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Influences of abiotic factors on the return, ocean abundance, and maturity of sockeye salmon (*Oncorhynchus nerka*) in the northern North Pacific Ocean

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Influences of Abiotic Factors on the Return, Abundance, and Maturity of Sockeye Salmon (*Oncorhynchus nerka*) in the Northern North Pacific Ocean

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Abstract

The fluctuations in return, ocean abundance, and maturity of sockeye salmon (*Onchorhynchus nerka*) were examined and related to wind stress curl, sea surface temperature (SST), sea level pressure, and cloudiness, in the area between 40°N-60°N and 160°E-140°W. Historical records, during two periods, 1971-76 and 1955-86, were the primary source of data.

Spectral analysis of a 360-month period of mean wind stress curl during 1955-85 showed 3.1- and 5.3-year cycles. The 5.3-year cycle was correlated (r=.32 to .44,P<.10) with the return of Bristol Bay sockeye salmon mostly at 0- (the year of spawning migration) and 1-year lag (the first year of lake residence).

The relative ocean abundance of sockeye salmon in the northwestern North Pacific during 1971-76 was lowest during the three periods: 1961-70, 1971-76, and 1977-85. Mature Kamchatka sockeye salmon were 24 % more abundant than mature Bristol Bay sockeye salmon during 1971-76. A significant relationship was found between the mean May-June SST and abundance of sockeye salmon (r=.56 to .66, P<.01) during 1961-85.

In the northern North Pacific, the SST was positively (r=.73 to .86, P<.001) related with the gonad weight of sockeye salmon.

The results indicated a close relation between the return, ocean abundance, and maturity of sockeye salmon and most of the abiotic factors.

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Chapter I: Sockeye salmon *Oncorhynchus nerka* in the Subarctic Pacific Ocean

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) fisheries have a major impact on the economy of North America. Of the six species, sockeye salmon (*O. nerka*) has been the focus of extensive studies in many countries (U.S.A., Canada, U.S.S.R., Japan) for several decades (Brannon, 1981), because of the diversity of their life history pattern, and of their great abundance and high economic value.

Each year from early summer to late fall, millions of sockeye salmon return to their home streams to spawn. Spawning of individual stocks occurs at about the same time each year. They spawn in tributaries and outlet streams to lakes. In North America, spawning occurs from the Columbia River in the south to the Bristol Bay area in the north. In Asia, spawning occurs from the north and the east part of Hokkaido in Japan to the northern Kamchatka coast (Hartman, 1971).

There have been studies on the habitat change in the freshwater and coastal regions (Groot, 1981), seaward migration of smolts (Straty, 1974), and the migratory route of adult fish in offshore waters (Straty, 1975). There is, however, a lack of study on the relationships between the large scale oceanic and atmospheric features and the return, ocean abundance, and maturity of sockeye salmon.

The objective of this study is to examine the fluctuations in return, abundance, and maturity of sockeye salmon in relation to the abiotic factors, wind stress curl, sea surface and subsurface temperature, cloudiness, and sea level pressure. The study

(1) examines the return, high seas catch and relative ocean abundance of the Bristol Bay and Kamchatka sockeye salmon;

(2) analyzes the spatial, seasonal, and annual variation of maturity of sockeye salmon at sea;

(3) analyzes fluctuations in wind stress curl, sea surface and subsurface temperature, cloudiness, and sea level pressure in the northern North Pacific; and

(4) examines the relationship between abiotic variables and the return, ocean abundance, and maturity of sockeye salmon.

LIFE HISTORY OF BRISTOL BAY SOCKEYE SALMON

Sockeye salmon have six major spawning systems in the Bristol Bay area: Togiak, Nushagak, Naknek, Kvichak, Egegik and Ugashik (Figure 1). Returns to these streams varied between 2.4 and 62.4 million fish during 1956-86 (Alaska Department Fish and Game, 1986). Spawning occurs from May to August with the eggs incubating in gravel beds. At the time the yolk sack is absorbed, the alevin emerge from the spawning gravels and migrate to lakes as fry in the following spring. A majority of young sockeye salmon spend one or two years in the nursery lake-stream systems before migrating to sea as smolts. The seaward migration of sockeye salmon from lakes into Bristol Bay occurs from mid-May to the end of August (Straty, 1974). After two to three years residence in the ocean, maturing sockeye salmon return to the coastal waters in late spring (French *et al.*, 1976; Burgner, 1978). The peak time for adults returning to their natal streams and lake systems is about two weeks between late-June and mid-July (Rogers, 1980; Nishiyama, 1984).

The combination of freshwater and ocean phases of sockeye salmon life history results in 22 different age groups (Healey, 1986). To express ages in this study, Koo's (1962) method has been employed in which freshwater residence precedes a decimal point and marine residence follows the decimal point. In the Bristol Bay area, most mature fish return in their fourth, fifth, or sixth year of life after one or two winters in freshwater. The dominant age groups are ages 1.2, 2.2, 1.3, and 2.3. Ages .2 and .3 are consistently used in this study to indicate that the mature sockeye salmon spent two and three winters in the ocean prior to returning to spawn.

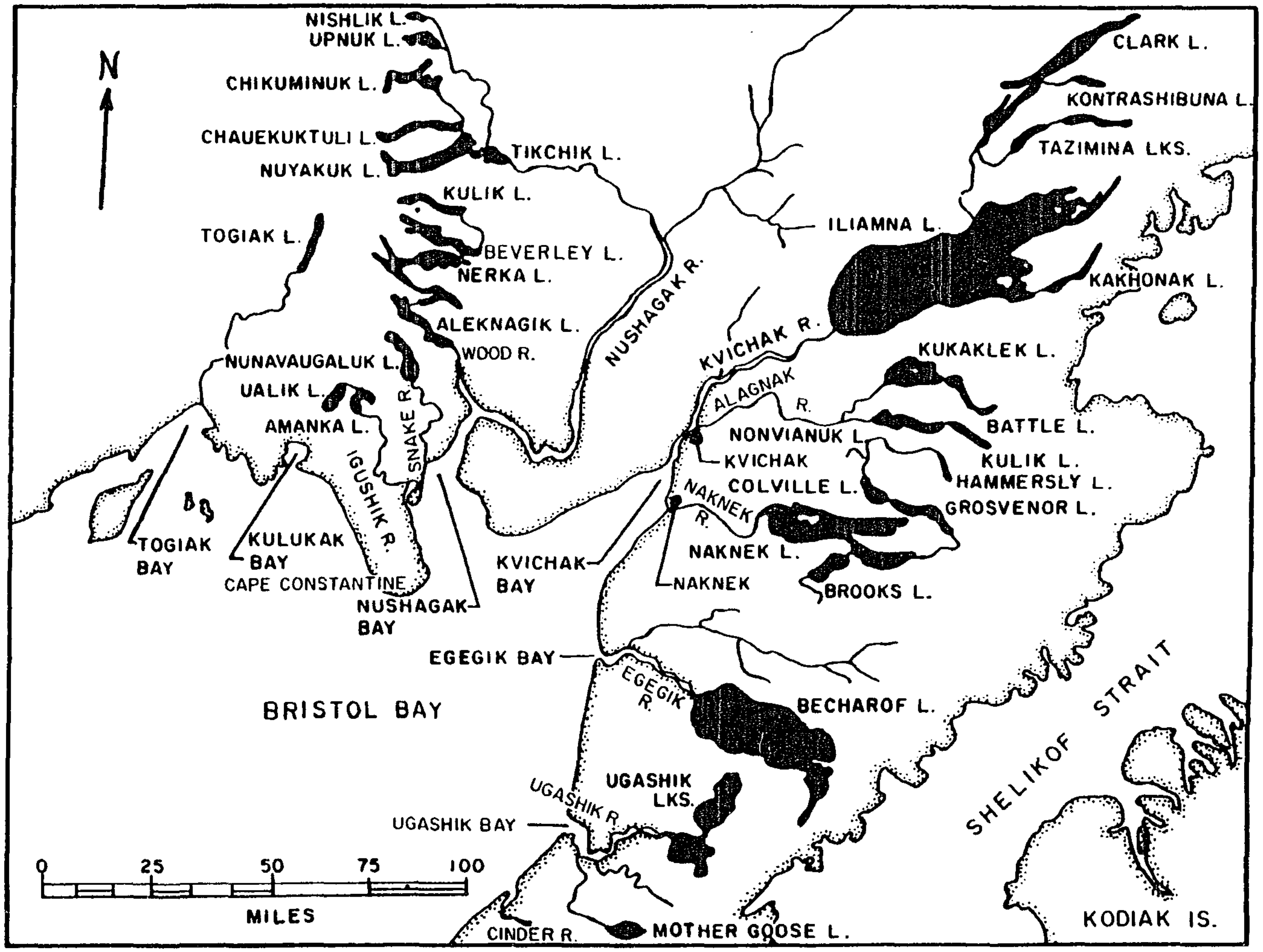

Figure 1. Major sockeye salmon spawning lake-stream systems in Bristol Bay, Alaska (from Straty, 1974).

