shown to move more rapidly seaward through the inner bay and at a more leisurely rate once they enter the outer bay of higher food abundance (Straty 1974).

3. Other Areas

There is certainly convincing evidence that oceanographic studies can play a vital role in fisheries investigations and it is obvious that the amount of knowledge obtained will be directly proportional to the effort expended. One of a number of interesting problems is the oceanic dispersion of down-stream migrants from the Columbia and Fraser Rivers. The divergence of on-shore flow that sends one branch northward and the other southward along the coast in this area changes seasonally as a result of normal wind systems and can change annually as a result of anomalous conditions. In addition, there is a relatively permanent northward undercurrent along the coast (Favorite et al 1976; Reed and Halpern 1976). Could it be possible that the apparent complexity of salmon movements in this area, based on tagging experiments, is simply a manifestation of salmon responding to, or searching out, specific oceanic flow regimes on a time scale much shorter than the tagging results are synthesized.

Only one salmon species has been selected to enumerate real and apparent or potential relations to environmental conditions and, thus, knowledge of behavior and life history characteristics of salmon that has been, or could be ascertained through planned environmental studies. And only selected relations have been noted; there are others and there are numerous similar examples that can be found with respect to other salmon species. Hartt and Dell (1977) have shown that the distribution of juvenile pink and chum salmon is similar to that of juvenile sockeye salmon in the Gulf of Alaska and Bering Sea; this was also noted during exploratory fishing by the National Marine Fisheries Service in the Bering Sea. Despite significant differences in the life history of these species and their initial size upon entering the sea, it would appear that they respond to similar environmental cues upon entering the sea. The timing of adult pink and chum salmon runs into Bristol Bay is somewhat later than that of sockeye salmon and their migration route during spawning migration has not been investigated in detail. It is logical to assume they would follow a route similar to that of the sockeye if destined for the same home-river systems. In fact, the adults of both species have been captured in association with sockeye salmon along their principal migration route into Bristol Bay.

Environmental features provide insight into salmon movements right into coastal waters where inevitably salmon are able to detect characteristics of natal streams although salmon are generally considered a near-surface fish and, thus, the edge of the continental shelf has not been considered an important guidepost for their movements. Except for seaward extensions of plumes from large river systems, the widely spaced oceanographic observations have not shown any marked changes in surface or subsurface water properties at the shelf edge. Yet there are numerous evidences of sockeye salmon milling about in this general location before commencing shoreward migrations off the west coast of Vancouver Island, and seaward migrants from this local area move northward around the Gulf of Alaska well off the coast. With the advent of continuously recording salinographs there is evidence off the west coast of Vancouver Island (Favorite 1969a) and the east coast of Kodiak (Favorite and Ingraham 1976) that dynamic processes at the shelf edge result in the formation

of a salinity front in the vicinity of the shelf edge that could serve as guidepost for such migrations. Further, extensive dilution caused by runoff from the Yukon River is evident south and west of St. Lawrence Island and can extend to the edge of the broad continental shelf.

The salinity front off the west coast of Vancouver Island is apparently associated with a massive concentration of oceanic forage (euphausids) that diminishes markedly seaward and shoreward (Favorite 1969a). Thus, the milling of Fraser River sockeye off Vancouver Island that has been attributed to a necessary "sixth sense" delay in coastal waters until stream conditions are satisfactory, may be simply an opportunity to feed extensively before beginning their final migration to spawning grounds, during which feeding is limited, if not curtailed completely. Further, pink salmon spend only one year in the ocean, yet body weights of pink salmon spawning in southeastern Alaska and British Columbia vary as much as 50%. This variability could be directly related to forage available in given years, a phenomenon that could be documented and forecast.

C. PACIFIC HERRING

The Pacific herring are believed to have originated in the Atlantic Ocean and moved eastward along the northern Asian coast to the Pacific Ocean during the Post-glacial Recession. Throughout Europe and North America considerable research has been devoted to the biotic and abiotic factors influencing the survival of herring. The results of much of this work are summarized and referenced in various publications (Counseil Permanent Internation pour l' Exploration de la Mer Vol. 154, 1963 and Fol. 160, 1971; International Commission for the Northwest Atlantic Fisheries Special Publication No. 6, 1965; and, Blaxter 1974). In addition, much of the knowledge on this subject with respect to the Pacific herring is discussed in numerous Canadian publications, particularly the Journal of the Fisheries Research Board of Canada. From this mass of accumulated information general impressions have emerged which appear to explain environmental causes for the occurrence of strong and weak year-classes in herring. The results of numerous investigations seem to contradict one another or point out the importance of one set of factors over another in determining year-class strength in herring. Investigators have generally used two approaches to explain environmental causes for the fluctuations in herring abundance--(1) direct correlation of environmental factors with year-class strength and (2) explanation of the physiological mechanisms involved in influencing stock size caused by variation in biotic and abiotic factors. The voluminous information on this topic does not permit more than a brief discussion of some of the more prevalent relationships which have emerged from both approaches. Rather extensive data are available in the Gulf of Alaska area, specially in southeastern Alaska, but data in the eastern Bering Sea are fragmentary and stem largely from foreign sources.

1. Background

Investigations of herring populations conducted throughout the world for more than 50 years have indicated that the most critical period for herring survival occurs during early life, usually during the first few months. Environmental variation occurring during this "critical period" is believed to be responsible for the observed variability in year-class strength in these populations. This variability may be attribted to variability in the abiotic environment of the herring during this period which in turn results in variability in its biotic environment.

Studies of Atlantic herring indicate that the abundance of larvae, and consequently the quantity of recruits to the spawning stock, depend on the quality and quantity of the reproductive products. The quality of the reproductive products is of great importance for the viability of the developing embryo and larvae (Benko and Seliverstove 1971). The qualitative characteristics of eggs are determined mainly by the yolk. The quality of the eggs depends on feeding conditions, on the amount of energy reserves stored as fat in the year preceding spawning and on the age and size composition of the spawning population (Hjort 1914; Blaxter and Hempel 1963). Presumably good feeding conditions result in a good growth rate and fat accumulation which in turn are manifested in increased fecundity for a given age (Hempel 1965) and more viable eggs than when poor feeding conditions exist. At least one investigator (Anokhina 1960) found the size of eggs more variable in thin herring than in fat herring. Survival time and size of larvae have been found to vary with egg size (Blaxter and Hempel 1963). Generally there is a tendency for the yolk:body weight ratio at hatching to increase with increasing egg size, permitting the larger larvae to put on more body weight during the yolk sac stage and to live longer on their body reserves despite their greater metabolic demands. Independent feeding of herring larvae after yolk absorption is normally timed to correspond with the time of spawning of zooplankton. The eggs and larval stages of this plankton comprise the food of herring larvae at this time. Laboratory studies have demonstrated that larvae deprived of food for a very short time (often only 1 or 2 days) after absorption of yolk reach a point of irreversible starvation resulting in complete mortality (Blaxter and Hempel 1963; Lasker et al 1970). This suggests that herring larvae may, at times, be susceptible to starvation and mass mortalities. Thus anomalous factors which would alter the normal timing of yolk absorption with arrival in areas of food abundance could account for mass mortalities and resultant variability in year-class strength. Environmental conditions which favor the production of large viable eggs are a definite plus in the survival of herring.

The availability of suitable food to larval herring at the appropriate time is essential to their survival. The possibility of mass mortality due to starvation occurring after yolk absorption has been mentioned as one possible factor in determining year-class strength. The availability of food after yolk absorption is related to phytoplankton production which in turn is closely related to seasonal changes in the amount of light. The abundance of zooplankton, the food of herring larvae, is related to phytoplankton abundance and the spawning period of adult planktonic animals

which in turn are controlled by temperature. There is evidence that huge
mortalities of yolk-sac larvae of pelagic fish occur which are not due to
a lack of food (Ahlstrom 1965). Theilacker and Lasker (1974) suggest that
predation on yolk-sac larvae may be the most important cause of mortality
during the early period in the life history of pelagic fish.

Certain macroplankters such as ctenophores, jellyfish, and chaetognaths
have been found to prey on herring larvae (Stevenson 1962). Copepods and
euphausids also have been reported to ingest anchovy larvae. From his work
on Pacific herring in British Columbia, Stevenson (1962) concludes, however,
that predation by macroplankton on herring larvae is not a serious source
of larval mortality. Although not well documented, predation by marine
birds and fish on herring larvae must obviously occur. The magnitude of
mortality by these sources of predation is unknown. Among other biological
features of the environment that affect the abundance of herring, disease
and parasite infestation may be of significance (Sindermann 1965). Certain
parasites and diseases are characteristic of either young, or older herring
or both. Additional studies of such things as the incidence of parasite
infestation and disease, its occurrence with age and locality, immune responses,
life cycle studies of parasites, and the role of environmental variables
are needed to provide a broad basis for understanding the importance of
these factors in the population dynamics of herring.

Abiotic environmental factors may influence herring abundance directly or
indirectly via the biotic environment. The general impression gained from
a review of the literature is that the occurrence of cold or below normal
sea temperatures during the early life of herring is conducive to poor survival.
Temperature may influence herring indirectly through its effect on growth
rate (see Section II-A-4); i.e., up to a point, growth rate increases with
increasing temperature, and good growth during the season preceding spawning
has been shown to increase fecundity for a given age and result in more
viable eggs.

Temperatures prior to spawning have a significant influence on the rate of
development of sexual products and therefore will influence the arrival of
a stock on the spawning ground and the time of spawning and hatching of
eggs. Cold temperature preceding spawning will result in late spawning and
shift the whole cycle of egg development through metamorphosis to later in
the season than when warmer temperatures prevailed. What effect this has
on herring survival remains speculative, but it will depend upon temperatures
prevailing after hatching. Various invesigators have shown that at low
temperatures larvae hatch at a later stage with smaller yolk supply than
at higher temperatures (Blaxter and Hempel 1961; Hempel 1962). Stevenson
(1962) found that Pacific herring larvae that hatched early grew more slowly
than those that hatched later in the spring. He reasoned that broods of
early hatched larvae would therefore have a longer period of larval life
than late broods. Thus, the various mortality factors would act on early
hatched larvae over a longer period of time than on later hatched larvae,
resulting in lower survival. Temperature can influence the survival of
herring larvae through its effect on the availability of food. The
availability of food suitable for larvae at the appropriate time is related

to phytoplankton production, which in turn is closely related to the seasonal changes in temperature and to the amount of light (which normally shows a close correlation with water temperature). Zooplankton, the food of herring larvae, is related to phytoplankton abundance and the spawning period of adult planktonic animals which is also controlled by temperature. Thus, too high or too low water temperatures may put larvae development out of phase so that development occurs before or after the peak population of the proper plankton. Finally, temperature, through its influence on metabolosm and therefore feeding activity and growth rate, influences larvae and juvenile survival. As with juvenile salmon, cold sea temperatures will reduce activity and growth of larval and juvenile herring, resulting in a reduced ability to avoid predators and extend the period of time that they remain of a size they can be eaten by predators.

It is obvious that investigators should look for, and in many instances will obtain, significant correlations between sea temperatures and year-class strength. However, sea temperature records along the shoreline of the Gulf of Alaska where spawning and early larval and juvenile herring development occur are scant and/or incomplete. The acquisition of sea temperatures for this region combined with studies of larval herring distribution and growth might afford a means of forecasting the relative strength of incoming year-classes several years in advance of recuitment to fished populations.

The direct influence of salinity on most fish species can be considered as minor (Laevastu and Hela 1970). Holliday and Blaxter (1960) found that fertilization, development, and hatching of herring eggs will occur over a wide range of salinities. Although herring larvae will tolerate a wide range of salinity, survival is greatest in water of 4/5 normal salinity (25.8 ^{o}/oo) (Fujita and Kokubo 1927). These investigators considered that their experimental results explained why larval herring thrive better under estuarine conditions than in open water of higher salinity. Assuming that these experimental results are applicable to conditions in nature, knowledge of those environmental conditions, i.e., currents which retain larvae within estuarine conditions, becomes apparent.

There are numerous other abiotic factors that influence survival. From the standpoint of herring survival, currents are primarily important as a mechanism for transport and concentration. The importance of currents for the transports of herring larvae to areas of food abundance by the completion of yolk absorption and the retention of larvae in areas of lower salinity has been mentioned. Hjort (1926) theorized that survival of Atlantic herring may be affected by young herring being transported out to the open sea where insufficient plankton is avilable. Laevastu and Hela (1970) point out that current convergences may bring about a "mechanical" aggregation of food organisms and small fish. With the exception of those areas being impacted by human development, little is known of the dynamics of currents in the U.S. inside waters of the Gulf of Alaska and their relation to herring distribution and survival. Herring eggs spawned in the intertidal zone may be subjected to the effect of wave action. It is well known that for many species of fresh water fish, eggs are very sensitive to vibration during the first 24 h of incubation. To what extent the eggs of herring will be destroyed by wave

action has not been extensively investigated. Because of their location in the inter-tidal zone, herring eggs are also subject to desiccation. The extent of egg mortality will vary with their location in the intertidal zone and the duration of sunny weather during incubation. Steinfeld (1972) reported a 20 percent mortality of exposed herring eggs sampled during a period in which the weather was cool and moist and a 50% mortality for those samples during a period when a dry warm climate prevailed. He concluded that desiccation of eggs was therefore a significant cause of mortality. Galkina (1971) reported the mortality due to siltation of herring eggs laid on low vegetation. The extent of such mortality on Gulf of Alaska herring has not been extensively studied. Low oxygen concentrations have been shown to influence the rate of development of embryos and larvae of many fish species. For herring, low oxygen concentrations have not been reported in the literature as a major source of mortality. Taylor (1971a) speculated that the decrease in hatching success as herring egg mass thickness increases may be due to reduced oxygen supply brought about by poor circulation of water around an increasing number of eggs.

All stages in the life history of herring, especially larvae and juveniles, are consumed by predators or are in competition with other marine animals for food. Therefore, fluctuations in the abundance of predators and competitors, which are themselves influenced by biotic and abiotic factors, must have a considerable influence on the survival rate of herring. Many of the most common food fishes and marine birds are known to prey heavily on herring or compete with them for food. Predation is obviously greater on younger and smaller herring than on the older and larger fish. Exploitation of herring stocks by man, of course, is a major source of mortality. Fisheries literature contains numerous accounts of the influence of fishing on recruitment. In at least one Pacific herring fishery, the increasing efficiency of fishing fleets increased total mortality to such a level that it resulted in decreased recruitment to adult stocks; e.g., Taylor (1968).

2. Gulf of Alaska

Pacific herring occur along the west coast of North America from San Diego, California, to Nome, Alaska. Herring occurring in the Gulf of Alaska are caught by U.S. fishermen primarily in bays, inlets, and waterways along the the coast and inside waters of southeastern and central Alaska (Figure 58). Herring apparently do not occur in large commercial concentrations very far offshore in the gulf. This was indicated by the poor catches made during several exploratory cruises in the offshore waters of the gulf (Rounsefell 1929; Powell 1957). In addition, foreign vessels fishing the offshore waters of the gulf have never been observed or reported catching substantial quantities of herring, nor have herring been considered a target species of foreign fleets; however, foreign vessels fishing off the coast of British Columbia have been reported to make substantial catches of herring. The apparent difference in the distribution of herring off British Columbia and Alaska defies explanation with our present state of knowledge.
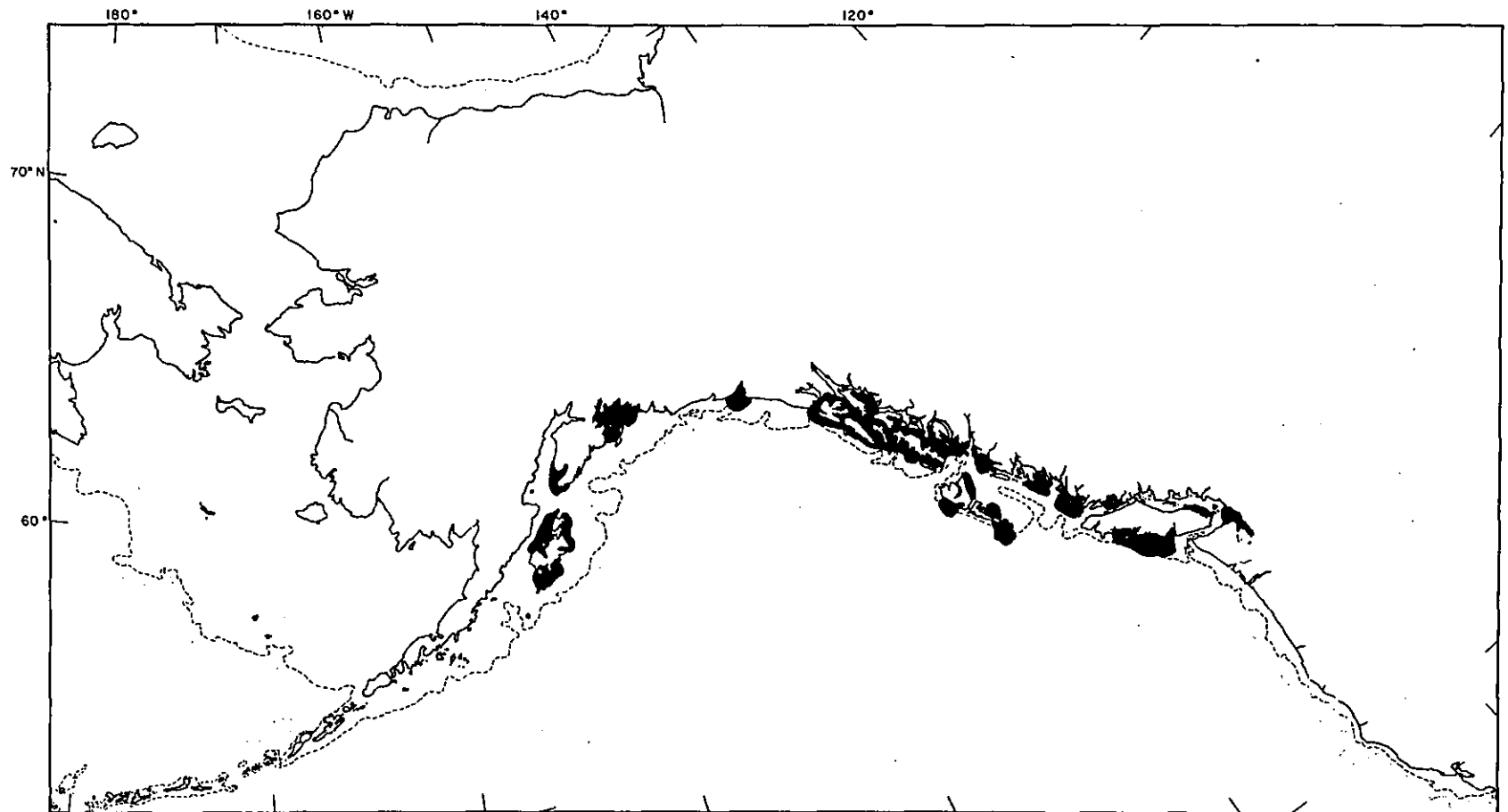
Figure 58. General locations of Pacific herring concentrations in the Gulf of Alaska area.

Information on the seasonal movements of adult herring in the Gulf of Alaska has resulted from numerous investigations conducted in southeastern Alaskan waters and off Canada by governmental research and management agencies. Environmental monitoring routinely conducted during many of these investigations has provided insight into those factors which appear correlated with the seasonal and vertical movements of herring and to fluctuations in their abundance. The seasonal movements of Gulf of Alaska herring stocks is best described by discussing what has been learned from investigations conducted in southeastern Alaska where adult herring are located seasonally in three geographically distinct areas--the spawning grounds, summer feeding areas, and overwintering areas.

Sometime during February to mid-March, schools of herring from large overwintering aggregations depart for the spawning grounds. Upon arrival in the vicinity of the spawning grounds they appear to congregate in the deeper waters and near the bottom. As spring approaches with rapidly increasing day length and resulting warmer temperatures, herring leave the deeper depths and begin moving continuously along the shoreline of their historic spawning grounds. At this time they usually occur at depths between the surface and 40 m and, upon final maturation of eggs and milt, spawning takes place.

Spawning occurs between March and April in southern southeastern Alaska and from late April to late May in northern southeastern Alaska and further north and west in the Gulf of Alaska. There is a progression in the time of spawning with larger and older herring spawning first, followed later by the smaller recruit spawners, which is consistent with what has been found by Devold (1963) for the Atlantic herring. There is evidence, although scant, which indicates that the identical spawning beaches are not used by both the larger and recruit spawners.

Spawning occurs in the intertidal and adjacent subtidal zone where their eggs are attached to the vegetative substrate, and the mortality of these eggs will vary depending upon such biotic factors as predator abundance and the thickness of the egg mass. Predation by marine birds in many areas is extremely heavy. Outram (1958) for example estimated that gulls alone accounted for 39% of the egg loss on the spawning grounds off Vancouver Island. Steinfeld (1972) reported a 99% loss of eggs by birds in Oregon. The thickness of the egg mass is dependent upon the size of the spawning population. Hatching success apparently decreases with increasing egg mass thickness (Taylor 1971a; Galkina 1971). Maximum larval production occurs at light to medium intensities of egg deposition. Thus, the higher the abundance of spawning fish and the thicker the spawn, the higher the relative mortality of embryos as compared to mortality at lighter egg densities. This has been offered as one explanation for the lack of or negative correlations obtained between the amount of eggs deposited and year-class strength for some herring stocks (Galkina 1971). Taylor (1971a) has speculated that the increased mortality in thick egg masses may be due to reduced flow or contact with the water, resulting in reduced oxygen supply or local increases in toxic material from dead eggs.

Herring do not feed during spawning--but after completion of spawning; spent herring break up into smaller schools and disperse over a wide area, eventually arriving at traditional summer feeding areas where zooplankton is abundant. These schools are constantly moving in search of food and do not occur in dense concentrations as observed in the wintering areas. The area around Point Gardner, at the southern tip of Admirality Island and the confluence of Chatham Strait and Frederick Sound, and off Cape Ommaney off the southern tip of Baranof Island are historic summer feeding areas for herring. Ocean-ographic conditions in these areas are apparently conducive to high primary and secondary (zooplankton) production. During the summer feeding period, June through October, herring may be found from the surface to a depth of about 30 m but appear to concentrate between 20 and 40 m. The herring feed heavily during this period, building up the energy reserves that must carry them through the winter and spring spawning season of low food abundance. Sometime during October, herring schools depart their summer feeding grounds for their overwintering areas in sheltered bays and inlets. This movement appears to coincide with the onset of the first severe fall storms which causes mixing of the water column and destruction of the thermocline. What influence, if any, the breakdown of the thermocline has upon herring behavior at this time remains speculative. It may serve as a cue which initiates the fall migration to the overwintering areas.

Herring appear to return to the same overwintering areas each year and their arrival in some areas is readily apparent by the significant increase in marine mammals, birds, and fish which feed on them. As the winter season approaches and sea temperatures decline, metabolism is reduced and herring become less active, and feeding all but ceases. During the day herring stay as deep as 120 m and at or near the bottom at lesser depths. They rise at night and on overcast days into the upper 20 m. Herring remain in the wintering areas until sometime between late February and early March when they again depart for the spawning grounds. At this time sea temperatures are at or near their seasonal low, zooplankton is minimal in abundance, and light is rapidly increasing. The seasonal movements of adult herring in other areas of the Gulf of Alaska, while not studied in detail, are generally consistent with those described for southeastern Alaska stocks.

The movements of larval and juvenile herring in the Gulf of Alaska have not been studied extensively. What is known of their movements has resulted from investigations conducted primarily off British Columbia and is consistent with limited observations made in southeastern Alaska. After the eggs of herring hatch, the semi-transparent larvae float passively in the water for up to 8 weeks while undergoing a gradual metamorphosis to the adult form. After metamorphosis, the larvae cease to exist as free-floating organisms and form schools which appear in the vicinity of the spawning grounds (Stevenson 1947; and unpublished data of the Auke Bay Laboratory of the NMFS Northwest and Alaska Fisheries Center). During the first summer, the young (juveniles) stay in inshore waters and concentrate in areas of relatively low salinity (Hourston 1959). They seem to prefer shallow bays and inlets and kelp beds where currents are weak (Outram and Humphreys 1974; and unpublished data of the Auke Bay Laboratory of the NMFS Northwest and Alaska Fisheries Center). In fall and winter they disappear from the inshore

coastal waters and move into deeper waters (Reid 1972; and unpublished data of the Auke Bay Laboratory of the NMFS Northwest and Alaska Fisheries Center). During their second summer as schools of immature fish, they reappear inshore. Recruitment to the mature stock occurs primarily during their third and fourth year. Juvenile herring do not appear to intermingle with adults; they generally occur in shallower water than the adults.

Throughout waters off Europe and North America considerable research has been devoted to the biotic and abiotic factors influencing the survival of herring. The results of much of this work are summarized and referenced in various publications (Counseil Permanent International pour l' Exploration de la Mer Vol. 154, 1963 and Vol. 160, 1971; ICNAF Special Publication No. 6, 1965; and Blaxter 1974). In addition, much of the knowledge on this subject with respect to Pacific herring is discussed in numerous Canadian publications, particularly the Journal of the Fisheries Research Board of Canada.

Variations in year-class strength are presumably due to variations in the environment at some time in early life. Failing or bypassing the information needed to make a direct study of the effect of various environmental factors on the survival of young fish, correlations between year-class strength and various environmental data have been made for several fisheries.

As pointed out by Gulland (1965) the use of correlations to establish a connection between environment and year-class strength is made difficult by the small number of pairs of observations available (one per year). On one hand, there is the statistical danger that with the wide range of possible environmental factors available, including the choice of precise season, a high degree of correlation between some factor and year-class strength is likely to arise merely by chance. On the other hand, the estimates of year-class strength, and probably also of the environmental factors, are likely to contain considerable observational variance. Despite these difficulties, it is worth examining the relation between year-class strength and some environmental factors in Pacific herring. As mentioned previously warm water temperatures prior to, during, and after spawning appear to be particularly conducive to good survival in herring. Therefore, it is natural to look at the relationship between sea temperature and herring abundance. Rounsefell (1930) reported a high degree of correlation (.73) between year-class strength and the mean annual temperatures for the combined months of March through June for Prince William Sound herring. Favorite and McLain (1973) have shown a close relationship between the relative abundance of year classes of herring in southeastern Alaska and anomalies of mean surface temperature (Figure 59). The 1953 and 1958 year-classes of herring which were spawned during warm years, dominated the fishery for 5 and 4 years respectively while the 1955 and 1956 year-classes were poor.

Ramey and Wickett (1973) have shown that it is possible to predict the year-class strength of herring stocks in the Gulf of Alaska with considerable success using an empirical/statistical relation derived from several environmental parameters—such as sea level records (indicative of currents and thermal stratification), stability of water stratification (indicative of primary productivity and phytoplankton standing stock density), and others.
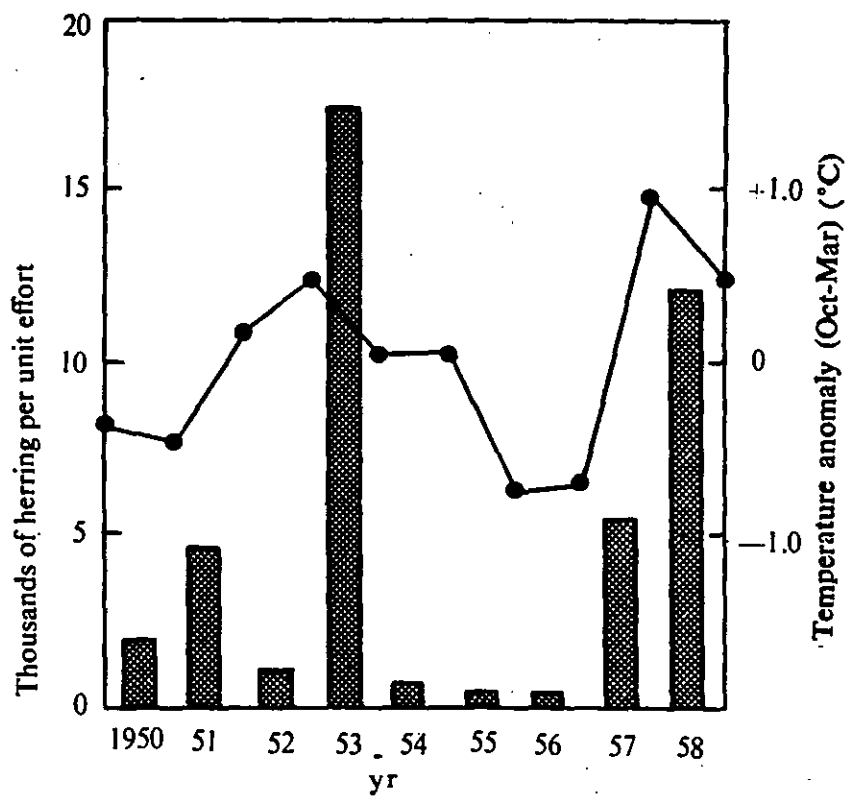
Figure 59. Comparison of relative abundance of year classes for Pacific herring from southeastern Alaska commercial fishery and anomalies of winter (October-March) mean sea surface temperature (from Favorite and McLain 1973).

However, the required data are not consistently available and this program is not operational. Wickett (1975) has presented data which show that year-class strength of herring stocks off the west coast of Vancouver Island appear to vary with changes in salinities. His data indicated that 85% of the variance in the annual mean British Columbia herring year-class is associated with the January to December mean salinity in the same year. However, salinity is used as an indicator of the magnitude of the "stirring up" effect brought about by wind driven currents which bring nutrients to the euphotic zone. Storm tracks in the 1960's were apparently unusual in that they didn't produce a "stirring up" effect required for nutrient growth and food chains. This was indicated by lower salinities and, therefore, nutrient supply in the upper waters resulting in conditions unfavorable for productive fisheries. Salinities apparently reversed their downward trend at Ocean Station P ($50^{o}N$, $145^{o}W$) and off Queen Charlotte Island in 1970, indicating increased nutrient supply to the euphotic zone and conditions conducive to increased stock size. Wickett's (1975) empirical relations suggest that the 1969, 1970, and 1971 year-classes should be on the increase.

3. Eastern Bering Sea

Historically, native herring fisheries were conducted in Norton Sound and Unalaska, and little was known about offshore distributions until the extensive Soviet fisheries investigations that commenced in the late 1950's. According to Shaboneev (1965) herring are found in winter northwest of the Pribilof Islands between lat 58 and $59^{o}N$ at depths of 105 to 137 m, an area of 1300-2800 km^2. They move shoreward in an early spring migration northeastward and southeastward and by May are found southwest of Nunivak Island and northwest of Unimak Island. The occurrence of only small amounts of herring seaward of a 20-mile coastal band in July is considered evidence that they remain in coastal embayments at this time.

Early studies suggested that spawning occurred at only several locations along the eastern Bering Sea shore, but air surveys by the Alaska Department of Fish and Game in late spring and early summer 1976 revealed that spawning occurs all along the coastline from Unimak Pass to Norton Sound; spawning capelin (Mallotus villosus) were also observed in this area. The older herring (7 years, or more, in age) migrate seaward in August. The younger herring move seaward later, but by September large numbers are found on the general wintering grounds at 70-90 m in temperatures of 2-3°C.

From a resource-environment relation standpoint there is only a little information. There appear to be many localized stocks with varying degrees of homing instinct (Kasahara 1961), and the present interpretation of two migrating routes may be drastically altered in the face of the evidence of widespread spawning. Typically, herring abundance varies from year to year and area to area, capable of supporting a fishery one year and scarce the next. This may be caused by distribution as much as abundance. For example, in late spring 1959, a Bureau of Commercial Fisheries salmon gill-net fishing vessel in the northern central Bering Sea, far from the shelf, caught several thousand adult herring in gillnets (Larkins 1964), an unprecedented event.

Although this could be considered evidence of a large but perhaps at times
dispersed herring population over the central Bering Sea basin, there is
evidence that the cold (-1.8°C) temperatures over the shelf in winter do
not restrict herring movements; in fact, there is speculation that herring
may be abundant under the shelf ice. Since the reported depths of herring
concentrations are all less than 200 m, it appears that the warm 3-4°C
temperatures at the shelf edge that apparently satisfy thermal requirements
of most flatfish, are of little significance to the herring. However, there
is evidence that such temperatures are of importance to herring during the
spawning period. Along the north coast of the Alaska Peninsula, spent
herring were found at 30-50 m depth in temperatures of 3-4°C; whereas,
2-, 3-, and 4-year-old herring at stage II maturity and immature herring
were found at 50-70 m in temperatures of 0° to -1°C. Takahashi and Konda
(1974) reported that year-class strength was dependent on water temperatures
in the spawning year.

D. DEMERSAL FISH

Historically, fisheries exploitation in this area, particularly in the Gulf
of Alaska and Bering Sea, has been selective even though indications of the
potential wealth of resources were documented in the eighteenth and nine-
teenth century. Ledyard (Munford 1963) reported that during Cook's third
Pacific voyage, the Resolution hove to south of Unimak Island in 1778 "...
and caught several hundred holybret [assumed to be halibut] and cod-fish..."
However, it was not until 1865 that a bottom fishery commenced in this area.

In 1888, while the U.S. Fish Commission Steamer Albatross conducted explor-
atory cruises in the vicinity of Unalga and Unimak passes, not only large
numbers of cod, halibut, salmon, and herring, but also small amounts of
flounder, squid, and walleye pollock, were caught (Tanner 1890). Although
the presence of king crab (Paralithodes camtschatica) was not reported, it
was suggested that the area was well suited for transplants of the "Atlantic
coast lobster." Further, two unusual biological phenomena, that have not
been clarified to this day, were also reported. Attempts to replace dory
(hand-line) fishing in the Bering Sea with trawls were considered unsuccessful
because ..."the sea fleas (Amphipod crustaceans) which were very abundant
on the bottom and devoured or injured the fish before the lines could be
hauled." In addition, a Slime Bank was reported about 20 miles northward
of Unimak Pass that not only yielded some of the largest cod taken in Alaska,
but was believed to be..."covered at a fathom or two above the bottom with
a dense layer of slimy Medusae, which generally prevents the hooks reaching
the bottom in a clean condition." It is perhaps too late to investigate
these phenomena and their niche in the ecosystem. No present day investigations
have reported (or perhaps even investigated) unusual abundances of amphipods
or medusae in this area. Nor do we have sufficient evidence to document
a possible succession of organisms from cod, to halibut, to crab, to pollock,
in the eastern Bering Sea.

1. Background

Here again, because of the paucity of information on local fisheries, it is useful to point out relations discovered in the Atlantic Ocean where considerable research on groundfish has been carried out. Many of the apparent effects of environment on roundfish (pollock, cod, etc.) are nature movements, such as seasonal migration, but they might be triggered by environmental changes (environmental stimuli), and this hypothesis is supported by several observations. McCracken (1965) found that spring and fall migrations of haddock (Melanogrammus aeglefinus) occur while rapid seasonal changes are taking place. Thus, year to year variation of the time of rapid change of e.g., temperature and its gradients, might affect the year-to-year variations of availability of groundfish, but not necessarily the stock size. Furthermore, Edwards (1965) also found that some fish species depart coastal areas in a relatively abrupt manner. The environmental extremes, such as cold bottom temperatures, are avoided by roundfish, but on the other hand the aggregation of fish is often influenced and/or determined by concentrations of preferred food (e.g., Beverton and Lee 1965). Summer distribution of large and small roundfish differ often markedly (McCracken 1965). Small fish seem to have greater tolerance to greater depths and lower temperatures. According to Edwards (1965) some roundfish species move inshore, where they occur during summer in the same temperature range as during winter in deep water. Some species, however, move offshore when temperature rises and different age groups, even different sexes, may have different temperature preferences. This observation substantiates Devold's hypothesis that many fish species select cooler temperatures because of the need to economize metabolic processes in relation to availability and demand for food. Edwards' observation is substantiated also by Tempelman and Hodder (1965), who found that in winter haddock escape into colder water at depth than occurs in shallows, and return from deeper water, which was warmer than the coastal water into which it moves in spring. The flatfish spend most of their adult life on the bottom where they feed mainly on benthos, although there is increasing evidence that flatfish actively move to the surface at night to feed (Fadeev 1970). Obviously, there is a spectrum of behavior and food habits in this group that varies with season. The diversity of demersal fish, their wide distribution, and the fragmentary data available make it difficult to present an effective summary of resource-environment relations; however, some pertinent comments can be made with respect to discrete stocks, year-class strengths, dispersal of eggs and larvae, distribution of juvenile stages, and general adult distributions.

When one considers that individual species exist around the northern rim of the Pacific Ocean and Bering Sea basin from California to Japan, or beyond, it is reasonable to assume that environmental conditions are of primary importance to discrete local stocks. The presence of discrete local stocks would imply discrete local environments, including proper currents for successful dispersal of eggs and larvae. However, the occurrence of adults throughout such a large area implies a compatible environment unique to the Subarctic Pacific Region with a constant or intermitten continuity of flow. The staff of the Northwest and Alaska Fisheries Center have just completed three voluminous reports on the status of knowledge on fish and shellfish resources of the Gulf of Alaska and the eastern Bering Sea (Pereyra et al 1976; Ronholt et al 1976; and, Macy et al 1977). Since these reports are readily

available, it is not useful or rewarding to repeat much of the information presented. But we will consider these resources from an ecological stand-point and, where possible, point out those areas wherein significant resource-environment relations are known. Perhaps the most significant aspect of demersal stocks is their continuity around the northern rim of the Pacific Ocean and Bering Sea basin from the California coast to the Okhotsk Sea or the Sea of Japan, completely within the Subarctic Pacific Region. Extensive migrations of sablefish from the Washington coast to the northern Bering Sea have been adequately documented (Sasaki et al 1975), and there is one instance of a walleye pollock being tagged in the western Bering Sea and recovered in the eastern Bering Sea. Although the routes of the former are considered to be along the rim of the basin, the route of the pollock cannot be precisely defined because some pollock are believed to be distributed in the surface and intermediate waters beyond the continental shelves during certain seasons of the year (Japan Fishery Agency 1974). Halibut tagging studies have suggested both short and moderately long migrations in the northeastern Pacific Ocean, and there is evidence of numerous local cod stocks. Before considering migrations it is useful to define continuous strata and discrete subsurface coastal domains.

Only northward of the Pribilof Islands do seasonal effects penetrate below 200 m depth. Generally, only when demersal fish move up over the continental shelf do they encounter markedly variable conditions; whereas, conditions below 200 m are relatively stable. Nevertheless, there are two features at depth that could influence demersal fish movements at depth, and these are the temperature-maximum and oxygen-minimum strata. The temperature-maximum stratum exists immediately below the maximum depth of winter overturn; and, over much of the region, it is in the 3-5°C range--the higher values existing southward of the Gulf of Alaska (Figure 60), and the lower values existing northward of the Pribilof Islands. In reality, this is not actually a stratum but merely the top of that part of the water column that has not been cooled by winter overturn. This is significant in that even when winter overturn extends below 200 m it rarely extends to 300 m (except in the Okhotsk Sea); and, thus, even in the northern Bering Sea, demersal fish can find 3°C temperatures at moderate depths along the continental slope. However, in order to do so they must sink lower and lower in the water column and by doing so they encounter the effects of the dissolved oxygen-minimum stratum. This is a true stratum that exists between 800 and 1000 m throughout the region (Figure 61). Surface values at or above 100% satur-ation fall to less than 10% saturation in this stratum and increase gradually to the bottom. The effect of this stratum on demersal fish is not known even though fishing is conducted at depths exceeding 1000-2000 m. However, off the Oregon coast there is a marked shift in relative abundance of sable-fish and of Pacific cod, Pacific hake, and grenadiers, or rattails (genus Coryphaenoides) near 500 ftm (914 m) (Alton 1972) and a marked reduction in the abundance of snow (Tanner) crab (Chionoecetes spp.) near 400 ftm (732 m) (Pereyra 1972) (Figure 62).
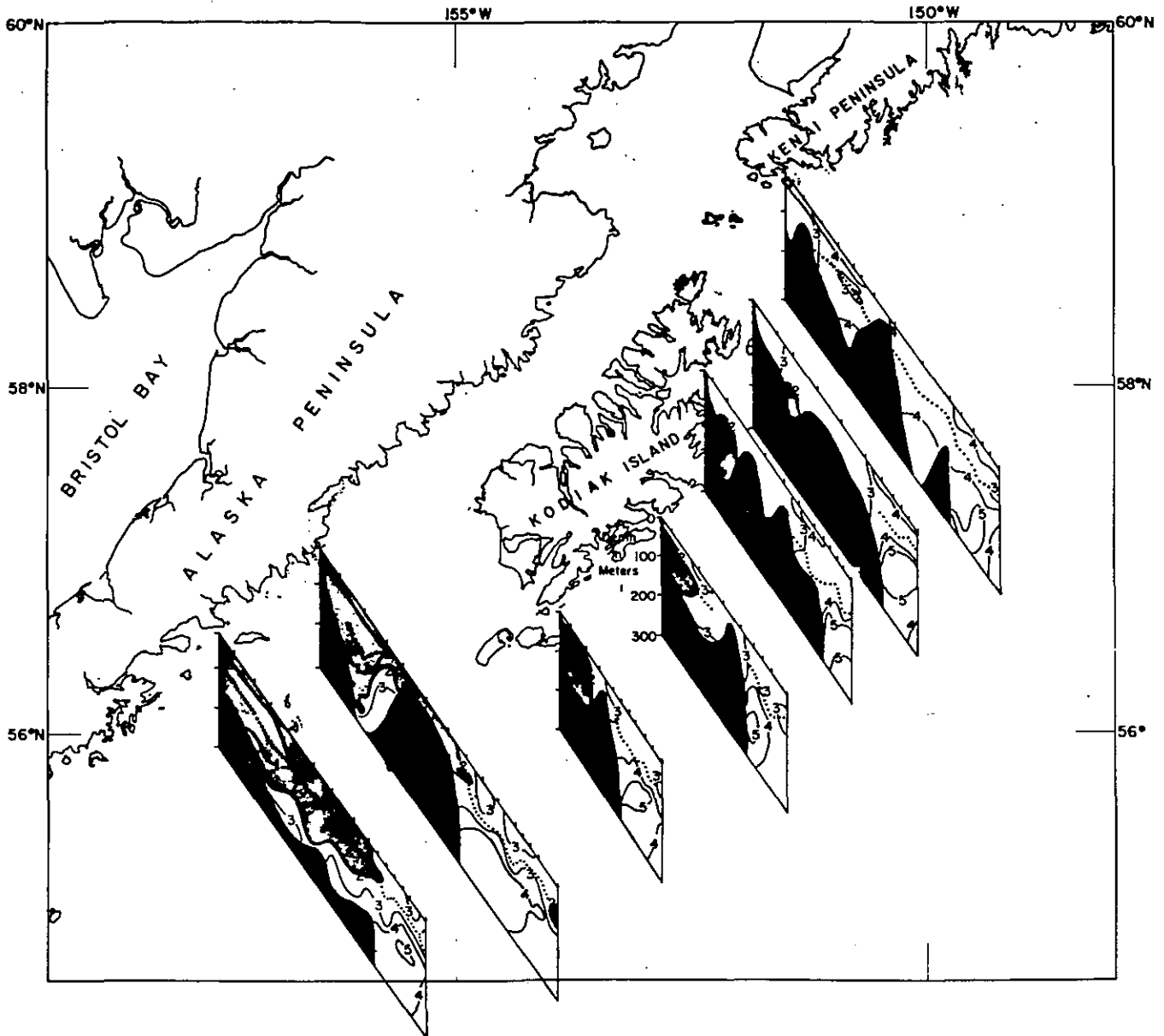
Figure 60. Vertical profiles of temperature (^{o}C) sections near Kodiak
in May 1972 indicating the 4–5°C temperature-maximum
stratum near the edge of the continental shelf (200 m).
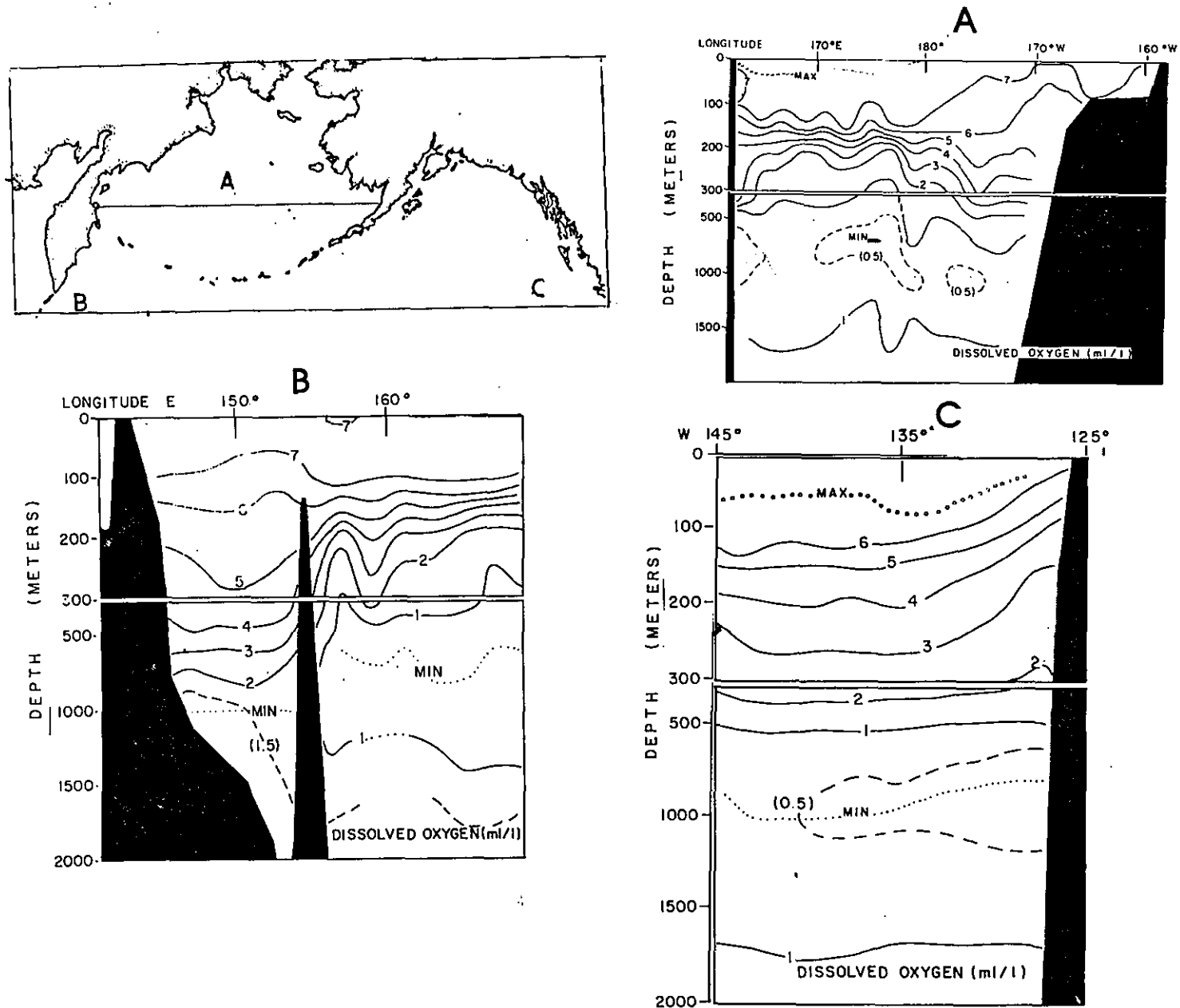
Figure 61. Vertical profiles of dissolved oxygen (ml/l) sections
across the Bering Sea at lat 57°N and at lat 49°N off
the east coast of Asia and the west coast of North America
indicating the oxygen-minimum stratum near 800-1000 m.
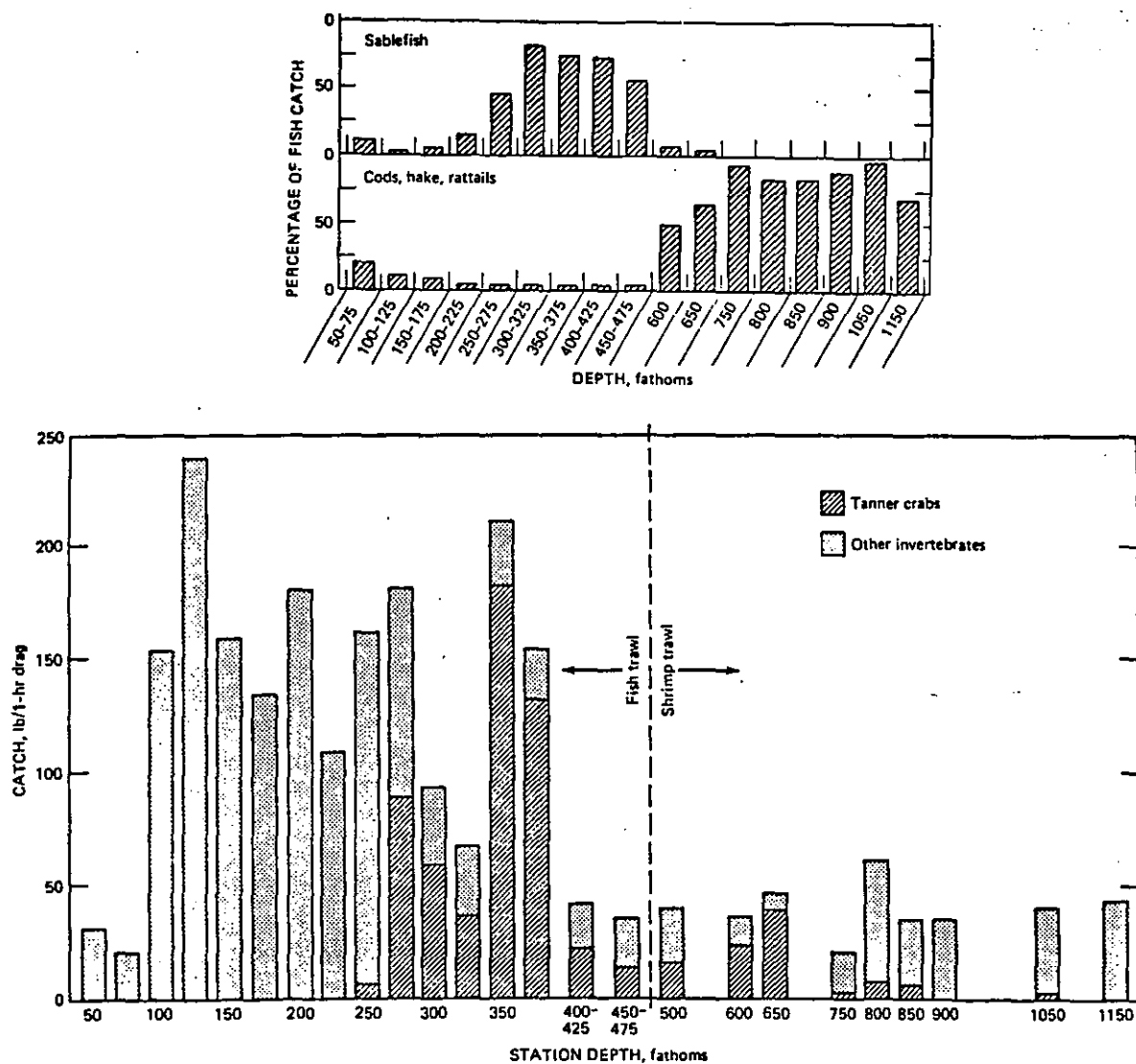
Figure 62. Depths of selected fish, and of snow crab abundances off the northern Oregon coast indicating marked changes near the depth of the oxygen-minimum stratum, 800-1000 m (437-547 m) — (from Alton 1972; and Pereyra 1972).

