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PART 1. COASTAL PELAGIC FISHES
(*Report of Working Group 3*)

Edited by John R. Hunter and Tokio Wada

PART 2. SUBARCTIC GYRE
(*Report of Working Group 6*)

Edited by Brent Hargreaves and Takashige Sugimoto

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Part 1

COASTAL PELAGIC FISHES

FORWARD

This is a report of PICES Working Group 3 (Coastal Pelagic Fishes) for 1993. The objective was to develop a report for review by the Fishery Science Committee based on the terms of reference (see Appendix 2) approved by Council at its 1992 meeting. The finalization of the report was at a meeting held in Nemuro, Hokkaido, Japan in conjunction with a Symposium on Subarctic Circulation, September 19-23, 1993. The secretary-general of the organizing committee was Dr. Makoto Kashiwai.

This report was written by the Working Group 3 members through their diligent efforts during 1993. The Co-Chairmen would like to thank all members (see Appendix 3) for their efforts in developing a good report that will provide the Fishery Science Committee with ideas for future consideration.

John R. Hunter and Tokio Wada
Co-Chairmen

EXECUTIVE SUMMARY

The goal of the PICES Coastal Pelagic Fishes Working Group is to evaluate how long term global changes in climate affect the pelagic fishes of the North Pacific. The goal of the committee matches the goal of GLOBEC International. Consequently, research and related activities of PICES Coastal Pelagic Fishes Working Group can be considered to be part of the GLOBEC International program in any PICES country.

Pelagic fishes currently considered by the Working Group include: Pacific herring, sardines, anchovies, saury, jack mackerel, and Pacific mackerel. The Working Group proposes to use comparative methods to determine how long term effects of climate may affect the dynamics of these North Pacific stocks.

The working group proposes to carry out analysis of the recruitment successes and failures of key Pan-Pacific pelagic stocks to determine if a pattern exists in population growth or decline. The ultimate goal of this work is to identify Pan-Pacific physical forcing functions. As a first step in this process, PICES Coastal Pelagic Fishes Group proposes to carry out an inventory of population time series for Eastern Pacific and Western Pacific stocks. It is important that Russian and Korean information is included in the inventory, although these nations were not represented in the workshop. After completion of the inventory, the time series will be analyzed for patterns and differences in recruitment and life table rates. These will be interpreted in terms of physical forcing and density dependent processes.

In the short term, a second style of comparative studies are planned. These include application of trophodynamics models to understand the production systems of different regions of the North Pacific and how they support pelagic fish biomass. Additional comparative approaches, which may be used in the future, are described in the Report.

The working group recognized that present trans-Pacific communication of PICES scientists was inadequate for successful completion of their goal of Pan-Pacific comparative studies. To improve communication, the Group proposed two actions: 1) conduct an inventory of PICES scientists working on projects relevant to the mission of the Coastal Pelagic Fishes Working Group; and 2) begin a visiting scientist program. The first will be done by working group members, but the second will require the support and administration by the Secretariat.

1.0 INTRODUCTION

The objective of the Coastal Pelagic Fishes Working Group of PICES (see terms of reference) is to determine the characteristics of the environment, other than fishing, that affect the dynamics of the pelagic fish stocks of the North Pacific. Long term population changes, such as those that may be produced by global climate change, are of particular interest. Consequently, the research and related activities of the Group can be considered to be part of the GLOBEC International program of any PICES country.

The pelagic fishes currently considered by the Working Group are: Pacific herring, (*Clupea pallasi*); sardines (*Sardinops spp*); anchovies (*Engraulis spp*); mackerels (*Scomber spp, and Trachurus spp*); and saury (*Colorabis saira*). The world catch of these pelagic fishes in 1990 was 25 million tons. This catch was 35% of the world catch of marine fishes (Table 1). About 7 million tons of small pelagic fishes are taken annually in the North Pacific (FAO Statistical Areas 61, 67, and 77), with the Japanese sardine accounting for 65% of the total. Only a small portion of the world catch of small pelagic fishes are used directly for human consumption, most of the catch is reduced to fish meal and oil with the meal being an important ingredient of animal feeds. In Japan, where 80-90% of sardine and anchovy catch is used for meal, meal is used to support a rapidly growing fish aquaculture industry. Aquaculture production of fish in Japan, which has tripled between 1970 and 1990, could be seriously affected by a major decline in the Japanese sardine stock.

The general research approach of the Working Group is the comparative method. Our terms of reference state we are "to develop a program for a comparative study of the population dynamics and production of small pelagic fishes in the coastal ecosystem along the western and eastern continental margins of the North Pacific". Comparisons of the dynamics of marine animal populations can be used to test a variety of hypotheses. Comparisons of the same or similar species in different ecosystems can be used to assess effects of population response to different forcing variables (Bakun & Parrish, 1982). Alternatively, comparisons can be made of recruitment success of different species within the same ecosystem to identify specific patterns in the responses to basin-wide environmental change (Hollowed et al., 1987; Koslow, l984).

Variation in abundance

Great variation in population size is characteristic of the major stocks of small pelagic fishes (Csirke, 1988). Considerable variability exists between species and regions. In Japanese waters, the catch of the sardine fluctuates over a two order of magnitude range while anchovy, mackerel, and saury are less variable (Table 2). In California, the same pattern emerges with the sardine population being much more variable than either anchovy or mackerel. Considering the differences in the data between Japan and California, the variability of the three stocks is remarkably similar in the two systems with the coefficient of variation for sardine about twice that for mackerel and with anchovy being roughly a third as variable as sardine. The most striking difference between the two systems is the much greater productivity of the Japanese stocks. On the average, landings of Japanese sardine, anchovy, and mackerel exceed the biomass of the equivalent California stocks.

The processes affecting the recruitment of year classes, and therefore population growth, have been researched for the last 20 years. This body of information on herring, anchovy and sardine, indicates that the recruitment success depends upon the survival of the early life history stages over the first 6 months of life with survivorship in the egg and larval stages being the most variable. Starvation as well as predation may be an important source of mortality during the first few weeks of life but thereafter survivorship is a function of larval growth and their size specific vulnerability to predators. Starvation and growth of early life history stages is fairly well documented but few quantitative estimates of predation exist.

A succession of strong or weak year classes over a decade or more are needed to realize the large and long fluctuations in population biomass, characteristic of many clupeoid populations. This pattern is also found in the physical oceanographic data where decadal periods of ocean climate exist (often called regimes) in which recruitment is either consistently lower or higher than the mean. In support of this argument authors point out correspondences between successions of strong or weak year classes and periods of lower or higher than average sea surface temperatures. How such temperatures affect recruitment remains obscure, however.

Persistent patterns in the success of year classes suggests to others that a positive feedback loop regulating population growth might exist, instead of the density-dependent negative feedback loop usually postulated as a regulatory mechanism. A positive feedback loop is possible in Japanese and California sardine since growth, migration, feeding habitats, and spawning habitats change as their populations grow. In the Japanese sardine energy allocation between growth and reproduction, egg and larval transport from spawning grounds to nursery grounds by the Kuroshio Current, may all be linked to population size. Thus, population response to changes in physical forcing variables may be modulated by internal population processes. Consequently, the long term effect of physical forcing variables on populations should be examined within the context of possible density dependent processes.

Lastly, it is important to recognize that these small pelagic fishes may be more closely linked to long term changes in primary and secondary production than are most other major stocks because they are planktivorous throughout their lives.

2.0 DESCRIPTIONS OF STOCKS

2.1 Eastern Pacific

2.1.1 California Sardine (*Sardinops sagax*)

Three stocks of sardine occur in the north eastern Pacific: a Gulf of California stock (Mexico); a southern Baja California stock (Mexico) [Punta Baja, Mexico to Cabo San Lucas]; and a northern stock (Punta Eugenia, Baja California, Mexico to Monterey, Alta California, USA). The northern stock, immortalized in Steinbeck's book, *Cannery Row*, has a summer feeding migration where fish migrate as far north as British Columbia, Canada.

In 1979, about 20 years after its near-total collapse, the northern stock showed the first signs of recovery. The beginning of the recovery is best illustrated by the average number of sardine eggs taken in CalCOFI cruises (Fig. 1, upper panel). The stock was probably less than 10,000 mt in the early 1970s. Currently, the spawning biomass may exceed 100,000 mt, which is still a small fraction of the maximum historic spawning biomass of 3.5 million tons. Some confusion exists regarding the timing of the recovery of the northern stock because FAO combines the landings for the northern and Gulf of California stocks. A new Mexican fishery on the Gulf of California sardine began in the early 70s, reaching a peak catch of over 300,000 tons by 1988 and has declined thereafter. The combined FAO landings give the impression that the northern stock underwent a striking recovery in the 70s and 80s coinciding with the striking recovery of the Japanese Stock (Kawasaki, 1991). The recovery of the northern sardine stock did not occur at the same time as the Japanese sardine; in fact, the northern stock did not exceed 20,000 mt until 1986 (Wolf, et al., 1987). Today (1993) the combined U.S. and Mexican catch of the northern sardine stock is about 60,000 mt. What was interpreted as a recovery was the development of a new Gulf of California fishery for sardine. Ironically, the Gulf of California stock, with catches declining since 1989, collapsed in 1993 with a total catch of less than 20,000 mt. It should be mentioned, however, that genetic analysis indicates that these stocks are part of a common population, but their dynamics are clearly different.

The current interpretation of the collapse of northern stock is that overfishing exacerbated a decline caused by environmental change, a decade of persistently cold sea water temperatures which were unfavorable to sardine recruitment. Recent work by Jacobson and MacCall (ms.) indicates that when sea surface temperatures (as measured at Scripps Pier) average 17.3°C the maximum sustainable yield (MSY) of sardine may be about five times the MSY when sea surface temperatures average 16.6°C. At this time the mechanisms responsible for the relation between sardine recruitment and sea temperature are unknown.

Smith, et al., 1992 estimated rates of California sardine population growth and decline using the scale deposition data from Baumgartner, et al., 1992 changes in standing crop of sardine eggs, and virtual population analysis. Fastest population growth was based on egg abundance of the northern stock of sardine (1975-1991) where annual growth was 70% per year, and fastest declines for the same population were 20-30% per year. Analysis of the effects of life stage specific differences in mortality and growth using Lefkovitch Matrix models indicate that population changes equivalent to those observed in sardine can be produced by altering early or late larval mortality or growth rates within the range of published values (Butler, et al., 1993). Thus, the central question for the California sardine from a climate change perspective is: what are the environmental conditions that persist over a decade or more, affect survival and growth of sardine larvae, and are correlated with three year average sea surface temperatures?

2.1.2 The Northern Anchovy (*Engraulis mordax*)

The northern anchovy population is divided into four stocks, a northern stock that extends from British Columbia to San Francisco; a central stock which extends from San Francisco to Punta Baja, Mexico; and a southern stock that extends south from Punta Baja to Cabo San Lucas. In 1986 a recent invasion of northern anchovy into the Gulf of California (Mexico) was documented by Hammann (1989) indicating the formation of a new Gulf stock of anchovy. Sedimentary scale evidence indicates anchovy have not been in the Gulf for over 100 years (Baumgartner, pers. comm.). The recent invasion is in rough correlation with a decline in the Gulf sardine stock.

The largest and best known stock is the Central sub-population. The biomass of this stock was low in the 1950's and 60's (200-500,000 mt) grew rapidly in the early 70's, reaching a maximum historic biomass of 1.2 million tons in 1973 (Jacobson and Lo, 1993), and declined thereafter. Over the last 5 years the biomass has stabilized in the 300-400,000 mt range. A 60,000-300,000 mt reduction fishery existed from 1969 through 1989, but landings have been less than 11,000 mt since 1989. Declines in biomass in recent years were probably due to low recruitment rather than high fishing mortalities (Jacobson and Lo, pers. comm.). The most striking feature of the 30 year anchovy time series was an extra-ordinarily large recruitment in 1972, ushering in a decade in which 7 years exceeded the mean. This period of high anchovy abundance coincided with the continuing decline of the sardine.

A pair of clupeoids, a sardine and anchovy, exist as part of the pelagic fish assemblages in many of the worlds oceans. The decline in one member of the pair, usually the sardine, has occurred in rough correlation with an increase in the biomass of the other (Blaxter and Hunter, 1982). This has led to considerable speculation regarding the potential interaction of these two species. Since their food overlap is broad, inter-specific competition for food has often been inferred. The only direct evidence of interaction is provided by Butler (1991). He found that mortality rates of sardine larvae (>20d) increased between 1951-1967 and the increase was positively correlated with the increase in biomass of the northern anchovy. He attributed the correlation to predation by anchovy on sardine eggs and larvae.

Life stage sensitivity analysis for anchovy using Lefkovitch Matrix models indicates that the most sensitive stages were the early larval (4-10 mm) where the fastest growth rate or lowest mortality rate leads to a 270% increase in population size (Butler et al., 1993).

2.1.3 Pacific Mackerel (*Scomber japonicus*)

Two major peaks in the biomass of Pacific mackerel have occurred over historical times, 1925-1935 when the stock exceeded 400 thousand mt and during the early 80's when the stock reached the same level (MacCall, et al., 1985). The paleo-sedimentary record of Pacific mackerel scales indicates the 1925-35 peak and another one around 1830. Thus, three major outbreaks of Pacific mackerel have occurred over the last 162 years. The 1925-35 and 1980s peaks coincided with warm water regimes. Minimum levels of abundance occurred in the late 60s reaching less than 10,000 mt by 1966, and remaining low until the late 70s. The 1976 year class that initiated the recovery of the fishery was in the upper 25% of all year classes, but it was produced by a spawning biomass of less than 10,000 tons. The stock has been declining slowly since the peak biomass in 1982; the estimated 1992 biomass was 124,000 mt.

Unlike sardine and anchovy, no dependable data exists on egg and larval mortality rates nor on larval and juvenile growth in the sea. Accurate estimates of larval mortality may never be practical because of the highly patchy distribution of the spawn. Preliminary work indicates that some mackerel females spawn daily (Dickerson, et al., 1992) but estimates of stock spawning rates would be difficult and costly due to the patchiness in the distribution of spawning and non-spawning fish. For these reasons either anchovy or sardine may be preferable to mackerel as a subject for cooperative research on effects of Climate Change on fish population dynamics.

2.1.4 Pacific Herring (*Clupea pallasi*) of the Northeastern Pacific Ocean

Distribution & Biology

In the Northeast Pacific herring are distributed along the west coast of North America from California to the Chuckchi Sea with some small stocks in estuarine arctic waters. The greatest abundance is from British Columbia to the Bering Sea. Stocks in California, Oregon, and Washington are small relative to the more northern stocks. Major aggregates of stocks are harvested in San Francisco

Bay, Northern Washington-Southeastern Alaska, Prince William Sound, Kodiak Island, Cook Inlet, and eastern Bering Sea in North America.

Pacific herring spawn exclusively in spring, in shallow inter- and subtidal waters. After a 2-3 week incubation, eggs hatch into pelagic larvae and disperse throughout local nearshore coastal waters. After a 1-2 month larval stage the young herring reside mainly in nearshore waters for a 1-2 year juvenile period. They mature sexually in 2-4 years (earlier in south) and spawn once per year for the remainder of their lives. Most herring live for 4-5 years with a few living to 15 years (Grosse & Hay, 1988).

Adults spend summers in a relatively large number of small, dispersed schools and feed mainly on copepods and euphausiids. Movement to summer feeding grounds for larger stocks may require extensive migrations of several hundred kilometers or more, to offshore banks, while migrations to feeding grounds of smaller stocks may be more geographically restricted. In the winter, adult herring form a small number of large aggregations in the same overwintering areas each year. In the spring herring move from these areas to spawning areas, that also are consistently occupied each year.

Stocks and fisheries

North American herring fisheries started as food fisheries in the early 1900s producing salt or dried herring. In the late 1920s industrial herring fisheries developed for oil and meal and catches rose rapidly in British Columbia to South-central Alaska where the largest fisheries occurred. Reduction fisheries persisted until the mid-1960s when the fishery closed due to economic competition from Peruvian anchovy and other cheaper meals, and the closure of some fishing areas to preserve herring for salmon forage. In British Columbia a moratorium on herring fishing was established, following a collapse of the herring stock in the mid-1960s (Fig. 2), and maintained until stocks recovered in the early 1970s (Hourston, 1980).

In the absence of fishing, the British Columbia stocks began to increase and in 1972 a roe fishery began which grew to a peak harvest of 80,000 t in 1976-78. In subsequent years the harvest was reduced to about 30-40,000 mt because of concern that high harvests could not be sustained.

Roe herring fisheries also developed in Alaska in the early 1970s, and harvests have been very conservative with exploitation at 10-20% of estimated biomass which has averaged less than 10,000 t annually. In the eastern Bering Sea a distant water fishery was established in the late 1950s by Russian and Japanese vessels. Catches rose rapidly to a peak in the early 1970s, and then declined, and the off-shore foreign fishery was replaced by an inshore roe herring fishery in the late 1970s.

Individual stocks of herring in the northeastern Pacific Ocean have exhibited wide variations in abundance. Sometimes, exceptionally large year classes, such as one in 1977, were synchronous over broad geographical ranges (from Vancouver Island to central Alaska). In other years there may be large differences in cohort strength between reinforcing stocks, such as the Queen Charlotte Island and the mainland of British Columbia. Year-class synchrony in the northeastern Pacific appears to correspond to hydrographic domains with distinctly different recruitment patterns between Alaskan and Canadian stocks (Zebdi and Collie, ms).

In the eastern Bering Sea only about a third of the variation in year class strength can be accounted for by variation in spawning stock size, indicating that environmental factors are important determinants of year-class size (Wespestad and Gunderson, 1991). Climatic effects of wind-driven transport and temperature describe a portion of the residual variation in recruitment, but about 50% of the total variation is left unaccounted. The remaining variation may relate to large-scale physical processes, or local variation in biological processes, for which accurate measures are unavailable.

In the middle part of their range, Washington to central Alaska (Prince William Sound) herring are the most abundant small coastal pelagic fish. They are consumed as principal or secondary prey by many piscivores such as the

Pacific cod (*Gadus macrocephalus*), the chinook and coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*), Pacific hake (*Merluccius productus*), as well as many sea birds and marine mammals (Hay et al., 1992). In this capacity they serve as a principal vehicle for energy transfer from lower to higher trophic levels. Predation has been shown to be a significant source of mortality and may contribute to variation in year-class size (Walters, et al., 1986; Ware 1991). Predation on herring is modified by environment in some cases. Ware and McFarlane (1989) found that in El Niño years hake extended their range into areas occupied by herring resulting in increased herring mortality.

2.2 Western Pacific

2.2.1 Japanese Sardine (*Sardinops melanostictus*)

A major part of this section is based on preliminary results of the BICOCOSMOS project, a ten year research project on Japanese sardine ecology and population dynamics, which began in 1989; results from this project will appear in journals in the near future.

Isozyme analysis for genetic divergence indicates that several stocks of Japanese sardine (*Sardinops melanostictus*) are a single population. The population fluctuated greatly over the last two decades; it began to increase in the mid-70's, reached a peak in the mid-80s, and has been declining since 1989. Total catch of the Japanese sardine was 20,000 mt in 1970. It increased to 2,210,000 mt in 1980 and reached a maximum of 4,490,000 mt in 1988. The catch declined after 1989, falling to about 2,000,000 mt by 1992.

On the Pacific side of Japan, sardine spawn along the Kuroshio Current in February and March. Eggs hatch two days after fertilization at 17-18°C and the larvae start feeding within two days after hatching. Egg and larvae are transported to the east by the Kuroshio Current as fast as 2-3 knots (1.0-1.5 m/sec) and in a few months when the larvae are 20-30 mm, they reach the Kuroshio Extension off the Boso Peninsula east of Honshu Island, Japan. Part of the cohort leaves the Kuroshio Current and enters the coastal waters along the Pacific side of Honshu Island forming shirasu fishing ground for sardine larvae.

While being transported by the Kuroshio Extension, the larvae metamorphose into the juvenile stage and in early summer they start a northward migration through the mixing water between the Kuroshio and the Oyashio fronts. They use warm streams and warm core rings derived from the Kuroshio Extension as migratory paths. They cross the Oyashio front and feed on abundant zooplankton and phytoplankton in the Oyashio water in summer. In autumn they migrate south to the waters off Boso Peninsula. The one year old sardines return to Oyashio waters the following summer.

The sardine mature in 2 or 3 years. Short day length and a decrease in water temperature in autumn induces sexual maturation and southward migration to the spawning grounds. Nutritional conditions of females at the beginning of sexual maturation have a major effect on the reproductive effort during the subsequent spawning season (Tsuruta, 1985). Batch fecundity varies from 20,000-40,000 eggs depending on nutritional condition (fat reserves) of females, but the number of batches spawned by females per season is not known). Eggs from fat females are of good quality having a larger yolk volume and higher content of poly-unsaturated fatty acids than those from thin females (Morimoto, 1991).

Since 1990 the percentage of the number of landed sardines older than 4 years has increased rapidly (Fig. 3). The percentage was about 30% or less in the years before 1989, but in 1991 and 1992 it increased to more than 90%.

The number of 1 year old sardine caught in waters east of Hokkaido Island is used as a recruitment index in Japan. From 1986 to 1988 the number of recruits ranged from 2,000-5,500 million fish, but decreased to 0-600 million in 1989-1992. Thus, the population has decreased since 1988 because of recruitment failure. Average egg production in the Pacific side of Japan in 1989-1992 was 4,600 trillion. The recruitment failure was assumed to be due to low survival rates in the stages between the egg to juvenile stage.

When the population was in the early phases of growth in the mid 1970's, the recruitment index (mentioned above) was stable as it ranged between, 1,500-2,000 million fish. When the population was in the older growth phase, reaching a peak biomass 1979-1987, the recruitment index was much more variable ranging between 32 million to 5.9 billion fish with a dominant year class occurring every three or four years. The recruitment failed in four successive years after 1988. In summary, three patterns in recruitment were evident during the rise and current fall of the population. Stable recruitment associated with a growing population, fluctuating recruitment associated with sustained high biomass, and recruitment failure associated with population decline. The population growth and decline of the sardine over the last two decades is considered to be caused by a variation of recruitment which might be due to changes in the mortality of early life stages.

2.2.2 Japanese Anchovy (*Engraulis japon-icus*)

The Japanese anchovy population is divided into four stocks which occur in the following four localities: northern Pacific, southern Pacific including Seto Inland Sea, East China Sea, and Japan Sea. Annual landings were high (350-450,000 mt) in 1950s and 1960s when the Japanese sardine (*Sardinops melanostictus*) population was very low, but landings decreased rapidly after 1975, as the sardine population increased. In the 1980s, the landings remained at a low level (150-200,000 mt). The landings have recovered since 1989 as the sardine began to decline. However, the maximum anchovy catch is only a tenth of that of the sardine, and the stock fluctuations are relatively moderate (see Table 2).

The north Pacific stock of anchovy is the largest and most studied. The spawning habits and demography of the stock change with population size, (Funakoshi, 1987). When the stock is small, almost all spawn at one year old in coastal waters and bays during summer and autumn and die after spawning. Their migration range is restricted to the spawning ground areas. On the other hand, when the stock is large they mature at one year old and spawn in coastal and offshore waters in spring. A large proportion survive after spawning and spawn again in next spring. Their migration range extends to the waters off southern Hokkaido.

Watanabe (1992) mentioned that the stock-recruitment relationship based on the total number of eggs spawned seemed to fluctuate clockwise around a certain equilibrium stock level. Funakoshi (1990) concluded that anchovy in plankton rich coastal waters have a higher fecundity, and spawned more frequently, than those spawning in offshore areas where food was less abundant. Laboratory experiments indicate that when food is reduced, anchovy spawn less frequently and the interval between spawning increases. The number of eggs spawned per female was reduced at high fish density even when food was held constant indicating density dependent affects on egg production (Tsuruta and Hirose, 1989).

A common belief is that anchovy populations vary inversely with sardine populations, but the long-term landing data of pelagic fishes in Japan seem to indicate a more complex pattern of interactions among pelagic species. These data indicate the following sequence: chub and spotted mackerels (*Scomber japonicus* and *Scomber tapaeinocephalus*, group A) was replaced by the sardine (species B); the sardine was replaced by a group of four species (group C), the anchovy (*Engraulis japonicus*), Pacific saury (*Cololabis saira*), and jack mackerels (*Trachurus japonica* and *Decapterus muroadsi*); and the four species in group C were replaced by the mackerel (Fig. 3). Matsuda, et al. (1991, 1992) proposed an inter-specific competition model for groups A, B, and C as a hypothesis for the species replacement. If species A causes a decline in the population of B, B causes a decline in C; and C causes a decline in A, the model predicts that the abundance of these three groups fluctuate forever and dominate in cyclic order. The kinds of interactions occurring among these three groups are not well understood, however. Improved understanding of their interactions seems to be an essential prerequisite for understanding the dynamics of these populations.

2.2.3 Japanese Common Mackerel (*Scomber japonicus*)

Two mackerel species are fished commercially around Japan, the common mackerel and the spotted mackerel (*Scomber japonicus* and *Scomber tapaeinocephalus*). The Japanese common mackerel is a widely distributed migratory fish, while the spotted mackerel has a much smaller range occurring principally in the southern part of Japan. The range for the common mackerel is even wider than that of the Japanese sardine. The northern limits to their distribution is about the same, but unlike the sardine, the common mackerel occurs in the East China Sea (recent catch is 110,000-250,000 mt).

The range of surface temperature for fishing common mackerel falls between 14-18°C. When the stock is large, common mackerel make large scale north-south migrations. The migration to the north is a feeding migration, while the southern migration is a wintering and spawning migration, similar to the sardine. The common mackerel population around Japan consists of four local stocks: Pacific; South Pacific; East China Sea; and Tushima Current (Japan Sea).

In recent years, the landings of the Pacific stock are 60-70% of the total Japanese landings. The catch from the Pacific stock increased remarkably in the 1970's reaching a peak of 1,300,000 mt in 1978; recent catches fluctuate between 200,000-300,000 mt.

2.2.4 Pacific Saury (*Cololabis saira*)

Pacific saury occurs throughout most of the northern Pacific. In the Western Pacific, saury is one of the major commercial species taken by Japanese, Russian, and Korean fisheries. No estimation of the population size exists because the distribution of the larvae, juveniles and adults is continuous from the Western to the Eastern Pacific.

After World War II, a new fishing gear, the stitch-held dipnet (bouke-ami), was introduced in Japan. Total catch increased remarkably after the introduction and reached a peak during 1955-63 with a maximum catch of 575,000 mt in 1958. Catch decreased in late 60s down to 52,000 mt in 1969. Annual fluctuation of the catch was quite large in 70s ranging between 87,000 to 427,000 mt. In the 80's, the catch stabilized because of landing regulations adopted by the saury fishermen association. Abundances of larvae, juveniles, and adults indicate that the population in the Western Pacific has been increasing since 1988.

Saury spawns off the northern Honshu Islands in autumn and spring, and in the Kuroshio area in winter. Juveniles from different spawning seasons start migrating north in early summer to the Oyashio area where they feed on abundant zooplankton, especially *Neocalanus plumchrus* and euphausiids. Otolith analyses (Watanabe, 1988), rearing experiments (Hotta, 1958, Watanabe and Kuji, 1991), and increase in body length of northward migrating groups (Fukushima, et al., 1990), all indicate that the Western Pacific saury reaches a length of 30 cm in one year. Three length modes occur in fish caught in fishing season from late August to early December. The large fish are assumed to originate from eggs spawned in the autumn, the medium sized fish from winter eggs and small fish from spring spawnings (Fukushima, et al., 1990). The three groups are not thought to be from different stocks because the genetic distances of size groups are too close to be regarded as separate stocks.

Size composition of landed sauries differs annually, and differences in size composition affect price and the total weight of the catch. The length composition of the catch is believed to be related to relative recruitment of autumn, winter and spring spawning cohorts. Pre-season forecasts of size composition of the catch is of great value to fishermen and fish processors. The Tohoku National Fisheries Research Institute provides forecasts of recruitment based on three parameters: larval production at hatching, growth and mortality rates in larval and juvenile stages. Using these parameters, they estimate daily production of 50 mm juvenile for autumn, winter and spring spawnings. Rearing studies indicate that by the time saury juveniles reach 50 mm and begin schooling, they have passed through the high mortality period.

2.2.5 Yellow Sea Herring (*Clupea pallasi*)

The Pacific herring in the Yellow Sea, which is traditionally called Yellow Sea Herring, has a long history of exploitation. The importance of herring is demonstrated by the existence of villages and localities named for their association with it. In this century, the commercial fishery has experienced two peaks (in about 1900 and 1938) followed by a period of little or no catch. In 1967, due to the recovery of the stock, a large number of 1-year old herring began appearing in bottom trawl catches. The catch increased rapidly to a peak of 200,000 mt in 1972. The high catches were due to the very strong 1970 year class and reached a historic maximum abundance estimate of 26.8×10^8 fish (at age 1). Since 1982, the stock has declined apparently due to the occurrence of a series of weak year classes. The catch has declined to below 1,000 mt in 1989-1990.

Obviously, Yellow Sea herring have been characterized by strong fluctuations in abundance. Tang (1981 and 1987) found that there is no strong relationship between spawning stock and recruitment and that environmental conditions such as rainfall, wind, and daylight are the primary causes of fluctuations in recruitment. Long-term changes in biomass may be correlated with the 36 year cycle of dryness/wetness oscillation in eastern China.

3.0 SCIENTIFIC QUESTIONS AND HYPOTHESES

The Working Group discussed the scientific questions and hypotheses required for an understanding the causes of variability of pelagic fish populations. Four key questions and their associated hypotheses are discussed briefly below.

3.1 What differences exist among Pan-Pacific pelagic stocks in biomass and stage specific vital rates? Implicit in this question, is the hypothesis that stage specific vital rates determine the variability of fish populations and density dependent processes play a subsidiary role. Pan-Pacific comparisons of vital rates might help answer the questions: 1) why does the western Pacific boundary system support a higher biomass of small pelagic fishes than does the eastern Pacific boundary system? and 2, Why do pelagic fishes show different fluctuation patterns in the same region? The group concluded that detailed descriptions and comparisons of fish biomass and stage specific vital rates, such as growth, mortality and fecundity are the first step in understanding the mechanisms underlying population fluctuations of small pelagic fishes.

3.2 How does physical forcing affect population processes? Implicit in this question is the hypothesis that variability in population size is determined largely by density-independent factors such as changes in regional oceanographic conditions. A further extension of this hypothesis is that a Pan-Pacific ocean climate influence on fish population dynamics exists and that regional comparisons are necessary to identify the details and modes of actions. Regional comparisons of similar species could lead to identification of the similarities in oceanographic conditions that correspond to population growth or failure, regardless of the validity of the Pan-Pacific hypotheses.

3.3 How do biomass specific changes in life history traits, such as expansion and retraction of spawning habitats or latitudinal extent of feeding migrations, affect population variability? Implicit in this question is the hypothesis that density-dependent processes play a major role in population growth. In coastal pelagic fishes important population traits seem to vary with population size, including: growth; age or size at maturity; spawning habitat selection; and the tendency to migrate. At high biomass levels, populations may have large migrations, slow growth, and older age at maturity with the opposite pattern at low biomass levels. A more specific hypothesis underlying this question is that density-dependent habitat selection affects reproductive success and population growth through the physical properties of the habitats selected.

3.4 How do the interactions between populations of small pelagic fishes affect their populations? No doubt exists that coastal populations of sardine, anchovy, and mackerel interact. As they all are pelagic planktivorus, their diets broadly overlap and they may consume each others egg or larval stages. In addition, large mackerel may prey upon adult anchovy and sardine as well as their early life stages. Thus, population interactions should affect the productivity and growth of pelagic fishes in the coastal ecosystem. The tacit assumption underlying this question is that species interactions play a role in population variability and shifts in dominance among pelagic fish.

4.0 CRITICAL GAPS IN INFORMATION AND KNOWLEDGE

A major challenge for marine science in the twenty-first century will be to forecast how long-term changes in ocean climate will affect our natural marine resources. The obvious first step is to explain past fluctuations in the abundance of stocks. Unfortunately, we lack the information, and the basic level of understanding necessary for a documented and coherent ecological explanation for the history of population growth and decline of North Pacific pelagic fishes. We do not know how physical forcing increased the survival of eggs or larvae to produce the great year classes of the past, nor do we understand the role played by population size and pelagic species interactions in the formation of those year classes. No shortage of plausible mechanisms exists and some have been validated by direct field measurement, but we lack the information needed to test these mechanisms analytically, and we lack the understanding necessary for a synthesis of physical forcing and density dependent mechanisms that would explain stock histories as we have observed them. We believe that the comparative studies we propose will help fill these gaps in understanding.

Initial requirements for a north Pan-Pacific investigation of climate effects on the dynamics of fish stocks are that estimates of abundance, recruitment, and vital population rates are available and that a strong Pan-Pacific communication network exists. Neither of these initial requirements are presently met. We lack data on some of the vital rates of even the best studied stocks, existing data on rates and population statistics are not generally available on a Pan-Pacific basis, and no adequate communication system exists for the development of Pan-Pacific comparative studies.

5.0 POSSIBLE SCIENTIFIC APPROACHES

The group identified various ways critical gaps in data understanding and communication might be filled and key scientific questions might be resolved. All approaches considered by the group are included.

5.1 Assembly of Data

The group placed a high priority on the assembly of time series of available data on annual biomass and recruitment levels, and on stage-specific vital rates for the key pelagic stocks. Such information may include: annual biomass, recruitment and catch; sex, first maturity and fecundity by length or age; spawning habitat characteristics such as temperature and season; egg incubation rates and mortality; and larval and juvenile mortality and growth.

This initial assembly of biological data should be followed by an assembly of time series of relevant oceanographic data for the areas occupied by the stocks. Relevant oceanographic indices could be selected for each area from results of detailed process studies, or by using forcing functions proposed in the literature. Biological data on zooplankton abundance, and the food habits of coastal pelagic fishes would also be desirable.

If fishery data, or data on specific vital rates, are missing for key populations, these data gaps could be filled by a directed program to collect and process such data.

5.2 Expansion of Scientific Knowledge

5.2.1 Pan-Pacific Comparisons of Recruitment

Exploratory comparative time series analyses of the biomass and recruitment for key coastal pelagic stocks need to be conducted to determine common patterns in stock fluctuations (using approaches similar to Hollowed et al., 1987). These analyses would be most fruitful if they focused on East-West (e.g. California sardine and Japanese sardine) and North-South (e.g. herring) comparisons. The next step may be to couple oceanographic data and models to the fishery analyses, to evaluate hypotheses concerning physical forcing of coastal pelagic stock fluctuations. For example, do similar oceanographic conditions and processes produce similar responses among different coastal pelagic fishes? Fish stock distributions and vital rates could be examined relative to latitude and longitude, seasonal temperature, and current patterns. Analyses of other aspects of the system (e.g. primary or secondary productivity) may also provide information for estimating upper or lower limits of fish production.

Inclusion of all possible spawning groups in Pan-Pacific comparisons, would greatly increase the richness of the comparison. Herring, sardine, and anchovy form a mosaic of habitat specific spawning groups, each with unique population dynamics and life table characteristics. Pacific herring are particularly prolific in this regard, with spawning groups associated with specific small intertidal areas, while spawning groups of sardine and anchovy are larger and more regional in character. Comparisons between these groups are useful because they reflect regional habitat differences, even though modern genetic studies often fail to find differences between them. For example, although genetic studies indicate that the sardine population around Japan belongs to one stock, a group of sardines spawn west of Kyushu Island and migrate into the Sea of Japan where oceanographic conditions are considerably different from the Pacific side. One would expect spawning and recruitment and vital rates to differ between the Japanese Sea and Pacific spawning groups.

Recruitment comparisons should not only consider single years of great recruitment success or failure, but should also consider successions of stronger than average year classes, or periods when year classes consistently failed. It is important to consider in such an analysis not only the environmental conditions that correlate with these periods, but also the affect of such successions of strong or weak year classes on population growth and stability. A number of strong year classes may stabilize the population while a small number of weak year classes may make the population more susceptible to environmental variability.

5.2.2 Life Table Analysis

Life stage matrix models, such as the Lefkovitch model (Lefkovitch, 1965; Caswell, 1989), provide a useful way to begin comparative work. First, they require an inventory of life table data and thereby identify critical gaps in knowledge. Second, they help assess the quality of the information by tests of population stability. Third, they permit assessment of the sensitivity of the population to changes in rates within each life stage. Lastly, they provide a simple standardized way to evaluate effects of physical forcing on population growth. For these reasons, completing a Lefkovitch matrix for each species to be compared would be a useful first step in the development of a PICES comparative study.

An important and recent refinement of life stage matrix models for fishes is to include variance as well as mean duration of stage and mortality (Lo, et al.; ms.). This approach adds new information, and the costs are low because the durations of early life history stages can be obtained from daily growth increment analysis of juveniles (Butler, 1989 and 1991). When variances are included the modeled population is generally less sensitive to changes in vital rates than when only the mean is used, and the results are probably more realistic.

5.2.3 Trophic Ecology

To examine the overall functioning of Pan-Pacific ecosystems an inter-regional comparison of the gross production and biomass at several trophic levels (primary and secondary levels, and small pelagic fishes) would be useful. This would provide a preliminary idea of the overall functioning of Pan-Pacific ecosystems and might help explain the differences in fish production between systems. A more thorough treatment of trophic relations using trophodynamics modeling is also strongly recommended. Trophodynamics modeling is defined as modeling of the food web linkages that support the production of key pelagic fish species. By trophodynamics modeling, the response of marine production systems to environmental changes can be analyzed, based on the flows and balance of biomass among the trophic levels. This technique will be useful for understanding the biological processes which control population fluctuations and species interactions. Model construction can also reveal the lack of knowledge on relationships among biological components and physical forcing functions. Once the model can generate the average annual cycle of fish production, various hypotheses on the relationships between environmental change and population fluctuations can be examined. This approach becomes more powerful when such models are constructed for several different regions with ecologically similar species.

5.2.4 Comparative Field and Laboratory Studies

The focus of most of the Working Group's discussions were on the analysis of existing data because such work is an appropriate starting point. The Group recognized in the long term, Pan-Pacific field and laboratory work using standardized methods and approaches would have great benefits. One approach might be to focus the field work on accurate interannual measurements of age specific fecundity and life stage specific growth or stage duration and their links to physical forcing. These fish population parameters are among the least expensive to measure, yet they might reveal substantial differences between populations and ecosystems. In contrast, mortality is an expensive parameter to measure directly by sampling larvae and juveniles requiring many more samples and days at sea. In addition, using modern otolith reading systems one can digitize long chronologies of daily growth records from a single otolith. When such data from a number of juveniles are combined, estimates of mean growth and variance for many life stages can be provided.

It also may be useful to collect larvae from stocks with different growth rates and rear them under identical conditions to determine if such growth rates are genetically or environmentally determined.

5.3 Sharing Knowledge and Technology

PICES has the opportunity for leadership in the Pan-Pacific exchange of knowledge among marine researchers. Presentations at PICES Annual meetings and workshops are important ways that PICES has opened the avenue of communication by providing a forum for exchange of ideas. In addition to these approaches, the working group considered several other ways to improve Pan-Pacific communication.

All members believed that informal scientific communication and possible collaboration would increase if a directory of key Pan-Pacific researchers were available. The Working Group proposed to compile a list of key researchers who study coastal pelagic fishes of the North Pacific within their respective geographic regions. The directory, would include not only agency or institution, address and FAX, but would include pertinent information such as species of interest, key-words describing broad topics of interest and areas of present research. This final compilation of researchers in all member countries should be made available in a paper copy and also maintained on a computer data base which should be updated annually.

Another way PICES could foster communication and build collaborative efforts is through Pan-Pacific exchange of the researchers. The Group believes that of all the activities sponsored by PICES, few could have as great and immediate benefit as a PICES visiting scientist program. The Group recommended that the Secretariat develop a PICES visiting scientist exchange program. Such a program might provide 2-4 visiting fellowships per year to the PICES community with a duration of a month or more. Selection of applicants would be competitive based on a short letter of intent, CV, and references. Applicants would include agency as well as academic scientists and funding would cover only travel and subsistence costs. If PICES does not have sufficient funds to support the program, some working Group members would be willing to work with the Secretariat to find outside funding. It would be preferable if the Secretariat managed the funds to minimize indirect costs.