OCEANIC DISTRIBUTION OF BRISTOL BAY SOCKEYE SALMON

Based on tagging experiments and catches in gillnet, long-line and purse seine, the distribution and migration patterns of Bristol Bay sockeye salmon in the ocean have been described (Aro *et al.*, 1971; Bakkala, 1971). French and Bakkala (1974) and French *et al.* (1976) summarized these studies and proposed models of oceanic migrations of sockeye salmon for various age groups. The fish make two or three circuits within an elongated east-west course in the North Pacific Ocean and the Bering Sea extending between latitude 40°N-60°N and longitude 165°E-140°W (Figure 2). The Bristol Bay sockeye salmon often extend far east to the area of 160°E-165°E (Cook, 1982). The information suggests that the sockeye salmon migration patterns are related to the ocean current. The general direction of movement is westward in the Alaska Stream and eastward in the Subarctic Current. As they approach Bristol Bay the schools of fish become more concentrated, and the center of abundance is about 74 to 111 *km* from the north side of the Alaskan Peninsula (Straty, 1974; French *et al.*, 1976).

CLIMATE AND WATER CIRCULATION OF THE SUBARCTIC PACIFIC

The general climate patterns in the Subarctic Ocean are characterized by the Aleutian Low and Pacific High in the eastern ocean (Figure 3), the Siberian High in the western ocean (Dodimead *et al.*, 1963; Favorite *et al.*, 1977) and the passage of frequent storms (Schumacher and Reed, 1983). In winter, the ocean is dominated by an intensive low pressure system (Aleutian Low). Two storm tracks prevail during winter, one parallel to the Aleutian Islands and one curving northward along the Siberian coast. In summer, the ocean is dominated by an intensive high pressure. During summer, the storms tend to migrate northward into the Bering Sea. The mean summer and winter winds are from the southwest in the North Pacific.

The central subarctic Pacific Ocean is frequently overcast in both winter and summer (Dodimead *et al.*, 1963; Karpova, 1963), and it appears to be cloudier than along the coast at either side of the ocean. Terada and Hanzawa (1984) showed a higher occurrence of total

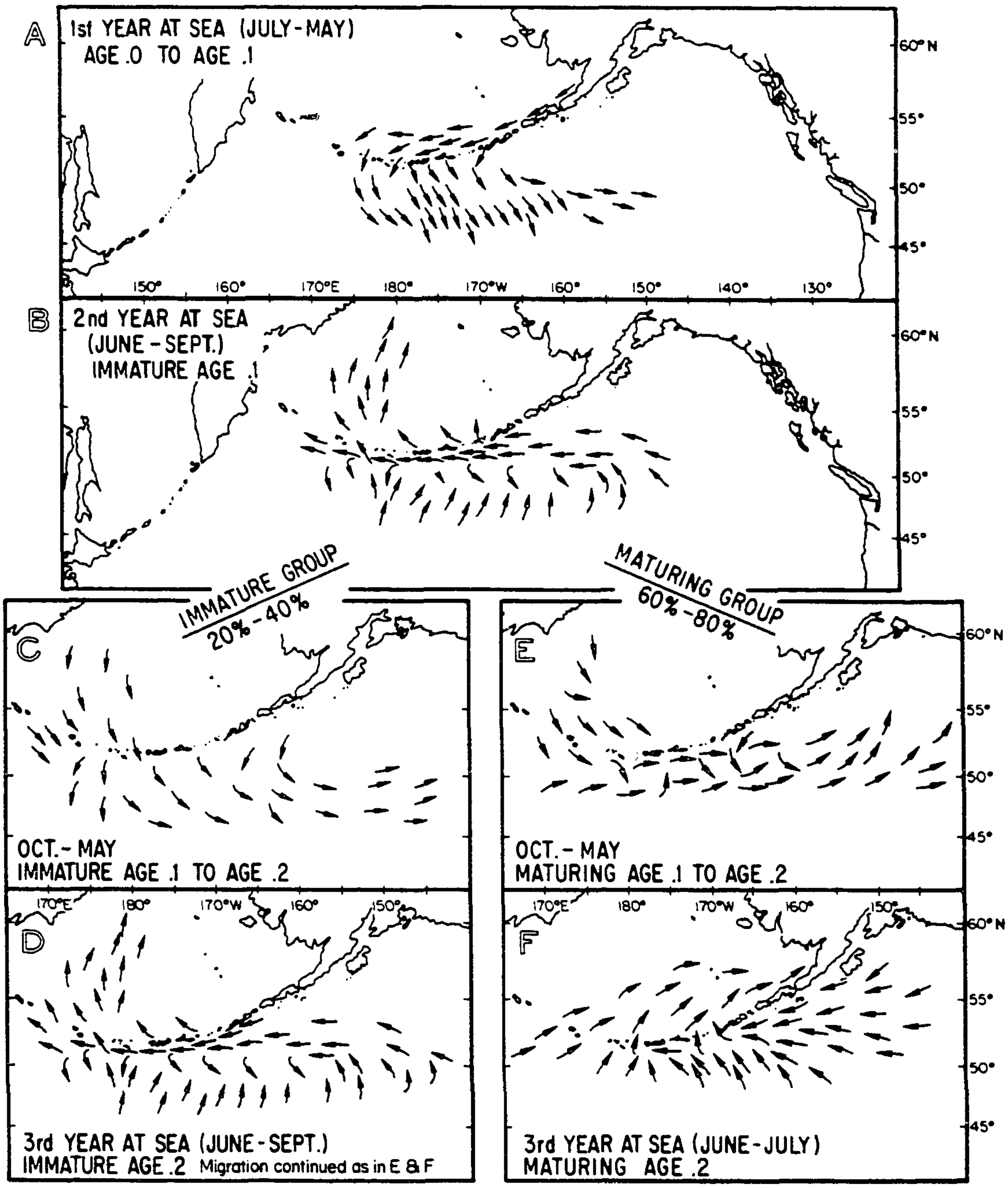

Figure 2. Model of migration of Bristol Bay sockeye salmon (from French *et al.*, 1976).