Any domain criteria are of course quite arbitrary, but the concept is useful and permits emphasizing environmental changes and 4 shelf-slope domains are suggested (Figure 63). The first domain (A) extends from the lower California coast, northward of cyclonic gyre off Baja California, and extends to the northern Vancouver Island. This domain is characterized by a number of environmental conditions and processes: a reversal of surface flow, northward in winter and southward in summer; major upwelling in spring and summer; a continual northward undercurrent below 200 m originating from the tropical, if not equatorial region; the absence of ice; and, temperatures at the edge of the continental shelf of 5-8°C. The second domain (B) is a transition zone, from northern Vancouver Island to the northern Queen Charlotte Islands where the surface reversal of flow may or may not occur, upwelling may or may not occur, the undercurrent terminates, and ice may form along the coast in winter. The third domain (C) extends from the Alexander Archipelago around the Aleutian Island portions of the Aleutian-Commander island arc and across the eastern Bering Sea to the Pribilof Islands. Here there is no seasonal reversal of surface flow, no major upwelling, no undercurrents, the presence of coastal ice, and temperatures at the edge of the continental shelf of 3-5°C. The fourth domain (D) extends from north of the Pribilof Islands westward around the Bering Sea basin to Cape Olyutorskiy, and the dominant feature in this area is the presence of ice in winter well seaward of the continental shelf. This causes winter overturn in the water column at the shelf edge to erode the warm temperature-maximum stratum (3-5°C) characteristic of the edge of the basin as far south as southeastern Alaska. Although there is a divergence in surface flow (<200 m) at Cape Navarin, as the Navarin Current turns eastward toward Bering Strait, flow largely below 200 m follows the bathymetry of the edge of the basin westward around the northern part of the Bering Sea. It is in this domain that we have for the first time a penetration of seasonal effects below the shelf edge. During the winter period, the loss of heat as a result of vertical winter overturn is greater than the horizontal advective effects of northward flow in the Transverse Current along the continental slope, thus, cooling occurs at the shelf edge during winter and spring and warming occurs during summer and autumn. This could result in essentially a seasonal opening and closure of a potential westward migration path at the shelf edge around the northern part of the Bering Sea basin. Because of the delay in removing the latent heat from the greater depths of the water column, minimum temperatures at depth will occur in late winter and, because of this delay, maximum advective effects occur up to this time. Thus, as the ice cover advances southward over the surface, the warm water (3-5°C) being advected northward over the continental slope is exerting a maximum warming effect on conditions at depth and one would expect the maximum northward penetration of demersal fish that require the higher temperatures (3-5°C) at this time. However, surface cooling is progressively eroding the heat content of the water column through convective and diffusion processes. When these exceed the effects of horizontal advective processes the entire water column cools; this occurs along the northern coast first and subsequently progressively southward along the eastern rim of the basin to the location wherein ice does not extend seaward of the continental shelf, essentially the Pribilof Island area.
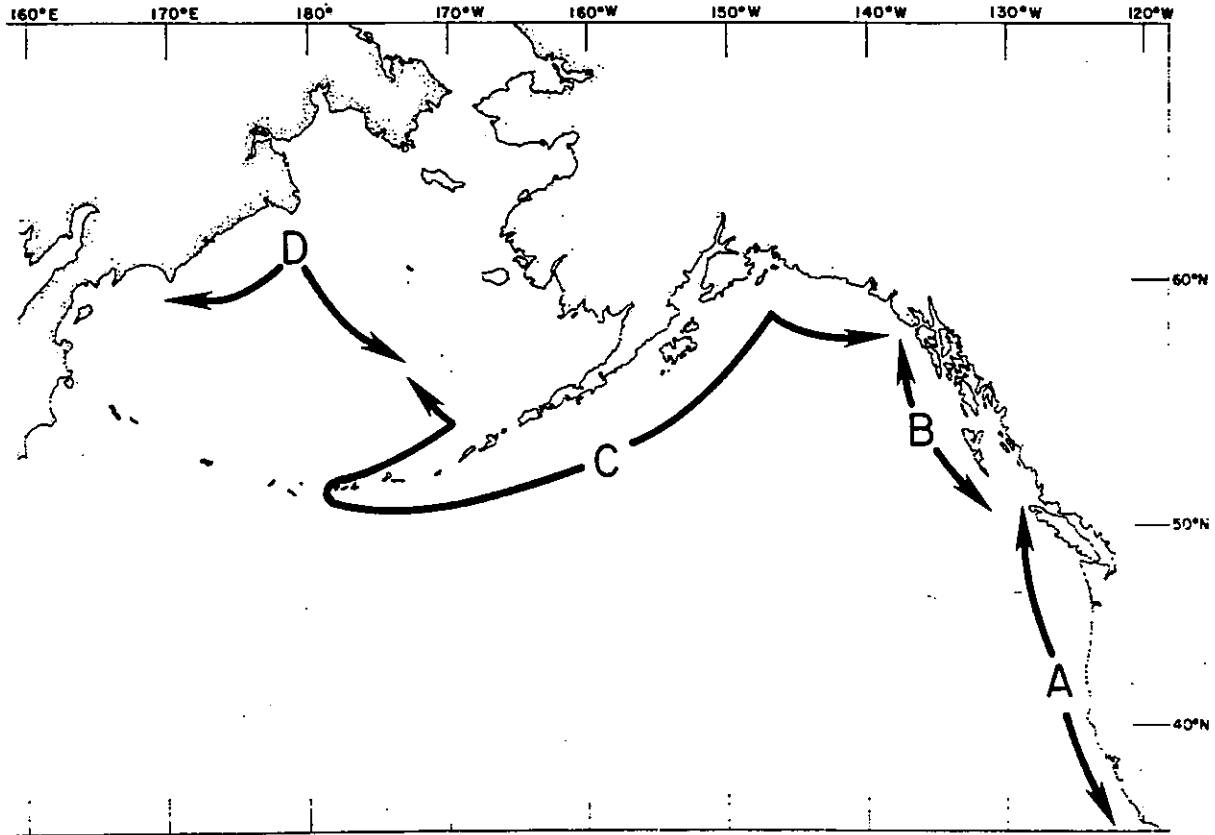
Figure 63. Four subsurface domains that influence the distributions of demersal fish.

In the absence of data to the contrary, it is assumed that winter winds in the ice free portion of the Bering Sea are adequate to insure uninterrupted flow over the slope around the basin, thus, in spring, when the ice cover is no longer present, the insolation and advective effects dominate and warm conditions are progressively restored not only at the surface but at depth. Disregarding diffusion effects and assuming an along slope flow of 10 cm/sec, the 3-5°C regime at the shelf edge could advance from the Pribilof Islands to Cape Olyutorskiy by late summer or early autumn and considerably beyond prior to February when vertical convection will commence to erode the heat content. Westward of Cape Olyutoskiy, extreme winter conditions prevail and temperatures below 0°C can occur at the shelf edge and similar conditions occur southward around the Kamchatka Peninsula and into the Okhotsk Sea.

Apparent resource-environment relations are discussed in relation to 4 important species and 1 family: the Pacific cod, Pacific halibut, Pacific ocean perch (Family Scorpaenidae), walleye pollock, and yellowfin sole. All extend from the California or British Columbia coast around the rim of the Pacific Ocean and Bering Sea basin to the Kamchatka Peninsula or Sea of Japan (Figure 64) and are representative of a large number of fishes that are found in this coastal regime.

2. Pacific Cod

Pacific cod extend from southern Oregon around the periphery of the Subarctic Pacific Region to Korea, including the Aleutian-Commander island arc, and are found in water temperatures of 0 to 10°C. One of the best treatments of ecology of cod in the northeastern Pacific is that of Ketchen (1961), but even this discussion suffers from infrequent and incomplete monitoring of the environment and, therefore, provides only general resource-environment relations.

Cod follow a seasonal bathymetric cycle of migration and are found at greatest depths during winter during spawning (January-March). They migrate into shallower regions of the shelf from spring to mid-summer and then return to deep water, completing the migration by December. The depth range off the Canadian coast (31-146 m) is small compared to that in the western Pacific (15-450 m) and the difference is assumed to be related to the amplitude of the seasonal temperature cycle. Ketchen found that main concentrations of Pacific cod on banks adjacent to the Canadian coast are to be found between the 6° and 9°C isotherms, seasonal depth distribution cycles (and depth migrations) were found to be synchronous with seasonal cycles of temperature in the bottom layers. He suggested that intrusions of water having temperatures much above or below this range would result in cod moving away from usual fishing grounds and could lead to erroneous estimates of year-class strength or recruitment. Thus, by monitoring the temperature changes and anomalies, prognoses on the distribution of individual cod stocks might be possible. This conclusion is substantiated by Moiseev's (1960) summary on the behavior of Pacific cod as well as Alverson's (1960) studies of cod distribution off the west coast of North America.
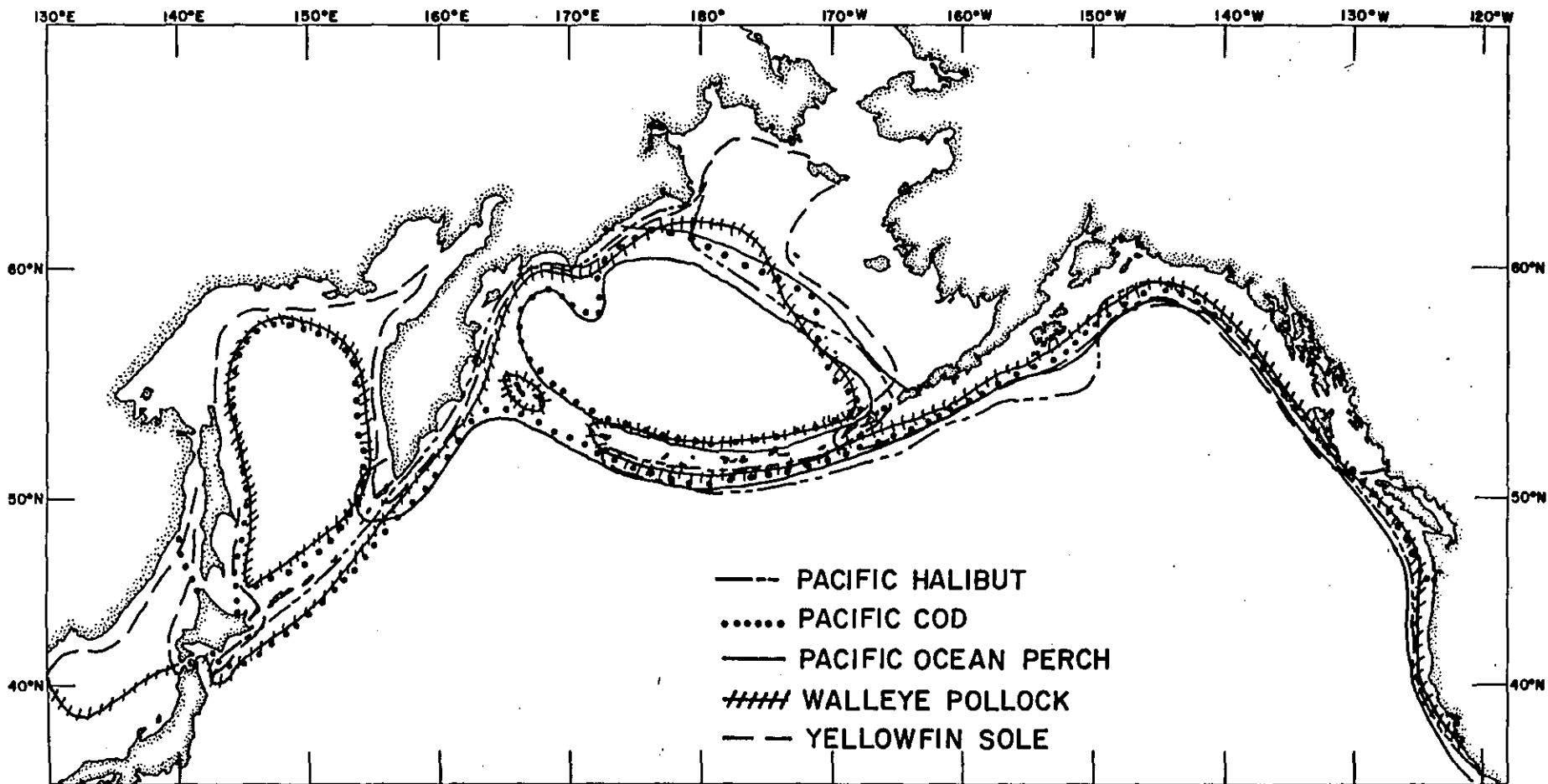
Figure 64. General geographic range of various demersal fish: (1) Pacific cod, (2) Pacific halibut, (3) Pacific ocean perch, (4) walleye pollock and (5) yellowfin sole (from Pereyra et al. 1976).

Also significant is that, compared to the more northern areas, cod off the Canadian coast have an early rapid growth rate, reach sexual maturity several years earlier, and have a shorter life span. But perhaps most important is that stocks acclimated to this regime, close to the southern limit of the geographical range, may have a northern limit to their distribution because north of southeastern Alaska temperatures at spawning depths are less than 6°C--whereas, from northward and westward around the Gulf of Alaska, out along the Aleutian Islands, and into the southeastern Bering Sea, temperatures at 100 to 250 m are in the 3 to 5°C range. However, ice cover that extends seaward of the shelf in winter in the northern Bering Sea, not only results in -1°C shelf temperatures, but also erodes the 3-5°C temperature-maxima at the shelf break; and temperatures of 0-2°C occur that extend around the Kamchatka Peninsula and into the Okhotsk Sea.

Salveson and Dunn (1976) noted that Pacific cod in Asian waters spawn at temperatures of 0° - 5°C, and Wilimovsky et al (1967) suggested on the basis of meristics characters that cod stocks in the northern and western Bering Sea were distinct from those in the eastern Gulf of Alaska. Evidence that cold water forms a barrier to cod distributions has been reported in the Spitzbergen area (Lee 1952), and Horsted and Smidt (1965) reported that in many Greenland fjords cod follow the capelin when the latter arrive there in May and June to spawn. When cold water is present, however, the capelin arrive in fjords without being followed by cod because the latter did not pass through the cold water barrier. Although the Pacific cod is not considered to undertake extensive geographic migrations and commonly form local populations whose seasonal migrations are limited to 300-500 km (Moiseev 1956), the subsurface domains defined (see Figure 63) suggest that the general distribution of Pacific cod presented by Salveson and Dunn (1976) may be separated into 4 areas. Obviously a number of local stocks could exist within these areas.

Cod eggs are demersal and even adhesive, and because in some areas, particularly the Canadian coast, spawning occurs well up on the continental shelf rather than near or over the continental slope, they are exposed to considerably less transport during early life history stages than fishes that spawn over the slope where high current speeds occur at the edge of the ocean basin.

3. Pacific Halibut

Although regulated by an international commission and not exploited as a trawl fishery, Pacific halibut has been studied extensively and provides insight into factors affecting groundfish in the Gulf of Alaska. The success of the halibut is entirely dependent on flow in the Alaska Current System.

Eggs are released in winter below the edge of the continental shelf and developing larvae remain at depths below 100 m for several months after which the larvae ascend into the surface layer and are carried onto the shelf and eventually into shallow water the following winter, a requirement for subsequent development. Those eggs deposited south of Vancouver Island are

subject to flow in the California Undercurrent and are carried northward
and shoreward as they rise to the surface layer in the Alaska Current System.
Those eggs released over the continental slope at the eastern side of the
Gulf of Alaska will be advected at speeds of roughly 5-10 cm/sec and thus
will emerge over the depth of the continental shelf and be swept into the
coastal regime at the head of the gulf. However, those eggs released in
the boundary current at the western side of the gulf, the Alaskan Stream,
will be advected at speeds of 50 cm/sec and thus carried west of the Alaska
Peninsula before rising into the surface layer. This implies that these
larvae will be subsequently carried along 3 routes: into the Bering Sea
through the Aleutian Passes, westward out along the Aleutian Islands in
the Alaska Stream, or southward and eastward across the Alaskan Gyre.

One of the dilemmas with respect to halibut spawning is that unless there
is a general southward migration of adults to areas where they were initially
spawned, there should be a progressive northward shift in the spawning area.
One could argue that if a southward spawning migration occurred this would
be manifestly clear in tagging and abundance studies, and there is no
consistent evidence of this. Further, it would appear that the end point
of such a southward migration would be associated with a frontal zone or
marked change in environmental conditions at some point along the continental
shelf, and this is difficult to identify. Thus, one is forced to look for
natural phenomena that permit perpetuation of the halibut stock.

Certainly one obvious environmental phenomenon is the Alaskan Gyre. Not the
small eddy the IFC scientists in the 1930's believed existed off Kodiak
(Thompson and Van Cleve 1936), but the large natural system clearly delineated
at the sea surface by salinity (Figure 65). This gyre would permit larvae
that rise to the surface layer 1-2 months after spawning (February-March)
to be carried from the slope area west of the Alaska Peninsula eastward
across the Gulf of Alaska at roughly lat 50°W and deposited on the California-
Oregon-Washington-British Columbia-Southeastern Alaska coast the following
winter. There is speculation that the larvae can remain in the upper portion
of the water column for such a long period of time, however, Hubbs and
Wilimovsky (1964) in a study of the Greenland turbot (Reinhardtius hippo-
glossoides) felt that young fish or perhaps even adults stemming from the
population in the northwestern Pacific as well as the population that likely
exists off the south side of the Aleutian chain were presumably carried
eastward by the North Pacific Drift to the west coast of North America. Those
larvae carried southward in the California current would serve to replenish
stocks south of lat 50°N, whereas those carried northward along the coast
in the Alaska Current System would replenish stocks north of lat 50°N.
Obviously the actual latitude of divergence would vary as would the relative
abundance of organisms carried to the north or south.

Those larvae not recirculated in the Alaskan Gyre are carried westward in the
Alaskan Stream; some will settle in the shallow embayments of the Aleutian
Islands, some will be carried westward into the Western Pacific Gyre and
possibly to die in an oceanic regime or to be carried to the east Kamchitka
coast, some will be carried northward through the eastern Aleutian passes to
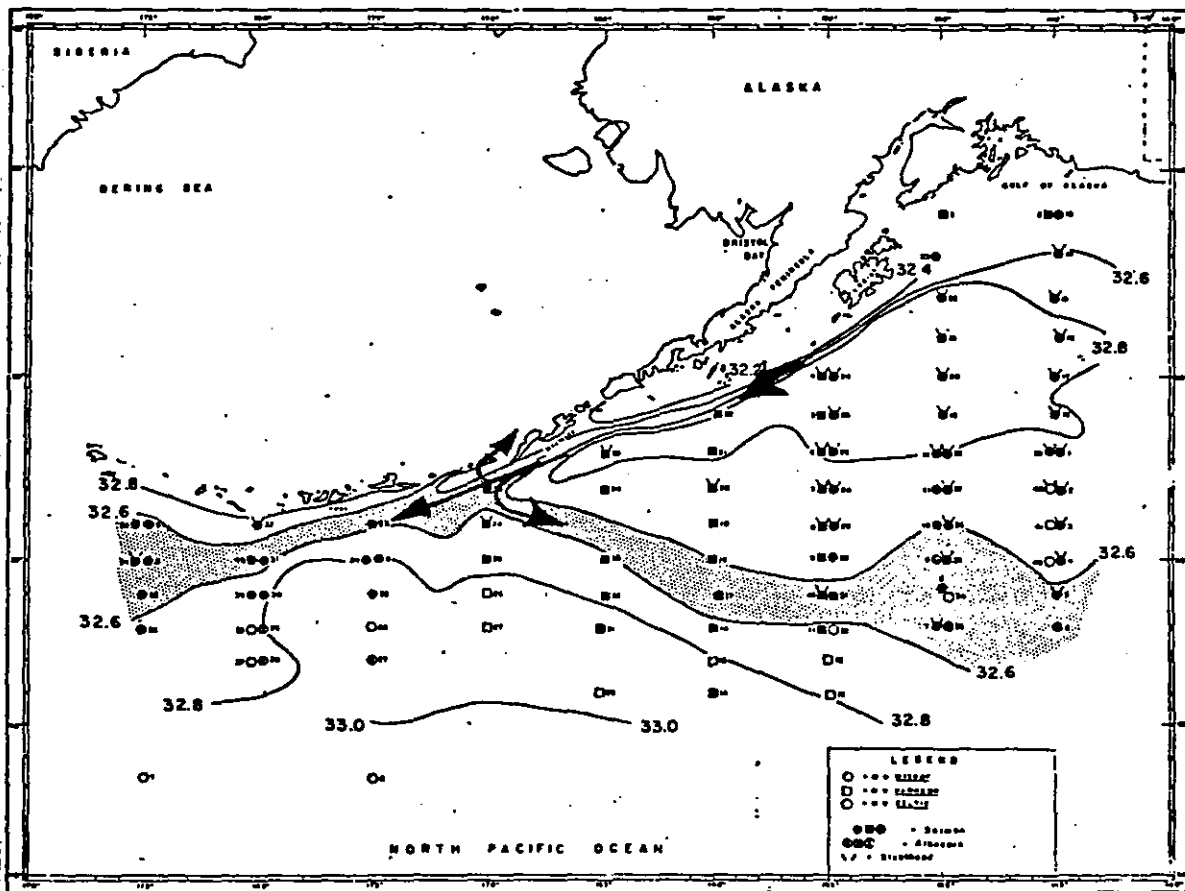
Figure 65. Horizontal distribution of surface salinity in summer
1956 showing recirculation of coastal water south of the
eastern Aleutian Islands eastward around the Alaskan
Gyre (adapted from Favorite and Hanavan 1960).

the eastern Bering Sea, and some will move through the western Aleutian passes and be carried to the western coast of Asia. Certainly the point at which the larvae die is open to question, but the dispersion patterns certainly auger well for perpetuation of the species.

Pacific halibut also spawn in winter over the continental slope in the southeastern Bering Sea. Eggs and larvae spawned in this area could be carried northwestward possibly as far as Cape Navarin before rising to the level of the continental shelf. Flow in the Navarin Current will carry them over the shelf to the required substrata and flow in the Olyutorskiy Current will also carry some larvae on to the Siberian coast.

This species also has a seasonally changing temperature requirement. During winter in the eastern Bering Sea adult halibut occur in high concentrations over the continental slope at temperatures greater than $3^{o}C$. After spawning they migrate into shallow water on feeding migrations where their movements are hindered by the cold regime ($>1^{o}C$) over the central portion of the shelf. By summer, the main concentrations of halibut are encountered in waters with a broad temperature range (4.5 to $10^{o}C$), but some are found in temperatures as low as $0.5^{o}C$ (Novikov 1964). Thus, during summer, attempts to predict halibut distributions from bottom water temperatures are less successful. But as the ice cover advances in late autumn and winter, the halibut retreat southward and westward to the continental slope at the southeast corner of the Bering Sea basin to repeat the spawning cycle. The concentration of halibut near the cold temperature front in the mid-shelf area of the eastern Bering Sea is apparent in IPHC data in June 1976 (Figure 66). Although there is a slight penetration of the temperature front, there is an obvious avoidance of the general area of low temperatures.

4. Pacific Ocean Perch

This ovoviviparous species spawns once a year, in winter off the Washington-Oregon coast and generally late winter and early spring northward along the coast as far west as the Kamchatka Peninsula, including the Commander-Aleutian island arc (Major and Shippen 1970). Adults are usually found along the outer continental shelf and on the upper slope at depths of 150 to 460 m, especially in and along gullies, canyons, and other depressions. Spawning in the Bering Sea was reported at 25 to 30 m off the bottom in depths of 390 to 400 m and the larvae ascended to roughly 250 m depth within a few hours. After a year in a planktonic stage largely at the mercy of ocean currents, during which they may be dispersed far offshore, juveniles are found near the bottom in water 125-150 m depth until reaching maturity. Adults remain well above the 1 ml/1 dissolved oxygen stratum in temperatures of 4 to $6.5^{o}C$ from depths of 350 m in summer to 420 m in winter.

Although little is known about the pelagic and benthic phases of juvenile Pacific ocean perch, it is apparent that the northward flow of warm water along the edge of the continental shelf and upper slope is important to the survival of the species, but here again we are faced with a northward transport
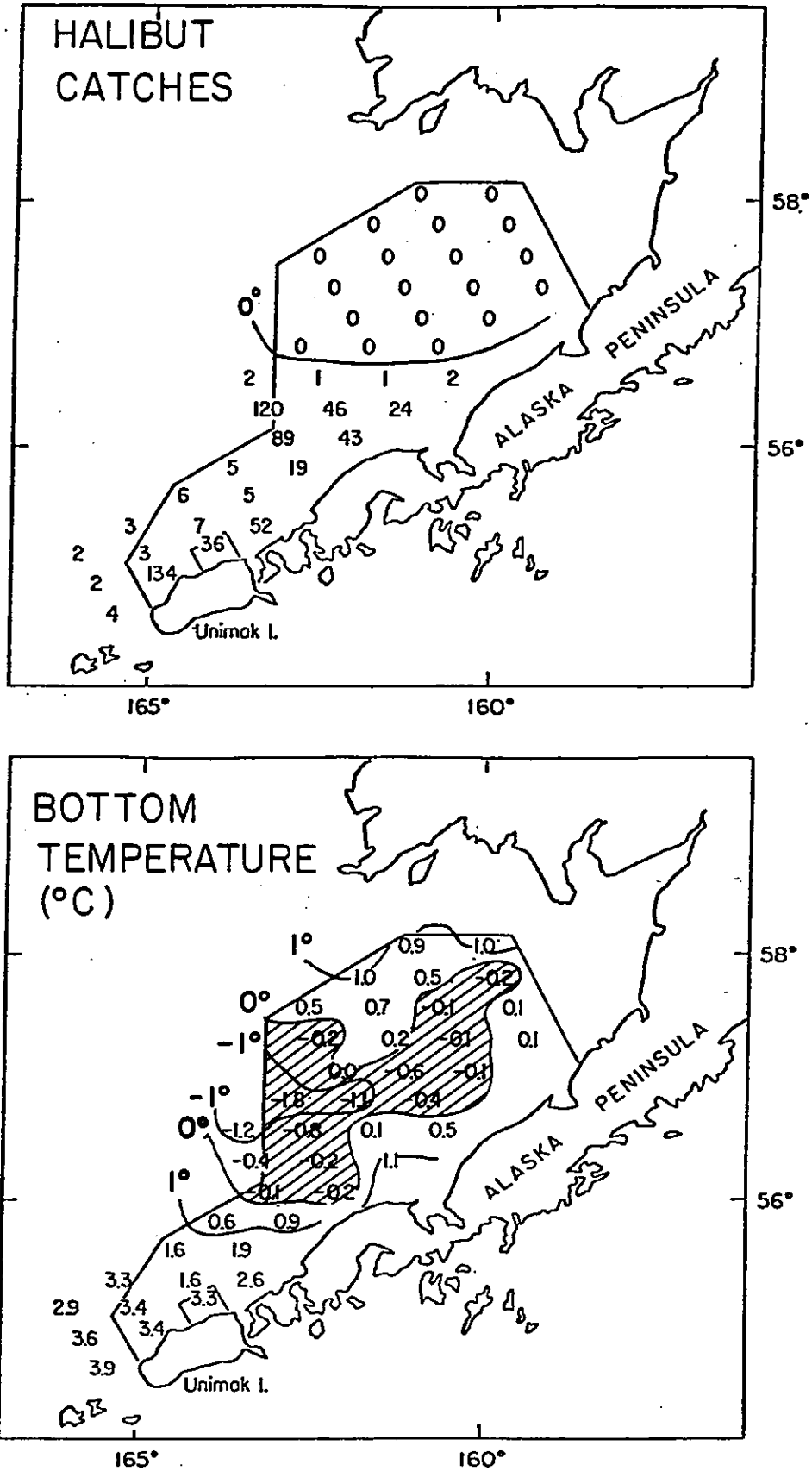
Figure 66. Halibut catches and bottom temperatures in eastern Bering Sea by IPHC in June 1976 indicating an initial penetration of the cold mid-shelf regime, but the concentrations indicate a reluctance to penetrate into the cold water area.

of larvae with only two possible explanations for replenishment of southern stocks along the west coast of the United States--migration of adults, or transport of larvae around the Gulf of Alaska gyre. And again, the time interval for pelagic existence, 1 year, is adequate to permit transport around the gyre.

5. Walleye Pollock

The walleye (or Alaska) pollock is endemic to the North Pacific Ocean and Bering Sea and are distributed from the California coast northward around the edge of the basin to waters off Japan and Korea. Although believed to occupy waters of the continental shelf and upper slope throughout its range, there is evidence that they are distributed in the surface and intermediate waters beyond the continental shelves during certain seasons of the year (Salveson and Alton 1976b).

As indicated earlier, the presence of pollock in the Aleutian Island area was noted about 90 years ago, but it was not fished extensively until the last decade. At the present time, roughly 90% of the catch in the eastern Bering Sea is pollock and there are reports that numbers of pollock in the Gulf of Alaska are increasing. Observations by the Ketchikan Trollers Association in 1976 indicate that the presence of pollock in the waters of southeastern Alaska is greater than at anytime in the last several decades. Whether this reflects an increase in the Bering Sea juvenile population that cannot be accommodated in that area, causing an increasing expansion of the stock into the Gulf of Alaska, or that this is a normal cyclic phenomenon that has not been adequately documented, is not known. Serobaba (1971) noted that pollock spawning occurred from March to July in a very restricted area north of Unimak Island, and subsequent data on commercial catches indicated that adult pollock were indeed concentrated in this area, particularly during the early part of the spawning period (Figure 67). In early spring 1976 investigations (for the Outer Continental Shelf Environmental Assessment Program--or OCSEAP) by the NMFS Northwest and Alaska Fisheries Center, in the eastern Bering Sea, found pollock spawning 30 km inside the ice field well north (>100 km) from Unimak Island, but subsequent collections of pollock eggs at the surface in late spring indicated maximum concentrations well north of Unimak Island, but not so distant that currents could not have carried them there from a location near Unimak Island. Nevertheless, this raises several questions--is the pollock spawning area in the eastern Bering Sea related to (1) the location of the ice field in early spring, (2) the geomorphology of the area north of Unimak Island (the Golden Triangle area in the southeastern corner of the Bering Sea basin), or (3) environmental conditions other than ice or bathymetry. It would be useful to know which of these is correct; for if spawning does occur in a limited area, ichthyoplankton studies could provide an estimate of the spawning population--thereby providing guidance to management decisions before intensive spring-autum fishing begins. Such studies might also provide insight into whether or not there are one (Takahashi and Yamaguchi 1972) or two (Maeda 1972) pollock stocks in the eastern Bering Sea (Figure 68). However, it should be pointed out that Iwata (1976) has reported that pollock tagged in the western Bering Sea were recovered in the eastern Bering Sea, and this suggests that we should be looking for migration routes of pollock.
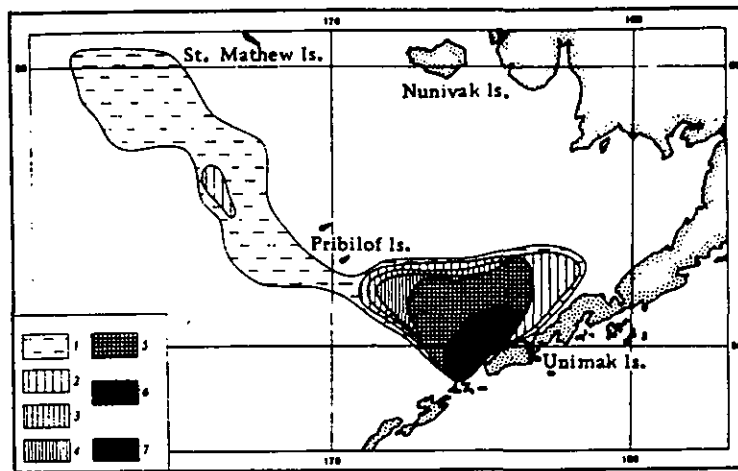
Figure 67. Distribution of walleye pollock eggs in the eastern Bering Sea in March-May 1965 – catch rates are: (1) 1-50, (2) 51-100, (3) 101-200, (4) 201-500, (5) 501-1000, (6) 1001-2000, and (7) more than 2000 (from Serobaba 1967).

ONE STOCK CONCEPT
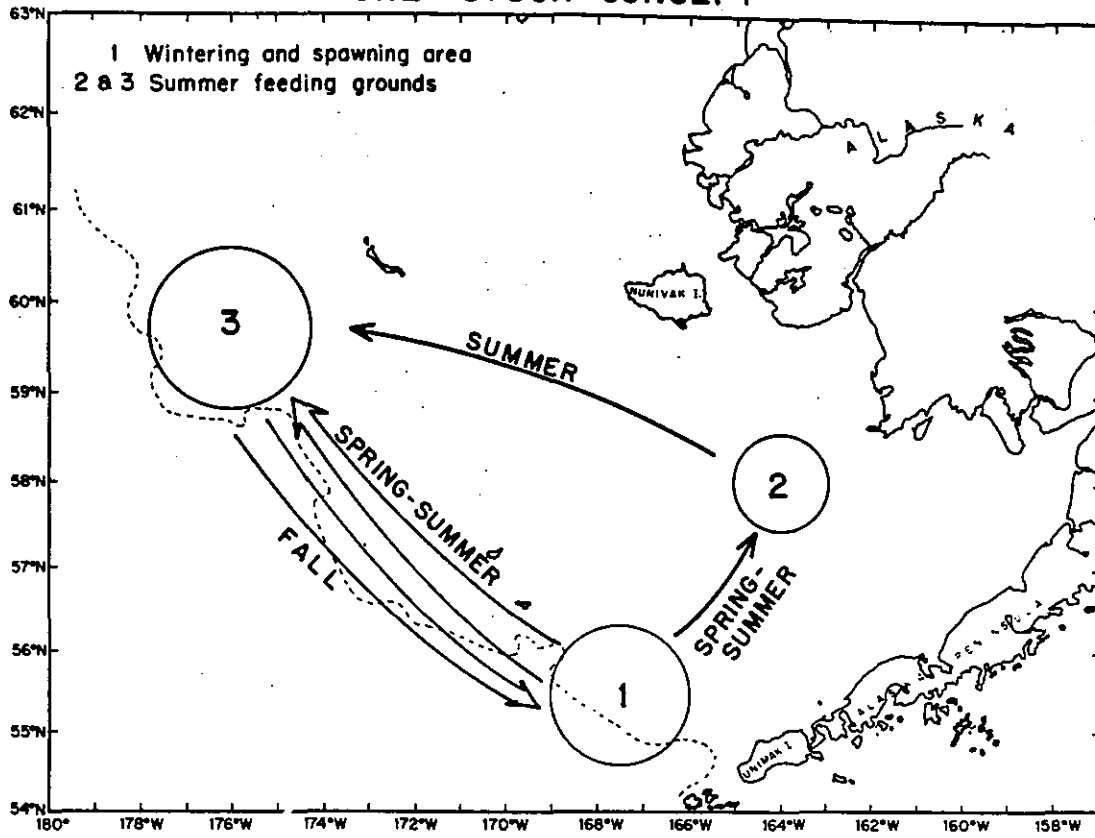
TWO STOCKS CONCEPT
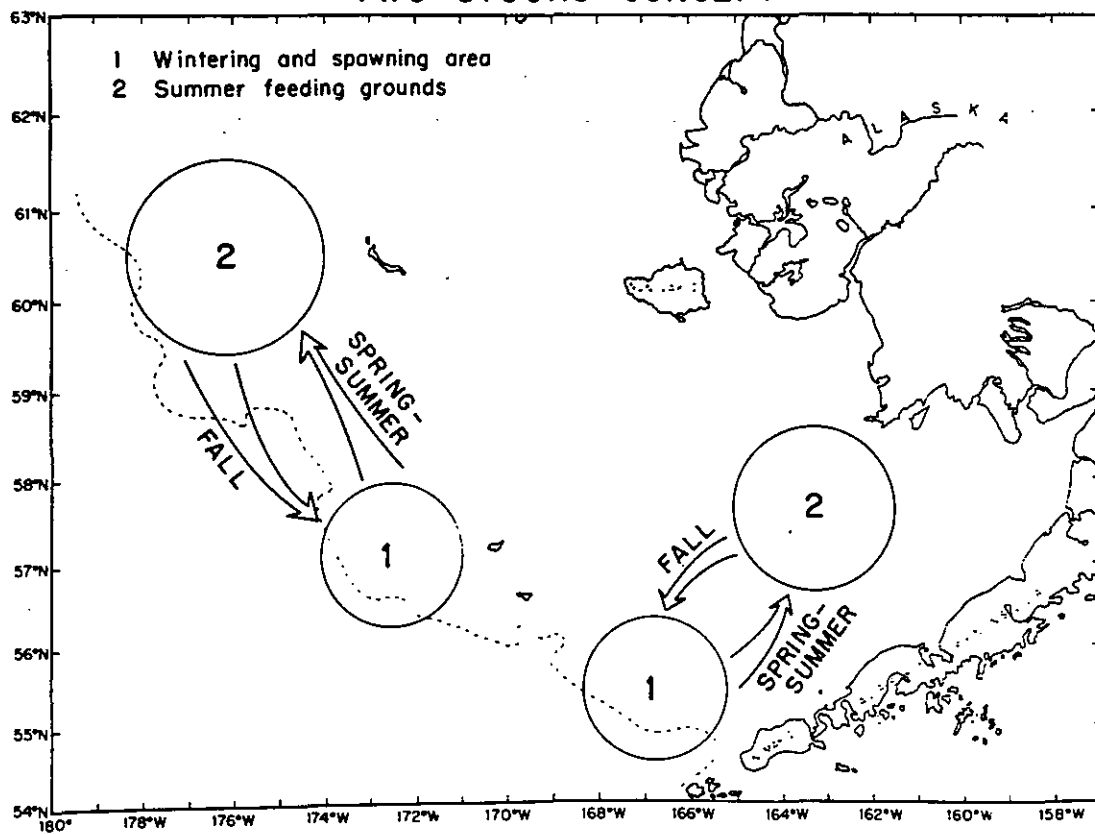
Figure 68. The movements of walleye pollock in the eastern Bering Sea based on (A) a one stock concept and (B) two stocks concept (from Salveson and Alton 1976b).

Little is known about pollock spawning areas in the northeastern Pacific
Ocean. During a cruise conducted by the NMFS Northwest and Alaska Fisheries
Center in the vicinity of Kodiak Island in May 1972 (Dunn and Naplin 1974;
Favorite et al 1975) pollock eggs were found at 29 of 67 stations and accounted
for 97.2% of the total egg catch. Eighty-three percent of the pollock
eggs were caught at one station off the Alaska Peninsula south of Shelikof
Strait (Figure 67), and the egg density ($1046/m^2$) was roughly 50% of the
maximum reported by Serobaba (1971) north of Unimak Island. Although surface
conditions were not anomalous ($1.3^{o}C$, 32.25 $^o/oo$), bottom temperatures
indicated a sharp frontal zone, values decreasing from $3^{o}-1^{o}C$ near 200 m.
It would appear similar conditions would occur at numerous locations along
the southern coast of the Alaska Peninsula.

At the present time there are two major environmental programs related to
the early life history stages of pollock in the eastern Bering Sea in addition
to ongoing programs by the NMFS Northwest and Alaska Fisheries Center; these
are the OCSEAP and Processes and Resources of the Bering Sea Shelf (PROBES)
programs.

6. Yellowfin sole

The most recent summary of information on this species (Salveson and Alton
1976a) indicates several interesting phenomena. The southern distribution
of yellowfin sole at the eastern side of the ocean is limited to northern
British Columbia, and in this general area its bathymetric range is limited
to 100 m or less. Whereas, in the eastern Bering Sea, the most recent area
of the largest biomass, there is an extensive migration of adults from the
continental slope from depths of 360 m in spring and early summer across
the continental slope to depths as shallow as 4 m; and a return in autumn
to the slope area. Salveson and Alton (1976a) note that the stimulus for
wintering fish to migrate to inner shelf waters during the spring apparently
is not the warming of these waters because the sole actually move from
relatively warm, deep water (3.5 to $4.5^{o}C$ in April) to shelf waters below
zero in April and May; and in addition, they report that large concentrations
of sole in near zero temperatures at times may be the result of the piling
up of fish near the border of cold water masses. However, it would appear
that during shoreward migrations the sole pass southward and around the
cold mid-shelf temperature regime (where bottom temperatures of -1 to $1^{o}C$
occur at this time) and spawn near Nunivak Island in the warm, dilute water
off the western Alaska coast. This spawning behavior is apparently so
different from stocks in the eastern Gulf of Alaska that one suspects that
the cold winter environmental regime in the eastern Bering Sea and other
northern areas necessitates the extensive onshore/offshore migrations of
adults if successful spawning is to occur. This appears to be an enigma
because one must then explain why the sole are not more abundant in the
gulf coastal areas. There are four possible answers: first, perhaps a cold
environment is beneficial to juveniles; second, perhaps the sole were abundant
there but lost their niche in the more southern regime, surviving only in
the northern areas where there was less competition; third, the sole are
presently adapting to a more southern regime, and in the absence of man's
exploitation it could eventually be quite successful; and fourth, over-
exploitation.

As noted above, the spawning area in the eastern Bering Sea is not along the coast, but at the edge of the mid-shelf cold water mass. Although it has been suggested that yellowfin sole may have a preference for the cold side of a temperature gradient, there are other possible explanations. First, extreme dilution occurs in inshore waters in spring as a result of extensive river runoff, and this moves northward along the coast at speeds attaining 50-100 cm/sec. Even though low salinities may not severely affect the eggs and larvae, the northward flow could quickly transport them out of the Bering and into the Chukchi Sea (Pruter and Alverson 1962). Any such transport is greatly reduced with distance from the shore; and, thus, spawning activity at the edge of the mid-shelf regime results in minimum northward transport. There is also another environmental phenomenon that may restrict northward drift of eggs and larvae, this is the existence of a trans-shelf surface flow in the vicinity of Nunivak Island, the Pribilof Current, and also west of the Yukon River Delta, the St. Lawrence Current, proposed by Fujii et al (1974) and Favorite et al (1976). Such east to west trans-shelf flows would aid in the retention of larval yellowfin sole in the southeastern Bering Sea where the juveniles reportedly overwinter in temperature regimes of $0^{\circ}C$ and less; however, the data on this point are fragmentary.

E. CRUSTACEANS

Crustaceans have been defined as water-breathing "insects" of the sea that have a segmented body and limbs at some stage of life, have gills or breathe in water through their skins, have no proper neck, never have wings, are born in locomotive freedom, and have an integument composed of chitin that may be flexible or brittle and may attain the hardness of bone (Schmitt 1965).

The copepods and euphausids that constitute a large part of the macro-holoplankton that serve as forage for both small (such as herring) and large fish (such as sockeye salmon), as well as the huge baleen whales, are crustaceans. Although of no immediate commercial importance to the U.S. fishing industry, the Japanese have for many years profitably harvested these forms, which supposedly are in plentiful supply throughout the region. However, biomass model studies (discussed in Section VI) indicate that starvation in the sea may be more commonplace than believed and intense harvesting of macroplankton in the eastern Bering Sea, for example, could affect ecosystem processes and balances (Laevastu et al 1976).

Of the thousands of marine species, we are interested primarily in the shrimps and crabs. Discussions will be limited to the Dungeness crab; the king crab; and the shrimp, *Pandalus borealis*.

1. Dungeness Crab

The success of the Dungeness crab appears to be inextricably linked to a prolonged period of spawning and the documented seasonal current reversal off the Washington-Oregon-California coast that assures confinement of larvae in the coastal regime. Dungeness crabs have been found on all bottom types from mean low water to approximately 100 m depth along the Pacific coast from lower California northward to the Aleutian Islands.

There have been several attempts to explain resource-environment relations with respect to Dungeness crab off the Oregon coast. Cleaver (1949) pointed out a strong dependence on the conditions affecting early life stages, but Reed (1969) noted that variations in temperature and salinity probably were not likely to cause large fluctuations in larval survival. Hubbard and Pearcy (1971) felt that annual upwelling fluctuations could result in changes in food availability; and Peterson (1973) felt that strong upwelling served to maintain a large crab population because this not only increased food availability but decreased competition for the food.

A local study off the Oregon coast by Lough (1976) indicates that egg-carrying females are found from October to March and maximum densities of larvae occur within 15 miles of the shore in late January. Thus, the larvae are present in the surface layer during the period of northward coastal flow; and this would not only retain early larvae in the coastal regime during the 4 to 5 months of planktonic existence prior to metamorphosing into benthic forms but could return larvae released after January near to the location they were released in July as a result of the subsequent reversal of coastal flow to the south in early spring. Of course, those larvae carried into the Alaska Current System (roughly north of lat $50^{\circ}N$) will continue to be carried northward along and around the coast of the Gulf of Alaska. Coastal flow off Oregon in winter not only tends to contain the larvae inshore, a necessary condition for survival, but is accompanied by a downwelling phenomenon--water piled up along the coast sinks and carries the warmer surface waters down over the continental shelf. The latter condition may even be favorable for the egg release in late autumn and early winter.

Also important to larvae survival off the Washington-Oregon-California coast is the timing of dropping out of the water column and the summer onset of coastal upwelling, May to October, which could carry planktonic forms in the surface layer seaward of the shelf out over the Pacific basin. The extensive seaward plume from the Columbia River must also be considered as a mechanism for transporting planktonic forms in the surface layer away from the shelf area. However, it is apparent that the larvae have a generous time span for assured onshore or alongshore transport and thus survival; however, it can be postulated that the duration and alongshore extent of such flow throughout the period October to March, could be an important factor in year-class strength.

Although wind-stress data may indicate periods of general onshore and offshore flow, actual current measurements along the coast would provide more precise data for estimating spawning success. Some moored current meter arrays are in place off Oregon as part of the Coastal Upwelling Ecosystem Analyses (CUEA) program and hopefully a number of arrays normal to the coast at various locations along the coast will be possible in the future.

In the Gulf of Alaska winter downwelling along the coast is considerably more intense (Bakun 1975) and surface temperatures are much lower than bottom temperatures. As water near the freezing point sinks and moves seaward over the bottom across the continental shelf, the crabs may advance seaward, away from the coastal fishery, even to the point of not being able to completely

return to normal inshore habitats when seasonal events result in warmer conditions because of dispersion or distance traveled. Possible evidence of this is the marked annual Alaska Dungeness crab landings vs the January upwelling index at the head of the Gulf of Alaska (lat 60°N, long 149°W) from 1955 to 1971 (Favorite 1975). Although the catch data in the late 1950's and early 1960's may reflect low or inadequate fishing effort rather than variability in crab abundance, the extreme downwelling index in 1966 and 1971 parallel the poor catches (Figure 69). It is also interesting to note that the recent years reflecting good catches, 1963 and 1968, were periods of warm oceanic conditions.

Thus, the success of the Dungeness crab along the west coast of North America is primarily due to the synchronization of spawning with the dynamics of surface flow along the coast. Variability in abundance of crabs off the Washington-Oregon-California coast will be due primarily to anomalies in flow during the critical autumn and winter periods. An increase in northward flow in winter could result in greater larvae dispersal northward, whereas, an unusually weak or short-term northward flow would result in a more southward dispersal of larvae. The latter could also result in small year-classes because there is a tendency for surface flow to turn seaward near Cape Mendocino rather than continue southward along the coast. In addition, an early onset of summer coastal upwelling along the Washington-Oregon-California coast could also result in a loss of larvae seaward. Obviously the availability of adults to the fishery is also important, but the data on adult movements are inadequate to ascertain specific environmental relations at this time.

2. King Crab

The three commercially important species of king crab are Paralithodes camtschatica, P. Platypus, and Lithodes aequispina and all inhabit the Subarctic Pacific Region on the continental shelves largely from the southern Gulf of Alaska to the Japan Sea in waters of 0 to 10°C. P. camtschatica is the most abundant and has been rather extensively studied in the eastern Bering Sea. Discussions will be limited to this species and this area.

P. camtschatica perform two dominant migrations, a spring migration to the inshore spawning areas near the Amak Island-Black Hills-Port Moller areas and a subsequent offshore migration to the deeper waters to feed (Bartlett 1976). The larvae are planktonic for roughly a 10-week period and generally drift northeastward along the north side of the Alaska Peninsula toward Bristol Bay. During the first juvenile stage (2-15 mm), the larvae inhabit the littoral zone, and on reaching 15 mm they form large aggregations (pods) of several up to several thousand near the shoreline to a depth of 30 m. Although there is speculation that podding is correlated with annual and seasonal changes in the environment, there is also evidence that podding may occur year round.
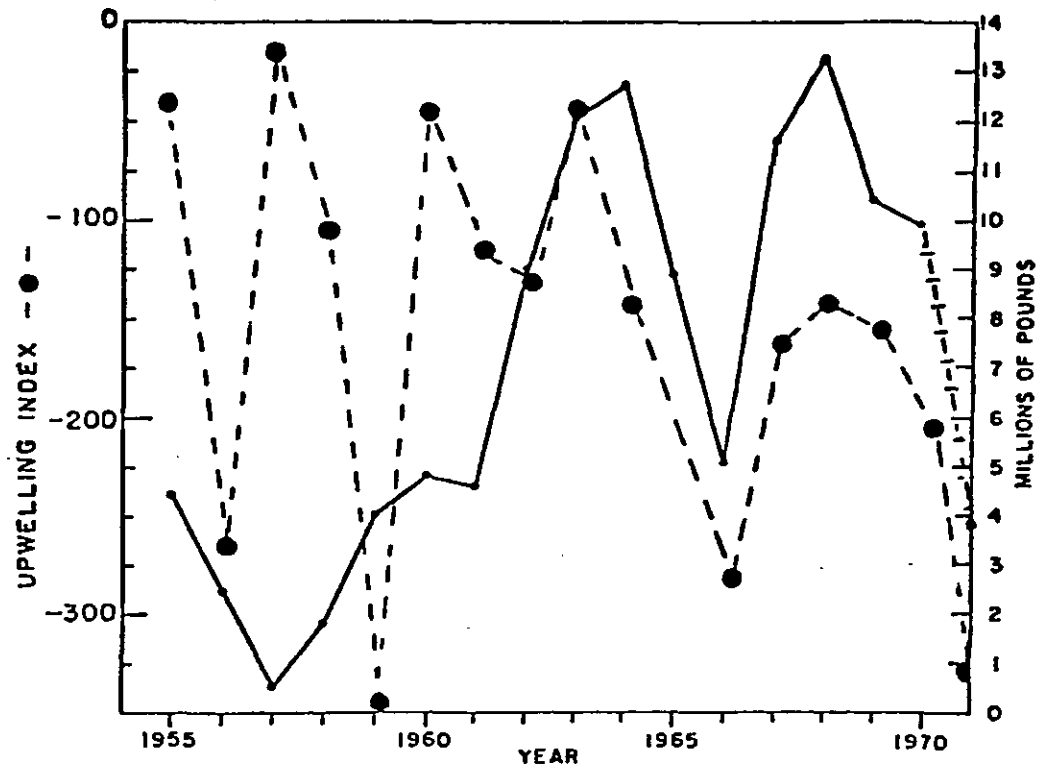
Figure 69. Annual Dungeness crab landings (from Hoopes 1973) vs
January upwelling index at lat 60°N, long 149°W (from
Bakun 1973).

It is recognized that water temperature and availability of food, both
environmental factors, play a major role in the molting frequency of larvae,
and nearly 20 molts are carried out in the first three years, during which
the crabs grow to 60 mm. They subsequently attain 170 mm at about 17 years.

Estimates of abundance of male and female crabs indicate nearly a 100-fold
increase in 60 mm crabs in 1975 compared to 1970 and 1972 (Figure 70). Also
apparent is an extensive increase in older crabs, which is explained as partly
an artifact caused by the use of a less efficient trawl in 1970 and 1972.
However, the maximum distance traveled by a crab in a single year is 666 km
(370 mi.); thus, even though temperatures in the eastern Bering Sea during
1970-73 were anomalously cold (McLain and Favorite 1976), one cannot positively
denote a crab-environment relation with temperature. It would appear that
invariably it is the inability to assess accurately the stock that prevents
ascertaining precise resource-environment relations, rather than the fact
that such relations do not exist.

   3. Shrimp

Ivanov (1969) noted that every water mass (or zone) in the eastern Bering Sea
shelf area was characterized by its own shrimp species. Crangon dalli is the
most common species on the inner shelf, to a depth of 50 m, which has sharp
seasonal fluctuations of seasonal temperatures and a sandy bottom (Zone 1).
Eualus macilentus and Pandalus goniurus are typical species in the mid-shelf
area from 50 to 70 m (or more) which has constant low temperatures and a
muddy bottom (Zone 2). And, Pandalus borealis is the dominant species, and
found in commercial concentrations, at the outer shelf area at depths of 70
to 120 m where relatively constant but warmer than mid-shelf temperatures
occur as a result of heating from waters along the continental slope (Zone 3).
Certainly excellent examples of resource-environment relations, and, as in
previous sections, our discussion will be limited to one species, in this
case P. borealis.