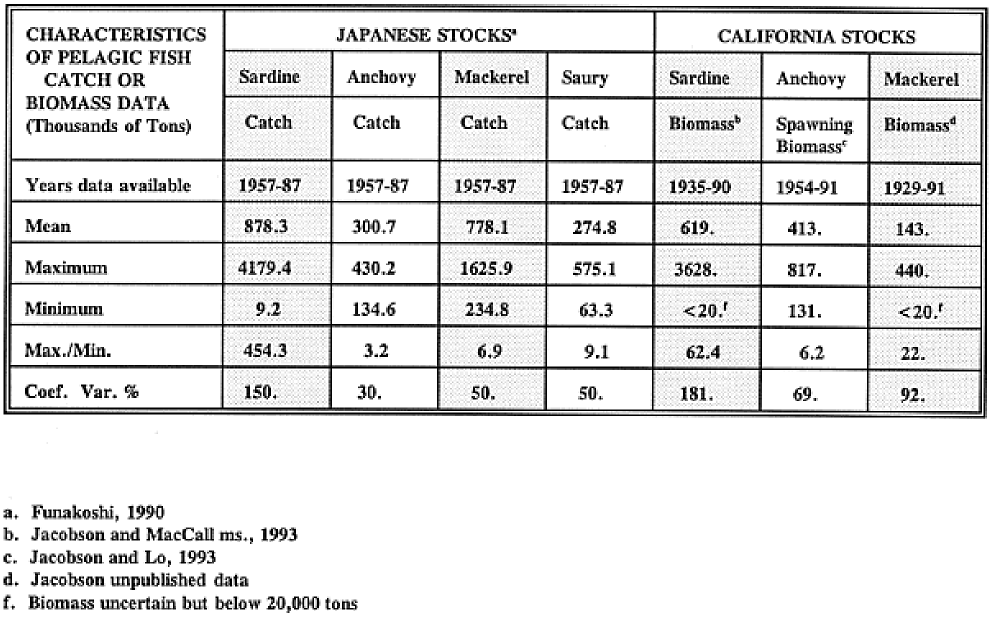
6.0 TABLES AND FIGURES

Table 1. Catch statistics of small pelagic fishes in 1990.

SPECIES		CATCH IN THOUSAND TONS	
Common	**Scientific**	**World**	**North Pacific**
Atlantic herring	Clupea harengus	1,538	***
Pacific herring	Clupea pallasi	199	199
Japanese sardine	Sardinops melanostictus	4,735	4,735
South American pilchard	Sardinops sagax	4,254	***
European pilchard	Sardina pilchardus	1,540	***
California sardine	Sardinops sagax	399	399
Anchoveta	Engraulis ringens	3,772	***
European anchovy	Engraulis encrasicolus	539	***
Japanese anchovy	Engraulis japonicus	442	442
South African anchovy	Engraulis capensis	201	***
Northern anchovy	Engraulis mordax	6	6
Japanese common mackerel	Scomber japonicus	1,391	751
Atlantic mackerel	Scomber scombrus	657	***
Chilean jack mackerel	Trachurus murphyi	3,828	***
Atlantic horse mackerel	Trachurus trachurus	420	***
Cape horse mackerel	Trachurus capensis	346	***
Japanese jack mackerel	Trachurus japonicus	250	250
Pacific saury	Cololabis saira	416	416
Small Pelagics Total		**24,933**	**7,198**
Marine Fishes Total		**70,666**	***

Source: FAO Yearbook of Fishery Statistics

Table 2. Comparison of the catch or biomass variability of small pelagic fishes from Japan and California.



CHARACTERISTICS OF PELAGIC FISH CATCH OR BIOMASS DATA (Thousands of Tons)	JAPANESE STOCKS[a]				CALIFORNIA STOCKS		
	Sardine	Anchovy	Mackerel	Saury	Sardine	Anchovy	Mackerel
	Catch	Catch	Catch	Catch	Biomass[b]	Spawning Biomass[c]	Biomass[d]
Years data available	1957-87	1957-87	1957-87	1957-87	1935-90	1954-91	1929-91
Mean	878.3	300.7	778.1	274.8	619.	413.	143.
Maximum	4179.4	430.2	1625.9	575.1	3628.	817.	440.
Minimum	9.2	134.6	234.8	63.3	<20.[f]	131.	<20.[f]
Max./Min.	454.3	3.2	6.9	9.1	62.4	6.2	22.
Coef. Var. %	150.	30.	50.	50.	181.	69.	92.

a. Funakoshi, 1990
b. Jacobson and MacCall ms., 1993
c. Jacobson and Lo, 1993
d. Jacobson unpublished data
f. Biomass uncertain but below 20,000 tons

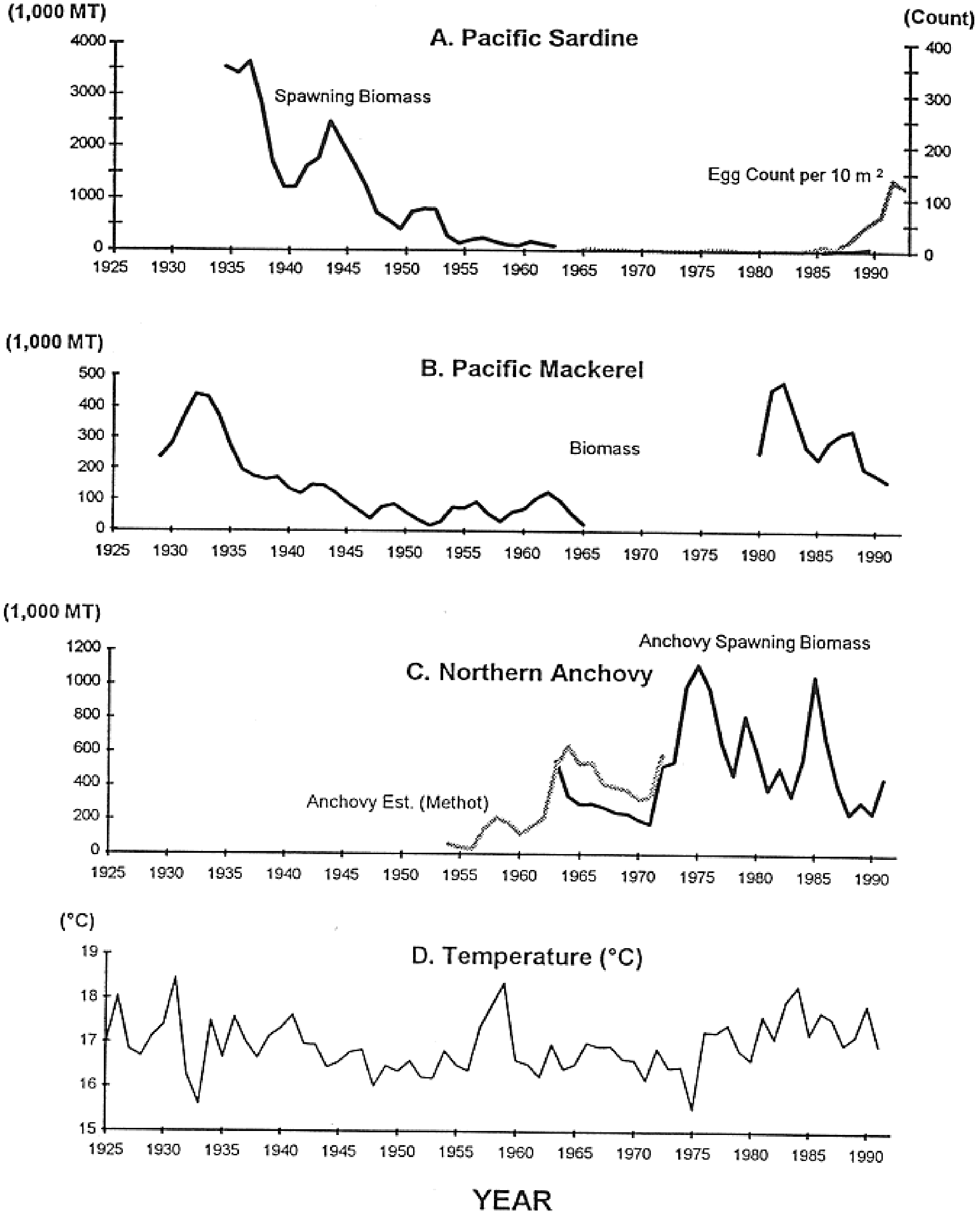


Fig. 1. Time series of estimates of the biomass of California coastal pelagic fishes and the average water temperature taken at Scripps Pier (La Jolla, California).

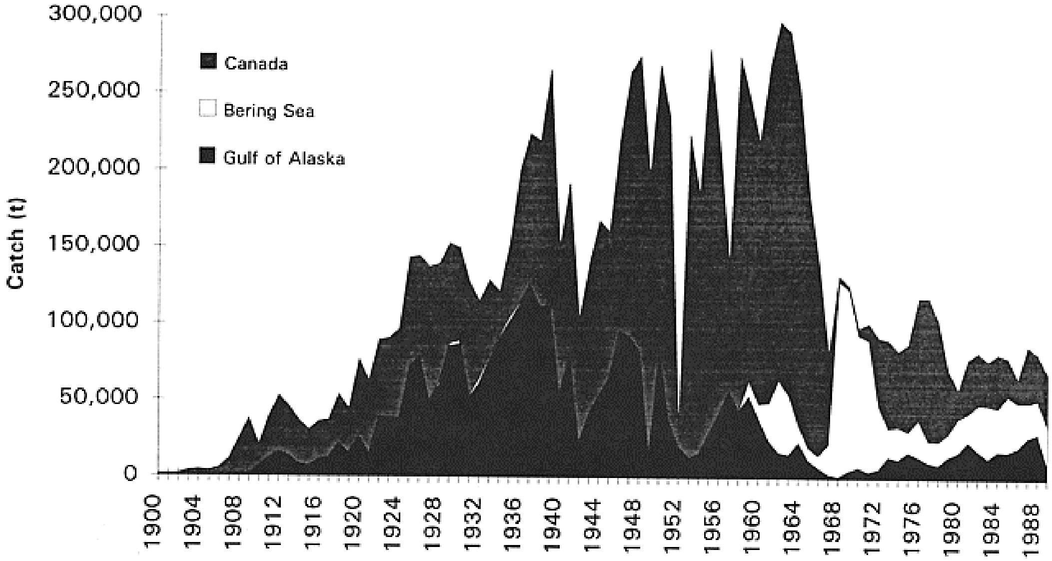


Fig. 2. Catch of herring off Canada, Gulf of Alaska, and in the eastern Bering Sea, 1900-1990.

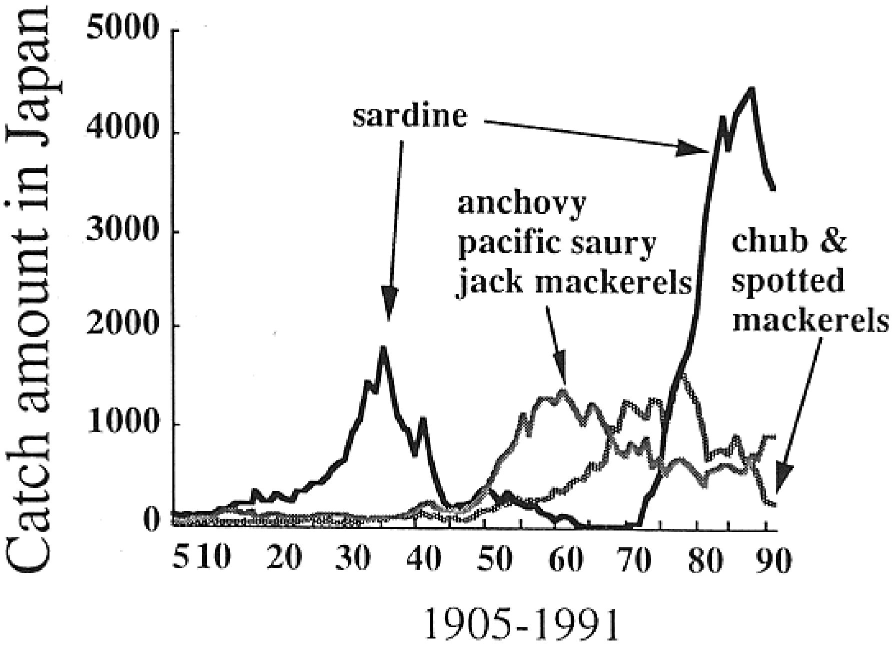


Fig. 3. The long-term fluctuation of annual catch of several species of pelagic fishes combining three groups: Japanese sardine; Japanese anchovy, Pacific saury, and jack mackerels; chub and spotted mackerels in 1905 to 1991 (after Matsuda et al., 1992).

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8.0 Appendices

Appendix 1

Recommendations and Actions

Science

- Assemble information on Western and Eastern Pacific Coastal pelagic fish populations. Fishery information shall include: stock size, catch, and recruitment estimates per year. Also, life table data containing life stage specific rates of growth, mortality and reproduction shall be required. PICES Working Group 3 agrees to produce a document containing these data for key coastal pelagic species of the Eastern and Western Pacific. The document shall be completed in time for PICES Working Group meeting in 1994.

- Encourage the inclusion of Russian and Korean fish population information data on herring and other northern coastal pelagic species in the data exchange described in item 1.

- Encourage development of relevant oceanographic time series to facilitate the interpretation of Pan-Pacific patterns in recruitment success.

- Apply trophodynamics models in Eastern and Western Pacific ecosystems to understand how the production systems of each region support pelagic fish biomass. This work may require inclusion of pollock and hake.

- In the annual 1994 PICES meeting Working Group 3 shall review the fish population document described in item 1 and establish plans to carry out Pan-Pacific comparisons of life table differences and recruitment.

Communication

- Members of Working Group 3 shall make an inventory of scientists working on key coastal pelagic fishes within their respective geographic area. Working Group 3 will compile a list of key persons, addresses and topics of study and make it available to all interested researchers.

- The PICES COASTAL PELAGIC FISH WORKING GROUP requests PICES Fishery Committee to seek support of the PICES Secretariat in obtaining funds for a visiting scientists program. The working group feels that working visits of PICES scientists to other PICES countries is essential. Recognizing that PICES may not have funds to directly support such an action, the working group stands ready to assist the Secretariat in preparation of proposals to foundations and agencies to support the visiting PICES scientist program.

Administration

- The proposed inventory of fishery time series data and life table information along with the PICES Nemuro Workshop Reports will constitute important working documents for PICES. Such documents need to be organized and archived in some consistent way. For that reason, we recommend to the Fishery Committee of PICES that the Secretariat establish an informal administrative report series. The minimum requirements for such a series are: each working document is assigned a unique administrative report number; a standard cover design is used on each copy of the report; a standard citation for the reports be established; report date; report number, and names of editors are clearly indicated. To reduce PICES costs, actual production of the report could be assigned to chairpersons, with a certain number of copies to the Secretariat. Of course, a more formal system could be adopted as well.

* Working Group 3 recommends continuation of the Working Group under the existing terms of reference but also recommends a name change to PICES COASTAL PELAGIC FISHES WORKING GROUP.

Appendix 2

Terms of Reference

Working Group 3
Dynamics of Small Pelagics in Coastal Ecosystems (FIS)

- develop a program for a comparative study of the population dynamics and productivity of small pelagics (focusing on herring, sardine, anchovy and mackerel) in the coastal ecosystems along the western and eastern continental margins of the North Pacific;

- review the present state of knowledge, identify the key scientific questions and hypotheses that could be tested, including environmental effects on fish production and ecosystem structure;

- identify who is working in this field, and what data are available for retrospective analyses;

- determine which member countries would be willing to participate in a coastal ecosystems program.

Appendix 3

List of participants

Working Group 3 members:

Canada
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Dr. R. Ian Perry

China
Prof. Qi-Sheng Tang

Japan
Dr. Ichiro Hara
Dr. Yasunori Sakurai
Dr. Tokio Wada (Co-Chairman)
Dr. Yoshiro Watanabe

U.S.A
Dr. John R. Hunter (Co-Chairman)
Prof. Brenda L. Norcross
Dr. Richard H. Parrish
Dr. Vidar G. Wespestad

Non-member:
Dr. Hideo Yoshida (Japan)

Part 2

SUBARCTIC GYRE

FORWORD

This is the first Annual Report of the Subarctic Gyre Working Group (WG-6). The initial Terms of Reference (Appendix 2) were finalized by the PICES Science Board in January 1993. The Co-Chairmen were named by Council in February 1993, and each nation subsequently designated additional members during March-April, 1993. No restrictions were placed on the number of members from each nation, and all countries were encouraged to include members from academic, industry and government sectors.

In 1993 the Co-Chairmen developed a short list of specific topics to be reviewed, based on the general Terms of Reference. The Co-Chairman asked members to write reviews on specific topics, and to propose a list of "Key Scientific Questions" on the Subarctic Gyre for consideration by all members. During 19-23 September 1993 the Nemuro Workshop on Western Subarctic Circulation was held in Nemuro, Japan. Japan also offered to host a concurrent workshop for PICES Working Groups. WG-6 accepted this invitation, and the first draft of this Annual Report was assembled and discussed by participants (Appendix 3) at the Workshop. WG-6 was required to submit this final Annual Report to the PICES Secretariat for review by the Science Board at the Second Annual Meeting. The Co-Chairmen commend all members for their efforts in 1993, and appreciate their patience and cooperation during this "start-up" year of the Subarctic Gyre Working Group.

On behalf of all members, we gratefully acknowledge the assistance of our many colleagues who generously contributed their time, energy, and ideas to WG-6 activities in 1993. We also appreciate the funding and logistic support provided to participants by Japan, the Organizing Committee for the Nemuro Workshop, and the citizens of Nemuro City. We thank the PICES Secretariat for assistance with WG-6 business, publication of this 1993 Annual Report, and for facilitating PICES communications. We thank David Welch for serving as Rapporteur, and A. Kasai and K. Tadokoro for technical assistance during the Nemuro Workshop.

Takashige Sugimoto and Brent Hargreaves
Co-Chairmen

1.0 INTRODUCTION

The physical oceanography of the Northern North Pacific Ocean is characterized by a large-scale cyclonic (anti-clockwise) circulation known as the Subarctic Gyre. This gross circulation pattern can be further resolved into at least four semi-closed sub-gyres: Alaskan Gyre, Bering Sea Gyre, Western Subarctic Gyre, and Okhotsk Sea Gyre (Fig. 1). In the eastern Pacific the Subarctic Water Mass includes both the Central Subarctic Domain and the Transitional Domain (Dodimead et al. 1963). The Alaskan Gyre is a portion of the Central Subarctic Domain. The currents associated with the Subarctic Gyre are generally weak, with speeds of 5-15 $cm \cdot s^{-1}$. However, the current is both baroclinic and barotropic with a volume transport of up to be $30 \cdot 10^6 \cdot m^3 \cdot s^{-1}$. Generally the southern boundary of the Subarctic region is defined in physical oceanographic terms by the position of the isohaline of 34.0 psu in the upper mixed layer, which typically runs east-west along about 40^oN.

The biological boundaries of the Subarctic Gyre are less precise and therefore more difficult to define. Many of the dominant fishes in the Subarctic Gyre are large nektonic species which undertake seasonal migrations over vast areas of the North Pacific Ocean. Some species such as salmon, salmon shark and some squids are typically found within or north of the Transitional Domain all year. These are generally regarded as Subarctic species, although seasonal migrations do occur into Subarctic waters. Several species (jack and Pacific mackerel, Pacific hake, Pacific sardine, pomfret, saury, blue shark, etc.) reside primarily in subtropical waters or the Transitional Domain during the winter, but migrate northwards to feed each summer in Subarctic waters. The extensive north-south migrations of migrant fish species also provide the opportunity for important interactions with other species not generally considered to be Subarctic species. For example, flying squid and albacore typically do not reside for significant periods in Subarctic waters, but comprise an important component of the ecology of the Transitional Domain. These species also frequently overlap in distribution with migrant Subarctic species during the winter.

The transitional zone is not only the region where both Subarctic and subtropical species occur, but it is also inhabited by a considerable number of endemic species of zooplankton and micronekton which have been zoogeographically recognized as "transitional species". This region is also a key part of the north-south migration route of nekton of commercial importance between the subtropical and Subarctic zones. These facts support the inclusion of the transitional zone within the PICES study area.

WG-6 activities therefore will focus mainly on the Subarctic region of the North Pacific, with the boundaries identified by physical oceanographic parameters (i.e. southern boundary identified by position of the isohaline of 34.0 psu in the upper mixed layer) and the transitional area between the Subarctic and subtropical areas. However, to fully understand processes in the Subarctic Gyre the boundaries of WG-6 investigations will be extended where necessary to include all areas and species of the North Pacific and marginal seas which currently are known to, or potentially could, significantly affect the physics, chemistry, or biology of the Subarctic Gyre.

1.1 Main Scientific Questions

In 1993 the WG-6 Co-Chairmen requested members to prepare written reviews on several specific topics, based on the Terms of Reference (see Appendix 2) provided by the PICES Science Board. The Co-Chairman also asked each member to propose a list of key scientific questions for the Subarctic Gyre for consideration by all members. These lists of Key Questions were discussed by participants at the "Nemuro Workshop on Western Subarctic Circulation '93" held during 18-23 September 1993 in Nemuro, Japan. Additional "Key Questions" were developed by members and colleagues who attended these meetings (see key questions in section 2.0).

As a result of discussions at the Nemuro meetings, three main questions were agreed:

1. **How do the various scales of physical variability affect biological processes and productivity of the Subarctic North Pacific Ocean ecosystem?**

2. **What is the structure of the food web in Subarctic waters and what controls its spatial, seasonal, and interannual variability?**

3. **What physical and biological oceanographic processes affect the production of salmon and other nekton in the Subarctic North Pacific Ocean?**

Based on discussion of these questions recommendation and action items were formulated (Appendix 1).

2.0 KEY SCIENTIFIC QUESTIONS FOR THE SUBARCTIC GYRE

In 1993 the Co-chairmen requested each member to prepare a list of key scientific questions for the Subarctic Gyre. These lists of Key Questions were discussed, modified, and additional "Key Questions" were developed by members and colleagues who attended the meetings at the "Nemuro Workshop on Western Subarctic Circulation '93" held during 18-23 September 1993 in Nemuro, Japan. These Key Questions are the foundation of the science activities and collaborative programs currently proposed by the Working Group. These Key Questions also represent an important resource for future planning and prioritizing of activities. Therefore the complete lists of Key Questions contributed by each participant in 1993 are included below:

T. Sugimoto:

1. What does the ENSO and decadal scale variation in the westerly wind system induce on the Subarctic ecosystem in each sub-gyre?

2. What physical parameters control vertical flux of nutrients, primary/secondary production, and population variations of pelagic fish?

3. What are the effects of the western boundary warm core ring region on biological production and fish migration?

J.D. Schumacher and T. Royer:

1. What is the interannual variability of the physical structure of the Subarctic Gyre with emphasis on the distribution of temperature and nutrients?

2. How do the continental shelves receive the required nutrients to support the growth of phytoplankton? Do the nutrients come from the vast quantities of fresh water entering the system? Do they come from upstream sources as might be found along the coastal regions of British Columbia and Washington? Are they brought into the photic zone from the deep ocean, where we know that their concentrations are quite high?

3. What mechanisms cause interannual variability in the Alaskan Stream which then alter the exchange of water into the Bering Sea? Are these mechanisms directly related to fluctuations in the westwind drift? What is the impact of changes in volume transport and its constituents (both chemical and biological) on the ambient ecosystem of the southeastern Bering Sea?

T. Yoshida:

1. What are the important oceanographical and meteorological processes which affect ecosystems in the upper mixed layer? How important is the intermittent mixing by strong wind during the heating season for the primary production?

2. How does the Subarctic Gyre respond to variations of the climate system over the Pacific Ocean? Does the Subarctic Gyre expand and contract?

3. How do the Subarctic and Subtropical gyres affect the global air circulation? Do the ocean circulations in middle and high latitude affect the global air circulation? How much does the Subtropical (Subarctic) gyre transport heat to the Subarctic (subtropical) sea? Where does the heat go?

A. Taniguchi:

1. Why is the Oyashio region so productive? Does deep ocean circulation enrich the Bering Basin waters and ultimately the Oyashio waters? Or is the confluence of Kamchatka-Kurile-Japan Archipelago and the Emperor Seamounts the site for upwelling of nutrient rich deep water?

2. *Phaeocystis poucheti* and *Emiliania huxleyi* rarely dominate the Oyashio and adjacent waters. Is it indicative of the difference in the biological oceanographical systems between Subarctic Pacific and Atlantic and/or between the eastern and western Subarctic Pacific?

3. Is there any long-term variation in zooplankton standing stock and species composition? And what are the causative factors?

4. How important are microzooplankton in the Oyashio and adjacent waters?

5. How does the plankton community change in time in warm core rings pinched off from the warm Kuroshio Current? How do warm core rings affect the plankton community in the surrounding water in terms of their life history and productivity?

D. Mackas and B. Frost:

1. What controls interannual variability in mesozooplankton abundance in surface waters of the oceanic Subarctic Pacific? What are the important linkages within the pelagic food web and what is the specific effect of interannual variability in the physical environment?

2. What physical and biological interactions trigger major changes in community structure within the Subarctic Gyre?

3. Does the pattern of oceanic plankton dynamics established at Ocean Station P in the Gulf of Alaska (50°N 145°W) apply generally to the open Subarctic Pacific? In particular, does it apply to regions where winter mixed layer depths are significantly deeper than at Station P, such as the western Subarctic region and the deep basin in the Bering Sea? Do the same underlying mechanisms pertain in all regions?

4. Why are there no blooms of large-sized phytoplankton cells in oceanic waters of the Subarctic Pacific, in contrast to shelf and coastal waters? What controls the abundance of large-sized phytoplankton species in oceanic waters, and in particular does size- or taxa- dependent limitation of phytoplankton specific growth rates by one or more trace nutrients (e.g., iron) play a role?

5. What are the connections between the oceanic microbial loop and the larger mesozooplankton (dominated by species of *Neocalanus*) in surface waters of the open Subarctic Pacific?

W. Pearcy:

1. How does circulation in the Subarctic Gyre vary in time and space? What are the variations on a climatic and interannual scale? What are the teleconnections between circulation in the eastern and western Subarctic Pacific, and with the California Current? What are the shapes of the frontal boundaries and how do they vary spatially from year-to-year?

2. What are the physical processes controlling productivity? What is the relative import of winter mixing vs. upwelling in gyre? How does volume transport in the Subarctic Current/North Pacific Drift relate to nutrient levels, upwelling and productivity? What are the major factors limiting primary productivity (iron limitation, microzooplankton)?

3. How do the communities and species respond to long-term and interannual variations in the ocean environment? Are there major changes in abundances, community structure or migrations?

4. What are the physical and biological features that are most important in influencing the distribution and abundances of major species?

5. Is the increased production of salmonids in the Gulf of Alaska since 1976 due to increased secondary production of zooplankton, or to a change in zooplankton distribution and availability?

6. How important is competition vs. predation in determining standing stocks and production? Is there evidence for competition among key species and salmonids?

7. What is the carrying capacity in biomass for salmonids during the 1980-90s? What stocks and what ocean regions show evidence for density-dependent growth or survival? What is the optimal number of salmon smolts that hatcheries should release in the future?

8. How much of the primary productivity eventually passes through salmonids and other top carnivores (pomfret, marine mammals, squids, sharks, etc.) vs. mesopelagics or fallout to the benthos?

R.D. Brodeur and A.B. Hollowed:

1. What is the taxonomic and size composition of the zooplankton that are advected onshore or through the Alaska Current by way of the Subarctic Current and what life stage of the dominant fish species present can utilize these prey most effectively? What is the taxonomic composition of the tertiary level of production in oceanic and coastal waters (e.g. small fishes and squid, myctophids, large pelagic shrimp and euphausiids) and does it fluctuate in phase with the secondary production?

2. What is the lag period between increased production in oceanic waters and the appearance of this production in coastal waters? What is the lag period between a change in atmospheric conditions and increased zooplankton production?

3. What is the connection between flow into the California Current and that into the Alaska Current? Is production out of phase between these two systems?

4. Does similar onshelf advection of zooplankton occur in the Western North Pacific and do pelagic and demersal fish stocks respond in the same way to this biomass flux? Are peak years in production in the Western Basin synchronous with those in the Eastern North Pacific?

5. Are there any anoxic basins with fish sedimentary records in the northern North Pacific that can determine whether the observed decadal shifts in dominance and biomass have occurred during the past millennia?

6. Are there shifts in the distribution of midwater and demersal fishes between years or major oceanographic regimes? How does the availability of suitable spawning habitat change?

7. How is growth affected by regime shifts on both sides of the ocean? Is the food available during any particular year above the amount needed to sustain optimal growth? Do several co-occurring species show synchronous good growth years? For the same species or species in a similar trophic position (e.g. hake and walleye pollock), is growth in the California Current out of phase with that of the Alaska gyre or is it related in any way to growth in the Western North Pacific? Is widespread density-dependent growth apparent for years of high fish biomass or low zooplankton production?

Y. Ishida, D.W. Welch and K. Shimazaki:

1. What factors are causing changes in the salmon production of the North Pacific?

2. What are the biological and physical factors controlling the distribution of Pacific salmon in the North Pacific? What are the implications of climate change on salmonid carrying capacity and productivity?

3. How are marine growth rates of salmon affected by changes in oceanic productivity?

4. What are the density-dependent interactions between salmonid species? What are the implications for the salmonid carrying capacity of the North Pacific?

B. Hargreaves:

1. What controls mortality of salmon and other important nekton species in the Subarctic? What is the location, timing, and variability of mortality?

2. Are there large geographic areas that consistently show different interannual rates of survival and/or growth for salmon? Are these regions consistent for other important nekton species?

3. Is there evidence for coherent patterns of ecosystem productivity and species/niche abundance patterns (trends, species replacement, etc. over larger space (e.g. basin-wide) and time

(e.g. decadal) scales (e.g. changes in average size of salmon, sardine abundance in eastern and western Pacific, etc.)?

4. What new approaches or technology can be used to continuously track the movements, growth, and status (e.g. living, dying or dead) of individual fish and entire stocks over space and time scales that are biologically meaningful (e.g. entire Subarctic Pacific Ocean and entire life span for salmon, pollock, saury, sardine, etc.) in the ocean?

5. What is the evidence for multiple stable states and for "regime" shifts for important fish species (particularly evidence from other than climate and harvested stocks)?

6. Is it valid to use historical catch data from fisheries (e.g. salmon catches) to estimate species abundance?

7. What is the evidence for top-down (natural predators and human fishing) versus bottom-up (physics/nutrient flux/zooplankton) control of ecosystem structure?

8. What are the effects of interannual and longer-term variability (e.g. global climate) on ecosystem productivity/composition (esp. fisheries)?

K. Kawaguchi:

1. What is the role of fish mesopelagic micronektonic animals in the food web of the Subarctic Pacific?

2. How much of the primary production is transferred to diel vertical migratory mesopelagic micronekton?

H. Nakata:

1. What are implications of mesoscale features such as oceanic fronts and eddies for biological production?

2. What are driving forces of decadal changes in community structure of plankton and fish populations?

3.0 REVIEW OF THE PHYSICS OF THE SUBARCTIC GYRE

3.1 Gross Structures And Decadal Scale Variations In The Basin-Scale Climatic and Oceanic Conditions (T. Sugimoto)

Gross oceanic environment in relation to primary production

Horizontal distribution of monthly mean sea surface wind velocity in the North Pacific in February and August are shown in Figs.2a and 2b, respectively. In winter, the Aleutian Low develops with its center around 45-50^{o}N, 170-180^{o}W and southerly wind prevails over the Alaskan gyre. On the other hand, northwest winter monsoon prevails around the Japanese Islands. In summer, however, a subtropical high develops in the mid-latitudes of the North Pacific from east to west and northerly wind prevails off the west coast of the North American continent. The horizontal distribution of the annual mean sea surface wind stress is shown (Fig. 3). Upper ocean circulation in the North Pacific, estimated from the sea surface dynamic height anomaly (Fig. 4). The anticlockwise Subarctic Gyre is observed north of 45^{o}N, which corresponds to the region of cyclonic rotation of the annual mean wind stress. Strong western boundary currents, the Kuroshio, the Oyashio and their extensions, are seen in mid-latitudes south and east of Japan. A wide transitional zone with many eddies is formed at 35-45^{o} N between the subarctic and subtropical gyres, as shown in Figs. 17 and 18.

Figures 5a and 5b show north-south sections of water temperature and salinity respectively along 180^{o}E in winter. Whereas Fig. 6a and 6b show those in summer. In the Subtropical Gyre, which extends from 15-35^{o}N, warm and highly saline water accumulates to depths of several hundred meters. In the Subarctic Gyre the water is generally more homogeneous. However, a strong halocline prohibits the deepening of the upper mixed layer due to winter cooling. An influx of fresh water through the sea surface is one of the specific characters of the Subarctic region in the North Pacific, and creates less saline upper layer. The vertical structure of the water mass is characterized by the sharp halocline at the bottom of the upper layer of about 100 m depth.

In the spring and summer, a sharp shallow seasonal thermo-halocline is formed by heating and net precipitation from the sea surface. The upward nutrient flux through this seasonal thermo-halocline is one of the most important processes in the primary production in the euphotic zone. The upward flux of nutrients from the deeper layer to the upper layer, due to winter mixing and subsequent formation of the shallow seasonal thermocline, combined with increasing sunlight in spring and summer, are essential physical factors for primary production, especially in the generation of the spring bloom.

In the vertical flux process, upward Ekman pumping in the Subarctic Gyre during winter is also important factor to lift up the deep nutrient rich water into the upper part of the permanent halocline. Figure 7 shows the horizontal distribution of monthly mean upward velocity at the bottom of the Ekman layer in February. This figure indicates that the water at the bottom of the Ekman layer in the Subarctic Gyre is lifted up by about 10-15 m for three months in winter. Upwelling velocity in the coastal upwelling region off the west coast of the American continent in summer (not shown here) is more than one order larger and much more effective to primary production.

El Niño events, meanders and variations in the westerly wind, the Kuroshio and the Oyashio on decadal scales

Figures 8a and 8b show monthly mean sea surface temperature anomalies in March and June in 1993. In this winter and spring, sea surface water in the eastern part and western boundary region of the Pacific was warmer by about 1^{o}C, and the central Pacific in the mid-latitudes was colder by about 1^{o}C than usual year. However, in this summer the surface water was colder than usual by about 1^{o}C in the central and western part of mid-latitudes. Cooler summers and calm warm winters in the Far East correspond to weak southeasterly and northwesterly monsoons in El Niño years. Figure 9 shows a time series of monthly mean sea surface temperature anomalies at the western and eastern parts of the equatorial Pacific since 1976. In recent years, the El Niño event which started in 1991 is persisting, although there was a short intermission. Figure 8 also shows that the El Niño-like situation has lasted for over ten years since 1976. But El Niño events were not dominant in the previous one and a half decades of 1960-75. Figure 10 shows about 50 El Niño events which occurred about every 10 years during the last 500 years, and that remarkable events have occurred once every 50 years. Although these long term variations are considered to be due to the variations in oceanic thermohaline circulation, which has a long response time, and variations in solar activity, the mechanisms are not yet well understood.

These events in low latitudes affect the oceanic and atmospheric phenomena in mid and especially high latitudes. Figure 11 shows the anomaly of the difference of monthly mean 500 mb height between 40 and 60°N. The positive values indicate small amplitudes, and the negative values indicate large amplitudes of the meandering of the westerly wind. This figure indicates that the amplitude of the meander of the westerly was large in 1956-65 and 1977-87, but was small in 1968-76 and in recent years.

The southward intrusion of the first branch of the Oyashio Current, indicated by the isotherm of 5°C at 100 m, usually occurs in spring. However, the interannual variation is also large (Fig. 12a). The southern limit of the first branch of the Oyashio extended more southward before 1966 and in the decade of 1977-86, but retreated northward in 1968-75, except during 1974 and 1988-90. Whereas the Kuroshio path south of Honshu did not show large meanders in the decade of 1964-74, it did follow a more meandered path in 1956-58, and in the decade of 1975-85 (except in 1981) (Fig.12b). The periods of intense southward intrusion of the Oyashio, and the meander/non-meander pattern of the Kuroshio path correspond well to the state of meandering of the westerly wind.

Figure 13 shows Sverdrup transport of the Kuroshio and the Oyashio Currents estimated from annually averaged wind stress during 1964-84, and the geostrophic transports of the Kuroshio and the Oyashio measured in the East China Sea and in the east of the Tugaru straits (Figure 14), four times a year. The transports in the decade since mid 1970s were larger than those before that decade. This tendency for decadal scale variation also corresponds to those of the meandering of the westerly.

Physical environments for early survival rate of Japanese sardine

Pacific sardine live in temperate waters of 10-20°C and are found around the Japanese Islands and off the California coast. Japanese sardine on the Pacific side spawn in the water between coastal water and the Kuroshio in winter, and migrate toward the northeast, across the Kuroshio-Oyashio transitional region, during spring and summer. Hence, the water between the Kuroshio and the coastal waters is important as the nursery ground. The Kuroshio-Oyashio transitional region and the Oyashio water are also an important feeding area for young and adult fish. Year to year variation in their biological and non-biological environments are considered to be important factors in the population variation through the recruitment success and failure.

During the period when a large meander of the Kuroshio Current persists, water exchange between the Kuroshio and its coastal waters is enhanced (Sugimoto and Kobayashi 1987). The water characteristics in the coastal boundary region become closer to offshore water than during periods when the Kuroshio meanders are smaller. For this reason, the dominant species of copepod shifts from coastal types of smaller sizes, to offshore larger size types (Nakata et al. 1994). This results in decreases in the number of nauplii of small copepods, which are the main food of sardine larvae, and increased the predation pressure by the large zooplankton.

In winter when the northwest monsoon prevails, the wind drift transports fish eggs and larvae toward offshore waters. As vertical mixing has already occurred due to winter cooling, strong wind mixing is thought to suppress the multiplication of phytoplankton and feeding condition of larvae, unlike the California coastal upwelling area. Figure 15 shows the computed retention rates of particles in coastal waters 20 days after release at the main spawning ground in each year. In this numerical model, offshoreward wind drift current, patterns of the Kuroshio path, horizontal diffusivity and spawning sites were taken into consideration. The result was compared with the survival rate of sardine larvae about 20 days after spawning in the field. In the years of strong westerlies (1981, 1984), both the retention rate and survival rate clearly decreased. Whereas in the years with calm winters (1979, 1980, 1982), the survival rate was relatively high.

Figure 16 shows multi-decadal scale variation of the Japanese sardine and two indices of the physical environment i.e. patterns of the Kuroshio path with/without large meander and the remarkable El Niño events which indicate a calm winter. In and around the 1972-73 El Niño year, the winter monsoon was extraordinarily weak for at least a month (Sugimoto et al. 1991). The Kuroshio did not meander between 1964-75. Under these physical situations in the early 1970s, survival rates of sardine larvae were enhanced and dominant year classes were formed. A similar situation occurred in the 1957-58 El Niño year, although the following years in that decade were not favourable.

In the summer of 1975, a large meander of the Kuroshio path started, which might have caused an upstream extension of the spawning ground toward the coastal water and the Kuroshio front south of Kyushu. This situation induced extremely large migrations of sardine, and increased the stock (Kobayashi and Kuroda, 1991), similar to that found in the late 1920s.

3.2 Review of processes of interannual variations in the eastern subarctic waters, including meso-scale phenomena and the shelf circulations which may affect the ecosystem (J.D. Schumacher and T. Royer).