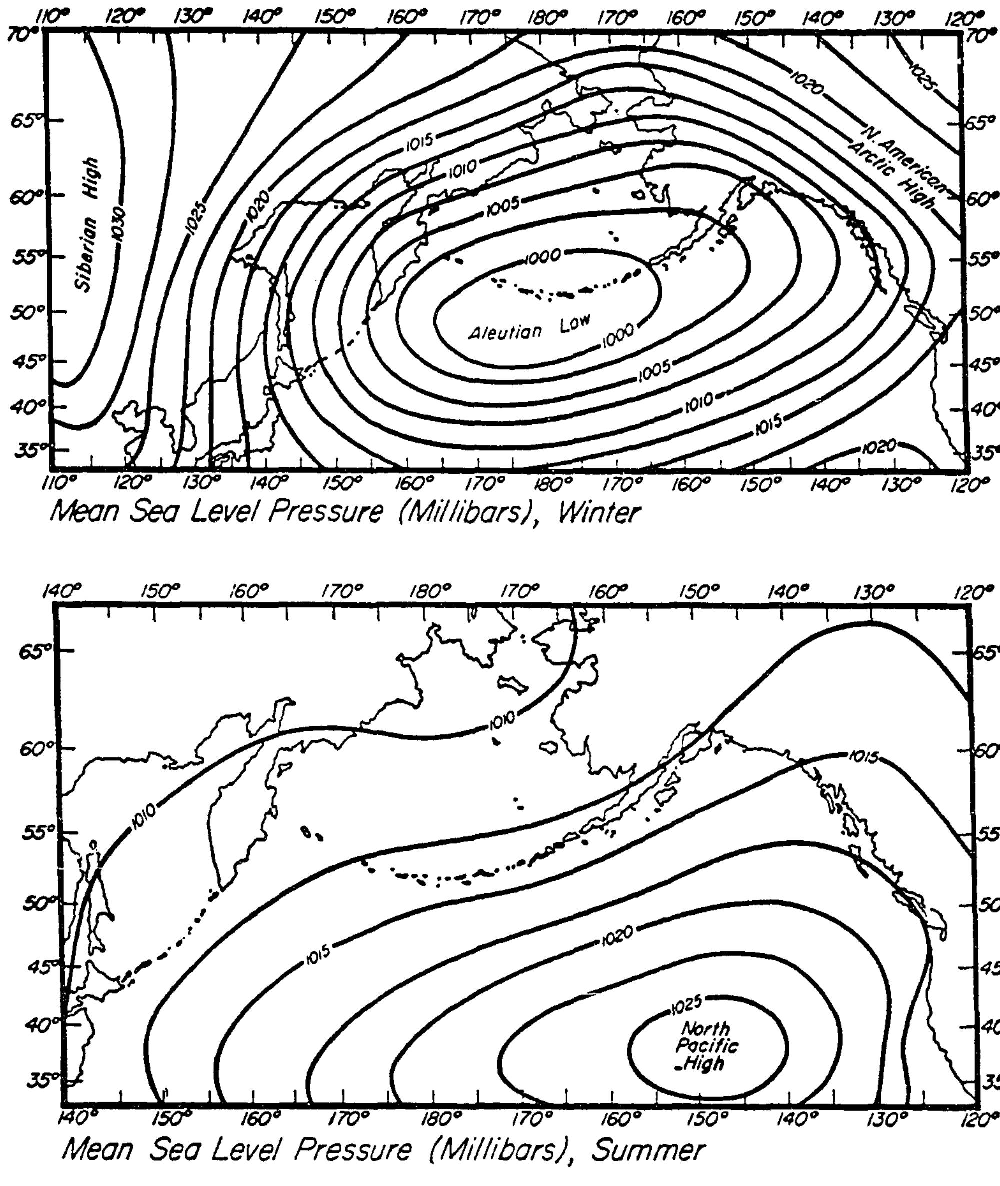

Figure 3. Mean atmospheric pressure distribution over the North Pacific for winter and summer (modified from Dodimead *et al.*, 1963; Royer, 1975).

cloudiness in summer than in winter. This higher occurrence is due mainly to frequent low stratus and fog in summer.

General water circulation of the Subarctic Pacific (Figure 4) was well studied in the 1950's (Dodimead *et al.*, 1963). The surface circulation in this region is characterized by a large cyclonic gyre existing just north of the mid-Pacific, and four subsidary gyres: Bering Sea, Western Subarctic, Okhotsk and Alaskan. Western boundary currents, which flow southward (Oyashio) and flow northward (Kuroshio) along the northeast coast of Japan, converge, mix, and turn eastward as the Subarctic Current. This current flows across the Pacific Ocean forming a transition zone between the cold, dilute Subarctic waters and the warm, saline Subtropic waters. The current is constrained by the coast of North America to turn northward as the Alaska Current, then westward out along the Alaskan Peninsula as the Alaskan Stream, or to turn southward as the California Current along the West Coast. The Alaskan Stream is continuous as far westward as longitude 170°E where it divides sending one branch into the Bering Sea through openings in the Aleutian-Commander Island Arc and one southwestward which joins the eastward flowing Subarctic Current at about longitude 165°E. After entering the Bering Sea, a portion of the Alaskan Stream discharges northward through the Bering Strait, but most of the stream continues to flow westward around the Bering Sea basin and southward along the east coast of Kamchatka, completing the gyre (Favorite, 1967; Favorite *et al.*, 1977).

In the Gulf of Alaska, the Alaska Coastal Current (Figure 4) is driven seasonally by freshwater discharge and winds (Royer, 1981). In summer, the wind appears to affect this current to a lesser degree than freshwater; winds are more important in winter.

FACTORS INFLUENCING FISH GROWTH, OCEAN ABUNDANCE, DISTRIBUTION, AND MIGRATION

Water temperature influences all facets of a fish's life history mediated through metabolism and behavior (Aggus, 1979; Straty, 1979), determining the feeding rate,

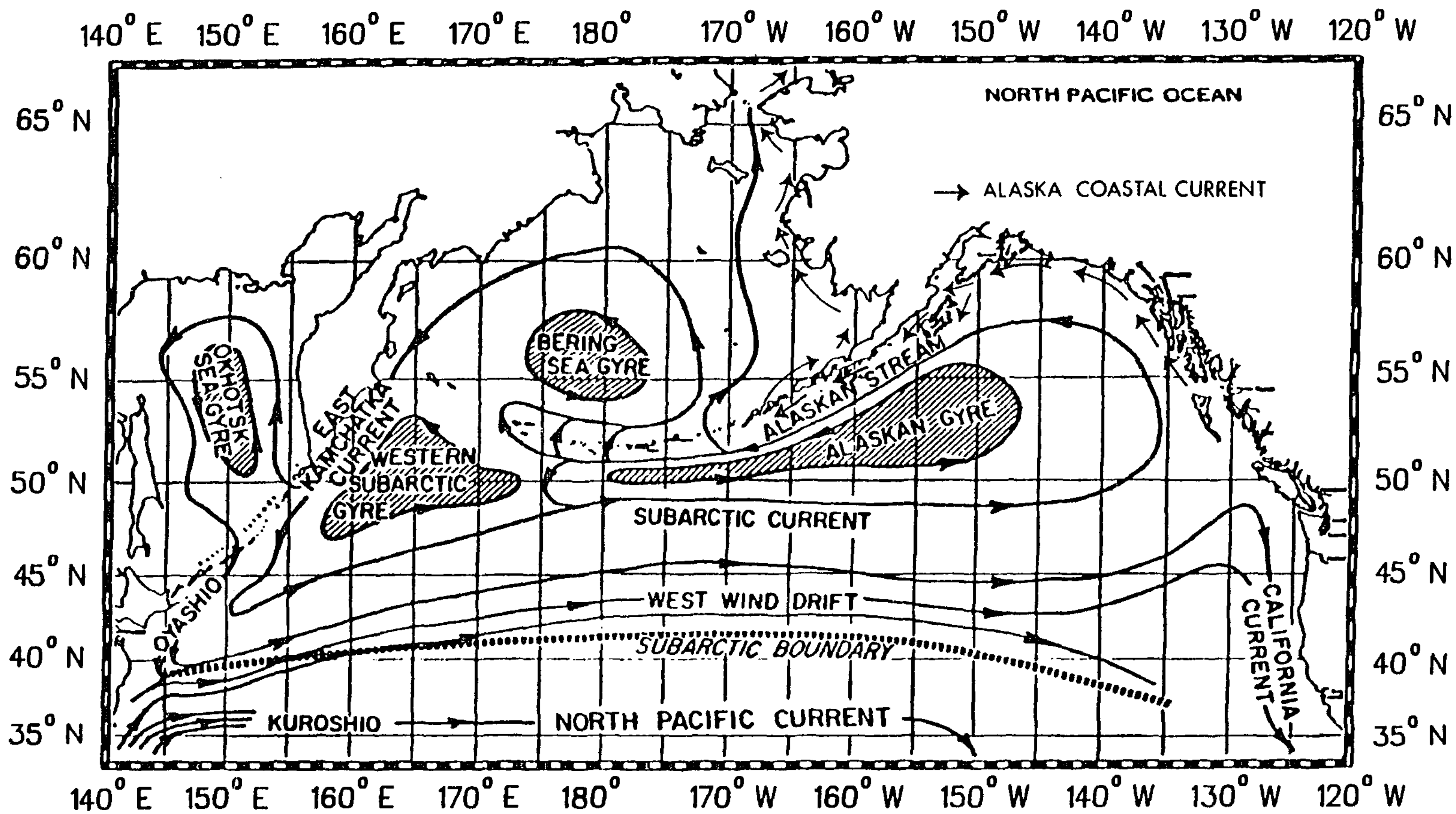

Figure 4. Schematic diagram of major surface circulation patterns of the northern North Pacific (modified from Dodimead *et al.*, 1963).

growth, development (Brett, 1956), and sexual maturation (Kruse and Tyler, 1983; Lam, 1983; Stacey, 1984). Temperature also acts as a directive element, causing fish to aggregate within thermal ranges, or directing them to new environmental conditions (Brett, 1956). Manzer (1964) and Machidori (1966) suggested that the formation of the thermocline acts as a physical barrier.

In winter, sockeye salmon are mainly distributed in three areas: the extension of the Oyashio and Subarctic Current areas, waters east of 160°E (Shimazaki and Nakayama, 1975), and the Alaskan Stream and the Alaskan Gyre (French and McAlister, 1970). In the early spring, sockeye salmon are widely distributed between 43°N and 48°N, in the northwestern North Pacific (Mishima, 1974; French *et al.*, 1976).