The commercial concentration of P. borealis off the Pribilof Islands is
attributed to 3 factors: a favorable temperature regime, a large muddy area,
and a closed water circulation restricting larvae drift. It is interesting
that these shrimp are not in the warmest part of the shelf area, which occurs
(as noted earlier) at the shelf edge, but in the inshore edge of this regime
that is not seriously affected by winter overturn. Since the latter is
primarily a function of ice cover which is highly variable south of the
Pribilof Islands (as noted earlier) it would appear that the safest area
for these shrimp (whose seasonal migrations appear to be limited to 56-74 km)
would be immediately north of the Pribilof Islands where a number of factors
contribute to a satisfactory environment. To the north of this area the
winter ice field forms earlier and is removed later, thus, winter overturn
extends to depths deeper than 150 m forcing these shrimp closer to the shelf
edge. Whereas, to the south of this area not only the ice field is extremely
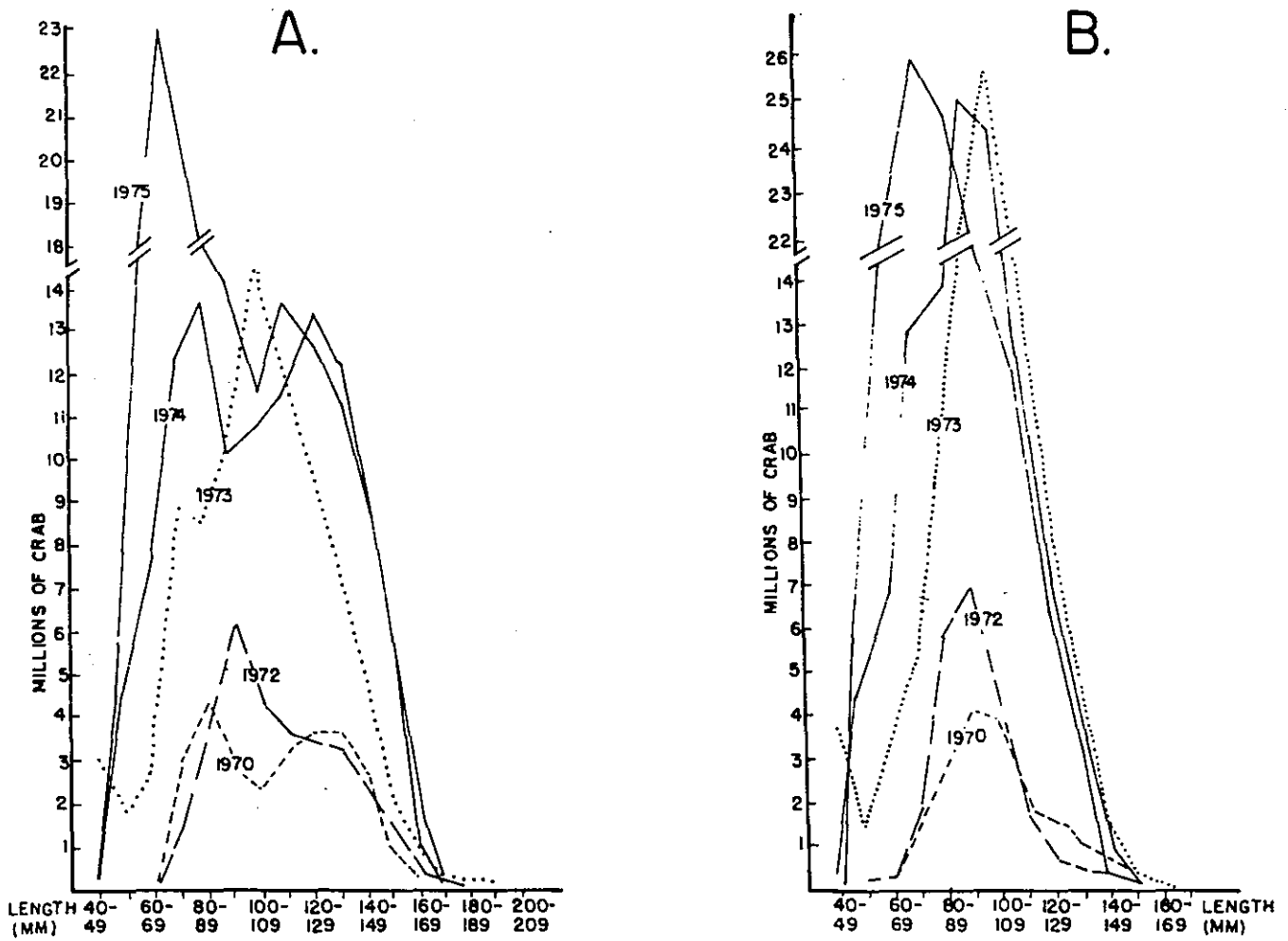
Figure 70.   Estimates of abundance of (A) male and (B) female king
crabs by 10 mm length classes, in the eastern Bering Sea
for 1970, 1972, 1973, 1974 and 1975 (from Reeves 1975)
showing low abundances during 1970.

variable and could necessitate immediate and far-ranging shrimp migrations, but also the onshelf penetration of warm slope water (also apparently avoided by these shrimp) can have large and variable excursions, also necessitating large migrations. Not surprisingly the area having the most stable conditions for these shrimp is the area of large concentrations--just north of the Pribilof Islands (Figure 71).

Even though this area may have the most stable environmental conditions at 50-150 m depth, long-term changes occur. In severe winters, below 0°C temperatures can envelop shrimp concentrations. Ivanov (1969) presents tentative but rather convincing evidence (based on data from 1951-61) that the strengths of different year-classes depend primarily on severity of the winter environment during the first year of life (severe conditions resulting in a poor year-class) and to a lesser degree on the abundance of the parent year-classes.

Although data on P. borealis in the Gulf of Alaska are too fragmentary for an equivalent analysis of resource-environment relations, there are indications that the similar behavior patterns exist. Winter cooling is not such a dominant factor because of the absence of an ice field, and stock fluctuations are not as extreme. The shrimp also avoid the warm (4-5°C) slope water that at times overrides the shelf edge, and maximum catches are usually made in areas of sharp temperature gradients. Maximum concentrations occur along the northern and western side of the Gulf of Alaska where environmental conditions are similar to the eastern Bering Sea (e.g. winter overturn results in below 0°C temperatures at the bottom), rather than in the eastern gulf areas where considerably warmer conditions at depth prevail. One major concern regarding the distribution of P. borealis is the fact that heretofore circulation studies have indicated that a continuous westward flow occurred in the inshore and offshore areas of the northern and western areas of the Gulf of Alaska. This implied a net transport of larvae downstream. In order to avoid a progressive displacement of shrimp stocks westward in this area (which is not apparent), the adult shrimp would be required to migrate intuitively back to original spawning grounds. Although not an impossible behavior, it is more convincing when areas of stock abundances are related to environmental conditions that prevent a wide or downstream dispersal of larvae. Favorite and Ingraham (1976b), as a result of an intensive ocean-ographic cruise in the vicinity of Kodiak Island in May 1972, showed that an extensive system of countercurrents occur over the shelf in that area that could retain shrimp larvae in the general area of spawning (Figure 72).
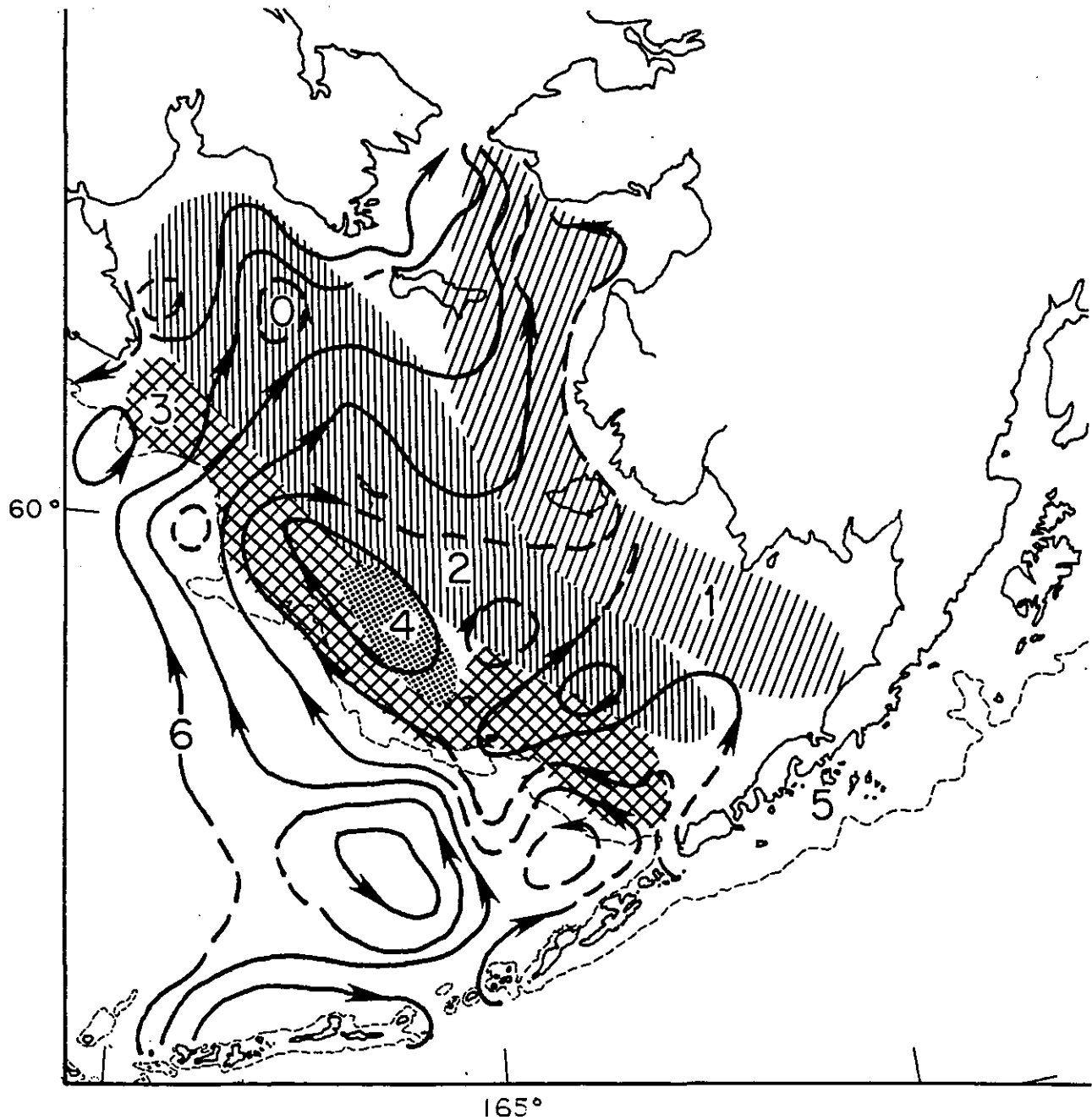
Figure 71. Schematic diagram of environmental zones in eastern Bering
Sea indicating: (1) (2) and (3) the zones (see text),
(4) the area of Pribilof shrimp population, (5) the 200 m
isobath, and (6) geostrophic flow — 10/1000 db (after
Ivanov 1969).
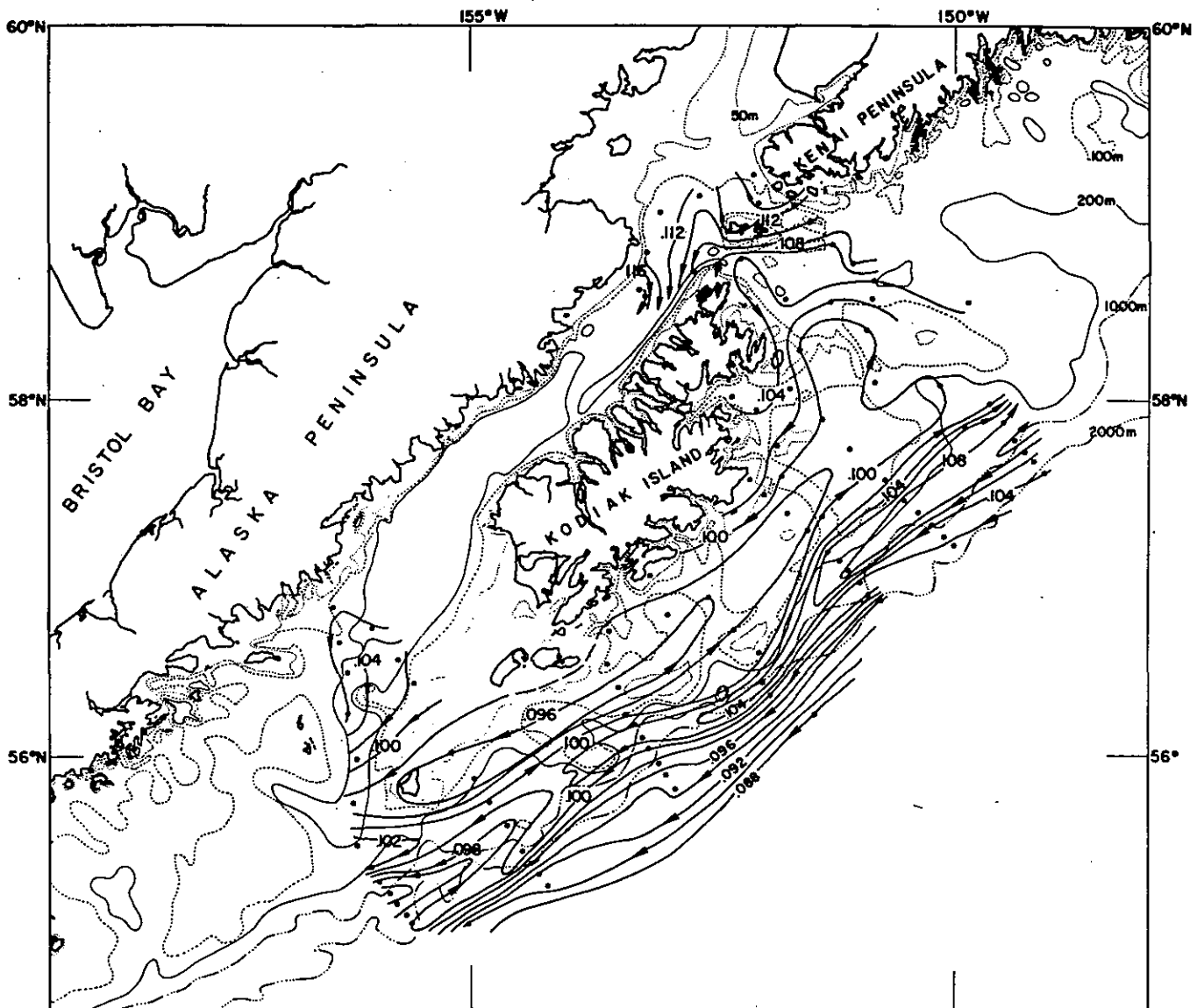
Figure 72. Geostrophic currents (0/50 db) over the continental shelf off Kodiak Island indicating the presence of gyres and counter-currents that could serve to retain demersal eggs and larvae in the area prior to settling on the bottom.

V.   OCEAN ENVIRONMENT VARIABILITY

There is a broad spectrum of time and space scales, from seconds to decades and centimeters to thousands of kilometers associated with environmental changes that are or may be expected to influence fishery resources with respect to abundance and temporal and spatial behavior such as distributions, migrations, and aggregations. The research and verification of the effects of the environment on fish in the northeastern Pacific Ocean has been scant in the past and most of the examples in this section have been derived at through rather indirect evidences.

The catches of different species vary widely in time and space, and much of this variability can be associated with environmental causes as shown schematically (Table 4). Neither the causes for migrations nor the actual migration paths of fish are clearly understood; however tagging studies indicate that even many demersal species, such as English sole, which were believed to be rather stationary, are undertaking extensive migrations (north-south) along the west coast of North America (Pattie 1969; Jow 1969). Many of these migrations may be triggered by environmental variability, specially availability of proper food in the lower levels of the food web (e.g., zooplankton) which is relatively sensitive to environmental changes. Some possible migration-triggering mechanisms have been schematically summarized (Table 5). One of the more important aims of environment-resource interaction studies is to be able to predict the abundance and availability of fishery resources from analyses of environmental conditions because the environment is easier to observe than the fishery resources per se.

A.   WATER PROPERTIES AND TIME AND SPACE SCALES

In pursuing environment-resource relationship studies, one deals with four groups of environmental variables that are easy to observe and/or can be obtained as routine environmental measurements and are known to affect fish (its physiology and behavior), as ascertained by laboratory experiments or empirical methods.

1.   Physical and Chemical Properties

The first group consists of physical and/or chemical properties: temperature, salinity, dissolved oxygen, other chemical constituents including odors, submarine illumination, and turbidity. The various processes which determine the sea surface temperature variability are listed in Table 6, and the approximate time and space scales of sea surface temperature changes are listed in Table 7. Temperature changes in the deeper layers are much smaller and slower, although an exception is the layer near the thermocline(s) where relatively sudden changes can occur due to mixing and/or convergence (see Figure 73, locations a and b). In fact, sudden changes in the depth of the surface layer and, thus, the thermocline, might act as triggering mechanisms or stimulus for the initiation of seasonal migrations of various fish. The factors which determine the mixed-layer-depth (MLD, and general effects of temperature on fish, are listed in Table 8 and Table 9.

Table 4. Resource-environment interactions

Fishing determining factors	Direct fishery factors	Biological and fish behavioral factors	Affecting environmental factors
Abundance		Migrations (spawning, feeding)	Environmental (e.g. temp.) change, anomalies (triggering migrations)
Aggregation	Availability		Temperature caused delay and dislocation of spawning Food availability
Depth Distribution		Fishable year class strength (including size distribution)	Spawning success as determined by food availability, grazing, etc.
Type of Bottom	Fishability	Seasonal and diurnal behavior (aggregation, dispersal in water mass, vertical migrations, etc.)	Aggregation at thermal gradients (horizontal and vertical)
Weather (storms)			Food distribution as determined by environment
Ice			

Table 5. Scheme of environmental causes for migrations and triggering of migrations by environmental changes.

Migrations	Range	Type	Reason
Seasonal migrations	Long distance	Spawning (aggregation)	(Inborne instincts)
		Feeding (dispersal)	Availability of food
		Search for optimum environment	Temperature, salinity
		(often separation of juveniles and adults)	Availability of food
			Escape from predators
	Depth	Spawning	Migration triggered by environmental rate of change
		Feeding	Food availability
		Optimum environment (search for)	Environmental factors, light
Short-term migrations		Feeding	Availability of food (e.g. plankton, benthos)
		Optimum environment	Environmental gradients
		Pursuit of prey and/or escape from predators	Presence of predators

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Table 6. Factors affecting the sea surface temperature (SST) and the resulting maximum SST changes in 48 hours

Basic cause	Contributing processes	Assumed value for computation of change in 48 hours	Maximum resulting SST change in 48 hrs ($^{\circ}$C)
Advection	Permanent (gradient) flow	Speed 1 knot; SST gradient 1.5°C/100 n. miles	0.7
	Wind currents	Speed 0.4 knots, SST gradient 1.5°C/100 n. miles	0.2
	Inertia and tidal currents	Speed 0.4 knots, SST gradient 3°C/100 n. miles	0.3
Heat exchange	Insolation (affected by clouds)	600 g. cal. cm^2 24 h^{-1} MLD 18 m	0.7
	Evaporation (affected by wind and $e_w - e_a$)	300 g. cal. cm^2 24 h^{-1} MLD 18 m	0.3
	Other heat exchange components	200 g. cal. cm^2 24 h^{-1} MLD 18 m	0.3
Mixing	Wave action	Deepening of shallow MLD by 8 m with sharp gradient below	1.6
	Convective stirring	Dependent on heat loss	0.5
	Currents	Dependent on sharpness of boundaries	0.2
Special causes	Upwelling and divergence/convergence	Gradient 2.5°C/30 m divergence 18 m	(1.3)
	Runoff	Important off estuaries	(0.2)
	Precipitation	(Important only in case of snow and hail)	(0.1)
	Freezing and melting of ice	(Important in limited areas in high latitudes)	(1.5)

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Table 7. Approximate time and space scales of sea surface temperature changes.

Process	Time scale	Space scale
Permanent (gradient) flow	—Seasonal, except near current boundaries and the coastal waters where dependent on insolation and runoff.	—Usually in oceanwide scale and in form of gyres, 500 to several thousand km. in diameter. Small off estuaries and modified near continental shelf.
Wind currents	—Cyclone belt – 2 to 8 days Anticyclone belt – 6 to 14 days	—Gyres correspond to the sizes of cyclones and anticyclones.
Inertia and tidal currents	—Tidal, diurnal, or semidiurnal. Inertia currents dependent on latitudes, (av. 30 hr.).	—Size of the amphidromic tidal systems. Smaller in semi-closed bays.
Insolation	—Seasonal and synoptic (see wind currents).	—Greatly determined by latitude and cloudiness patterns; in general 1/2 cyclone and 1/4 anticyclone size.
Evaporation	—Mainly seasonal; synoptic periods (see wind currents).	More rapidly changing smaller patterns in tropical storms, at coasts and occasionally at sharp current boundaries.
Other heat exchange components	—Seasonal and synoptic as above. The synoptic periods also vary seasonally, especially at low latitudes.	
Wave action	—Cyclone belt – 2 to 8 days Anticyclone belt – 6 to 14 days	—Generally the size of cyclones and their wind fields.
Convective stirring	—Mainly seasonal in medium and high latitudes.	—Generally latitudinal pattern; at the periphery of cyclones (about 1/2 of their size).
Currents (mixing by)	—Seasonal, except near current boundaries and in coastal waters.	—Usually important near major current boundaries. Scale from a few miles to a few hundred miles.
Upwelling and divergence/convergence	—Seasonal and synoptic (see wave action	—Usually narrow and elongated areas near coasts, oceanic and atmospheric fronts; from tens to hundreds of miles wide, several hundred to thousands of miles long.
Runoff	—Mainly seasonal	—Off estuaries and along the coast; few miles to a few hundred miles wide.
Precipitation	—Seasonal and synoptic (see wave action).	—Of minor importance only in high latitudes during the winter; the size or precipitation (snow) area.
Freezing and melting	—Mainly seasonal	—Important only near coasts and near ice boundaries.

TEMP ⟶

Winter ⟶

Sea?onal Thermocline

⟵ Summer

MLD

Effect of convergence

A

Effect of sudden mixing (e·g storms)

Permanent Thermocline

B
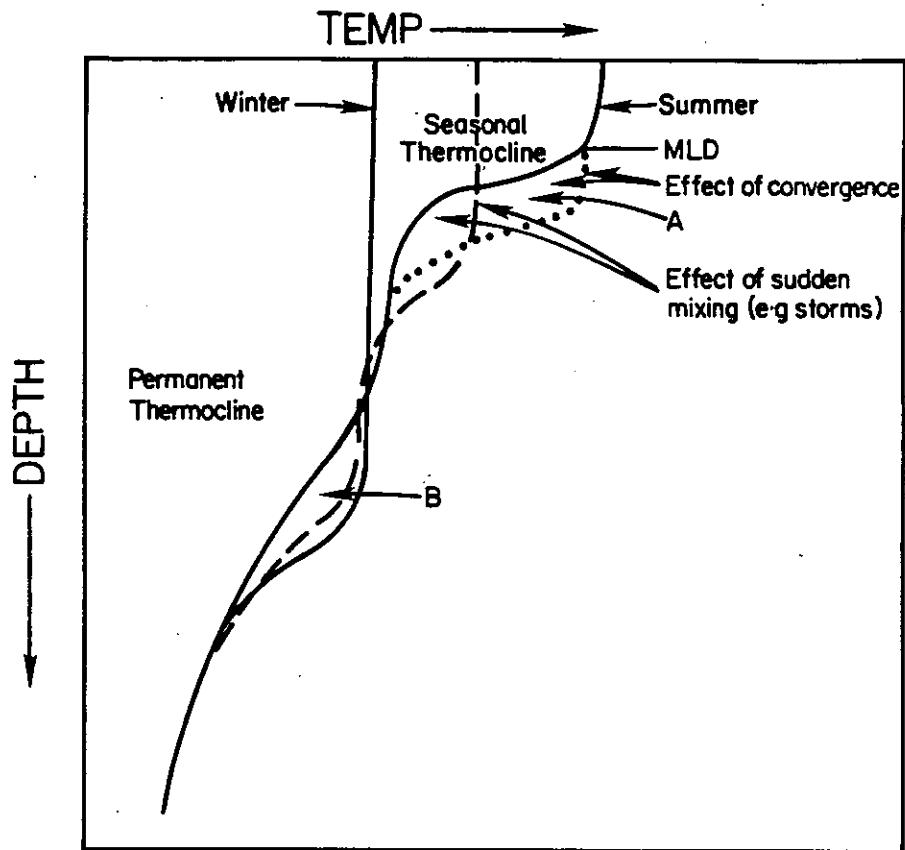
DEPTH

Figure 73. Schematic diagram of thermal structure with depth indicating effects of conditions and processes in the water column.

Table 8. Factors determining the mixed layer depth (MLD) and its changes.

Basic cause	Processes and factors
Heat Exchange	Heating Season-Formation of transients and seasonal thermocline Cooling Season-Convective stirring; deepening of thermocline
Mixing by Wave Action	Mechanical mixing (deepening) Decay of transients
Advection (Currents)	Divergence/convergence "Overflow" (inversion) Decay of transients Deformation by advection (below MLD)
Internal Waves	Tidal fluctuations and mixing
	Other causes (short-term, irregular fluctuations)

Table 9. Major effects of temperature on fish.

Process	Affecting
Spawning	Development of gonads Delay or displacement of spawning
Survival of larvae	Time for hatching Availability of food
Growth	Metabolism Uptake of food
Optimum temperature	Migrations Activity (agility) Aggregation
Lethal temperature	Mass mortalities Migrations

The horizontal variability in salinity is largely a coastal phenomenon and this might affect fish in various ways, such as physiological changes, stimuli for behavioral changes, and buoyancy of eggs. The factors affecting the variability of salinity are listed in Table 10.

Submarine illumination is altered by time of the year, cloud cover and amount of suspended matter, minerological as well as detrital (i.e., turbidity). Submarine illumination affects the search for food, is an important factor in basic food production (phytoplankton), and also affects stimuli for seasonal behavior (maturation, migration, etc.). It affects also catchability coefficients of certain fishing gear (e.g., gillnets).

2. Dynamic Factors

The second group consists of dynamic factors: currents and turbulence. Currents are affected by surface winds and by thermohaline distributions. The prevailing current, however, in most areas, specially over continental shelves, is the tidal current. Turbulence in the upper mixed layer is caused by currents and wave action (i.e., the same factors affecting MLD, see Table 8). Currents affect the fish by transport of eggs and larvae and smaller fish and as stimuli for orientation in most species; such orientation may be directly related to purposeful migrations. Currents also affect the transport of plankton forage for many fish species. The time and space scales of current variabilities are closely related to the time and space scales of surface temperature variability as listed in Table 7.

3. Biological Variables and Processes

The third group consists of biological variables and processes which are intimately connected to and affected by the environment: plankton and benthos. The variability of plankton and benthos (species composition, abundance, patchiness, etc.) are determined by physical-chemical environmental parameters, grazing and reproduction cycles. Benthos variability is in addition determined by depth of the bottom and substrata. The variability scales of plankton, though having seasonal and large-scale features, are mainly a relatively small-scale phenomena, patchiness. Zooplankton abundance is largely determined by the abundance of phytoplankton (primary production), their consumption by predators, and their transport by currents. The availability of zooplankton as forage for fish can affect greatly the migrations of juvenile fish and spring and/or fall blooms may provide triggering mechanisms for migration of maturing fish.

B. TEMPORAL CHANGES

Specific examples of long-term, seasonal and short-term changes in environmental conditions can be documented, but the effect of these changes on the various fisheries is not known and numerous studies should be instigated to ascertain specific resource-environment relations.

Table 10.   Factors affecting salinity changes in the sea.

Basic causes of salinity change	Processes, factors and other remarks
Precipitation	Location and season dependent
Evaporation	Season dependent, greatly affected by surface winds
Runoff	Near-coast phenomena, location dependent, seasonal
Advection	Currents
Mixing	Wave action, currents

1. Long-Term

Studies of long-term, and consequently large-scale environmental changes in
the northeastern Pacific Ocean suffer from the lack of an adequate environ-
mental data base. An indication of long-term trends in oceanic conditions
is afforded by annual mean air temperatures at a coastal site; data at Sitka
(Figure 74) extend back (with gaps) as far as 1828 and reflect: 3-5 year
temperature cycles, pronounced warm periods (1828, 1869, 1885, 1915, 1926,
1940-41), recent cold periods (1955, 1971), and extended cooling trends
(1828-1850, 1926-1955). The longest records of oceanic conditions are those
of surface temperatures from ships-of-opportunity, and the earliest quasi-
periodic, oceanic, sea surface temperatures are available from the trans-
pacific voyages of the "China Steamer" from San Francisco to Yokohama from
1871-75 (Dall 1882). Comparisons of data off San Francisco for the same
months in different years reflect differences of 1-2°C, but the data series
is too short to allow assessments of long-term changes. The accumulation
of temperature data from various vessels has permitted the compilation of
numerous atlases of mean conditions, the most recent and best being that
of Robinson (1976) showing mean monthly values at several depth levels, as
well as, other data analyses. However, in most instances, the data base
for temporal and spatial comparative purposes over large oceanic areas is
limited to surface temperatures, extends back essentially to 1930, and has
reasonable continuity only when averaged in 5x5° quadrants.

Within the last several decades there are three generally recognized periods
of extreme anomalous sea surface temperature conditions in the northern Pacific
Ocean: (1) cold conditions in the vicinity of Japan 1934-36, (2) warm
conditions along the east coast of the United States in 1957-58, and (3)
cold conditions in the eastern Bering Sea and off the California coast in
1970-71. When all sea surface temperature data are compiled into annual
means by 5x5° quadrants (Figure 75) these, as well as, other cool and warm
periods are evident; certainly the cold conditions off Japan in the mid-1930's
are striking. A plot of the years in which the maximum negative anomalies
from annual mean sea surface temperatures in individual 5x5° quadrants
occurred during the years 1930-1974 (Figure 76) indicates that with few
exceptions the cool conditions in the 1930's were a transpacific phenomena
with cold conditions occurring at both sides of the ocean from 1932-34. It
is also interesting that the actual negative anomalies by 5x5° quadrants for
1936 which should reflect effects of eastward advection, indicates the cold
regime trended southeastward and didn't result in marked negative anomalies
off the California coast. However, the warm period, along the east coast
of the United States in 1957-58, showed a different pattern. If one
considers only the years 1953-60 and ascertains the years of maximum positive
anomalies in individual 5x5° quadrants (Figure 77) there is an apparent,
orderly eastward shift in maxima from 1955 to 1958 that results in anomalous
warming all along the west coast from California to the Gulf of Alaska.
Thus, it is obvious that there are marked long-term changes in the environ-
ment of the northeastern Pacific Ocean, and these are transpacific phenomena
whose causes are not known at this time. There are speculations that the
warming is caused by an increase in transport in the warm, Kuroshio Current
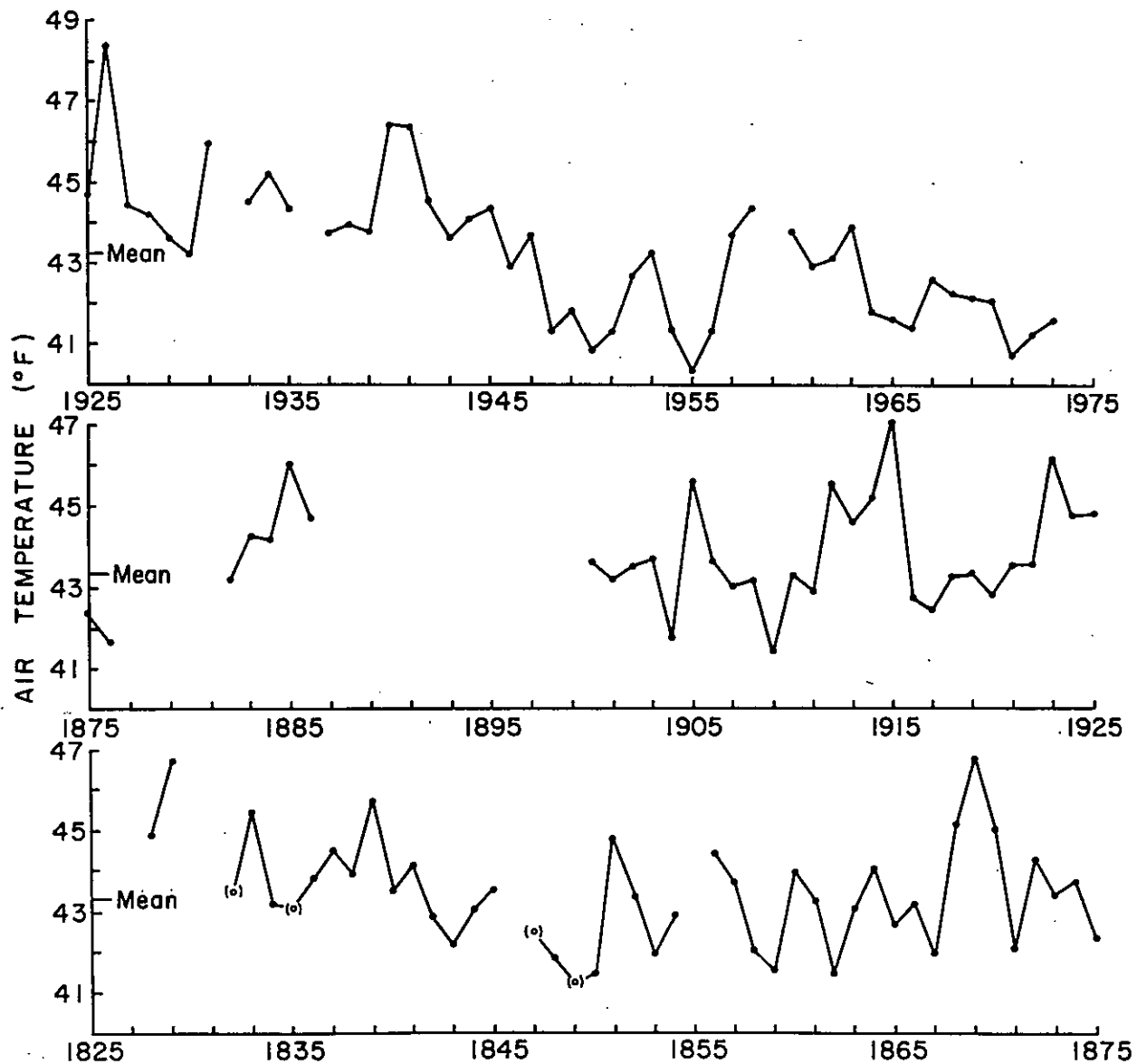
Figure 74. Annual mean air temperatures at Sitka (New Archangel) from 1828 to 1974 indicating short- and long-term environmental fluctuations.
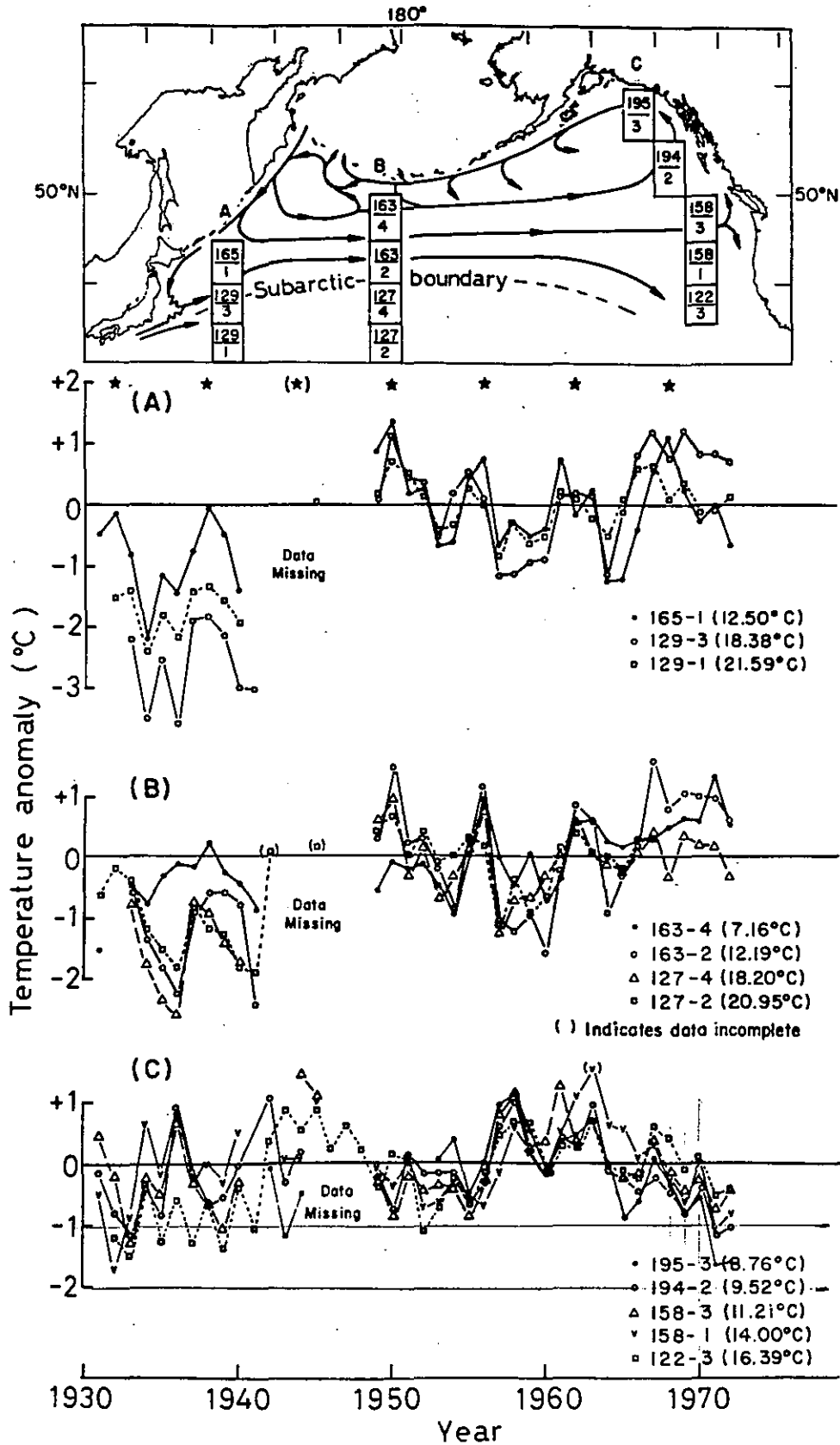
Figure 75. Deviations from annual mean sea surface temperatures in the numbered 5x5° quadrangles, 1930-1972 indicating the long-term variability, and the transpacific continuities and discontinuities of specific events (from Favorite and Ingraham 1976).

130°E 140 150 160 170 180 170 160 150 140 130 120°W

N 60°

50°

X × × × × ×

X × × X × X X 71 38 38 33 33 33 34 49

40 37 32 32 31 60 31 58 70 70 69 69 33 55 33 39 44

X × 41 34 32 36 36 36 41 41 40 40 40 40 40 38 38 54 32 45 33

34 34 36 36 34 36 36 36 35 34 36 36 40 40 40 40 39 37 33 33 33

43 32 31 36 34 40 36 36 43 36 36 40 40 40 40 40 40 39 39 33 39 33

X × 39 × × × 34 × × × 36 36 × × × 36 33 39 × × × ×

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130°E 140 150 160 170 180 170 160 150 140 130 120°W

N 60°

50°

40°

+1

0

-4 -3 -2

-2

-1 1

X × × × × × × × X X X × × × X × × ×

X × × × × X × × × ×

Figure 76. Map showing the year (numbers indicate last two digits, 36 = 1936) in which maximum negative anomalies (1948-67 mean) from annual mean sea surface temperatures occurred during 1930 to 1974 in individual 5x5° quadrants indicating the cold period in the 1930's, and the distribution of annual mean temperature anomalies for 1936 suggesting the general eastward drift of cold conditions off Japan.
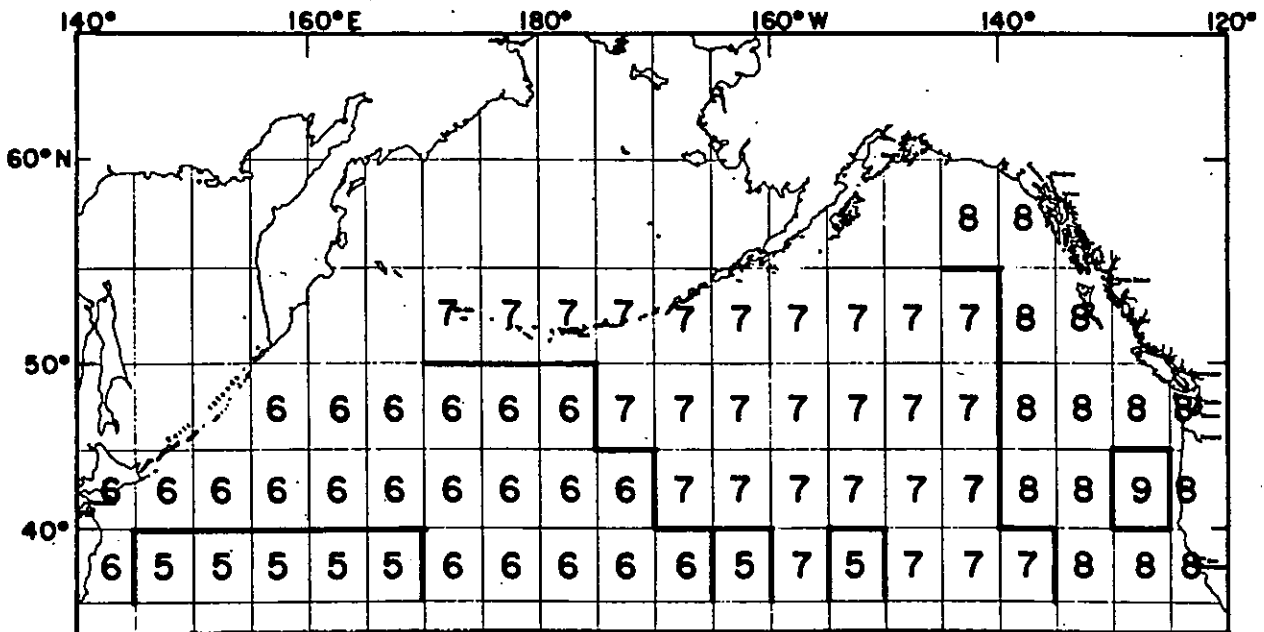
Figure 77. Map showing years from 1953 to 1960 (numbers indicate last digit, 7 = 1957) in which maximum positive anomalies (1948-67 mean) from annual mean sea surface temperature occurred in individual 5x5° quadrants, indicating the transpacific advection of warm conditions from 1955 to 1958 (from Favorite and McLain 1973).

and that cooling may be due to an increase in transport in the cool, Oyashio Current. Since the former is a northward flow and the latter a southward flow, these conditions would reflect the more dominant influence of the former on conditions along the west coast of North America. Similarly, the cause for the recent cooling (1970-71) along the west coast of North America is not known. Sea surface temperature data in the eastern Bering Sea are sparse except for the last decade or so, but McLain and Favorite (1976) have shown the cooling trend evident in that area since 1968 (Figure 78) and the marked effects of this cooling on various living resources.

Favorite et al (1976) have shown that a transpacific temperature cycle of about 5 years has occurred for several decades: warm years-1957-8, 1962-3, 1967-8, and cold years-1955-6, 1960-1, 1964-5. These cycles are characterized by temperature anomalies of 1-3C^o, unfortunately the paucity of data in the northern Gulf of Alaska, the offshore divergence of the Subarctic Current, as well as processes in the Upwelling Domain along the west coast of the United States masks the continuity of such changes into the coastal regime. However, one cannot help but believe that these large oceanic pools or areas having positive and negative anomalies of 1-3C^o that move across the Pacific Ocean, should contain and support different abundances of planktonic forage organisms, possibly different rations of subarctic and subtropic forms; perhaps some at lethal threshold temperatures. Changes in abundance, size groups, and other characteristics of these forms that are swept northward or southward along the coast could markedly affect the larval survival of various fish stocks.

The above discussions have been limited to sea surface temperature but there are other long-term changes that occur deeper in the water column, although these data are quite fragmentary. If one considered the stratum under the temperature-minimum stratum characteristic of the Subarctic Pacific Region, there are two regimes--a cold water one ($<4^oC$) that intrudes eastward from an oceanic area into the Gulf of Alaska and a warm water one ($>5^oC$) that intrudes northward along the coast into the Gulf of Alaska (Figure 79). It is apparent that the interactions between these two water masses govern not only the flow, but the water characteristics--and thus the environment-- along the continental slope in the Gulf of Alaska. The eastward penetration of the 3.75^oC isotherm from long 170^oW to the vicinity of Yakutat from 1955-62 is ample evidence of long-term changes in the water properties of the deeper layers. Unfortunately data obtained in this area since 1962 are too sparse to permit subsequent analyses of this phenomenon.

In addition, one can use oceanographic features at depth to assess long-term changes. For example, from inspection of the vertical distribution of salinity data at oceanographic stations, one can quickly ascertain (A) the northern boundary of the salinity-minimum stratum, (B) the northern boundary of the salinity-maximum stratum as defined by the 34 $^o/oo$ isohaline regardless of its location in the water column, and the location at which the 34 $^o/oo$ isohaline occurs at the surface (see Figure 47). Even though diffusion as
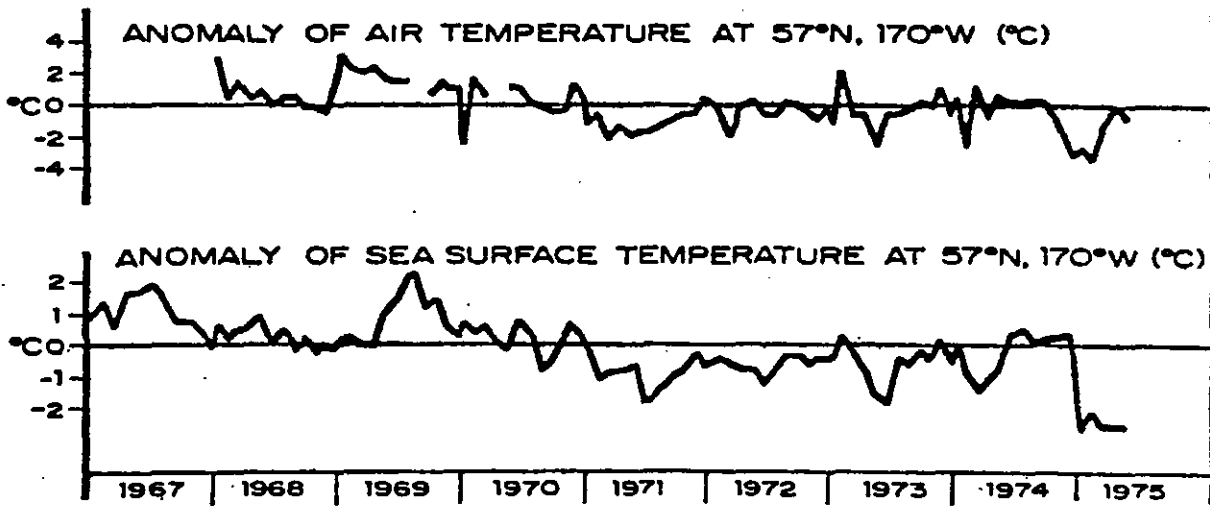
Figure 78. Anomalies of air and sea surface temperature 1967 to 1975 in the eastern Bering Sea indicating the long-term downward trend, the first major negative anomaly in 1971 and the maximum negative anomaly in 1975 (from McLain and Favorite 1976).
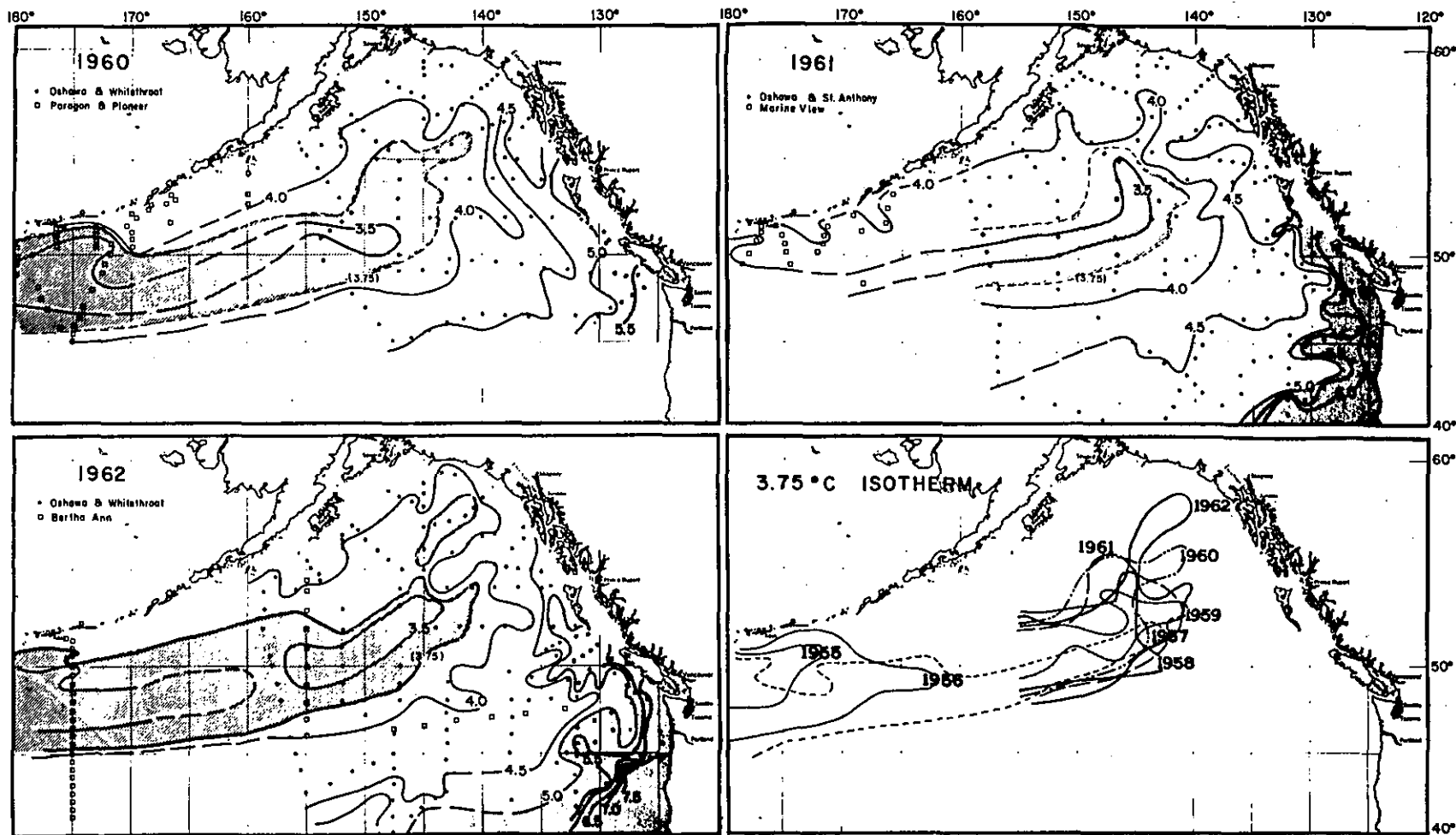
Figure 79. Temperatures ($^{\circ}$C) in the surface of salinity = 34.0 $^{\circ}$/oo
(approximately 200-300 m) in 1960, 1961, and 1962, and
the configuration of the 3.75°C isotherm in years 1955
to 1962 indicating the long-term advection of cold water
at depth from the central Pacific Ocean in 1955 to the
continental slope in the Gulf of Alaska in 1962 (from
Favorite 1975).

well as advective processes are occurring simultaneously, one can obtain an
indication of the variability and continuity in the location of these phenomena
in individual years in which adequate data are available. Unfortunately one
must refer back to the period of intense oceanic studies conducted for the
INPFC (1955-1962) in order to obtain adequate data (Figure 80), but it is
apparent that wide fluctuations in these boundaries occur. Particularly
noticeable is the shoreward extent of boundary A in 1961 and 1962 which is
analogous to the shoreward protrusion of the 3.75°C isotherm on the 34 $^{\circ}$/oo
isohaline surface (see Figure 79), even though these two phenomena exist over
750 km apart. Although the effects of these phenomena on behavior of fish
are not known, we cannot stress too strongly that if these water structures,
which (except for the surface location of the 34 $^{\circ}$/oo isohaline) occur at
roughly 200-400 m, do indeed affect fish that it is only through oceanographic
surveys, not satellite data, that data required to ascertain the location of
these boundaries can be obtained.