The Northeastern Pacific Subarctic Gyre experiences some of the largest seasonal variations in atmospheric forcing in the world. The atmospheric system is dominated by an intense low pressure system in winter, the Aleutian Low. In summer the atmospheric circulation is influenced primarily by the North Pacific High. Coastal topography assists in the containment of the winter low pressure systems over the Gulf of Alaska. Seasonally, the oceanic driving changes from a strong central upwelling with strong coastal downwelling in winter, to a very weak central downwelling and coastal upwelling in summer. In addition to the wind forcing, the Aleutian Low in fall and winter brings high rates of precipitation. The precipitation is especially intense in the coastal regions, where the moisture laden air masses interact with the coastal mountains. This non-uniform distribution of precipitation and runoff creates a cross-shelf salinity gradient that drives the coastal circulation. Annual precipitation rates of more than 8 m have been reported.

Given the very large seasonal signal in atmospheric forcing, it is surprising to discover that the seasonal variability in the Subarctic ocean circulation is quite small, generally less than 10% of the mean. The most probable explanation is that the ocean at these relatively high latitudes does not have enough time to respond to the atmospheric forcing. We do see a response of the circulation on the Gulf of Alaska shelves to this forcing, however, with greatest nearshore flows occurring in fall and winter (Schumacher and Reed 1980; Royer 1981; Johnson et al. 1988; Schumacher et al. 1990).

Since we know that the biomass production on the shelves of the Subarctic Pacific are very great, an important question is "How do the shelves receive the required nutrients to support this growth?". Do the nutrients come from the vast quantities of fresh water entering the system? Do they come from upstream sources as might be found along the coastal regions of British

Columbia and Washington? Are they brought into the photic zone from the deep ocean, where we know that their concentrations are quite high?

While some attention over the past two decades has been devoted to the measurement of physical parameters on the shelves in the Gulf of Alaska, little or no resources have been used to gather information on the chemistry or biology. Fortunately, a WOCE cruise (P17N) recently (May-June 1993) obtained nutrient and CFC data for the central part of the Gulf of Alaska and across the shelves near the Shumagin Islands and Sitka. This was the first time that high precision nutrient sampling has been done synoptically for the shelf and deep ocean in the Gulf of Alaska. While it cannot reveal much about the important processes controlling the nutrient distributions, it does provide the first "snapshot" of their distribution.

Interannual variability of temperatures in the upper layers of the northern Gulf of Alaska have been observed and attributed to the 18.6 year lunar nodal tide forcing. This tidal forcing can account for about 60% of the variance of the halibut biomass in the Gulf of Alaska. The exact mechanism of this influence on the biomass is not known, but it is likely that it operates through some other method than a direct temperature effect. We need to pursue the question of interannual variability of temperature and other parameters including nutrients, primary production and larval fish. These investigations should also address the shorter period fluctuations due to ENSO forcing. Attempts should be made to map the propagation of ENSO events up the west coast of North America from the tropics to the Gulf of Alaska and possibly into the Bering Sea. We also need to evaluate the role of the Subarctic Gyre in any possible global climate change processes and the potential impact on the fisheries.

Recent numerical models and observations of Subarctic ocean circulation indicate the presence of mesoscale eddies in the Subarctic North Pacific (Cummins 1989; Musgrave et al. 1992). The eddies are usually formed along the eastern boundary of the Gulf of Alaska. They are several hundred kilometers in diameter and are analogous to warm core rings. They do not have a temperature signal, but instead are relatively fresh, giving them a lower density than the surrounding water. They tend to propagate slowly westward across the Gulf of Alaska at about 2 $\mathrm{cm} \cdot \mathrm{s}^{-1}$. Ultimately, after several years, they enter the Alaska Stream, where they are carried to the southwest along the Aleutian Island Arc. The ultimate fate of these eddies is unknown. Several questions arise that are related to these eddies. First, do they represent a significant mechanism by which the wind stress enters the gyre? Second, are they important for mixing in the subarctic? Third, are they important biological habitats? The latter question arises since they are so long lived.

Knowledge of the exchange of waters between the North Pacific Ocean and the Bering Sea is limited because of the lack of reliable measurements (Reed 1990). Since the late 1980s however, several research efforts have been conducted in support of the National Oceanic and Atmospheric Administration (NOAA) Fisheries Oceanography Coordinated Investigations (FOCI; Reed et al. 1989, 1992; Schumacher and Kendall 1992). Because the focus of this program is to understand how the physical environment influences survival of early life history stages of pollock and their eventual recruitment to various stocks, the impact of interannual variations in Subarctic waters on the ecosystem is a central issue. In the following review we present results which describe flow through Amukta Pass, Amchitka Pass and Near Strait (Fig. 17), with emphasis on interannual variations, impact on the physical environment of the Bering Sea, and speculation on processes which cause the observed fluctuations.

The Bering Sea is partially separated from the North Pacific Ocean by the Aleutian Island arc (Fig. 17). Three passes have water depths >700 m (Amchitka Pass, Near Strait, and Kamchatka Strait), and only Kamchatka Strait permits exchange of deep (>2000 m) water (Favorite 1967). Although topographic features limit exchange, clearly the Bering Sea is not an isolated, self-contained system (Stabeno and Reed 1992). The two major circulation features over the basin, the Kamchatka Current in the western Bering Sea and the Bering Slope Current (Kinder et al. 1975; Schumacher and Reed 1992; Overland et al., in press) in the eastern Bering Sea, are extensions of the Alaskan Stream. Inflow into the Bering Sea ($12 \cdot 10^6 \cdot m^3 \cdot s^{-1}$) is balanced by outflow through Kamchatka Strait, so that flow in the Bering Sea basin may be aptly described as a convoluted continuation of the North Pacific Subarctic Gyre (Stabeno and Reed 1993). An insignificant volume ($<1 \cdot 10^6 \cdot m^3 \cdot s^{-1}$) flows northward through Bering Strait. Furthermore, the interannual variability of the sea surface temperature in the Bering Sea and Gulf of Alaska tend to fluctuate in unison (Royer 1993).

The Alaskan Stream is the northern boundary of the cyclonic Pacific Subarctic Gyre (Favorite et al. 1976). It is a narrow (about 75 km), deep (>2000 m), swift (peak speeds 75 $cm \cdot s^{-1}$) flow that extends from the head of the Gulf of Alaska to the western Aleutians (Reed 1984). The Alaskan Stream transports relatively fresh surface water and warm subsurface water into the western Pacific Ocean. If it were absent from the Bering Sea for any considerable period, there would be a substantial alteration of circulation and of water properties in the Bering Sea, with potential impacts on the ecosystem (Stabeno and Reed 1992).

The Bering Sea is characterized by a temperature-minimum layer (from the surface to near 200 db) and by a temperature-maximum layer below the minimum, typically cantered at 300 to 400 db. The temperature minimum is deepest and has the most extreme (lowest) temperatures off the coast of Siberia and Kamchatka (Sayles et al. 1979). Although it is formed by winter convection, it persists year-round, and its distribution is altered by subsurface advection and diffusion (Reed 1991). On the other hand, the subsurface temperature-maximum layer is mainly affected by horizontal advection of water from the North Pacific through the Aleutian Island passes (Sayles et al. 1979). Kinder et al. (1975) concluded that in the eastern Bering Sea the maximum occurred near the sigma-*t* density surface of 26.80, but Reed and Stabeno (1989) observed a maximum (in a similar location during spring 1988) that had a mean sigma-*t* density of 26.62. Thus the depth and density of the maximum can vary considerably, likely as a result of variations in the source waters.

The magnitude of the temperature minimum suggests an aspect of transport into the Bering Sea. During three cruises conducted in the southeastern Bering Sea between fall 1989 and fall 1990, temperatures at sigma-t of approximately 26.8 were relatively low (generally <3.7°C). Conversely, during fall 1986 and spring 1988 (Reed et al. 1988; Reed and Stabeno 1989) temperatures were >4.0°C in places. The warmer temperatures indicate an inflow of warm Alaskan Stream water through Amukta Pass. Relatively low temperatures during 1989-1990, during August 1972 (Kinder et al. 1975), and during June 1987 (Reed et al. 1988), however, suggest the absence of inflow through Amukta Pass.

Appreciable variability exists in transport through Amukta Pass as well as variability in flow and water properties all along the slope (Schumacher and Reed 1992). Recent results from a numerical model (Spillane, pers. communication) indicate that eddies are formed during periods of inflow. High concentrations of pollock larvae have been found to coincide with eddies both in the Gulf of Alaska (Schumacher et al. 1993) and in the southeastern Bering Sea (Reed and Stabeno 1989), and there are suggestions that the eddy environment is conducive to survival (Schumacher and Kendall 1992). Furthermore, the depth of the temperature maximum is near the depth that pollock spawn; the observed temperature differences up to 0.5°C would impact the time it takes for eggs to hatch. Since eggs and larvae may be separated vertically by more than 300 m, differential transport would occur. The consequences of such are unknown. Although inflow through Amukta Pass may be important regionally, its transport is relatively small ($<1 \cdot 10^6 \cdot m^3 \cdot s^{-1}$).

Recent results indicate an average of 2-$3 \cdot 10^6 \cdot m^3 \cdot s^{-1}$ of Alaskan Stream water flow into the Bering Sea through Amchitka Pass (Reed 1990). While this is only 10-15% of the total volume transport of the Alaskan Stream, it provides the majority of the flow which flows eastward along the north side of the Aleutian arc (Stabeno and Reed submitted) and is continuous with the Bering Slope Current. Interannual fluctuations in the volume transport through Amchitka Pass seem not to be linked to either wind stress or wind stress curl. Reed (1990) suggests that fluctuations in the location of the Alaskan Stream interact with a spur-like feature in the bathymetry upstream from the pass. The curvature resulting from fluctuations in potential vorticity would then cause variations in northward transport.

Satellite tracked buoy observations (Stabeno and Reed 1992) and water property observations (Reed et al., in press) indicated that the Alaskan Stream was not flowing through Near Strait for more than a year (mid-1990 to fall 1991; Stabeno and Reed 1992). The presence of the Alaskan Stream in this region is clearly indicated by temperature >4°C to depths in excess of 200 m with a mean transport of approximately $5 \cdot 10^6 \cdot m^3 \cdot s^{-1}$. The anomaly of inflow through Near Strait resulted in dramatic changes in the western Bering Sea Current System, including a reduction of transport in the Kamchatka Current of approximately $5 \cdot 10^6 \cdot m^3 \cdot s^{-1}$ (Verkhunov and Tkachenko 1992). The anomaly was thought to result from an inertial effect on the Stream rather than from wind stress (Stabeno and Reed 1992).

Clearly, fluctuations in the position of the Alaskan Stream have great impacts on transport into the Bering Sea. Further, such variations cause significant changes in circulation and water properties in the Bering Sea. The connection between such variations in the ecosystem, in particular the environment in which pollock spawn and live their early life stages are not know but are potentially of importance. To address such processes requires an enhanced understanding of causes of fluctuations of inflow through Amukta and Amchitka Pass for pollock in the southeastern Bering Sea, and through Near Strait for pollock stocks in the western Bering Sea.

The important questions revolve around understanding what mechanisms impact the time/space behaviour of the Alaskan Stream? This can be separated into the following questions:

What mechanisms cause interannual variability in the Alaskan Stream which then alter the exchange of water into the Bering Sea? Are these mechanisms directly related to fluctuations in the westwind drift? What is the impact of changes in volume transport and its constituents (both chemical and biological) on the ambient ecosystem of the southeastern Bering Sea? To answer these questions requires pragmatic knowledge of the physical environment as it influences biota. We stress understanding the impact of natural fluctuations in the physical environment on biota. Examination of this impact should extend up the food chain to sea birds, marine mammals, and commercially important fishes. To answer these questions requires broad, long-term collaborative programs. GLOBEC type studies could serve as a guideline.

3.3 Oceanographic structure of the upper layer in the western North Pacific subarctic region and its variation (T. Yoshida)

Circulation pattern

The circulation pattern of the upper layer in the western North Pacific Subarctic region from Ohtani (1970) is shown in Figure 18. This gives more detailed information for the western part of the circulation than Ohtani (1991), including recent knowledge of the whole North Pacific Subarctic circulation. The Western Subarctic Gyre is a triangular cyclonic gyre, which is located off southeast of Kamchatka. The Subarctic Current flows eastward south of the Western Subarctic Gyre, and the West Wind Drift flows eastward south of the Subarctic Current. The southern boundary of the West Wind Drift is the Subarctic Boundary. The Subarctic Boundary is usually defined by the location of the 34.0 psu isohaline which runs almost vertically in the upper layer in the north-south vertical sections (Nagata et al. 1992), but the character is not clear in seas adjacent to Japan. The circulation pattern in Figure 18 is based upon winter observations, but the summer pattern is almost the same (Ohtani 1970).

There are two wide eastward flows in the southern part of the Western Subarctic Gyre: the Subarctic Current and the West Wind Drift. Ohtani (1970) estimated their speeds were 5 cm · sec^{-1} or less (Fig. 18). Ohnishi et al. (1992) showed that there were two fast eastward flows at 45-46°N and 40-42°N whose speeds were calculated at more than 10 cm · sec^{-1} based on their baroclinic geostrophic flow distribution along the 180° meridian. Because the positions of the two fast flows coincide with the temperature fronts (see next section), it may be better to replace the wide eastward flow pattern in Figure 18 with the pattern of two fast flows at the borders of water masses.

The barotropic flow should be taken into account to get the real flow pattern, but it is difficult to estimate based on conventional observational data. We expect to obtain new knowledge on the real flow pattern from the altimetry data obtained by satellites and the satellite tracked buoy observations.

Division of the regions on the basis of oceanographic structure

Miyake (1989) reviewed the investigations on the frontal structure in the central North Pacific Subarctic region. He concluded that "the Polar Front by Roden et al. (1982) was the southern boundary of the Subarctic water, the Kuroshio Front was the northern boundary of the subtropical water, and the Subarctic Boundary (or the Subarctic Front) existed in the region between the Polar Front and the Kuroshio Front". In the temperature sections along 155°E and 165°E meridians (Fig. 19), the Polar Front and the Subarctic Front are clearly seen as the temperature fronts around 5°C and 10°C respectively.

The western North Pacific Subarctic region north of the Kuroshio Front is divided by these two fronts into three regions. The first is the Subarctic Water Region: north of the Polar Front (Roden et al. 1982). The second is the West Wind Drift Region: between the Polar Front and the Subarctic Boundary. The third is the Subtropical Water Region: south of the Subarctic Boundary.

Relation between the three regions and the regions in the Tohoku Sea Area

The Oyashio Water Region in the Tohoku Sea Area is the western part of the Subarctic Water Region. Because the frontal structures at the south boundary of the Subarctic Water Region and the Oyashio Front in the Tohoku Sea Area are the same, and the Subarctic water characterized by the dichothermal structure in warming season distributes both in the Oyashio Water Region and in the Subarctic Water Region (Kono 1991). But the relation between the other two regions and the Perturbed Area (Kawai 1972) and the Kuroshio Region in the Tohoku Sea Area is not well known (Nagata et al. 1992). Kawai (1972) said that the Subarctic Boundary might be connected with the Secondary Kuroshio Front, which was a northern branch of the Kuroshio Front. The path of the northern branch of the Kuroshio Extension by Mizuno and White (1983) (Fig. 20) supports Kawai's (1972) idea because the path coincides with the Subarctic Boundary in the region east of 165°E. Zhang and Hanawa (1991) concluded that the Subarctic Front by Roden et al. (1982), which coincided with the Subarctic Boundary, was the same front with the Secondary Kuroshio Front from the water mass analyses.

Variation of the circulation

Recent investigations of the Oyashio and the Subarctic Gyre illustrate that variation of the Subarctic Gyre correlates with the wind system over the Pacific ocean. Sekine (1988a) showed that the wind stress in the years of the anomalous southward intrusion of the Oyashio caused the southward expansion of the gyre in the magnitude of 300-500 km. Sekine (1988b) also showed that the southward expansion of the Subarctic Gyre was a barotropic response to the change of the wind stress field caused by the anomalous development of the Aleutian Low. From Ogawa (1989), the magnitude of the variation of the first Oyashio intrusion near Japan coast is estimated to be the same magnitude as Sekine (1988a) showed. But Yoshida (in press) estimated from the movements of the SST fronts that the movements of the south boundary of the Subarctic Water

Region and the Subarctic Boundary were within one degree in latitude.

The variation of the Subarctic Gyre is still not well investigated. Ogawa's (1989) data on the southern limit of the first Oyashio intrusion is quite useful as the unique index of the Subarctic Gyre, and it has contributed much to progress in the investigation of the Subarctic Gyre. In the early stage of the investigation (our understanding is that the investigation on the Subarctic Gyre is just in early stage!), it is useful to transform phenomena into numerical indices and analyze them. The usefulness of these indices is easily understood from the fact that many indices such as zonal index, polar vortex index, SOI and NINO-3 SST play an important role in the fields of meteorology and tropical oceanography even in the mature stages of investigation. We would appreciate receiving information concerning any new indices which have recently been developed.

Variation of the upper mixed layer

The Subarctic water is characterized by the dichothermal structure in warming season. The depth of the upper mixed layer is more than 100 m in winter (Fig. 21). The sharp halocline, which has a thickness of 70-100 m below the wintertime upper mixed layer, prevents the wintertime mixed layer from deepening (Ohtani 1989). In the warming season, the seasonal thermocline grows in the upper part of the wintertime mixed layer, and a thin upper mixed layer is formed over the seasonal thermocline. In cooling season, water temperature of the thin upper mixed layer decreases and the thickness increases. Besides the formation/ destruction of the seasonal thermocline by the warming/cooling from the air, intermittent mixing by strong wind in the warming season, which causes the temporal destruction of the seasonal thermocline and supplies nutrient salts from lower layer, is important for primary production (Taniguchi 1991). There should be interannual variation of the upper mixed layer. It is commonly thought that the meteorological interannual variation causes some change in the upper mixed layer, because the mixed layer is mainly affected by the meteorological condition. But it is not well investigated.

To describe the annual and interannual variation, long period monitoring of the oceanographical structure and meteorological condition is essential. But we do not have enough data obtained over such long periods to describe the annual and interannual variation in the Subarctic region, except the SST data (which are the same as the temperature data in the upper mixed layer). Long period operation of moored buoys which are equipped with oceanographical and meteorological observation systems would provide us with precious data. In the following sections we describe the variations in SST.

Annual variation in SST

The monthly mean SST maps for February and August, derived from thirty years of data (Japan Meteorological Agency 1991), are shown in Figure 22. We can see that in February the 5°C isotherm almost coincides with the southern boundary of the Subarctic Water Region. This indicates that the region with wintertime SST less than 5°C represents the Subarctic Water Region. This region extends southwestward along the Kuril Islands to the southeast of Hokkaido, where the Subarctic water takes its southernmost position. The 3°C isotherm is almost parallel with the 5°C isotherm, but it runs northward along the 170°E meridian from 45°N to 52°N. This feature is caused by the northward flow of warm water transported by the Alaskan Stream along the south border of the Aleutian Islands (Ohtani 1970). From February to May this feature is seen on the SST map, but it is masked by the seasonal thermocline and can not be seen in other months. The SST along the central Kuril Islands is lower than that of the neighbouring area in August (Fig. 22). The low SST is thought to be caused by the continuous tidal mixing in the channels of the central Kuril Islands (Ohtani 1989).

The mean annual SST cycles are shown in Figure 23 for the four areas: A, the Western Subarctic Gyre; B, the Oyashio Region; C, the West Wind Drift Region; and D, the south of the Subarctic Boundary (calculated from the SST data by the Japan Meteorological Agency 1991). The SST is lowest in March and highest in August or

September in all the areas. The amplitude of the cycles is around 10^{o}C.

SSTs in areas A and B (both in the Subarctic Water Region) are the same in winter. But the SST difference is more than 3^{o}C in summer. The SST difference is thought to be brought about by the latitudinal difference in heating. The wintertime SST in areas B and C (in the West Wind Drift Region) is different by more than 3^{o}C. But the two areas located at almost the same latitude, and therefore the difference of the SSTs between the two areas decrease in summer. The shape of the annual cycle curve in area D resembles that of area C. The difference between the SST in areas D and C is about 6^{o}C all year long.

Interannual variation of SST

The SST anomaly map in July 1993 (Japan Meteorological Agency 1993) in Figure 23 shows that an area of negative anomaly less than -2^{o}C extends broadly east of Japan from 30^{o}N to 45^{o}N. Besides the annual variation, which dominates the SST variation as mentioned in the above section, strong SST anomalies sometimes appear over large areas (Fig. 24).

The time series of monthly mean SST anomalies in the areas defined in Figure 23 are shown in Figure 25. The anomalies are around 1^{o}C or less in ordinary years. They are about 10% of the amplitude of the mean annual cycle. But anomalies more than 2^{o}C sometimes appear in areas B, C and D.

The results of correlation analyses (Table 1) show that the SST anomalies in these four areas are correlated with each other. It is estimated that a variation with large scale affect the four areas. Atmospheric variability is probably the cause of such large scale variations in the SST anomalies. The relation between SST variation in the western North Pacific and the atmospheric variation is well investigated (Iwasaka et al. 1987, 1988; Hanawa et al. 1988, and Hanawa 1989a, b), and it is noted that the global scale atmospheric phenomena (e.g., ENSO events) affect SST variations. Because the upper mixed layer has direct contact with the atmosphere, weather conditions connected with the global scale atmospheric phenomena give a direct effect to a certain extent.

Besides the direct effect from the atmospheric variation, the variation of the heat transport by the Subarctic and subtropical gyre and the expansion/contraction of the gyre can cause the SST variation. These are the themes to be investigated in the near future.

4.0 REVIEW OF THE BIOLOGY OF THE SUBARCTIC GYRE

4.1 Phytoplankton And zooplankton in the western Subarctic Gyre (A. Taniguchi)

Introduction

The Subarctic Pacific is one of the most productive areas in the world oceans (Figs. 26 and 27). However, the most characteristic feature of plankton dynamics in this area is the large amplitude of seasonal variation in productivity which occurs every year. Fishes distributed in this area should incorporate this seasonal variability of food conditions into their life history strategy (Taniguchi 1981, 1991, 1993). This aspect is particularly important for the planktivorous fishes like Jack mackerel, Pacific saury, sardine, etc. which migrate between the Subarctic area in the north and the Subtropical seas in the south (Fig. 28). These species can build huge populations and support massive harvests. In other words, the plankton dynamics in this area governs the life history strategy and productivity of migratory Subtropical fish as well as endemic Subarctic fish.

In the western North Pacific east of northern Japan, a transition zone is recognized which extends from about 37°N to 42°W in average summer and is bordered by the Oyashio front in the north and the Kuroshio front in the south. Hydrographic features within this zone are very complicated because of the presence and mixing of four different water masses: Subarctic Oyashio, subtropical Kuroshio, Tsugaru Warm water from the Sea of Japan and coastal water around Hokkaido and Northeast Honshu. There usually are many warm and cold core rings of different sizes and ages (Fig. 29) (Kawai 1991; Nagata et al. 1992). This area is within the migratory routes of the pelagic fishes mentioned above. Therefore, this area, though located at the margin of the Subarctic Gyre, should be included in this review.

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Primary productivity in the western Subarctic Pacific

The main area included in this brief review is the western Subarctic region around northern Japan, including the Oyashio Current and its adjacent regions. The Oyashio Current, including its predecessor the East Kamchatka Current, is one of the most productive currents of the world ocean because of an ample supply of nutrients from the surrounding Bering and Okhotsk Seas, which in turn are enriched by winter convection of water. It is reported that nutrients in the surface layer are never depleted during (Kawarada and Sano 1972) or after (Taniguchi and Kawamura 1972) vigorous spring blooms of diatoms (Taguchi et al. 1992 and unpublished data).

In the western Bering Basin region upwelling of deep water can occur. This deep water contains high concentrations of nutrients accumulated during the long journey of the deep ocean circulation (Nagata et al. 1992). This may enrich the Bering Basin water and ultimately the Chukchi Sea and Oyashio waters. Furthermore, since the Kamchatka-Kurile-Japan Archipelago in the west, and Emperor Seamounts in the east, form a wedge-shaped basin opening toward the upper stream of the deep current flowing from the south (Stommel 1958). Therefore, the deep water may ascend at the vortex (located just southeast of Kamchatka) where the Oyashio Current flows through.

Phytoplankton Community

It is well known that the dominant primary producers in the Oyashio region, and the Bering and Okhotsk Seas as well, are chain-forming diatoms such as *Nitzschia* (*Fragilariopsis*), *Odontella*, *Thalassiosira* in spring, and *Chaetoceros* (*Hyarochaete* and *Phaeoceros*), *Denticulopsis*, and *Rhizosolenia* in warm seasons. Several dinoflagellate species of the genera *Ceratium* and *Protoperidinium* are also dominant in summer/fall. The general range of numerical abundance of these primary producers is from 10^2 cells · l^{-1} or less in winter, to 10^5 cells · l^{-1} or more in spring, with intermediate values around 10^3 cells · l^{-1} in summer/fall (e.g. Aikawa 1949; Ohwada 1957; Zenkevitch 1963; Karohji 1972; Kawarada and Sano 1972; Sambrotto et al. 1986).

Phytoplankton density sometimes reaches 10^8 cells · l^{-1}, particularly in the seasonally ice-covered area of the Bering and Chukchi Seas, suggesting the sea ice fosters and then releases dense phytoplankton populations into the water column below (Saito and Taniguchi 1978). It is also reported that local wind-driven upwelling, generated particularly at the ice edge, plays an important role in the enrichment of the upper water column in the northern Bering Sea (Niebauer et al. 1981; Niebauer and Alexander 1985). Investigation is needed to determine if the same condition exists in the Okhotsk Sea.

The composition of the ice-algal community in the Okhotsk Sea is different from the Bering Sea, because the mechanism of sea ice formation is different in these two seas. Pennate diatoms are dominant and build dense populations in the Bering Sea ice community (Horner 1980). On the other hand, many centric diatoms and pennates were found but these rarely formed dense populations in the Okhotsk Sea drift ice community (Tamura 1951). The role of sea ice in phytoplankton dynamics may be a matter worthy of consideration in future PICES programs (cf. Horner 1976, 1982). Because the area of shallow shelf water is limited in the Okhotsk Sea, any algae released as dense clumps would sink directly down to the deep-sea ecosystem.

The likely great importance of nano- and pico-phytoplankton in the Subarctic Pacific during warm seasons was recently reported (Furuya and Marumo 1983; Taguchi et al. unpublished). However, quantitative data are not yet sufficient to fully assess the significance of this production.

Most of the diatoms listed above are reported to form resting spores (cysts). However, this phenomenon seems paradoxical because cysts work effectively only in shallow sea areas (cf. Smayda 1958), whereas the Oyashio and adjacent regions are relatively deep. There may be a regular supply of diatom seed populations from the shallow shelf waters in the northern Bering Sea and along Kamchatka-Kurile coast, where cysts would work effectively. Some particular hydrodynamic conditions perhaps also exist which keep the cysts suspended within the upper water column. Upwelling and convection of water, or a sharp pycnocline at the bottom of the upper mixed layer, may act as such agents.

Among the phytoplankters which have been reported to bloom in the discoloured water in the Subarctic Atlantic (e.g. Fraser 1962; Lancelot et al. 1987; Ackelson et al. 1988) and the eastern Bering Sea (Sambrotto et al. 1986), prymnesiophytes *Phaeocystis poucheti* and *Emiliania huxleyi* rarely dominate in the Oyashio and adjacent regions. This fact indicates that their bloom may be controlled by some factor(s) other than macronutrients like nitrate and phosphate, which are more abundant in the Oyashio region. To define these factors, it is helpful to understand the basic difference between the biological oceanographic systems in the Subarctic Pacific and Atlantic, and/or the difference between the eastern and western Subarctic Pacific.

Primary Productivity

Recent knowledge about primary productivity in the Bering Sea and adjacent region has accumulated mainly due to activities of the Universities of Alaska and Washington. It is now known that horizontal transport of nutrients from the highly eutrophic shelf break water and/or basin water is essential to maintain higher productivity during warm seasons in the inner shelf region of the Bering Sea and the Chukuchi Sea (cf. Hood and Calder 1981; McRoy 1993).

On the other hand, few attempts have been made to directly measure the primary productivity in the Oyashio region since the early 1970s, when new laws were introduced in Japan which strictly regulates the field use of radioactive isotopes. Data obtained before these strict regulations show that the daily productivity in the Oyashio and adjacent regions was fairly high (1-2 $g \cdot C \cdot m^{-2} \cdot day^{-1}$) in the vernal blooming season in April-May, but lower (0.3-0.5 $g \cdot C \cdot m^{-2} \cdot day^{-1}$) in summer/fall (Fig. 30) (Saijo and Ichimura 1960; Saijo et al. 1972; Taniguchi and Kawamura 1972). No fall bloom has been observed in this region (Figs. 31 and 32) (Taguchi et al. unpublished). Although no data on mid-winter production is available, it must be negligibly low due to the combined effects of reduced phytoplankton biomass and unsuitable environmental conditions such as limited flux of solar energy and deepened convection of water (cf. Sverdrup 1953). The available data at HNFRI indicate that the chlorophyll-*a* crop in winter is about 1/20 of the spring crop in the Oyashio region.

Annual production in this region, calculated from the data cited above, is high, being about 156 $g \cdot C \cdot m^{-2} \cdot yr^{-1}$ (Taniguchi 1972). Annual production in the Bering Sea has been estimated as 89 $g \cdot C \cdot m^{-2} \cdot yr^{-1}$ for most of the basin region (Taniguchi loc. cit.), and 162-166 $g \cdot C \cdot m^{-2} \cdot yr^{-1}$ for the shelf region (Walsh and McRoy 1986).

In conclusion, primary productivity in the western Subarctic Pacific, as represented by the Oyashio region, is very high in an annually integrated value. It varies very widely with the seasons, from negligibly low values in winter to high values reaching 2 $g \cdot C \cdot m^{-2} \cdot day^{-1}$ in spring, and intermediate values of 0.5 $g \cdot C \cdot m^{-2} \cdot day^{-1}$ in summer. The amplitude of this seasonal variation therefore typically exceeds a factor of 20 (Taniguchi 1981, 1991).

Such highly productive and highly variable productivity also occurs in the coastal upwelling systems in the eastern Pacific (e.g., off California, Peru, etc.), where the amplitude is about 10-20 (cf. Raymont 1980; Valiela 1984). Community structure of the primary and secondary producers, mainly chain-forming diatoms and large-sized copepods, is also similar in both the Subarctic and upwelling regions. However, because the effects of ENSO events are not as prominent in the Oyashio region (unlike the eastern Pacific, e.g. off Peru), the Oyashio region may be an ideal area to determine the intrinsic long-term trend of the biological elements, eliminating much of the highly significant "noise" of ENSO events in other regions.

Secondary productivity in the western Subarctic Pacific

Zooplankton community

The principal secondary producers or zooplankters grazing the primary producers in the Subarctic Pacific are calanoid copepods. Among them three calanoids *Eucalanus bungii_bungii*, *Neocalanus cristatus* and *N. plumchrus* are the predominant species. In addition to these three, other calanoids such as *Acartia clausi*, *Clausocalanus arcuicornis*, *Metridia lucens*, *Paracalanus parvus*, *Pleuromamma scutullata*, *Pseudocalanus minutus* and *Scolecithricella minor* are also dominant in the Oyashio region. In the northern Subarctic region, *Acartia longiremis* and *Calanus marshallae* must be added to this list instead of *A. clausi* and *P. parvus*.

Cyclopoid copepods *Oithona plumifera* and *O. similis* and some amphipod *Parathemisto* spp., euphausiid *Euphausia* and *Thysanoessa* spp., pteropod *Clione* and *Limacina* spp., and planktonic prochordates *Oikopleura* and *Salpa* spp. are also important occasionally (e.g. Minoda 1971; Morioka 1972; Takeuchi 1972; Motoda and Minoda 1974; Cooney and Coyle 1982: Smith and Vidal 1984; Hattori 1985, 1991; Vidal and Smith 1986; Kawamura 1988; Shiga 1990; Brodeur and Ware 1992; Odate 1993). The general size range of these herbivorous zooplankters at later growth stages are 1-8 mm for copepods and 1-3 cm for the other taxa.

All the reports listed above demonstrate that zooplankton biomass in the Subarctic Pacific is very large in summer (Fig. 27). For instance, Motoda and Minoda (1974) report that the biomass in the upper 80 m water column in the Bering Sea, and down to near bottom in the shelf water region shallower than 80 m, was 22-67

$g \cdot m^{-2}$ wet wt. A few exceptionally small values of 13-15 $g \cdot m^{-2}$ were observed in some areas (e.g., Alaskan coastal waters). These were average values for 15 summers from 1956 to 1970. The biomass in the southern Aleutian Chain (14-20 $g \cdot m^{-2}$) was generally lower than in the north, but values may be larger in the Oyashio region (Fig. 33). This regional variation was roughly opposite to that of phytoplankton, indicating the so-called top-down control of the primary production in this area. They also reported interannual fluctuations with a period of 2-3 years in the zooplankton biomass (Fig. 34).

Brodeur and Ware (1992) report the summer zooplankton biomass in the upper 150 m water column of the Gulf of Alaska. The mean biomass was 80-102 $g \cdot 1000m^{-3}$ wet wt for 1956-1962 and 230 $g \cdot 1000m^{-3}$ wet wt for 1980-1989. This is converted into 12-15 $g \cdot m^{-2}$ wet wt and 35 $g \cdot m^{-2}$ wet wt, respectively. Although the biomass was low near the southern Aleutians during 1956-1962 (Motoda and Minoda 1974), it increased significantly during 1980-1989. A clear trend of long-term increase at Ocean Station P was also detected (see also cf. Frost 1983). If this also occurred in the Bering Sea, the biomass would have doubled after the period reported by Motoda and Minoda (1974). It is important to determine this kind of long-term variability, particularly for future estimation of the carrying capacity of the entire Subarctic Pacific.

Odate (1993) reported a long-term trend in zooplankton biomass between 1952 and 1990 in the top 150 m in the sea east of North Japan. This area could be divided into three subareas, based on temperature at 100 m depth: Oyashio Region (<5°C), Mixed Water Region (5-15°C) and Kuroshio Region (>15°C) (cf. Fig. 29). In addition to regular and wide seasonal variation, long-term fluctuations were observed rather than a constant increase, particularly in the Oyashio Region (Fig. 35). When only summer (May-July) values (or the seasonal maxima) were extracted, this long-term fluctuation is evident in the Oyashio Region. In the other two regions, and especially the Kuroshio Region, a more regular increase is more likely the case (Fig. 36). The mean summer biomass over this period was 33, 13 and 7 $g \cdot m^{-2}$ wet wt, respectively, for these three regions (from north to south) (Fig. 36). The values in the Oyashio Region were comparable to those in the Bering Sea, and in the Mixed Water Region south of the Aleutian Is., during 1956-1970, and in the Gulf of Alaska before 1980.

Many authors have reported that zooplankton biomass in the surface layer decreases to low levels in winter. However, winter biomass in the subsurface layer (150-300 m) is as large as 22-176 $g \cdot m^{-2}$ wet wt in the Bering Basin region (Kitani and Komaki 1984), which is significantly larger than the summer biomass in the surface layer (cf. Fig. 33). Ontogenetic vertical migration of the annually breeding dominant zooplankton represented by Neocalanus spp. (Fulton 1973) is the reason for this phenomenon. Since their ontogeny is mostly synchronized with the seasons, the adult individuals which have attained their maximum body weight descend simultaneously to the subsurface layer in late summer and stay there during fall and winter (but cf. Miller et al. 1984).

On the other hand, small-sized copepods (Acartia, Pseudocalanus, etc.) typically reproduce several times a year (Ikeda and Motoda 1978b), so that the synchronized winter descent is not always the case, and they may be distributed in the surface layer throughout the year.

These facts suggest that both the average body size and total biomass of the zooplankton community in the surface layer are large in summer but small in winter. Therefore, the nature of the zooplankton communities is quite different between summer and winter.

Secondary Productivity

Although there is no ideal method to directly measure the production of natural zooplankton communities, several indirect methods for calculating production are available (Omori and Ikeda 1984). Because there is a balance between feeding and metabolism when the food supply is sufficient, their production can be calculated from the easily measurable rates of respiration or feeding by a simple proportional equation (e.g. Winberg 1956; Ikeda and Motoda

1978a; and also cf. Schmidt-Nielsen 1972; Peters 1983).

Metabolic rate or respiration rate of marine zooplankton is a function of body weight and ambient temperature (Ikeda 1974). Therefore, secondary production is indicated by the respiration rates, which can be calculated by using appropriate formulae which relate temperature and biomass and size composition of the herbivorous zooplankton community. The mean production in the Bering Basin region calculated in this way was 13.3 g · C · m^{-2} · yr^{-1} (Ikeda and Motoda 1978b). Another estimate based on data for feeding rates yielded a value of 19.6 g · C · m^{-2} · yr^{-1} for zooplankton in the same region (Cooney 1981, cited in Springer 1992), which is comparable to the value estimated by Ikeda and Motoda (1978b).

These values can be converted, using a carbon/wet weight ratio of 0.045 (Omori and Ikeda 1984), into values of 295.5 - 435.5 g · m^{-2} · yr^{-1} wet wt. Numerically, the latter values are roughly ten times larger than the summer biomass (cf. Fig. 33). The secondary production in the Oyashio region may be similar in the Bering Basin region, while that in the Subarctic water south of the Aleutian Chain is 50% lower (Ikeda and Motoda 1978a,b).

Microzooplankton community

The main deficiency in the above estimates is microzooplankton, which are too small to collect by conventional zooplankton nets (330-350 µm mesh). Recent knowledge about microzooplankton in the Subarctic Pacific is reviewed by Taniguchi (1989) and Zeitzschel (1990).

Microzooplankton, defined as zooplankton less than 200 µm in body size, form an important food item (together with phytoplankton) of the net (i.e. larger) zooplankton listed above. First feeding fish larvae also feed on microzooplankton. On the other hand, the feeding habits of microzooplankton are not necessarily clear. Although it has been confirmed that many microzooplankton graze on smaller phytoplankters in culture experiments, it is not clear if they actively feed on bacteria or bacterivorous pico-/nano flagellates. The possibility of direct uptake of dissolved organic matter by microzooplankton also has not yet been precisely examined.

One of the major components of the microzooplankton community is ciliated Protozoa, which spend their entire life as microzooplankton. The other is Copepoda nauplius stages, which later grow into net zooplanktonic copepodite stages. The former are the holo-microzooplankton and the latter are the meso-microzooplankton. Since the functional roles of these two groups are different in marine food webs, both should be separately counted. Abundance of holo-microzooplanktonic ciliates may be rather constant throughout the warm seasons. On the other hand, the abundance of mero-microzooplanktonic copepod nauplii varies temporarily in the Subarctic Pacific, being large in spring but decreasing in summer/fall.

The relative biomass of microzooplankton to net zooplankton in the Subarctic Pacific in summer is not large (about 15%) (cf. Figs. 37, 38). The relative biomass in the Subtropical seas (about 27%) is also small, though still significantly larger than in the Subarctic (Taniguchi 1989). However, the physiological rate per unit biomass is significantly higher in the microzooplankton than in the net zooplankton, so that the relative importance of microzooplankton in total metabolism should be high.

A few data on productivity of microzooplankton in nature have been reported for the coastal assemblages. Annual feeding rates of holo-microzooplanktonic ciliates are equivalent to 26-27 % of total phytoplankton production. The ratio becomes 52% when only nanophytoplankton smaller than 10 mm, which are the potential food of microzooplankton, is taken into account (Capriulo and Carpenter 1983; Verity 1985). The latter value undoubtedly is meaningful. From the values reported by the last authors, the annual ecological efficiency (the ratio of annual ciliate production to annual phytoplankton production) can be calculated as 7% for total phytoplankton production and 16% for nanophytoplankton.

Based on the data obtained by laboratory experiments done under abundant supply of favourable food at 17°C, the following values are calculated for the holo-microzooplanktonic ciliates: 19-60 % for the gross growth efficiency (k1) or ratio of growth to ingestion, and 1.9-19.2% h^{-1} (45.6-460% day^{-1}) for the minimum and maximum values of hourly (or daily) weight specific growth rate of growing populations. These maximum and minimum values are applicable to populations at the climax and last stages of the logarithmic growth phase, respectively. Values applicable to normal growth of natural populations are probably somewhere in between (Taniguchi 1989).