Saltwater growth of Bristol Bay sockeye salmon during the first year of life is related to the sea surface temperature in the eastern Bering Sea, but not in the North Pacific (Barber and Walker, 1980). Annual deviation in timing of sockeye salmon runs to Bristol Bay is correlated with the May-June sea surface temperatures immediately south of the Aleutian Islands, and the mean air temperature in Adak-Cold Bay in late spring (Burgner, 1978). Nishiyama (1982) found a positive relation between gonadsomatic index of ocean age .2 sockeye salmon and the sea surface temperature in the eastern Bering Sea. He also found an inverse relationship of temperature to an increased rate of maturity in mid-June to early July. This relationship suggests that the high sea temperature accelerates feeding activities, digestion rate, and growth potential of sockeye salmon (Straty and Jaenicke, 1980).

The catch of fish in the ocean is related to sea level pressure (Harden Jones and Scholes, 1982). Pati (1982) and Lassig (1983) found that a passage of storm causes rapid hydrographic changes and high turbid conditions in the coastal region, thus limiting and influencing fish distribution and movement. Peterson (1972) found that changes in barometric pressure were related to the spawning activities of rainbow trout (*Salmo gairdneri*) in a pond in Wyoming. The onshore or offshore wind apparently alters the distribution and concentration of odorants from rivers. The largest runs of chum salmon occur during strong onshore winds which concentrate the freshwater plume near the river mouth (Leggett, 1977). The influence of winds on the timing of the migration of the Atlantic salmon (*Salmo salar*) and kokanee salmon (*O. nerka*) has also been reported (Hayes, 1953; Lorz and Northcote, 1965).

Photoperiod has been considered a prime factor in controlling gonadal development in fishes (Woodhead and Woodhead, 1965; Scott, 1979). A number of investigators (Combs *et al.*, 1959; MacQuarie *et al.*, 1978 and 1979; Clarke *et al.*, 1981) have demonstrated in the laboratory that maturation in salmonids can be induced by exposing them to an accelerated light regime followed by decreasing photoperiod several months in advance of the normal time. Little is known about the effect of cloudiness or photoperiod on the maturation of salmon in the ocean.

Sockeye salmon use estuarine salinity as directive cues in their migration to and from the river systems (McInerney, 1964; Straty, 1974). The migratory route of maturing sockeye salmon was related to the position of water of high salinity flowing eastward into Bristol Bay (Straty, 1974; Fujii, 1975) where a wedge of high salinity water extends into inner Bristol Bay. The outer Bay was marked by higher and more uniform salinity distribution.

In the open ocean, migration of salmon is related to the flow pattern of the Alaskan Stream and Subarctic Current (Royce *et al.*, 1968; Favorite and Ingraham, 1972; Favorite *et al.*, 1977). Mature fish are present in large numbers all along the southern side of the Aleutian Islands heading westward in the dilute waters of the Aleutian Stream. Therefore, changes in flow rate would influence the rate at which these fish move. Fujii (1975) found that the fish caught in high numbers were all along this current bounded by high salinity and low temperature gradients and proposed that this gradient acted as a barrier. This temperature-salinity barrier disappears when a rapid and continuous northbound flow of the Alaskan Stream water enters the Bering Sea. The breakdown of this barrier coincides with the movement of sockeye salmon into the Bering Sea. Sockeye salmon tend to migrate within the low salinity and high temperature zone of the Alaskan Stream. Since the position of this water varies from year to year (Favorite, 1974), movement of sockeye salmon through the Aleutian Passes into the Bering Sea is likely to vary between years.

The abundance and distribution of food (mainly zooplankton) influence the rate of marine growth and the survival of sockeye salmon (Straty and Jaenicke, 1980). Hoar (1957), Woodhead (1960), and Purdom (1979) reported that gonad maturation in fish requires large quantities of food. In the ocean, adult sockeye salmon feed actively (Nishiyama, 1972), but no feeding occurs during upstream migration (Idler and Tsuyuki, 1958).

Larger forms of food items are more abundant in outer Bristol Bay than in the inner bay. Salmon that feed on larger organisms, such as fish and squid, have higher caloric intake per energy expenditure than those feeding on smaller organisms, such as amphipod and chaetognath (Straty and Jaenicke, 1980). Therefore, the growth potential of sockeye salmon would be positively related to the size and abundance of food.

The abundance of sockeye salmon in the ocean is thought to be affected by their predators, which include belukha whale (Alaska Department of Fish and Game, 1956 and 1957), Alaska fur seal, sea lion, dolphin, salmon shark, blue shark, swordfish, marlin, Pacific cod, and Pacific halibut (Sano, 1959). For example, belukha whale is reported to consume 3 million Bristol Bay sockeye salmon smolts (Alaska Department of Fish and Game, 1956). However, no quantitative study has been conducted on the influences of other predators on the abundance of Bristol Bay sockeye salmon.

Chapter II: Variations in Return, Ocean Abundance, and Maturity of Sockeye Salmon

INTRODUCTION

This chapter examines the abundance cycle of four major age groups of Bristol Bay sockeye salmon. The relation between the return of sockeye salmon to the Bristol Bay area and catch of sockeye salmon on high seas by the Japanese fishery is also examined. Further, this chapter examines age composition and maturity annual and seasonal change in abundance, and gonad weight of sockeye salmon in their ocean residence.

The long-term cyclic fluctuation in abundance of sockeye salmon is an apparent phemonenon in North America, but not in Kamchatka. In British Columbia, Canada, the abundance of sockeye salmon shows a 4- and 5-year cycle. The dominant cycle is about 65 times the off cycles (Larkin and McDonald, 1968). In Bristol Bay, the total return of sockeye salmon peaks every fifth year (Mathisen and Poe, 1981), but little information is available on the abundance cycle of four major age groups of sockeye salmon in that area.

The landing of sockeye salmon varied extensively in temporal and spacial scale. Before 1978 North America produced three times more sockeye salmon than Asia (Fredin and Worlund, 1974; Fredin, 1980). Asian catches of sockeye salmon declined drastically after 1979. The production of Bristol Bay sockeye salmon changed significantly since 1965 and a sharp decline occurred in the 1970's (Rogers, 1984). Since 1978, a resurgence of Bristol Bay sockeye salmon has been observed (Eggers *et al.*, 1984; Rogers, 1984).

Seasonal variation of gonad weight of sockeye salmon in the North Pacific and Okhotsk Sea has been analyzed. Based on frequency distribution of the gonad weight of sockeye salmon taken in the Japanese high seas fishery in summer, Ishida and Miyaguchi (1958) and Takagi (1961; 1978) found two groups of maturing sockeye salmon with different ovary weights. In the early fishing season, the group with heavy ovary weight was traced migrating northward and it disappeared from the commercial catch in the late fishing season.

DATA SOURCES AND METHODS

Two areas were delineated to study variations in abundance and gonad weight of sockeye salmon (Figure 5). Study area 1 was chosen from latitude 40^oN-60^oN and longitude 160^oE-140^oW, since this area is inhabited by Bristol Bay sockeye salmon throughout their oceanic life stages (French *et al.*, 1976). Study area 2, covered 46^oN-62^oN and 160^oE-175^oW, was the area for the Japanese high seas salmon fishery during 1971-76. Within area 1, a subarea was selected as study area 3 between 40^oN-52^oN and 160^oE-170^oW. Distribution of both Kamchatka and Bristol Bay sockeye salmon occurs in this subarea. Catch and environmental data have been accumulated within these areas.

Two sources of data were used to examine the abundance, catch, composition, and gonad weight of sockeye salmon. The landing and abundance data of the Japanese high sea and land-based fisheries were obtained from the Fishery Agency of Japan (1986). The coastal catch and escapement data in the Bristol Bay area were obtained from the Alaska Department of Fish and Game (1986). The age and origin of sockeye salmon in high seas were determined by the scale patterns of adult fish.

The Fishery Agency of Japan (1986) data were acquired from gillnet operations of the Japanese mothership fleets and salmon research vessels from May to July, 1971 to 1976. Gillnet mesh sizes, used by the mothership fleets whose catch was primarily adult fish, are 106, 111, and 121 *mm* in stretched measure, whereas the research vessels employ 10 sizes, ranging from 29 to 204 *mm* in stretched measure. The unit of gillnet length is called a *tan*. One *tan* is 50 *m* in length and 5 *m* in depth. Usually, the nets are set one hour after sunset, and retrieved the next morning before sunrise. Catch per unit fishing effort (CPUE) refers to the number of fish per one *tan* of net during a given night.