It is clear that there are long-term and cyclic changes in the surface and
subsurface oceanic environment that could provide considerable insight into
the survival of year classes, phases of life history, and behavioral character-
istics of fish. For example, the marked northward shift into the Gulf of
Alaska of tropical forms, normally limited to the California coast, in
1957-59 provided insight not only into preferential environmental conditions,
but also the mobility of these forms. Radovich (1976) noted that annual move-
ments of certain species, as well as the distribution of spawning success,
are affected by subtle differences in water temperatures. Most long-term
changes are regional by nature, caused by shift of mean positions of semi-
permanent atmospheric features, such as the Aleutian Low, and initial studies
can be made using surface pressure data, which are now readily available.
The variability in the frequency of monthly mean sea level pressure minima
(in terms of 3 arbitrary pressure levels--<995 mb, <990 mb and <985 mb)
of the Aleutian low pressure system for the period 1899-1972 (Figure 81)
suggests that marked changes do occur, not only in oceanic and coastal flows,
but also in temperature regimes.

Another approach is the study of variability of surface driving forces (e.g.,
wind speed). Monthly standard deviation of surface wind speed square and
twelve-month running mean of this standard deviation in an ocean region off
the Washington and Oregon coasts to about long 175°W are shown (Figure 82)
and the long-term variability of the "variability" (standard deviation of
wind speed square) as well as the differences of the onset of greater fall
and winter variability of wind speed from year to year are readily apparent.
Again, it has not been possible to analyse these data together with pertinent
fisheries data. The monthly mean wind speed square from 1964 to 1971 in
the same area indicates the year to year differences in the onset of stronger
winds in autumn that affect significantly the behavior and availability of
the fishery resource as well as vessel operations.

Dominant weather cycles, other than annual, on earth may be largely controlled
by forces acting beyond our immediate solar system. The earth is subject to
a definite sunspot cycle of roughly 11 years, and a 22-23 year magnetic or
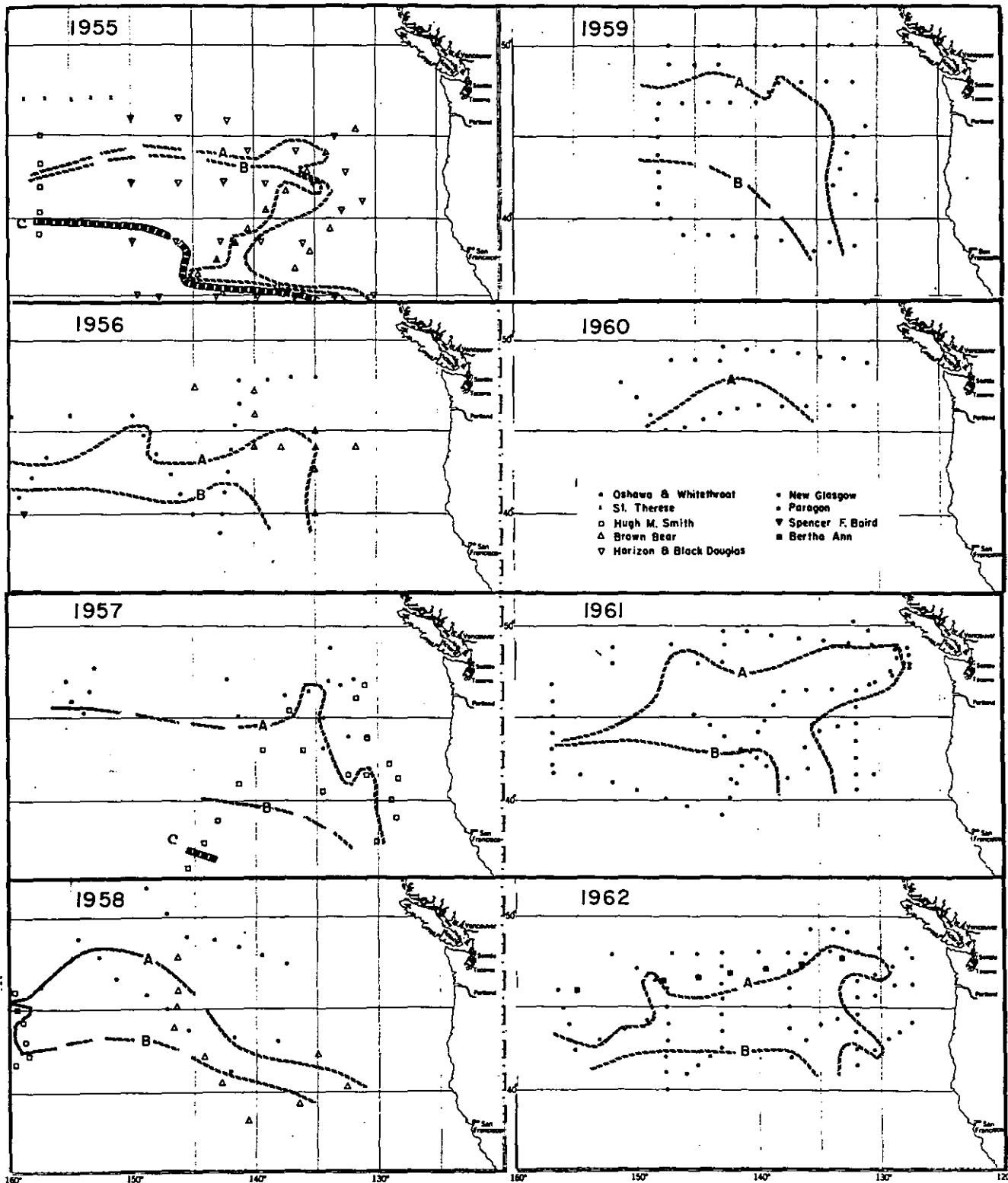
Figure 80. Boundaries of (A) salinity-minimum stratum, (B) salinity-maximum stratum and (C) the 34 ^{o}/oo isohaline at the surface (see Figure 47) indicating the extreme variability in location of these water structures that could influence the movements and dsitribution of fish (e.g., salmon, albacore, pomfret, etc.).
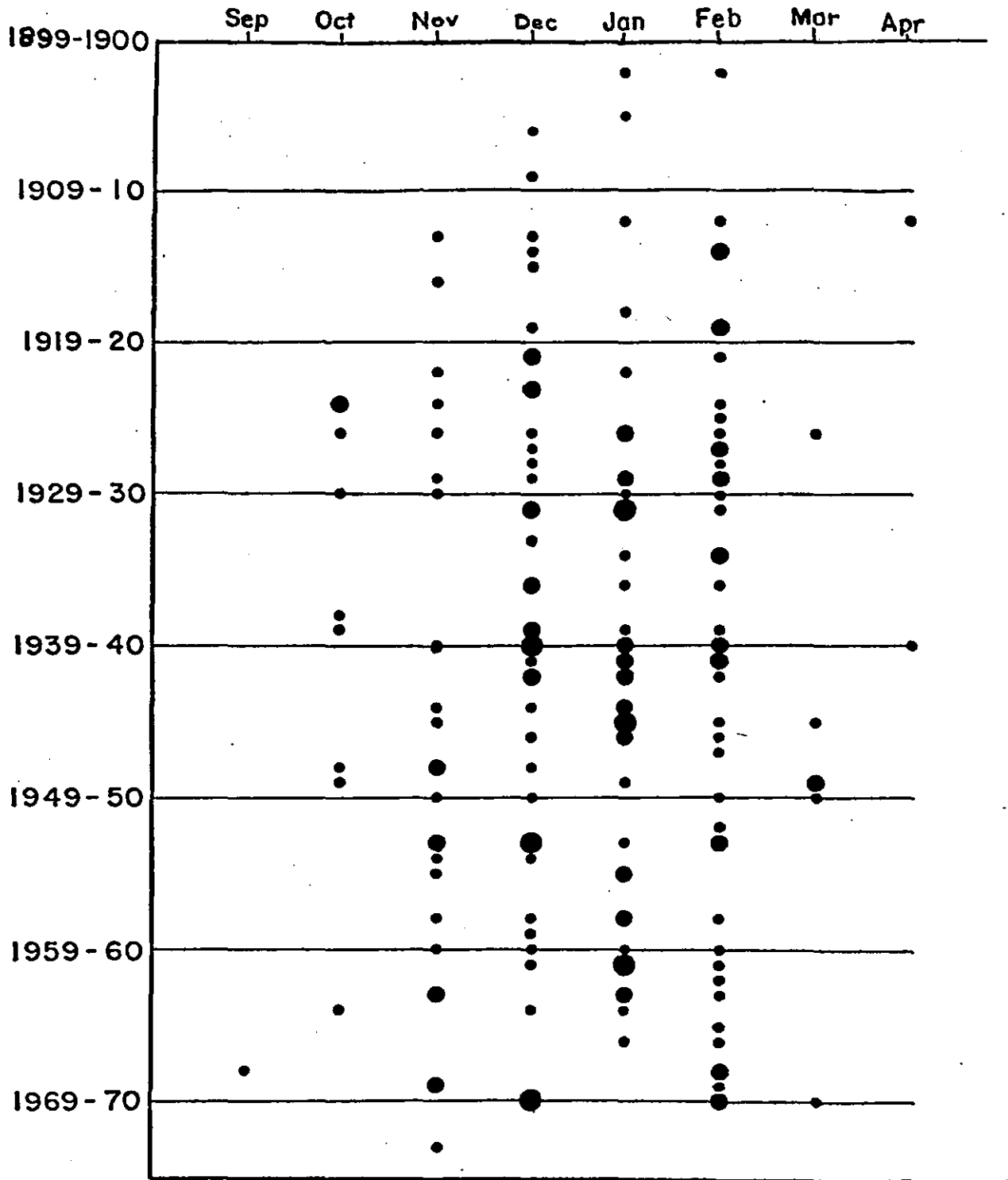
Figure 81. Variability in frequency of monthly mean sea level pressure minima in terms of 3 arbitrary pressure levels (<995 mb, <990 mb, and <985 mb) of the Aleutian low pressure system for the period 1899 to 1972 reflecting the variability in wind-stress on the sea surface and thus water transport (from Ingraham et al. 1976).
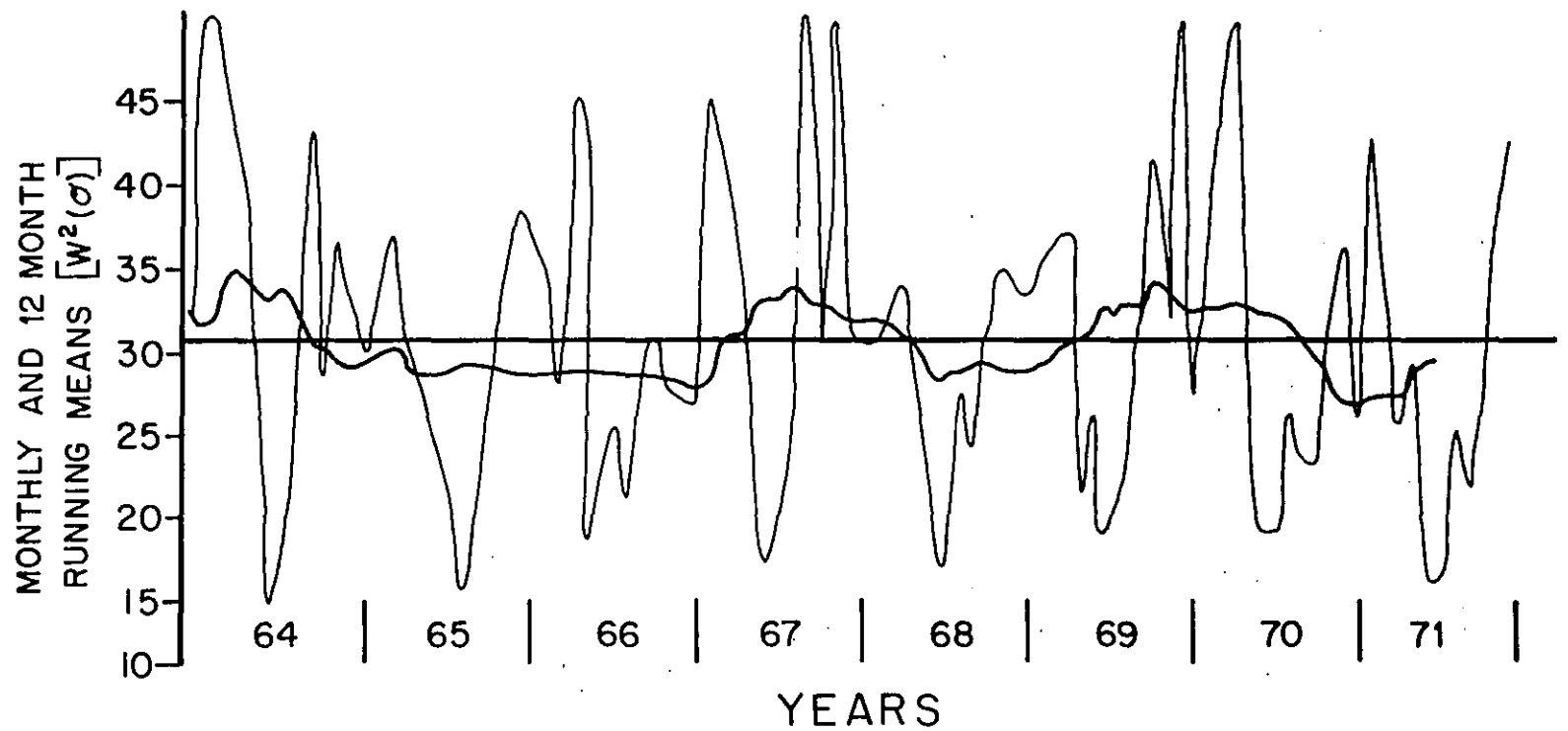
Figure 82. Monthly mean standard deviation of surface wind speed square and 12-month running means off the Washington-Oregon coast from 1964 to 1971, indicating the variations in winter wind speeds.

double sunspot cycle that can be traced back over 2 millennia. Favorite and Ingraham (1976a)using data since 1899, have shown that during period of sunspot maxima the mean winter position of the center of the Aleutian low pressure system shifts from the Gulf of Alaska to the western Aleutian Islands. This alters a number of environmental conditions: (1) mean cyclonic wind-stress transport in the Gulf of Alaska is reduced 20%, which, not only reduces the volume of warm water normally advected into the area, but reduces the intensity of the vertically upward divergence in the Alaskan Gyre; (2) since the upwelled water is cold, these temperature effects would be counteracting, but the replenishment of nutrients to the surface layer may be considerably reduced; and (3) there is an increase in the southwestward transport along the Asian coast that should result in cold conditions that will subsequently be advected across the Pacific Ocean. The effects of these conditions on various living marine resources are not known and long-term sampling efforts and designs will be required; however, some aspects may be discussed. Wickett, Taylor, and Ramey (1975) have indicated that the average year-class strength of British Columbia herring populations varied with mean surface salinities between 1957 and 1966 and concluded that air-sea inter-actions which induce greater vertical velocities in the Gulf of Alaska produce more nutrients and food in the euphotic zone and greater survival of young fish that are moving offshore. Thus, periods of sunspot minima would be more favorable than sunspot maxima to these fish. Further, the apparent changes in the intensity and locations of current systems could affect the ultimate drift of planktonic eggs and larvae, as well as, migration paths of juvenile and adult fish.

2. Seasonal

The seasonal changes of most surface environmental parameters follow a regular pattern over large areas. Seasonal changes below the surface and specially near the bottom, the main domain for demersal fish, are usually considerably smaller in magnitude and lag behind the changes at surface. The seasonal changes of thermal structure with depth and the delay in warming of the deeper layers are schematically shown (Figures 83 and 84). This warming does not necessarily follow a smooth seasonal pattern, but might occur within a day or two when the first winter storm passes through a given area. Thus, some seasonal changes may be quite abrupt, and their timing can vary considerably from year to year. These changes appear to have a great influence on fish and their behavior by triggering seasonal migrations, which are known to begin rather abruptly in many species.

Biological changes in the sea (e.g., abundance of a species, or start of a plankton bloom, etc.), as well as changes of environmental parameters in subsurface layer, follow a stepwise pattern; the decline being relatively sharp, the recovery slow (Figure 85). This condition does not apply to the changes of environmental parameters at or near the sea surface, which are caused by advective processes. The year to year timing of the more abrupt changes and their variability is also indicated indirectly by the variation of the monthly mean meridional component surface wind speed square off Oregon and Washington coasts (see Figure 82). These pronounced seasonal changes are also the main causes of various environmental anomalies that, once established during a transition season, spring or autumn, usually persist through the following season, summer or winter.
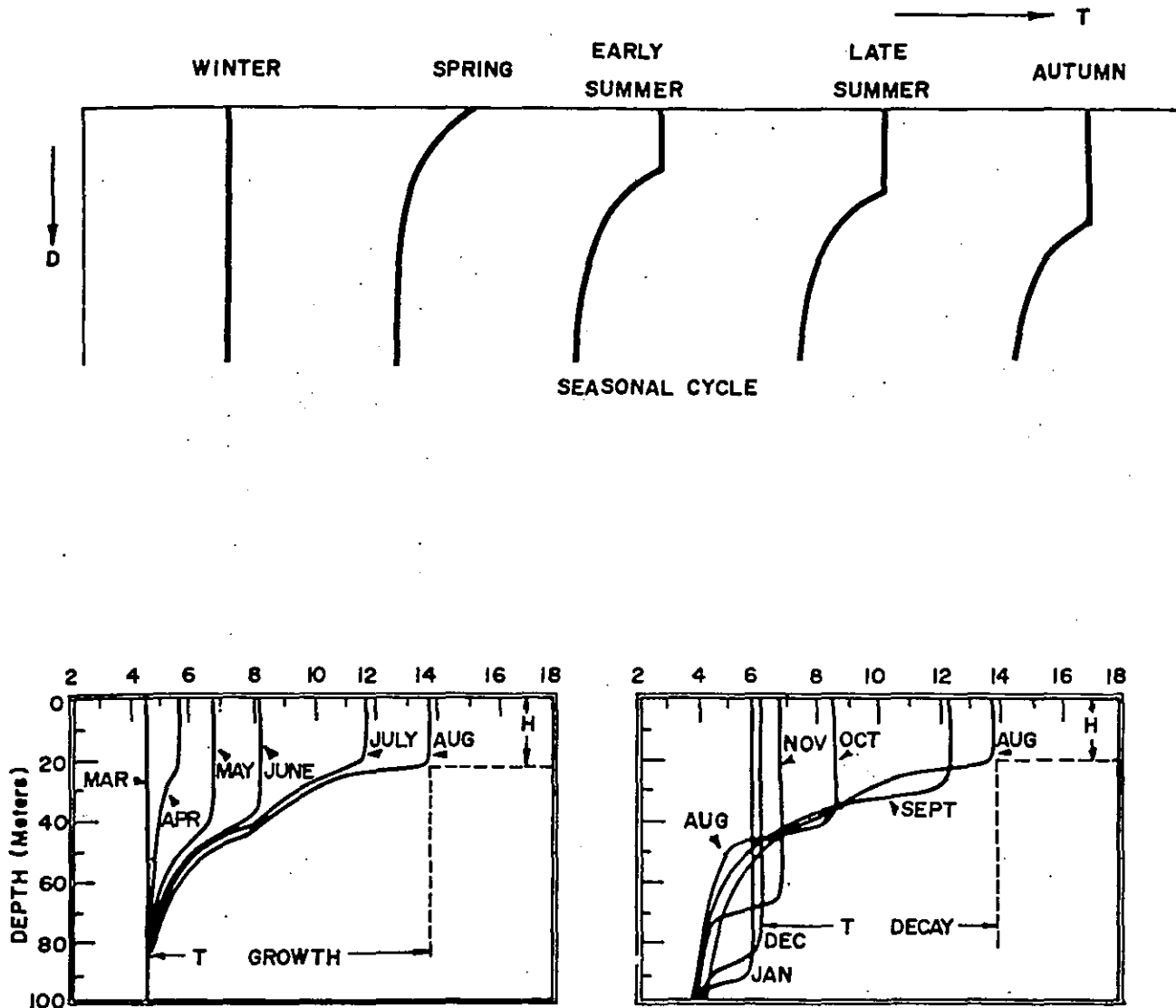
Figure 83. Seasonal types of vertical thermal structures and growth and decay of the thermocline at Ocean Station "P" (after Dodimead et al. 1963).
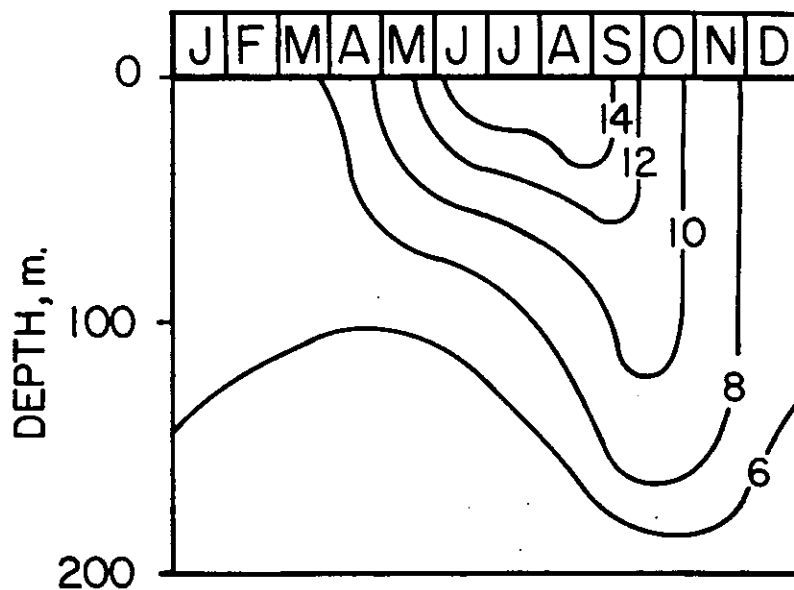
Figure 84. Annual shift of temperature with depth at a mid-latitude
location indicating the maximum temperatures at depth
occur long after seasonal cooling commences at the sea
surface.

ABUNDANCE CHANGE
WITH TIME ⟶

Rapid decline

Slow recovery

ABUNDANCE

+

0

−
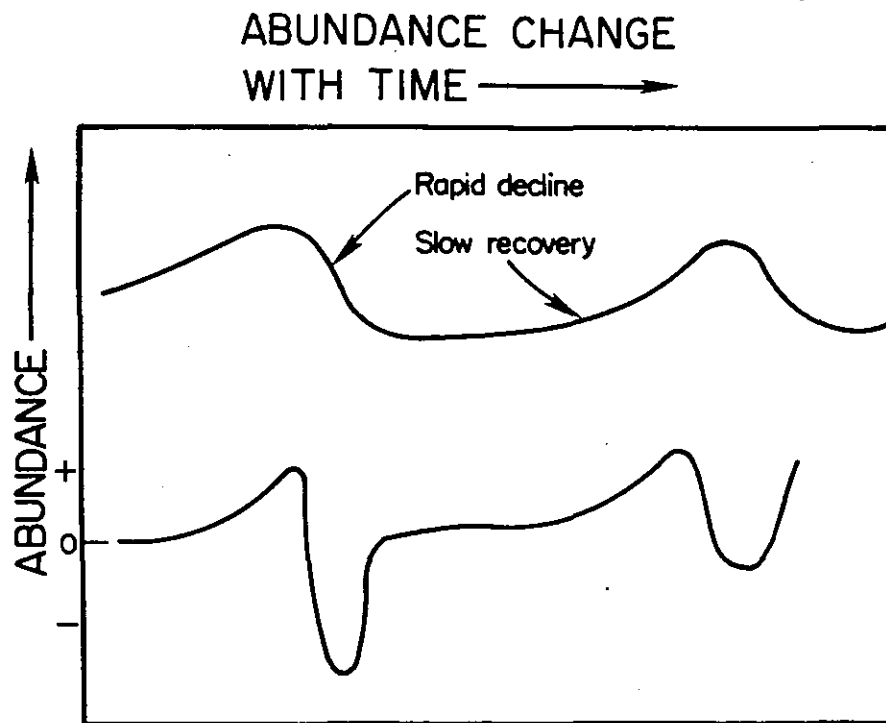
Figure 85. Schematic diagram of typical changes and rate of change in abundance of standing stocks in the sea.

Seasonal changes in total transport in oceanic areas have been discussed (see Section IV-A-2), but changes in surface winds had additional effects. The surface wind drift (Ekman transport), or flow in the surface layer of the ocean, is driven by the direct action of the wind (the net effect occurs at right angles to the wind—to the right looking downwind, in the northern hemisphere) and has a marked effect on not only the drift of eggs and larvae, but also movements of juvenile and adult fish. Because of its limited vertical extent, this flow is always almost negligible in terms of total transport in the water column, but it results in very large convergence and divergence patters. Computer techniques (Bakun 1973) permit compilations of data on a daily basis (Figure 86) that are assimilated into longer time periods of general analyses. Although winter intensification in wind-stress dominates the annual cycle of this flow, the seasonal shifts in winds result in various combinations of inshore and offshore convergences and divergences near the coast because of the physical barrier imposed by the land. When high southerly winds occur near a north-south oriented coastline, the increased shoreward Ekman transport piles up water along the coast that sinks (down-welling), and the seaward flow at depth satisfies in part the local increased requirement for surface flow (Figure 87). Three other conditions are also presented. When the offshore winds are more intense than those at the coast (Situation B), sinking occurs along the coast and offshore as well. The reverse occurs when north winds occur; when the north winds offshore are more intense than those inshore (Situation C), surface flow both at the coast and offshore has a seaward component and local continuity is satisfied by a vertically upward (upwelling) from depth, in both areas. And, finally, when northerly winds are most intense at the coast (Situation D), there is an intense seaward flow at the coast that diminishes off shore and results in upwelling both on the coast and offshore. The monthly mean types of convergence-divergence couples for various coastal areas are shown (Table 11) and intricate downwelling along the coast (A or B) occurs at nearly all locations from October to March, and upwelling occurs at most locations from June to August.

Statistical analyses of such data are presented in Ingraham et al. (1976) and indicate that strong downwelling occurs in winter and that the area of greatest intensity extends from the Kenai Peninsula (lat 59°N, long 151°W) to south-eastern Alaska (lat 57°N, long 137°W) and reaches a maximum near Yakutat (lat 59°N, 141°W). The summer upwelling period is longest in the southwest portion of the gulf extending from April to December near the extremity of the Alaska Peninsula, and exhibits three separate maxima, in April, August, and November. The season of mean upwelling becomes progressively shorter and less intense with distance clockwise around the gulf, lasting 3 months off the Kenai Peninsula and essentially vanishing off southeastern Alaska. Generally in these data the standard deviations are larger than the means, particularly in winter, indicating highly energetic pulsations and relaxations of vertical flow along the coast. Extreme events during fall and winter are predominately downwelling events and during spring and summer are pre-dominately upwelling events.

3. Short-term

A high rate of change of environmental parameters can in some cases affect a biological subject more profoundly than a large, slow rate of change; the
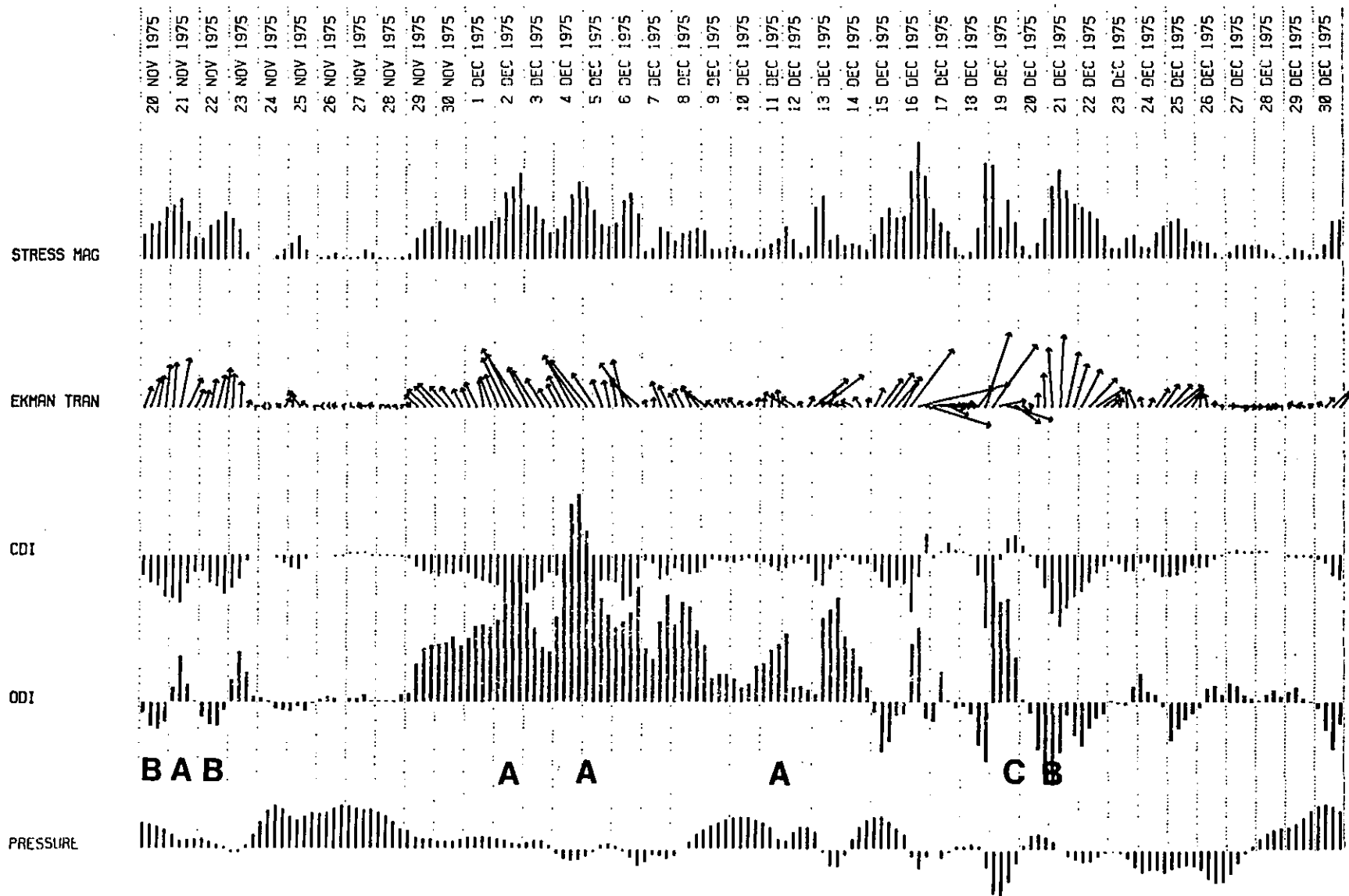
Figure 86. An example of compilations of 6 hourly sea level pressure
observations at 60°N 146°W for November 20 to December 30,
1975 translated into: wind stress magnitude, Ekman trans-
port, coastal divergence index, offshore divergence index;
large letters indicate type of event that occurs (see
Figure 87).
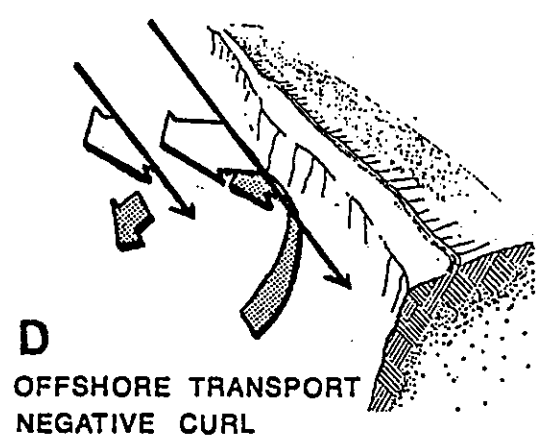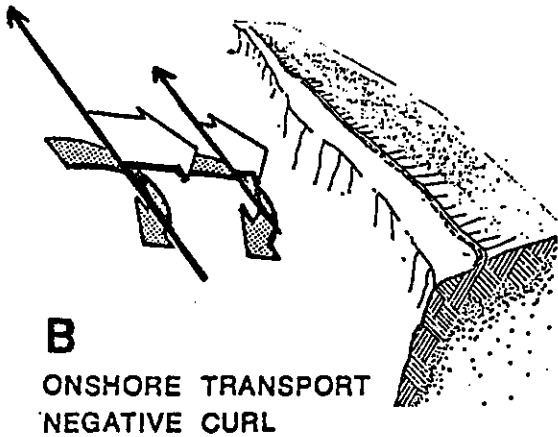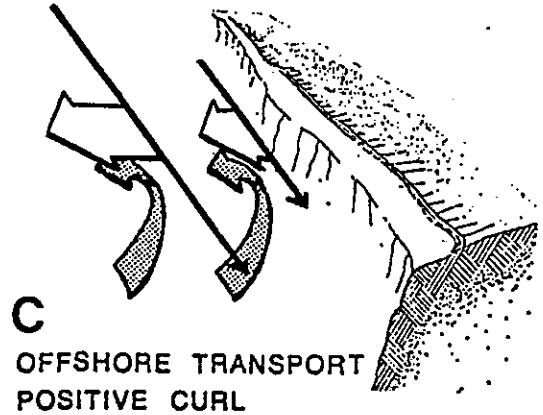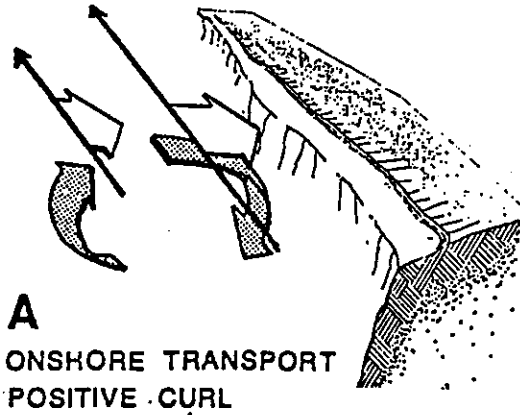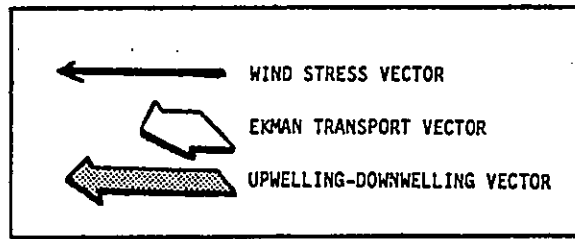
Figure 87. Classification of indicated events according to the combination of coastal and offshore convergence or divergence (from Ingraham et al. 1976).

Table 11. Monthly mean "types" of convergence-divergence couples according to classifications in Figure 87

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
54N, 164W	B	A	A	C	C	C	C	C	C	C	C	C
55N, 160W	B	A	A	C	A	C	C	C	C	C	C	A
57N, 156W	B	A	A	C	C	C	C	C	C	A	A	A
59N, 151W	A	A	A	A	B	D	D	C	A	A	A	A
60N, 140W	A	A	A	A	B	D	D	D	A	A	A	A
59N, 141W	A	A	A	A	B	D	D	B	A	A	A	A
57N, 137W	A	A	A	B	B	B	B	B	B	A	A	A
54N, 134W	A	A	A	A	B	B	A	A	A	A	A	A

former often causing shock effects, whereas, the latter allows some acclima-
tization. Thus, sudden changes, as well as abrupt environmental gradients,
are known to trigger behavioral changes (migrations, changes in feeding
habits, etc.) in fish which inevitably affect their abundance and avail-
ability. Short-term changes in environmental parameters in the sea are
caused by passing atmospheric systems and are caused mostly by advective
and mixing processes. An example of an advective type, short-term change
of sea surface temperature at weather ship November is presented (Figure 88).
The two surface pressure charts verify that the changes of sea surface
temperature must have been caused mainly by advection rather than by violent
mixing or stirring locally. If the readjustment by a driving force is not
operative, an anomaly, caused by a short-term change, can be rather persistent.
Furthermore, it follows that the magnitude of short-term advective changes
is large where the horizontal gradients of a given environmental property
are large (e.g., at current convergences and in coastal areas). The
relative magnitude and duration of short-term changes of sea surface
temperature are illustrated (Figure 89) showing that these short-term
changes can exceed one quarter of total annual range of the change of sea
surface temperatures at any given location and even, in some occasions,
they can exceed half the annual range of monthly mean values in a few days.

There are profound changes in availability of many pelagic species within
short periods at given locations, and these availability changes have been
for a long time accredited by fishermen to changes of weather and weather
caused changes in the sea. Although short-term changes in the ocean can
be forecast from weather predictions, more research must be conducted on
the relation between short-term meteorological and oceanographic changes,
and the behavior and availability of fish species affected by such changes.
Experiences have also indicated that the behavioral characteristics of a
given species to short-term changes may vary in relation to geographic
areas. Sea level observations at coastal stations indicate changes in
flow along the coast and these reflect some gross patterns as well as marked
deviations from station to station (Figure 90).

C. OCEAN MODELS

Conditions and processes in the oceans are changing continuously on all space
and time scales. Although the magnitude and rate of change of environmental
variables, such as temperature in the sea, are smaller than the corresponding
changes in the atmosphere, organisms are adapted to or respond to these
changes. It is not feasible to observe all the changes directly in the
ocean. Therefore, we must turn to various numerical models (National Academy
of Sciences 1975) which allow us to use all pertinent observations and
knowledge on interactions of various parameters to derive at the essential
changes of environmental conditions.

In order to utilize knowledge of resource-environment relations, either in
fisheries management or directly for fishing operations, it is necessary to
obtain timely, pertinent observations and to analyse them in space and time
into coherent, physically correct entities and, in some instances, make
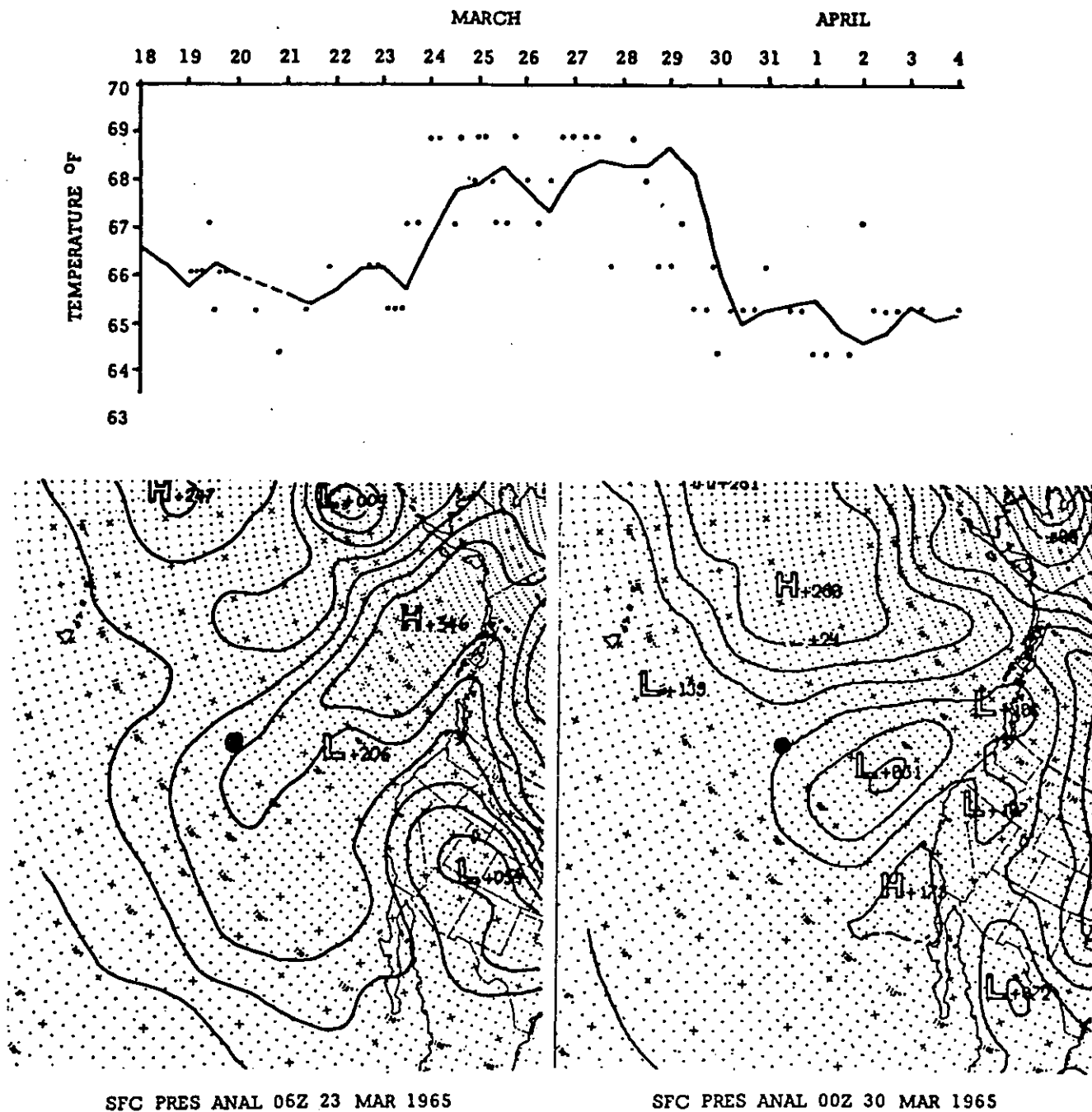
SFC PRES ANAL 06Z 23 MAR 1965   SFC PRES ANAL 00Z 30 MAR 1965

Figure 88.   Sea surface temperature (SST) at Weather Ship NOVEMBER
             from March 18 to April 4, 1965 and surface pressure analysis
             on 0600Z, March 23 and on 0000Z, March 30 (dots on upper
             figure indicate actual SST reports and the line indicates
             the analysed SST.
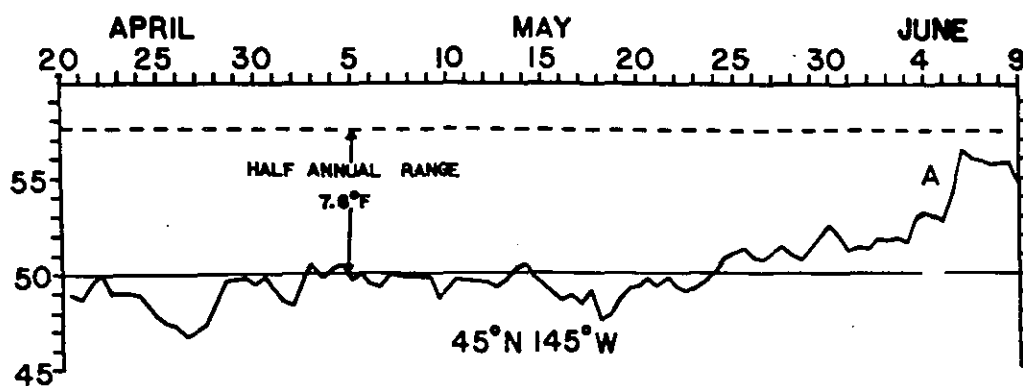
Figure 89.   Sea surface temperature changes at Weather Ship NOVEMBER
             April 20 to June 1965.

SFC PRES ANAL 06Z 23 MAR 1965   SFC PRES ANAL 00Z 30 MAR 1965
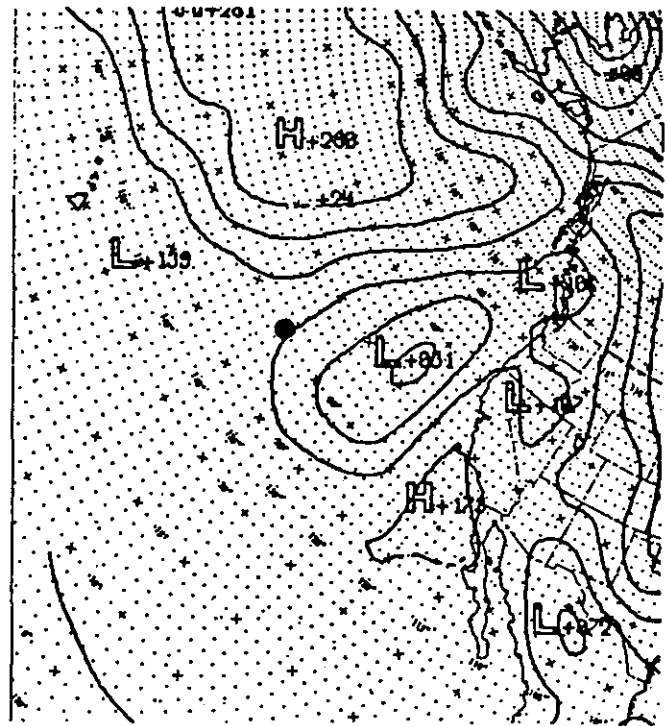
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the analysed SST.
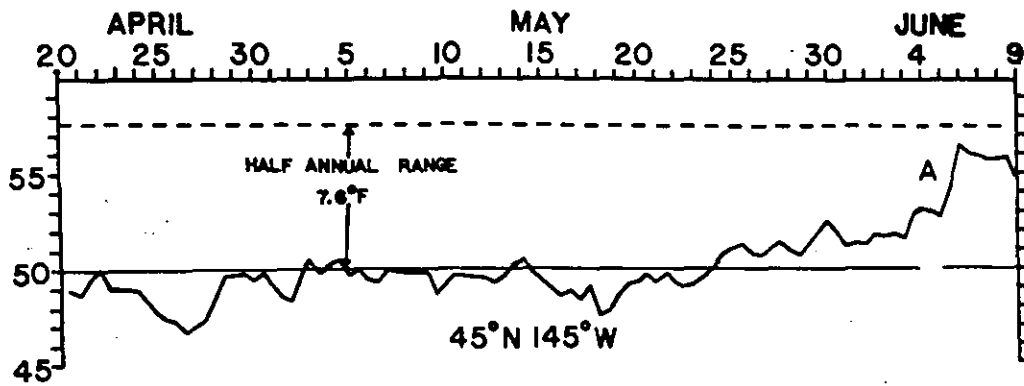
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April 20 to June 1965.
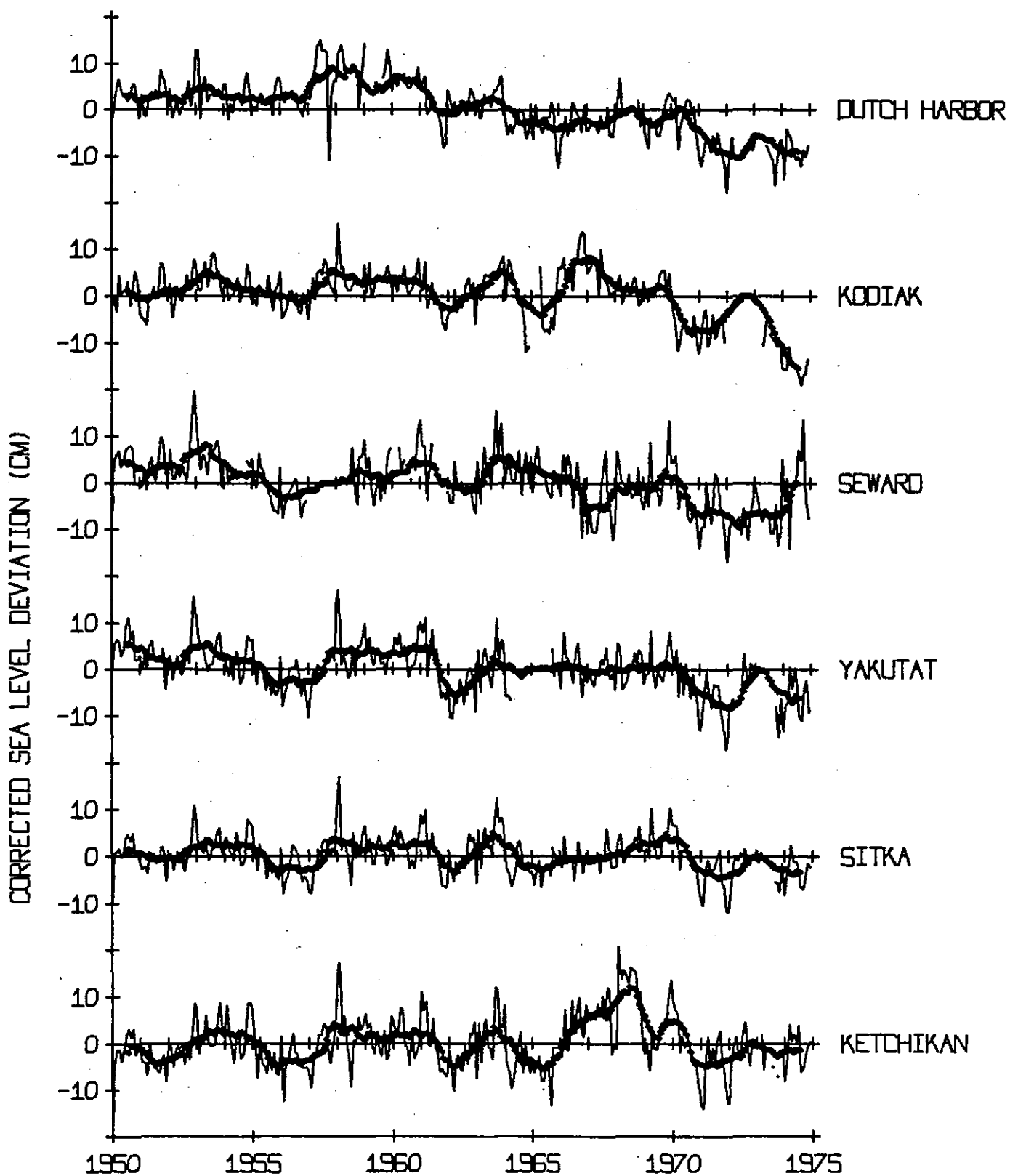
Figure 90. Deviations in corrected sea level (cm) at Dutch Harbor, Kodiak, Seward, Yakatat, Sitka and Ketchikan from monthly mean (1950-74) values (bold line indicates 12-month running mean) showing both coherence and lack of coherence between stations, and marked short-term (monthly) and long-term changes (from Ingraham et al. 1976).

extrapolations into the future (i.e., forecast). This requires relatively routine treatment of a considerable amount of information, usually in numerical form, and extensive computations have to be made using quantitative knowledge on sea-air interactions. Numerical computerized models are used, which not only speed the analysis process and reduce manpower, but carry out the task objectively with prescribed procedures, eliminating subjective interpretations which may vary from person to person.

Truly synoptic oceanographic observations are scarce, consequently the variability of the ocean conditions must be derived using knowledge of, and relation to, meteorological driving forces. Furthermore, many resource-environment problems require the direct use of specific surface meteorological data, such as winds. The meteorological analyses and forecasts are nearly exclusively accomplished using computerized models. The earlier, simpler barotropic/baroclinic models are now replaced with primitive equation (PE) models, using hemispheric grid nets with grid size of about 380 km.