All of the values cited above indicate that the growth efficiency and productivity of microzooplankton are substantially higher than those of net zooplankton. However, because temperature is the dominant factor affecting metabolic rates of zooplankton (e.g. Ikeda and Motoda 1978a, b), much lower values should be expected in the Subarctic Pacific. The physiological rates of Subarctic microzooplankton in situ are virtually unknown at this time.

Succession of Plankton Communities in Warm Core Rings

The longevity of warm core rings (WCR) in the sea east of North Japan is often longer than one year, commonly reaching two or three years. This longer duration favours the monitoring of temporal change of a particular plankton community within an isolated water parcel. This kind of monitoring is valuable in two aspects: (1) dynamics of the community composed of greater varieties of species and niches, and (2) time-course of vertical mixing/stratification of the phytoplankton standing crops. The ecological, and probably also evolutionary, meaning of the former aspect is obvious. The latter will be very important in future analyses of satellite imagery. Once we know the time-series of relationships between surface and subsurface phenomena, it may be possible to determine the subsurface features from the surface information which appear in satellite imagery.

This kind of monitoring is not easy, because it requires a well organized mobile fleet of research vessels which can frequently visit the same WCR, which may be moving in an unforeseen way. A floating ocean laboratory or robot buoy which followed the same WCR would be a powerful tool. This has not been done in the past but is recommended as a future activity in PICES programs.

4.2 Distributions and seasonal/ interannual variations in the phytoplankton and zooplankton biomass and species composition. (D. Mackas and B. Frost)

Present information base

Over the past thirty-five years, several major multi-cruise oceanographic research programs have examined the biological oceanography of the eastern and central Subarctic Pacific, and are the basis for most of our present understanding. These include the U.S.-Canada NORPAC spatial surveys 1956-62 (LeBrasseur 1965); the 1957-1980 Canadian Ocean Weather Station P time series (McAllister 1969; Fulton 1983; Frost 1983; Parsons and Lalli 1988); spatial surveys mounted by Hokkaido University 1980-89 (Kawamura 1988); and detailed within-season time series obtained by the 1984-88 U.S.-Canada Subarctic Pacific Ecosystem Research program (Project SUPER; Miller et al. 1988, 1991a-b; Miller 1993a). There have also been important added insights provided by individual research cruises and ship-of-opportunity sampling of the Alaska gyre and the cental Subarctic region (e.g. Anderson et al. 1969; Larrance 1971; Anderson and Munson 1972; Booth et al. 1982; Taylor and Waters 1982), and by research programs in more westerly and northerly regions of the Subarctic Pacific (e.g. Heinrich 1962; Smith and Vidal 1986; Cooney 1988).

Seasonal Cycles of phytoplankton biomass and species composition

In contrast to coastal waters, where intense phytoplankton blooms occur, oceanic waters in the Alaska gyre exhibit remarkably little seasonal variation in phytoplankton biomass. Average mixed layer chlorophyll concentrations are near 0.3 mg · m^{-3} throughout the year; typical variations are about three-fold and the total observed range of variation is only about a factor of ten (see reviews and interpretation by Sambrotto and Lorenzen 1986; Parsons and Lalli 1988; and Miller et al. 1988, 1991a-b). Frost (1991) notes that variations observed at time scales less than a week and space scales of tens of kilometers are roughly comparable to the amplitude of the seasonal signal, and also summarizes evidence that this constancy of primary producer biomass occurs despite significant seasonal variation of surface irradiance, mixed layer depth, primary production rate, grazer biomass and upper layer macronutrient concentration (although the latter probably never reach levels that would strongly limit phytoplankton growth rate).

The mechanism responsible for preventing seasonal phytoplankton blooms in the oceanic Subarctic Pacific has been a long-standing scientific issue. The original explanation was that the unusual life-cycle of the dominant copepod taxa allowed them to maintain a continuous balance between phytoplankton growth and "major grazer" removal rate (Heinrich 1962; Parsons and Lalli 1988). But phytoplankton biomass in the Alaska gyre is dominated by small cells from taxonomic groups other than diatoms (Booth et al. 1982, 1993; Taylor and Waters 1982). Nearly all of the biomass consists of particles <10 µm diameter, and most consists of naked flagellates <5 µm and cyanobacteria <2µm (Booth 1988). Results from SUPER and a few earlier studies have now shown conclusively that the original "major grazer" explanation cannot be correct. Because of their small size, the dominant Subarctic Gyre phytoplankton cannot be grazed effectively or directly by the resident copepods (Dagg and Walser 1987; Landry and Lehner-Fournier 1988; Frost 1991; Dagg 1993). At most, the copepods may control the relatively small component of phytoplankton standing stock that consists of large diatoms and dinoflagellates.

Two replacement hypotheses have recently been advanced for the year-round control of total phytoplankton standing stock: a) limitation of phytoplankton growth by atmosphere- or land-derived micronutrients such as iron, either directly or through possible resulting effects on nitrate utilization (e.g. Martin and Gordon 1988; Martin 1991; Morel et al. 1991), and b) direct micrograzer control by heterotrophic flagellates and ciliates (Banse 1982; Miller et al. 1991 a-b; Frost 1991, 1993).

The relative merit of these two hypotheses is at present hotly debated, in part because of their differing implications for potential human manipulation of the rate of CO_2 removal from the atmosphere by the oceanic "biological pump". Based on present evidence, it appears that both of these new mechanisms may be important causes of the observed phytoplankton time variability. But it is unclear which, or both, consistently dominates.

Seasonal Cycles of larger zooplankton biomass and species composition

The species composition of the net (1 mm to 5 cm body size) zooplankton of the Alaska gyre is very similar to that found in the rest of the oceanic Subarctic Pacific. Total biomass is strongly dominated (especially in spring and early summer) by five large-bodied copepod species: *Neocalanus plumchrus*, *Neocalanus flemingeri*, *Neocalanus cristatus*, *Eucalanus bungii*, and *Metridia pacifica*. Euphausiids (*Euphausia pacifica*), pteropods (*Limacina* and *Clione*), chaetognaths (*Eukrohnia hamata* and *Sagitta elegans*) and salps (*Salpa fusiformis* and *Cyclosalpa bakeri*) are also common and can be major contributors to net zooplankton biomass at some times and locations.

The seasonal cycle of total zooplankton is set by the seasonal cycle of the four major copepods. Most transfer of food energy to higher trophic levels probably also passes through these species. In contrast to the relative seasonal uniformity of phytoplankton biomass, there is about a twenty-fold seasonal variation in net zooplankton biomass (February minimum about 5-20 mg · m^{-3} wet weight, May-June maximum about 100-500 mg · m^{-3}; Frost 1983). The annual peak coincides with when late copepodites of *Neocalanus* spp. are most abundant in the upper 100 m. The three *Neocalanus* species and *E.*

bungii are "interzonal migrators" (Vinogradov 1968) with a shared pattern of extensive seasonal ontogenetic vertical migration. They complete most or all of their feeding and somatic growth above the permanent pycnocline (i.e. 0-100 m) in spring and early summer, and then descend from the upper layer to spend the late summer, autumn and early winter at depths below about 400 m. The *Neocalanus* species all appear to have a purely annual life cycle in the Alaska gyre. They migrate downward from the surface layer as fattened fifth copepodites sometime in the summer, then molt to adults, mate and spawn at depth in early winter using metabolic reserves laid down in the preceding spring and summer. Their annual supply of early juveniles is therefore decoupled from current year phytoplankton supply and the abundance and biomass of young-of-the-year copepods increases roughly in phase with the spring increase in phytoplankton productivity. This was the rationale behind the original "major grazer" hypothesis for the lack of spring phytoplankton blooms in the region. The timing of spawning and development varies by a few weeks between species, and within species over their zoogeographic range (Fulton 1973, Miller and Clemons 1988, Miller and Terazaki 1989, Miller 1993b). Life cycles in the southern part of the Alaska gyre (Station P, 50°N, 145°W) have been described in detail by Miller and Clemons (1988) and Miller (1993b). There, *N. flemingeri* is the earliest to complete it's upper ocean growth, reaching fifth stage copepodite and starting it's downward migration in May to early June. *N. plumchrus* lags *N. flemingeri* by about 25 days. The departure of *N. flemingeri* and *N. plumchrus* from the upper layer is completed within a few weeks. Developmental timing of the very large copepod *N. cristatus* is similar to *N. plumchrus*. However, some late copepodites of *N. cristatus* persist considerably longer in the upper water column (to mid-August at Station P). The developmental sequence of *E. bungii* is more complex and probably involves some mixture of annual and biennial life cycle (Miller et al. 1984). In contrast to the three *Neocalanus* species, *E. bungii* adults migrate back to the upper layer in spring, and feed prior to spawning.

What do these copepods eat to fuel their annual population growth? A major conclusion from Project SUPER, based on several independent methods and lines of evidence, was that direct ingestion of phytoplankton plays only a small role in their diet in the Alaska gyre (Dagg and Walser 1987; Landry and Lehner-Fournier 1988; Miller et al. 1991a-b, Dagg 1993). This is in strong contrast to the dependence of *Neocalanus* and *Eucalanus* spp. on phytoplankton in more nearshore regions, and perhaps also in the oceanic western Subarctic Pacific. The most important food source for *N. flemingeri* and *N. plumchrus* is probably microzooplankton (Gifford and Dagg 1991; Dagg 1991; Gifford 1993), while *N. cristatus* may feed on large sinking detrital particles (Dagg in press).

Seasonal cycles of microzooplankton biomass and species composition

Microzooplankton are abundant in the Alaska gyre, both as 5-10 µm heterotrophic flagellates and as >35 µm ciliates (LeBrasseur and Kennedy 1972; Taniguchi 1984; Booth 1987; Booth et al. 1993; Strom 1993). Another major conclusion from Project SUPER, again based on several independent sets of measurements, was that the growth and feeding rates of microzooplankton make them the most plausible grazers on the small-celled phytoplankton that are dominant in the Alaska gyre (Miller et al. 1991b; Strom and Welschmeyer 1991; Landry et al. 1993).

How are microzooplankton in the Subarctic Pacific able to maintain through the winter sufficient standing stocks to limit the spring increase of phytoplankton? The present understanding is based on a small amount of data, plus inferences from the numerical models of Evans and Parslow (1985) and Frost (1991, 1993). Because the water column in the Subarctic Pacific is capped year-round by a ca. 100 m low-salinity upper layer, it does not experience the deep (>>200 m) winter mixing that is characteristic of the North Atlantic at similar latitudes. Integrated over the mixed-layer, winter light limitation of primary production is therefore less severe in the North Pacific, and winter phytoplankton production and standing stock are greater. Microzooplankton in the Subarctic Pacific therefore experience the three-fold benefits of higher winter food concentration, faster winter food production, and reduced downward mixing away from their food supply. LeBrasseur and Kennedy (1972) also note that the ontogenetic seasonal migration of the dominant copepod species result in relatively low autumn and winter predation pressure on the microzooplankton. However, there is a clear need to test these ideas by extending to the autumn and winter seasons the range of detailed rate measurements carried out in spring and summer by Project SUPER.

Vertical distributions

Vertical distributions of phytoplankton, microzooplankton, and net zooplankton are all closely tied to physical structure of the water column. The average seasonal progression of water column structure at Station P is well known from the 30 year weathership time series (Tabata 1961, Tully and Giovando 1963). The following summary of their conclusions is taken from Mackas et al. (1993):

The depth of winter mixing in the Subarctic Pacific is much less than in the Subarctic Atlantic. Salinity stratification of the layer above the permanent pycnocline is weak throughout the year, and stability of the upper water column is controlled mostly by the temperature profile. Breakdown of the thermal stratification from the summer season lags the solar calendar by several months and is cumulative from early autumn to early spring. By March-April of each year, the water column is isothermal and isohaline from the surface down to the top of the permanent halocline. In mid- to late-spring, seasonal increases of insolation plus (slightly) moderating winds start a new cycle of thermal stratification of the upper water column. But the physical stratification process is not steady. Rather, it is episodically interrupted by storms in April-June that re-establish a surface mixed layer and, by downward mixing of warmed surface water and erosion of the underlying layer, produce transient and relatively weak, step-like subsurface thermal gradients at depths ranging from near-surface down to the permanent halocline (Tully and Giovando 1963, Denman and Gargett 1988). Spring-season storms can be violent and the resultant mixing of salt and nutrients across the permanent pycnocline very strong compared to any other season.

Detailed sampling by Booth (1988) and Booth et al. (1993) showed that phytoplankton at Station P extend broadly from the surface down to about 80-100 m. In spring, biomass is highest in the upper mixed layer. In late summer it is usually highest between the seasonal thermocline and the permanent pycnocline. But vertical gradients in phytoplankton biomass and species composition are not particularly strong (roughly factor of two range around the upper water column average). Vertical variations in physiologic state and rates are stronger. Denman and Gargett used vertical variation in fluorescence yield to interpret the rate and depth penetration of upper layer mixing. They concluded that weak upper layer stratification (about 0.25°C over about 5-10 m) is sufficient to inhibit vertical transfer of mixing energy downward from the surface layer. Booth et al. (1988, 1993), Forbes et al. (1988) and Welschmeyer et al. (1991) showed that carbon fixation and net phytoplankton growth rate are highest in the upper 20 m, and near-zero below about 40 m. Vertical differences reflect gradients in light rather than macro-nutrient availability.

Booth et al. (1993) reported on vertical distribution of microzooplankton biomass, including heterotrophic flagellates, dinoflagellates, and ciliates, at Station P. Total microzooplankton were broadly distributed in the upper 100 m, but were often most abundant in the mixed layer and upper portion of the seasonal thermocline. Concentrations were 10-60 µg-C $\cdot$ l^{-1} in near-surface maxima and usually <1 µg-C $\cdot$ l^{-1} below 80 m. Strom (1993) examined vertical distributions of the larger ciliate microzooplankton in greater detail. She found maximum ciliate biomass (about 4 µg-C $\cdot$ l^{-1}) in the mixed layer and <1 µg-C $\cdot$ l^{-1} at depths well below the upper (seasonal) thermocline. Some, but not all, profiles had a weak subsurface maximum near this temperature step. The general pattern of mixed layer or upper thermocline maximum, and low ciliate biomass below the thermocline was present in both spring and late summer profiles.

Net zooplankton biomass is strongly concentrated above 100 m during the spring-summer growing season of the dominant copepods. The most detailed vertical distributions are reported by Marlowe and Miller (1975), Forbes et al. (1988) and Mackas et al. (1993). Of the dominant taxa, only a few show detectable diel vertical migration. *Metridia pacifica*, *Euphausia pacifica*, *Sagitta elegans*, and *Cyclosalpa bakeri* migrate consistently from near surface (night) to >100 m (day). Diel migration over several tens of meters by *Neocalanus cristatus* and/or *Eucalanus bungii* was observed on a few occasions but was absent on many others; there may be a seasonal component with diel migration by *N. cristatus* and *Eucalanus* more likely in mid-summer than in spring or early summer (compare Marlowe and Miller 1975 with Mackas et al. 1993).

A striking feature of the copepod profiles is the vertical partitioning of the upper 100 m by the biomass dominants *Neocalanus plumchrus*, *N. flemingeri*, *N. cristatus*, and *Eucalanus bungii*. In spring and early summer, there is consistently a near-surface pair (*N. plumchrus* and *N. flemingeri*) distributed between the sea-surface and about 25-40 m depth, and a subsurface pair (*N. cristatus* and *E. bungii*) extending from the lower limit of the surface pair down to about 150 m. The exact depth of the boundary between these groups shifted vertically depending on sampling date and location, but was sharply defined and was very often coincident with the weak and transient thermocline (25-40 m depth) defining the base of the upper mixed layer. Mackas et al. (1993) present evidence that the cause for this vertical stratification of copepod species is direct and differing behavioral response to the local intensity of turbulence.

Horizontal distributions

Horizontal spatial pattern at gyre scales of 1000s of km is controlled by the large-scale patterns of upper layer circulation and nutrient input (McGowan 1971). Zooplankton species composition remains relatively uniform to the continental margins along the east, north, and west margins of the Alaska gyre, but changes rapidly near the continental shelf breaks (to a more coastal fauna) and along the southern margin of the gyre (to an oceanic Transition Zone fauna). The phytoplankton community becomes more seasonally variable and dominated by larger cells with decreasing distance from the coast (Sambrotto and Lorenzen 1986).

Three- to ten-fold biomass gradients due to small-scale (1-50 km) patchiness are normal in both zooplankton and phytoplankton distributions (Kawamura and Hirano 1985; Frost 1991; Mackas et al. 1993). We do not yet have a good theoretical understanding of how these patches form and evolve in the Alaska gyre, but several studies (e.g. Mackas and Louttit 1988, Hamner and Schneider 1986) indicate interaction between plankton swimming behaviour and small-scale flow-field perturbations such as convergences and fronts. There is evidence of the presence of mesoscale, long-lived (>2 yr) eddies (Cummins 1989, Musgrave et al. 1992) that might have significant influences on plankton distributions in the Gulf of Alaska.

Interannual variability

This is clearly a question of major practical significance for PICES, because of its relevance to fisheries and climate-change issues. To date, we know almost nothing about the intensity and cause of interannual variability of the Subarctic Pacific phytoplankton community. Several studies have examined low-frequency variability of zooplankton biomass (Wickett 1967; Longhurst et al. 1972; Fulton 1983; Frost 1983; Fulton and LeBrasseur 1985; and Brodeur and Ware 1992) and body size (Miller, Fulton and Frost 1992) in the Alaska gyre. All conclude that there is substantial variability at time scales between interannual and decadal. Unfortunately, much of our interpretation is based on the Station P time series. Because Station P is located very near the southern margin of the Alaska gyre, it is difficult to interpret how much of the observed variability represents changes in the entire gyre, and how much is caused by small (or large) north-south shifts in the Subarctic Boundary (Fulton and LeBrasseur 1985). Brodeur and Ware (1992) include spatially-distributed data, so their conclusions may be the most broadly applicable. They find an approximate doubling of zooplankton biomass over the three decade time span from 1959-1962 to 1980-1989, and a positive correlation between the intensity of winter winds and zooplankton biomass in the following summer.

What causes these variations? Year-to-year body-size fluctuations of two of the dominant copepods, *N. plumchrus* and *N. flemingeri* (Miller et al. 1992) are particularly provocative. These species do not appear to be well-nourished in the open Subarctic Pacific, where their body size is very much smaller than in more productive environments such as the Bering Sea. The smaller year-to-year body size variations at Station P are correlated between the two copepod species, despite about a month's offset in their seasonal developmental cycles. So we might expect their mutual size variation to reflect rather broad and persistent year-to-year differences in primary productivity. But the size variations are NOT correlated with total zooplankton biomass fluctuations, nor with upper layer temperature, salinity, and Ekman transport anomalies. They are correlated, but negatively, with estimates of annual new production based on oxygen concentration.

There is increasing evidence for coupling between decadal-scale anomalies in large-scale winter atmospheric pressure patterns over the North Pacific, and upper ocean circulation and water properties. Project SUPER observed large between-year differences in upper layer nitrate that were attributable to the presence or absence of strong storms in early spring (Wheeler and Kokkinakis 1990; Miller et al. 1991b). Improved process studies are needed to sort out the real linkages, including possible interannual variations in the input of limiting trace nutrients.

4.3 Distributions and seasonal/interannual variations in the biomass of dominant species in the higher trophic levels of the Alaskan Gyre and marginal seas. (W. Pearcy)

The Subarctic Pacific ecosystem is simple and productive. It is characterized by a large biomass but a low diversity of nektonic animals, such as fishes and squids, compared to tropical or subtropical waters. Much of what is known about the nekton of the Subarctic Gyre has been obtained from the catches of gill nets and purse seines that sample near-surface waters. Most of these collections are from summer months, so our knowledge is limited seasonally.

Seasonal Variations

According to Dodimead et al. (1963), the Subarctic Pacific Water Mass in the eastern Pacific includes both the Central Subarctic Domain and the Transitional Domain. The Alaska Gyre is a portion of the Central Subarctic Domain. Many of the common species of nektonic animals that are found in the Transitional Domain, or even subtropical waters during the winter, undertake feeding migrations into gyre waters during the summer. These transient species are important constituents of structure and dynamics of the gyre region during the season of peak production.

Some species, such as salmonids, salmon shark and some gonatid squids are usually found north of the Transitional Domain all year, although seasonal north-south migrations occur within Subarctic water. Other common species, e.g. Pacific pomfret, Pacific saury, and blue shark migrate into the Subarctic Gyre during the summer and retreat to warmer waters of the Transitional Domain or the subtropics during the winter. Other species, e.g. flying squid and albacore may overlap in distribution with migrant species, especially during the winter, but usually do not penetrate into central Subarctic waters and are considered transitional species. Because of these extensive migrations, species inhabiting central gyres may interact, directly or indirectly, with species found far to the south during the winter. These north-south movements of common species are correlated with seasonal warming and cooling events.

Interannual variations

Year-to-year variations in the catches of salmonids and other species in gill nets have been documented in this region. These are due to variations in actual abundances as well as variations in catchability and availability. The distribution of salmonids is known to be influenced by oceanographic factors, such as temperature, resulting in interannual fluctuations in the southern and northern boundaries of catches.

Long-term variations in the carrying capacity of the North Pacific and abundances of salmonids have been pronounced in the Subarctic Gyre in recent years. Commercial salmon harvest of Alaska increased dramatically after 1976 and has remained high through much of the 1980s and 1990s, exceeding the historic high catches in the 1930s. Changes in atmospheric circulation associated with a deep Aleutian Low displaced to the east, and changes in ocean circulation associated with increased advection from the Subarctic Current into the Alaskan Current and intensification of gyral circulation are correlated with this regime change in salmon production. Apparently these physical changes have resulted in warmer oceanic temperatures and increased production or availability of zooplankton, leading to increased salmon production. These changes appear to be out-of-phase with those in the California Current, where weak upwelling and warm temperatures have resulted in poor ocean conditions for stocks of coho and chinook salmon since 1976.

Ranching of pink and chum salmon around the Pacific Rim has contributed to the record returns of salmon in Subarctic waters since 1976. In recent years, the average size of fish returning to some hatcheries has decreased. This raises the question of the carrying capacity of the Subarctic Pacific and its ability to produce even more salmon. Density-dependent growth and mortality may become a serious concern, especially if the carrying capacity declines to a lower, pre-1976 level.

The gillnet fishery for flying squid in the North Pacific resulted in the death of over a billion Pacific pomfret during some years. Since pomfret and salmon often feed on the same prey during the summer, a reduced pomfret population may have benefited salmon stocks. Also, reduced population of fur seals and northern sea lions may have positive effects on salmonids. Such changes may influence the growth and survival of salmonids and other key species in the ecosystem.

Some of the main problems and questions that need to be solved include:

1. How is the trophic/species structure of the Alaskan Gyre affected by climatic regime changes? A review of our knowledge of the numbers, biomass and production of the nektonic species in the gyre during the summer is needed along with better information on the food web, estimates on the amount of primary and secondary production consumed directly or indirectly by common species, and estimates of the degree of dietary overlap among species. Such a review should help to us to model changes in trophic structure and production after major regimes shifts.

2. Is the increased salmon production in the Alaskan Gyre caused by increased primary and secondary productivity? Studies are needed to describe the physical and biological causes of the increased carrying capacity for salmonids. How much of the increased production can be ascribed to intensification of the gyre and Ekman pumping of nutrients into the euphotic zone? Since major nutrients are not thought to limit plant production in the Gulf of Alaska, what factors are responsible for higher production levels. Is it availability of iron? Or has advection of zooplankton into coastal regions by intensification of gyral circulation caused increased survival of juvenile salmon in their coastal migration corridors independent of oceanic productivity?

PICES should review existing oceanographic research in regions of interest and consider collaborative, long-term programs to effectively monitor productivity and climate change in the Subarctic Pacific Ocean during the next decade.

3. We need to examine the evidence for density-dependent growth and survival of salmon to learn what species and stocks are affected. When in their life history is density dependence most obvious - during juvenile stages in coastal seas or in oceanic phases? Does the recent phenomenal increase in production apply to stocks feeding in both the eastern and western gyres, or to mainly to the Alaskan Gyre and only a few stocks? Is it reflected in larger sizes for a given age of fish? What stocks have been negatively affected? Such a study will help to detect critical stages in the life history of salmon, and areas where competition for food may be acute.

Since pomfret populations have been intensively fished, and pomfret and salmon potentially compete for food during the summer, a reliable method of aging pomfret is needed to enable a study of density-dependent growth of this important species. Have their growth rates increased concomitant with increased salmon production, or with intensified mortality of their stocks?

4. If present trends of salmon ranching and enhancement continue, and the carrying capacity of the ocean is exceeded, adults salmon may return at increasingly smaller sizes in the future. To avoid a "tragedy of the commons" scenario, PICES should study the effects of releasing optimal numbers of juvenile salmon from hatcheries to maximize economic benefits.

4.4 Review of the studies of variations in Benthic and Midwater fish populations (R.D. Brodeur and A.B. Hollowed)

Evidence is accumulating that coastal fish populations in the northeast Pacific Ocean undergo major shifts in abundance level that appear to be related to large-scale oceanographic conditions (Hollowed et al. 1987; Hollowed and Wooster 1991; Beamish 1993). Large-scale changes in the physical environment (Hanawa 1991) and pelagic fish production (Terazaki 1989; Kawasaki 1991) have been noted in the western North Pacific, but few data exist to confirm similar long-term changes in demersal fish populations in this region. Numerous studies have found significant relationships between indices of year class strength of individual stocks of marine fish and large-scale factors (see Table 2 for examples from the Eastern North Pacific). Many hypotheses have been advanced to explain these relationships (Wooster and Bailey 1989). One hypothesis is that the large-scale oceanic circulation influences secondary production available to coastal fish stocks. A link between atmospheric conditions and plankton production in the Subarctic Gyre has been established (Brodeur and Ware 1992) and this relationship has been extended to the production of a coastal fish species (McFarlane and Beamish 1992).

This increased secondary production may translate into increased production of coastal fishes in several ways. First, the increase in food available may increase survival of the larval and pelagic juvenile stages of many species leading to higher numbers recruiting to the fishery. Second, increased food for adult fishes increases growth and allows fish to reach a larger size for a given age increasing yield. Finally, larger fish show greater fecundity and produce more offspring, thus potentially increasing production yet further in cases where a strong relationship exists between spawners and recruits.

The main distribution of many of the dominant demersal stocks is within the Coastal Downwelling Domain (Ware and McFarlane 1989) so that, unlike many of the pelagic fisheries which are dependent on production occurring from local upwelling (e.g., Nickelson 1986; Hollowed and Bailey 1989; Ware and Thomson 1991), these species appear to rely on production cycles forced from outside their distribution range. Cooney (1984) has calculated that coastal production along the Northern Gulf of Alaska is not sufficient to sustain the large numbers of juvenile salmon which migrate through the area each summer and that offshore copepods advected onto the shelf supplement the food resources at that time. This onshore advection of production may result in part from increased the spin of the gyre. Brodeur and Ware (1992) found the highest biomass of zooplankton around the edge of the gyre during the 1980s, a period of high wind stress.

Another source of oceanic production may come from advection through the Subarctic Current and its divergence into the Alaska and California Current. A band of increase primary production is evident in satellite images in the area of the Subarctic front and a similar band is seen in maps of zooplankton biomass distribution. The mechanism generating this enhanced productivity is unknown but if this oceanic production is advected to coastal regions, then the area downstream from it may benefit greatly. Chelton (1984) has hypothesized that the flow into the Alaska Gyre and California Current fluctuate out of phase suggesting that the divergence flow may not be equal between the two systems. Hollowed and Wooster (1992) have found that different oceanic and production regimes may be associated with each condition. It is not known whether these changes in fish production are mediated through changes in temperature or food production, or both.

Proposed research

A concerted effort on the part of all PICES member states and many laboratories will be needed over several years in order to answer some of the questions posed. We propose the following research to address each of the topics listed above.

1. A large-scale physical and biological oceanographic program will be needed to monitor a series of key transects around the North Pacific rim at least through the spring and summer months but preferably once a month for a whole year. These transects would extend out a sufficient distance to encompass the major currents in coastal waters with an additional 1-2 transects in oceanic waters across the Kurushio Extension/Subarctic Current.

   Some likely transects are given in Table 3 along with some possible institutions/countries that might be able to conduct the sampling (given sufficient funding). We propose that the following suite of measurements and samples be made along these transects: 1) current speed and direction, 2) temperature and salinity profiles, 3) nutrients, 4) chlorophyll, 5) zooplankton collections, and 6) micronekton collections. A high degree of consistency in sampling techniques among laboratories would be a necessity.

2. We will need to construct long time series of spawner biomass and recruitment for as many stocks of pelagic and demersal fishes as possible from the western North Pacific to see if there are any synchronous strong year classes and if so, how do these years match with those in the Eastern North Pacific and Atlantic Oceans. These time series may be constructed from stock surveys or data available from the fisheries (cohort analysis) but should include data from all nations involved.

3. We need to locate all possible sites with anoxic basins throughout the Pacific rim similar to those found off Southern California and take representative core samples from each. Analysis of the sedimentary record could be done by a team of paleobiologists from several nations working together at one laboratory.

4. We will need to examine historical groundfish and pelagic surveys to examine how species distributions change through time, particularly at the transitional periods between environmental regimes. Adult spawner or early pelagic egg distributions could be examined to determine changes in spawning habitat.

5. The available otolith data from all laboratories needs to be inventoried and comparisons then made of yearly growth patterns among several species which occur over a wide distributional range. We might expect to find major changes in growth patterns associated with regime shifts or

dramatic changes in the abundance of that species or some trophically-similar species.

4.5 How To Estimate Carrying Capacity For Nektonic Species? (Y.Ishida, D.W. Welch, and K. Shimazaki)

Introduction

Recent production of Pacific salmon has reached more than 300 million fish, or about 800,000 metric tons. This is similar to or exceeds the peak historical catches made in the 1930s (Pearcy 1992; Welch 1992; Ishida 1992). This increase in salmon production in the North Pacific raises several scientific questions which need to be clarified for both scientific and economic reasons. One of these questions concerns whether the carrying capacity of the North Pacific ocean can be quantified for fish in general, and salmonids in particular.

This paper summarizes information relevant to assessing the salmonid carrying capacity of the North Pacific, and the potential response to climate change in the North Pacific Ocean.

Dominant Fish Species

Based on FAO catch statistics from 1986 to 1990, the major fish species in the Northeast (40N° - 65°N, 175°W - 125°W; Area Code 67) and Northwest (20N° - 65°N, 115°E - 175°W; Area Code 61) Pacific Ocean are six species of Pacific salmon (sockeye, *Oncorhynchus nerka*; chum, *O. keta*; pink, *O. gorbuscha*; coho, *O. kisutch*; chinook, *O. tshawytscha*; and steelhead, *O. mykiss*), flatfishes (Pleuronectiformes). Pacific halibut (*Hippoglossus stenolepis*), yellowfin sole (*Limansa aspera*), rock sole (*Lepidopsetta bilineata*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), North Pacific hake (*Merluccius productus*), Pacific ocean perch (*Sebastes alutus*), scorpionfishes (Scorpaenidae), Arabesque greenling (*Pleurogrammus azonus*), sablefish (*Anoplopoma fimbria*), Pacific herring (*Clupea pallasii*), Pacific saury (*Cololabis saira*), Japanese sardine (*Sardinops melanostictus*), and Japanese anchovy (*Engraulis japonicus*) .

Ware and McFarlane (1989) estimated that average catch/biomass (C/B) ratio in the Central Subarctic Domain in the northeast Pacific, which is dominated by sockeye, chum and pink salmon, is 0.33. If we apply this ratio to all the FAO catch statistics, the biomass of the major salmon species in the North Pacific Ocean would be about 3 times the FAO average catches.

In addition to these species, Japanese research vessel data show that pomfret (*Brama japonica*), flying squid (*Ommastrephes bartrami*), boreal clubhook squid (*Onychoteuthis borealijaponica*), blue shark (*Prionace glauca*), and salmon shark (*Lamma ditropis*) are dominant species in the subarctic North Pacific Ocean (Shimazaki 1986; Brodeur 1988). Also marine mammals such as sperm whale (*Physeter catodon*), Dall's porpoise (*Phocoenoides dalli*), Stellar sea lions (*Eumetopias jubatus*), and northern fur seal (*Callorhinus ursinus*) are significant components of the subarctic North Pacific ecosystem (Laevastu and Larkins 1981; Springer 1992).

Among these species, salmon are economically important to Canada, Japan, the United States, and Russia, and probably to China and Korea in the future.

Identifying Density-Dependent Interactions (Carrying Capacity)

Enhancement programs for salmon are based on the assumption that the ocean has adequate productive capacity to support more salmon. This assumption is supported by theoretical calculations of food chain efficiencies based on plankton production data for the North Pacific Ocean suggest that salmon use only a small fraction of the food production available to them (Sanger 1972).

In essence, a practical limit to the carrying capacity of the North Pacific (or some sub-regions) will occur when oceanic production is insufficient to support the stock and species aggregates that are present, each of which will have its own freshwater stock-recruitment relationship. Identification of individual stock-recruitment relationships for specific stocks in freshwater does not preclude the potential for ocean carrying capacity limitations to also significantly limit salmon production.

Sanger (1972) reviewed the pertinent literature on the primary production and fishery potential of the Subarctic Pacific Region. He estimated the annual primary production of the Subarctic Pacific Region, which is defined as the portion of the North Pacific Ocean north of 40°N including the Bering Sea, the Sea of Okhotsk, and the Sea of Japan, was estimated at $1.28 \cdot 10^9$ $t \cdot C \cdot yr^{-1}$ in the early 1970s. Assuming a simplified food chain relation for biological production, the potential fish production of the Region was estimated at 26-78 million $t \cdot yr^{-1}$. Taking as a rough estimate that 50% is potentially harvestable, average landings (6.6 million $t \cdot yr^{-1}$ in recent years) would have to have increased four-fold to equal this potential. Landings for the Region were formerly stable at about 0.4 million $t \cdot yr^{-1}$. An assumed total salmon production (catch + escape + mortality) of 1.2 million $t \cdot yr^{-1}$ equals about 1.5% of the estimated total fishery potential.

Based on Sanger's (1972) analysis, salmon would appear to play a small role in the ecology of the North Pacific, and there would appear to be little likelihood that the oceanic production of salmon would be impacted by density-dependent (carrying capacity) effects except possibly for certain times and places. However, as Mackas and Frost (this report) note, much of the primary production is now recognized as flowing into the micro-zooplankton community, which is a highly inefficient link in the food chain. Earlier food chain calculations, which did not recognize the existence of this link and suggested that there must be an over-abundance of the forage base relative to the abundance of salmon, are therefore in error. ***Furthermore, as we review below, this prediction of an overabundance of food relative to salmon densities does not agree with observations that oceanic salmon production (as measured by somatic growth rates) is in fact affected by salmon density in many regions of the subarctic Pacific.***

Empirical Evidence for a Finite Ocean Carrying Capacity

Despite Sanger's theoretical calculations, density-dependent growth and survival process occur in the ocean within and among stocks and species of Pacific salmon and other fishes. These density-dependent processes can generate lower benefits than expected from the increases in abundance that result from extensive enhancement projects (Peterman 1991). For example, the size of adult Japanese chum salmon has decreased by roughly 25% since 1970. The size of Russian chum salmon has also fallen in recent years (Ishida et al. 1993; Kaeriyama 1989). In both cases the cause of these changes is unknown, but the potential effect of efforts to enhance salmon populations that are currently occurring around the Pacific Rim needs to be considered carefully.

Evidence for large scale density-dependent interactions on the high seas comes primarily from studies demonstrating inverse relationships between the terminal size at capture of various salmon species. These studies indicate that growth rates must be depressed at some point or points during the marine life history phase. The available evidence points to this density-dependent reduction in growth occurring primarily during the specific year of life on the high seas (Ishida *et al*. 1993)

Data exist to demonstrate apparent between-species trophic competition with pink salmon in the western North Pacific for coho (Ogura *et al*. 1990 a and b), and sockeye (Krogius 1960; Bugaev *et al. MS*). In both species growth rates were lower in years of large pink salmon populations in the western North Pacific. There is also good evidence for intra-specific trophic competition occurring for the abundant salmon species, with growth rates inversely related to stock size for pink (IPSFC 1984; Peterman 1987), sockeye (Peterman 1984), and chum salmon (Kaeriyama *in press*; Ishida *et al.* 1993). In contrast, we have found no reports of chum salmon abundance influencing the growth rates of other salmon species, although evidence for self-depression of chum salmon growth by chum abundance is well documented.

Empirical evidence also indicates that the mean weight of stomach contents changes much less for chum salmon than for sockeye in years when pink salmon populations are high in the western North Pacific (Sano 1963; Ito 1964; Tadokoro, *pers. comm.*). This suggests that the unusual diet of chum salmon may help to buffer their populations, by reducing direct trophic competition with other salmon (Welch *et al, in press*).

The key point from these studies is that although theoretical calculations based on typical food chain considerations suggest that the ocean should **not** be limiting salmon production, marine rates of growth and feeding clearly do indicate that such limits do exist. As net production can be defined as the product of survival x growth, these limts can directly impact rates of salmon production by Pacific Rim states. What is unclear is the extent to which these interactions occur between species, and the degree to which different salmon stocks will be impacted.

Methods for Estimating Salmon Carrying Capacity

Limitations to Statistical Analysis

There are six species of Pacific salmon, of which three (sockeye, pink, and chum) are abundant and form the majority of the salmonid biomass production in the North Pacific Ocean. There are also, however, four countries whose salmon production is of significance, and who may consider large scale increases in salmon production in the future. However, each countries' salmon occupy different parts of the North Pacific, and the degrees of overlap are not symmetrical.

At a minimum, a complete description of the salmonid carrying capacity of the North Pacific Ocean would require estimating 12 interaction coefficients per species and country, in order to describe the impact of further production increases on other species and other countries. This calculation includes self inhibition of growth or survival. As a result, a total of 12^2, or 144 interaction coefficients would have to be estimated simply to take into account the most abundant species.

Such estimations go far beyond what the available data can support. Alternative approaches to estimating the impacts of different stocks on each other must therefore be used, in order to reduce the number of possible interactions that need to be considered. For example, species of salmon that feed higher up the food chain are unlikely to be trophic competitors with species that feed farther down the food chain. As a result, species feeding higher up the food chain are unlikely to have a major impact on the growth and somatic production of species feeding lower down, whereas the reverse may be true.

In general, the greater the trophic separation the lower the probability of competition. Sockeye tend to feed higher up the food chain than pink salmon (Azuma 1992; Pearcy *et al.* 1988), thus enhanced production of pink salmon is more likely to impact sockeye production than vice versa. In contrast, chum salmon feed at an indeterminate position, because their diet includes a large, but currently poorly quantified, amount of gelatinous zooplankton (Black and Low 1983).

As the trophic role of gelatinous zooplankton is not well understood, it is unclear just how important feeding on these organisms is for the production dynamics of chum salmon. However, Japan produces primarily chum salmon. If chum salmon feed higher up the food chain than pink salmon, and primarily on a branch of the food chain not exploited by other salmon species, then it is reasonable to expect that further production of chum salmon might not impact the production of other salmon species to the extent that it might otherwise have (Welch and Parsons 1993). This conjecture needs to be tested and further evaluated.

Bottom up estimation

A schematic presentation of a conventional food web model is given in Figure 39 (from Fig. 7 of Laevastu and Larkins 1981). Although there are some weaknesses in this approach, the following is an example of its application in coastal and open waters.