The mean annual CPUE ($\bar{C}$) from the Japanese high sea fishery is expressed as follows:

$$\bar{C} = C / E \qquad (1)$$

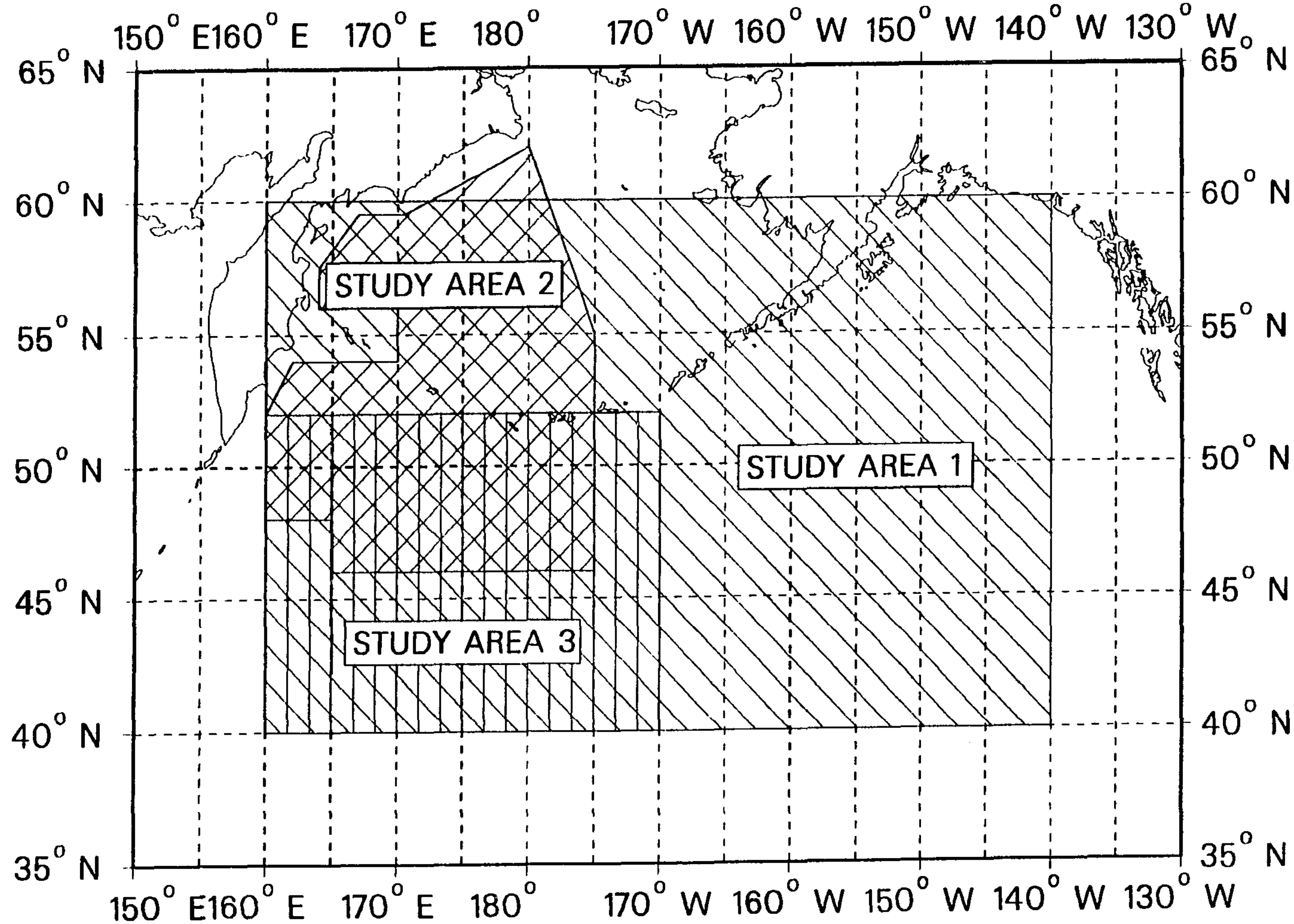

Figure 5. The study area in areas 1, 2, and 3.

where C is the yearly total catch of fish in number and E is yearly total fishing effort in *tan*. The monthly mean CPUE ($\bar{C}_d$) was separately calculated for mature and immature fish.

$$\bar{C}_d = C_d \, / \, E_d \tag{2}$$

where C_d is the monthly total catch of fish in number and E_d is the monthly total fishing effort in *tan*.

The mean monthly CPUE ($\bar{C}_d$) in May, June, and July was multiplied by the percentage of mature (P_m) and immature ($1-P_m$) fish to yield the monthly CPUE of mature (C_m) and immature (C_{im}) fish.

$$C_m = P_m \times \bar{C}_d \tag{3}$$

$$C_{im} = (1 - P_m) \times \bar{C}_d \tag{4}$$

The percentage of age .2 (R_2) and .3 (R_3) is given by

$$R_2 = [N_2/(N_2 + N_3)] \times 100 \tag{5}$$

$$R_3 = [N_3/(N_2 + N_3)] \times 100 \tag{6}$$

where N_2 and N_3 are the total sample numbers of age .2 and .3 fish, respectively.

The monthly mean CPUE of age .2 (C_2) and .3 (C_3) sockeye salmon is obtained by multiplying equations (5) and (6) by equation (4):

$$C_2 = R_2 \times C_m \tag{7}$$

$$C_3 = R_3 \times C_m \tag{8}$$

Gonad weight (GW) data of female sockeye salmon were excerpted from Tagaki (1978). The mature and immature fish are separated by particular GW values (Ishida *et al.*, 1965). The females with GW greater than 33 to 40 *g* are considered to be mature, and vice versa. The number of age .2 and .3 immature and mature fish was presented for each unit area of a $2^{o} \times 5^{o}$ quadrant, and the GW were given for mature fish in logarithmic transformed values.

The gonad weight of age .2 and .3 fish is denoted as GW_2 and GW_3, respectively. To compare longitudinal difference, the average GW in actual values and average values was calculated for each 5^{o} longitude quadrant. For a statistical comparison of the GW in latitudinal direction, the logarithmic values of GW were averaged for each 2^{o} latitude quadrant and were tested by the Student *t* test.

RESULTS

Abundance of sockeye salmon

There is a long-term fluctuation of abundance of sockeye salmon returning to Bristol Bay (Figure 6) with high abundance occurring about every 5 years. The lowest return was 2.43 million fish in 1973 and highest of 62 million in 1980. In the Kamchatka area, however, the total return showed no apparent cycle, and displayed a long-term decline from 15.21 million fish in 1961 to a low of 4.64 million fish in 1977.

In Bristol Bay, the return of age .2 sockeye salmon was about 75 % higher than age .3 fish (Figure 7A), and the low return in 1973 was largely due to the low abundance of age .2 fish. For freshwater-age fish, the highest return occurred in 1960 (29.97 million) for age 1.2 fish and in 1965 (47.62 million) for age 2.2 fish (Figure 7B & 7C). Age 1.3 and 2.3 sockeye salmon (in millions) varied from 0.97 in 1962 to 13.87 in 1981, and from 0.67 in 1962 to 9.61 in 1966, respectively.

Five peak returns of Bristol Bay sockeye salmon occurred between 1960 and 1980. Age 2.2 was the primary age group contributing to peak returns occurring in 1965, 1970, 1975, 1980. There was a peak return of age 1.2 in 1983. There was also a cyclic return of age .3, but this return occurred for five years beginning in 1961, one year after the peak return of age .2 fish. Unlike age .2 fish, age 2.3 fish only contributed to one of the high returns in 1965, whereas age 1.3 fish contributed to the peak returns in 1961, 1971, 1976, and 1981.