Over open ocean areas the hemispheric, "standard mesh" models are sufficient for fisheries oceanography purposes. In these areas the surface meteorological features are large in scale and the available synoptic data from voluntarily observing and reporting vessels are sparse. In coastal areas, where most fishery is conducted, the meteorological conditions are more variable than further offshore and over the land, and are influenced by local factors, such as mountainous coasts and intensive sea-air interaction over coastal waters. Thus, the dimensions of the significant environmental features, such as wind and temperature fields, are considerably smaller in coastal areas and the coarse mesh hemispheric models are not adequate to analyse and predict this environment. Consequently, small-mesh numerical models must be used for meteorological and oceanographic analyses and forecasts in coastal areas.

Proven, excellent numerical small-mesh surface meteorological analysis forecasting programs are in existence, but unfortunately not in use on the North American continent; one reason for the latter condition being the absence of enough demand for these analysis/forecasts from the fishery community. The small mesh analysis/forecasting models, with grid size from 50 to 125 km, are usually baroclinic models, utilizing among other factors, quantitative knowledge on sea-air interactions. The boundary conditions, and at times the initial guess fields, are derived from hemispheric models. In a forecasting mode these models are useful and more accurate than hemispheric PE models for about 48 hours. Thereafter, the prescribed boundary conditions (i.e., the atmospheric systems which move into the area from the boundaries) dominate the prediction.

For several decades numerous numerical models have been proposed for reproduction of the general circulation in the oceans. The purposes of these models have also been varied, e.g., from attempts to determine the relative importance of the driving forces (wind, thermohaline gradients), and the effects of continental boundaries, to genuine attempts to reproduce all the dynamic processes in the ocean. These types of models are, however, of little direct use to fisheries problems. Even the best ones have not yet reached the stage where they can reproduce the available climatic information on

general circulation and distribution of properties as presented in available atlases. The best general circulation models are designed for research on long-term changes in the ocean and in the atmosphere, and these are used together with atmospheric general circulation models. Furthermore, the input into these models is often too generalized (e.g., flat bottom) and grid nets are too coarse.

Two types of quasi-synoptic oceanographic numerical models have, however, proven to be capable of reproducing processes and conditions in the ocean and are useful to fisheries oceanography problems: the rational (semi-empirical) models and the Hydrodynamical Numerical (HN) models. The rational methods, which can be applied for analysis/prediction of few, essential parameters (conditions) in the oceans use all available pertinent surface meteorological observations and available quantitative knowledge of sea-air interactions. The methods for analysis of sea surface temperature (SST) use the SST reports from meteorological messages and, in special cases, observations by fishing vessels. The satellite infrared observations, as well as heat exchange computations, have not yet proven to be useful for this analysis. Due to scarcity of observations and due to the fact that SST changes relatively slowly, 3 to 7 day composite observations can be used in one given analysis to increase the data density and information in surrounding areas can be obtained by interpolated climatology. The grid size of any oceanographic analysis should normally not exceed 50 km as oceanographic features and processes have smaller space scales than corresponding atmospheric features. The SST analysis is usually subtracted from time interpolated SST climatology to obtain anomalies, which have more direct use in fisheries ecology problems than absolute SST values.

The analyses of mixed-layer-depth (MLD, depth of the thermocline) and surface currents can be computed, using mainly surface wind data from meteorological analyses, but also other auxillary data, especially from ocean climatology. The methods for these computations are relatively complex and their description does not fall within the scope of this summary. The few directly synoptic observations on MLD (bathyothermagraphs (BT's), expendable bathyothermagraphs (XBT's), or temperature-salinity-depth (TSD) records) and surface currents are usually used to refine analysis/prediction methods, rather than to use them directly in synoptic analysis.

The advanced, multilayer Hydrodynamical Numerical (HN) models compute the currents, the thermohaline structure at each grid point in each time step, as well as tidal inputs. They require, however, the use of large computers and are expensive. As these models can depict in detail the distribution and dispersal of e.g., fish eggs and larvae or pollutants, they could be used in special application cases and in more accurate research tasks. Furthermore, the HN models can provide environmental input to ecosystem models, specially where tidal currents, mixing by tides, and net tidal drifts are of concern.

Due to increasing amounts of various fisheries related data and the need to use these data in quasi-real time, in various fisheries management problems, it is necessary to computerize the storage, retrieval and analysis of not

only environmental but also various fisheries and biological data. Therefore, certain standardization (specially in respect to format) of numerical storage and retrieval models is in progress in fisheries centers. The models for objective analysis of, in space and time, randomly spaced data are an important part of these data handling programs. Although initially developed for analysis of environmental observations, these analysis programs have been adapted for objective analysis of great variety of special data, such as catch statistics and results from exploratory fishing.

Two developments in data handling field with respect to fish-environment relations seem to be in need of additional attention and acceleration: first, all past fisheries biological data, including catch and other fisheries economical data, must be put into computer accessible form (environmental data is already fully available in this form) so that these data, among others, can be incorporated into complex ecosystem models, as well as, specialized correlation and other analysis. Second, various computerized analyses, objective as well as statistical, should be carried out on various fisheries data in association with corresponding environmental data to test and prove various existing theories and hypotheses on resource-environment relations, to extend this knowledge, and to create a basis for various fisheries forecasting methods.

VI.   NUMERICAL ECOSYSTEM MODELS

It has long been recognized that the productivity of any marine resource
is a complex function of the synergism between species and stocks and their
physical and biological environment as well as intra-stock (or intra-species)
interactions.   Ideally, production models for any species should consider
the totality of these interactions.   These ecological relationships are,
however, extremely complex and difficult to describe, let alone quantify.
Moreover, since most of the processes are beyond human control, the pragmatic
necessity for resource management has resulted in the evolution of yield
models developed around the one controllable source of mortality, the quantity
and quality of fishing effort.   The conventional models deal with single
species and express yield principally in terms of the resultants of population
increments (recruitment and growth) and decrements (natural and fishing
mortality), with almost total disregard for the ecological processes which
determine these population parameters.

Although single species management models have provided and will continue
to provide a basis for rational management decision, current and future
decisions concerning marine resources, even for the management of single
species, will require short- and long-term forecasts of yield which extends
beyond the scope of the conventional single species models and requires a
better understanding of the interaction of any species with its physical
and biological environment.   Furthermore, the scope of pressing marine
resource management decisions has increased beyond considerations of fisheries
alone and include assessment of the effects of fishing not only on target
species but on other animals in the community including not only fishes,
but commercially important invertebrates, mammals and birds as well.

The marine ecosystem contains a complex web of interactions among species
(e.g., one species preying upon the other) and between the species and
environment as summarized in previous Sections.   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 fishery alters the balance
(or imbalance) in the ecosystem and can result in an increase and/or decrease
in other components.   Thus, in order to evaluate changes in abundances and
distributions of different living marine resources and devise wise management
criteria, realistic, quantitative, numerical ecosystem models must be used
because the conventional single-species models are no longer adequate.

A.   DYNAMICAL NUMERICAL MARINE ECOSYSTEM (DYNUMES) MODEL

A dynamic marine ecosystem model that permits simulation of the statics and
dynamics of standing stocks of various species and groups of species (i.e.,
abundance and distribution) in space and time as affected by interspecies
interactions (e.g., predation), environmental factors (e.g., temperature,
currents) and the activities of man (e.g., fishing) which are depicted in
model outputs has been formulated at NMFS's Northwest and Alaska Fisheries
Center (Laevastu and Favorite 1976a).   Thus, energy requirements of trophic
levels and realistic hypotheses as to constraints on population growths can
be formulated.

The main objectives of any numerical modeling scheme of the marine ecosystem are connected with its prospective use in solving practical as well as scientific problems: (1) the evaluation of the effects of exploitation to achieve optimum management of marine resources; (2) the evaluation of the effects of environmental changes (e.g., climatic changes) and short and medium range anomalies on the exploitable resources and on the marine ecosystem at large, and quantitative comparison of man-made and environment-caused changes in this system; (3) the reduction of all quantitative and descriptive data into easily accessible and reviewable form; and, (4) the determination of additional research needs and priorities.

The size of the basic grid is determined by the economy of the computer core and time requirements/availability, but it is often necessary to look at the distributions and dynamics of a given species at a given location (e.g., on spawning grounds) in much greater detail than the relatively coarse basic grid allow. For this purpose a zooming technique must be provided in the model and detailed computations are carried out in fine grid inserts by special instructions for which the boundary and initial values are obtained from a large scale model and its subroutines. The fine mesh computation will also use a shorter time step than the large scale model. Zoomed approaches have both scientific and model-improving (tuning) as well as practical applications. They allow modeling and consequent verification of research planning of the small- (and meso-) scale effects of environmental changes, determining the consequences of a displaced (and delayed) spawning, and formulating detailed prognostications of the location and time of fish aggregations that aid in management decisions.

No problem exists in obtaining static input parameters for the model (e.g., depth) and the dynamic environmental input parameters are mostly obtained from separate environmental analysis/forecasting models. Subroutines are provided for the input of environmental data (e.g., in form of anomalies), obtained either as observational data at a few points, or as test and research modes, to study the response of the ecosystem to possible changes and/or anomalies. This is usually accomplished with an analysis subroutine, which uses a first-guess field (e.g., time interpolated climatology) and analyses the new introduced "observations" at specified locations into the first-guess field with a variable (determinable) smoothing coefficient.

The input of biological information into the model is either in form of first-guess fields of distribution and abundance, computed from available description, often as fragmented information, or as dynamic variables such as migration directions and speeds (migration routes), including aggregation and dispersal also estimated from available descriptive data (e.g., from known seasonal distribution changes). The latter information although given initially as direction and speed, is decomposed into u and v (east-west and north-south) components. Furthermore, some preliminary (first-guess) decomposition is made by "movement" caused or affected by currents, movements such as route and speed caused by environmental properties (e.g., selection of optimum temperature by a species), and "active" movements associated with either a search for food or a spawning migration. Much of the other biological information input is given either as time-dependent variables for a given

species or group of species in the form of seasonal variation of composition
of food and changes of growth rate with time and/or age, or as predetermined
coefficients, such as feeding rates or food requirements for maintenance
and growth and optimum temperature requirements (temperature preference
limits).

Several of the initially prescribed input coefficients in the models do not
usually remain constant during the computation, but are made dependent
variables in certain conditions with the use of restrained functions, such
as composition of food and feeding rates, which can become functions of
food (prey) density as well as predator density. The natural mortality
coefficents can also be initially estimates and introduced into the model
as time and location dependent variables for a given year-class, species
or group of species, which can then be changed during the course of computation.

Fishing mortality is used in the model as a time and space variable input,
to be easily changed by the operator during the course of the use of the
model. When using the model as a decision making tool, variations in fishing
mortality will determine the resultant abundance and distribution of the
given species under consideration and will affect, in most cases, the statics
and dynamics of the whole ecosystem.

The model outputs can be tailored to the principal use of the model, both
in a research as well as in a decision making mode. Spacial distributions
of abundance of any species can be extracted and displayed at any desired
time step (e.g., weekly or monthl). Furthermore, time series outputs could
be taken at any given point, or the static and dynamics of the entire stock
could be summarized over the entire area of the computational grid. A
simple, (at this time) somewhat hypothetical example of such output is shown
(Figure 91) which depicts the effects of monthly fishing mortality changes
on the biomass of a fish species together with the effects of this change
on the growth of the biomass.

The concept and general processes computed (Figures 92 and 93) consist of
five basic groups: (1) static factors which are prescribed in digital form,
and do not change during computations such as the grid net with sea-land
table and depth of water; (2) dynamic environmental factors, which are either
extracted from other environmental analysis/forecasting models or computed
with special subroutines on an ecosystem model (e.g., mean monthly temperature
and its anomalies, current); (3) various biological components, which are
nearly all dynamic as is the case with living organisms in general; (4)
components consisting of factors dependent on man, such as fishing mortality;
and, (5) "feedback channels" (i.e., interconnected computational loops),
which allow iterative solutions to be sought if, when, and where factors
and interactions are changed which affect the changes of other processes
and quantities.

The model is initialized with the best available data on standing stocks of
essential components and their spatial distributions at an initial stage
(e.g., January). The best available information on trophic relationships,
feeding rates and other interspecies interactions, seasonal migrations,
sensitivity to environmental changes, and/or optimum environmental require-
ments for the various components, are prescribed in numerical form on a
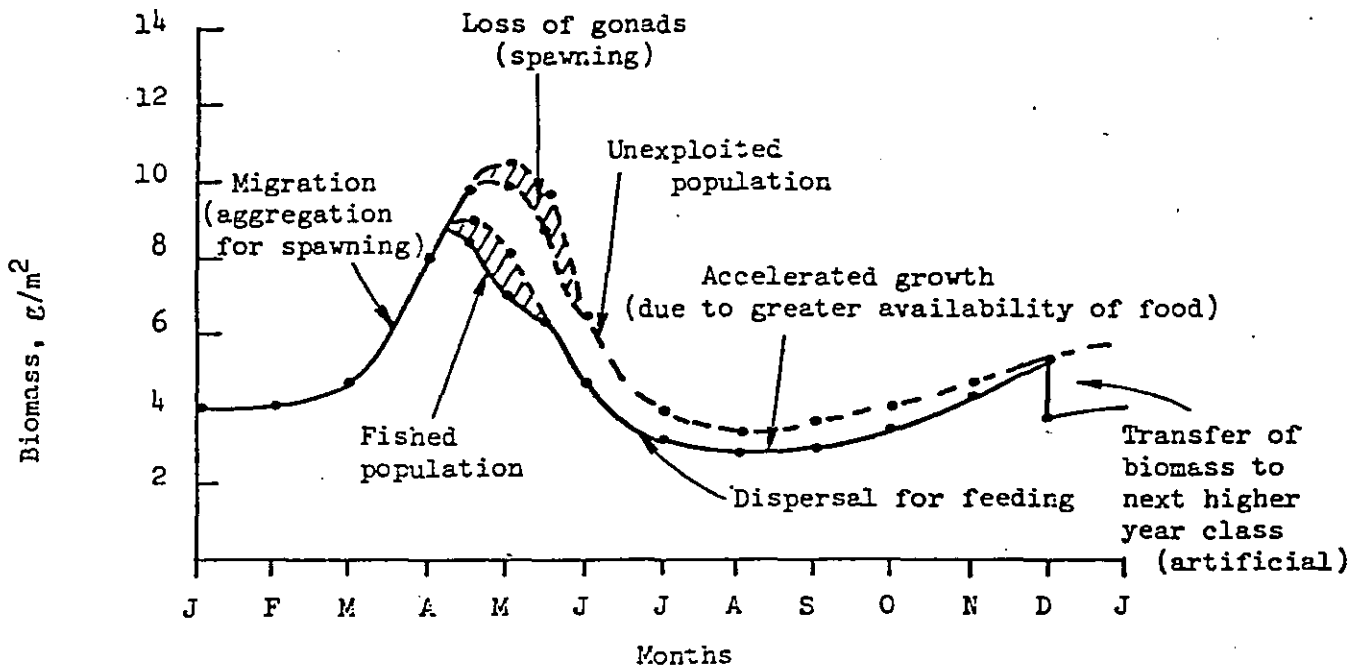
Figure 91. Schematic diagram of a model output showing monthly biomass change of a given age group of a species at a grid point.
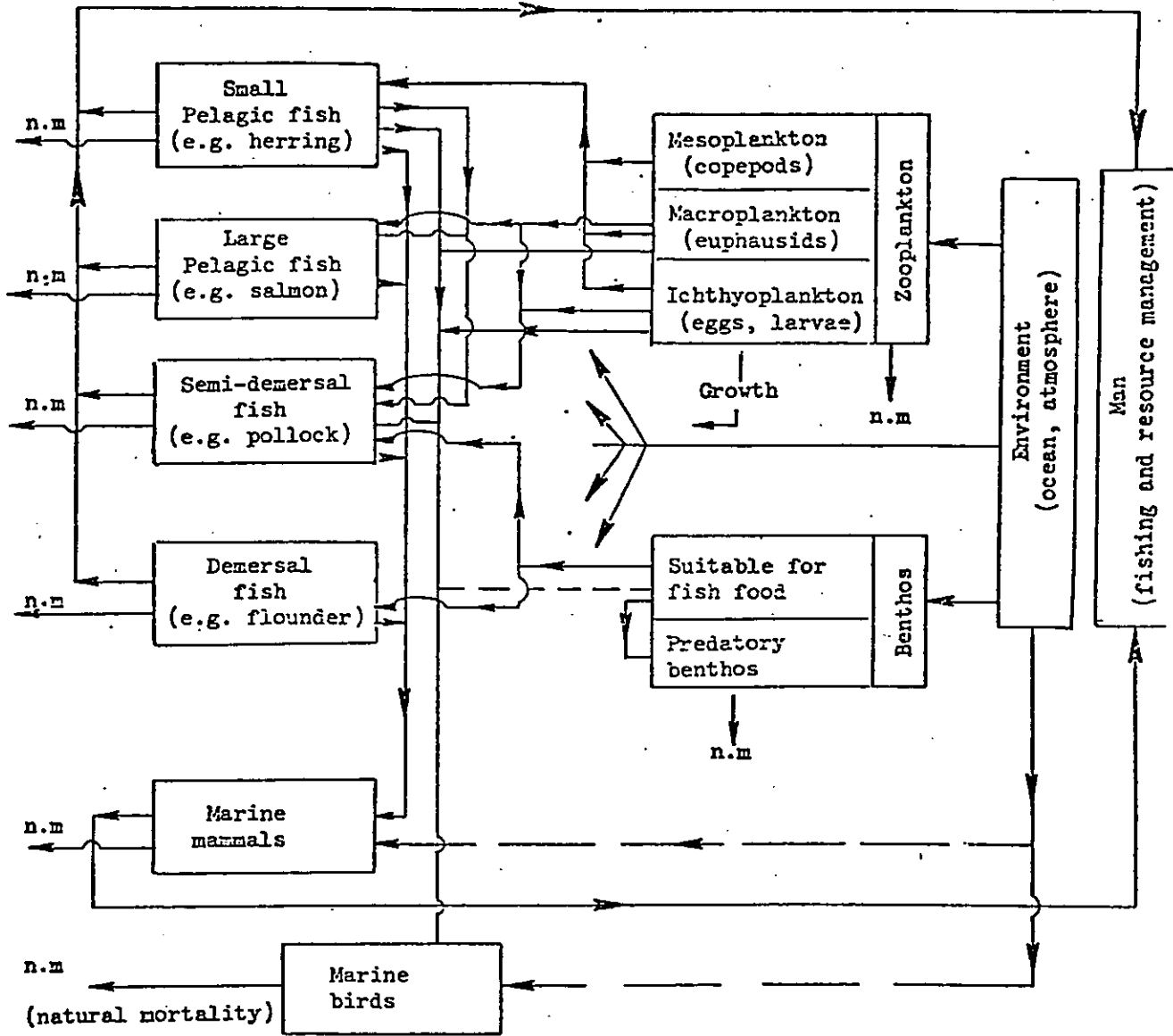
Figure 92. Generalized scheme of major components of dynamic marine ecosystem model (from Laevastu and Favorite 1976a).
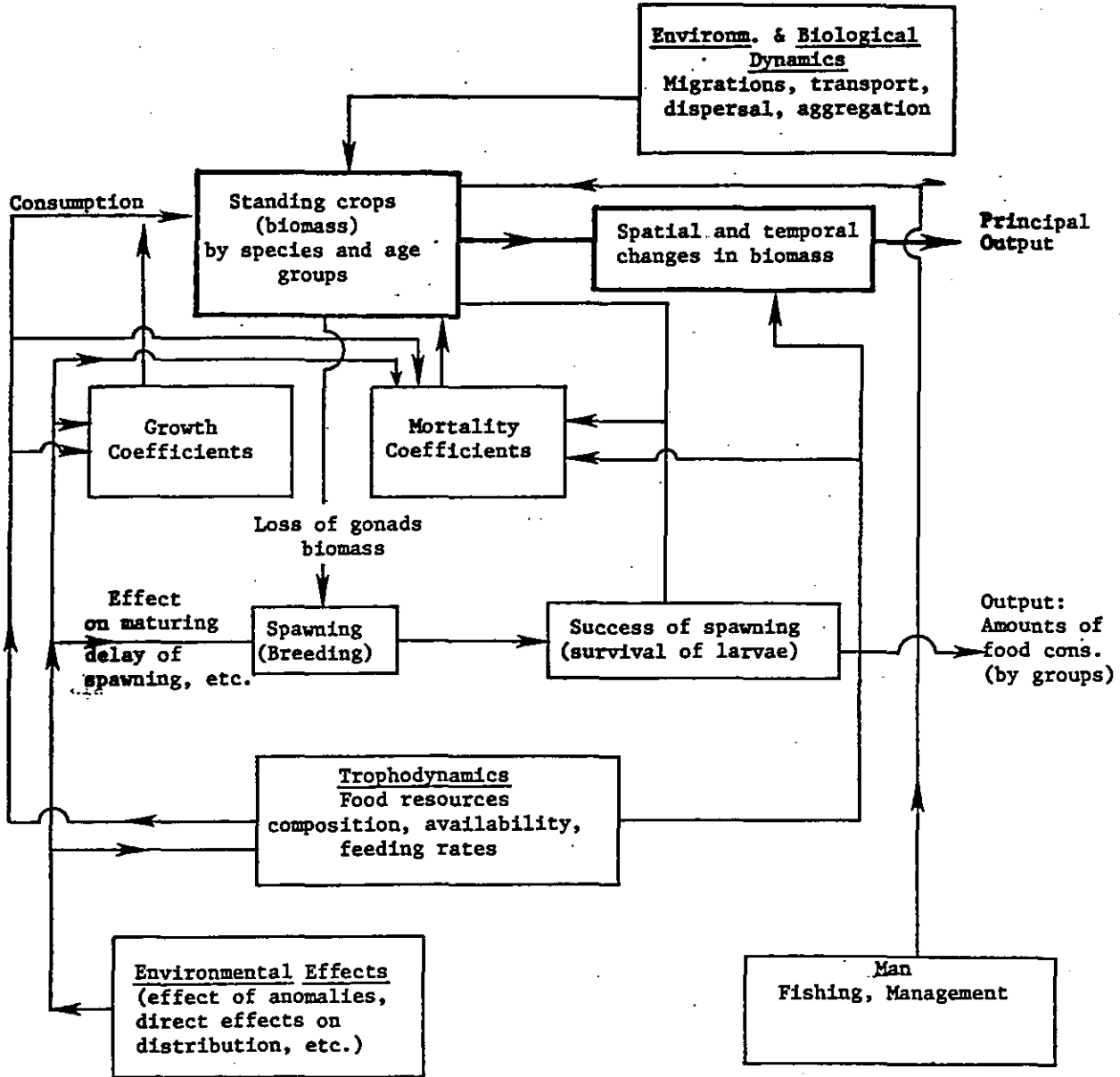
Figure 93. Principal processes in a dynamic marine ecosystem model
(from Laevastu and Favorite 1976a).

month to month basis. In addition, all available pertinent models and modeling techniques, such as the conventional population dynamics models, are used in modified form as part of various subroutines. Some concepts of "energy flow" models have also been used, but in different form--i.e., in the form of the "flow" of biomass.

In the initial formulation, the model is essentially a time-dependent, two dimensional model, whereby the third dimension (e.g., depth distribution of species, distribution of temperature and currents, etc. with depth) applies implicitly in some parts of the model.

B. BERING SEA MODELS

The eastern Bering Sea provides a somewhat optimum area for model studies-- the available data are adequate for initial first-guess fields, present studies provide information to test some aspects of initial formulations, and on-going studies could verify the validity of model results.

1. Bulk Biomass

Our first model is a relatively simple, Bulk Biomass standing stock and trophodynamics evaluation Model (BBM) (Laevastu and Favorite 1976b). This model attempts to evaluate the mean standing stocks (e.g., average standing stock of roundfish in terms of kg/km^2 in the eastern Bering Sea), using a first best guess of this standing stock, monthly growth rates, removal by fishery, natural mortality and above all internal ecosystem consumption (i.e., grazing). The plausible (usually minimum) standing stock is derived at by iterative computations.

Obviously, results are dependent on the initial inputs and the following principal inputs (Tables 12 to 14) should be considered as preliminary: the estimated number of mammals in the eastern Bering Sea, and estimated food composition (Table 12), assuming a low food requirement of 6% of body weight daily; the estimated mean composition of food, as introduced into the present model runs (Table 13); and the growth and food coefficients, as used in preliminary model runs (Table 14). The food coefficients are the lowest plausible values ascertained from the literature, thus, the model generates a low estimation of plausible standing stocks of forage organisms, including fish.

The growth coefficients are the highest reasonable estimates although the small pelagic fish (herring, capelin, Pacific sand lance (Ammodytes hexapterus), smelt (e.g., eulachon (Thaleichthys pacificus), and rainbow smelt (Osmerus mordax), and other Osmeridae species)) growth coefficient, 14.6% per month, is somewhat too high--a value of 12% would be the highest supported by available data. High growth coefficients on the other hand would allow the iteration of low standing stocks. Furthermore, high growth coefficients are typical for young populations (1 to 3 years) and thus indicate that the bulk of population biomass seems to be of young age (prefishery juveniles).

The BBM model was run with monthly time steps and the standing stocks were iteratively adjusted so that quai-steady state was reached in the model.

Table 12.—Mammals in the eastern Bering Sea and their food composition (input to BBM model).

Species	Average number of animals		Mean weight (kg)	Roundfish	"Herring"	"Salmon"	Squids	Benthos	Others
	Summer	Winter							
Fur seal	550,000	96,000	65	80	5	2	11	–	2
Sea lion	100,000	50,000	400	80	10	10	–	–	–
Harbor seal	190,000	315.000	140	30	12	2	30	21	5
Ringed and ribbon seals	175,000	350,000	70	35	34	1	10	15	5
Bearded seal	75,000	200,000	240	8	8	1	8	70	5

Table 13.--Composition of food of major ecological groups in the eastern
Bering Sea (input to BBM model).

Ecological Group	Food item	Percentage
Megaloplankton (squids, etc)	Copepods	30
	Phytoplankton	60
Small pelagic fish (herring, etc.)	Copepods	60
	Euphausids	30
	"Others"	10
Large pelagic fish (salmon, etc.)	Euphausids	10
	Squids	15
	"Herring"	40
	Roundfish	15
	"Others"	15
Benthos	(Detritus, other benthos)	
Roundfish (pollock, etc.)	"Herring"	20
	Benthos	20
	Euphausids	15
	Copepods	10
	"Others"	10
	Roundfish (cannibalism)	25
Flatfish (yellowfin sole, etc.)	Benthos	85
	Flatfish (cannibalism)	15

Table 14.--Growth, mortality and food coefficients for major ecological
groups in the eastern Bering Sea (input to BBM model)

Ecological group	Growth coefficient[1]	Mortality coefficient[1]	Food coefficients	
			Growth	Maintenance[2]
Megaloplankton	15.6	4.5	1:6	–
Small pelagic fish	14.6	1.5[3]	1:3	1.0
Large pelagic fish	6.0	3.6	1:3	1.3
Benthos	13.2	6.0	–	0.67
Roundfish	9.2	2.2	–	1.3
Flatfish	8.4	2.2	–	1.0

1/ % per month

2/ % body weight daily

3/ excludes fishery

Thereafter various outputs, among others the ecosystem internal consumption, were taken and the results are presented in Tables 15 to 17. Some of the preliminary results and indications from this numerical model exercise were:

The quasi-equilibrium standing stocks of most ecological fish groups (e.g., pelagic, demersal, etc.) are very sensitive to change of growth coefficients, consumption and the fishery. Minimum plausible standing stock size of any one of the ecological fish groups depends largely on these two factors collectively for all ecological groups (i.e., a standing stock of roundfish (e.g., pollock) cannot be determined alone, without determining also herring, mammal, etc. standing stocks, their growth and specially consumption of roundfish by these other ecological groups).

The growth coefficients are high in the present model run. This implies that the populations are relatively young. This statement translated to fisheries problems means that bulk of the biomass (usually >50% of it) consists of prefishery "juveniles". These juveniles are growing faster than older fish and consume food from higher stages of food pyramid (e.g., zooplankton) than older fish do, thus the juveniles are more effective utilizers of the organic production. Furthermore, the rapid growth of juveniles, together with considerable standing stocks of them, is an important consideration in mesh size regulations.

The model demonstrates directly that availability of proper food for all ecological groups below secondary production level is the limiting factor of the maximum standing stock size, and the quasi-equilibrium standing stock iterated with the present model would not differ greatly from the maximum possible standing stock due to food availability limitations.

The consumption of fish by mammals is about the same order of magnitude as the present fishery in the eastern Bering Sea.

There must be much more small pelagic fish (forage fish) in the eastern Bering Sea than generally recognized at present (i.e., the dispersed standing stock of young herring (1 to 4 years), capelin, smelt, and Atka mackerel must be considerable (>1 million metric tons). Part of the ecosystem food requirements are satisfied by assumed considerable dispersed standing stock of squids (>3 million metric tons), which occur frequently as food items in stomach analyses of fish, mammals and birds.

The more varied and flexible the feeding habits and the wider the seasonal migrations occurring in an ecological group, the larger the standing stock (e.g., pollock).

2. 8-Component Submodel

Our present 8-component marine ecosystem submodel (DYNUMES) for the eastern Bering Sea constitutes a conceptual model and is another step in the development of a total ecosystem model. The selection of the biological components was somewhat arbitrary in view of the diversity of organisms in the Bering Sea. Two organisms in each of four categories (plankton, fish, mammals,

Table 15. Annual consumption kg/km^2 in the eastern Bering Sea (as computed with BBM model).

Consumer	Phytoplankton	Zooplankton	"Squids"	"Herring"	"Salmon"	Benthos	Roundfish	Flatfish	"Others"
Birds	-	(150)	540	390	(25)	780	260	-	340
Mammals		-	500	480	130	1,310	1,570	-	150
Zooplankton	33,800	-	-	-	-	-	-	-	-
"Squids" (megaloplankton)	-	15,000	-	-	-	-	-	-	-
"Herring" (small pelagic fish)	3,050	68,670	2,290	-	-	-	-	-	7,620
"Salmon" (large pelagic fish)	-	-	800	2,130	-	-	800	-	800
Benthos	-	-	-	-	-	(122,590)[1]	-	-	-
Roundfish (pollock, etc.)	-	11,810	-	9,460	-	9,460	1,990	-	4,720
Flatfish (sole, etc.)	-	-	670	500	-	14,430	670	-	670
Total	36,850	85,630	4,800	12,960	155	25,980 (148,570)[2]	5,290	(1,200)[3]	14,300

Parenthesis indicate uncertain and/or incomplete values.
[1] Consumption by predatory benthos.
[2] Includes consumption by predatory benthos.
[3] Cannibalism, etc. computed as part of "others".

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Table 16. Annual mean consumptions, standing stocks and mean annual turnover
          rates (kg/km^2) in the eastern Bering Sea (as computed with BBM model).

Ecological group	Monthly mean standing stock	Annual consumption [1]	Mean natural annual turnover rate [2]
Phytoplankton	100,000	36,850	(0.4)
Zooplankton (copepods, euphausids)	20,000	85,630	4.3
Megaloplankton (squids, etc)	3,800	4,800	1.3
Small pelagic fish (herring, etc.)	8,200	12,960	1.6
Large pelagic fish (salmon, etc.)	760	155	(0.2)
Benthos	200,000	25,980	–
(Predatory benthos)	(50,000)[3]	(148,570)[4]	(0.8)
Roundfish	9,800	5,290	0.5
Flatfish	4,700	(1,200)[5]	(0.3)
"Others"	?	14,300	?

Parentheses indicate uncertain, incomplete, and nonsignificant values
[1] All exclude fishery
[2] Standing crop/consumption (excluding fishery)
[3] Predatory benthos
[4] Total consumption, including consumption by predatory benthos
[5] Cannibalism and consumption by roundfish, mammals ("incidental")

Table 17. Ecosystem internal consumption and fishery, kg/km^2, in the eastern Bering
          Sea, assuming 800,000 km^2 area (as computed with BBM model).

Ecological group	Standing stock	Ecosystem internal consumption	Fishery	Fishery in % of internal consumption	Monthly mean Fishing mortality coefficient (%)
Pelagic fish (e.g.herring)	8,200	12,960	63	0.5	0.06
Roundfish	9,800	5,290	2,075	39	1.76
Flatfish	4,700	(1,200)	215	(18)	(0.38)
"Salmon"	760	155	50	33	0.55
"Others"(crabs,etc)	?	(14,300)	(250)	(1.8)	–

Parentheses indicate incompete and nonsignificant values

and birds) were selected, primarily as a result of dominance and/or distinctly different migration patterns so as not only to achieve representativeness, but also to tax the dynamic capabilities of the model. It is recognized that the omission of benthonic components may be a shortcoming of the present model, but provision for incorporation has been made.

a   Subroutines

Mammal--Northern fur seal (Callorhinus ursinus) and bearded seal (Erignathus barbatus) were selected as representative of marine mammal populations. Monthly distribution of the numbers of fur seal are prescribed, whereas monthly distribution of bearded seal was created in the program in relation to the ice edge. These bearded seal fields are also read from cards in the main (control) program and stored on discs. The numbers of mammals are converted to weight of biomass per unit area (e.g., kg/km^2).

Although provision is made in the program for computation of growth and mortality of mammals, this provision is not used, as the errors (uncertainty) of monthly numbers of animals present in the Bering Sea would entirely mask the effects of growth and mortality computations. Food consumption per unit time by mammals is assumed only as 4% of body weight daily in the model run, which is presented in this report, whereas the data available in literature indicates 6 to 8% of body weight daily. The latter data originates from feeding experiments of mammals in captivity. The composition of fur seal food is assumed in the presented run as 77% of pollock, 5% of herring, and 18% other fish. The composition of bearded seal food is 8% pollock, 8% herring, mackerel, and other related pelagic species, and 70% of benthos. All the above mentioned numbers are variable inputs and are changed in different runs for the study of their individual effects on the ecosystem as a whole and for testing of the reported data to find the plausible numerical values.

Fish--Walleye pollock and Pacific herring were selected as representative of fish populations. The initial distribution of pollock in January was prescribed. The population was divided into three size (age) groups in the reported model run as follows: group 1, <30 cm, 38% of total biomass; group 2, 30 to 50 cm, 43% and group 3 >50 cm, 19%. Thereafter the computations were carried out separately on each size group. Again this quantitative division is preliminary and subject to further tuning in future use of the model. The pollock biomass was moved from deep water (winter) to the continental shelf (summer) and back to deep water for next winter with a migration speed and pattern, ascertained from literature; the migration speed (u and v components) being generated within the pollock subroutine. The same migration speed was used initially in the present submodel for all three size groups. The numerical advection scheme, used in the model, has been developed earlier for studies of pollutants and is one of the few available tested advection schemes which permit the conservation of biomass. The growth, intergroup transfer, and consumption of each size group was computed in monthly time steps with the following coefficients (subject to future tuning):

Size group	Bulk growth (% monthly)	Transfer to next group (% monthly)	% of total pollock consumption by other groups applied*	Fishery* (% of total)	Natural mortality (% monthly)
Group 1	9.7	3	40	--	--
Group 2	3.9	3	50	40	--
Group 3	0.8	-	10	60	2.8

*e.g., of the total consumption of pollock by mammals 40% is taken from size group 1; the same applies to fishery.

It was assumed that food coefficient for growth is 1:2 and 1% of body weight of food daily is required for maintenance. These coefficients can be changed with ease in the program. The composition of pollock food in the present program can also be changed. The model runs were made with the following food composition:

Group 1. 30% copepods, 70% euphausids.

Group 2. 18% copepods, 56% euphausids, 10% herring, 8% benthos and 8% of pollock from Group 1.

Group 3. 5% copepods, 30% euphausids, 10% herring, 25% benthos, and 30% pollock (Groups 1 and 2).

Pollock biomasses from Groups 2 and 3 are affected by the fishery, and these data were tuned to available fishery statistics.

The pollock subroutine allows various outputs, either for tuning of the model or as results of a particular model application. The implications of the presently used numerical values and the preliminary results are described at the end of this section.

The herring subroutine is in many aspects similar to pollock subroutine, except no division into different size groups was made. Growth of herring biomass was assumed to be 8.5% per month, no natural mortality from "old age" was computed and the consumption of herring was computed in other subroutines as dictated by composition of food of different species. The fishery on herring was computed in two seasons only (i.e., winter offshore fishery and summer fishery on spawning stocks near the coast). The composition of herring food was assumed to be 70% of copepods and 30% of euphausids, as ascertained from literature. The effect of growth coefficient on total standing stock of herring is described at the end of this section.

Zooplankton--The consumption of zooplankton (copepods and euphausids) was computed in other subroutines as dictated by composition of food and food requirements of corresponding species feeding on zooplankton. In zooplankton subroutine, a monthly mean zooplankton abundance was created, which was used for comparison with consumption. The distribution and magnitude of the abundance was tuned to the corresponding data (available in literature). The numerically created field was a function of latitude, time (month), and specific location (e.g., depth of water, distance from coast, and continental

slope). In converting the consumption from unit area (kg/km^2) to unit volume (mg/m^3), a uniform depth distribution of 50 meters (approximate mean shelf depth) was assumed.

Bird--Shearwaters (family Procellaridae) and murres (family Alcidae) were selected as representative of marine bird populations. The monthly numerical spatial distributions was created using the available estimates on the number of birds in the Bering Sea and their geographic distribution on one hand and special index field (i.e., distance from the coast, depth of water, etc.), ice field, and latitude on the other hand.

No growth or natural mortality was computed for the birds as the results from these computations would be entirely masked by the uncertainties in the estimates of the numbers of birds present in the area. The composition of food for birds in this submodel was: shearwater--50% euphausids, 10% small herring, 10% small pollock, and 30% other small fish; murres--10% small herring, 30% other small fish, 30% benthos, and 30% other various food items.

The food consumption was assumed to be relatively low--9% of body weight daily in the presented test run. The values of food requirements of birds, given in literature, reach up to 20% body weight daily. However, the consumption by birds affects marine ecosystem relatively little. The model serves as a powerful tool for investigation of various processes within the ecosystem and their effects on the marine ecosystem as a whole, and for determination of magnitudes of standing stocks and their dynamics.

b. Preliminary Results

This initial 8-component submodel of DYNUMES has been used for preliminary study of pollock and herring in the eastern Bering Sea (Laevastu and Favorite 1976a). Some of the preliminary results of interest to fisheries management, are the following:

During the winter the greatest part of the herring and pollock population in the eastern Bering Sea are apparently off the continental shelf over deep water. A considerable part of the pollock biomass remains there also during the summer. In addition, it can be prognosticated that part of the capelin population must reside there at least part of the year (as concluded from food requirements for pollock population). As availability of food is one of the limiting factors for the pollock population size, as the model indicates, it can be postulated that rather widespread starvation prevails in some parts of this population. Thus, all fish which theoretically should spawn each year, might not do so because of hampered development of sex products due to inadequate nourishment. The shortage of available food might be one of the causes of cannibalism in larger pollock.

As a result of interaction between seasonal migration, consumption by mammals and fishery, there is a spatial separation of major adult population of pollock from the juveniles (Figures 94 and 95). As pollock is rather cannibalistic, this separation has a saving effect on juvenile population (i.e., prevention of grazing by larger adults).
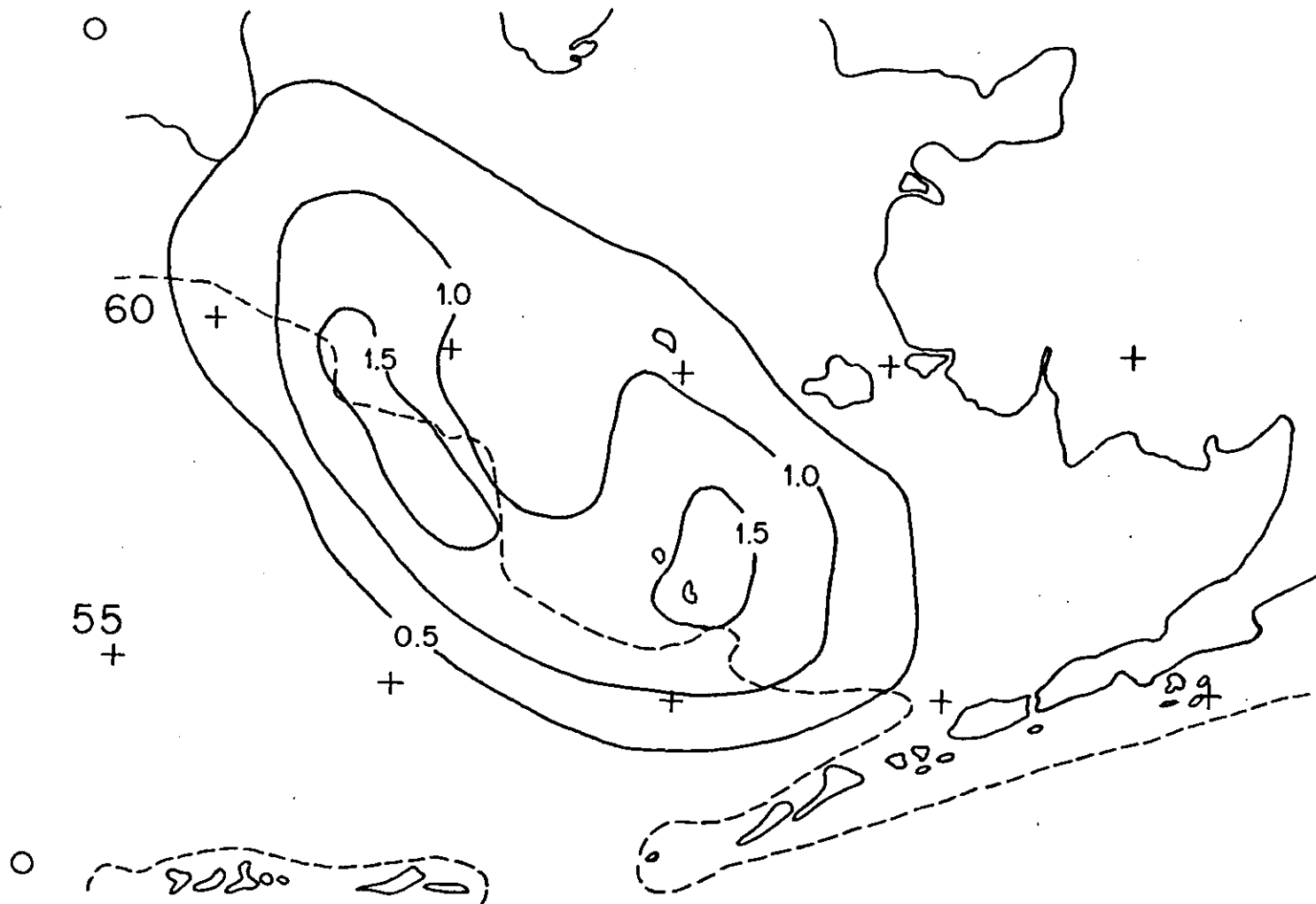
Figure 94. Distribution of walleye pollock of group 3 (>50 cm) in August (DYNUMES submodel).
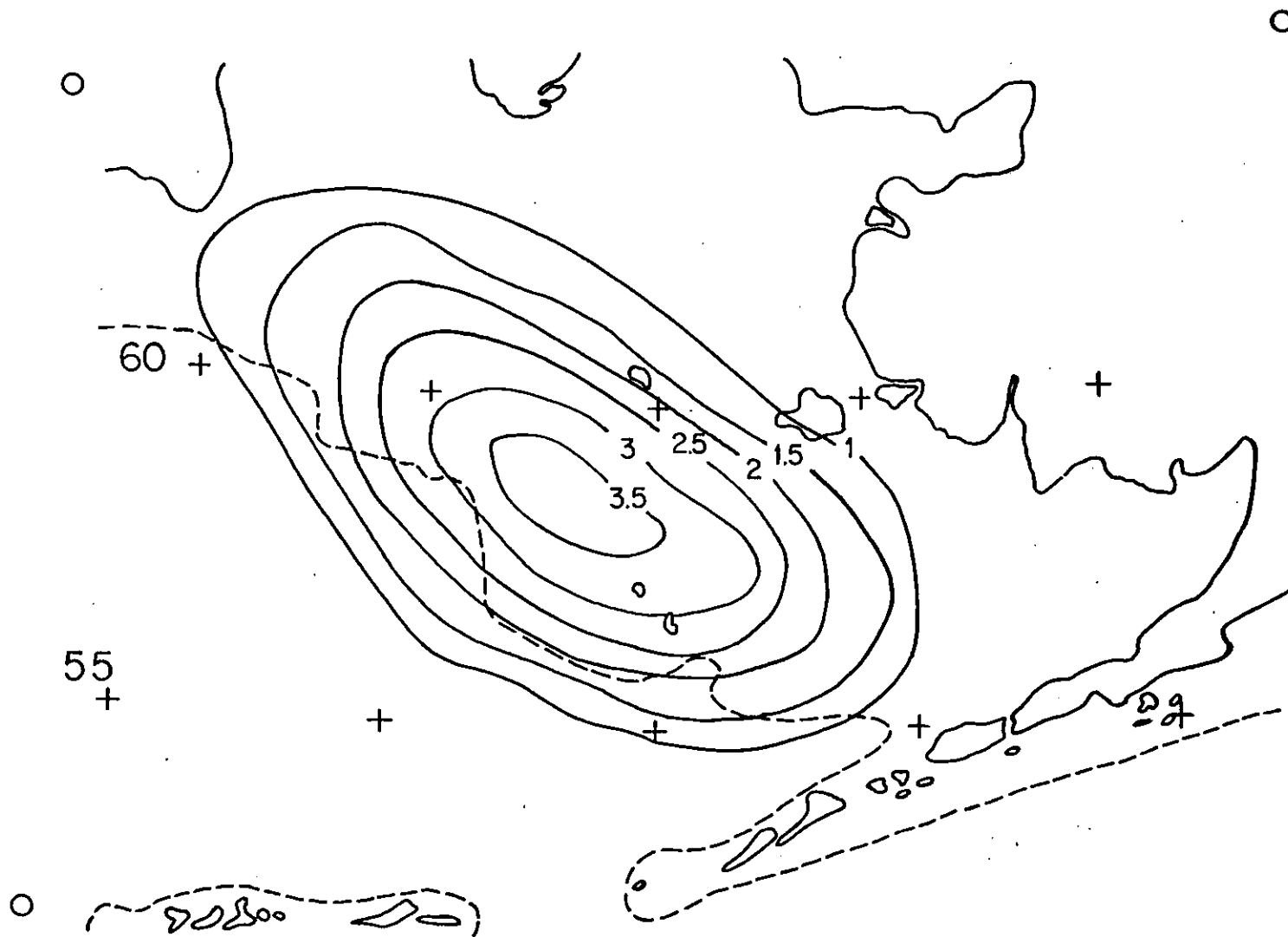
Figure 95. Distribution of walleye pollock of group 1 (juvenile) in August (DYNUMES submodel).

With the increased fishing effort on pollock, part of the older (and medium age) pollock is removed. As these large pollock are cannibalistic on juveniles, by decreasing their (older) population the grazing (cannibalism) on juveniles is diminished; thus, as juvenile part of the population has faster growth, it grows bigger than it was in unfished population due to decreased grazing (cannibalism) on them, thus increasing the total population of pollock until availability of food for juveniles (and presumably also decreased spawning population size due to fishery on mature fish) becomes a limiting factor (Figure 96). Thus, here we have an example where fishery increases the production of biomass of a species (to certain limits)!

In an unfished (and/or slightly fished) pollock population the older age groups are relatively large and graze (cannibalism) the juvenile (prefishery) part of the population to a lower level (Figure 97). Thus, before the start of the intensive pollock fishery in the early 60's, the total pollock biomass in the Bering Sea was apparently at a lower level than at present and the age composition shifted with increased fishery to younger (smaller) fish. This model result is partly supported by observations.

An overall increase of pollock biomass causes a decrease of herring (and possibly also shrimp) biomass due to increased grazing.

The fringe population of herring is consumed first by increased grazing by pollock and the population "shrinks" toward the center of its mass distribution.

The numerical model indicates that there are natural long-term fluctuations in the pollock biomass size in the eastern Bering Sea and the magnitudes and periods of these fluctuations are influenced by the fishery. This periodicity is being investigated.

These are only a few preliminary examples of the use of numerical ecosystem model and indications/conclusions obtained with the DYNUMES model.