Simenstad and Salo (1982) estimated the carrying capacity of juvenile chum salmon in Hood Canal, Washington, U.S.A. Juveniles entering the Canal early in the outmigration period (February and March) encounter relatively meagre prey resources in shallow sublittoral and neritic habitats. Rapid migration rates (7 - 14 $km \cdot d^{-1}$) during this period suggest a behavioral response to low prey availability might be immediate migration into regions with more prey. In spring, epibenthic and neritic zoo-plankton increase, and migration rates decline (3 - 5 $km \cdot d^{-1}$) as the juvenile salmon spend more time foraging in estuarine and nearshore habitats, but upon growing to 45 - 55 mm FL, move into neritic habitats and start eating pelagic and nektonic organisms such as calanoid copepods, hyperiid amphipods, and larvacians. This transition is theorized to be the result of prey resource depression and growth of the fish to the point that they can feed upon larger neritic organisms and avoid predators. Assuming the size-dependent daily rations between 15 and 25 percent of the total body weight per day, the estimated carrying capacity of juvenile chum salmon in Hood Canal for two week periods ranged from 0.03 - 0.65 fish $\cdot m^{-2}$ in shallow sublittoral habitats and from 0.01 - 0.07 fish $\cdot m^{-2}$ in neritic habitats based on the total biweekly prey production.

Theoretically, using this type of approach it is possible to estimate the salmonid carrying capacity of the North Pacific Ocean, but detailed estimation of the total prey production is not feasible, owing to the vast area of salmon distribution in the North Pacific Ocean. However, satellite monitoring of primary production might provide a useful index for matching with the changes in salmon production.

Top down estimation

The principles of trophodynamic computations are schematically shown in Figure 40 (from Fig. 5 of Laevastu and Larkins 1981). These computations permit determination of who eats what and how much and, consequently, how much of each (consumed) species must be present in order to produce the eaten amounts, using empirically determined growth coefficients (Laevastu and Larkins 1981).

Favorite and Laevastu (1979) developed a transpacific, numerical, salmon ecosystem simulation model (NOPASA) and they concluded that the forage base of the North Pacific is far from being reached by Pacific salmon and that salmon production can be increased significantly above present levels. However, predation on salmon (e.g. by mammals) may seriously limit salmon production.

Estimation based on historical peak catches

Salo (1991) estimated that the total biomass of immature and mature chum salmon (standing stock in the North Pacific would have weighed between 860,000 and 1,300,000 mt based on peak historical catches in 1936, using a catch:escapement ratio of 2:1, and the estimated age composition for the catch in the 1930s.

However, the assumptions used are not necessarily valid because changes in ocean productivity, changes in relative abundance of food species, competitors, and predators, and "fishing-up" effects reflected in the peak historical catches (Peterman 1991) will all tend to distort these estimates.

Several papers have also shown that the abundance of marine mammal predators, such as the northern fur seal (*Callorhinus ursinus*) and Stellar sea lions (*Eumatopias jubatus*) has declined during the past 15-20 years. These species consumed salmon as one of their food resources, although they utilized other species such as walleye pollock (Springer 1992; Kajimura and Loughlin 1988). Their decline may improve the marine productivity of salmon stocks.

Changes in North Pacific Salmon Productivity:

The subarctic Pacific is the feeding and nursery grounds for the majority of salmon production. Some two-thirds or more of the life history of Pacific salmon is normally spent in the pelagic environment of the open Pacific Ocean. During this time most somatic growth is completed (Ricker 1962, 1976), and a significant fraction of total cohort mortality also occurs (Parker 1962; Ricker 1962, 1976). However, despite the length of this period in the life cycle, relatively little is known about the biological dynamics underlying the pelagic period of the life history, and their influence on the production dynamics of Pacific salmon.

(i) Changes in productivity per unit area

Unlike the North Atlantic, phytoplankton biomass in the North Pacific remains quite constant throughout the year, including the spring bloom (Mackas and Frost, this report). However, analysis of Secchi disk data also suggests that phytoplankton productivity has remained essentially unchanged in the North Pacific this century (Falowski and Wilson 1993).

Several lines of evidence point to a change in North Pacific productivity at higher trophic levels. The amount of chlorophyll in the central North Pacific gyre doubled between 1965 and 1985 (Venrich et al. 1987), and a similar doubling in zooplankton biomass in the Gulf of Alaska also occurred between the 1950s and 1980s (Brodeur and Ware 1992). A similar trend in zooplankton abundance is apparent in the western North Pacific (Odate 1986) - although perhaps not in the central North Pacific (Kawamura 1988). The productivity of many fish populations in the NE Pacific has also shown sharp increases, beginning in the late 1970s (Beamish 1993). Taken together, this evidence suggests that the North Pacific is a tightly coupled system, where the effects of physical changes in upper ocean dynamics can be quickly passed up the food chain to influence fish production. Salmon, as the dominant high level predators within this system, may therefore provide an excellent focus for studies of the effects of the ocean environment on fish production.

Similar changes in a wide range of physical oceanographic variables have also occurred in the eastern Pacific (Kerr 1992). These changes may be associated with the intensification of the Aleutian Low (Trenberth 1990), a major meteorological system which dominates the weather of the North Pacific region.

The detailed reasons for these increases in productivity at higher trophic levels are currently unknown. They could involve increased levels of wind-driven mixing of sub-surface nutrients through the thermocline, shifts in phytoplankton community structure towards more intrinsically productive species, increased insolation or, at least in costal regions, shifts in food web structure (Brodeur and Pearcy 1992). However, the net result is that in tightly coupled systems such as the North Pacific, there have been striking changes in biological productivity at higher trophic levels, the mechanisms for which have not yet been fully explained. These changes should influence the dynamics of Pacific salmon, and need to be better understood.

(ii) Changes in the Productive Area of the North Pacific for Salmon

In addition to changes in the productivity per unit area of the north Pacific, changes in the amount of ocean habitat available to Pacific salmon may have also occurred. Although salmon are widely distributed in the North Pacific Ocean, the southern limit of their distribution is sharply limited by temperature (Welch, Chigirinsky and Ishida, *submitted*; Welch, Ishida and Nagasawa, *in prep.*). Figures 41 and 42 demonstrate the sharp thermal limits found in the spring that define the southern boundary to the oceanic distribution of Pacific salmon, while Figure 43 shows the sharp changes in salmon abundance by species that result when these thermal limits are applied to the spring 1990 sea surface temperature field for the Gulf of Alaska. The subarctic boundary, traditionally defined as the southern boundary to the salmon distribution, occurs at about 39°N, or at the southern edge of this plot. The sharp southern edge to the salmon distribution clearly lies well to the north of this position. As a result, the area of the subarctic north Pacific lying within the thermal limits of Pacific salmon, or their thermal habitat, is only a fraction of the total area of the subarctic North Pacific in at least some seasons.

Climate change, on any time scale, could influence the productivity of salmon populations by restricting the area of the north Pacific available to salmon. This could happen if the oceanic forage base of salmon is already limiting, and salmon were prevented from foraging in some parts of their former range. Alternatively, if the distribution of Pacific salmon should change so that greater numbers of salmon were restricted to specific parts of their former range, then localized overabundance relative to their food supply could still occur.

Analysis of AVHRR satellite imagery for the Gulf of Alaska shows that very large interannual changes in the position and area of thermal habitat available to salmon have occurred since 1982 (Welch, Thomson, LeBlond, and Jardine, *in prep.* and Fig. 44). For example, in the El Niño years 1982-3 the amount of warming that occurred reduced the amount of thermal habitat lying within the range found in recent field experiments by Welch, Ishida, and Nagasawa (*in prep.*) to zero (Fig. 44). Under such conditions, which are similar to those predicted to occur as ***average*** conditions under global warming for the region, salmon must have violated the sharp thermal boundaries found in recent surveys. This restriction of thermally available habitat seems to have had a large negative impact on the growth of pink salmon (Welch and Morris *in prep*. and Fig. 45), and on the survival of sockeye salmon (Rogers 1984).

Changes in Marine Growth Rates:

The scales of Pacific salmon contain an annual record of growth rate variations that reflect the combined effects of changes in oceanic production and density-dependent interactions. As we have reviewed above, although the density of salmon on the high seas seems to be too low for interactions to occur, there is considerable evidence for such interactions, reflected in both changes in the amount of stomach contents present when competitors are in abundance, and in the terminal sizes of adult salmon on both sides of the Pacific (Fig. 45).

The changes in the terminal sizes of Pacific salmon that are shown in Fig. 45 provide a natural index of oceanic productivity, and one which integrates those oceanographic conditions that are specifically relevant to their production biology over their entire marine life. It is interesting that all of these salmon species show substantial differences, both between years and between populations. There is therefore quite a large and varied signal which might provide sufficient data to permit some of the rigorous statistical analysis of growth interactions in the open ocean that we earlier indicated is currently infeasible. In addition, early marine survival of salmon seems to be related to their growth in at least some times and places (cf. Henderson and Cass 1991; Henderson 1992). The effects of changes in oceanic productivity on growth in subsequent years should also be measurable and, unlike changes in marine survival rates, can be readily measured and identified with the period in which they occurred (Ishida *et al.* 1993). Considerable insight might therefore be obtained from a coordinated study of scale-based growth patterns from salmon populations around the Pacific rim.

Recommendations

- ***Factors causing changes in the productivity of the North Pacific should be monitored and the causes of the doubling of primary, secondary, and tertiary (fish) production between the 1950s and 1980s should be identified.***

The salmon fishing industry in the north Pacific and their markets are cantered on a salmon resource that is currently highly productive. If the factors that caused the doubling of productivity in the 1970s were to revert to their pre-1970 levels, severe economic dislocations would ensue. Satellite monitoring of SST and primary production levels (i.e. chlorophyll-*a* measurements) might provide some lead time for industry, as well as providing important scientific understanding of the factors causing the shift in fish production.

- ***Further analysis of the factors controlling the distribution of Pacific salmon in the North Pacific is necessary, from both biological and physical viewpoints.***

Joint Japanese-Canadian work to date has shown very sharp thermal limits to the southern distribution of Pacific salmon. The sharp decline in abundance with temperature, and the remarkably low temperatures at which the response occurs, suggests that thermal barriers form an effective limit to the offshore distribution of salmon, and can limit the distribution of Pacific salmon to a much smaller area of the subarctic Pacific than previously believed

The strength of this response is presumably the direct result of strong evolutionary selection, and should therefore have a direct impact on the production biology of Pacific salmon. Global climate models predict increases in ocean temperatures that could prevent salmon from occupying almost all of the North Pacific Ocean. Future temperature changes in the North Pacific could therefore have a direct impact on the production dynamics of Pacific salmon, both by restricting the area of the north Pacific that is available to forage within, and by increasing the density of salmon.

In order to identify a critical season for salmon production, improved monitoring of salmon distributions, food availability, and prey densities is required in the winter, spring, and fall, where our data bases are currently weakest.

- ***Studies of marine growth rates using salmon scales provide a cost-effective and detailed method of assessing changes in oceanic productivity in the regions salmon inhabit.***

Scale studies have not been done as often as they should; they provide useful data for multiple-year comparisons with those oceanographic variables directly relevant to salmonid production biology, and for identifying the stocks and ages of salmon where density-dependent interactions occur. When initiated on a Pacific-Rim wide basis, they have the potential for synoptic studies that could provide considerable insight into the degree to which changes in salmon production are shared between countries.

- ***The relative trophic positioning of different salmon species must be quantitatively assessed in order to determine the potential for density-dependent interactions (i.e. a carrying capacity effect).***

Empirical evidence indicates that the mean weight of stomach contents changes much less for chum salmon than for sockeye in years when pink salmon populations are high in the western North Pacific. This suggests that the unusual diet of chum salmon may help to buffer their populations, by reducing direct trophic competition with other salmon. Further work is also needed to assess the magnitude of trophic overlap between species, and the direction of any interactions.

5.0 TABLES AND FIGURES

Table 1. Correlations between monthly mean SST anomalies in the four areas in Figure 6.

	A	**B**	**C**	**D**
A (in the Western Subarctic Gyre)	-	0.51	0.53	0.28
B (in the Oyashio Region)	0.51	-	0.58	0.50
C (in the West Wind Drift Region)	0.53	0.58	-	0.69
D (south of the Subarctic Boundary)	0.28	0.50	0.69	-

Table 2. Summary of studies of oceanic influences on recruitment of commercially exploited fish and shellfish stocks in the northeast Pacific Ocean.

Species	**Reference**	**Proposed Mechanism**	**Variable**
Bluefin tuna	Mysak 1986	Alteration of migration routes	El Niño-Southern Oscillation
Coho salmon	Nickelson 1986	Reduced predation offshore, increased prey availability and thus faster growth	Upwelling during spring & summer
Dover sole	Hayman and Tyler 1980	Prey concentrations, location of settling	Upwelling
Dungeness crab	Johnson et al. 1986	Transport of zoea	Wind stress
	Jamieson et al. 1989	Transport	Current patterns
English sole	Kruse and Tyler 1983	Alteration of spawning period, rates of gonadal development	Temperature
	Hayman & Tyler 1980	Prey concentrations	High storm frequency, low mean wind speed
	Botsford et al. 1989	Prey concentrations	Productivity
	Forrester 1977	Egg viability	Temperature
	Ketchen 1956	Pelagic stage duration & transport	Temperature
Jack mackerel	Zwiefel & Lasker 1976	Incubation period, larval growth	Temperature
	Theilacker 1986	Starvation, predation	Productivity
	Hewitt et al. 1985	Starvation, predation	Productivity
Northern anchovy	Lasker 1975, 1981	Prey concentration	Wind driven turbulence
	Peterman & Bradford 1987	Prey concentration	Wind driven turbulence
	Husby & Nelson 1982	Transport & prey concentrations	Turbulence, upwelling, strength of thermocline
	Power 1986	Larval transport	Upwelling
	Fiedler 1984	Extension of spawning range	El Niño-Southern Oscillation
	Zweifel & Lasker 1976	Incubation period, larval growth	Temperature
	Methot 1986	Maturity schedule	Temperature
Pacific cod	Tyler & Westrheim 1986	Larval transport, survival of eggs & larvae	Transport & temperature
Pacific hake	Bailey 1981	Larval transport	Upwelling, temperature

Species	Reference	Proposed Mechanism	Variable
	Zwiefel & Lasker 1976	Incubation period, larval growth	Temperature
	Bailey & Francis 1985	Larval transport, growth, spawning location	Upwelling, temperature
	Hollowed & Bailey 1989	Larval transport, growth, prey concentration	Upwelling, spring transition
Pacific halibut	Parker 1989	Larval transport	Wind
Pacific herring	Pearcy 1983, Mysak 1986	Wide range of factors	El Niño-Southern Oscillation
	Alerdice & Hourston 1985	Embryonic & larval survival	Temperature, salinity
	Stocker et al. 1985	Physiological effec, prey production	Temperature, river discharge
	Schweigert & Noakes 1991	Transport	Ekman transport, upwelling
	Tanasichuk & Ware 1987	Ovary weight & fecundity	Temperature
Pacific mackerel	Sinclair et al. 1985	Reduced southward transport	El Niño-Southern Oscillation, temperature
	Parrich & Mac Call 1978	Prey concentrations, vulnerability to predation, change in distribution	Temperature, upwelling, wind stress
Pacific sardine	Zweifel & Lasker 1976	Incubation period	Temperature
	Bakun & Parrish 1980	Prey conditions and circulation	Annual upwelling 39°N February - June upwelling and stress curl
Petrale sole	Alderdice & Forrester 1971	Incubation, hatching success	Temperature & salintiy
	Forrester 1977	Pelagic stage duration, settling time, prey concentrations	Temperature
Rock sole	Fargo & McKinnell 1989	No proposed mechanism	Temperature
	Forrester 1977	Egg development, larval retention	Temperature (Feb. - Apr.). transport
Sablefish	McFarlane & Beamish 1986	Prey concentrations	Transport & temperature
Sockeye salmon	Mysak 1986	Alteration of migration routes	El Niño-Souther Oscillation
	Thomson et al. 1992	Alteration of migration routes	Wind driven current
Walleye pollock	Ingraham et al. 1991	Egg transport, spawning location	Large scale atmospheric forcing
	Kim 1989	Depth distribution of eggs & larvae	Density
	Hinckley et al. 1991	Larval transport	Advection
	Schumacher & Kendall 1991	Larval transport, larval retention	Advection, storm frequency
Widow Rockfish	Norton 1987	Larval transport	Advection, atmospheric circulation

Table 3. List of geographic locations of possible transects to sample biological and oceanographic parameters. The institutions or countries listed after each reflect those which either have a historical time series along these transects or a general scientific interest in these areas and do not represent a commitment to do them.

Transect Number	Location	Institution/Country
1	San Francisco	PFEG and NMFS Tiburon/USA
2	Newport, OR	Oregon State University/USA
3	Vancouver Island	Institution of Ocean Sciences/Canada
4	Southeast Alaska	NMFS Auke Bay/USA
5	Seward, AK	University of Alaska/USA
6	Alaska Peninsula	PMEL and NMFS Seattle/USA
7	Aleutian Islands	Hokkaido Univeristy/Japan
8	Kamchatka Pen.	TINRO/Russia
9	Kurile Islands	TINRO/Russia
10	Hokkaido Island	Hokkaido University/Japah
11	Honshu Island	Ocean Research Institute/Japan
12	Kyushu Island	Japan and China
13	Kuroshio Extension	Far Seas Fisheries Institute Shimuzu/Japan
14	Subarctic Current	NMFS Honolulu/USA or PBS Nanaimo/Canada

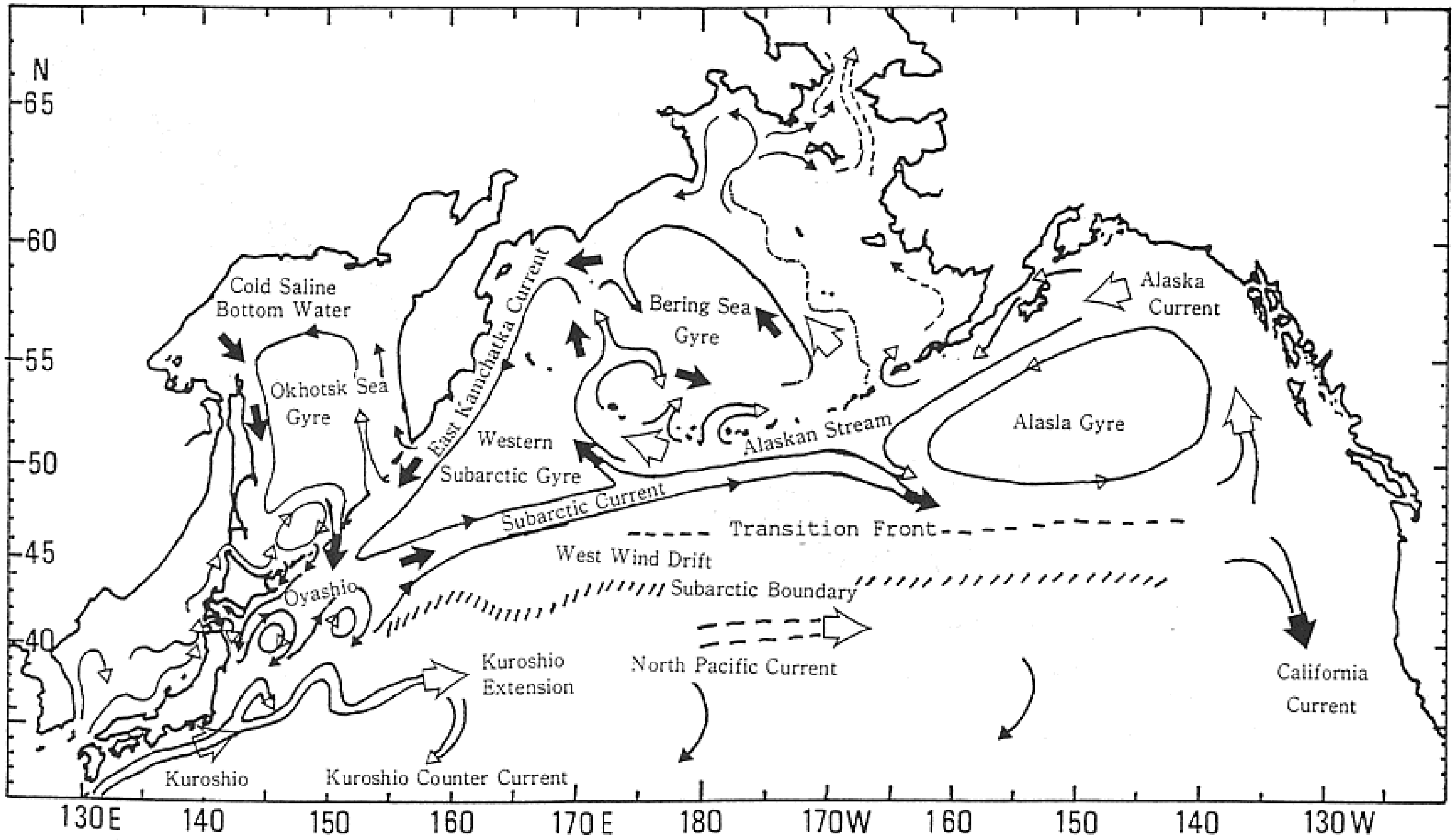


Fig. 1. General circulation of the subarctic North Pacific Ocean (after Dodimead et al., 1963; Favorite et al., 1976; as revised by Ohtani, 1991).

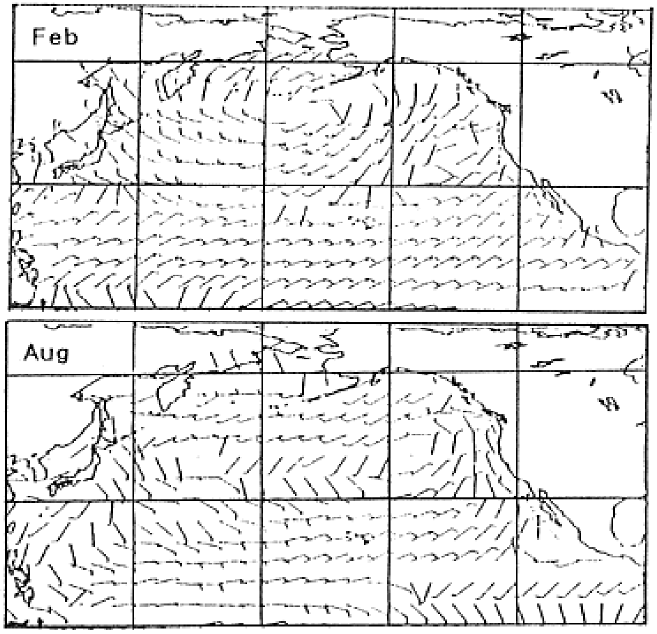


Fig. 2. Monthly mean sea surface wind velocity (after JWA). (a) February (b) August

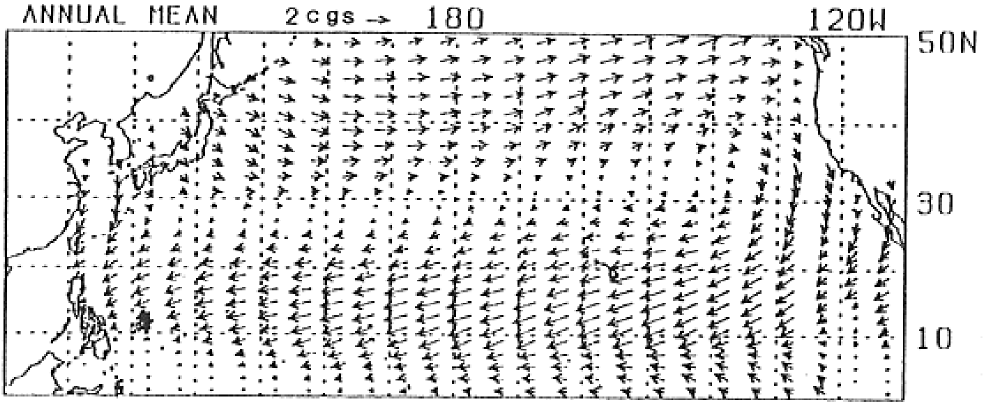


Fig. 3. Annual mean sea surface wind stress during 1961-84 (after Kutsuwada and Teramoto, 1987).

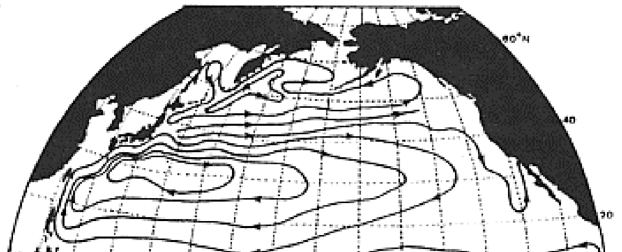


Fig. 4. Upper ocean circulation in the North Pacific indicated by the distribution of dynamic height anomaly (modified from Reid, 1961).

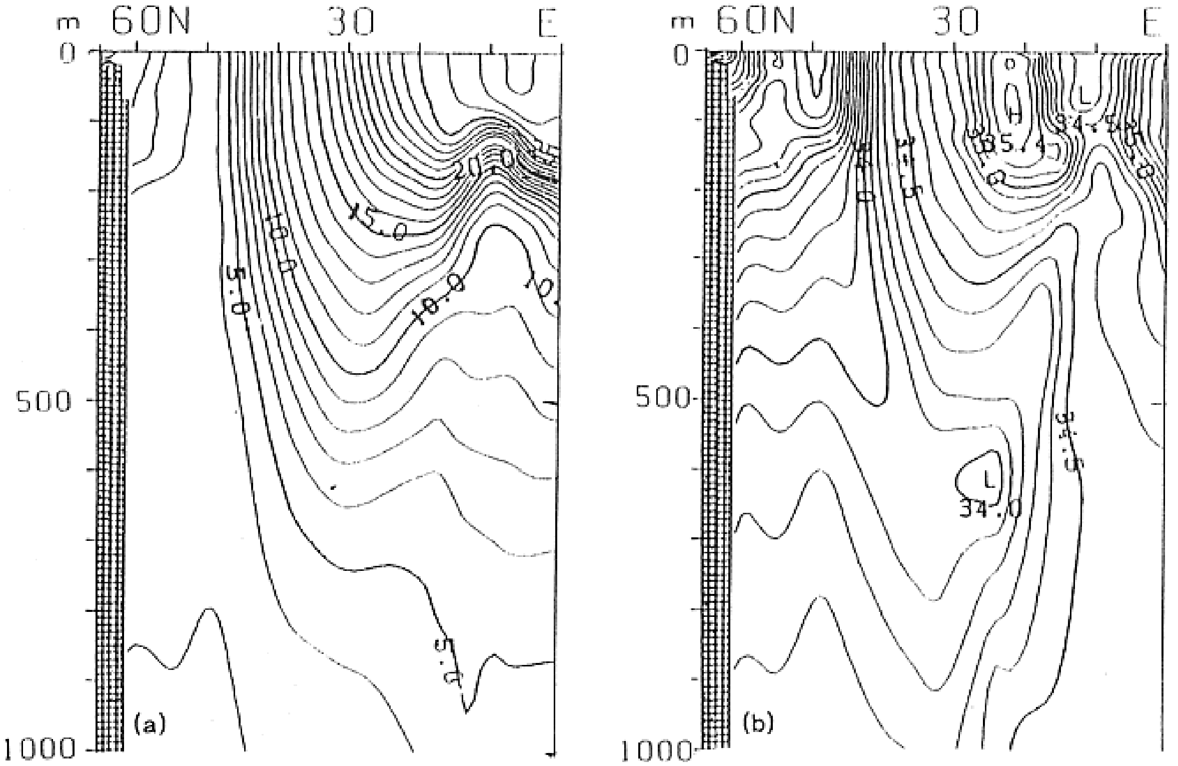


Fig. 5. North-south sections of water temperature (a) and salinity (b) in winter along 180°E (after MRI-JMA).

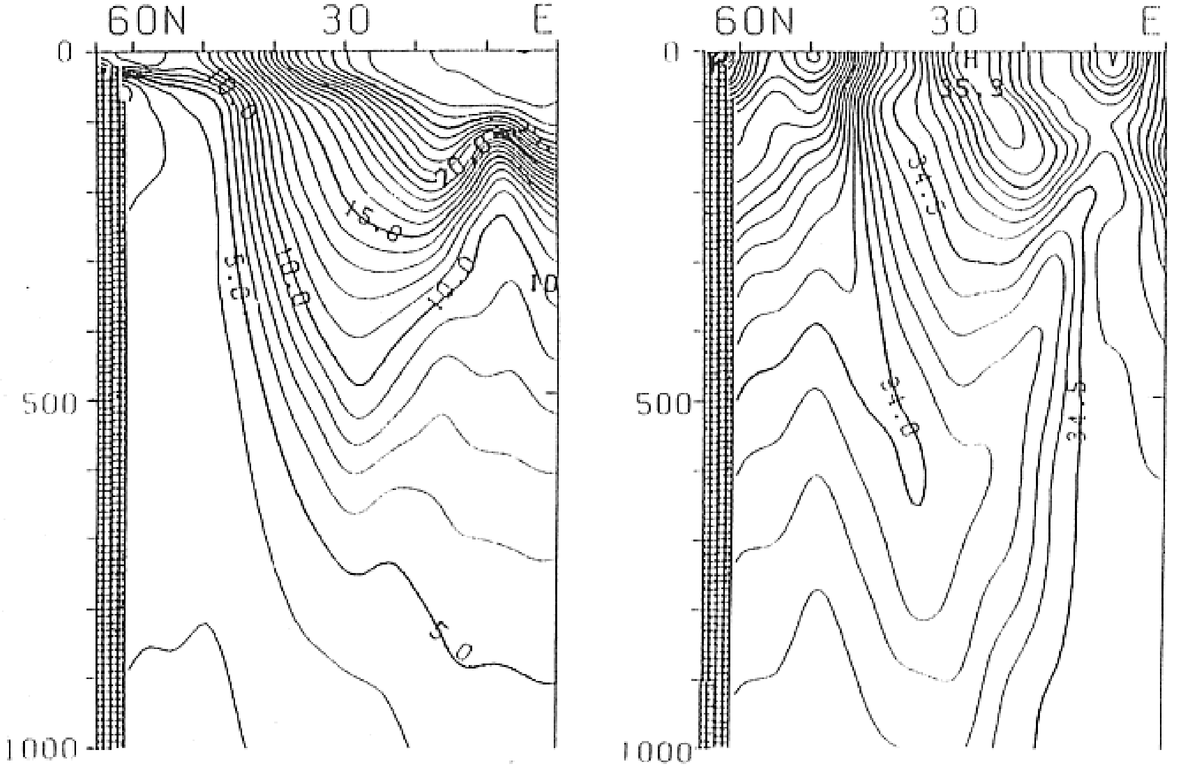


Fig. 6. North-south sections of water temperature (a) and salinity (b) in summer along 180°E (after MRI-JMA).

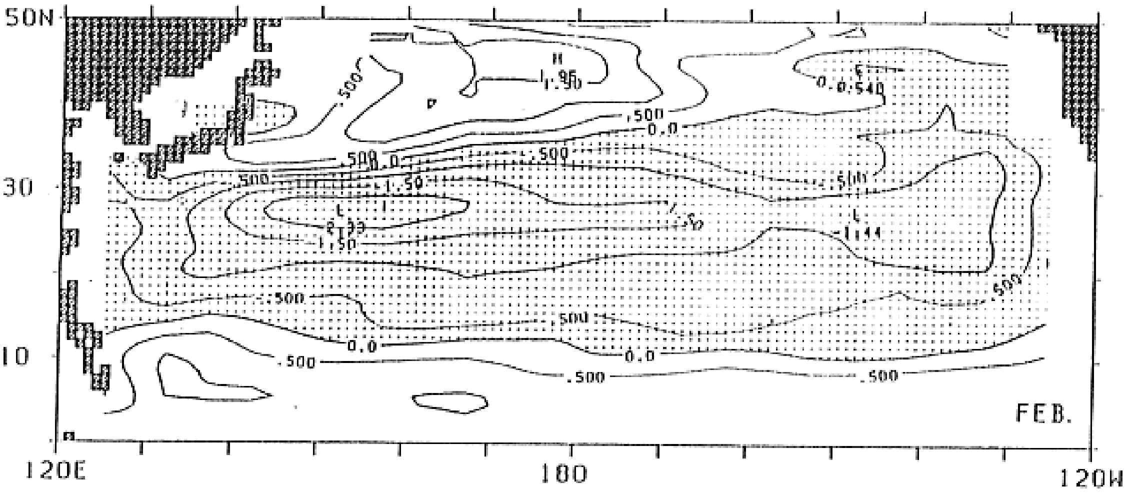


Fig. 7. Monthly mean upward velocity due to Ekman pumping in February (after MRI-JMA).

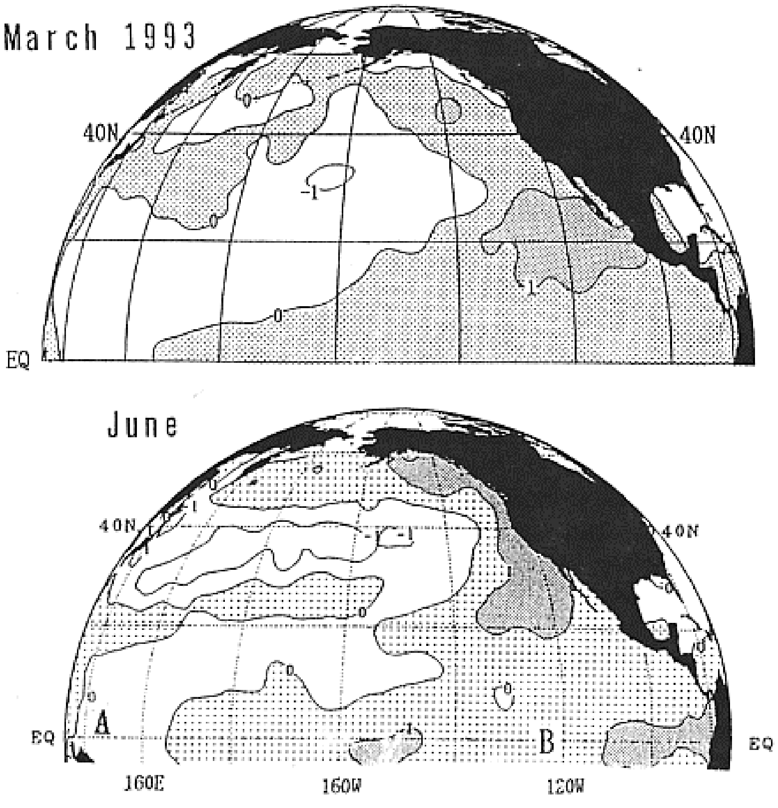


Fig. 8. Monthly mean sea surface temperature anomaly in March (a) and June (b) in the North Pacific in 1993 (after JMA).

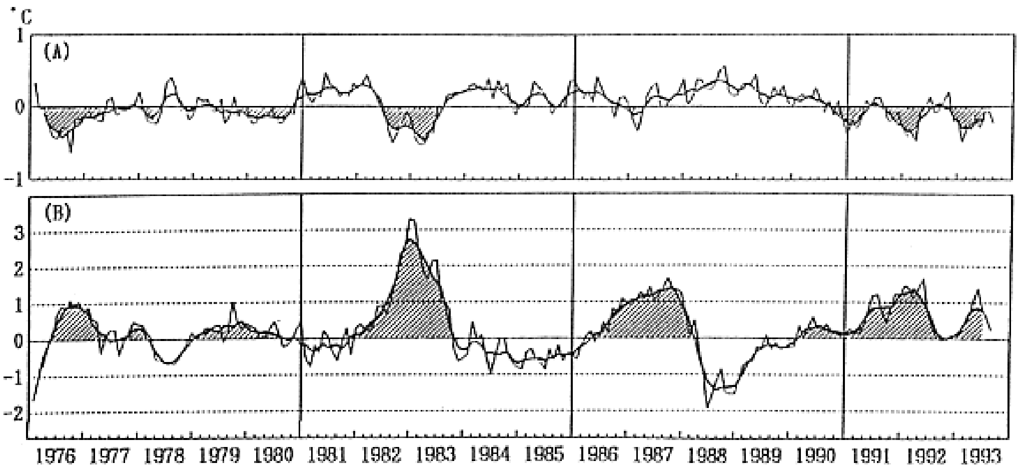


Fig. 9. Time series of monthly mean sea surface temperature anomaly in the western (a) and eastern (b) equatorial Pacific in Fig. 8 (b) (after MRI-JMA).

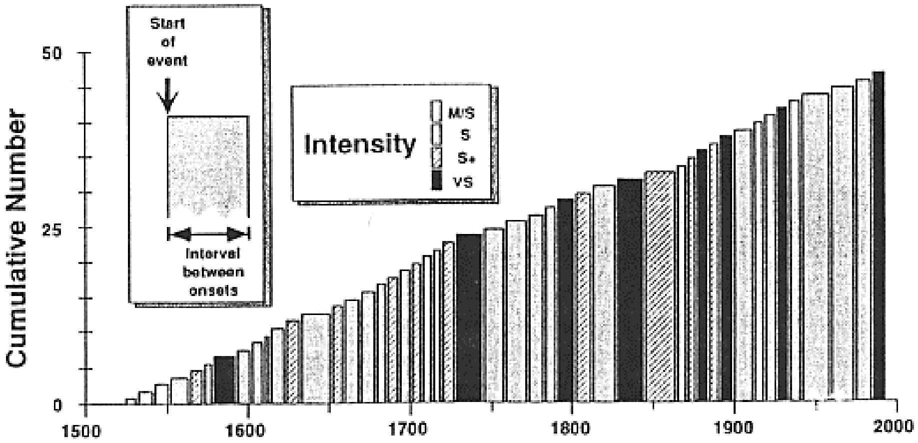


Fig. 10. Decadal and multi-decadal scale variations of the appearance of El Ninõ events (after Enfield, 1988).

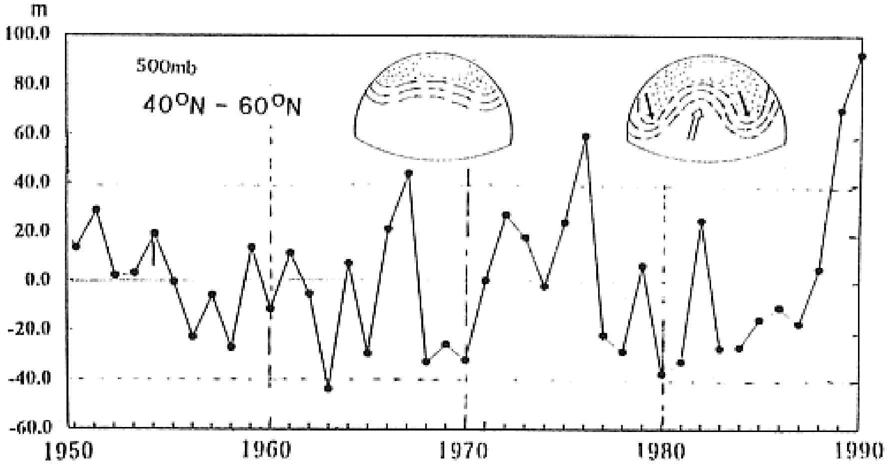


Fig. 11. Decadal scale variations in the anomaly of 500 mb height difference between 40°N and 60°N called east-west index, based on the JMA data in 1946-90.

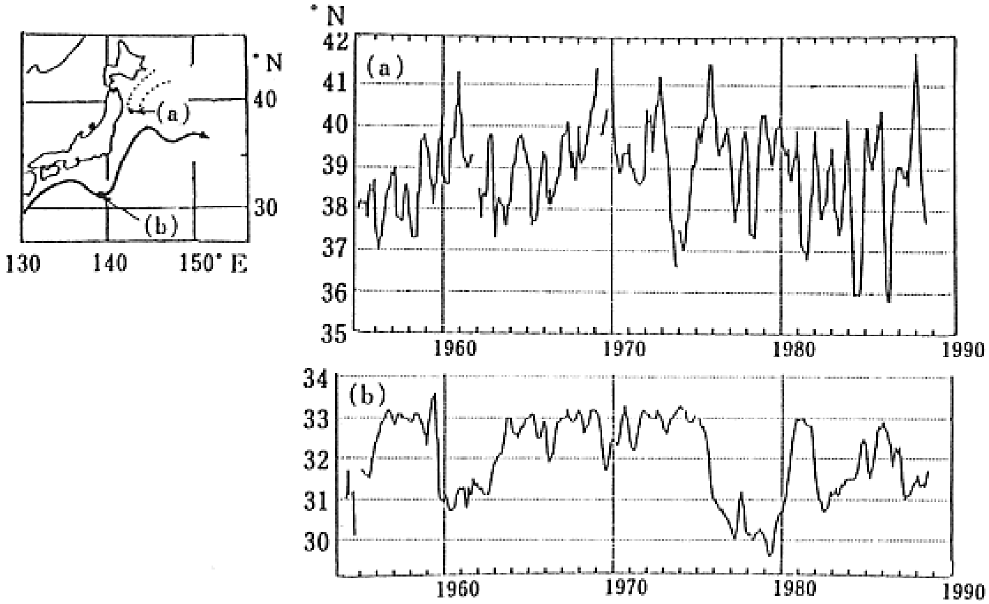


Fig. 12. Year to year and decadal scale variations in the southward intrusions of the Oyashio (a) and the latitude of the trough of the Kuroshio path in the south of Honshu (b) (after JMA).