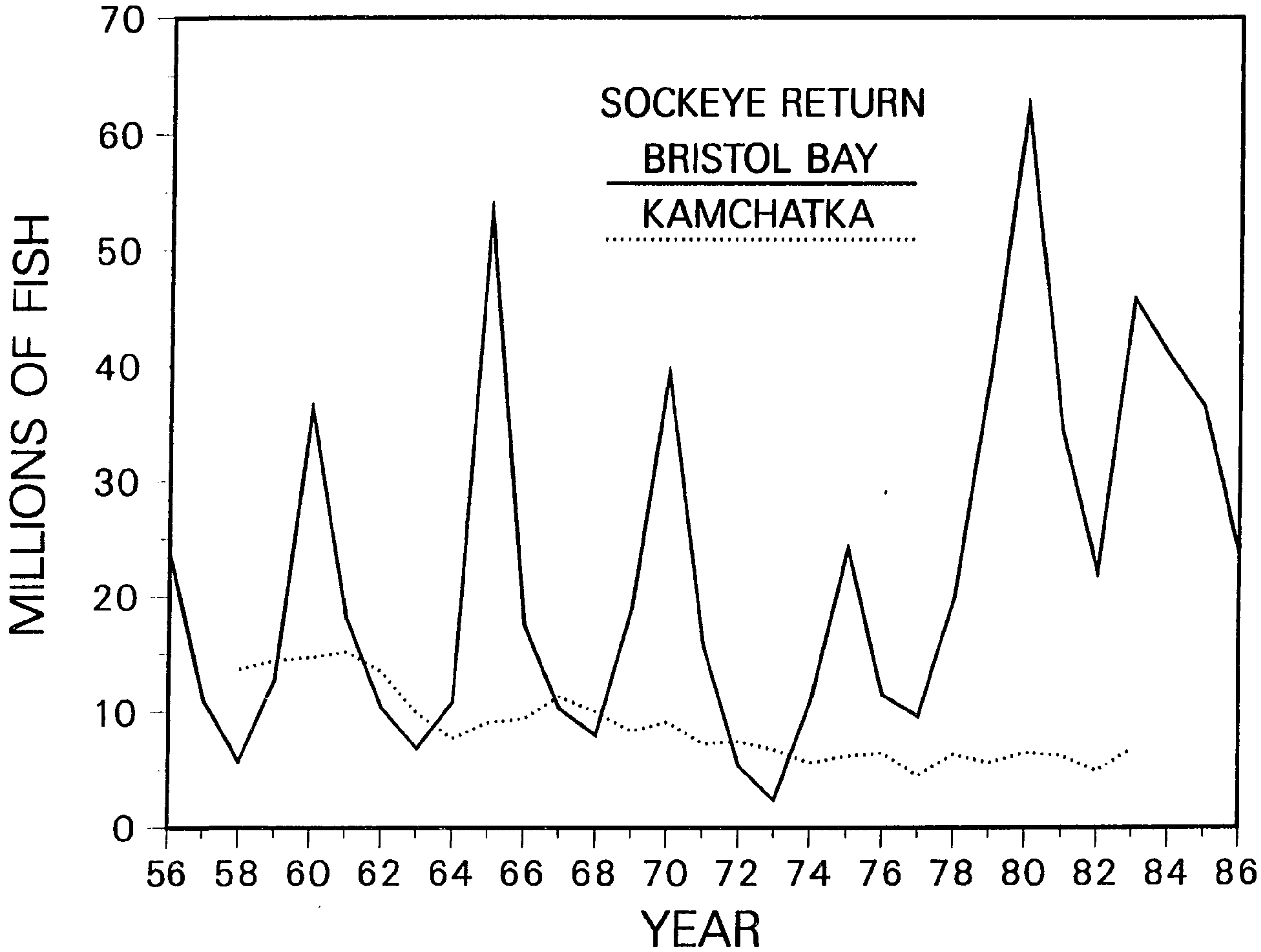

Figure 6. The total return of sockeye salmon to Bristol Bay in 1956-86 and to Kamchatka in 1958-83.

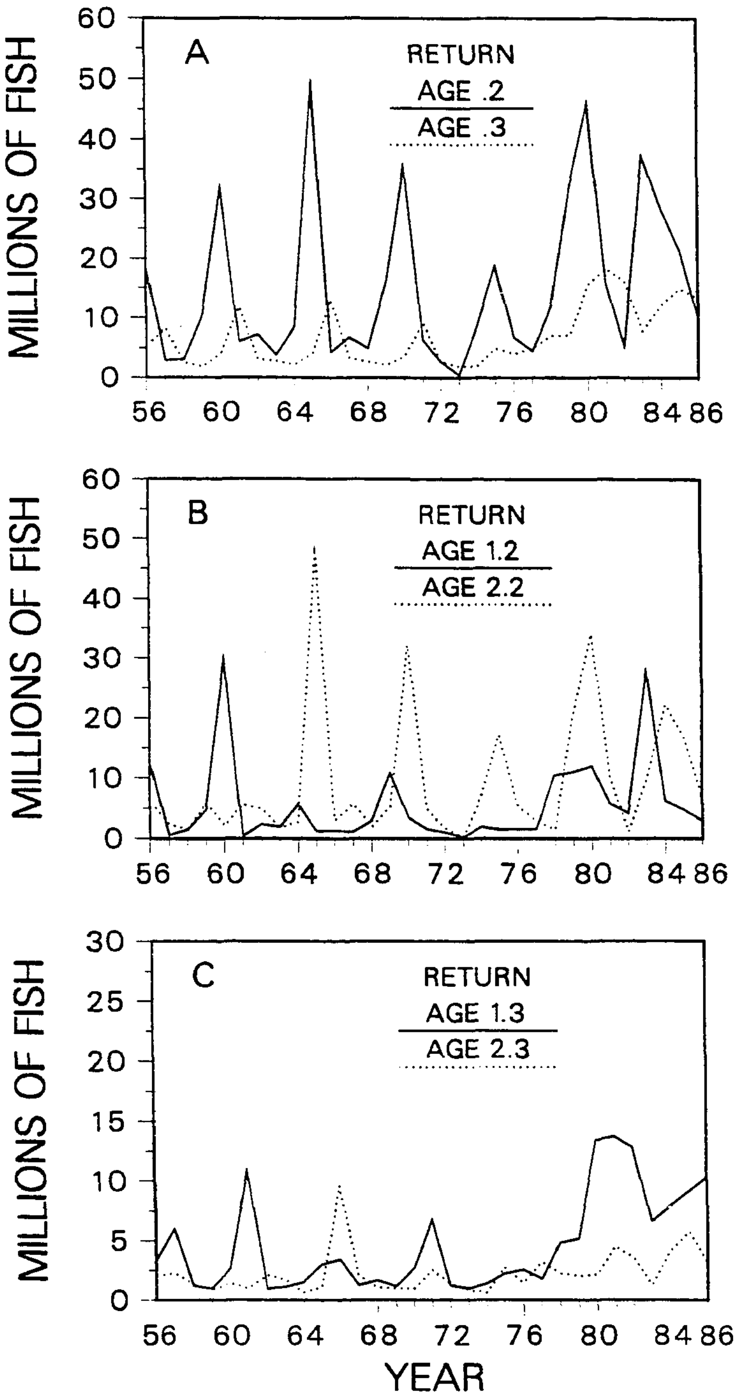

Figure 7. The total return of Bristol Bay sockeye salmon in 1956-86 for ocean age .2 and .3 (A); for age 1.2 and 2.2 (B); and for age 1.3 and 2.3 (C).

During the period from 1961 to 1985 $\bar{C}$ (annual mean CPUE) for Bristol Bay and Kamchatka sockeye salmon combined varied from .02 to 2.5, depending on year and maturity (Figure 8A). A decreasing trend of $\bar{C}$ for mature fish exists which may be divided into three periods: 1961-70, 1971-76, and 1977-85 (Table 1). Among the three periods, the $\bar{C}$ of mature fish was the largest between 1961 and 1970, while it was the lowest in the six years from 1961 to 1976. This lowest $\bar{C}$ was caused by the decrease of mature fish. After 1977, the $\bar{C}$ slightly increased. The trend was not clear in immature fish, but resembled the pattern for mature fish, except in 1963 when immature fish outnumbered mature fish.

Table 1. Average CPUE of sockeye salmon by maturity in three periods, 1961-70, 1971-76, and 1977-85.

MATURITY	1961-70	1971-76	1977-85
Mature	.577	.304	.316
Immature	.170	.161	.208
Total	.748	.465	.623

Before 1978, mature Kamchatka sockeye salmon taken in the high-sea fishery were generally more abundant than mature Bristol Bay sockeye salmon, but the order reversed in 1961, 1965, and 1970 (Figure 8B). The relative ocean abundance of Kamchatka sockeye salmon was consistently higher than Bristol Bay sockeye salmon during the 1971-77 period. The $\bar{C}$ was lowest in 1971-76, and the highest in 1961-70 (Table 2). The average $\bar{C}$ of mature fish in 1971-76 was 0.372 for Kamchatka and 0.224 for Bristol Bay. In other words, 62 % of the fish are considered to have originated from the Kamchatka area and 38 % from the Bristol Bay area, which means 24 % more of the mature fish are from the Kamchatka area than from the Bristol Bay area. The abundance of immature sockeye fluctuated in different ways as compared with mature fish (Figure 8C).