3. Extended Submodel

One of the most pronounced interspecies interactions in the marine food web is the grazing of one species upon another. The grazing involves also intra-species interaction via cannibalism. In the present 8-component submodel the food coefficients (i.e., the food requirements for growth and maintenance) have been selected generally as lowest plausible values reported in literature. Furthermore, the composition of food has been kept constant throughout the year and in all locations (i.e., not a function of space and time). Despite these limitations the submodel indicates that availability of food is a limiting factor for most components in the marine ecosystem (i.e., limiting the possible population size, as well as growth and, indirectly reproduction). Furthermore, it follows that a marine ecosystem model must include all major components of a system as food sources and grazers in order to simulate real highly competitive conditions in the sea. Thus, the next steps in the completion of the DYNUMES ecosystem model will be:
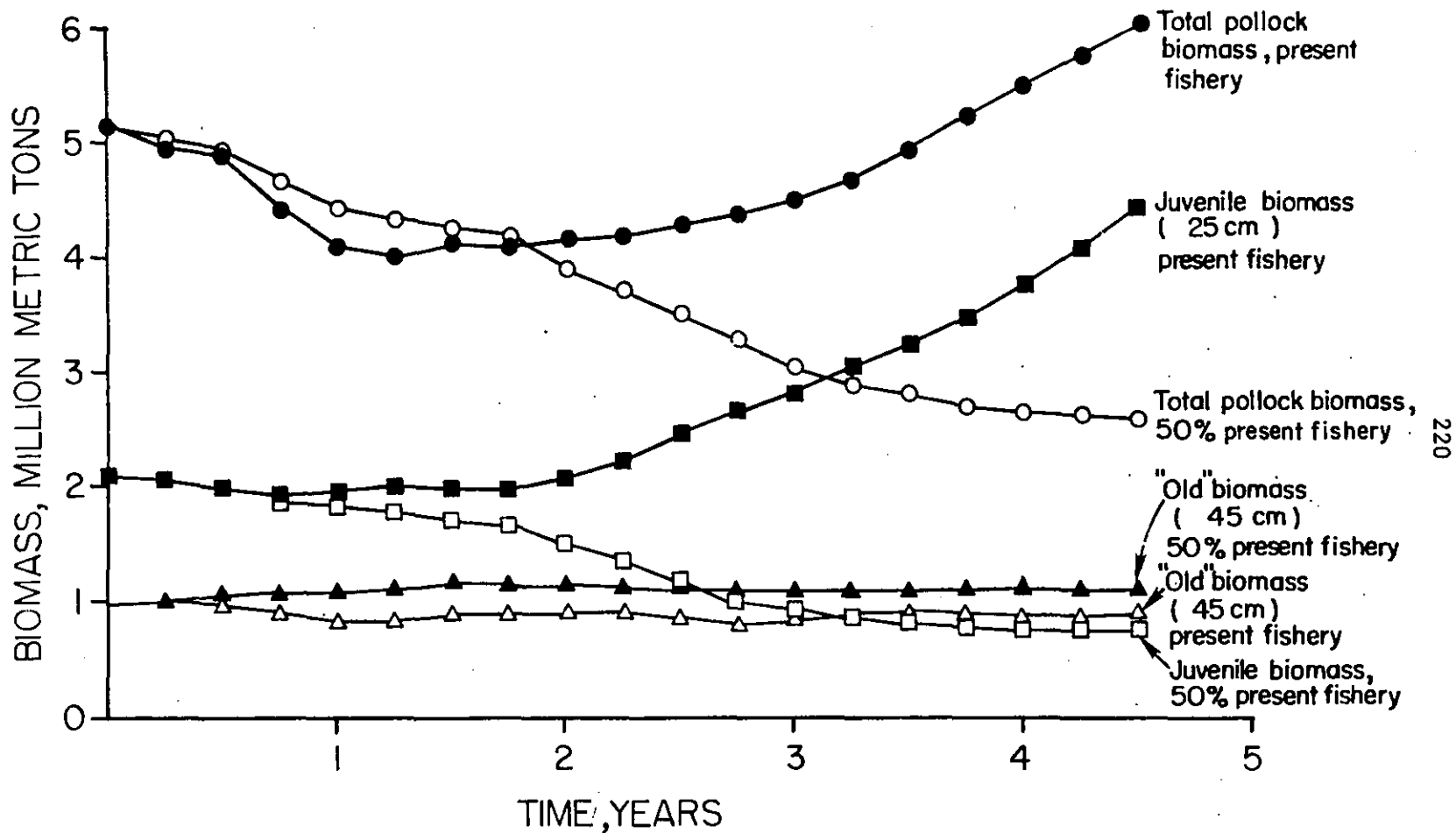
Figure 96. Change of biomass of juvenile, old and total walleye
pollock in the eastern Bering Sea with simulated present
fishing intensity and half present intensity (DYNUMES
submodel).
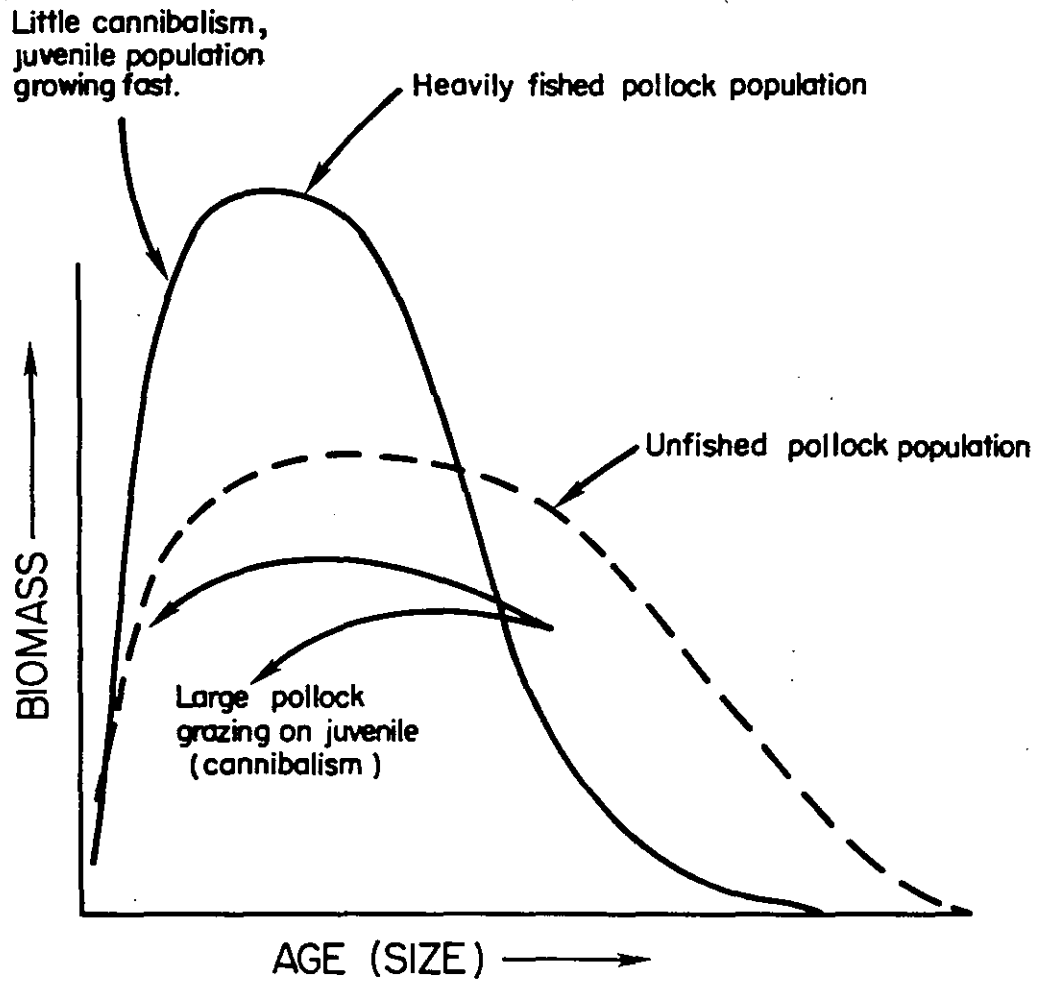
Figure 97. Schematic diagram of age (size) composition of heavily fished and unfished stocks of walleye pollock.

Inclusion of benthos and demersal fish subroutines.

Completion of the mammal subroutine with inclusion of northern sea lion (_Eumetopias jubatus_), harbor seal (_Phoca vitulina_), and other seal in "bulk" form; inclusion of other pelagic species (e.g., capelin) to "herring" subroutine and other roundfish (semi-demersal) to pollock subroutine.

Inclusion of more environmental effects to all subroutines (such as the effects of cold bottom temperatures, effect of seasonal temperature changes and its anomalies on migrations, effect of temperature on feeding, growth, and spawning, effects of currents on transport of eggs and juveniles, etc.).

Refinements of feeding and growth computations by (a) making the feeding rate dependent on availability of food (food concentration) and season (temperature effect, spawning), (b) making food composition a function of food availability in space and time (incl. preferred substitution), (c) making growth rate dependent on available food supply and temperature of the environment.

The ecosystem model can be used to evaluate the priorities of future research. This is done mainly by evaluating the importance (and influence) of given parameters, processes and distributions on the results of the model outputs. The indicated research needs fall into three categories:

Literature search and testing and evaluating of data obtained (e.g., standing stocks and migrations; food requirements and composition, etc.).

Field work (verification of model results, such as abundance (distribution) of euphausids, under-ice distribution of plankton and fish, feeding under ice, hunger-dependent non-maturation, effects of environmental anomalies, etc.).

Laboratory work (food coefficients; cannibalism; experiments in tanks and their verification of findings in the field; stomach analysis; etc.).

Considering the need for various data for the numerical model, a general list of major research tasks in the eastern Bering Sea is presented (Table 18).

C. PROPOSED MODELS

It is intended to adapt the extended DYNUMES model (which at present includes only the eastern Bering Sea) to the Gulf of Alaska, with proper local inputs. However, the DYNUMES model is already a very large and extensive one, requiring considerable computer core and time; thus, it can be run only on large computers and is relatively expensive. Often urgent, well-defined questions occur in fisheries management complex for which specific answers can be obtained with somewhat simplified specialized ecosystem models. For the above reasons, three additional ecosystem models are in conceptual development stage in Resource Ecology Task.

Table 18.--Baseline studies and research tasks required to improve the 8-component eastern Bering Sea ecosystem model.

A. Mammals

1. Estimation of abundance and distribution of toothed and baleen whales.

2. Food composition of toothed whales.

3. Study of spatial and temporal changes of composition of food (stomach content analysis) of dominant mammal species (e.g., sea lion, fur seal, bearded seal, and harbor seal) including better estimates on food requirements.

4. Quantitative evaluation of major factors affecting the mortality of adult seals and sea lions.

B. Fish

1. Estimation of abundance and distribution of unexploited resources especially pelagic species (smelt, capelin, sand lance, etc.).

2. Studies on growth rates of juvenile and adult stages, and food requirements.

3. Identifications of eggs and larvae.

4. Studies of spawning behaviors, temporal and spatial distributions.

5. Study of the differences in distribution of juveniles and adults of major species (pollock, groundfishes, herring, etc.) both on and off the shelf.

C. Zooplankton and Nekton other than Fish

1. Distribution and seasonal abundance of squids.

2. Temporal and spatial variation of vertical distribution of copepods and euphausids (including patchiness).

3. Study of the reproduction cycle of euphausids and its dependence on environmental factors.

D. Benthos

1. Abundance and distribution of mobile epifauna.

2. Study of the spatial and temporal variation of the quantitative relations between predatory benthos (e.g., starfish) and "fish food" benthos (e.g., annelids, small bivalves).

E. Birds

1. Behavior of birds during heavy storms and the effect of storms on mortality.

2. Study of predation by birds on plankton and nekton.

1. Salmon Ecosystem Model (SEM)

This model will permit one to investigate, model, and determine quantitatively the following:

— Seaward migration of smolt: timing of migrations as affected by run-off and other environmental anomalies, coastal migration routes, predation by birds and estuarine/coastal fish populations, and year-to-year variations in this predation.

— Oceanic life of salmon: migrations and distributions, as affected by environmental factors and boundaries (e.g., temperature, currents, their anomalies), relative food availability as affected by environment and its anomalies, and the effects of food availability on growth and maturation.

— Return runs: timing as might be affected by environmental anomalies and past history of offshore distributions.

Among additional objectives of this model is the testing of possibilities to predict possible different offshore distributions of salmon originating from different rivers, and possible prediction of the size of runs as affected by oceanic conditions.

2. Open Coast Ecosystem Models (OCEM)

This model is intended for evaluation and prediction of the abundance and monthly availability of selected, commercially important resources off the open coasts. It will be adapted to four specific areas: (1) southeastern Alaska coast, (2) Gulf of Alaska coast, (3) Aleutian Island area, and (4) Washington-Oregon-California coast. This model will be in many respects similar to DYNUMES, with some simplifications: Instead of the equal area grid in DYNUMES, OCEM will have "boxes" which correspond to fisheries statistical subareas as well as to ecological divisions (such as depth distribution and oceanic boundaries-convergences/divergences). This model will not compute steady migrations of resources, but subjective "mass" movements from "box" to "box" as derived from existing empirical evidence. The open boundary conditions will be prescribed.

Among the objectives of the use of these models (OCEM) are: to determine the month-to-month production, abundance, and availability of commercially important resources as affected by environmental anomalies, fishery, and interspecies interactions. Some emphasis in these models will be placed on demersal resources. The models will include for each species:

— Growth, grazing (consumption) and fishery.

— Seasonal movements (including seasonal depth migrations of demersal resources.

— Effects of environmental anomalies (ascertained from various "point observations" on individual species.

— Interspecies interactions and effects of food availability (specially plankton and benthos).

3. Northeast Pacific and Bering Sea Ecosystem Model (NPEM)

This model will be a large-scale model with relatively coarse mesh size. Its main objectives are to investigate (and/or predict) the effects of large-scale environmental anomalies (e.g., temperature, currents) on the resources (mainly pelagic) and to provide open boundary inputs to the OCEM models. Various environmental models, being developed in the Resource Ecology Task (e.g., surface currents in the Gulf of Alaska and in the northeast Pacific), would be subroutines for this model. A large part of the salmon ecosystem model (SEM) will become a subroutine of this large-scale model. Emphasis will be placed on offshore pelagic resources, either exploited at present or potential resources (saury, squids, etc.).

VII. RESOURCE-ENVIRONMENT RESEARCH

Optimum resource assessment and fishing occurs when man permits natural fish
behavior to perform the function of concentrating fish; this may occur in
a number of ways: during periods of spawning, aggregations in the vicinity
of concentrations of food and at oceanic and coastal frontal zones, and
orderly migrations along narrow routes. However, perpetuations of a species
depends on inherent behavior or response to constant or cyclic natural
phenomena that permit continual spawning success. All of these activities
are related to the environment. Successful spawning depends on optimum
environmental conditions for maturing fish that aids maximum gonad develop-
ment and optimum conditions at the time of spawning, not only for fertiliz-
ation, but survival of eggs. Microscopic organisms of the right size and
abundance must literally surround the larvae during early life stages to
prevent starvation, and adult spawning sites must be such that the subsequent
planktonic drift will provide conditions necessary for survival and develop-
ment of the organism until it can actively maintain an optimum environment.
At the present time little effort is expended on these phases of the life
history of fish for various reasons, usually because limited funds are
necessarily used in observing and assessing later life stages that are more
stable and accessible. However, even though the fisheries biologist feels
that he hasn't any control over early life stages, it is always rewarding
in the long run to know why things occur rather than what, and research
plays several important roles in this regard. When a large year-class
reaches maturity, it is assumed that prolific spawning will result and
equivalent progeny be produced, but in many cases this does not occur.
However, rarely are reasons known or given, and incomplete studies on adult
components continue as before. However, in the future it may well be desirable,
perhaps even necessary, to know whether the failure of a large year-class
to produce another was due to environmental conditions, behavior, physiology,
pollution, or predation.

Although some fishery biologists argue that statistical assessments of adult
populations are adequate for management purposes, and that deviations caused
by environmental conditions only result in minor fluctuations or "noise" in
the data, it is apparent that such statistics are largely "first guess"
fields that must be improved. Improvement can only come through better
understanding of multi-species interactions because exhaustive surveys using
specialized gear at critical times and critical places for all species is
extremely difficult, if not impractical. And, if multi-species studies are
required, knowledge of the total environment (not just bottom temperatures
for groundfish and surface temperatures for pelagic fish) is required. Obviously
a complete study of the environment is a huge undertaking beyond the present
support of fisheries studies and much of the specialized knowledge lies
beyond the capability of fisheries groups. However, because fisheries
interests can demonstrate a real and immediate need and use for studies
covering the entire ecological spectrum, it is apparent that any and all
environmental studies have a bearing on fishery problems. The important
point here is that fisheries groups must identify and point out priorities.
These priorities can be expressed in general or specific terms. The entire
marine science community, including fisheries, should be encouraged to aid
in the solution of the former, and the fisheries interests should be willing
to directly support or actually conduct the latter.

A. LARGE-SCALE OR LONG-TERM STUDIES

Most of the principal environmental conditions and processes that affect
fisheries can be summarized into three general categories; those influencing
resource distribution, behavior, and abundance. Resource abundance, the
total biomass of a given species and the time-change variability as affected
by the environment and interspecies reactions, has two major aspects: the
production of the biomass as affected by the availability of food and food
distribution, and the survival of eggs, larvae, and juveniles as affected
by the availability of food, the characteristics of the water mass. The
resource distribution, or the large scale availability is affected by a
number of factors: seasonal migrations and their timing as affected by
the environment, aggregations at oceanic boundaries or fronts as related
to water properties or food concentrations, the location and timing of
spawning, the delays or accelerations in maturation as affected by temper-
ature and food availability, and the transport of eggs, larvae, and juveniles
by currents. The resource behavior is of primary importance in the local
availability, such as: seasonal depth migrations and the possible triggering
mechanisms (e.g., autumn storms), reactions to fronts and in frontal areas,
timing of peak spawning as affected by past and present environmental conditions,
and diurnal migrations and their temporal and spatial differences as affected
by the environment. The planning and actual investigations of general resource-
environment relations are more productive if cause and effect relations are
studied in relation to principal oceanographic features.

1. Oceanic Boundaries

These are coastal and offshore fronts denoting convergences and divergences.
The most obvious frontal zone is the surface interface caused by river run-
off, the boundaries of river plumes. The extent to which this dilute water
is carried seaward or confined to the coastal area is dependent on the volume
of discharge and the oceanic circulation. For example, the effects of the
Columbia River discharge is evident hundreds of kilometers seaward, whereas,
much of the dilution from Copper River and Cook Inlet is confined to the
broad shelf in that area. Another frontal zone occurs at the edge of the
continental shelf, although sometimes denoted by salinity and/or temperature,
it is probably more readily identified by changes in the structure of horiz-
ontal and vertical flow, transmission of sound, and other physical factors.
In the oceanic regime the major frontal zones are found at the boundaries
of dominant current systems and are generally evident in the distributions
of water properties. As pointed out, relative spawning success, larvae
survival, and fish behavior in these zones are relatively unknown, responses
may be due to physical, biological or chemical differences. Satellite
imagery has proven very effective in delineating fronts, but experimental
fishing synchronized with satellite data has been limited.

2. Current Systems

Although there is a general uniformity or gradient of water properties within
a current system, there are numerous large and small gyres that spin within

the general flow, coalescing and breaking up. These are difficult to detect
by present research methods yet are probably directly associated with the
heterogenity of oceanic fish catches made at random or predetermined locations.
Further, because most assessments of currents are made by calculations of
geostrophic flow rather than by direct methods, little is known concerning
the interleafing of current systems. Such behavior is probably not unlike
that of the less dense "fluid" air, where in some instances overriding and
underriding of air masses occur as well as clearly defined strata with
different and/or opposing flow. The extent of such intrusions may signal
disasterous consequences for some species whereas for others it may provide
the only mechanism for survival.

3. Environmental Anomalies

Anomalies of any and all water properties whether caused by advection,
diffusion, mixing, stirring, insolation, precipitation, or a number of other
reactions to global forces, can affect not only the abundance, distribution
and behavior of all species as well as cause anomalous interactions between
species. These are primarily instigated by meteorological processes and
extensive data are available on winds, wind-stress, cloud cover, etc., that
could not only be a source for a better understanding of ocean conditions
and processes, but also be related to anomalous biological events. Most
NMFS Fisheries Centers have limited studies related to anomalies, but
these programs are fragmentary.

4. Availability of Forage

The success of most marine organisms is primarily due to their fecundity.
Confronted with not only massive predation and extensive cannibalism, larvae
and juvenile fish are also subject to widespread hunger and starvation. The
importance of ample food during the various early life stages of year classes
of various sizes is a subject that has been only recently addressed and a
difficult one to resolve, primarily because there are few field programs
designed to capture and analyse early life stages. This area between the
extensive sampling of plankton by oceanographers and the massive sampling
of adult fish by resource assessment teams and the various fisheries should
receive immediate attention. For example, the removal of millions of tons
of hake from the coastal waters of Washington and Oregon by foreign fishing
fleets must considerably reduce the stress on planktonic forage in this
area, yet there are no biomass studies that permit assessing the effect of
this change on the ecosystem.

5. Organic Pollution

Very little progress has been made in recent years in relation to organic
matter in the sea and some marine scientists feel that if these studies
are left purely to the organic chemists, only some sort of patchwork picture
of the compounds that are present with no ideas of sequences, mechanisms,

and rates for the processes that are associated, would result. However, in addition to natural organic dissolved matter, several hundreds of different organically structured compounds are able to exist as organic pollutants and some of these have been detected in the most remote parts of the world ocean. These stem from organic chemical industries, oil industries, transport of oil products, application of pesticides and herbicides, and other sources, and have been summarized by Duursma and Marchand (1974). Although the concentrations of these pollutants will be relatively small in both the surface and deeper waters of the open ocean in comparison to natural organic matter in solution, dangerous concentrations can occur in some local areas.

All crude oils and oil fractions, except highly purified petroleum materials, are to some extent poisonous to marine organisms, and very often the most toxic compounds are more water-soluble than the non-toxic fractions. Some organisms are more susceptible than others (unicellular algae, death after 5 days of hydrocarbon concentrations of about 0.1-1000 ppm; zooplankton, complete mortality in one day at 50-100 ppm; crustacean larvae, susceptible at 10-100 ppm although adults might survive at 2-3 times higher concentrations).

Because pesticides are selective poisons and do not necessarily cause genetic damage, there is little information concerning the possible genetic effects of pesticides on marine organisms. However, the presence of several pesticides at low levels can sometimes be detected by smell and it is believed that aquatic organisms can detect some pesticides at certain levels of concentration that could result in attraction or avoidance reactions which change the behavior. Although little work has been done on herbicides, the concentrations of DDT and metabolites found in the marine environment is about $0:002$ ppb (2 mg/m^3) in open ocean water, and toxicity effects of DDT start for phytoplankton at the ppb level for influencing primary productivity, for zooplankton the lethal concentrations are from about 0.1 ppb, for shrimps and mollusks at 3 ppb upwards and for fish at 0.1 ppb. Thus, at the present level there is only a safety factor of 5 for zooplankton and 50 for fish. Of course these are only gross levels but certainly evidence for alarm.

Sewage is a general term for a complex and diverse mixture of compounds having various effects on the marine ecosystem. Although human wastes may enrich the nutrient content of the water and result in an increase in primary productivity if no poisonous substances inhibit phytoplankton growth, many sewage effluents contain heavy metals and other components that may cause diseases. Abnormalities in different fish species, tumour-like sores and weight-length relations, have been detected in the vicinity of the Los Angeles City sewage outfalls, and organic compounds have indicated different physiological effects on fish, such as upset of plasma balance, inhibited cell respiration, and greater metabolic rate. Detergents seek contact with any surface organisms that have less polar properties than water and greatly affect the surface tension of water. Growth of unicellular algae is inhibited and chronic exposure to the 0.1 ppm level at coastal sewage outfalls can result in the absence of some flora over distances of some kilometers. Reduced surface tension and accompanying detergent compounds can destroy epithelial gill cells of fish and cause death in several hours.

Polychlorinated biphenyls (PCB's), which have substantially the same toxic and chemical properties of pesticides, are carried into the ocean by sewage outfalls and by airborne fallout, and there is some question that PCB's may be a degradation product of DDT. Levels of 2 kg PCB's per day have been estimated in several sewage outfalls in California. There is evidence that near-coastal strains of specific flora are more resistant than open-ocean strains. At concentrations above 10 ppb primary production is gradually depressed with increasing concentrations, and above 300 ppm toxic effects to fish can occur.

There is a large group of additional compounds present in industrial organic wastes, 120 have been identified in the Rhine River alone, and the number that have up to now escaped detection, as well as the number yet to be produced, is unknown.

Obviously organic pollution is a problem confronting fisheries yet one that is difficult to address without a considerable shift in present emphasis or the influence of new funds and personnel. Although the chemical aspects are difficult to address at this time, controlled experiments in the laboratory are possible and are being carried out. However, the tracing of the ultimate fate of these pollutants from a specific source is a problem that can be addressed by fishery groups and will require extensive knowledge of not only small scale but also large scale environmental and ecosystem processes.

B. SMALL-SCALE, SHORT-TERM STUDIES

There are a number of specific applied resource-environment studies in addition to those already mentioned that could be carried out during a single time period, either independently on a dedicated vessel as part of a multi-ship program, or even a dedicated multi-ship program. Although further amplification might be desirable with respect to temporal and spatial variations, definitive answers to basic questions would result.

1. Drifting Telemetry Buoys

Oceanographers are prone to draw flow fields based more on imagination than fact, usually rather smooth streamlines are drawn in areas where eddies are commonplace. Obviously this is because of insufficient data. Thus, there is a need for drifting, satellite tracked, telemetry buoy studies similar to those recommended to the INPFC a decade ago. One has to ask, if Federal funds support drifting buoy programs in the mid-Pacific and Antarctic areas, why can't we afford one to solve more immediate fishery problems in the northeastern Pacific Ocean? One of a number of buoy experiments proposed by the NMFS Standing Committee on Oceanography in 1972 was a Buoy Experiment in the Eastern Pacific (BEEP), which called for drifting, satellite-tracked, telemetry buoys to be released at 100 km intervals along a north-south line off the west coast of North America in order to illuminate not only onshore, but alongshore flow, during a winter and summer period. This is still considered an excellent experiment (Figure 98). These buoys are relatively inexpensive ($\sim$ $3-5K) and can be recovered and used again, unless lost through
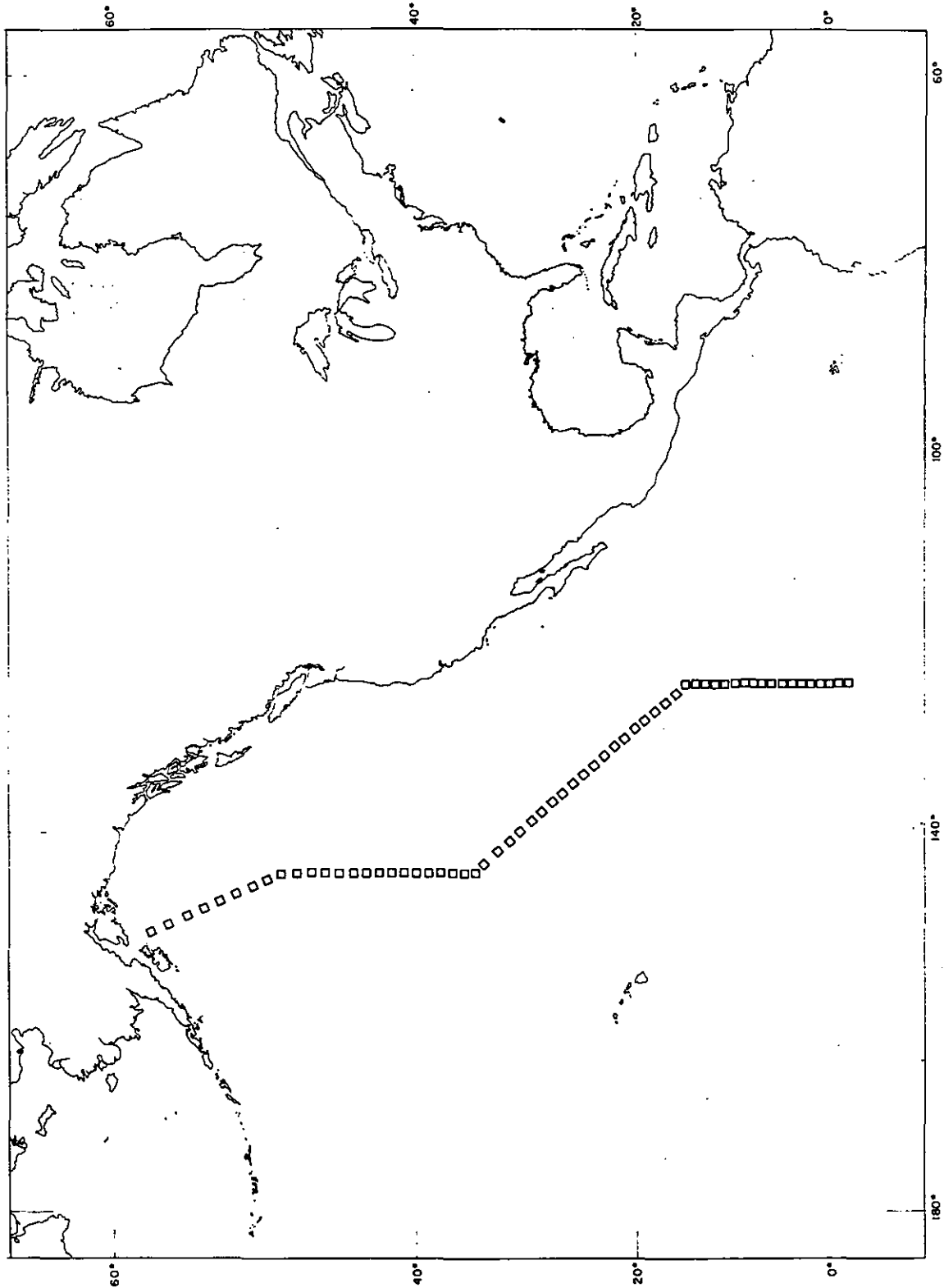
Figure 98.   Drifting telemetry, satellite tracked, data Buoy Experi-
ment in the Eastern Pacific (BEEP) proposed by the NMFS
Standing Committee on Oceanography in 1972 in order to
ascertain offshore and coastal flow patterns.   Squares
show locations buoys were to be released during a winter
and a summer period in order to relate migrations of
salmon, albacore, and other fish to environmental conditions.

battery failure or other damage. Because these buoys are recoverable, it
is possible that they can be borrowed from the National Data Buoy Center,
other national programs have access to them. Buoy release at sea should
not prove to be difficult with all the present vessel activity in relation
to ongoing Federally funded marine programs.

Although there have been a number of successful and significant buoy tracking
experiments, an example of a single buoy released in the Gulf of Alaska by
the Atlantic Oceanographic and Meteorological Laboratory (Figure 99) is more
than adequate to show the information on flow that could result. Here is
an example of a drift trajectory that not only moved from an offshore regime
but swept inshore and along the coast, clearly defined an eddy west of Sanak
Island, moved into and around Prince William Sound and went aground just
before exiting the Sound. With only a little bit of luck it could have re-
entered the coastal flow and been carried into the complex flow in the Cook
Inlet-Kodiak Area. Certainly this one buoy has provided more information
on flow in the northern Gulf of Alaska than all of the previous inshore
studies combined, and shown a well ordered flow that could not be pieced
together from the most extensive drift bottle study. The insight into
larval drifts, as well as possible juvenile and adult fish migrations that
could be obtained by selected buoy experiments, is more than amply demon-
strated. The important point to remember here is that such techniques are
not new and have been in many instances proposed and developed by fisheries
groups; however, this study was funded by the Bureau of Land Management in
relation to potential oil pollution studies and conducted by a group far
removed from the local scene, even though the program was well coordinated
with local marine groups. There are a number of areas where drifting
telemetry buoy programs would be of considerable benefit to fishery programs.

2. Satellite Data

Satellite imagery has been available for over a decade and has provided
considerable insight into ocean conditions and processes. An example has
already been given of upwelling off the west coast of the United States
(see Figure 37). Initially, the imagery provided cloud cover data. When
the large-area daily synoptic pictures that delineated not only the extent
of low pressure systems, but also an indication of the intensity and location
of the centers of these systems, were combined with the fragmentary ship
reports of sea level pressure, much of the guess-work in constructing trans-
pacific pressure fields was eliminated. Although more accurate pressure
fields were obtained, this advance made many of the old data rather obsolete
for comparative purposes because in most instances the intensities of the
highs and lows had been generally greatly underestimated (only when a ship
report was made at the center of the low, which most ships tried to avoid,
was the intensity of the low ascertained).

Considerable interest was shown (primarily by individual investigators) in
the trade wind zones and monthly mean charts of cloud cover were constructed
for the area lats 20S to 20N, but only the daily imagery was available for
the Subarctic Pacific Region. Visual interpretations of daily cloud cover
for the year 1969 were integrated into monthly mean charts in the eastern
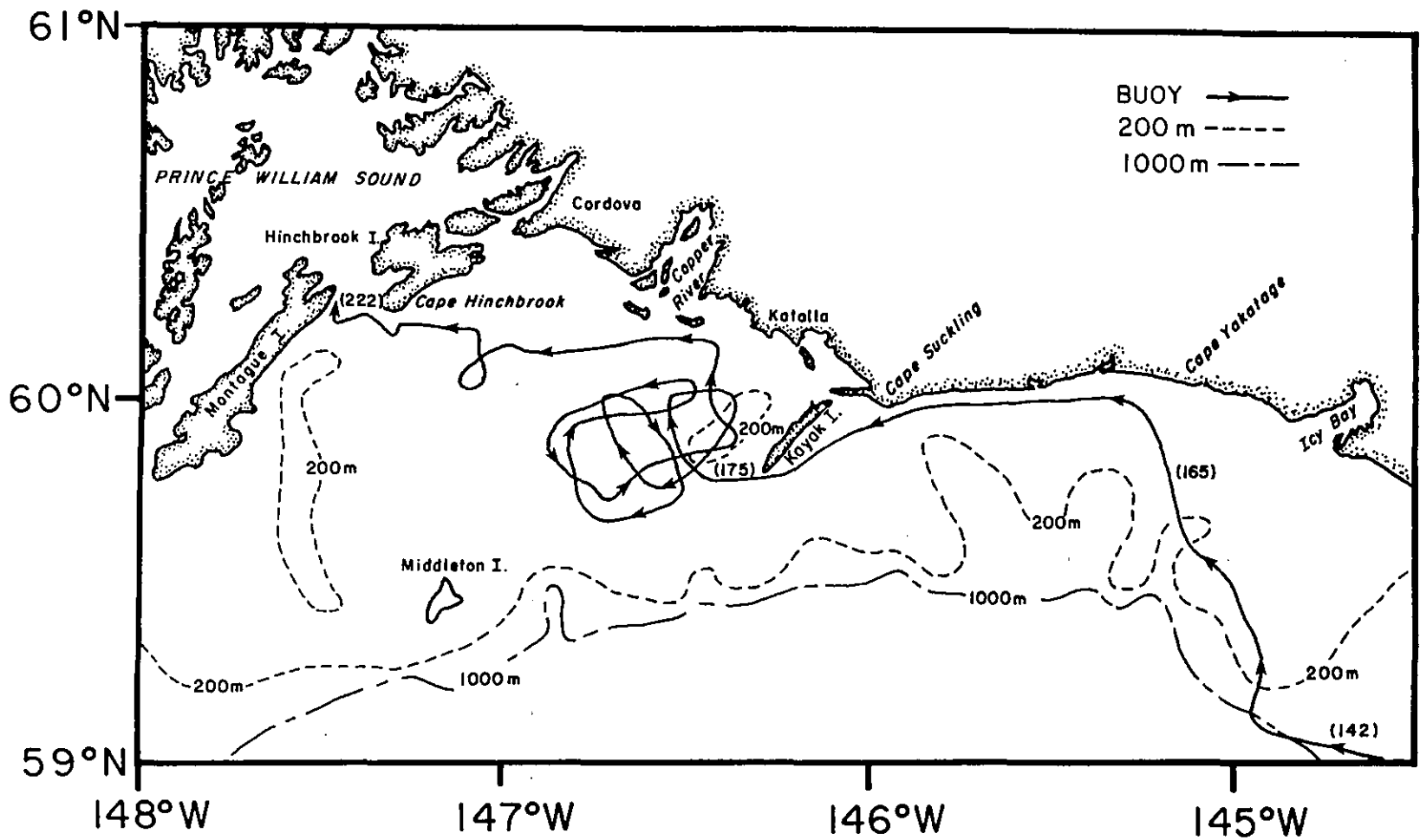
Figure 99. Track of a drifting, satellite tracked, buoy released
in the Gulf of Alaska in summer 1976 showing the extensive
along coast flow near Cape Suckling; the large, non-tidal
eddies west of Kayak Island, and the movement into Prince
William Sound indicating the complex flow demersal eggs
and larvae are subject to in this area (numbers indicate
days from starting point – from Hansen 1976).

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part of the region to determine if oceanic areas of warming or cooling could be indicated (Favorite et al 1971); however, individual interpretations of the imagery obtained from the Seattle weather office were considered too inconsistent to justify a continuing program. In 1973, a contract was given to the National Climatic Center to compile transpacific monthly mean cloud cover for the year 1968, directly from the data tapes, that showed considerable departure from existing cloud atlases, but the cost ($500/month) prevented continuing this project after several attempts to get the National Weather Service to provide the monthly data compilation at no cost failed (the NWS was only interested in operational forecasts and having accomplished this objective the data were archived).

The ERTS satellite from which data is available from 1971 has considerable resolution and multi-spectral lands that permits observing the ice fields in the eastern Bering Sea, and even detecting mammals on the ice, as well as, sediment laden river plumes discharging into coastal waters. An excellent example of this is the vast coastal area in the eastern Bering Sea influenced by discharge from the Yukon River (Figure 100). However, this non-synchronous satellite makes a pass over individual areas (or swaths) only every 16 days.

Subsequently, sea surface temperature fields were capable of being detected by satellite imagery and marked frontal zones, such as the Gulf Stream front, were clearly delineated and as indicated above upwelling zones are also clearly evident. Although not quite as distinct, warm water in the Alaskan Stream flowing westward seaward of the continental shelf south of the Alaska Peninsula can also be detected (Figure 101).

At the present time satellite instrumentation proposed for NIMBUS-G will provide color imagery in bands selected to detect not only sediments but also chlorophyll. There is considerable speculation as to how accurately the chlorophyll data will estimate productivity because only the surface concentrations are measured and in many places a chlorophyll maximum occurs at depth. But areas and times of significant phytoplankton blooms should be clearly evident and imagery will be available on a 1-3 day basis. Because such data can only be obtained from sporadic research vessel cruises, the addition of these data (when techniques and calibrations are perfected) will provide far more new information with respect to primary productivity in the ocean, than the cloud imagery did in relation to sea level pressures. This is an experimental satellite scheduled for 1978 whose components are designed to last only for a year, but both the Northwest and Alaska Fisheries Center and the Pacific Marine Environmental Laboratory are involved in test programs that should result in operational programs in the future that will provide valuable resource-environment information.

There are three comments that should be made with respect to satellite programs. First, they appear to be hardware oriented, in other words, the engineers are determining what instruments they wish to design rather than what instruments the marine science community may want. The new satellite will have a space resolution of 800 meters as a compromise for color spectral resolution. Perhaps fisheries groups would have preferred to detect porpoise or whales. Evidently no satellite planners have considered this. Second, satellite data, as indicated
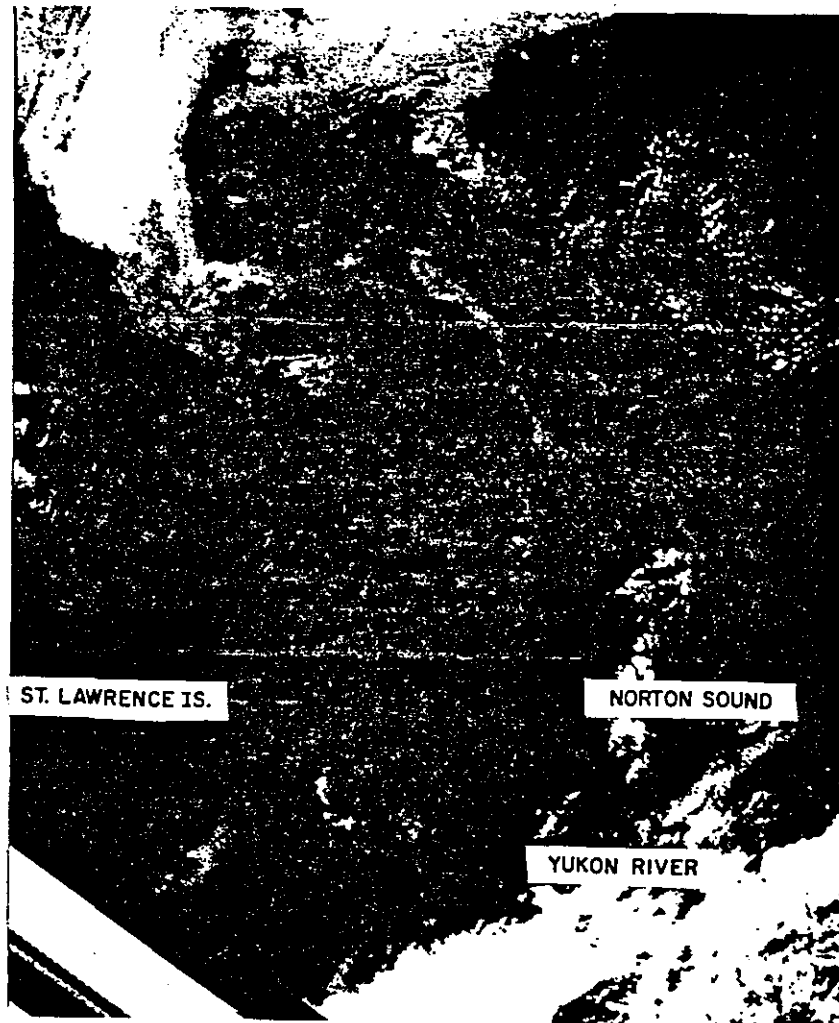
Figure 100. Satellite imagery showing the extent of influence of
the discharge of the Yukon River on the coastal environ-
ment.
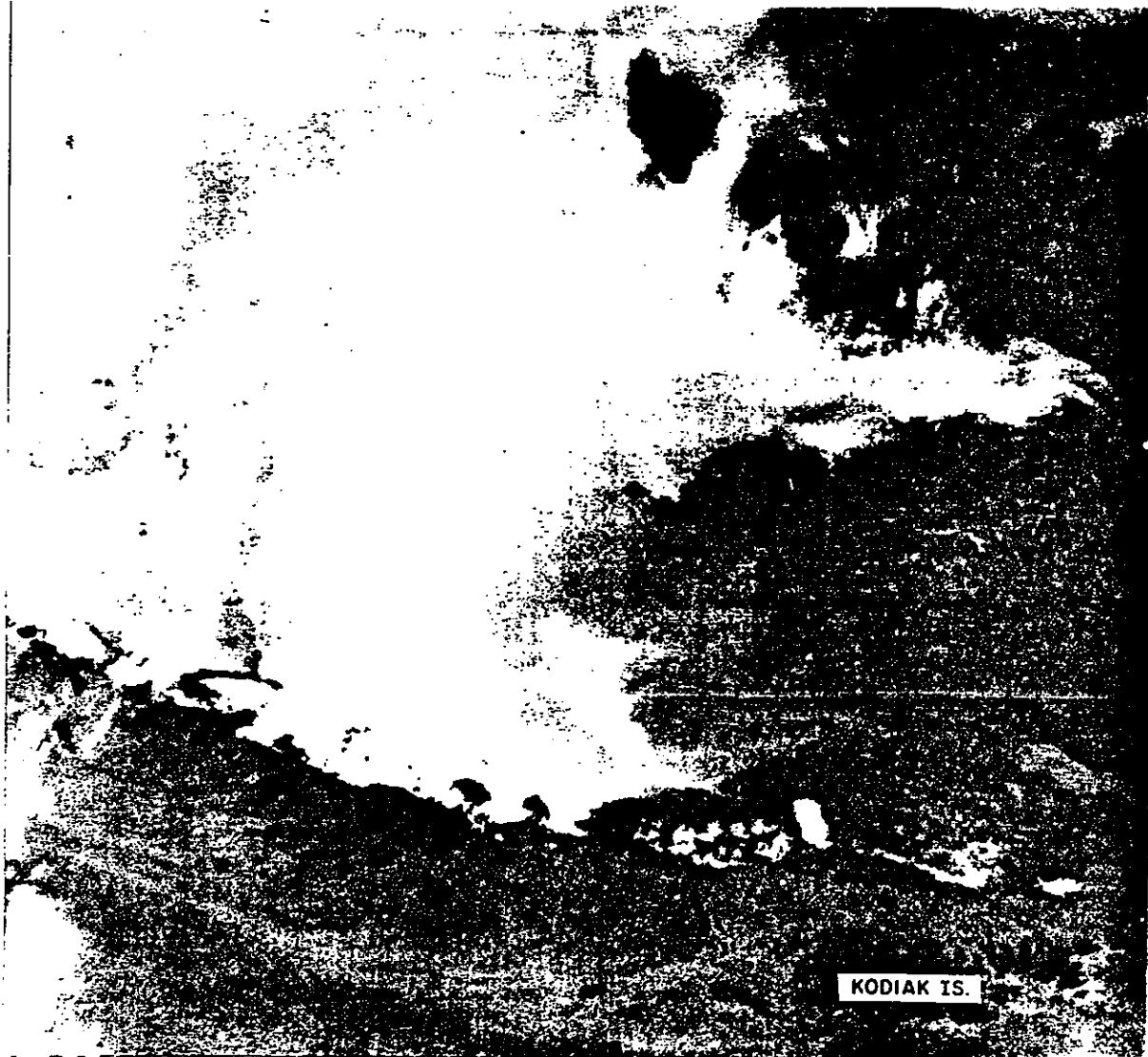
Figure 101. Satellite imagery on August 21, 1976 showing the edge of the Alaskan Stream flowing westward south of the Alaska Peninsula.

above, are not only expensive to obtain, but expensive to process into a useable form. It does fisheries groups little good for the planners to say this technology will be useful to fisheries, if fisheries groups can't afford to obtain, process, or use them in an effective manner. Third, there is a real need for cooperative analyses of satellite data. A regional team of users should meet on a monthly basis to evaluate these data in order to obtain maximum benefit from this costly technology. Obviously the imagery is of interest to meteorologists, oceanographers (biological, geological, and physical), as well as fishery groups, and the various processes each is concerned with are all interrelated. Such a meeting would also result in bringing into focus individual problems and interests. Eventually one would like to see a vessel available on a monthly basis that could be dispatched to investigate anomalous phenomena detected in satellite imagery; such costs would be small in relation to satellite hardware and launch costs. It is only through such cooperative efforts that the synergistic studies that are required to justify the costs of satellite data will come into being.

3. Salmon Studies

It is impossible to summarize briefly the results of INPFC oceanic salmon investigations conducted by three nations (Canada, Japan and the United States) over a span of nearly a quarter of a century, but several interesting aspects of resources—environment relations have been pointed out with regard to Bristol Bay sockeye salmon; these, of course, raise more questions than they answer. Even though there is an apparent hiatus in oceanic salmon research, we are still a long way from ascertaining how salmon find their way in the sea. Certainly the results obtained from the limited oceanographic studies conducted indicate that further studies would be rewarding and there are a number of approaches that are within the present capabilities of both oceanographic and fisheries research groups.

First, it would be rewarding to investigate the behavior of sockeye and other species at the sharp inshore front south of the Aleutian Islands. It is apparent that salmon move westward in the Alaskan Stream in spring and are associated with the dilute water moving westward in this current (Figure 102). Although Unimak Pass is the first large opening into the Bering Sea, it is a shallow pass and relatively uninfluenced by the main flow in the Alaskan Stream, which occurs 75 km southward of the pass at the edge of the continental shelf and over the slope. As the width of the shelf narrows to the westward, the flow in the Alaskan Stream has a greater and greater effect on inshore flow. The first major northward flow into the Bering Sea occurs through Samalga and adjoining Passes where a sharp frontal zone occurs between the dilute Alaskan Stream water (<32.6 ^{o}/oo) and Bering Sea water (>33.0 ^{o}/oo). Here bottom topography has a marked effect on surface conditions and could markedly affect salmon migrations. The impingement of high velocity flow on the shoal south of Chuginadak Island has been shown to bring deep, high salinity (33.3 ^{o}/oo) water to the surface (Figure 103). This water also had a high nutrient content and could influence the productivity of coastal flora in this area. Also at this general location there is a pronounced loss to the southward that
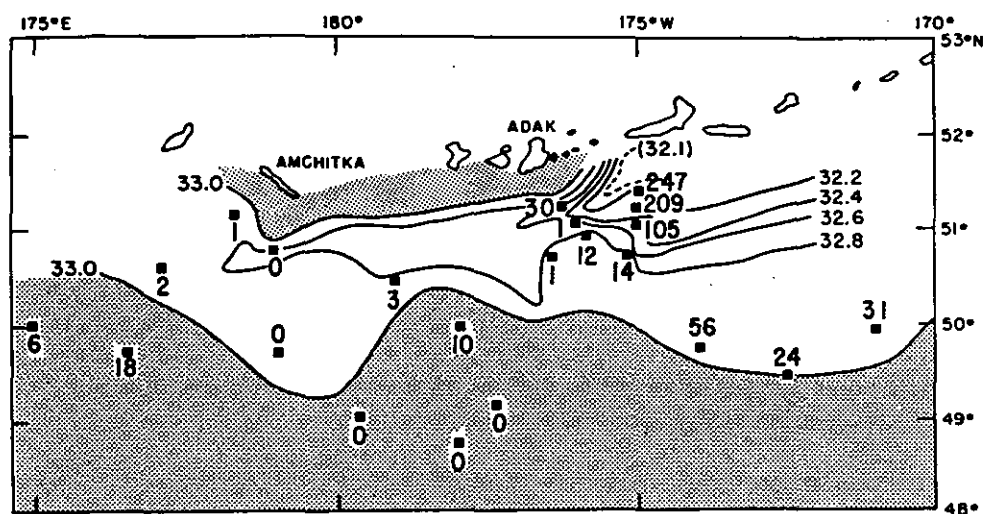
Figure 102. Surface salinity (^{O}/oo) and sockeye salmon catches May 9
to June 9, 1970 showing westward penetration of dilute
water and the accompanying concentrations of sockeye
salmon (squares indicate fishing locations, adjacent
numbers indicate sockeye salmon catch in gill nets;
shaded portion shows areas south of Aleutian Islands
where salinity values exceeded 33 ^{O}/oo)(from Favorite
and Ingraham 1972).
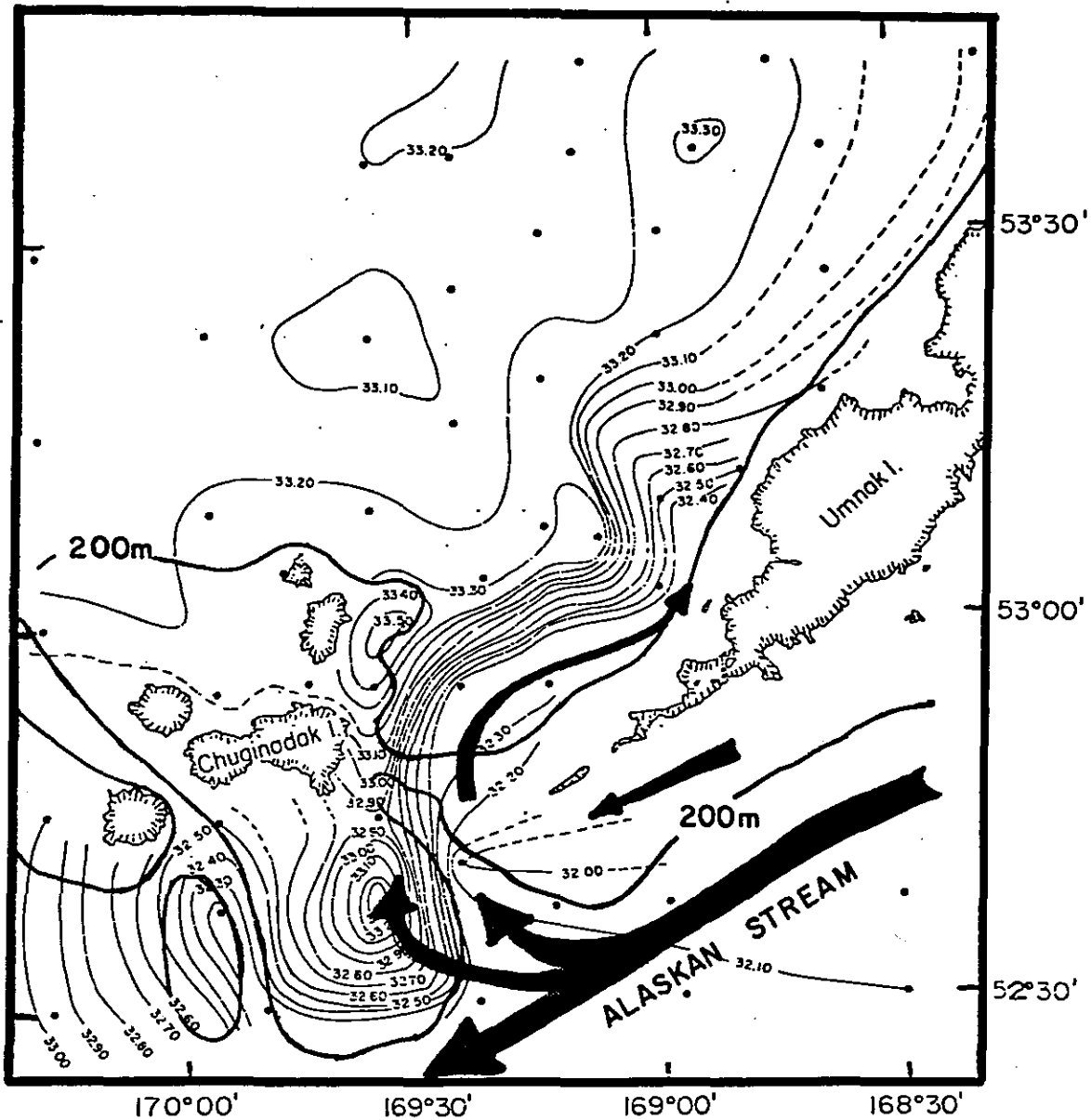
Figure 103. Horizontal distribution of surface salinity in the
eastern Aleutian Islands (June–July, 1971) indicating
a marked increase in salinity values (nutrient values
also increased) as the Alaskan Stream reaches the first
pass area with depths greater than 200 m and irregular
bathymetry results in vertical displacement of flow
(from Kelley et al. 1973). This suggests that fishing
stations in this area should be selected with knowledge
of environmental conditions.

that recirculates around the Alaskan Gyre (see Figure 65). It is difficult
to assess whether the flow through the passes into the Bering Sea permits
a northward shift in regimes south of the Aleutian-Commander island arc that
in effect constricts the westward flow. And, there is another conflicting
factor in that there is evidence of a southward flow of cold, saline water
out of the Bering Sea at the western side of Amutka Pass that displaces the
warm, dilute westward flowing Alaskan Stream offshore and results in sharp
temperature and salinity frontal zones in the Adak Island area (Figure 104).
It would appear that intensive fishing in this area based on the locations
of these environmental features would greatly expand our knowledge of the
shoreward migration of Bristol Bay sockeye salmon. One hypothesis being
that because of the anomalous westward movement of Bristol Bay sockeye salmon,
environmental features have a significant influence on their movements and
migration paths. This information could result in rational bases for
closures in critical areas at critical times as well as aiding in forecasts
of timing and abundance of specific runs.