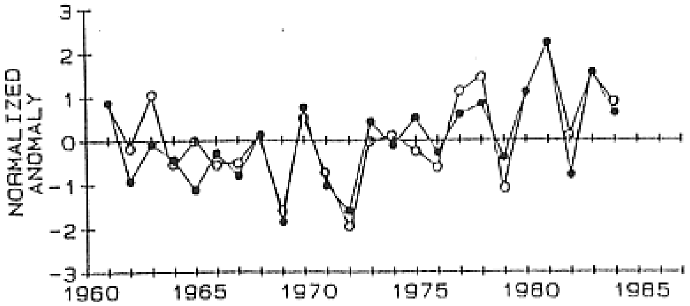


Fig. 13. Normalized anomalies of Sverdrup transport of the subtropical (closed circles) and the subarctic (negative value with open circles) gyres estimated from annual mean wind stress in 1964-84 (after Hanawa et al., 1993).

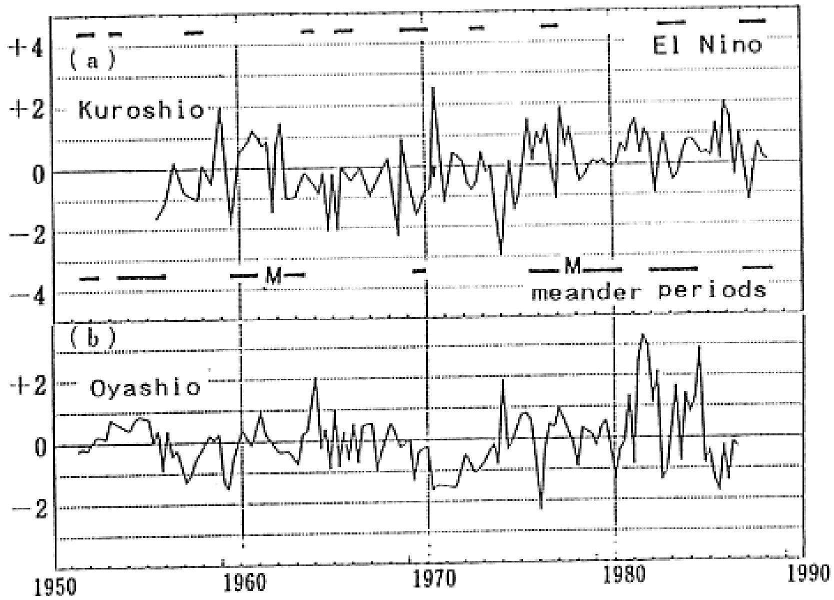


Fig. 14. Normalized anomalies of interannual variations in the volume transport of the Kuroshio in the East China Sea (a) and the Oyashio in the east of the Tsugaru straits (b) observed seasonally by JMA.

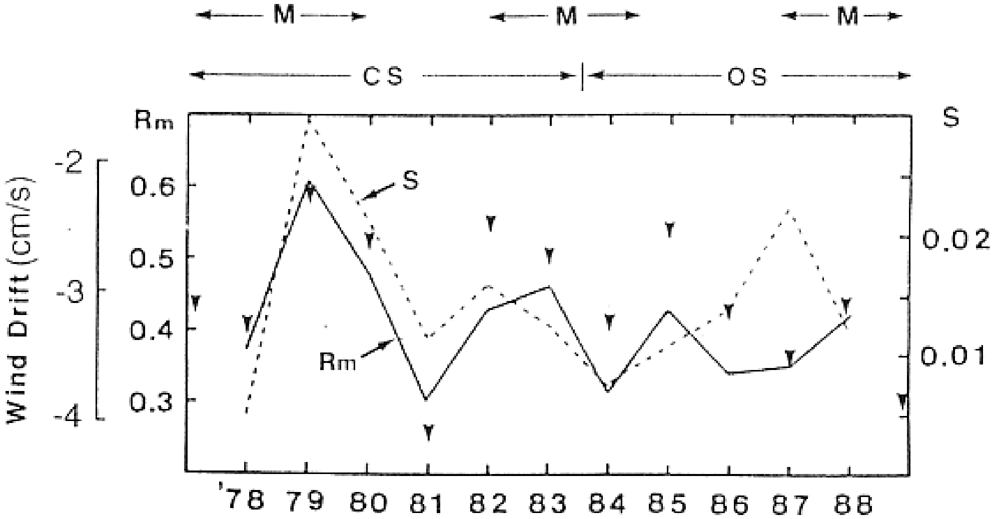


Fig. 15. Survival rate of sardine larvae about 20 days after spawning in the Kuroshio and its coastal water, which is compared with the computed retention rate of particles in the coastal water 20 days after release in the spawning sites. S and Rm indicate survival and retention rates respectively. Ms indicate periods of large meander of the Kuroshio path and downward arrows offshore wind drift velocity. CS and OS indicate period of coastal and offshore spawning respectively (after Kasai et al., 1992).

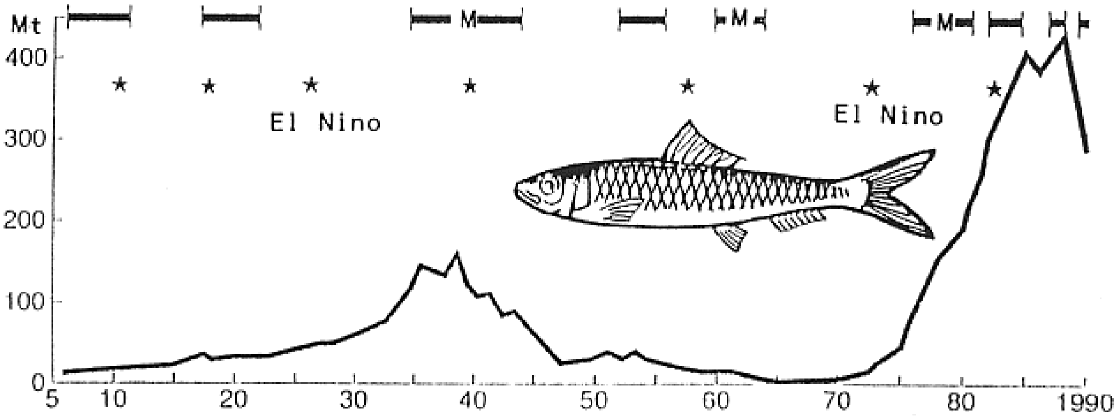


Fig. 16. Multi-decadal scale variations in the sardine's catch around Japan with meander and non-meander pattern of the Kuroshio path and El Ninõ years (after Sugimoto, 1993).

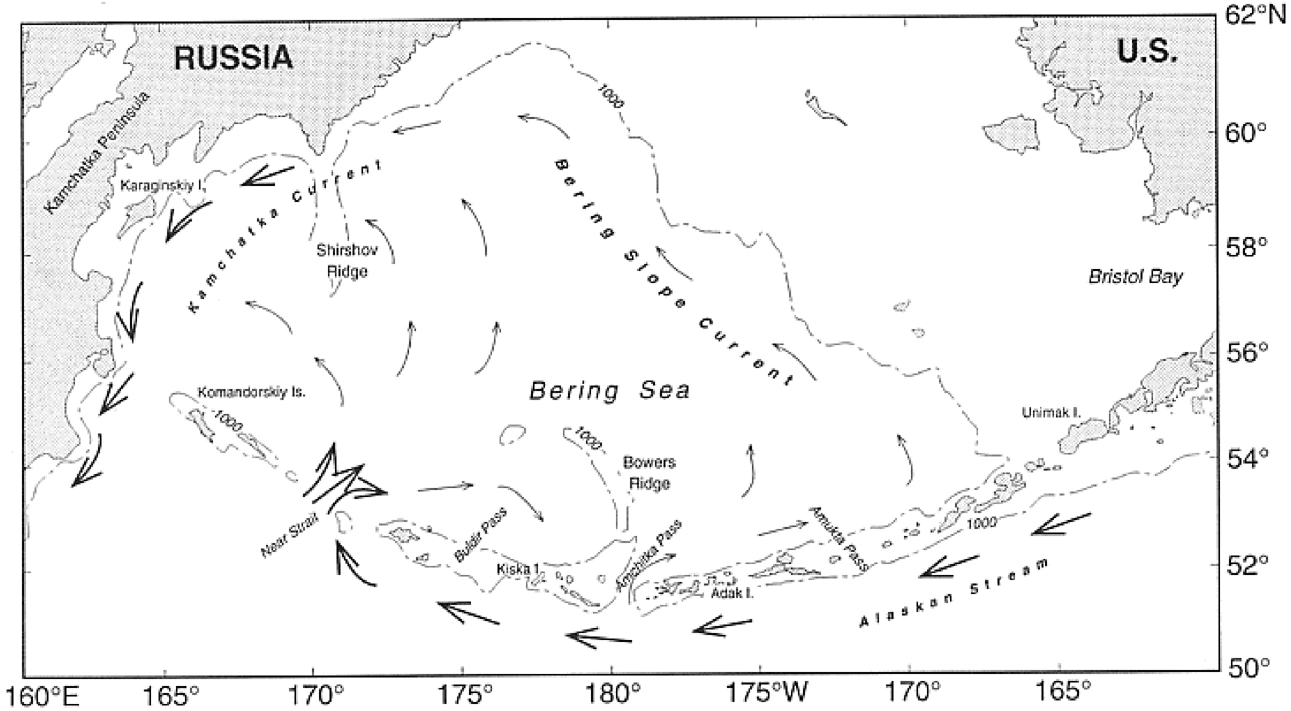


Fig.17. A schematic of the mean circulation in the Bering Sea [modified from Stabeno and Reed (1992)]. The major currents and topographic features are indicated. (Figure provided by P.J. Stabeno.)

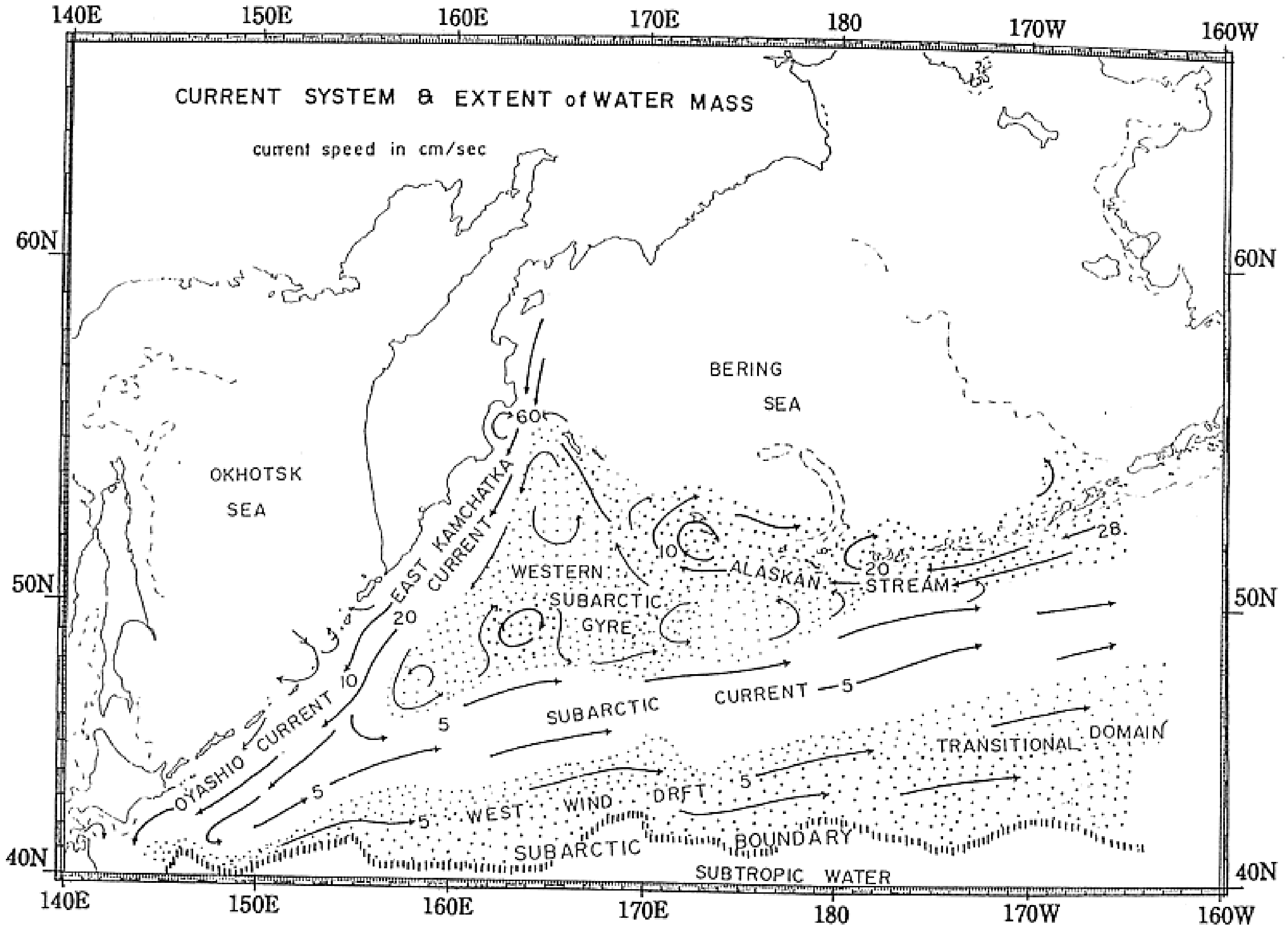


Fig. 18. The current systems and the extent of the water masses in the western subarctic region in winter (Ohtani, 1970).

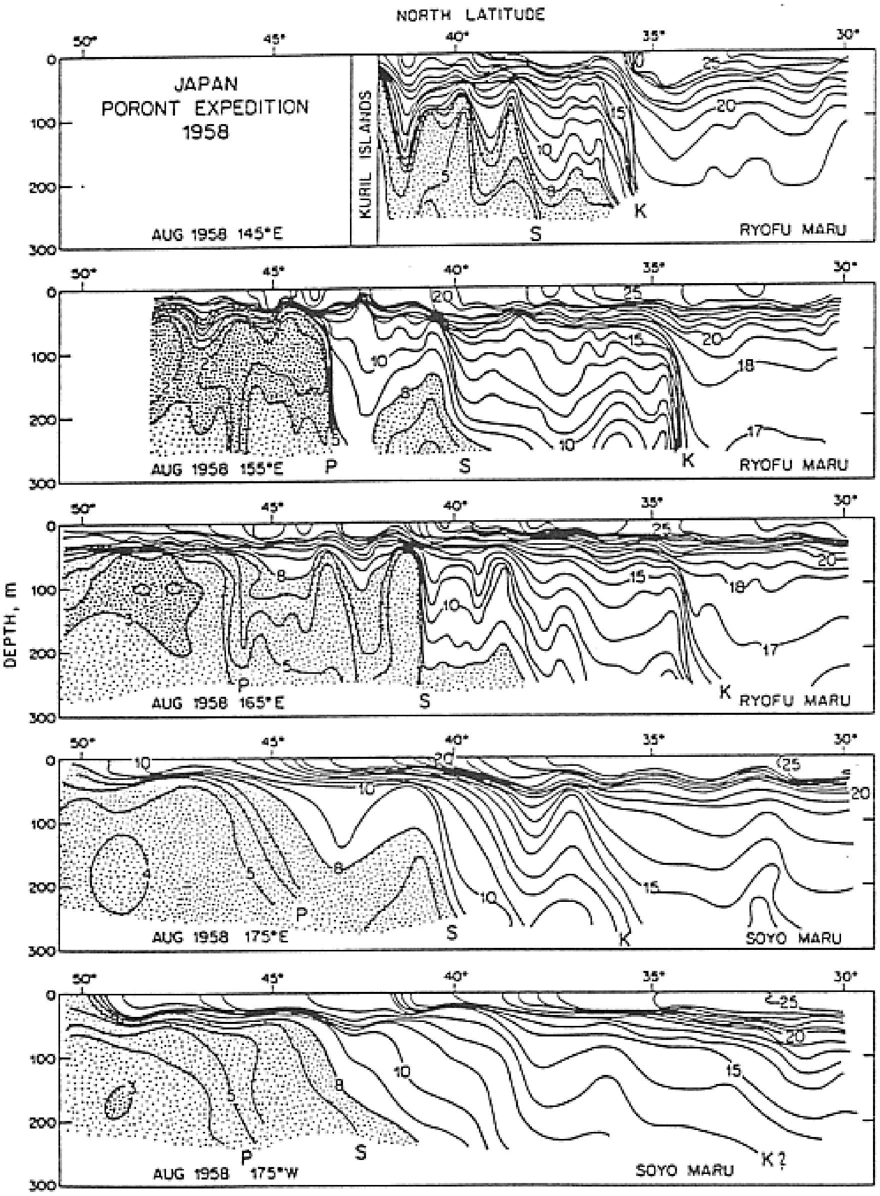


Fig. 19. Longitudinal variability of the meridional thermal structure in the western and central North Pacific (Roden et al., 1982). Locations of the fronts are indicated: P, polar front; S, subarctic front; and K, Kuroshio front.

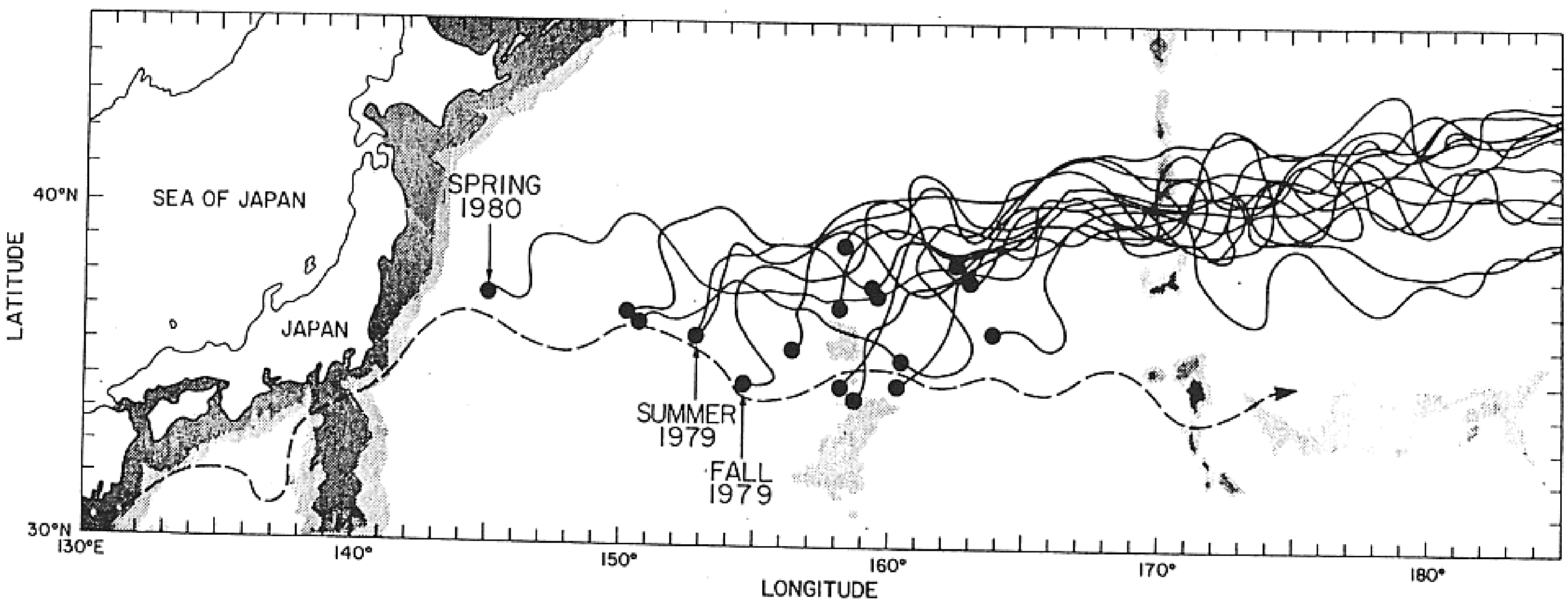


Fig. 20. Composite of the bifurcation point for each season and of the northern branch of the Kuroshio Extension (Mizuno and White, 1983). Solid circles indicate bifurcation points. Dashed line indicates the mean Kuroshio path.

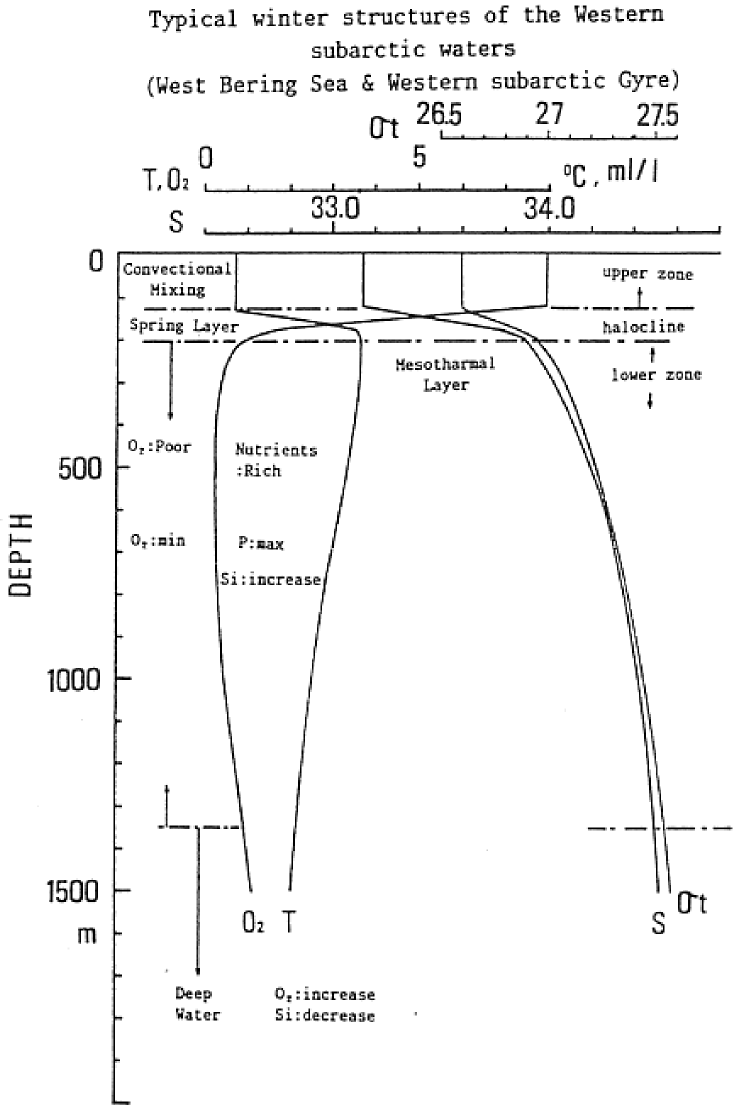


Fig. 21. Representative vertical profiles of temperature, salinity, dissolved oxygen and sigma-t in the western subarctic waters in winter (Ohtani, 1989).

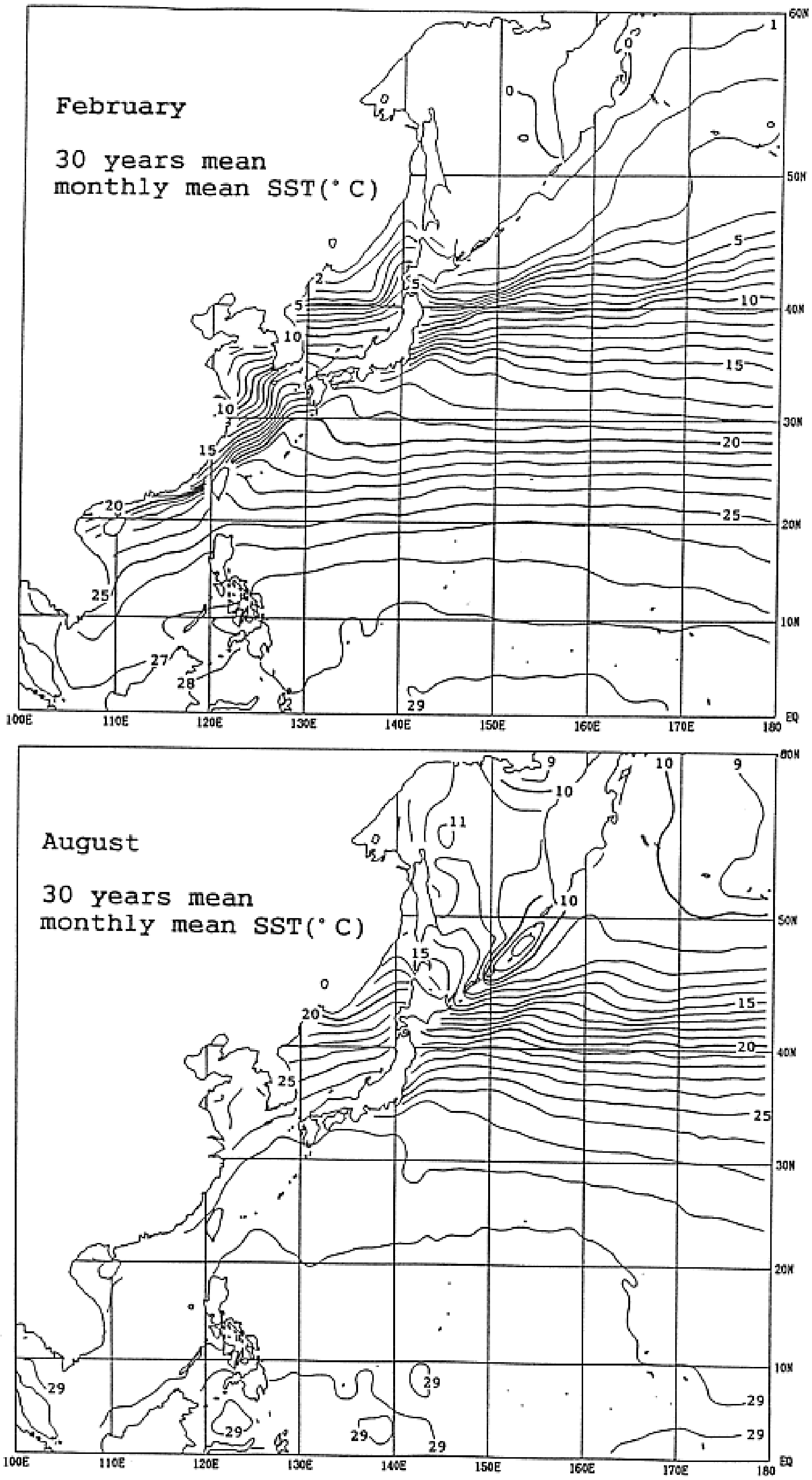


Fig. 22. Thirty years mean monthly mean SST for February and August in the western North Pacific (JMA, 1991)

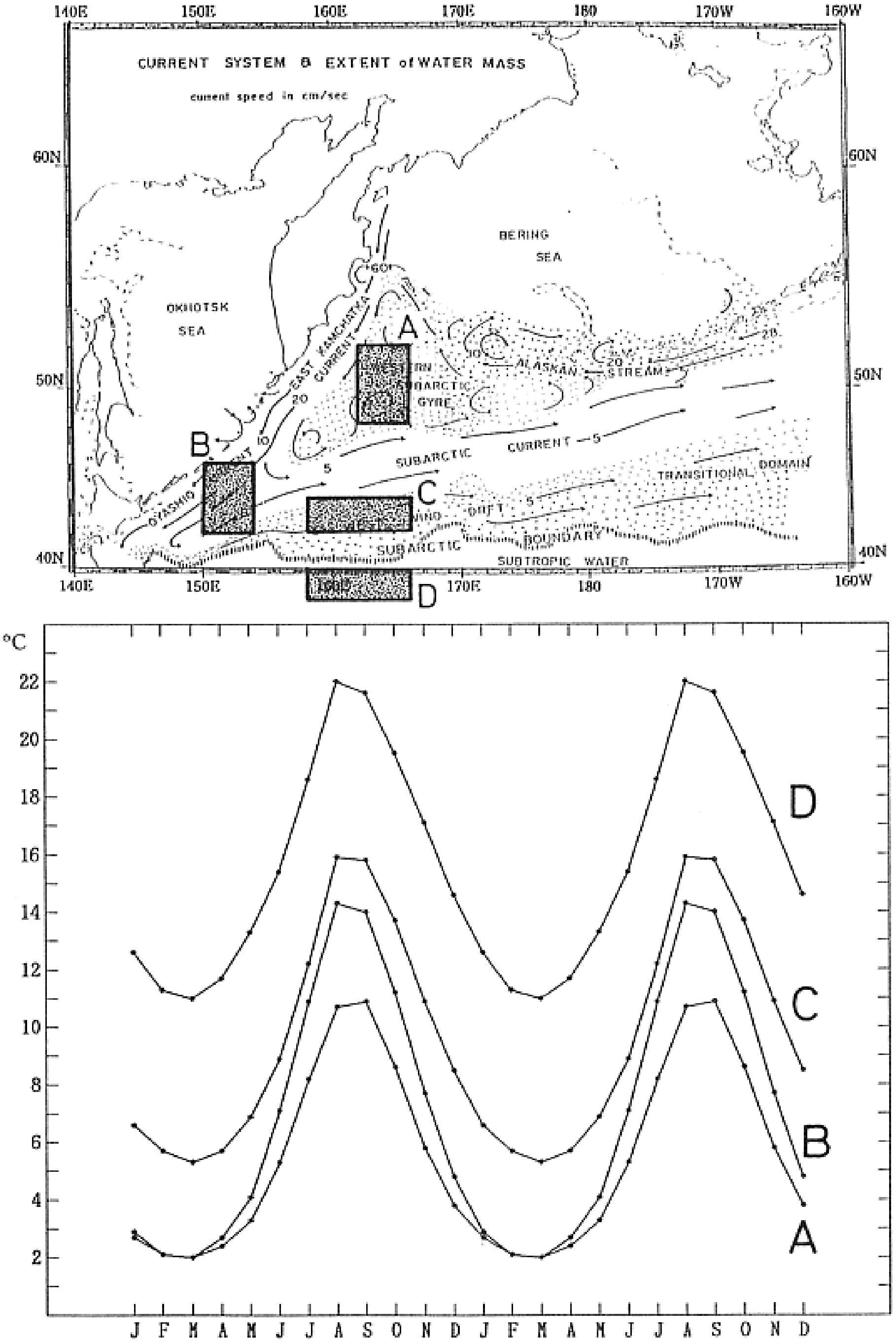


Fig. 23. Thirty years (1961-90) mean annual cycles of the SST in the four areas indicated in upper panel: A, in the western subarctic gyre; B, in the Oyashio region; C, in the west wind drift; and D, south of the subarctic boundary. Mean annual cycles are made from the SST data set of the Japan Meteorological Agency (1991).

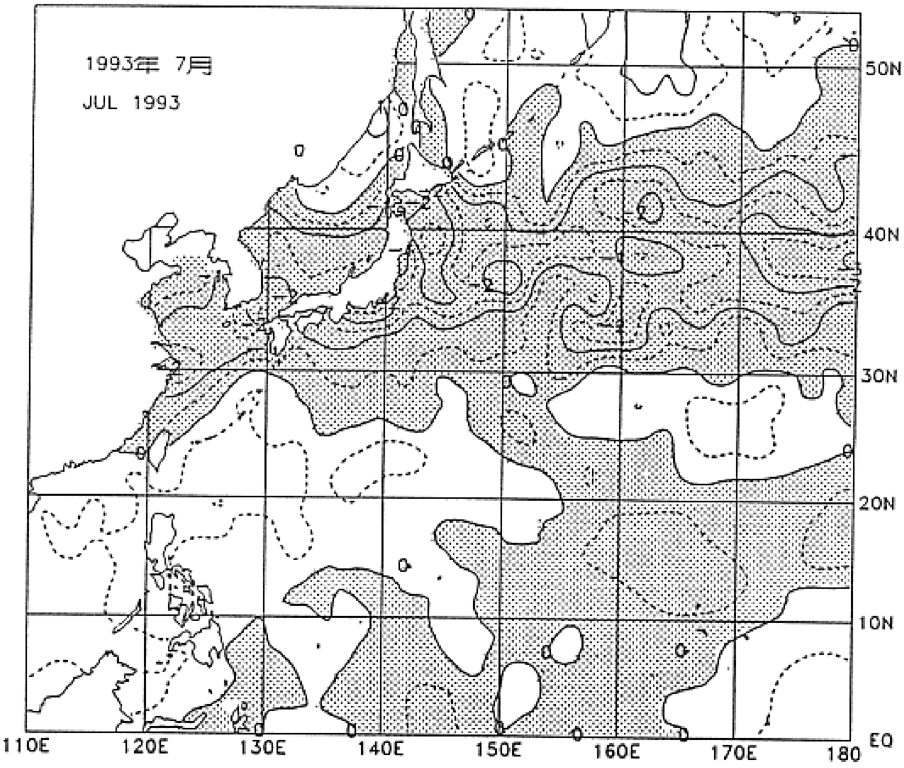


Fig. 24. Monthly mean SST anomalies in the western North Pacific for July 1993 (JMA, 1993). Anomalies are computed with respect to the JMA climatology (1961-90).

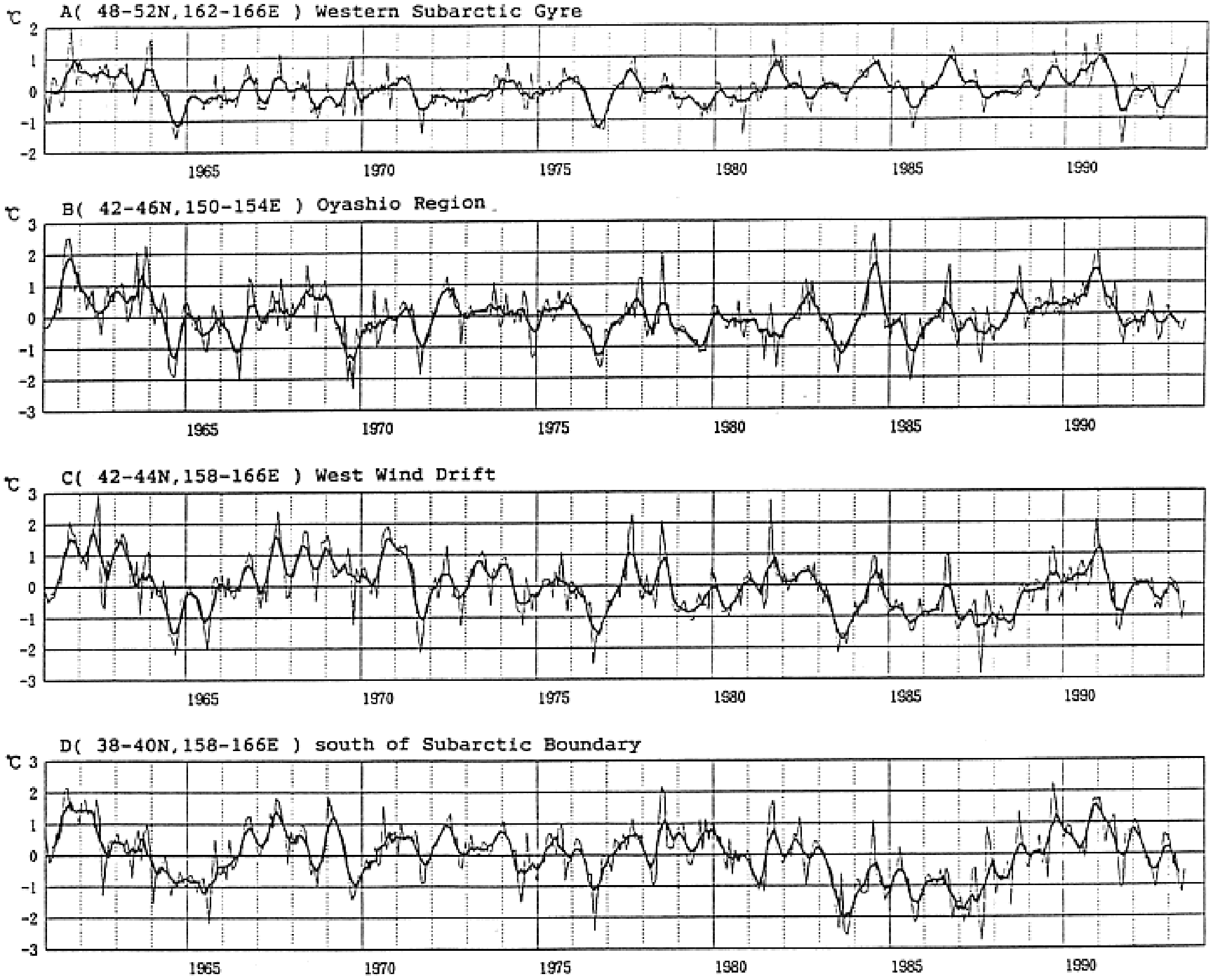


Fig. 25. Time series of monthly mean SST anomalies in the four areas in Fig. 23. Anomalies are computed with respect to the JMA climatology (1961-90). Thick lines show the five months running mean.

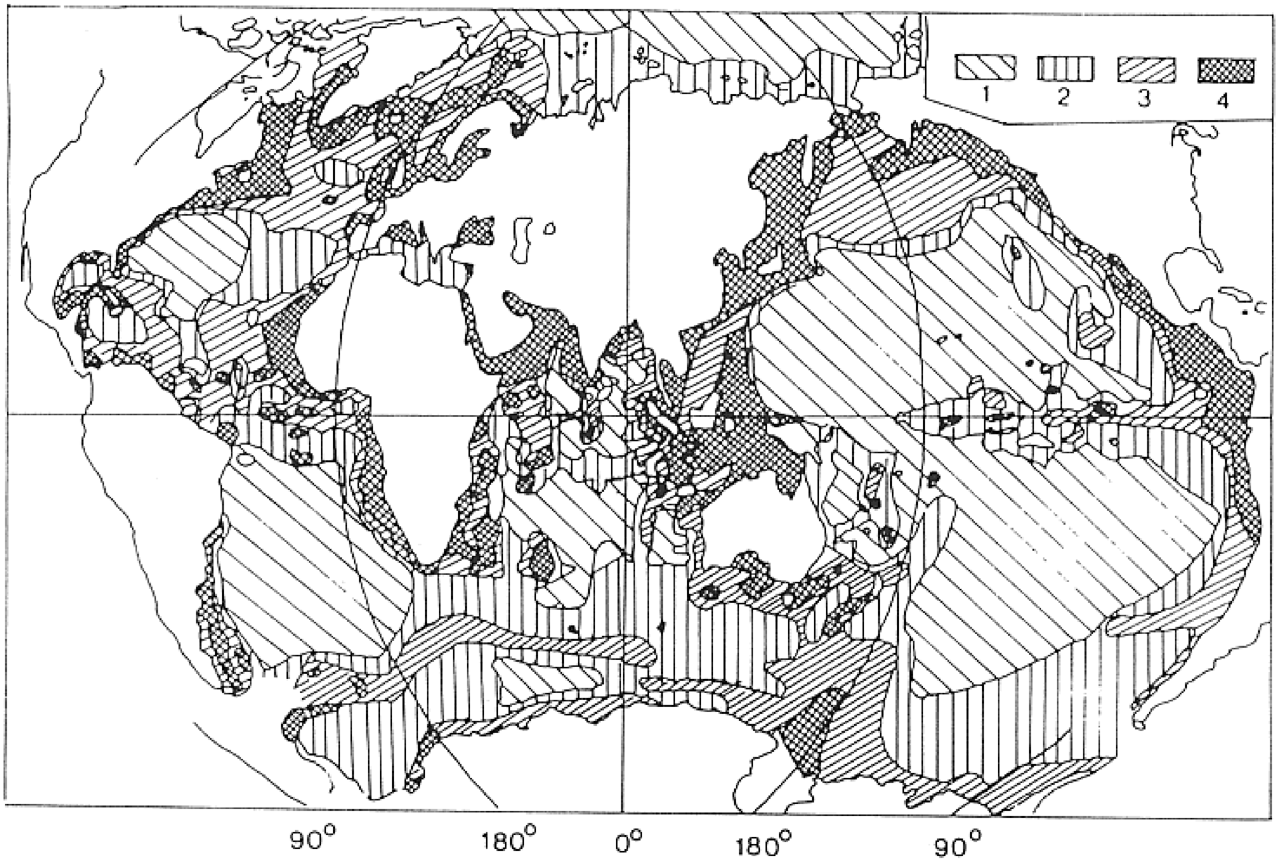


Fig. 26. Distribution of primary production in the world oceans in terms of mg C·m^{-2} day^{-1}. 1: less than 100; 2: 100-150; 3: 150-250; 4: more than 250 (Koblentz-Mishke et al., 1970; cited from Steemann-Nielsen, 1975).