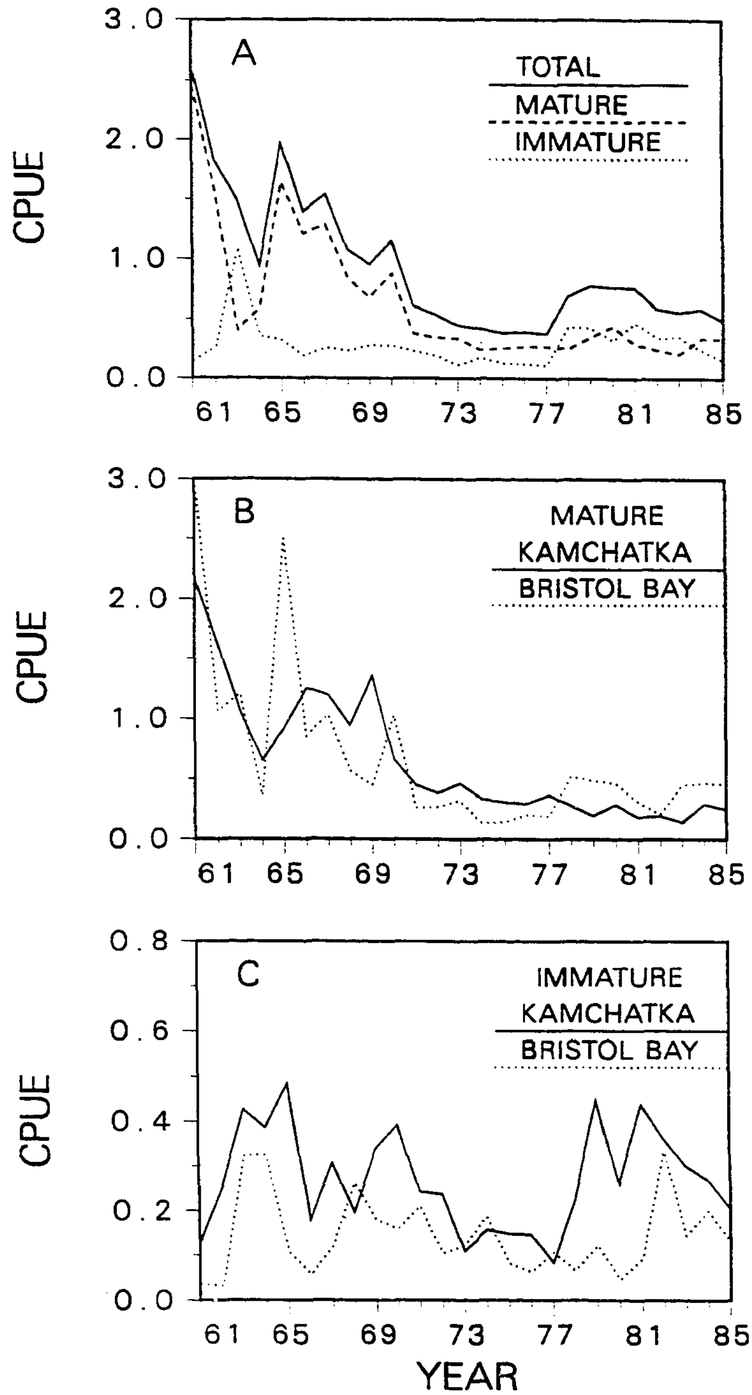

Figure 8. Sockeye salmon CPUE by the Japanese high sea fishery, 1961-85. Mature and immature fish (A); mature Kamchatka and Bristol Bay fish (B); and immature Kamchatka and Bristol Bay fish (C).

Table 2. Average CPUE of sockeye salmon by origin and maturity in three periods.

POPULATION	1961-70	1971-76	1977-85
Kamchatka Mature	1.183	.372	.245
Kamchatka Immature	.309	.173	.288
Bristol Bay Mature	1.204	.224	.359
Bristol Bay Immature	.160	.128	.138

In general, the Bristol Bay immature fish were less abundant than the Kamchatka immature fish. During the period of 1971-75, there was a steady decrease in $\bar{C}$ for both the mothership fleet and research vessels (Figure 9A; Appendix Table A-1). In 1976, the $\bar{C}$ from the research vessels (.444) was slightly higher than that of the mothership fleet (.392), suggesting an increase in abundance for that year. The ocean abundance of the immature and mature fish combined generally decreased, but differed from May to July and varied between years (Figure 9B; Appendix Table A-2). In May, the $\bar{C}_d$ (monthly mean CPUE) was generally the highest among the three months. The $\bar{C}_d$ in June was generally lower than that for May and higher than the $\bar{C}_d$ for July. The $\bar{C}_d$ of age .2 and .3 fish generally increased with season (Figures 9C & 9D; Appendix Table A-3).

Landing and escapement of sockeye salmon

The Japanese high seas fishery catch throughout 1957-85 decreased from 20 to 1.1 million, while land-based fishery catches varied between 16 thousand and 3.5 million fish (Figure 10A). In comparison with the high seas fishery, the catch of the land-based fishery was consistently lower, except during the period of 1972-77. During this period, the land-based fishery recorded a catch of 0.6-1.2 million fish higher than that of the motherships.

During the years 1956-86, the coastal catch of sockeye salmon in Bristol Bay varied from 0.75 to 36.9 million fish. The catch revealed a minor 5-year cycle in 1960-70 (Figure

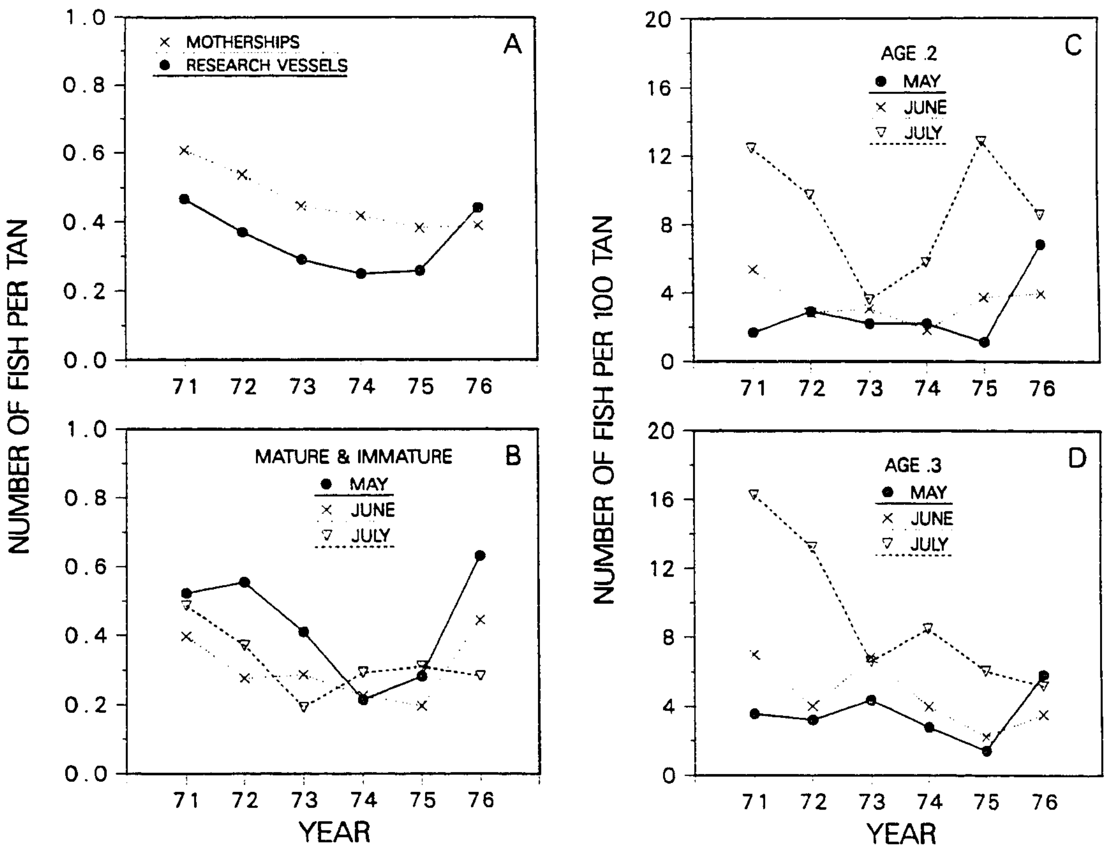

Figure 9. Annual mean CPUE ($\bar{C}$) of sockeye salmon during 1971-76 for Japanese motherships and research vessels (A) and monthly mean CPUE ($\bar{C}_d$) for immature and mature fish (B); age .2 (C); and .3 fish (D) during 1971-76.