Second, and an extension of the above, it would be useful to ascertain the
influence of Alaskan Stream water northward of the Aleutian Islands on
migration paths. It has been shown that at least at Amchitka Pass this
water maintains continuity through the turbulent passes and across the
eastern Bering Sea. If combined oceanographic and fisheries studies revealed
maximum catches associated with the axis of flow through Amchitka Pass, one
could ascertain the general area sockeye salmon approached the continental
shelf in the eastern Bering Sea (movements over the shelf are discussed in
Section IV). One hypothesis being that if salmon suffer heavy predation
when exposed to the mammal populations of the Pribilof Islands, one might
conclude that the closer their onshore migration path is to the vicinity
of the Pribilof Islands, and the narrower the width of the predominant
migration path, the greater the potential predation.

Third, one of the greatest dilemmas associated with the distribution of salmon
is that most theories indicate that salmon retreat or migrate to the warmer
waters in the eastern and southern portions of the Subarctic Pacific Region
during winter, this would imply a concentration of stocks in a smaller area
than that during summer when supposedly wide-ranging feeding migrations
occur, yet consistently smaller catches occur during winter regardless of
the area sampled. One hypothesis that could be tested is that salmon remain
deeper in the water column; specifically, in the area of the salinity-minimum
(Figure 105) that represents surface subarctic water that sinks to the south-
ward under the more saline Central Pacific Water Mass and forms Pacific
Intermediate Water. It is generally accepted that the absence of macro-
plankton in the region in winter is because diel migrations to the surface
layer are not carried out, and that the organisms remain below 100 m and
extend to depths as great as 800 m. Perhaps vertically upward-migrations
by subarctic forms carried southward at depth into the salinity-minimum
stratum are limited by interface at the base of the surface lens of high
salinity water and this results in concentrations of forage; instances
similar to this have been reported based on visual observations made from
diving chambers in the area of the Kuroshio. Although there is speculation
that winter annuli on salmon scales indicate considerable reduction in food
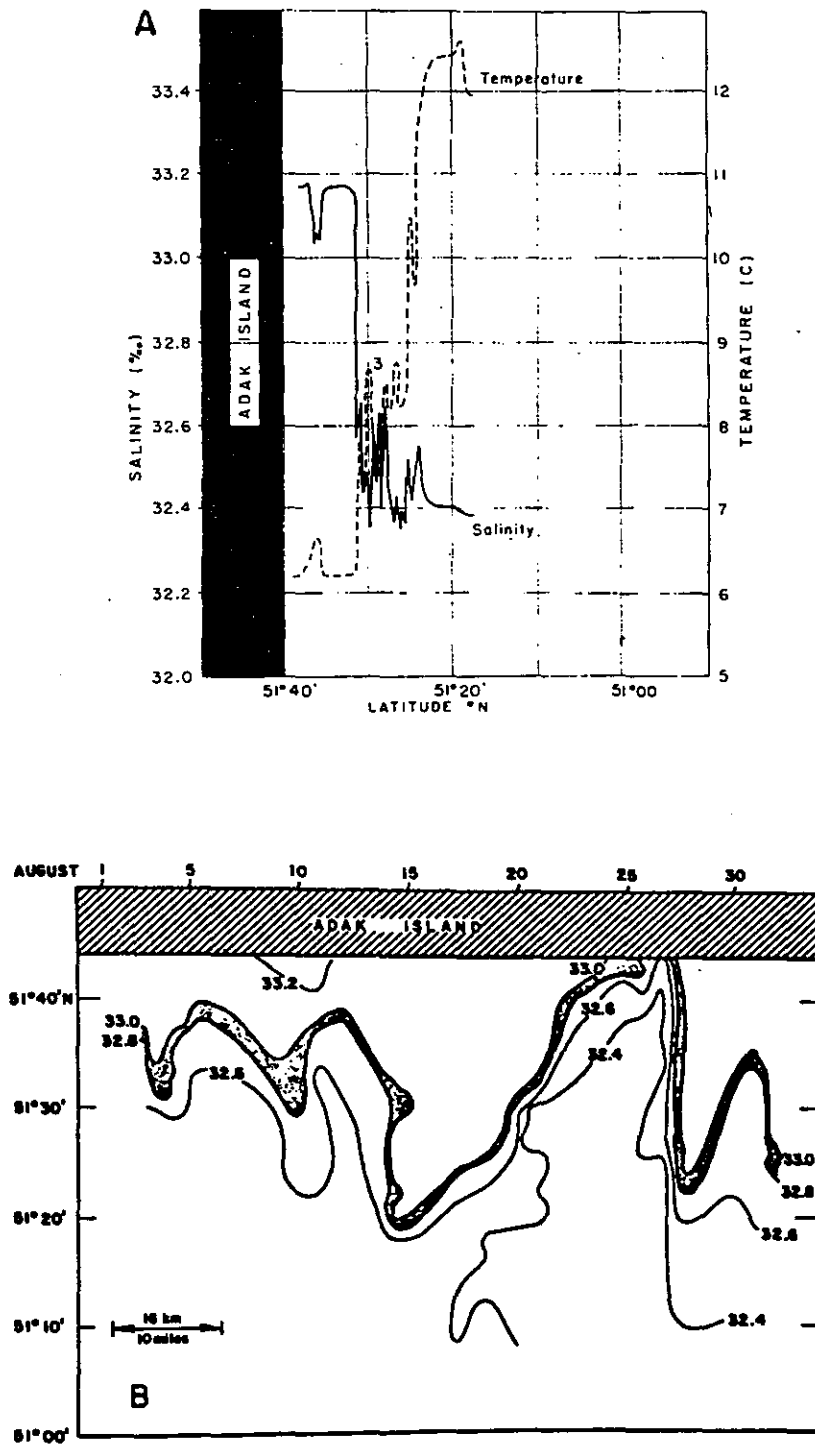
Figure 104. Surface temperature and salinity data south of Adak
Island in summer 1969 showing (A) the synchronous
temperature and salinity front at lat 51°32'N and
the isolated temperature front 10-15 km southward; and
(B) time-series data on the salinity front (32.8 - 33.0
o/oo isohalines) from August 1 to 30 indicating the
location of this front varies from the coast to over
40 km offshore. This suggests fishing stations in this
area should also be selected with knowledge of environ-
mental conditions.
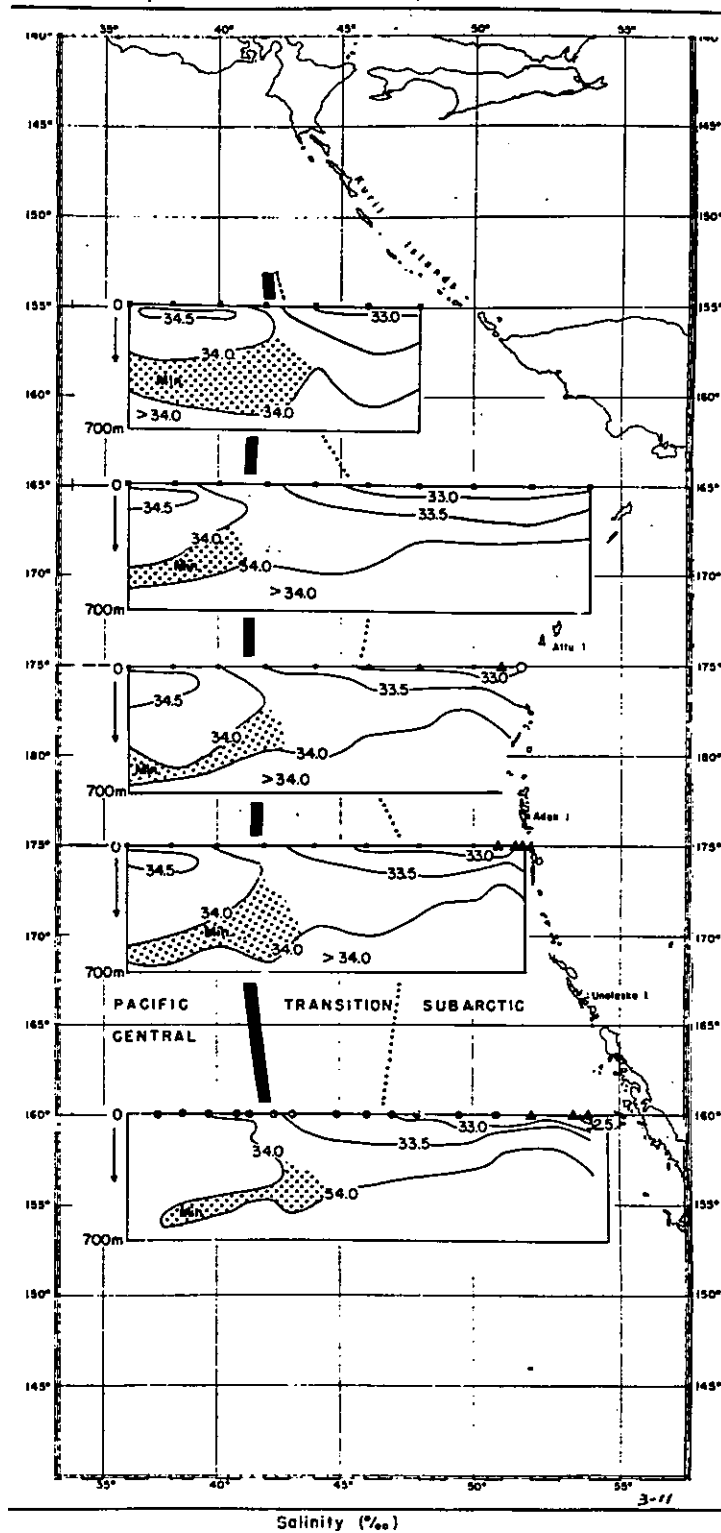
Figure 105. Transpacific north-south vertical sections of salinity
(⁰/oo) in summer 1958, arrows indicate the zone of the
salinity-minimum stratum that could denote a winter
habitat for Pacific salmon.

consumption during winter, there is no evidence of unusually empty salmon
stomachs during winter. The sudden appearance of large numbers of sockeye
salmon in spring at the northern edge of the Transition Domain also suggests
a return to the surface layer prior to instigating spawning migrations.

Fourth, although the concentrations of sockeye salmon in the Gulf of Alaska
challenge this general hypothesis of a southward retreat in winter to deeper
waters associated with the salinity-minimum stratum, it is interesting that
this stratum doesn't exist in the Gulf, where acceptable surface temperatures
of 2-3°C persist throughout the winter but concentrations of sockeye salmon
are only found in the area of the temperature-minimum stratum. Salmon
stomachs obtained in this area during winter 1962 indicated active feeding
primarily on amphipods, although it must be pointed out that digestion
rates are not known. The reasons for the apparent concentration of sockeye
in this area of active, vertically upward movement is not known, nor is the
reason for a similar distribution of immature salmon during summer; only
during shoreward migrations in spring do maturing sockeye salmon appear to
leave this area. Whether the seaward extensions of coastal plumes of dilute
water through Dixon entrance and from the Columbia River are used by salmon
returning to streams in those areas is not known (Favorite 1961).

It should be apparent that in spite of extensive international investigations,
there are still a number of basic questions that remain unanswered in relation
to the oceanic distributions and movements of salmon. For example, Straty
(1975) has indicated that mature Bristol Bay sockeye salmon move eastward
over the continental shelf to the north and south of the Pribilof Islands,
but not in the vicinity of those islands--is this due to mortality by the
large resident mammal stocks, the result of learned behavior, or the existence
of a northern and southern migration path related to river systems in the
area? If a northern migration path exists, this might provide some insight
into reasons why the only place concentrations of adult Bristol Bay sockeye
salmon (identified by biological characteristics) have been found off the
Asian coast in summer is in the northern Bering Sea; might these salmon
have sought and continued past (because of their immaturity) evidences of
discharges of coastal water from the St. Lawrence Current and continued
around the cyclonic, subarctic gyre for another year? Some people feel
that if seasonal river discharges enter the ocean and are circulated around
the region any chemical signatures would shortly become ubiquitous and
ambiguous; however, these chemical characteristics or odors could be short-
lived or altered as a result of not only chemical but also physical (temper-
ature) changes. Certainly the ability of salmon to detect the presence of
some substances in concentrations of less than parts per billion has been
demonstrated (see Section II-F-4) and maximum river discharges in spring
are of short duration.

In addition, one must ask that if sockeye salmon in the Gulf of Alaska are
present largely within the area of the temperature-minimum stratum during
spring just before the home migrations of matures occurs, and in summer
when only immatures remain, what mechanism provides clues to the shoreward
migrating paths? Is there any significance to the large concentrations of
sockeye salmon at the head of the Gulf of Alaska in spring 1963 (see Figure

26), do eastward and westward shoreward or along-shelf migrations occur at this point? What is the role of the salinity front detected at the edge of the continental shelf off Kodiak (and believed to exist around the rim of the Gulf of Alaska) on shoreward migrating adults as well as seaward migrating juveniles?

Of course, one must consider also potential pollution effects. Certainly it is obvious that all sockeye salmon returning to streams in the northern and western Gulf of Alaska, the Aleutian Islands and the Bering Sea must pass into or through the high velocity Alaskan Stream that has well defined continuity through this area. If an extensive oil spill, or seepage, over the continental slope at the head of the Gulf of Alaska remained uncontrolled for a period of several weeks, and the pollutant products remained in the surface layer for this period, a continuous streak could extend westward to the end of the Aleutian Islands. And if the pollutants caused an avoidance reaction, or impairment to physiological functions controlling homing behavior in sockeye salmon, there is an excellent chance that the entire maturing population, which at times can number in excess of 50 million (and have a market value of many times that amount in dollars), could be wiped out, and the effect on immature salmon representing 1-3 year-classes equally disastrous as a result of loss of ocean forage. Also, it must be realized that other salmon stocks and species are also present in this area. The possible far-ranging effects of oil pollution products (tar balls) is suggested by release of drift bottles in the central Gulf of Alaska, some of which were recovered not only on the Washington-Oregon coast, but also in the central part of the ocean (Figure 106).

Certainly the documentation of the nature and extent of the Alaskan Stream was accomplished almost entirely through INPFC studies, and, in addition to aiding in our understanding of oceanic salmon movements, its discovery provides clear rationale for extraordinary safeguards in relation to oil exploration and exploitation in the Gulf of Alaska and Alaska Peninsula areas.

There is controversy today as to whether or not salmon have short memory spans (on the order of seconds) and that all responses are predicated on creature "comforts" until maturity triggers spawning migrations. If so, present migration models (e.g., Royce, et al 1968; French and Bakkala 1974) that reflect highly ordered geographical movements should be reevaluated. Thus, perhaps the highest priority in salmon research should be the formulation of mathematical or simulation models that provide spatial and temporal salmon movements according to varying environmental parameters. A conceptual model being developed jointly by the Northwest and Alaska Fisheries Center and the Fisheries Research Institute was discussed in Section VI.

4. Salmon-Albacore-Saury Study

Some examples of resource-environment relations in the oceanic regime of the Subarctic Pacific Region have been presented and, although limited to a few commercial species, they reveal that past research has demonstrated
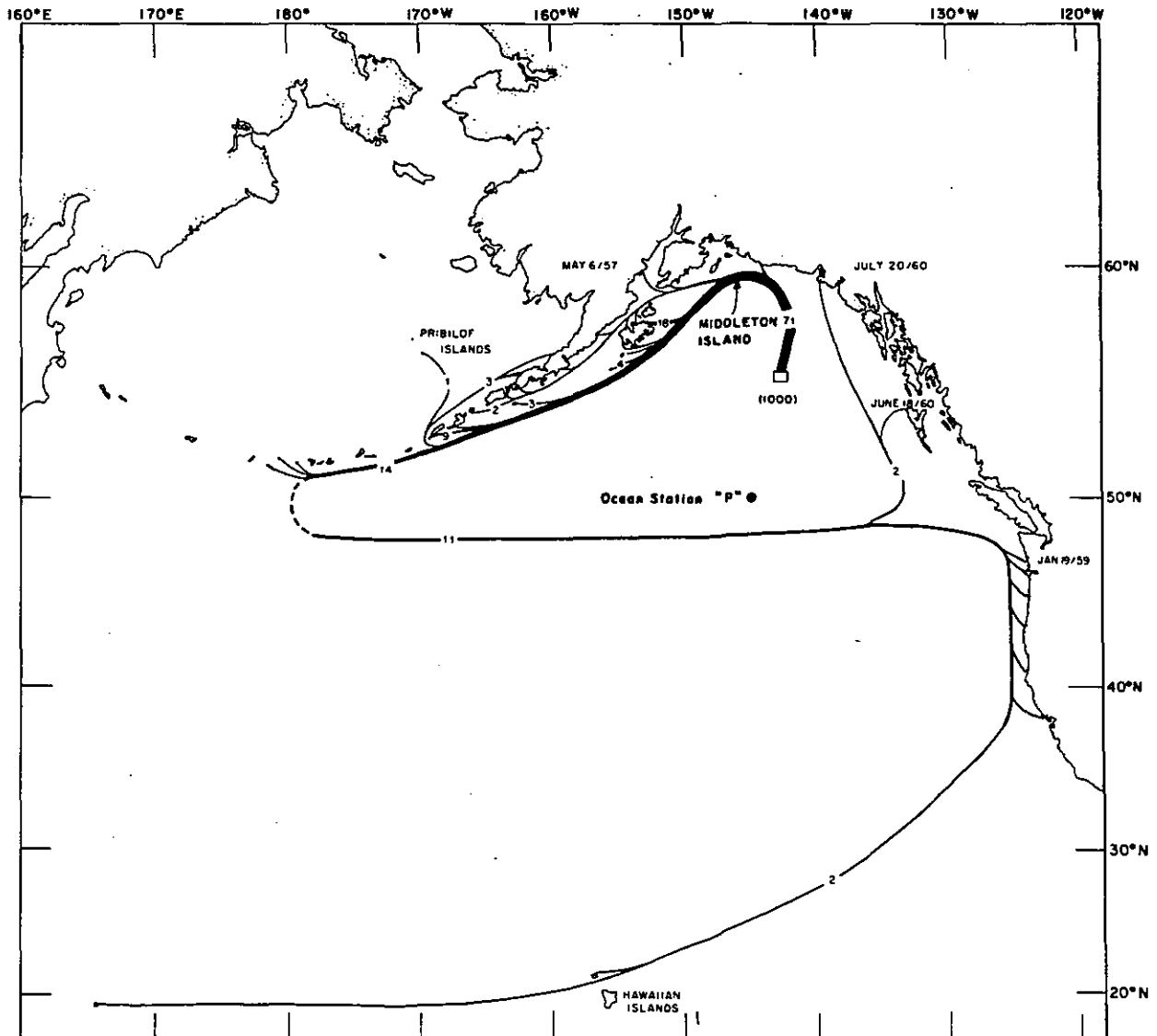
Figure 106. Drift bottle experiment in February 1957 showing wide
dispersal of 1000 bottles from a release point in the
central Gulf of Alaska particularly along the axis of
the Alaskan Stream south of the Alaska Peninsula (from
Dodimead and Hollister 1962). The effects of an oil
spill in this area could seriously affect the movements
of Pacific salmon as well as other organisms.

an inherent order to the physical-chemical environment and the biological
systems that was not even imagined possible a few decades ago. Because these
species represent only a small percentage of the total pelagic biomass in
the region, considerably more knowledge will be forthcoming with additional
research on migration routes, spawning areas, the role of specific organisms,
and multi-species interactions. Although short-term management decisions
must be made on individual species and stocks, long-term management requires
more complete knowledge of conditions and processes in the ecosystem.

It would appear that multi-disciplinary environmental studies and multi-species
fishing efforts during two prolonged multi-ship operations north and south
of the Subarctic Boundary in the central part of the ocean during a spring
and autumn seasons, would provide much of the knowledge required to ascertain
the continuity or discontinuity of pelagic stocks that occur and are subject
to extensive fisheries on each side of the ocean. If continuity exists,
national management plans must be based on transpacific conditions and
activities. Obviously, it would be useful if oceanographic studies provided
additional rationale for such an investigation, and there are two instances
wherein even relatively widely spaced observations indicate environmental
features that might influence or guide movements of fish. The first is the
zone of a surface, salinity-minimum band discovered along long 175°W in the
vicinity of the Subarctic Boundary during April 1962 (Figure 107). At no
other time have observations in this area been taken at sufficiently closely
spaced intervals that permit one to say that such a feature does not exist
or that it doesn't have an extensive transpacific continuity. Of course,
the large water masses have continuity, but these areas are too broad to
be of any great aid in selecting sites for selective fishing. However, as
observations are made at more closely spaced intervals, continuities in
water properties have become quite clear (fronts in the Alaskan Stream have
already been discussed). A second example that demonstrates the kind of
continuity of water properties that can exist at depth is the seaward
extension of the narrow tongue of cold water from the Okhotsk Sea-Kuril
Island area into the central Pacific Ocean ascertained in 1966 (McAlister
et al 1970), the discreteness of this flow also being apparent in the salinity
distribution (Figure 108). Selective fishing in and across the boundaries
of these features should provide insight into numerous biological conditions
and processes.

5. Herring

There are a number of problems concerning the assessments of herring spawning
that may be resolved by present and future satellite technology. Recent
attempts by the Alaska Department of Fish and Game to detect spawning
areas in the eastern Bering Sea proved remarkably successful in that spawning
was apparent nearly all along the coast from Unimak Pass to Norton Sound,
rather than only in a few selected areas along this coast as heretofore
believed to be the case. However, there still are little data concerning
the oceanic distribution of herring subsequent to spawning when they depart
from coastal areas. It is important to ascertain how far from the continental
shelf and slope they migrate, if they disperse, and what depths they occupy--
both in the Gulf of Alaska and the eastern Bering Sea.
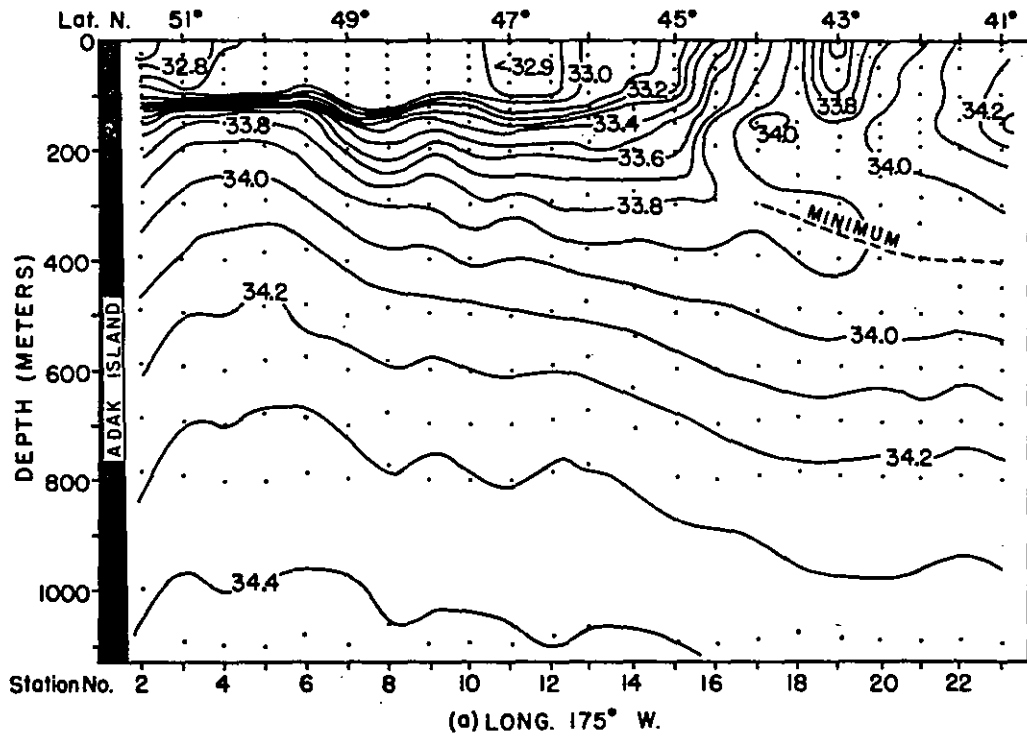
Figure 107. Anomalous band of reduced salinity surface water along long 175°W at lat 43°N (April 1962) and thus at the southern boundary of the Subarctic Pacific Region. This is a definitive feature that, if continuous and a quasi-permanent phenomenon, could influence not only salmon but albacore behavior.
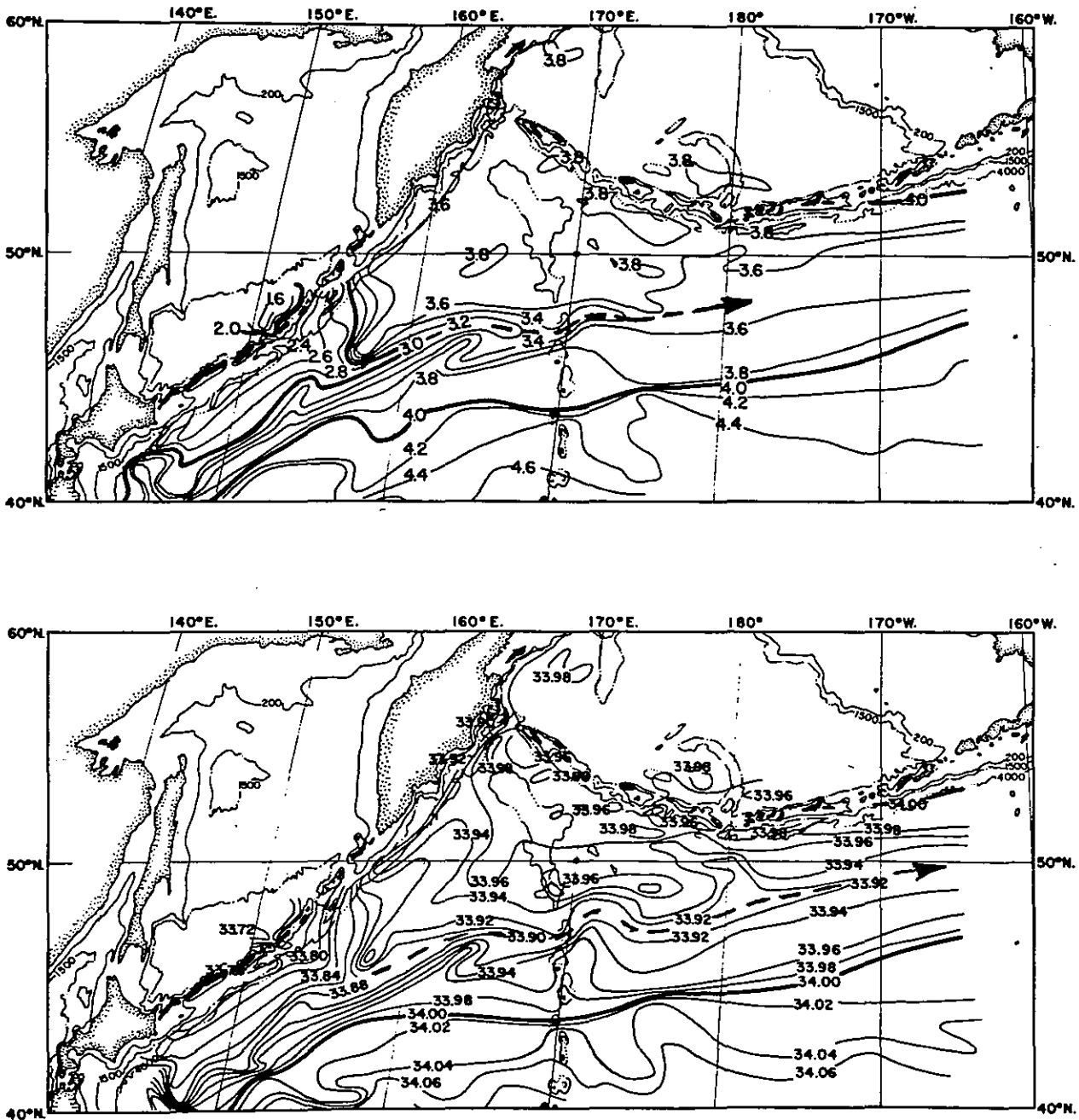
Figure 108. Distributions of (A) temperature and (B) salinity on a
constant density surface (sigma-t = 27.0; winter 1966)
that indicate the continuity of water properties that
can be shown to exist in the ocean when adequate obser-
vations are obtained. The relatively filamentous but
obvious continuity of discrete properties could be used
by fish to guide migrations or to orient themselves in
mid-ocean areas (from McAlister et al. 1970).

6. Demersal Fish

The role of the temperature-maximum stratum at the edge of the continental shelf in the Gulf of Alaska and eastern Bering Sea with regard to the success of bottomfish and crustaceans is not known. By providing a constant year-round warm (3-5°C) environment in a subarctic region, it could be the site of concentrated spawning activity, as well as providing a path for extensive migrations. If indeed stocks do aggregate in this stratum during winter it would provide an easier and more accurate estimate of abundance because only a small percentage of the shelf and slope area is associated with this stratum (Figure 109). Although it has been shown that oceanic intrusions may interrupt the coastal continuity of this stratum (see Figure 109), basically it may be considered a permanent environmental feature. New information required are data on actual current speeds in this stratum, this would permit assessments of alongslope egg and larvae drifts. Temporal and spatial data on vertical velocities at the shelf edge would permit ascertaining where and when demersal ichthyoplankton would be transported on or off the shelf edge.

The role of the oxygen-minimum stratum on the distributions of resources (see Figure 61) should also be examined. All along the continental slope at depths of 800-1000 m there is a relatively finite zone where saturation values of 5-10% occur. It is obvious that organisms are found in this zone such as Tanner crabs off Oregon (Pereyra 1972), but it is apparent that the most dense concentrations in this area occur at shallower depths. This is in marked contrast to dissolved oxygen concentrations of roughly 30-50% saturation that occur on the continental shelf in the eastern Bering Sea where these crabs occur in the tens of millions.

In addition to environmental features already noted, it is apparent that there are a number of areas that warrant ecosystem studies. The southern terminus of the California Current System with respect to hake spawning; the divergence of the Subarctic Current off British Columbia with respect to cod and the northern extent of hake and the southern extent of pollock distributions, and the transport of ichthyoplankton: (1) out of the Gulf of Alaska, not only along the Aleutian Islands and through island passes, but in the narrow band of surface recirculation in the Gulf of Alaska (see Figure 65); (2) along the west coast of Alaska; (3) along the edge of the eastern Bering Sea shelf from the Pribilof Islands to Cape Navarin, and from Cape Navarin to Cape Olyutorski; and, through Bering Strait.

C. DIFFICULTIES ENCOUNTERED OR EXPECTED

When one considers the above suggestions it is apparent that small- and large-scale, and short- and long-term environmental studies are required by fisheries. That such a broad spectrum of studies is necessary is not new, the Bureau of Commercial 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 multi-disciplinary studies needed, to present the rationale for conducting such studies, and to justify the funds, vessel-time, and manpower needed.
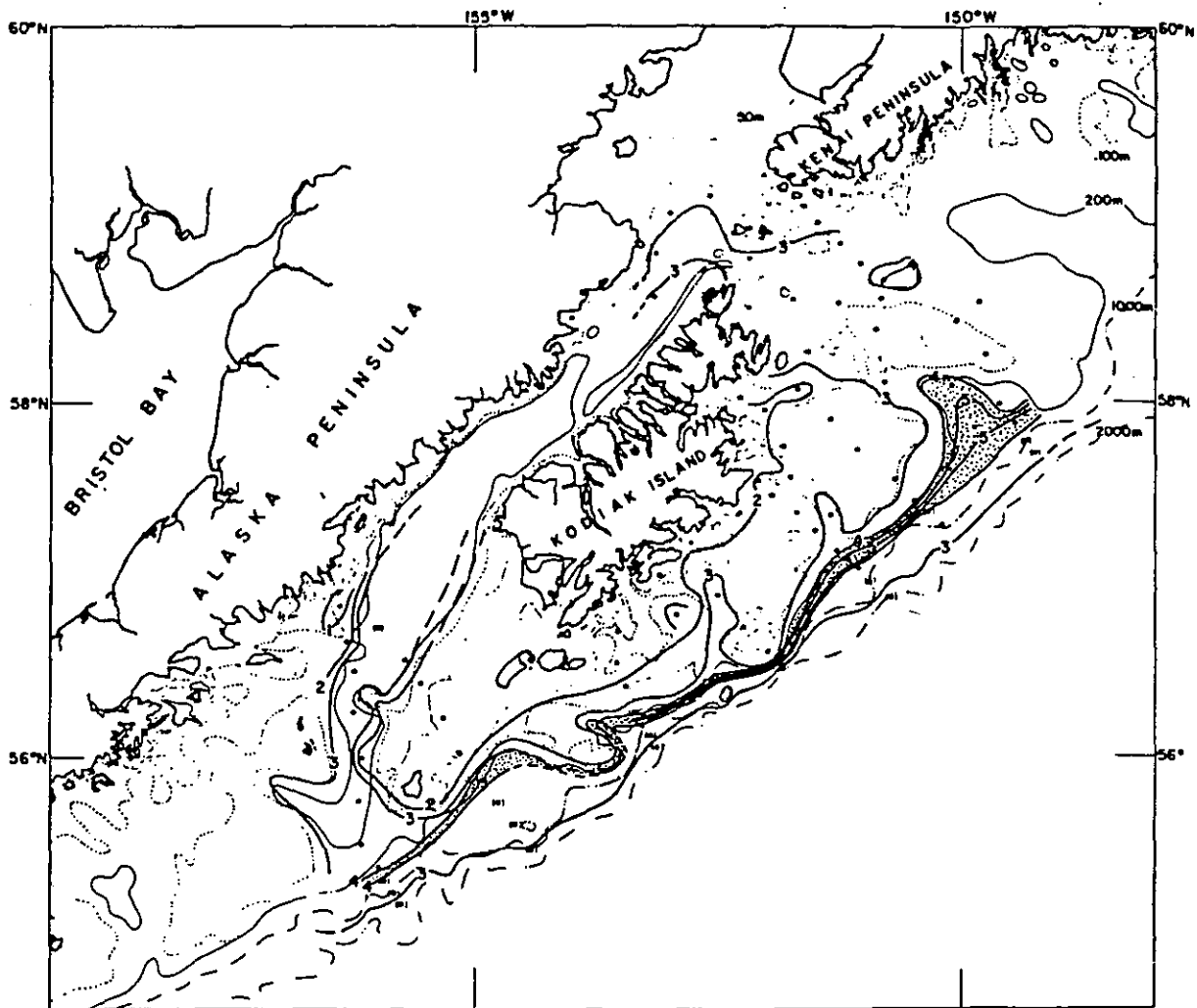
Figure 109. Bottom temperatures off Kodiak in May 1972 showing
the narrow zone (stippled) affected by the temperature-
maximum stratum where temperatures of 4-5°C occur
year round. The environmental conditions in this zone
may attract demersal fish during the winter and serve
as a necessary condition for survival of numerous species
around the Gulf of Alaska.

Scientists involved in Fisheries Oceanography, the environmental phases of fisheries studies, have always encountered two dilemmas: first, other Federal agencies have always received the larger share of the oceanographic funds and; second, fisheries groups have been required to spend their limited funds on small-scale, short-term fisheries related problems. For example, 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 aboard vessels in excess of 100 m in length. These multi-million dollar studies resulted in a single research paper (Barbee 1965) that was of minor relevance to INPFC studies.

Another example is the inability of fisheries units to establish environmental data-buoy programs. It was apparent that resource-environment relations pertaining to salmon migrations were largely dependent on knowledge of oceanic circulation patterns in the northern North Pacific Ocean that were, and still are, inadequately understood. Transpacific buoy drifts were proposed (Robinson 1964; INPFC 1965) and satellite-tracked buoys were developed and used at the BCF, Seattle Biological Laboratory in the mid-1960's (Favorite, Fisk and Ingraham 1965; McAlister 1968). However, this fisheries environmental data-buoy program was terminated in 1967 when the responsibility for the data buoy program was assigned to the U.S. Coast Guard. Although recently the national program has been turned over to NOAA, data-buoy development has been dominated by meteorological interests, subsurface sensors are still not operational, and fisheries requirements for data buoys outlined by the NMFS Standing Committee on Oceanography in 1972 have been left unheeded.

The frustrating aspects of large-scale, and expensive environmental studies, to the fisheries-oceanographer is not that such studies cannot or are not being conducted (because they are), but that most agencies involved have little interest in fisheries problems, even though results expected are heralded to have far-reaching effects or benefits to fisheries. There are a number of such programs: Processes and Resources of the Bering Sea (PROBES) being funded by the National Science Foundation ($500 K/yr) is primarily a study of basic physical, chemical, biological, and geological processes with some emphasis on relations with pollock only as a result of NWAFC input; the NOAA/BLM Outer Continental Shelf Environmental Assessment Program (OCSEAP) is a multi-million dollar coastal program from California to Prudhoe Bay, Alaska, supporting baseline and other studies, but environmental studies are primarily designed to ascertain how oil spills disperse and affect resources but little funds are available as yet for integrated studies on natural environmental affects on resources; Coastal Upwell Ecosystem Analysis (CUEA), a well funded program off the Oregon coast, is primarily a physical study but involves biological processes related to plankton not fisheries; and the North Pacific Experiment (NORPAX), another

multi-million dollar study, is focused primarily on air-sea interactions, initially, in the northeastern Pacific Ocean, but ultimately throughout the entire Pacific Ocean. Most of these programs are of limited duration, usually less than 5 years. This is roughly the life span of only one generation of some pelagic and anadromous fish, but others, like the halibut, live several decades. Thus, it is obvious that the above studies are not crucial to long-term studies of life histories of fish, but with adequate planning the studies could contribute substantially to our knowledge of specific phases of life history studies, as well as responses of fish to environmental conditions, because there is a national need to protect our fisheries, because they are an important source of food for mankind, and because they have an impact on our national economy--it would appear that all Federally-funded marine studies should contribute directly or indirectly to the management and conservation of our fisheries. In order to accomplish this fisheries interests should have an opportunity to comment on, and recommend inputs to, all major Federal marine environmental programs that affect fisheries before they are funded.

VIII. SUMMARY

Until man can see through water, as easily as he can through air, two
basic problems confronting the fisheries biologists are the temporal and
spatial distribution and abundance of stocks. And, it is only through
knowledge of accurate resource assessments of what is in the ocean that one
can rewardingly proceed to the more difficult questions of why fish are
where they are, when they are, and how they interact—the basic knowledge
required for implementation of ecosystem models and resource predictions
based on environmental factors. Total stock assessments are a vast problem
and can be made only through the extensive data obtained from commercial
fishing or from sophisticated acoustic surveys. Such techniques have been
used for decades with various degrees of success and failure, and one must
constantly ask whether or not man will ever be able to assess and comprehend
nature with sufficient accuracy to permit forecasting of conditions and
events. However, although forecasting may be a desirable target or ultimate
goal for resource-environment studies, this does not imply knowledge in-
sufficient for forecasting does not have considerable value. Knowledge
that permits stock conservation, savings of time at sea, and selection of
profitable opening and closing dates of processing plants, etc., has
considerable demonstrable value.

Knowledge that permits wise conservation of stocks is difficult to assess
in terms of actual value, but intelligent use and protection of existing
resources may be equivalent to the value of the total resource in question,
only the time frame is not precisely known. Before the advent of major,
highly organized, government supported fishing expeditions, typified by
the recent Soviet fishing operations, productive fishing grounds were rather
well kept secrets of individuals or groups of individuals whose fishing
success was actually dependent on seasonal or annual repetitions of natural
events. Most scientific studies were either conducted only after trends
in a specific fishery were altered disastrously, or were of extremely narrow
scope (e.g., single species, small area, etc.). However, now large-scale
multidisciplinary information is required to protect stocks from the diverse
effects of not only foreign exploitation, but also world-wide pollution.
There is a practical limit to the extent to which areal studies can be
expanded, but certainly it's obvious that proper study of fisheries in the
northern Pacific Ocean must incorporate the transpacific area north of
lat 35°N, essentially the Subarctic Pacific Region. Of particular interest
are the significance and interrelations of: the various gyres on egg and
larval drift; the migrations of salmon to mid-ocean and beyond; the
transpacific migrations of albacore; the transpacific drifts of saury and
Greenland turbot; the movements of pollock, herring, saury, and hake seaward
of as well as on the continental shelf; and, the responses of demersal fish
and crustaceans to conditions along the continental shelf and slope, up
and down canyons, and over and around banks and shoals.

Some obviously productive studies have been pointed out but a complete
"shopping list" would be endless as witness the small area and short time
interval studies required for specific life stages of crustaceans, herring,
salmon, and other stocks. However, we have advanced well along from the

stage when M. Schaeffer, W. M. Chapman, and O. E. Sette used to sit in the sardine loft and think about the myriad factors and processes in the sea that did and might influence the various oceanic and coastal fisheries.

First, in regard to fish behavior and physiology studies, some of these must be taken out of the laboratory and conducted at sea. Certainly today ships are of adequate size to conduct studies at sea in relation to spawning environments and thresholds, identification of eggs and larvae, and factors related to their survival. Certainly a number of fragmentary studies have been carried out at various times and places, but relatively few have been adequately planned and thoroughly carried out.

Second, there is much to be gained from multi-species studies that obtain complete environmental data, from the surface to the bottom in inshore areas, and to at least 1500 m in oceanic areas, because of the need of surface data for studies of ichthyoplankton, stratification data at depth for studies of forage and pelagic fish, and data at the sea floor for demersal fish and crustaceans. It must be recognized that unless studies of ecosystems are initiated rather, for example, than isolated studies of only bottomfish and the accompanying records of only bottom temperatures, it will be decades before we have an understanding of resources, their interactions, and their responses to fluctuations in environmental conditions that is adequate to provide inputs to rational management of stocks.

Third, in regard to oceanic and coastal field studies there is a real need for communications, cooperation, and consolidation. This must extend beyond the Satellite Data Analysis group discussed in Section VII-C-2. Although the right of the universities to conduct basic research is acknowledged, advances in marine science are rapidly accelerating and no longer can one assume that university faculties are completely aware of new knowledge or the demands for additional knowledge in specific areas. And, there is some question as to whether the rapidly expanding marine sciences have adequate continuity today to provide the extensive background information required to plan integrated marine studies without "reinventing the wheel". One can easily argue that few university researchers have access to, or the ability to keep up with the rapidly expanding fisheries and oceanographic data that are being collected by foreign fleets off our coast and are available to fisheries centers; sometimes perhaps with caveats against publication, but not against informal transmittal or communication. In fact, there is ample evidence that Soviet knowledge of oceanographic conditions off the west coast of the United States is far more complete than that of U.S. investigators, but U.S. oceanographic research vessels continue to conduct independent operations of a general or specific nature without the benefit of such information. Since nearly all marine programs receive some support from Federal funds, and in many instances the justification for such studies frequently note that the information obtained will benefit fisheries, it would seem reasonable that local fisheries interests should have an opportunity to see, or pass judgement on, such proposals--certainly long-range proposals or those in excess of a certain dollar amount. This does not imply that a veto power be given, but that communications be established,

and both fishery interests and the principal investigators know what work
will be conducted, whom it will actually benefit, and in what manner. This
would also permit an exchange of ideas and the possibility of cooperation
and even consolidation of resources—manpower, vessel time, equipment, etc.
Hopefully this does not sound naïve, because a pertinent example can be
given. Because of extended jurisdiction, local fisheries interests no
longer are responsible for shallow, local fishing grounds, but a large
segment of the ocean having highly variable and complex features and
processes. These areas are also subject to extensive exploration by: (1)
various universities conducting basic research studies, (2) various state
fisheries and ecology agencies concerned with local problems, (3) various
Federal and privately funded studies in relation to oil exploration and
exploitation studies, (4) U.S. Navy studies related to defense, (5) U.S.
Coast Guard studies related to vessel safety and lifesaving programs, (6)
ocean buoys positioned largely to obtain data for meteorological forecasts,
(7) environmental studies by organized fishing groups (e.g., Ketchikan
Trollers Association), (8) foreign research vessels and fishing fleets
(Soviet, Polish, East German, Canadian, Japanese, Korean, etc.), and (9)
satellites. Now the question arises, if fisheries groups are interested
in all aspects of conditions and processes in the ocean, how are they to
assess the information obtained? Much of the task of assembling the data
is resolved by the National Oceanographic Data Center, but the subsequent
presentation of these data takes so many forms, time and space dimensions,
that it must be done by individual groups. It is apparent that groups
concerned with ascertaining time-changes of environmental conditions all
along the coast could cost-effectively be associated with the regional NMFS
Fishery Centers. Although environmental groups exist at these Centers,
they have yet to assume the responsibility for such overall analyses except
for the superficial surface temperature analyses produced by the Southwest
Fisheries Center. One step toward obtaining data pertaining to assessments
of conditions in the extended jurisdiction zone has been made by a Resolution
of the Sixteenth Meeting of the SEA USE Council that reads as follows:

> "Recognizing the developing need for observed data as to the ocean's
> physical, biological, and chemical parameters which provide a basis
> for knowledge of ocean conditions and hence the ability to manage
> and use the ocean's resources, the SEA USE Council urges the appropriate
> authorities of the United States and Canada, in reaching agreements
> with foreign nations relative to use of the 200 mile fisheries zone,
> to arrange for using the capability of the larger foreign flag fishing
> ships to gather such atmospheric, oceanographic, and biological data
> as are considered of value for management of the 200 mile fishing zone
> and for marine weather forecasting and scientific investigations."

Yet to be resolved is what group or agency should be responsible for the
analysis and dissemination of these and other data with regard to resource-
environment relations.

Fourth, in regard to studies of ocean variability and ecosystem models, there
is also an obvious need for communications, cooperation and consolidation of
resources—manpower, data bases, computer programs and analyses. For example,

no one knows how many students or investigators today are using basic files
of oceanographic and fisheries data, or constructing or contemplating con-
struction of models--certainly hundreds if not thousands of individuals. The
interest here is not to interfere with an individual's right to investigate,
but to challenge the usefulness of deriving basic data--sea level pressure
fields, surface temperature fields, or catch data, for example--over and
over again just because everyone's computer can do it easily and quickly
(albeit not inexpensively). Fisheries groups have unique problems to solve
and, usually, other restrictions that make it mandatory for specific studies
to be carried out; with respect to ocean variability, temporal and spatial
dimensions, although derived from basic data, are usually unique to fisheries
interests. This is also true with respect to resource-environment (ecosystem)
models. Although some of the more advanced physical models are quite intricate
multi-layer types, these are not only very expensive to run, but provide
more theoretical than practical results. At this stage of our knowledge
there is a need for operational resource-environment models that provide
factual knowledge that can be used and updated on a daily or weekly basis,
yet the costs involved should remain equivalent to the application; these
should be developed and be accessible at Fishery Centers.

This report would be incomplete without a statement with regard to cost-benefits
of resource-environment studies and applications of results to the fishing
industry. It is obvious that the most significant and immediate asset to
resource-environment relations (other than obtaining multi-million dollar
research funds such as those that are available to OCSEAP investigations)
would be the apparently simple but, in reality, awesome task of insisting
that a substantial part of the relatively uncoordinated marine science
activities focus a portion of their attention on providing data on the con-
tinuity of large- and small-scale ocean and coastal features and processes
that fishing interests can apply directly to a better understanding of the
factors influencing the distributions and abundances of living marine resources.
This would result in guidelines for protection of resources from pollutants
and for management practices. The use of this knowledge by the fishing
industry is clearly summarized in the introduction to a report on The Coho
Project, an attempt to forecast favorable salmon fishing areas off the
Oregon coast (Woodworth, n.d.).

> "The application of scientific or technological advancements to the
> practical problems facing a business or industry is appropriate only
> if they are economically justified. There is no question that pure
> science will ultimately benefit mankind as it progressively unlocks
> the secrets of nature. To a businessman, however, the incorporation
> of scientific discoveries, with their attendant costs, into his mode
> of operations, must provide benefits which not only cover these costs
> but are sufficient to induce a change from established patterns."

Statistical analyses of attempts to forecast the location of bodies of water
off the Oregon coast in 1973 that contained relatively higher concentrations
of coho salmon indicated that the mean catch rate in the forecast areas on
key days (those wherein a major change in ocean conditions is predicted to
occur the following day) was significantly higher than the mean catch rate
in non-forecast areas on those same days, and this resulted in an estimated

increased monetary value in excess of $1,000/boat/season. Although a
majority of participants were in favor of such a forecasting system, there
were three pertinent unfavorable comments. Some fishermen were so skeptical
of the usefulness of the information that they were unwilling to risk long
transit times to get to the recommended areas. Others who believed that
they were either above average fishermen or had better equipment, resented
the predictive system because it aided primarily those fishermen of lesser
caliber, or sportsfishermen. Further, some people felt that the concentration
of boats in a forecast area would increase risks of collision.

In regard to reliability of forecasts, confidence can only come from results.
This experiment was not repeated, and, although not apparent in the report,
much of the expense of obtaining, processing, and disseminating the data
was largely absorbed by a concurrent research program on coastal upwelling
sponsored by the National Science Foundation and the Office for the Inter-
national Decade of Ocean Exploration. However, this effort and the accom-
panying vessel and aircraft expenses may be soon replaced by satellite
imagery and the data will be available directly to individual fishermen for
their own interpretation and analysis. Thus, science has pointed the way
to useful fishing information without expense to the individual fisherman.
Particularly encouraging in regard to fishermen collecting their own data
is the present effort by the Ketchikan Trollers Association to have members
keep log books documenting fish catches, surface temperatures, whale sightings,
stomach contents, etc. Nearly 50 boats participated in this program in 1976,
and 100 are expected to be involved in 1977. The Northwest and Alaska
Fisheries Center, Alaska Sea Grant and State fisheries are initially assisting
in this program, which hopefully will not only provide a much needed data
base, but also lead to forecasts of fishing conditions.

The problem of forecasting finite areas of favorable fishing based on
environmental data has also been encountered by a cooperative program between
the Japanese government and the Japanese fishing industry in which forecasts
of productive fishing areas off the Japanese coast were transmitted to
fishing vessels reporting environmental data. The industry quickly noted
that the forecasts were very useful, but requested that only the general,
not the specific, area of favorable environmental conditions be forecast
so that the more skilled fishermen would have an opportunity to take advantage
of some of their own knowledge. However, although this procedure is apparently
adhered to, the information obtained from the independent fishing and the
continued reporting of environmental conditions still becomes part of the
scientific data base to be used to improve future forecasts, to augment
studies of physical and biological conditions and processes, to enhance
knowledge of fisheries movements and behavior--all of which, in addition
to the immediate benefits to the industry and the fishermen, ultimately
provides real and yet to be discovered benefits to mankind. For example,
much of the environmental data obtained in the past in relation to fishery
programs also provide the basis for the present studies of energy exchange
at the sea surface, attempts to understand world weather and causes for
climatic change, and environmental impact statements designed to protect
living resources from man-related pollutants such as oil and mineral explor-
ations and exploitations.

IX. ACKNOWLEDGMENTS

X. LITERATURE CITED

Ahlstrom, E.H.
  1965. A review of the effects of the environment of the Pacific sardine.
  ICNAP, Spec. Publ. 6:53-74.

Alander, H.
  1952. Fisheries hydrography in the Baltic. Rapp. P.-V. Reun. Cons.
  Inter. Explor. Mer. 131:61-62.

Alton, M.S.
  1972. Characteristics of the demersal fish fauna inhabiting the outer
  continental shelf and slope off the northern Oregon coast, p. 583-634.
  In A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary
  and adjacent ocean waters. Univ. of Wash. Press, Seattle and London.

Alverson, D.L.
  1960. A study of annual and seasonal bathymetric catch patterns for
  commercially important groundfishes of the Pacific Northwest coast of
  North America. Bull. Pac. Mar. Fish. Comm. (4):66 p.

  1961. Ocean temperatures and their relation to albacore tuna (Thunnus
  germo) distribution in waters off the coast of Oregon, Washington, and
  British Columbia. J. Fish. Res. Board Can. 18(6):1145-1152.

Alverson, D.L., and H.A. Larkins.
  1969. Status of knowledge of the Pacific hake resource. Calif. Coop.
  Oceanic Fish. Invest. Rep. 13:24-31.