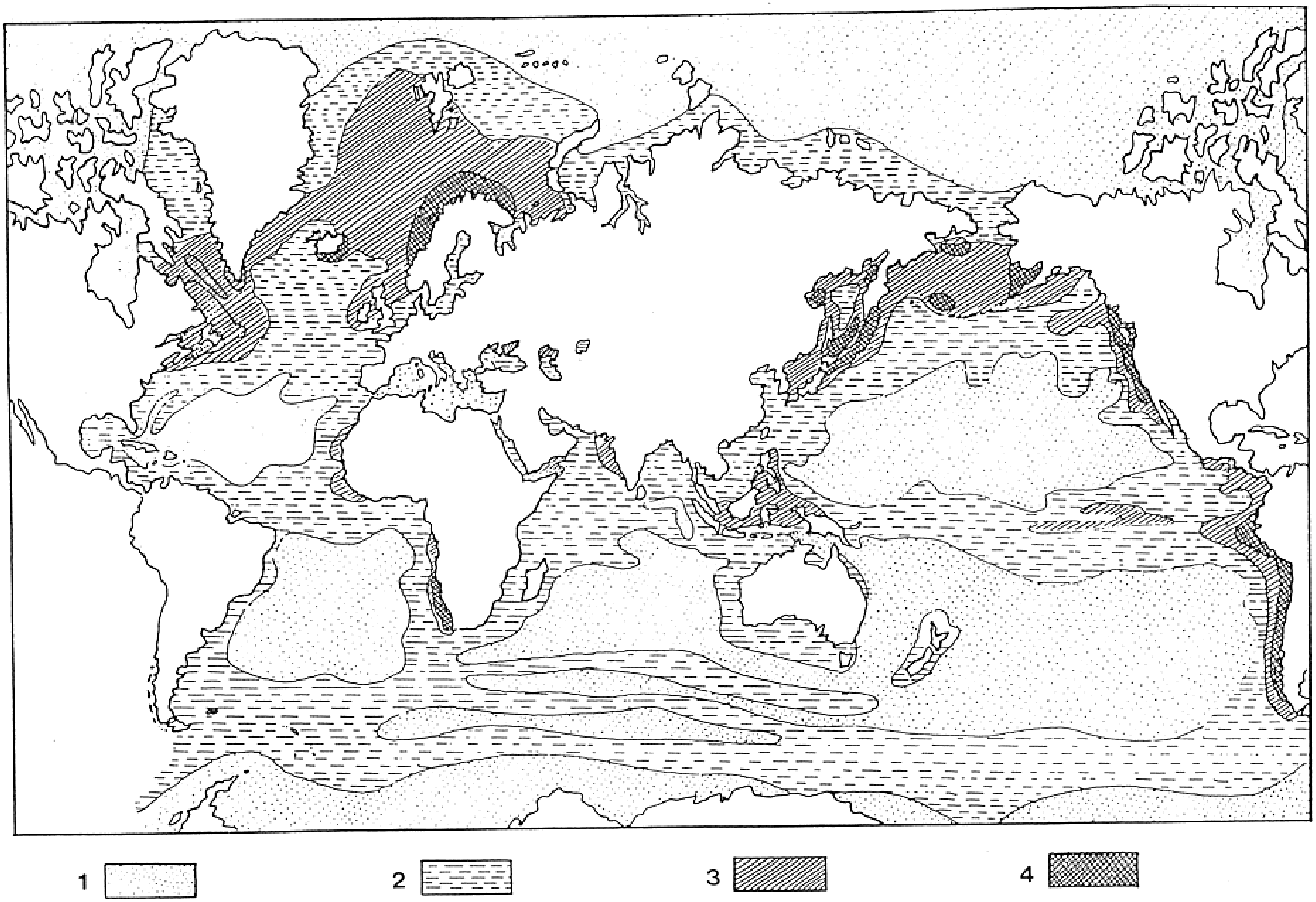


Fig. 27. Distribution of net zooplankton biomass in the upper 100 m water column in terms of mg wet weight·m^{-3}. 1: 0- 50; 2: 51-200; 3: 201-500; 4: over 500 (Bogorov et al., 1968; cited from Gulland, 1970).

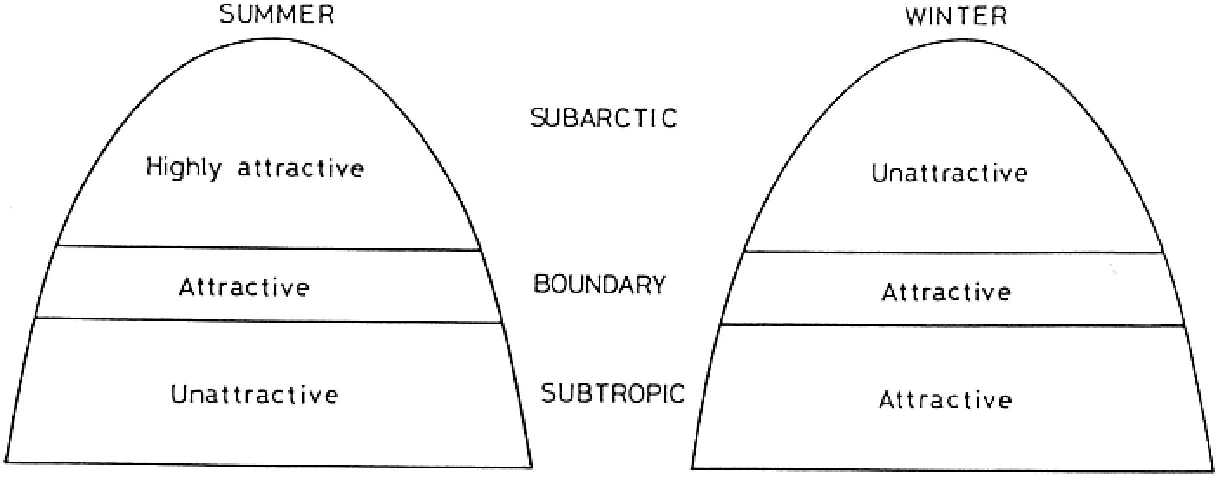


Fig. 28. Seasonal difference of food conditions for migrating pelagic fish over the subarctic, boundary and subtropical sea areas of the North Pacific (Taniguchi, 1981).

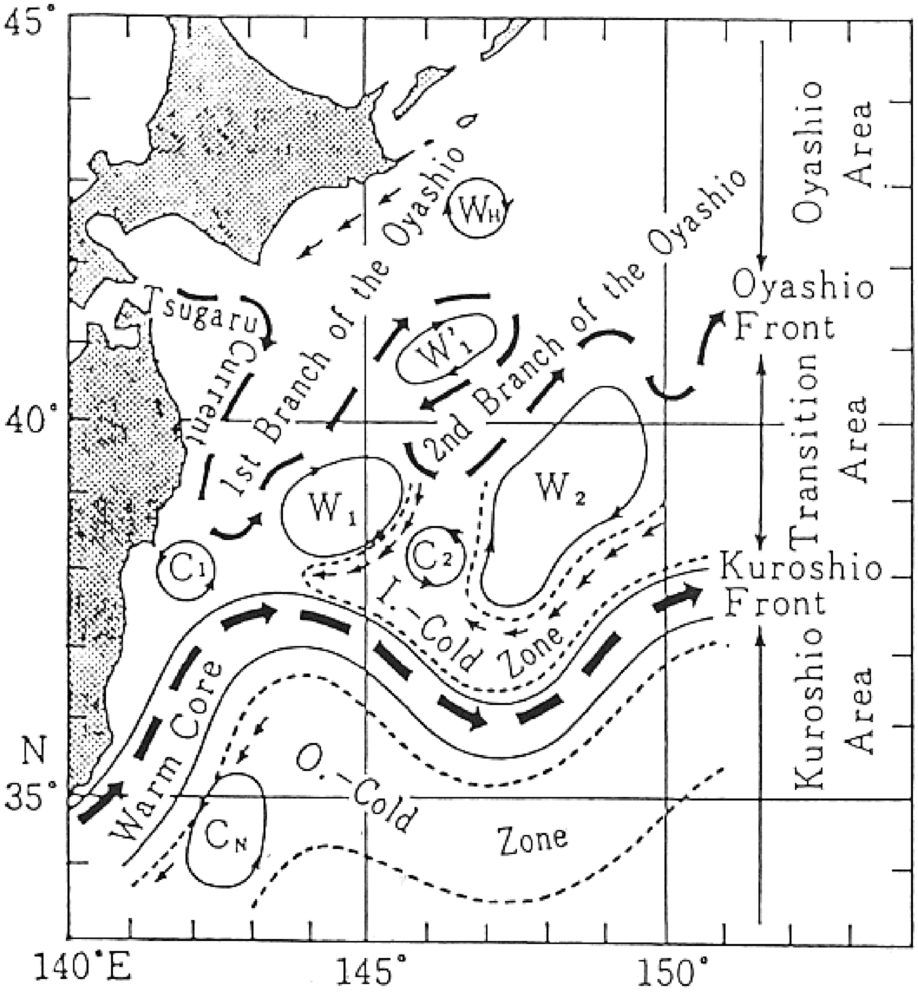


Fig. 29. Schematic diagram showing complicated hydrographic conditions in the sea area east of northern Japan (Kawai, 1955; cited from Kawai, 1991)

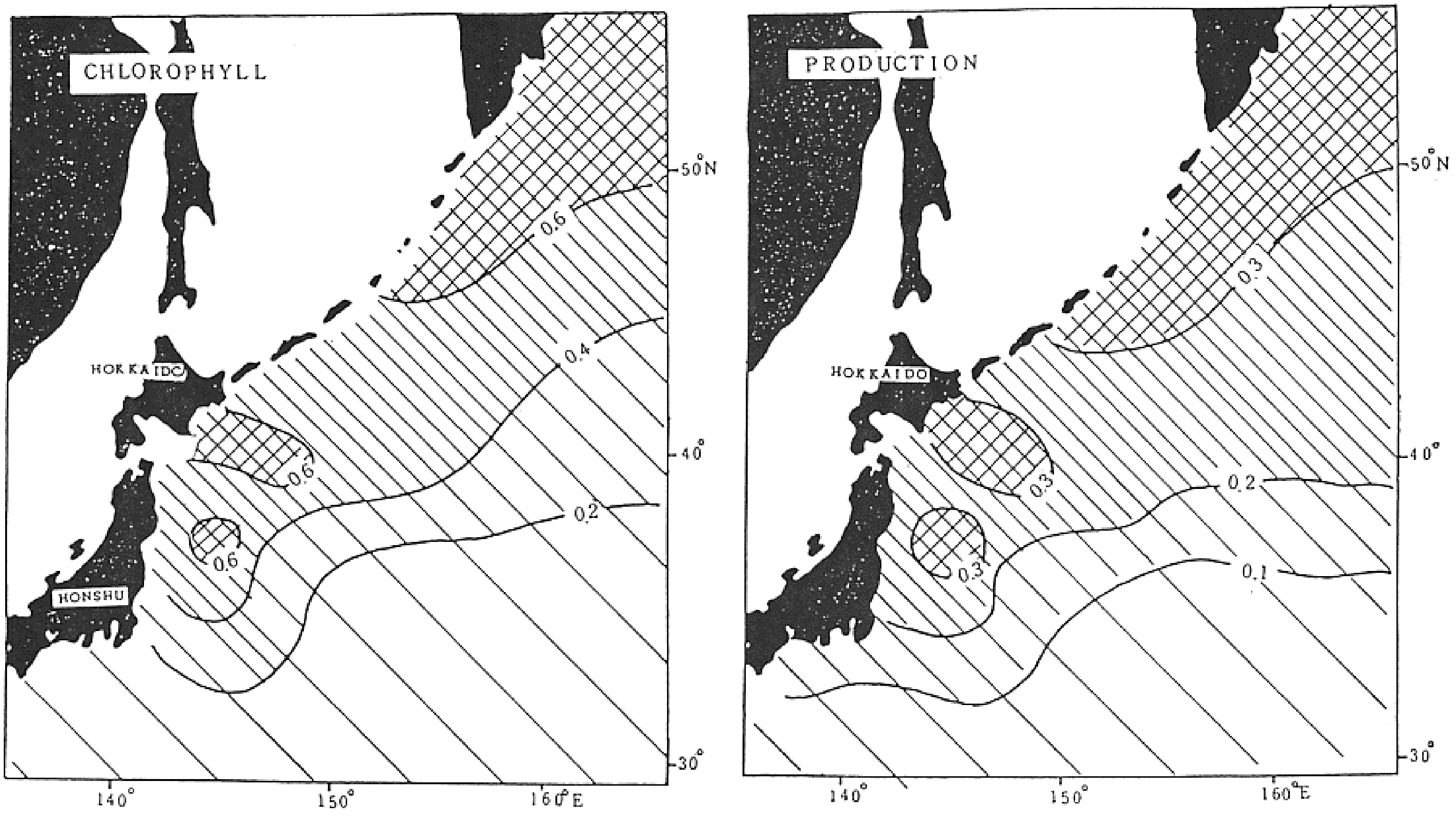


Fig. 30. Distribution of primary productivity in terms of chlorophyll *a* standing crops (left: mg·m^{-3}) and daily production (right: gC·m^{-2} day^{-1}) in the western subarctic Pacific in summer (Saijo and Ichimura, 1960).

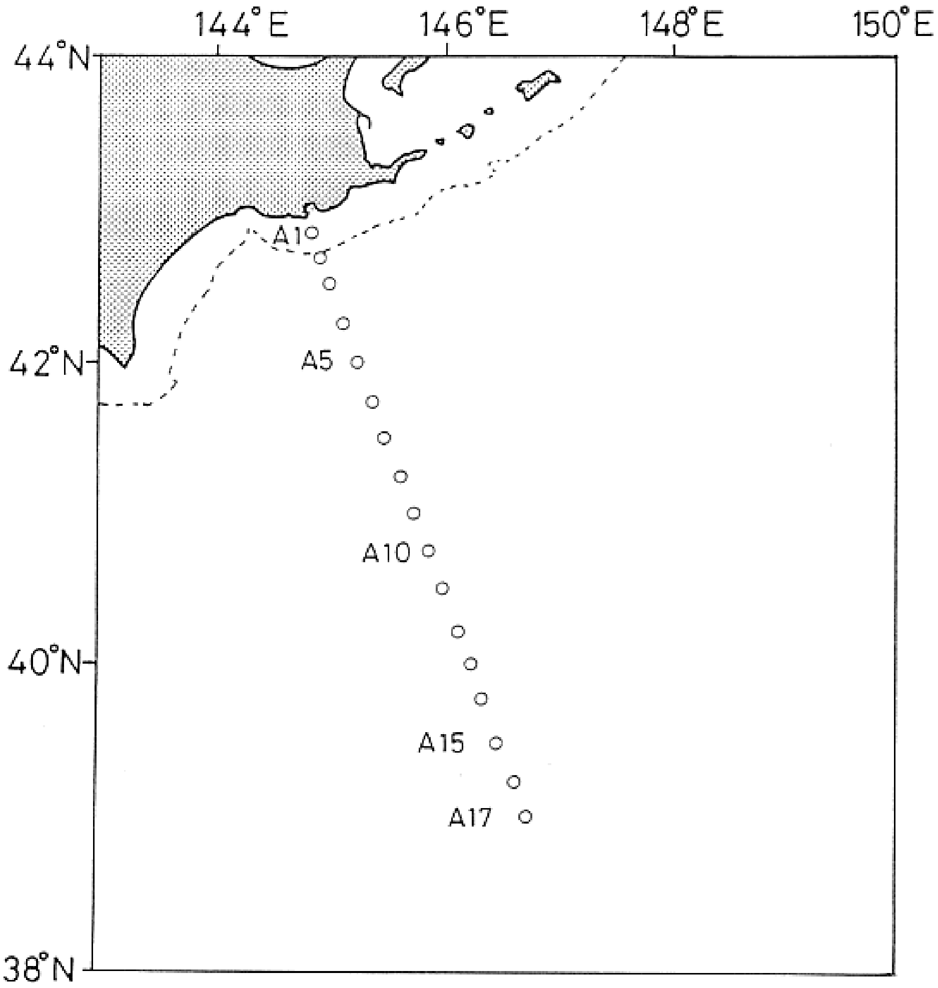


Fig. 31. Location of sampling stations in the Oyashio and adjacent regions off Hokkaido, where the data shown in Fig. 32 were obtained (Taguchi et al., unpublished).

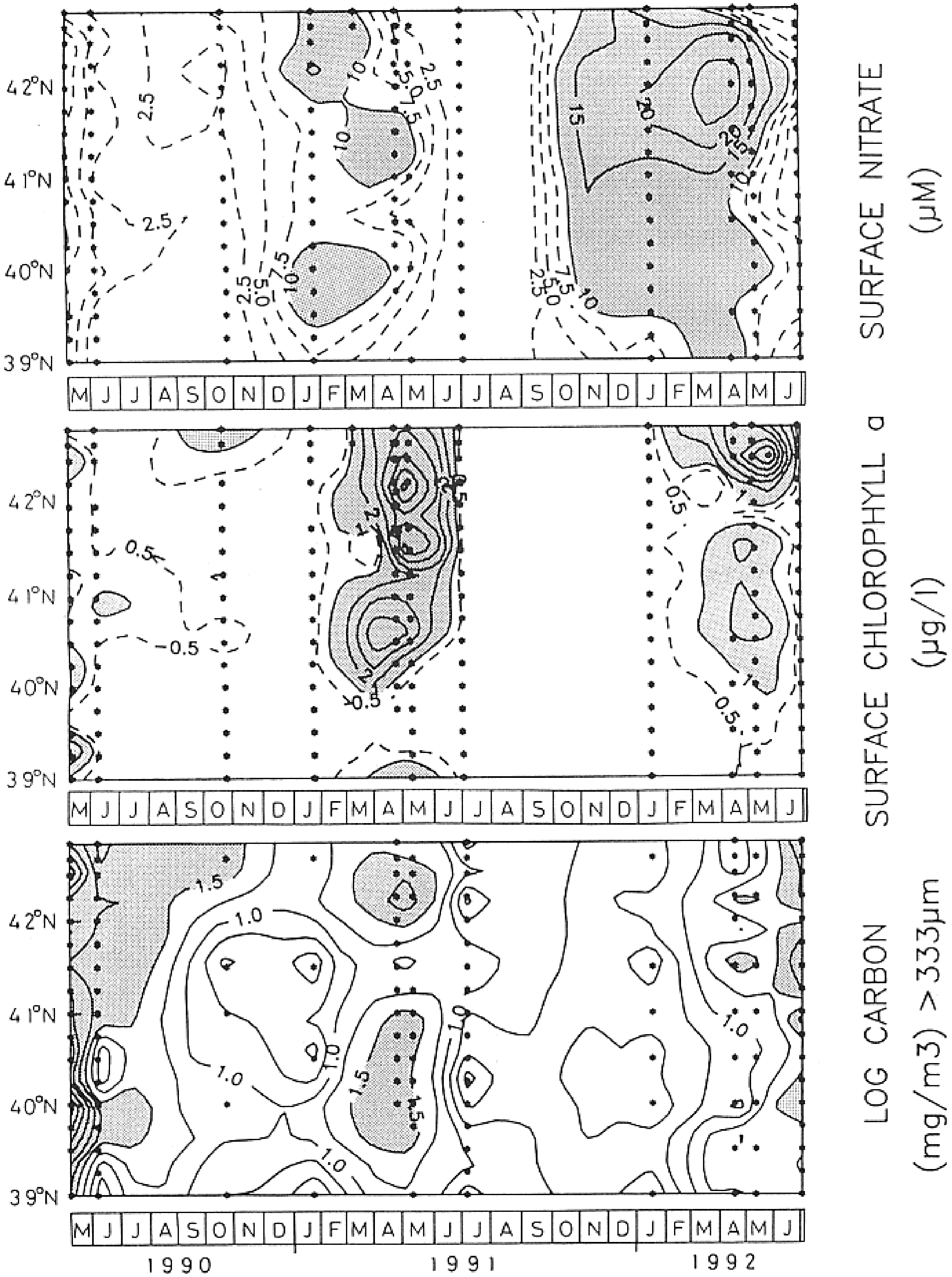


Fig. 32. Spatial and temporal variation of stocks of surface nitrate (top: μM), chlorophyll *a* (middle: μg/l) and net zooplankton carbon (bottom: mgC·m^{-3}) in the Oyashio and adjacent regions (Taguchi et al., unpublished).

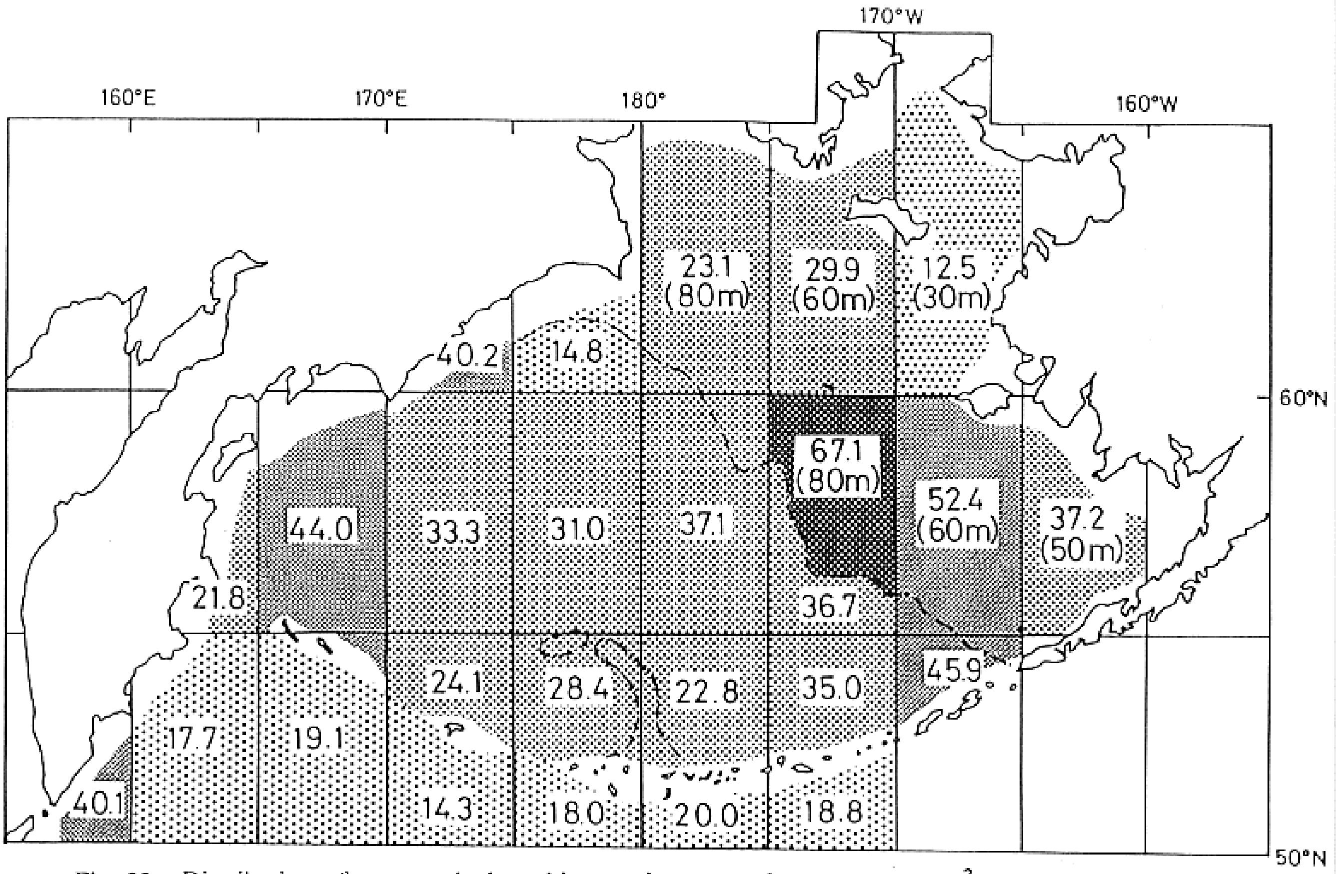


Fig. 33. Distribution of net zooplankton biomass in terms of g wet weight·m^{-2} in the upper 80 m water column averaged for 15 summers from 1956 to 1970 in the Bering Sea and western North Pacific (Motoda and Minoda, 1974).

Fig. 34. Interannual variation of mean summer net zooplankton biomass in the upper 150 m water column of the Bering Basin region from 1956 to 1979 (Motoda and Minoda, 1974).

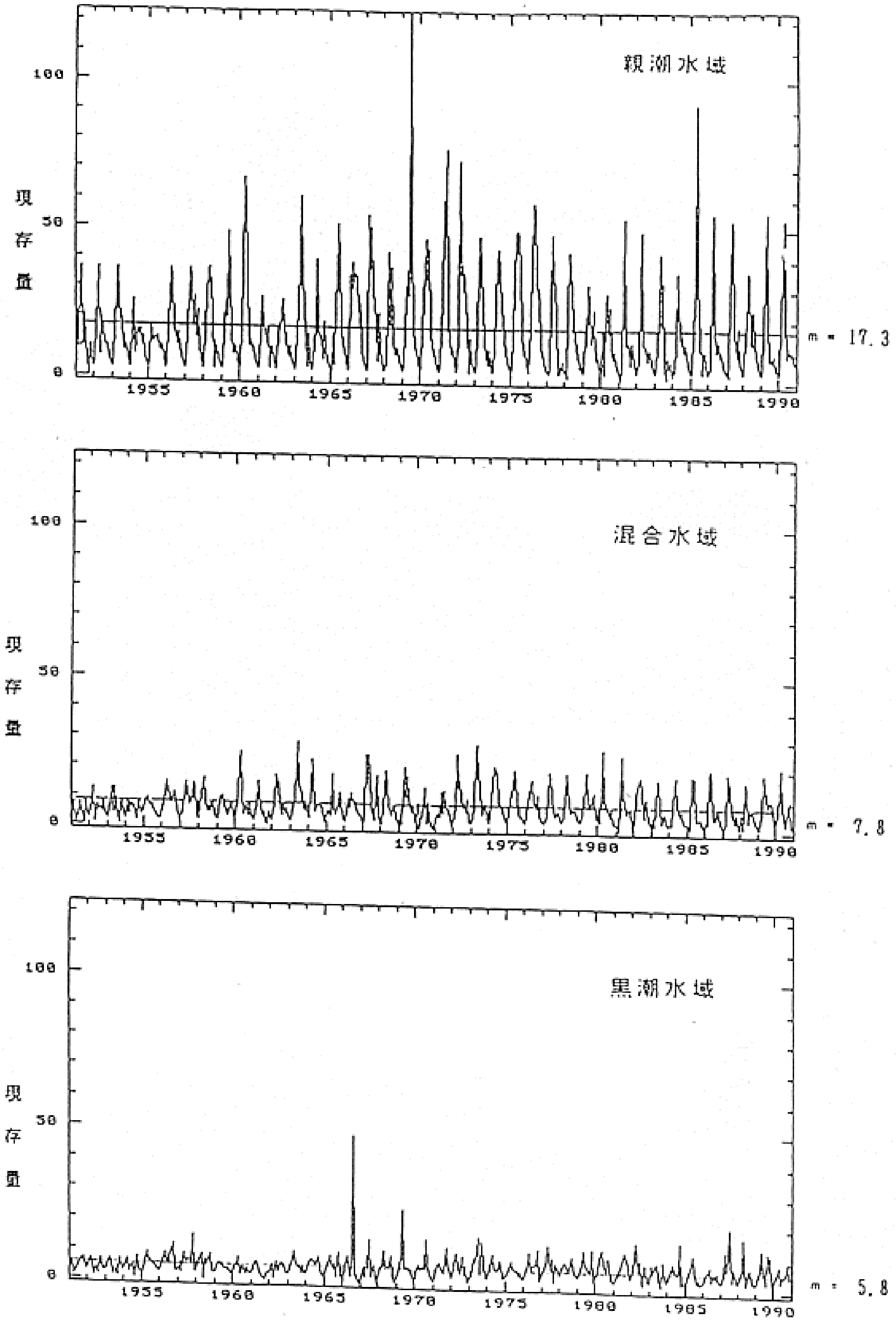


Fig. 35. Seasonal and interannual variations of net zooplankton biomasses in the upper 150 m water column (ordinates: g wet weight·m^{-2}) in the Oyashio (top), mixed water (middle) and Kuroshio (bottom) regions east of northern Japan recorded from 1951 to 1990. Overall means for three regions are respectively 17.3, 7.8 and 5.8 g wet weight·m^{-2} (Odate, 1993).

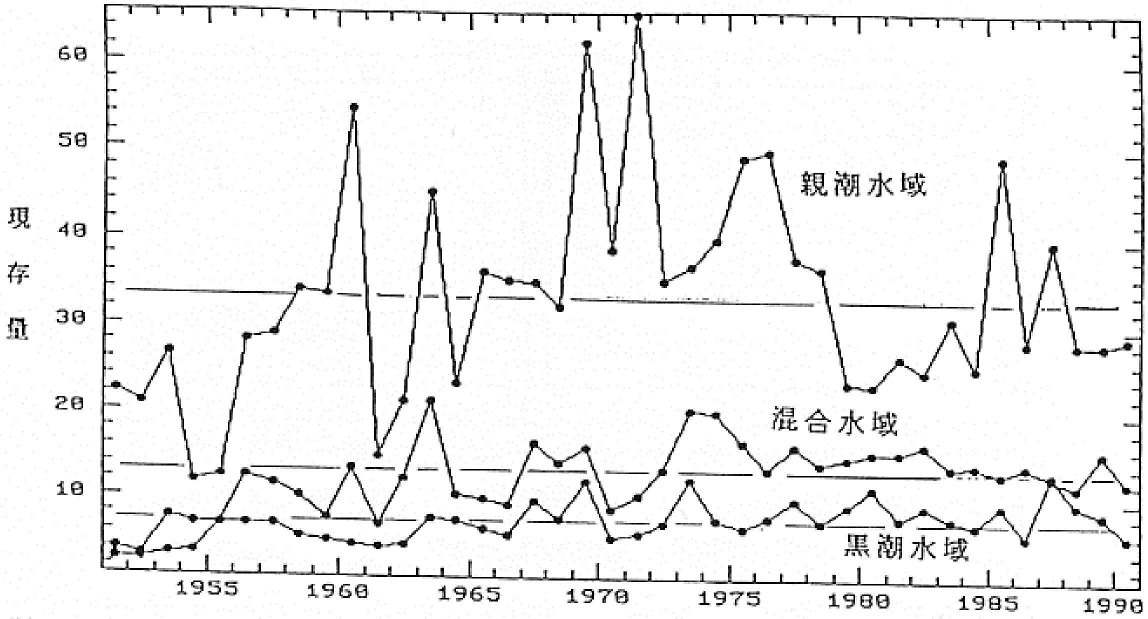


Fig. 36. Interannual variation of summer (May-July) net zooplankton biomasses in the upper 150 m water column (ordinates: g wet weight·m^{-2}) in the Oyashio (top line), mixed water (middle line) and Kuroshio (bottom line) regions. Three cycles can be seen (Odate, 1993).

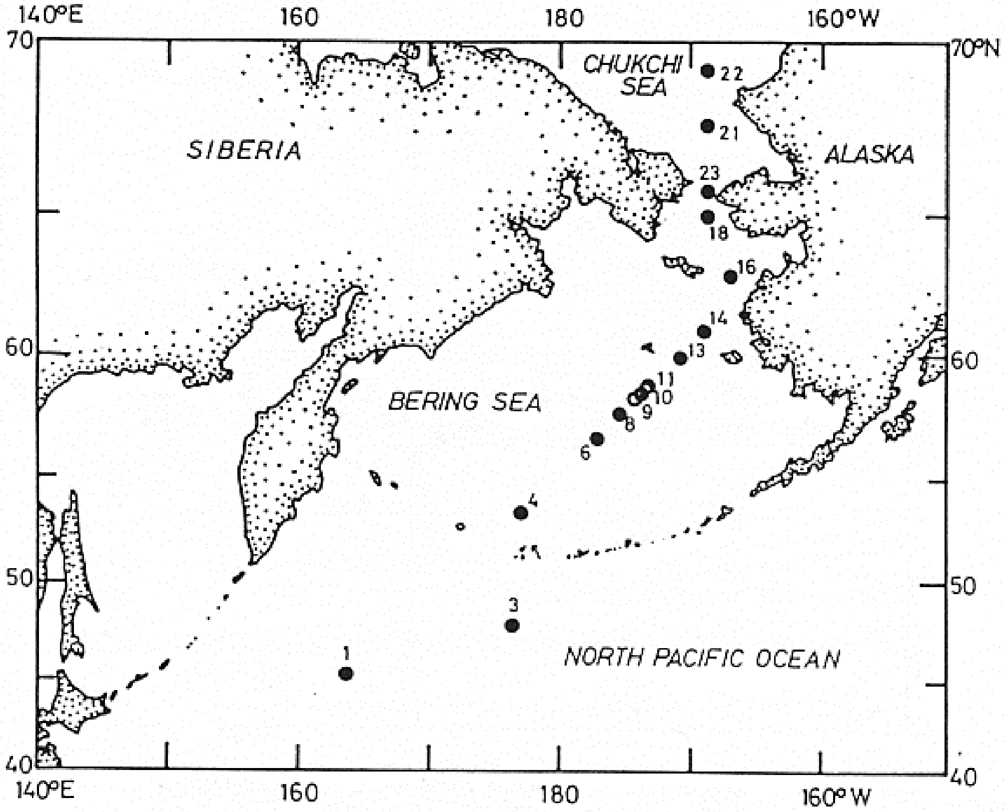


Fig. 37. Location of microzooplankton sampling stations in and around the Bering Sea, where the data shown in Fig. 38 were obtained (Taniguchi, 1984).

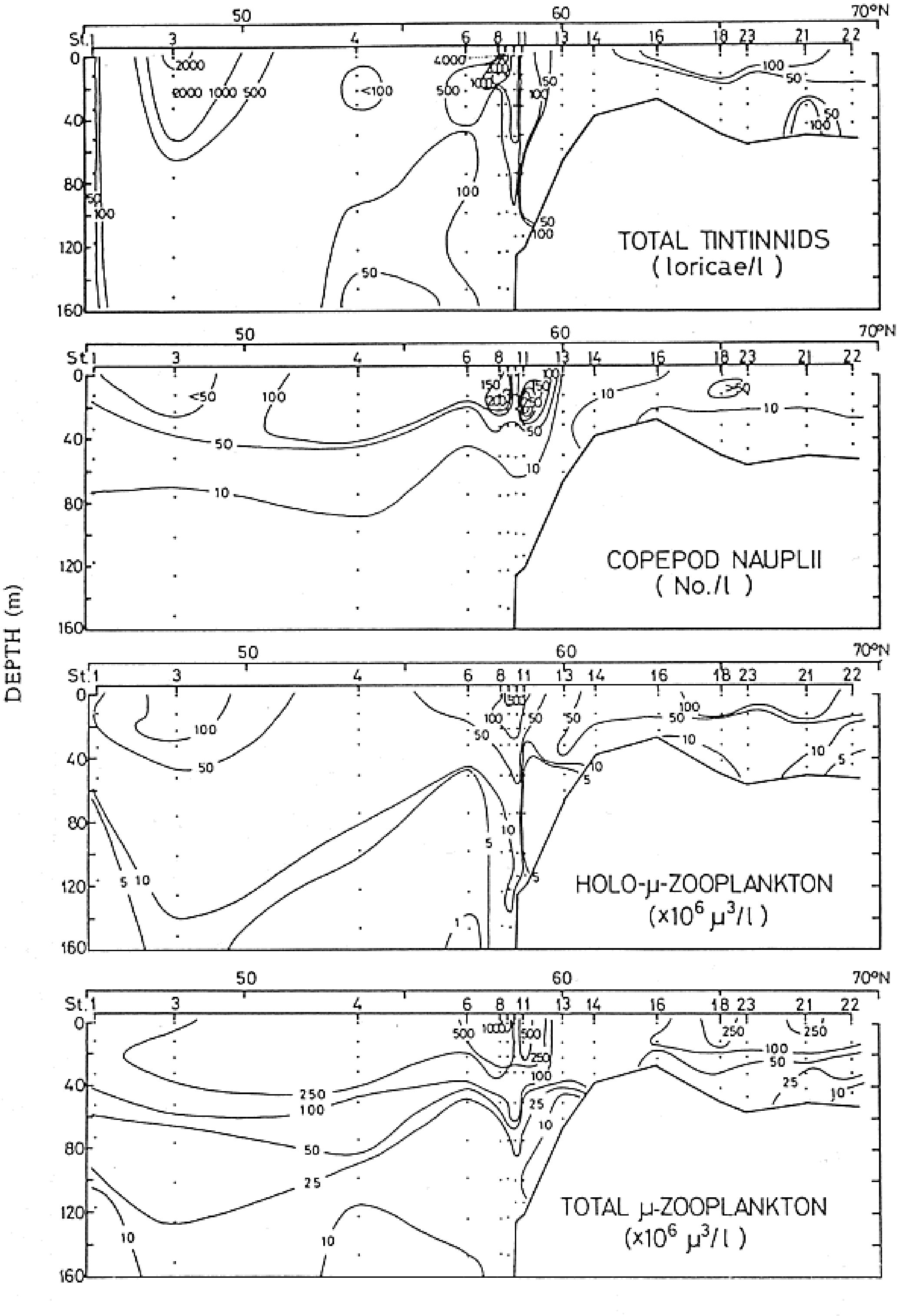
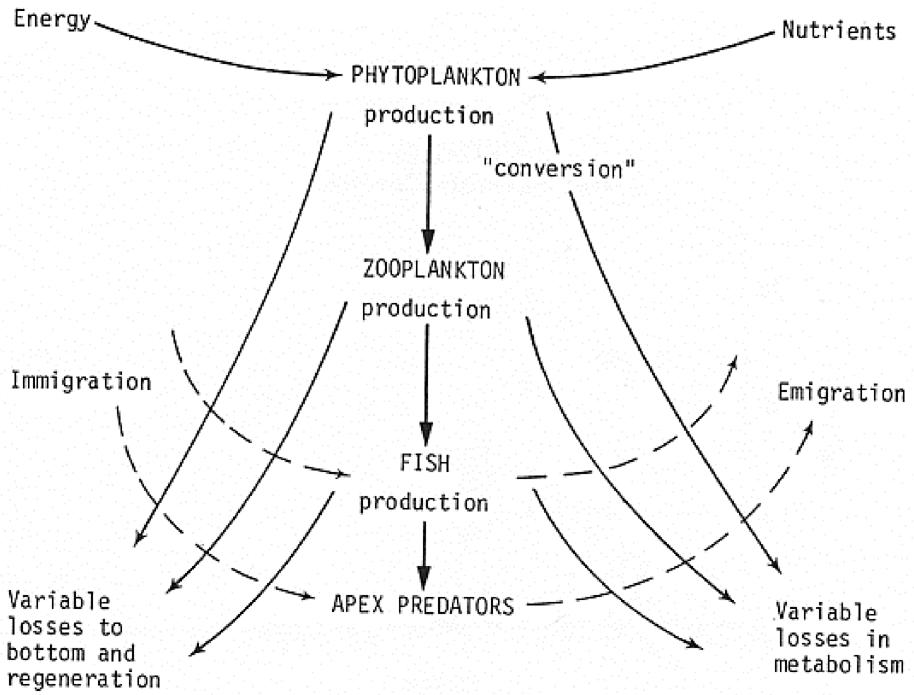


Fig. 38. Distribution in vertical section of major components of microzooplankton community in and around the Bering Sea in July 1978 (Taniguchi, 1984).