Anokhina, L.E.
  1960. Interrelations between fecundity variability of the size of the
  eggs and fatness of mother fish in Onega herring. C. R. Acad. Sci.
  USSR 133(4):960-963.

Bakkala, R.G.
  1969. Distribution, abundance, and migrations of immature sockeye salmon,
  Oncorhynchus nerka, in offshore waters investigated by the Bureau of
  Commercial Fisheries. Int. North Pac. Fish. Comm., Doc. 1183, 154 p.

Bakun, A.
  1973. Coastal upwelling indices west coast of North America 1946-71. U.S.
  Dep. Commer., Natl. Oceanic Atmos. Admin. Tech. Rep., Natl. Mar. Fish.
  Serv., Spec. Sci. Rep. Fish.-671. 103 p.

  1975. Daily and weekly upwelling indices, west coast of North America,
  1967-73. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin. Tech. Rep.,
  Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish.-693. 114 p.

Barbee, W.D.
  1965. Deep circulation, central North Pacific Ocean 1961, 1962, 1963.
  U.S. Dep. Commer., Environ. Sci. Serv. Admin., Coast Geodetic Surv.
  Res. Paper. 104 p. U.S. Govt. Print. Off., Washington, D.C.

Bardach, J.E.
  1967. The chemical senses and food intake in the lower vertebrates, p.
  19-32. In M.R. Kae and O. Maller (editors), The chemical sense and
  nutrition. John Hopkins Press, Baltimore, Maryland.

Bardach, J.E., and J. Case.
  1965. Sensory capabilities of the modified fins of squirrel hake
  (Urophycis chuss) and searobins (Prionotus carolinus and P. evolans).
  Copeia No. 2:194-206.

Barnes, C.A.
  1936. Review of dynamical consideration of ocean currents and physical
  and chemical investigation in Bering Sea and portions of the North Pacific
  Ocean. Ph. D. Thesis, Univ. Wash., Seattle, 254 p.

Bartlett, L.D.
  1976. King crab (family Lithodidae), p. 531-544. In Walter T. Pereyra,
  Jerry E. Reeves, and Richard Bakkala (editors), Demersal fish and shellfish
  resources of the eastern Bering Sea in the baseline year 1975. U.S. Dep.
  Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest
  Fish. Center, Seattle, Wash., Proc. Rep.

Benko, Y.K., and A.S. Seliverstov.
  1971. Influence of some factors on the abundance of Atlanto-Scandian
  herring year-classes. Symposium on the Biology of Early Stages and
  Recruitment Mechanisms of Herring. Rapports et Proces-Berbaux des
  Reunions, Cons. Int. Explor. Mer. 160:152-157.

Beverton, R.J.H., and A.J. Lee.
  1965. The influence of hydrographic and other factors on the distribution
  of cod on the Spitzbergen shelf. Int. Comm. Northwest Atl. Fish., Spec.
  Publ. 6:225-245.

Black, Y.S.
  1957. Excretion and osmoregulation, p. 163-205. In M.E. Brown (editor),
  The physiology of fishes, Vol. 1. Academic Press, New York.

Blaxter, J.H.S.
  1965. Effect of change of light intensity on fish. Int. Comm. Northwest
  Atl. Fish. Spec. Publ. 6, p. 647-661.

Blaxter, J.H.S., Editor.
  1974. The early life history of fish. Proceedings of an International
  symposium, Dunstaffnage Marine Research Laboratory of the Scottish Marine
  Biological Association, Oban, Scotland, May 17-23, 1973. 765 p.

Blaxter, J.H.S., and G. Hempel.
  1961. Biologische Beobachtungen bei der Aufzucht von Heringsbrut. Helgo-
  land wiss. Meeresunters 7(5):260-283.

Blaxter, J.H.S., and G. Hempel.
  1963. The influence of egg size on herring larvae (Clupea harengus L.).
  J. Cons. Cons. Int. Explor. Mer 28:211-240.

Blaxter, J.H.S., and F.G.T. Holliday.
  1963. The behavior and physiology of herring and other clupeids, p.
  261-393. In F.S. Russell (editor), Advances in marine biology. Vol. 1.
  Academic Press, New York.

Breder, C.M., Jr.
  1959. Studies on social groupings in fishes. Bull. Am. Nat. Hist.
  117:397-481.

Brett, J.R.
  1956. Some principles in the thermal requirements of fishes. Q. Rev.
  Biol. 31:75-87.

  1958. The effect of temperature on the cruising speed of young sockeye
  and coho salmon. J. Fish. Res. Board Can. 15:587-605.

Brett, J.R., and C. Groot.
  1963. Some aspects of olfactory and visual responses in Pacific salmon.
  J. Fish. Res. Board Can. 20:287-303.

Brett, J.R., and D. MacKinnon.
  1952. Some observations on olfactory perception in migrating adult coho
  and spring salmon. Fish. Res. Board Can., Prog. Rep. Pacific Coast Stn.
  No. 90:21-23.

Brown, M.E.
  1957. Physiology of fishes. Vol. 1. Metabolism. Academic Press, New York.

Burt, W.V., and B. Wyatt.
  1964. Drift bottle observations of the Davidson Current off Oregon, p.
  156-165. In Kozo Yoshida (editor), Studies on oceanography. Univ. Tokyo
  Press.

Cannon, G.A., N.P. Laird, and T.V. Ryan.
  1975. Flow along the continental slope off Washington, autumn 1971. Mar.
  Res. 33:97-107.

Carlson, H.R.
  1976. Food of juvenile sockeye salmon, Oncorhynchus nerka, in the inshore
  coastal waters of Bristol Bay, Alaska, 1966-67. Fish. Bull. 74:458-462.

Carlson, H.R., and R.E. Haight.
  1976. Juvenile life of Pacific ocean perch in coastal fiords of south-
  eastern Alaska: Their environment, growth, food habits, and schooling
  behavior. Trans. Am. Fish. Soc. 105:191-201.

Clarke, G.L., and E.J. Denton.
  1962. Light and animal life, p. 456–468. In M. N. Hill (editor), The
  sea, Vol. 1, Physical oceanography. Intersciences Publishers, New York.

Cleaver, F.G.
  1949. Preliminary results of the coastal crab (Cancer magister) investi-
  gation. Wash. Dep. Fish., Biol. Rep. 49A:47–82.

Dall, W.H.
  1882. Report on the currents and temperatures of Bering Sea and adjacent
  waters. U.S. Coast Geodetic Surv., Annu. Rep. 1880, App. 16:297–340.

Davidson, F.A., and S. J. Hutchinson.
  1938. The geographic distribution and environmental limitations of the
  Pacific salmon (genus Oncorhynchus). Bull. U.S. Bur. Fish. 48:667–692.

Davis, G.E., J. Foster, C.E. Warren, and P. Doudoroff.
  1963. The influence of oxygen concentration on the swimming performance
  of juvenile Pacific salmon at various temperatures. Trans. Am. Fish.
  Soc. 92:111–124.

Dell, M.B.
  1963. Oceanic feeding habits of the sockeye salmon, Oncorhynchus nerka
  (Walbaum), in Aleutian waters. Masters Thesis, Univ. Mich., Ann Arbor,
  40 p.

Devold, F.
  1963. The life history of the Atlanto-Scandian herring. In Contributions
  to Herring Symposium, 1961. Rapports et Proces-Berbaux des Reunions.
  Cons. Int. Explor. Mer 154:98–108.

Dodimead, A.J., F. Favorite, and T. Hirano.
  1963. Salmon of the North Pacific Ocean--Part II. Review of oceanography
  of the Subarctic Pacific Region. Int. North Pac. Fish. Comm., Bull. 13.
  195 p.

Dodimead, A.J. and H.J. Hollister.
  1962. Canadian drift bottle releases in the North Pacific Ocean. Fish.
  Res. Board Can., Manucr. Rep. Ser. (Oceanogrp. Limnol.) 14, 64 p. + 44
  figs. (Processed)

Donaldson, L.R., and F.J. Foster.
  1940. Experimental study of the effect of various water temperatures on
  the growth, food, utilization, and mortality rates of fingerling sockeye
  salmon. Trans. Am. Fish. Soc. 70:339–346.

Dudnik, Y.I., and E.A. Usal'tsev.
  1964. The herring of the eastern part of the Bering Sea. Transl. in,
  Sov. Fish. Invest. Northeast Pac., Part II, p. 236–240.

Dunlop, H.A., F.H. Bell, R.J. Myhre, W.H. Hardman, and G.M. Southward.
1964. Investigation, utilization, and regulation of the halibut in southeastern Bering Sea. Int. Pac. Halibut Comm., Rep. 35, 72. p.

Dunn, J.R., and N.A. Naplin.
1974. Fish eggs and larvae collected from waters adjacent to Kodiak Island, Alaska, during April and May 1972: NWFC MARMAP Survey I. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. Unpubl. manuscr. 61 p.

Duursma, E.K. and M. Marchand.
1974. Aspects of organic marine pollution, p. 315-431. In Harold Barnes (editor), Oceanography and Marine Biology. Vol. 12. Hafner Press, New York.

Edwards, R.L.
1965. Relation of temperature to fish abundance and distribution in the southern New England area. ICNAF Spec. Publ. 6:95-110.

Engstrom, K.
1963. Cone types and cone arrangements in the teleost retinae. Acta. Cool. 44:179-243.

Fadeev, N.S.
1965. Comparative outline of the biology of flatfishes in the southeastern part of the Bering Sea and the condition of their stocks. Transl. in Sov. Fish. Invest. Northeastern Pac. Ocean, Part IV, p. 112-129.

1970. The distribution pattern of yellowfin sole (Limanda aspera Pallas) in the northern part of the Pacific Ocean. Izv. Tikhookean. Nauchno-issled. Inst. Rybn, Khoz. Okeanogr. 74:32-1. (Transl., 1973, avail. Lang. Serv. Div., Natl. Mar. Fish. Serv., Wash., D.C.)

Favorite, F.
1961. Surface temperature and salinity off the Washington and British Columbia coasts, August 1958 and 1959. J. Fish. Res. Board Can. 18(3):311-319.

1964a. Oceanography. Int. N. Pac. Fish. Comm., Annu. Rep. 1963:141-148.

1964b. Drift bottle experiments in the northern North Pacific Ocean, 1962-1964. J. Oceanogr. Soc. Japan 20(4):160-167.

1966. Oceanography, p. 101-105. In Int. N. Pac. Fish. Comm., Annu. Rep. 1964.

1967. The Alaskan Stream. Int. N. Pac. Fish. Comm., Bull. 21:1-20.

1969. A preliminary bibliography of papers pertaining to relationships between Pacific salmon and the marine environment. BCF Biol. Lab., Seattle. 20 p. (Processed).

1969a. Fishery oceanography II, Salinity front at entrance to Washington's Strait of Juan de Fuca. Commer. Fish. Rev., 31(8-9):36-40.

Favorite, F.
  1969b. Fishery Oceanography III. Ocean temperature and distribution of
  Pacific salmon. Commer. Fish. Rev. 31(1):34-40.

  1969c. A preliminary bibliography of papers pertaining to relationships
  between Pacific salmon and the marine environment. Int. N. Pac. Fish.
  Comm. Doc. No. 1184, 20 p.

  1970. Fishery Oceanography VI. Ocean food for sockeye salmon. Commer.
  Fish. Rev. 32(1):45-50.

  1972. A mass stranding of Velella. Pac. Search 6(5):12-14.

  1974. On flow into Bering Sea through Aleutian Islands passes, p. 3-37.
  In D. W. Hood and E.J. Kelley (editors), Oceanography of the Bering Sea.
  Inst. Mar. Sci. Occas. Publ. No. 2, Univ. Alaska, Fairbanks.

  1975. The physical environment of biological systems in the Gulf of Alaska.
  Proc. Arctic Inst. of N. Amer. Symp. on Sci. and Nat. Resour. Gulf of
  Alaska. Oct. 16-17, 1975. Anchorage.

Favorite, F., A. Bakun, and W.B. McAlister.
  1971. Oceanography, p. 102-108. In N. Pac. Fish. Comm. Annu. Rep. 1969.

Favorite, F., A.J. Dodimead, and K. Nasu.
  1976. Oceanography of the Subarctic Pacific Region, 1960-72. Int. North
  Pac. Fish. Comm., Bull. 33, 187 p.

Favorite, F., D. Fisk, and W.J. Ingraham, Jr.
  1965. First transponding oceanographic buoys in the Pacific. J. Fish.
  Res. Board Can. 22(3):689-694.

Favorite, F., and D. M. Fisk.
  1971. Drift bottle experiments in the North Pacific Ocean and Bering Sea--
  1957-60, 1962, 1966, and 1970. U.S. Dep. Commer., Natl. Oceanic Atmos.
  Admin., Natl. Mar. Fish. Serv., Data Rep. 67, 20 p. on 1 microfiche.

Favorite, F., and M. G. Hanavan.
  1960. Oceanographic conditions and salmon distribution south of the
  Alaska Peninsula and Aleutian Islands, p. 57-72. In Int. North Pac.
  Fish. Comm., Bull. 11.

Favorite, F., and W.J. Ingraham, Jr.
  1972. Influence of Bowers Ridge on circulation in Bering Sea and influence
  of Amchitka Branch, Alaskan Stream on migration paths of sockeye salmon,
  p. 13-29. In A. Y. Takenouti et al., (editors), Biol. Oceanog. of the
  northern N. Pac. Ocean. Idemitsu Shoten, Tokyo.

Favorite, F. and W.J. Ingraham, Jr.
  1976a. Sunspot activity and oceanic conditions in the northern North
  Pacific Ocean. J. Oceanog. Soc. Japan 32(3):107-115.

Favorite, F., and W.J. Ingraham, Jr.
  1976b. On flow in the northwestern Gulf of Alaska, May 1972. J. Oceanogr.
  Soc. Japan.

Favorite, F., W.J. Ingraham, Jr., and D.M. Fisk.
  1975. Environmental conditions near Portlock and Albatross Banks (Gulf
  of Alaska) May 1972. U.S. Dep. Commer., Natl. Oceanic. Atmos. Admin.,
  Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash., Proc.
  Rep. 45 p.

Favorite, F., W.B. McAlister, W.J. Ingraham, Jr., and D. Day.
  1967. Oceanography, p. 89-99. In N. Pac. Fish. Comm. Annu. Rep. 1966.

Favorite, F., and D.R. McLain.
  1973. Coherence in transpacific movements of positive and negative
  anomalies of sea surface temperature, 1953-60. Nature 244 (5412):139-143.

Favorite, F., B.A. Morse, A.H. Haselwood, and R.A. Preston, Jr.
  1964. North Pacific oceanography, February-April, 1962. U.S. Fish.
  Wildl. Serv., Spec. Sci. Rep. Fish. 477. 66 p.

Fishery Agency of Japan.
  1974. Summary report on research conducted by Japan in 1972 for the
  International North Pacific Fisheries Commission, p. 45-65. In Int.
  N. Pac. Fish. Comm., Annu. Rep. 1972.

Fofonoff, N.P.
  1962. Machine computations of mass transport in the North Pacific Ocean.
  J. Fish. Res. Board Can. 19(6):1121-1141.

Fofonoff, N.P., and S. Tabata.
  1966. Variability of oceanographic conditions between ocean station "P"
  and Swiftsure bank off the Pacific coast of Canada. J. Fish. Res. Board
  Can. 23(6):825-868.

French, R.R., and R. G. Bakkala.
  1974. A new model of ocean migrations of Bristol Bay sockeye salmon.
  Fish. Bull. 72(2):589-614.

Fry, F.E.
  1957. The aquatic respiration of fish, p. 590-606. In M.E. Brown (editor),
  Physiology of Fishes. Vol. 1. Metabolism. Academic Press, New York.

Fujii, T.
  1975. On the relation between the homing migration of the western Alaska
  sockeye salmon Oncorhynchus nerka (Walbaum) and oceanic conditions in
  the eastern Bering Sea. Memoirs Fac. Fish., Hokkaido Univ. 22(2):99-191.

Fujii, T., K. Masuda, T. Nishiyama, G. Kobayashi, and G. Anma.
  1974. A consideration on the relation between oceanographic conditions and
  distribution of Bristol Bay sockeye salmon (Oncorhynchus nerka) in the
  eastern Bering Sea, with special reference to its poor return in 1973.
  Bull. Fac. Fish. Hokkaido Univ. 25(3):215-229.

Fujita, T., and S. Kokubo.
  1927. Studies on herring. Bull. School Fishery, Hokkaido Imperial Univ.
  1(1).

Fukuhara, F.M.
  1953. Japanese 1952 North Pacific salmon-fishing expedition. Comm. Fish.
  Rev. 15(2):1-17.

Galkina, L.A.
  1971. Survival of spawn of the Pacific herring (Clupea harengus pallasii
  Val.) related to the abundance of the spawning stock. Symposium on the
  Biology of Early Stages and Recruitment Mechanisms of Herring. Rapports
  et Proces-Verbaux des Reunions, Cons. Int. Explor. Mer. 160:30-33.

Gilbert, C.H.
  1924. Experiments in tagging adult red salmon, Alaska Peninsula Fisheries
  Reservation, Summer of 1922. Bull., U.S. Bur. Fish., 39:39-50.

Gilbert, C.H., and W.H. Rich.
  1927. Second experiment in tagging salmon in the Alaska Peninsula
  Fisheries Reservation, Summer of 1923. Bull., U.S. Bur. Fish., 42:27-75.

Gilbert, P.W., E.S. Hodgson, and R.F. Mathewson.
  1964. Electroencephalograms of sharks. Science 145:949-951.

Gray, I.E.
  1954. Comparative study of the gill area of marine fishes. Biol. Bull.
  107:219-255.

Gulland, J.A.
  1965. Survival of the youngest stages of fish, and its relation to year-
  class strength. ICNAF Environmental Symposium Spec. Publ. 6:363-371.

Hall, F.G.
  1931. The respiration of the puffer fish. Biol. Bull. 61:457-467.

Hansen, D.V.
  1976. Quarterly Report, p. 689-704. In Environmental Research Laboratories
  environmental assessment of the Alaskan continental shelf, Vol. 3, Principal
  investigators' reports, July-September 1976. U.S. Deps. of Comm. and Int.,
  Boulder.

Hara, T.J.
  1971. Chemoreception, p. 79-120. In W. S. Hoar and D. J. Randall (editors),
  Fish physiology. Vol. V. Sensory systems and electric organs. Academic
  Press, New York and London.

Hara, T.J., K. Ueda, and A. Gorbman.
  1965. Electroencephalographic studies of homing salmon. Science 149:884-885.

Harden Jones, F.R.
   1956. The behaviour of minnows in relation to light intensity. J. Exp. Biol. 33:271-281.

   1968. Fish migration. St. Martin's Press, New York, 325 p.

Harris, G.G., and W.A. van Bergeijk.
   1962. Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. J. Acoust. Soc. Am. 34:1831-1841.

Hartman, W.L., W.R. Heard, and B. Drucker.
   1967. Migratory behavior of sockeye salmon fry and smolts. J. Fish. Res. Board Can. 24:2069-2099.

Hartt, A.C.
   1962. Movement of salmon in the North Pacific Ocean and Bering Sea as determined by tagging, 1956-1958. Int. North Pac. Fish. Comm., Bull. 6, 157 p.

Hartt, A.C.
   1966. Migrations of salmon in the North Pacific Ocean and Bering Sea as determined by seining and tagging, 1959-1960. Int. North Pac. Fish. Comm. Bull. 19, 141 p.

Hartt, A.C., and M.B. Dell.
   1977. Life history of juvenile Pacific salmon and steelhead trout during their first summer in the open sea. Univ. Wash., Fish. Res. Inst., Seattle, Wash., Unpubl. manuscr.

Hasler, A.D.
   1957. Olfactory and gustatory senses of fishes, p. 187-209. In M.E. Brown (editor), The physiology of fishes. Academic Press, New York.

   1966. Underwater guideposts. Univ. Wisconsin Press, Madison, 155 p.

Healey, E.G.
   1957. The nervous system, p. 1-119. In Margaret E. Brown (editor), The physiology of fishes. Vol. II.

Hela, I., and T. Laevastu.
   1961. Fisheries hydrography. How oceanography and meteorology can and do serve fisheries. Fishing News (Books) Ltd., London, 137 p.

Hemmings, C.C.
   1966. The mechanism of orientation of roach, Rutilus rutilus L. in an odour gradient. J. Exp. Biol. 45:465-474.

Hempel, G.
   1962. Uber die biologishsche Bedeutung der Eigrosse beim Hering (Clupea harengus) Habilitationsschrift Math. nat. Fak. Univ. Hamburg.

Hempel, G.
  1965. Fecundity and egg size in relation to the environment. ICNAF
  Environmental Symposium Spec. Publ. 6:687-690.

Hjort, J.
  1914. Fluctuations in the great fisheries of northern Europe. Rapports
  et Process-Berbaux des Reunions. Cons. Int. Explor. Mer. 20:228.

  1926. Fluctuations in the year classes of important food fishes. J. Cons.
  Cons. Explor. Mer. 1:1-54.

Hoar, W.S. and D.J. Randall (editors).
  1969. Fish physiology. Vol. I, Sensory systems and electric organs.
  Academic Press. New York and London. 465 p.

  1971. Fish physiology. Vol. VI, Environmental relations and behavior.
  Academic Press, New York. 559 p.

Holliday, F.T.T.
  1969. The effects of salinity on the eggs and larvae of teleosts, p.
  293-311. In W.S. Hoar and D.J. Randall (editors), Fish physiology, Vol. 1.
  Academic Press, New York.

Hoopes, D.T.
  1973. Fishery Facts-6. Alaska's fishery resources--the Dungeness crab.
  U.S. Dep. Commer. Nat. Ocean. Atmos. Admin., NMFS Extension Pub., 14 p.

Horsted, S.A. and E.Smidt.
  1965. Influence of cold water on fish and prawn stocks in West Greenland.
  ICNAP Spec. Publ. 6:199-207.

Hourston, A.S.
  1959. Effects of some aspects of environment on the distribution of juvenile
  herring in Barkley Sound. J.Fish. Res. Board Can. 16:283-308.

Hubbard, L.T., and W.G. Pearcy.
  1971. Geographic distribution and relative abundance of Salpidae off
  the Oregon coast. J. Fish. Res. Board Can. 28:1831-1836.

Hubbs, C. and N.J. Wilmovsky.
  1964. Distribution and synonymy in the Pacific Ocean and variation of the
  Greenland halibut, Reinhardtius hippoglossoides (Walbaum). J. Fish. Res.
  Board Can. 21(5):1129-1154.

Ingle, D.
  1971. Vision: The experimental analysis of visual behavior, p. 59-77.
  In W.S. Hoar and D.J. Randall (editors), Fish physiology, Vol. V. Academic
  Press, New York.

Ingraham, W. J.
  1968. The geostrophic circulation and distribution of water properties off
  the coasts of Vancouver Island and Washington, spring and fall 1963. U.S.
  Fish Wildl. Serv., Fish. Bull., 66(2):223-250.

Ingraham, W.J., A. Bakun, and F. Favorite.
1976. Physical oceanography of the Gulf of Alaska. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv. Northwest Fish Center, Seattle, Wash., Proc. Rep. 132 p.

Ingraham, W.J., Jr., and J.R. Hastings.
1973. Seasonal surface currents off the coasts of Vancouver Island and Washington as shown by drift bottle experiments in 1964-65. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash. Unpubl. manuscr. 26 p.

Inoue, M.S. and S. Hughes.
1971. Pacific saury (Cololabis saira), a review of stocks, harvesting techniques, processing methods and markets. Eng. Exper. Sta. Bull. 43. Ore. State Univ., Corvallis. 102 p.

International North Pacific Fisheries Commission.
1957. Annual report for 1956. 88 p.

1965. Proceedings of the twelfth annual meeting, 1965. 256 p.

Ivanov, B.G.
1969. The biology and distribution of the northern shrimp (Pandalus borealis br.) in the Bering Sea and Gulf of Alaska. FAO Fish. Rep. 3(57):799-810.

Iwata, M.
1976. Species structure. Marine Sciences Monthly, Symposium 81:39-46. (In Japanese).

Jaenicke, H.W., and M.B. Bonnett.
/1977./ Food of sockeye salmon outmigrants in Bristol Bay, Alaska, 1969-70. U.S. Dep. Commer.,Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest and Alaska Fish. Center, Auke Bay Laboratory, Auke Bay, Alaska. Unpubl. manuscr.

Japan Fishery Agency.
1974. Pacific pollock stocks in the eastern Bering Sea. Japan Fishery Agency, Tokyo, 1974. Unpubl. manuscr., 33 p.

Jensen, A.J.C.
1952. The influence of hydrographical factors on fish stocks and fisheries in the transition area, especially on their fluctuations from year to year. Rapp. P.-V. Reun., Cons. Int. Explor. Mer. 131:51-60.

Jow, T.
1969. Results of English sole tagging off California. Pac. Mar. Fish. Comm. Bull. 7:15-34.

Joyner, T.
1964. The determination and distribution of particulate aluminum and iron in coastal waters of the Pacific Northwest. J.Mar. Res. 22:259-268.

Kasahara, H.
 1961. Fisheries resources of the north Pacific Ocean. Inst. Fish. Univ.
 B.C., Vancouver, 202 p.

Kashkina, A. A.
 1965. Reproduction of yellowfin sole (Limanda aspera (Pallas))and changes
 in its spawning stocks in the eastern Bering Sea. Transl. in, Sov. Fish.
 Invest. Northeast Pac., Part IV, p. 182-190.

Keenleyside, M.A.A.
 1955. Some aspects of the schooling behavior of fish. Behaviour 8:183-248.

Kelley, J.J., D.W. Hood, J. Groves, and L. Longerich.
 1973. Oceanography of the Bering Sea. Phase 2. Turbulent upwelling and
 water mass identification in the vicinity of Samalga Pass, eastern
 Aleutian Islands, Vol. 2, Part. 1. Univ. Alaska, Fairbanks, Inst. Mar.
 Sci. 118 p. (Processed).

Ketchen, K.S.
 1961. Observations on the ecology of the Pacific cod (Gadus macrocephalus)
 in Canadian waters. J. Fish. Res. Board Can. 18(4):513-558.

Kleerekoper, H.
 1969. Olfaction in fishes. Indiana Univ. Press, Bloomington.

Kodolov, L.
 1968. Reproduction of the sable fish (Anoplopoma fimbria (Pall.)).
 Izv. Tikhookean. Nauchno-Issled. Inst. Rybn, Khoz. Okeanogr.

Kondo, H., Y. Hirano, N. Nakayama, and M. Miyake.
 1965. Offshore distribution and migration of Pacific salmon (genus
 Oncorhynchus) based on tagging studies (1958-1961). Int. N. Pac.
 Fish. Comm. Bull. 17, 213 p.

Koo, T.S.Y.
 1962. Age designation in salmon, p. 41-48. In Ted S.Y. Koo (editor), Studies
 of Alaska red salmon. Univ. of Wash. Press, Seattle.

Kramer, D. and P.E. Smith.
 1970. Seasonal and geographic characteristics of fishery resources.
 California current region--II. Pacific Saury. Commer. Fish. Rev.
 32(6):47-51.

Krinner, M.
 1935. Über die Geschmacksempfindlichkeit der Elritze. Z. vgl. Physiol.
 21:317-342.

Kulikov, M.Y.
 1965. Vertical distribution of sablefish (Anoplopoma fimbria (Pallas))
 on the Bering Sea continental slope. Transl. in, Sov. Fish. Invest.
 Northeast Pac., Part IV, p. 157-161.

Laevastu, T., J. Dunn, and F. Favorite.
 1976. Consumption of copepods and euphausids in the eastern Bering Sea
 as revealed by a numerical ecosystem model. ICES. C.M. 1976; Plankton
 Committee L:34.

Laevastu, T., and F. Favorite.
  1976a. Summary review of Dynamical Numerical Marine Ecosystem Model
  (DYNUMES), p. 118-148. In Proceedings of the NMFS/EDS workshop on climate
  and fisheries, April 26-29, 1976. U.S. Dep. Commer., Natl. Oceanic Atmos.
  Admin., Washington, D.C.

  1976b. Evaluation of standing stocks of marine resources in the eastern
  Bering Sea - using a static-trophic numerical Bulk Biomass Model (BBM).
  Natl. Mar. Fish. Serv., NOAA, Northwest and Alaska Fish. Center, Seattle,
  Wash. Unpubl. manuscr. 35 p.

Laevastu, T., and I. Hela.
  1970. Fisheries Oceanography. New Ocean Environmental Services. Fishing
  News (Books) Ltd. London. 238 p.

Lagler, K.F., J.E. Bardoch, and R.R. Miller.
  1962. Ichthyology. John Wiley and Sons, Inc., New York. 545 p.

Larkins, H.A.
  1964. Some epipelagic fishes of the north Pacific Ocean, Bering Sea, and
  Gulf of Alaska. Trans. Am. Fish. Soc. 93:286-290.

Larson, S.
  1970. Surface drift circulation in the North Pacific Ocean. Flt. Num.
  Wea. Cent. Tech. Memo No. 28, Monterey, California. 6 p. + 5 figs. (Processed).

Lasker, R., H.M. Feder, G.H. Theilacker, and R.C. May.
  1970. Feeding, growth and survival of Engraulis mordax larvae reared in
  the laboratory. Mar. Bio. (5):345-353.

Laurs, R.M. and R.J. Lynn.
  1977. Seasonal migration of North Pacific albacore, Thunnus alalunga, into
  North American coastal waters, their distribution, relative abundance, and
  association with Transition Zone waters. Fish. Bull. (In Press).

Lee, A.J.
  1952. The influence of hydrography on the Bear Island cod fishery. Rapp.
  et. Proc. ICES, 131:74-102.

Lindroth, A.
  1942. Sauerstoffverbrouch der Fishe. II. Verschiedene Entwicklungs-und
  Alterstadien vom Lachs und Hecht. Z. vergleich. Physiol. 29:583-594.

Lisovenko, L.A.
  1964. Distribution of larval Pacific ocean perch (Sebastodes alutus G.)
  in the Gulf of Alaska. Transl. in, Sov. Fish. Invest. Northeast Pac.,
  Part III, p. 217-225.

Lough, R.G.
  1976. Larval dynamics of the Dungeness crab, Cancer magister, off the
  central Oregon coast, 1970-71. Fish. Bull., U.S. 74:353-376.

Loukashkin, A.S., and N. Grant.
  1959. Behavior and reactions of the Pacific sardine, Sardinops caerula
  (Girard), under the influence of coloured lights and darkness. Proc.
  Calif. Acad. Sci. 29:509-548.

Lyubimova, T.G.
  1963. Basic aspects of the biology and distribution of Pacific rockfish
  (Sebastodes alutus Gilbert) in the Gulf of Alaska. Transl. in, Sov.
  Fish. Invest. Northeast Pac. Ocean, Part I, p. 308-318.

Macy, P.T., J.M. Wall, N.D. Lampsakis, and J.E. Mason.
  1977. Resources of non-salmonid pelagic fishes of the eastern Bering Sea
  and Gulf of Alaska--a review of literature and historical data. U.S.
  Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest
  and Alaska Fish. Center, Seattle, Wash., Final Report for Contracts #R7110811
  and R6120812, Task A07, Res. Unit 64/354, for Outer Continental Shelf
  Energy Assessment Program, U.S. Dep. Int., Bur. Land Manage. In 2 parts-
  Part I. Review of literature and analysis of historic fishing data; Part II.
  Appendices A-C.

Maeda, T.
  1972. Fishing grounds of the Alaska pollock. Bull. Jap. Soc. Sci. Fish.
  34:362-371.

Major, R.L., and H.H. Shippen.
  1970. Synopsis of biological data on Pacific ocean perch (Sebastodes alutus).
  U.S. Fish Wildl. Serv. Circ. 347 (FAO Fisheries Synopsis No. 79): 38 p.

McAlister. W.B.
  1968. Buoy telemetry for environment prediction in fisheries research.
  Proc. Int. Telemetering Conf., Los Angeles, Calif., Oct. 8-11, 1968,
  Vol. 4:650-657.

McAlister, W.B., F. Favorite, and W.J. Ingraham, Jr.
  1970. Influence of the Komandorskie Ridge on surface and deep circulation
  in the western North Pacific Ocean, p. 85-96. In John C. Marr (editor),
  The Kuroshio: a symposium on the Japan Current. East-West Center Press,
  Honolulu.

McCracken, F.D.
  1965. Distribution of haddock off the eastern Canadian mainland in relation
  to season, depth and bottom temperature. ICNAP Spec. Publ. 6:113-129.

McGary, N.
  1971. An atlas of the Columbia River effluent and its distribution at
  sea. Univ. Wash., Seattle, Dep. Oceanogr., Spec. Rep. 47. 57 p.

McGowan, J.A.
  1974. The nature of oceanic ecosystems, p. 9-28. In Charles B. Miller
  (editor), The biology of the oceanic Pacific. Oregon State Univ. Press,
  Corvallis.

McInerney, J.E.
1964. Salinity preference: an orientation mechanism in salmon migrations.
J. Fish. Res. Board Can. 21:995-1018.

McLain, D.R., and F. Favorite.
1976. Anomalously cold winters in the southeastern Bering Sea, 1971-75.
Mar. Sci. Commu. 2(5):299-334.

McMynn, R.G., and W.S. Hoar.
1953. Effects of salinity on the development of the Pacific herring. Can.
J. Zool. 31:417-431.

Meyer, H.
1935. Die Atmung von Uranoscopus scaber und ihre Abhangigkeit vom Sauerstoffdruck.
Z. vergleich. Physiol. 22:435-449.

Moiseev, P.A.
1953. Cod and flounders of far-eastern waters, Part I and II. Fish. Res.
Board Can., Transl. Ser. 119, 576 p.

1956. Factors of population dynamics of the commercial fauna in the northwest
Pacific Ocean. Zool. Zh. 35(11):1601-1607.

1960. The behavior of the Pacific cod in various zoogeographical areas.
Zool. Zhuin. 31(4):558-562.

Moulton, F.R.
1939. The migrations and conservation of salmon. Publ. Amer. Assoc. Advan.
Sci. No. 8. The Science Press. 106 p.

Mukhocheva, V.A., and O.A. Zayayina.
1960. Development of the Pacific coast cod. Tr. Inst. Okeanol. Akad. Nauk.
SSSR. 31:145-165.

Munford, J.K.
1963. John Ledyard's journal of Captain Cook's last voyage. Oregon State
Univ. Press, Corvallis, 264 p.

Munz, F.W.
1971. Vision: Visual pigments, p. 1-32. In W.S. Hoar and D.J. Randall
(editors), Fish physiology, Vol. V. Academic Press, New York.

Murray, R.W.
1971. Temperature receptors, p. 121-133. In W.S. Hoar and D.J. Randall
(editors), Fish physiology, Vol. V. Academic Press, New York.

Musienko, L.N.
1963. Ichthyoplankton of the Bering Sea (Data of the Bering Sea expedition
of 1958-59). Transl. in, Sov. Fish. Invest. Northeast Pac., Part I, p.
251-286.

Musienko, L.N.
  1970. Reproduction and development of Bering Sea fishes. Transl. in,
  Sov. Fish. Invest. Northeast Pac., Part V, p. 161-224.

National Academy of Sciences.
  1975. Numerical models of ocean circulation. Nat. Acad. Sciences, Wash.,
  D.C. 364 p.

Nelson, M.O. and H.A. Larkins
  1970. Distribution and biology of Pacific hake: A synopsis, p. 23-34. In
  Pacific hake, U.S. Fish Wildl. Serv., Cir. 332.

Nicol, J.A.C.
  1963. Some aspects of photoreception and vision in fishes, p. 171-208.
  In F.S. Russell (editor), Advances in marine biology, Vol. 1. Academic
  Press, New York.

Novikov, N.P.
  1964. Basic elements of the Pacific halibut (Hippoglossus stenolepis
  Schmidt) in the Bering Sea. Transl. in, Sov. Fish. Invest. Northeast
  Pac., Part II, p. 175-219.

Novikov. N.P. and Yu. M. Kulikov.
  1966. Perspektivny i raion promysla sairy (Prospective region for saury
  fishing). Ryb. Khoz. 42(7):20-21. (Translation, Bur. Commer. Fish.,
  Off. Foreign Fish., Dep. Interior, Wash., D.C.).

Oshima, K., W.E. Hahn, and A. Gorbman.
  1969. Electroencephalographic olfactory responses in adult salmon to
  waters traversed in the homing migration. J. Fish. Res. Board Can.
  26:2123-2133.

Outram, D.N.
  1958. The magnitude of herring spawn losses due to bird predation on the
  west coast of Vancouver Island. Pacific Coast Stations of the Fisheries
  Research Board of Canada, Progress Rep. (111):9-13.

Outram, D.N., and R.D. Humphreys.
  1974. The Pacific herring in British Columbia waters. Fisheries and Marine
  Service Pacific Biological Station, Nanaimo, B.C. Canada. Circ. 100, 26 p.

Parker, G.H.
  1914. The directive influence of the sense of smell in the dogfish. U.S.
  Bur. Fish., Bull. 33:63-68.

Pattie, B.H.
  1969. Dispersal of English sole, Parophrys vetulus, tagged off the Washington
  coast in 1956. Pac. Mar. Fish. Comm., Bull. 7:11-14.

Pearcy, W.G.
  1973. Albacore oceanography off Oregon - 1970. Fish. Bull. 71(2):489-504.

Pereyra, W.T.
  1972. Bathymetric and seasonal abundance and general ecology of the Tanner
  crab, Chionoecetes Tanneri Rathbun (Brachyura:Majidae), off the northern
  Oregon coast, p. 538-582. In A.T. Pruter and D.L. Alverson (editors), The
  Columbia River estuary and adjacent ocean waters. Univ. of Wash. Press,
  Seattle and London.

Pereyra, W.T., J.E. Reeves, and R.G. Bakkala.
  1976. Demersal fish and shellfish resources of the eastern Bering Sea in
  the baseline year 1975. Natl. Mar. Fish. Serv., NOAA, Northwest Fish.
  Center, Seattle, Wash., Proc. Rep. 619 p.

Peterson, W.T.
  1973. Upwelling indices and annual catches of Dungeness crab, Cancer magister,
  along the west coast of the United States. Fish. Bull. 71:902-910.

Poulsen, E.M.
  1930. Investigations of fluctuations in the cod stock in Danish waters.
  Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 68:20-23.

Powell, D.E.
  1957. Alaska offshore herring exploration by the John N. Cobb--July-August 1957.
  Operations Report. U.S. Fish Wildl. Serv., Bur. Comm. Fish., Alaska Region,
  Juneau, Alaska. Unpubl. manuscr.

Pruter, A., and D. Alverson.
  1962. Abundance, distribution, and growth of flounders in the southeastern
  Chukchi Sea. J. Conseil 27:81-99.

Radovich, J.
  1976. Water temperature and fish distribution: an epilogue to the warm
  water years (abstr.) p. 264-265. In 13th Pac. Sci. Cong. Record of
  Proceed. Vol. 1, Abstracts of Papers, Pac. Sci. Assoc., Vancouver, Canada.

Ramey, C.W., and W.P. Wickett.
  1973. Empirical relations between physical factors in coastal waters and
  herring population size. Fish. Res. Board Can., Tech. Rep. 381:1-55.

Reed, J.R.
  1969. Alarm substances and fright reaction in some fishes from the south-
  eastern United States. Trans. Am. Fish. Soc. 98:664-668.

Reed, R.K., and D. Halpern.
  1976. Observations of the California Undercurrent off Washington and
  Vancouver Island. Limnol. Oceanog. 21(3):389-398.

Reeves, J.E.
  1975. King and Tanner crab research in the Bering Sea. Natl. Mar. Fish.
  Serv., NOAA, Northwest Fish. Center, Seattle, Wash. Unpubl. manuscr. 25 p.

Reid, G.M.
  1972. Alaska's fishery resources. The Pacific herring. Fishery Facts 2.
  Natl. Mar. Fish. Serv. Extension Publ. Seattle, Wash., 20 p.

Robinson, M.K.
  1964. Physical oceanography: plans for U.S.-Japan Cooperation. Science
  146:1371-72.

  1976. Atlas of North Pacific Ocean monthly mean temperatures and mean
  salinities of the surface layer. Naval Ocean. Off. Ref. Publ. 2, XIX p.
  + 173 figs.

Ronholt, L.L., H.H. Shippen, and E.S. Brown.
  1976. An assessment of the demersal fish and invertebrate resources of
  the northeastern Gulf of Alaska, Yakutat Bay to Cape Cleare, May-August
  1975. NOAA, Northwest and Alaska Fish. Center, Seattle, Wash. Unpubl.
  manuscr. 184 p.

Rounsefell, G.A.
  1929. Contribution to the biology of the Pacific herring, Clupea pallasii,
  and the condition of the fishery in Alaska. Bull. U.S. Bur. Fish. 45:227-320.

  1930. The existence and causes of dominant year classes in the Alaska
  herring. Contributions to Marine Biology. Stanford Univ. Press,
  September 1, 1930:260-270.

  1975. Ecology, utilization and management of marine fisheries. C.V. Mosly
  Co., 516 p.

Royce, W.F., L.S. Smith, and A.C. Hartt.
  1968. Models of oceanic migrations of Pacific salmon and comments on
  guidance mechanisms. U.S. Fish Wildl. Serv., Fish. Bull. 66:441-462.

Saila, S.B., and R.A. Shappy.
  1963. Random movement and orientation in salmon migration. J. Cons.
  28:153-166.

Salveson, S.J., and J.R. Dunn.
  1976. Pacific cod (Family Gadidae), p. 393-405. In Walter T. Pereyra,
  Jerry E. Reeves and Richard Bakkala (editors), Demersal fish and shellfish
  resources of the eastern Bering Sea in the baseline year 1975. U.S. Dep.
  Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest
  Fish. Center, Seattle, Wash., Proc. Rep.

Salveson, S.J., and M.S. Alton.
  1976a. Yellowfin sole (Family Pleuronectidae), p. 439-459. In Walter T.
  Pereyra, Jerry E. Reeves, and Richard Bakkala (editors), Demersal fish
  and shellfish resources of the eastern Bering Sea in the baseline year 1975.
  U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv.,
  Northwest Fish. Center, Seattle, Wash., Proc. Rep.

Salveson, S.J., and M.S. Alton.
   1976b. Pollock (Family Gadidae), p. 369-391. In Walter T. Pereyra, Jerry
   E. Reeves, and Richard Bakkala (editors), Demersal fish and shellfish resources
   of the eastern Bering Sea in the baseline year 1975. U.S. Dep. Commer.,
   Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center,
   Seattle, Wash., Proc. Rep.

Sasaki, T., L.L. Low, and K.N. Thorson.
   1975. Sablefish (Anoplopoma fimbria) (Pallas) resources of the Bering Sea
   and northeastern Pacific Ocean. U.S. Dep. of Commer., Natl. Oceanic Atmos.
   Admin., Natl. Mar. Fish. Serv., Northwest Fish. Center, Seattle, Wash.,
   Proc. Rep., 56 p.

Scharfe, J.
   1953. Uber die Verwendung Kumstilichen lichtes in der Fischeri. (Concerning
   the use of artifical lights in the fishery). Protokolle zur Fishereitechnik
   8:1-29.

Schmitt, W.L.
   1965. Crustaceans. The Univ. of Michigan Press, Ann Arbor, 204 p.

Schwassmann, H.O.
   1971. Biological rhythms, p. 371-428. In W.S. Hoar and D.J. Randall
   (editors), Fish physiology, Vol. Vi. Academic Press, New York and London.

Serobaba, I.I.
   1967. On the spawning of Alaska pollock Theragra chalocogramma (Pallas)
   in the northeastern part of the Bering Sea. Vopr. Ikhtiol. 8(6(53)):992-1003.

   1971. About reproduction of walleye pollock (Theragra chalocogramma) (Pallas)
   in the eastern part of the Bering Sea. Izv. Tikhookean. Nachno-issled.
   Inst. Morsk. Rybn. Khoz. Okeanogr. 75:47-55 (Transl. 1973, Fish. Res. Board
   Can. Transl. Ser. 2470, 20 p.).

Shaboneev, I.E.
   1965. Biology and fishing of herring in the eastern part of the Bering Sea,
   p. 139-154. In Soviet fishery investigation in the northeast Pacific, Pt. 4.
   Avail. Natl. Tech. Inf. Serv., Springfield, Va. as TT67-51206.

Shaw, E.
   1961. Minimal light intensity and the dispersal of schooling fish. Bull.
   Inst. Oceanogr. Monaco, No. 1213, 8 p.

Sheldon, R.E.
   1911. The sense of smell in selacians. J. Exp. Zool. 10:51-62.

Sindermann, C.J.
   1965. Effects of environment on several diseases of herring from the
   western north Atlantic. ICNAF Environmental Symposium Spec. Publ.
   6:603-610.

Steinfeld, J.D.
  1972. Distribution of Pacific herring spawn in Yaquina Bay, Oregon, and
  Observations on mortality through hatching. M.S. Thesis, Oregon State
  Univ. 74 p.

Stevens, D.M.
  1959. Studies on the shoaling behavior of fish. I. Responses of two
  species to changes in illumination and to olfactory stimuli. J. Exp. Biol.
  36:261-280.

Stevenson, J.C.
  1947. Preliminary survey of larval herring on the west coast of Vancouver
  Island, 1947. Fish. Res. Board Can., Pacific Prog. Rep. 73:64-67.

  1962. Distribution and survival of herring larvae (Clupea pallasii) in
  British Columbia waters. J. Fish. Res. Board Can. 19:735-810.

Straty, R.R.
  1969. The migratory pattern of adult sockeye salmon, Oncorhynchus nerka.
  in Bristol Bay as related to the distribution of their home-river waters.
  Ph.D. Thesis, Oregon State Univ., Corvallis, 243 p.

  1974. Ecology and behavior of juvenile sockeye salmon, Oncorhynchus nerka,
  in Bristol Bay and the eastern Bering Sea with emphasis on renewable
  resources. Univ. Alaska, Inst. Mar. Sci., Occas. Publ. 2:285-319.

  1975. Migratory routes of adult sockeye salmon, Oncorhynchus nerka, in
  the eastern Bering Sea and Bristol Bay. Natl. Ocean. Atmos. Admin. Tech.
  Rep./Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish.-690, 32 p.

Straty, R.R., and R.E. Haight.
  In Press. Interaction of marine birds and commercial fish in the eastern
  Bering Sea. Wildlife Research Dep., U.S. Fish Wildl. Serv.

Straty, R.R., and H.W. Jaenicke.
  1971. Studies of the estuarine and early life history of sockeye salmon in
  Bristol Bay, 1965-67. Northwest Alaska Fish. Cent., Auke Bay Fish. Lab.,
  Natl. Mar. Fish. Serv., Natl. Oceanic Atmos. Admin., Unpubl. manuscr., 137 p.

Taguchi, K.
  1956. A report of drift-bottle surveys off Kamchitka, USSR, in 1940 and
  1941. Bull. Jap. Soc. Sci. Fish. (Tokyo). 22:393-399.

Takahashi, Y., and H. Yamaguchi.
  1972. Stock of the Alaskan pollock in the eastern Bering Sea. Bull. Jap.
  Soc. Sci. Fish. 38(4):418-419.

Takahashi, T. and M. Konda.
  1974. On the age composition and the hourly changes of the catch of the
  herring by the trawl net in the northwestern area of the Pribilof Islands,
  North Pacific in the 1971-72 winter. Bull. Fac. Fish., Hokkaido Univ.
  25(1):47-54.

Tanner, Z.L., et al.
   1890.   Explorations of the fishing grounds of Alaska, Washington Territory,
   and Oregon, during 1888, by the U.S. Fish Commission steamer Albatross.
   Bull. U.S. Fish Comm. 8:1-95.

Taylor, F.H.C.
   1968.   What happened to the herring? Western Fisheries, February:24-32.

   1971a.   Variation in hatching success in Pacific herring (Clupea pallasii)
   eggs with water depth, temperature, salinity and egg mass thickness.
   Symposium on the biology of early stages and recruitment mechanisms of
   herring.   Counsul Inter. pour l' Exploration de la Mer.   Rapports et
   Proces-Verbaux des Reunions.   Cons. Int. Explor. Mer. 160:34-45.

   1971b.   Offshore distribution of Pacific herring (Clupea pallasii) on
   basis of records from fur seal stomachs.   J. Fish. Res. Board Can.
   28(10):1663-1665.

Teichmann, H.
   1957.   Das Ruchvermogen des Aales (Anguilla anguilla L.).   Naturwissenschaften
   44:242.

   1962.   Die Chemorezeption der Fische.   Ergeb. Biol. 25:177-205.

Templeman, W. and V.M. Hodder.
   1965.   Distribution of haddock on the Grand Bank in relation to season,
   depth and temperature.   ICNAF Spec. Publ. 6:171-187.

Theilacker, G.F. and R. Lasker.
   1974.   Laboratory studies of predation by euphausiid shrimps.   In The early
   life history of fish.   Proceedings of an international symposium, Dunstaffnage
   Marine Research Laboratory of the Scottish Marine Biological Association,
   Oban, Scotland, May 17-23, 1973:286-299.

Thompson, W.F. and R. Van Cleve.
   1936.   Life history of the Pacific halibut.   (2) Distribution and early
   life history.   Rep. Int. Fish. Comm., No. 9, 184 p.

Todd, J.H., J. Atema, and J.E. Bardach.
   1967.   Chemical communication in social behavior of a fish, the yellow
   bullhead (Ictalurus natalis).   Science 158:672-673.

Tomita, T.
   1971.   Vision: Electrophysiology of the retina, p. 33-57.   In W.S. Hoar
   and D.J. Randall (editors), Fish physiology, Vol. V., Academic Press,
   New York.

Ueda, K., T.J. Hara, and A. Gorbman.
   1967.   Electroencephalographic studies on olfactory discrimination in adult
   spawning salmon.   Comp. Biochem. Physiol. 21:133-144.

Van Bergeijk, W.A.
  1964. Directional and non-directional hearing in fish, p. 281-299. In
  W.N. Tavolga (editor), Marine Bio-Acoustics, Pergamon Press, Oxford.

von Frisch, K.
  1938. Zur Psychologie des Fischschwarmes. Naturwissenschaften 26:601-606.

Walford, L.A.
  1946. Correlation between fluctuations in abundance of Pacific sardine
  (Sardinops caerulea) and salinity of the sea water. J. Mar. Res. 6:48-53.

Whitworth, W.R.
  1968. Effects of diurnal fluctuations of dissolved oxygen on the growth
  of brook trout. J. Fish. Res. Board Can. 25:579-584.

Wickett, W.P.
  1975. Recent changes in the marine climate affecting herring. Fish. Res.
  Board, Can., Manuscr. Rep. Ser. 1342. Proceedings of the Second Annual
  Pacific Coast Herring Workshop, Oct. 30-31, 1974. Unpubl. manuscr.:39-43.

Wickett, W.P., F.H.C. Taylor, and C.W. Ramey.
  1975. Simultaneous changes in B.C. herring year-class-strengths and the
  marine climate of the northeastern Pacific Ocean (abstr) p. 269-270. In
  13th Pac. Sci. Cong. Record of Proceed. Vol. I. Abstracts of Papers.
  Pac. Sci. Assoc., Vancouver, Canada.

Wilimovsky, N.J., A. Peden, and J. Peppar.
  1967. Systematics of six demersal fishes of the North Pacific Ocean. Fish.
  Res. Board Can., Biol. Sta., Nanaimo, B.C. Tech. Rep. 34, 95 p.

Woodhead, P.M.J.
  1965. Effects of light upon behavior and distribution of demersal fishes
  of the north Atlantic. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6,
  p. 267-287.

Woodworth, B.M.
  (n.d.) The coho project, living resources prediction feasibility study,
  Vol. III, system evaluation report. Florida State University and
  Oregon State University. 57 p.

Wooster, W.S. and J.L. Reid, Jr.
  1963. Eastern boundary currents, p. 253-280. In M. N. Hill (editor), The
  sea: Ideas and observations on progress in the study of the sea, Vol. 2.
  Interscience Publ., New York.

Wrede, W.L.
  1932. Versuche uber den Artduft der Elritzen. Z. vgl. Physiol. 17:510-519.