Principles: Estimation of organic production and its "conversion" to other trophic levels

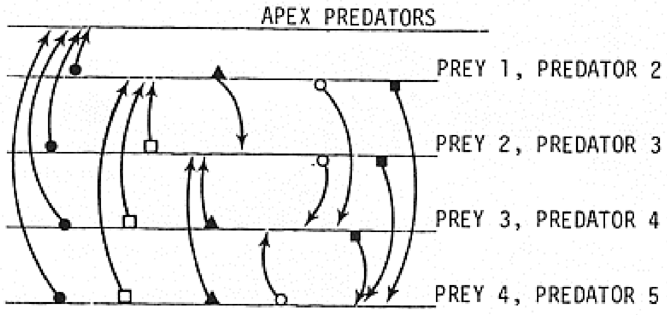
Shortcomings: Primary production sampling incomplete.

Conversion efficiencies variable and badly known

Magnitudes of "losses" nearly unknown.

Proportioning between trophic levels highly variable.

Fig. 39. Principles of a conventional food chain or food pyramid model based on production (Laevastu and Larkins, 1981).



Principles: Determine who eats what and how much and then determine how much of the prey must be there to produce the eaten amounts.

Advantages: Minimum values of the production and standing stocks of all prey can be computed.

Amounts of noncommercial (and nonsampled) species can be estimated.

Changes in one prey biomass are related to changes in other prey biomasses.

Fig. 40. Principles of trophodynamic computation based on consumption (Laevastu and Larkins, 1981).

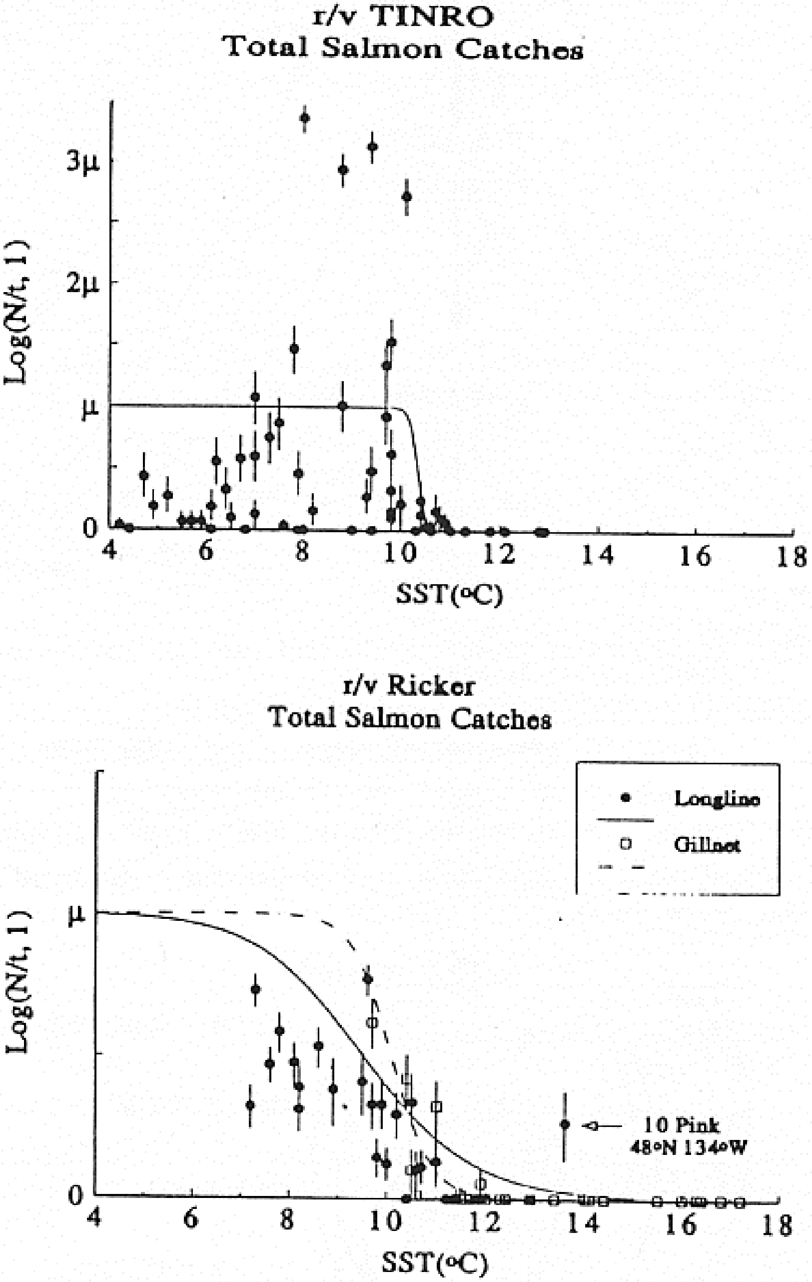


Fig. 41. Comparison of total salmonid catch vs. temperature for the R/V TINRO and the 1987, 1988, and 1990 W.E. RICKER cruises (after Welch, Chigirinsky, and Ishida, *in press*).

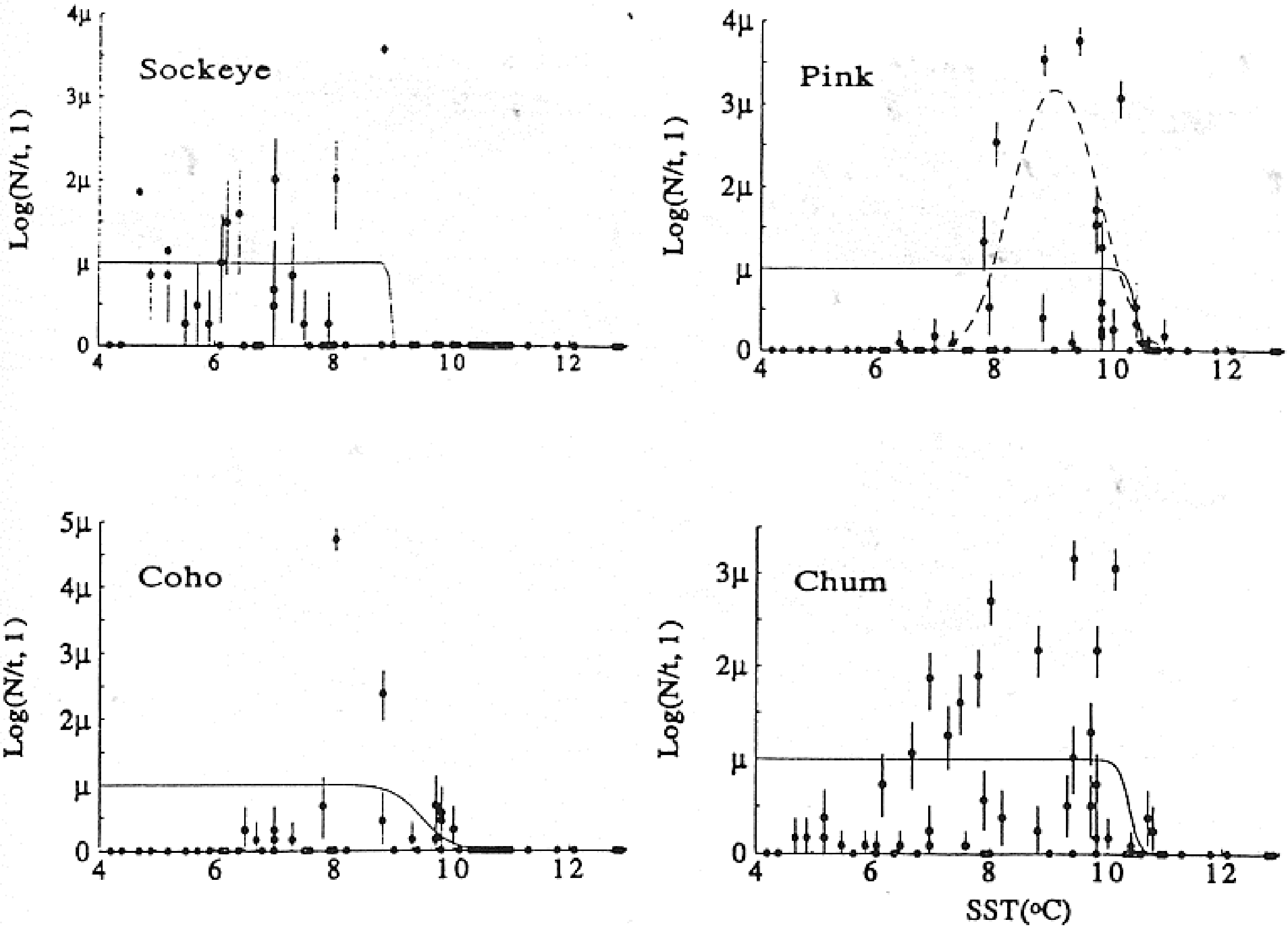


Fig. 42. Salmonid catch vs. temperature. Non-zero catches are expressed in terms of the logarithm of numbers trawled, after normalizing by the fishing time (t). Zero catches are plotted as log(1), and μ indicates mean abundance. Under this transformation the vertical range of positive catches is compressed to emphasize the sudden drop in density at the threshold temperature. Vertical bars indicate the 95% confidence limits on the individual catch estimates, calculated using the negative binomial distribution. Lines show the maximum likelihood estimates of salmon abundance as a function of temperature (after Welch, Chigirinsky, and Ishida, *in press*).

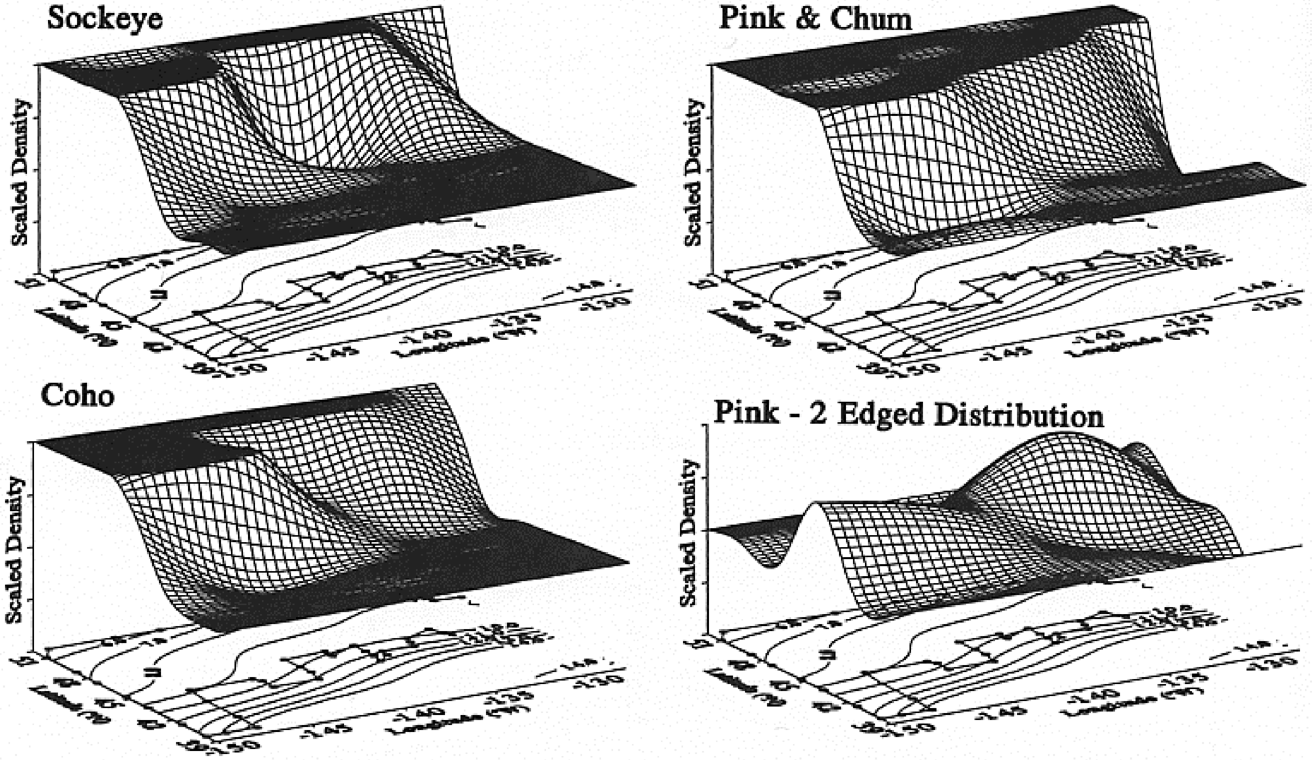


Fig. 43. The predicted geographic distribution of salmon in April 1990, based on the R/V TINRO data. Contour plots show the predicted temperature field, while the surface plot shows the predicted mean response of salmon abundance to temperature, using the parameter estimates reported in Tables 2 and 3. Note the sharp drop in abundance well to the north of the subarctic boundary, which lay south of 40°N. Fine details in the abundance surfaces are dependent on the accuracy of the interpolation of the temperature field (after Welch, Chigirinsky, and Ishida *in press*).

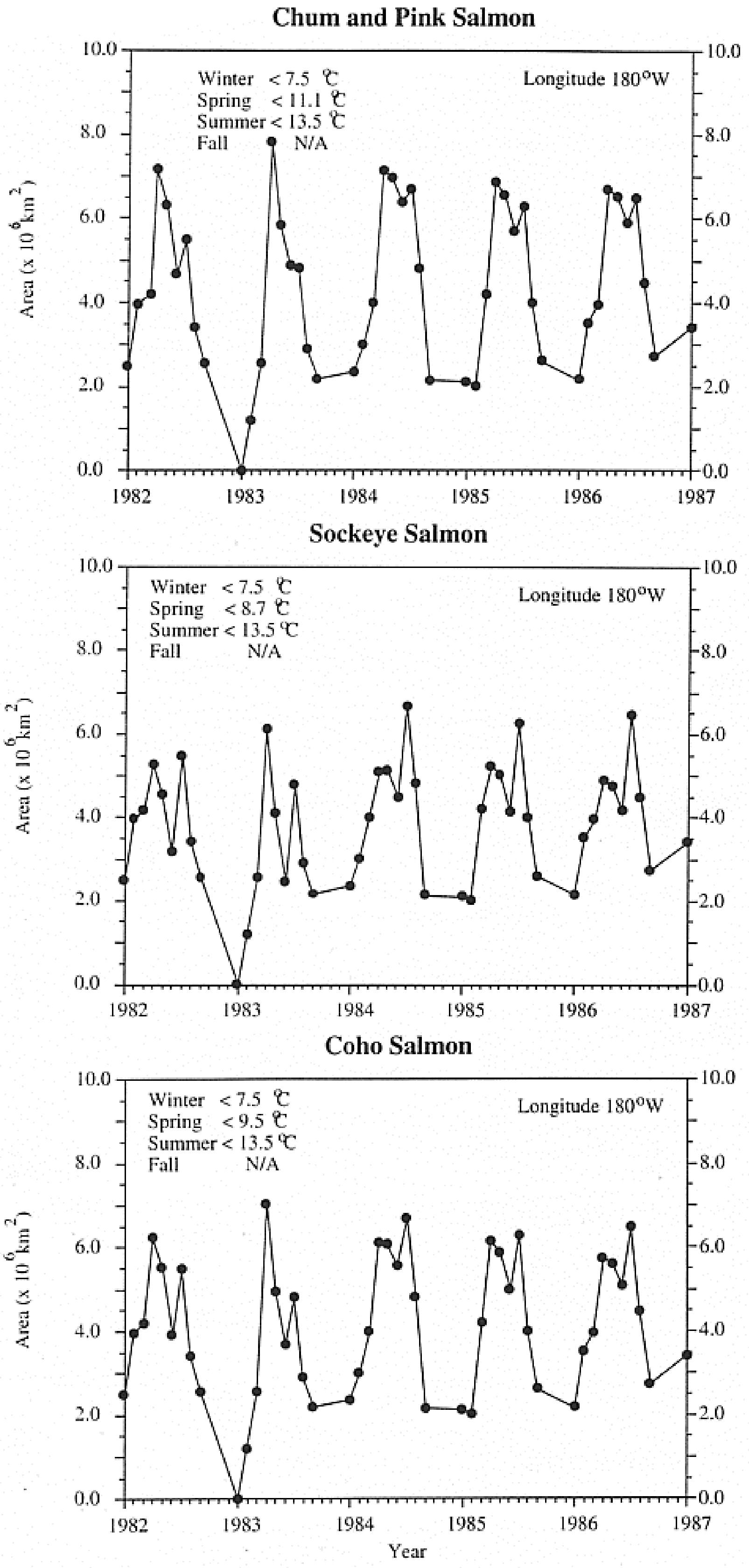


Fig. 44. Variation in the amount of thermal habitat available to Pacific salmon in the Gulf of Alaska, 1982-87. The region is taken as bounded on the west by the dateline, and the position of the southern limit to the salmon distribution is calculated from AVHRR satellite data (Welch, Thompson, LeBlond, and Jardine, *in prep.*).

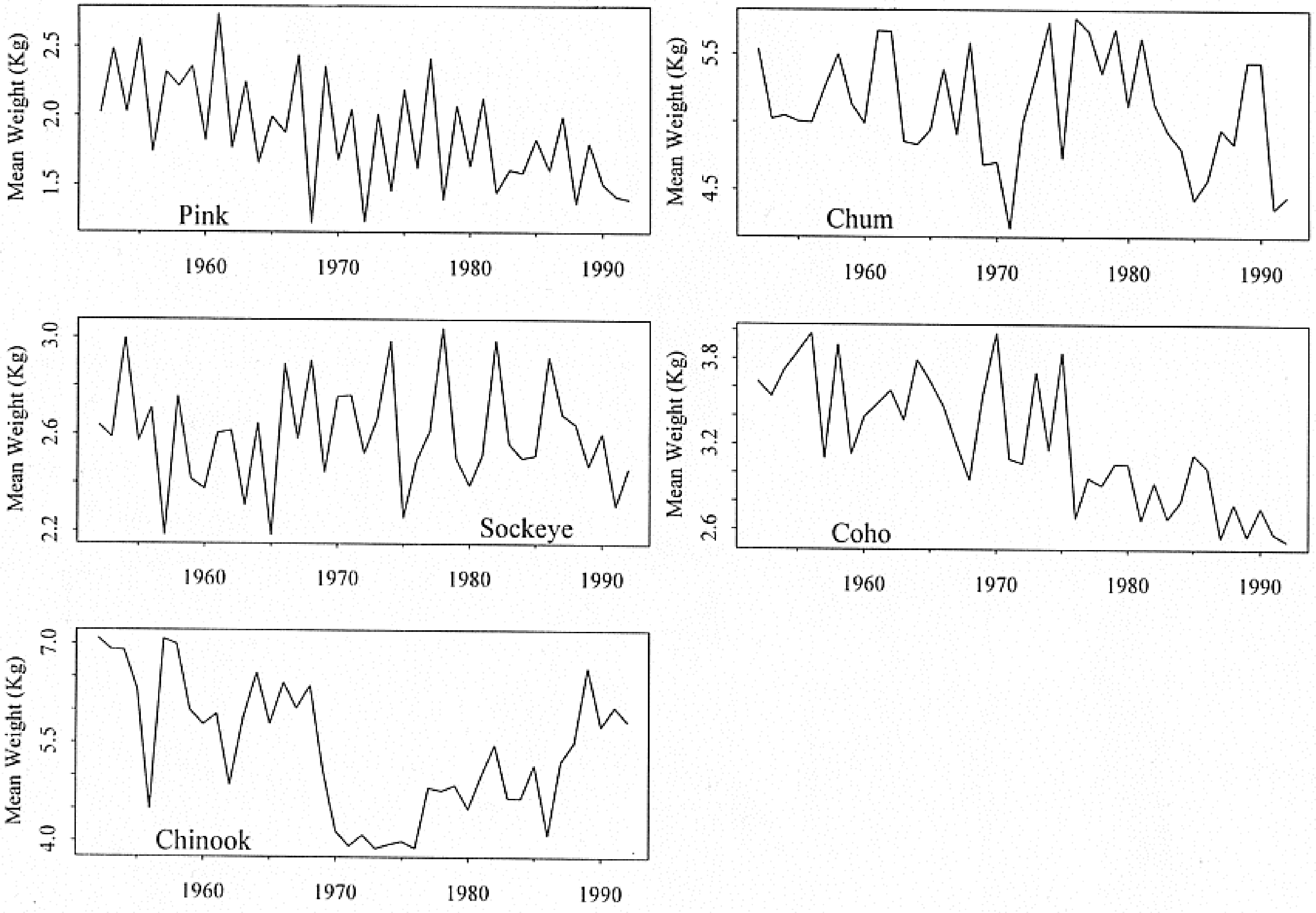


Fig. 45. Variation in the mean annual weight of seine-caught salmon returning to British Columbia, 1952-92. Note the large annual fluctuations in terminal size, and the large declines in average size over the 40 year period for some species. The average body weight of pink and coho salmon has declined by 40% and 30% respectively, over this period. Sockeye salmon have also shown similar large declines since 1990. Their cause is unknown.

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7.0 APPENDICES

Appendix 1

Recommendations and Action Items

General Recommendations

GR.1 WG-6 strongly recommends that the relationship between the North Pacific Anadromous Fish Commission (NPAFC) and PICES be clarified as soon as possible. PICES should support the science needs of NPAFC.

GR.2 WG-6 recommends that PICES support GLOBEC activities in the North Pacific region, especially those directed towards understanding the physical and biological oceanographic linkages to long term variations in zooplankton and fish populations.

GR.3 WG-6 recommends cooperation and coordination of activities between PICES and existing international programs, such as Global Ocean Ecosystem Dynamics (GLOBEC), the World Ocean Circulation Experiment (WOCE), Joint Global Ocean Flux Study (JGOFS) and Global Ocean Observing System (GOOS).

GR.4 WG-6 recommends that PICES should encourage and support long-term monitoring programs required to assess the biological productivity of the Subarctic North Pacific Ocean. PICES should ensure that current, cost-effective programs are maintained, and essential new programs initiated to measure key parameters at the critical time and space scales.

GR.5 PICES should strongly encourage and support the exchange of scientific data, information, plans and ideas between Pacific Rim countries. Reliable, detailed, and timely information about ongoing and planned national and international research activities is required to achieve maximum scientific benefits for minimum cost and effort. Formal international technical committees may be needed to achieve this goal (e.g. Ship Committee to organize, plan, and coordinate scientific cruises within the Subarctic Pacific).

GR.6 WG-6 should organize a scientific workshop in 1994: "PICES-GLOBEC Program for the North Pacific Ocean". The purpose is to further develop and plan collaborative research programs between PICES and International GLOBEC for the North Pacific Ocean.

GR.7 WG-6 should plan and organize a scientific symposium: "Structure, Trophic Linkages, and Ecosystem Dynamics of the Subarctic North Pacific" for the PICES Third Annual Meeting in 1994. This symposium would review and summarize current knowledge of the structure of the Subarctic food web, and the physical and biological processes which control the spatial and temporal (annual, interannual, decadal, etc.) variability.

GR.8 WG-6 should continue working in 1994 to complete scientific reviews of the physics and biology of the Subarctic Pacific, and prepare detailed proposals for collaborative research programs.

Specific Recommendations For Collaborative Programs

WG-6 endorses the following proposals for collaborative research, based on the discussions of participants at the 1993 Nemuro Workshop. These programs are at various stages of completion, including work that is ongoing or planned to start soon. In each case members considered both the scientific and practical importance of the proposed research, the likelihood of success, and whether or not the results would be useful. For convenience these proposals were classified into 2 categories: (1) short term programs (expected to be completed within 2-3 years); and (2) long-term programs (>5 yrs). These categories were based on the probable times required for planning and carrying out the research, and also the expected short vs.

long term pay-offs. WG-6 also carefully considered the extent to which PICES member states collectively and individually have the necessary resources to conduct the proposed work, both currently and in the foreseeable future. Each of these specific research proposals is preceded by a question (numbered Qx:). These questions were identified as the highest priority among the longer lists of key questions identified by each member (see section 3.0 for full lists of "Key Questions").

Q1: What processes control western and eastern boundary current system, including meso-scale processes and productivity of the ecosystem?

WG-6 strongly recommends and endorses continuation and future expansion of comparative studies among the following four key Pacific Rim ecosystems: Kuroshio-Oyashio Current, Western Subarctic Gyre, Alaskan Gyre, and California Current. In particular, WG-6 recommends comparisons between the Western and Eastern Subarctic Gyre ecosystems, between the western and eastern Boundary Current ecosystems, and between the California Current and the Alaskan Current ecosystems. Members view these comparative studies as the best approach to determining the main factors which control both long-term (e.g. global climate change) and short-term (e.g. interannual) variation in the structure and productivity of the Subarctic ecosystems. WG-6 recommends that these comparative studies also be extended in the future to include the marginal seas: Bering Sea, Okhotsk Sea, and East China Sea. WG-6 also recommends these PICES comparative studies be closely linked to, and coordinated with, other international research programs such as GLOBEC, WOCE, JGOFS, and GOOS.

Action:

1. WG-6 recommends that PICES support ongoing and expanded comparative studies of the Kuroshio-Oyashio Current and California Current ecosystem. These studies should focus on determining how the physical environment affects the productivity and composition of the nutrient and plankton dynamics, and production and recruitment of major fishes (e.g. sardine and anchovy) in these ecosystems. In the short term (within the next 2-3 years), existing physical and biological data (routine national surveys, U.S.A. CalCOFI, Canada LaPerouse Bank project and Line P, Alaskan GAK-1 hydrographic line, Hokkaido University sampling series, etc.) should be continued. The data from these series should be analyzed to assess the important spatial/temporal scales of changes in these ecosystems. Much historic data is available for the Eastern and Central Pacific, but there is a critical need for more data from the Western Pacific. Therefore, WG-6 strongly recommends that intensive field programs be initiated there immediately, focusing on determining the effects of physical oceanography on biological processes and fisheries dynamics. These new studies should include the Hakuho-maru cruises planned for the Kuroshio and Kuroshio Extension areas in 1994.

2. For the longer term, WG-6 recommends that PICES support initiation within 5 years of more detailed comparative studies on the Subarctic ecosystem dynamics, encompassing larger space and time scales. These expanded studies should include maintaining existing and establishing additional long-term monitoring and data exchange programs. These studies should also develop numerical models describing the ecosystem dynamics to determine what triggers major ecosystem changes (e.g. "regime shifts" in important fish species).

3. For both 1. and 2. above, WG-6 should prepare detailed research proposals (background, requirements, participants, schedule, costs, etc.). Proposals for immediate implementation should be prepared in 1994 and reviewed by all WG-6 members at the 1994 WG-6 meeting. The revised proposal should be included in the WG-6 1994 Annual Report for further consideration by the PICES Science Board.

Q2: What is the interannual variability of the physical parameters in the Subarctic Gyre, especially those related to biological productivity?

WG-6 recommends PICES support the continuation of existing programs and platforms designed to improve understanding of interannual and interdecadal variability in the physics of the upper 250 m in the northern Northeast Pacific Ocean. WG-6 also recommends PICES encourage expansion of these programs to include additional measurements designed to assess the effects of physical variations on biological productivity. Important projects include: 1) the ongoing 23 year record of coastal temperature and salinity versus depth from the GAK-1 hydrographic line at Resurrection Bay, Alaska (60°N, 149°W), 2) the U.S.A. WOCE Volunteer Observing Ship (VOS) program that will conduct quarterly transects from Valdez, Alaska to Honolulu, Hawaii from 1993-1998. This VOS section is particularly significant to WG-6 as it will allow determination of the position of the Subarctic boundary, and also the meridional upper layer thermal structure.

Action:

1. WG-6 recommends PICES endorse continuation of the GAK-1 hydrographic line series. This is one of the few long-term data series in this region, and continuation of this series is vital to understanding the upper ocean variability in the northern Northeast Pacific. PICES should also strongly encourage the U.S.A. to expand the current measurements to include nutrients, dissolved oxygen, larval fish, plankton and ocean color.

2. WG-6 recommends PICES endorse the continuation of the current U.S.A. VOS section. PICES should also strongly encourage expansion of the current measurements to include sea surface temperature, salinity and fluorometry. Continuous plankton recorders should also be added, if possible. PICES should also encourage use of these current VOS platforms for other types of observations important to PICES member states.

3. PICES should immediately begin planning to address anticipated changes in the ongoing U.S. VOS program. PICES should carefully consider a recommendation to the U.S.A. that this VOS section be continued beyond 1998.

4. WG-6 recommends PICES support and encourage initiation of additional VOS sections in the North Pacific as soon as possible. Currently the U.S.A. VOS section is complemented in the central North Pacific only by a Japan VOS section between Tokyo and Vancouver.

5. PICES should support and encourage development of additional instrument "packages" which can be routinely placed on current VOS and other ships of opportunity, as part of an ongoing PICES commitment to VOS-type programs. These new instrument "packages" should be capable of measuring physical, biological and chemical parameters in the upper ocean. WG-6 recommends this could be a very cost-effective and valuable approach to measuring upper ocean variability in the North Pacific.

Q3: What controls interannual variability in mesozooplankton abundance in surface waters of the oceanic Subarctic Pacific?

WG-6 recommends that new collaborative work be initiated to observe the dynamics of species composition, abundance and production of plankton in controlled shipboard experiments involving manipulations of key processes and properties. Microcosms containing natural assemblages of plankton should be treated in experiments of multi-factorial design with different combinations of light, nutrients (trace nutrients and ammonia), and abundance and composition of mesozooplankton. Sufficient effort should be devoted to field (***in situ***) measurements of rates and distributions to verify interpretations derived from these "enclosure" experiments. The biological responses should be monitored for several days to a week. The potential effects of spatial variation in some physical properties (light field, mixed depth layer) utilizing undulating towed vehicles to measure ***in situ*** fluorescence, irradiance, temperature and salinity in underway surveys should also be explored. The results from this work would determine not only the types of observations required in future investigations of plankton production in the open Subarctic Pacific, but also whether crucial missing information compromises the value of extant long term data sets and samples (such as those from Ocean Station P).

Action:

1. WG-6 recommends that this proposal be given high priority for immediate action. To begin, selected members should prepare a detailed research proposal (background, requirements, participants, schedule, costs, etc.) in 1994. This proposal should be reviewed and discussed by all members at the 1994 meeting, and the revised proposal included in the 1994 Annual Report for further consideration by the PICES Science Board.

Q4: How do processes occurring in oceanic regions of the Subarctic Pacific affect the production of coastal marine nekton?

WG-6 recommends that a large-scale physical and biological oceanographic program should be initiated to monitor a series of key transects around the North Pacific rim once a month (or at least through the spring and summer months), for several complete cycles (3-5 years). These transects would extend offshore sufficient distances to encompass the major currents in coastal waters with an additional 1-2 transects in oceanic waters across the Kuroshio Extension/Subarctic Current. We propose that the following suite of measurements and samples be made along these transects: 1) current speed and direction, 2) temperature and salinity profiles, 3) nutrients, 4) chlorophyll, 5) zooplankton (including ichthyoplankton) collections, and 6) micronekton collections. A high degree of consistency in sampling techniques among laboratories would be a necessity.

Action:

1. This project is a long-term objective which will require much planning to achieve the maximum benefits. WG-6 recommends that selected members prepare a detailed research proposal (background, requirements, participants, schedule, costs, etc.) in 1994. This proposal should be reviewed and discussed by all WG-6 members at the 1994 meeting, and the revised proposal included in the WG-6 1994 Annual Report for further consideration by the PICES Science Board. Upon approval by the Science Board, WG-6 should initiate detailed planning and formal requests for support (e.g. ship time) from all PICES member states.

Q5: What is the structure of the Subarctic food web and what controls its spatial, seasonal and interannual variability?

WG-6 recommends that increased emphasis be placed on improving our knowledge of the structure and dynamics of the Subarctic food webs, including oceanic and mesopelagic animals, and how trophodynamic processes affect the production of nektonic animals such as salmonids, other fishes, seabirds, and marine mammals. Mesopelagic and bathypelagic animals such as myctophids, shrimp, and squids likely form a critical, but currently poorly understood, role in the trophic structure of the Subarctic region.

Action:

1. The highest priority for immediate action is to conduct further analyses of the existing zooplankton data of Dr. Odate (40 yr. monthly series of zooplankton wet weight and taxonomic group composition). The relationship between zooplankton variation and environmental factors should be analyzed. Fishery statistics should also be examined to determine if there are significant relationships between zooplankton and fish variability.

2. The second priority for immediate action should be initiation by WG-6 of new work to

inventory existing plankton/ micronekton/ nekton collections and data in PICES member states. These existing samples and data should enable at least preliminary examination of food habits and long term variations in trophic relationships and species composition.

3. PICES should insure adequate curation of existing historic sample and data collections in PICES member states (e.g. plankton samples from Ocean Station "P" and CalCOFI). Such collections are irreplaceable and their immense value in addressing current and future questions (e.g. effects of climate change on fisheries) is not always apparent to those responsible

4. In the longer term, additional routine research surveys are needed determine the long-term variation in food web structure and the causative factors. These new samples and data are especially needed to estimate the future carrying capacity of the Subarctic Pacific, and could also test theories developed from trophodynamic modelling. WG-6 should develop or solicit detailed research proposals (background, requirements, participants, schedule, costs, etc.) for these new surveys, and should try to link and coordinate these surveys with other PICES and WG-6 proposals and activities (e.g. Pacific Rim experiment outlined in Q3 section above). Upon approval by the Science Board, WG-6 should initiate detailed planning and formal requests for support (e.g. ship time) from all PICES member states.

Q6: What processes affect the production of salmon and other nekton in the Subarctic Pacific?

Action:

1. WG-6 recommends PICES support continuation of the ongoing analyses of ocean growth of salmon using the time series of salmon scale samples accumulated by Canada, Japan, the United States, and (if possible) Russia. These data provide insight into the variations in growth that have occurred in different salmon stocks, patterns of co-variation, and whether the types of oceanographic data products currently collected are correlated with variations in oceanic growth. WG-6 should contact PICES member states to obtain information about existing collections of salmon scales in each country. PICES should encourage additional new collaborative research using salmon scales. After ongoing scale analyses projects are completed, WG-6 should prepare and/or solicit detailed research proposals (background, requirements, participants, schedule, costs, etc.) for new activities. Proposals endorsed by WG-6 should be included in the 1994 Annual Report for further consideration by the PICES Science Board. Upon approval by the Science Board, WG-6 should initiate detailed planning and formal requests for support (e.g. additional collection of scales) from all PICES member states.

2. WG-6 recommends that PICES support continuation of ongoing collaborative research between PICES member states on salmon distributions in the Subarctic region. Recent results from joint work between Japan and Canada show sharp thermal limits to the distribution of Pacific salmon in the North Pacific. Therefore, the potential impacts of expected warming trends in the Subarctic Pacific could have important impacts on the production dynamics of Pacific salmon. These results need to be verified, and their impact on salmon yields clarified by additional analyses of existing data in order to better understand their possible future impact.

3. WG-6 recommends that PICES support and facilitate expanding the information collected by fishery research vessels to include the collection of more physical and biological data relevant to the understanding of the changes that have occurred at lower trophic levels in recent decades. WG-6 should prepare and/or solicit a detailed research proposal (background, requirements, participants, schedule, costs, etc.) for these expanded biological and physical measurements, for further consideration by the PICES Science

Board. Upon approval by the Science Board, WG-6 and other appropriate PICES Working Groups (e.g. WG-4: Data Collection and Quality Control) should initiate detailed planning and coordination of activities by all PICES member states.

Q7: What new approaches and technology can be used to track the movements and fate (e.g. living, dying, or dead) of migratory nekton species over large regions of the North Pacific Ocean?

WG-6 recommends PICES support the development of new technology designed to solve significant fundamental physics, biology, and fisheries management problems. This is a strategic, ongoing and long-term objective: new technology and methods are needed to support both current and proposed WG-6 activities. One example, among many, is development of new "intelligent" fish tags, which would continuously record or transmit the real-time position (location, depth) of a fish over the entire lifetime of the fish.

Action:

1. In the short term, WG-6 recommends that detailed research proposals (background, requirements, participants, schedule, costs, etc.) should be prepared for all proposed new methods and technology. These proposals should be reviewed and discussed by all members at the annual WG-6 meetings, and proposals endorsed by members should be included in the WG-6 1994 Annual Report for further consideration by the PICES Science Board. Upon approval by the Science Board, WG-6 should initiate any detailed planning and formal requests for support (e.g. ship time, collaborative field experiments, etc.) from PICES member states.

2. For the longer term, we recommend that WG-6 form a new Methods and Technology Sub-Committee for assessing the potential value and costs of all proposed new methods and technologies. This MTC would implement a standard review procedure, such as:

- identification of required data
- review relevant existing methods and technology
- identify requirements to solve specific problem
- identify and assess technical problems
- develop or invite detailed R/D proposals
- review and endorse/reject R/D proposals
- recommend R/D proposals to PICES Science Board
- coordinate/facilitate PICES collaborative efforts to develop and test resulting new methods and technology

Appendix 2

Terms of Reference

Many important phenomena which link layer of the North Pacific were identified by the physical and biological processes in the upper PICES Climate Change group and the Physical Oceanography group in the PICES workshop in 1991, and also in the 1992 BIO Committee report to the PICES first annual meeting in Victoria, B.C. (see PICES Annual Report, 1992). The initial mandate of WG-6 is to further clarify the present state of scientific knowledge about the Subarctic Gyre region, to facilitate and promote future studies of the physical environments, the dynamics of the primary and secondary production, the trophic linkages and transfer functions, and fisheries recruitment and population dynamics in response to climatic change. WG-6 is also tasked with identifying and evaluating methods of determining the carrying capacity of the Subarctic Gyre for nekton, and assessing the effects of climate and oceanic change on primary and secondary production in this region. Other PICES working groups (WG-5 and WG-1) deal with the Bering Sea and Okhotsk Sea, respectively. Therefore WG-6 will focus on the physical fluctuations of the Alaskan Gyre and Western Subarctic Gyre, and the effects on the ecosystem.

The PICES Science Board provided the following seven specific Terms of Reference for WG-6 for 1993:

- Review the existing level of description of ocean circulation and climate variability in the Subarctic North Pacific and identify gaps in knowledge;

- Review the present level of knowledge of the important processes determining ocean circulation in the Subarctic North Pacific and identify gaps in knowledge;

- Review existing information on the biomass of major trophic levels, and distribution of the dominant species within each level;

- Review existing information on the carrying capacity for salmon and other nektonic species in the subarctic, and what is known about variations in the carrying capacity of this region in response to climate change. Advise on how changes in carrying capacity could be quantified;

- Review existing level of knowledge of the processes affecting primary and secondary production in this region and identify information gaps. Advise on how these gaps could be studied;

- Identify key scientific questions, and propose collaborative programs which can be conducted to advance knowledge and test major hypotheses;

- Determine relationship to GLOBEC. Advise which PICES and GLOBEC objectives could be linked.

Appendix 3

Participants of Subarctic Gyre Working Group

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#denotes participated in Working Group 6 discussions at 1993 Nemuro Workshop