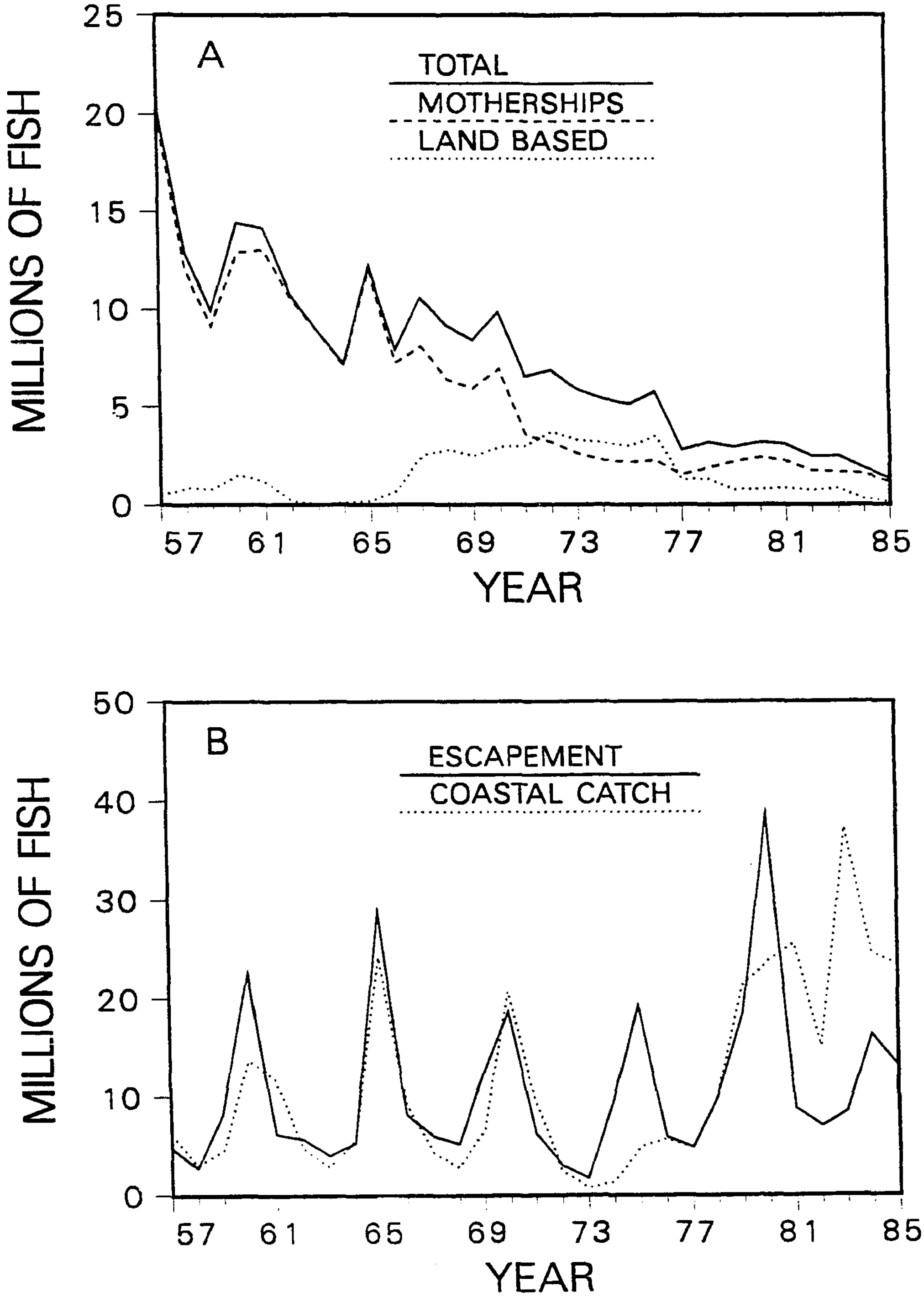

Figure 10. The catch of sockeye salmon by the Japanese high seas and land based fisheries in 1957-85 (A); and the escapement and coastal catch of Bristol Bay fish (B) in 1957-85.

10B), whereas the escapement data showed a clear 5-year cycle in 1960-80. The highest escapement occurred in 1965 and 1980. From Figures 10A and 10B, the relation between the Japanese high seas fishery catch and the total return of sockeye salmon in Bristol Bay is obscure. A resurgence of Bristol Bay sockeye salmon has occurred since 1979, while the catch by high seas and land-based fisheries has shown a continuous decrease because of continual restriction on fishing since 1957, and has levelled off since 1977.

Composition by age and maturity

Monthly mean ocean age composition of sockeye salmon during 1971-76 varied from year to year. Age .2 sockeye were proportionally lower in number than age .3 sockeye salmon during 1971-74 (Figures 11A & 11B). Throughout the years 1971-76, age composition was consistent, except in 1975 and 1976 (Appendix Table A-4). In 1975, age .2 fish outnumbered age .3 fish in May, but the situation reversed in June and July. In 1976, age .2 fish constituted more than 53 % of the total catch.

The proportions of immature to mature fish were relatively consistent during 1971-76 (Figures 11C & 11D). Immature fish prevailed both in May and June with 68-92 % of the total catch, but decreased to 40-53 % in July. Inversely, mature fish were fewer in number in May and June with 8-32 % of the total catch, but increased significantly in July to 47-60 % (Appendix Table A-5). The difference in the monthly proportions of immature to mature fish is obvious, with extreme cases occurring in 1971 and 1974. In 1971, only 8 % of the fish were mature in May, whereas in 1974 less than 20 % of fish were mature in May and June, and the number of immature fish were four times higher than that of mature fish.

Seasonal change in gonad weight

The mean GW_2 in May was low and almost constant (between 22 and 28 g) without a yearly difference. The mean gonad weight for age .2 fish (GW_2) and age .3 fish (GW_3) within the 6-year period between 1971 and 1976 is given in Figures 12A & 12B and

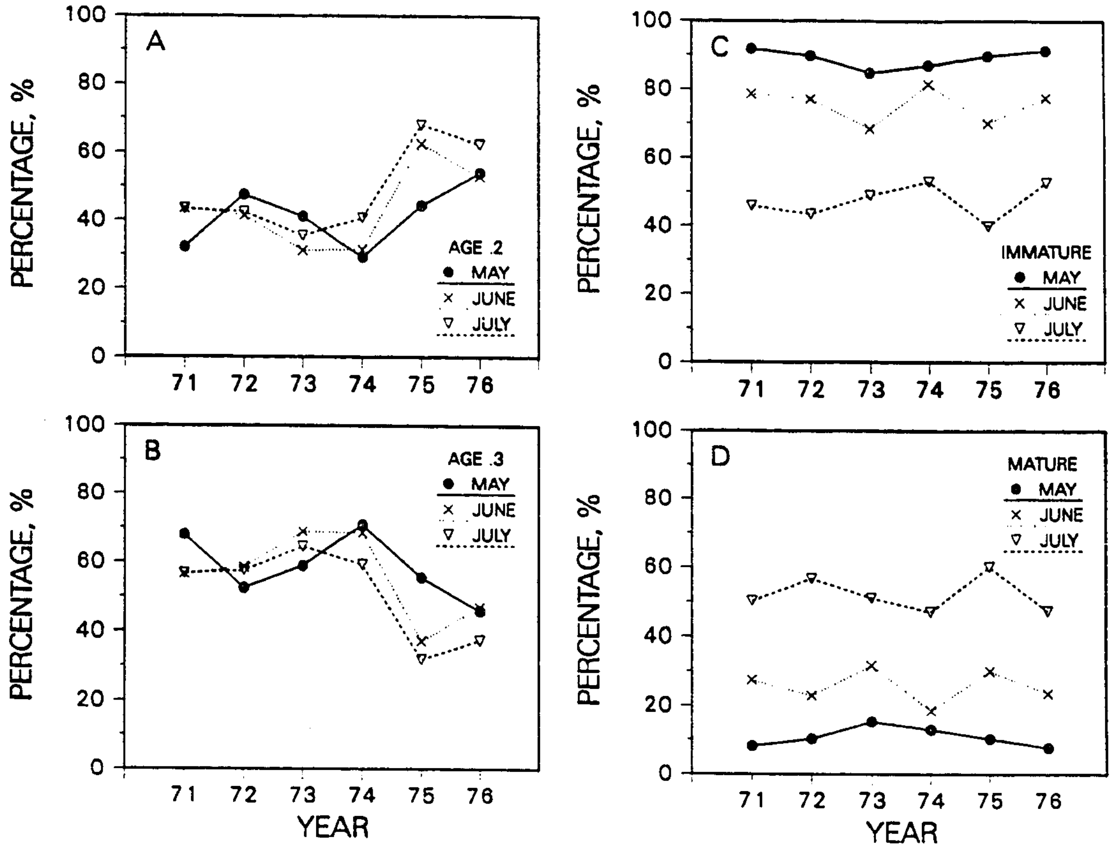

Figure 11. Percentage catch of age .2 (A) and .3 (B) and immature (C) and mature (D) sockeye salmon, 1971-76.

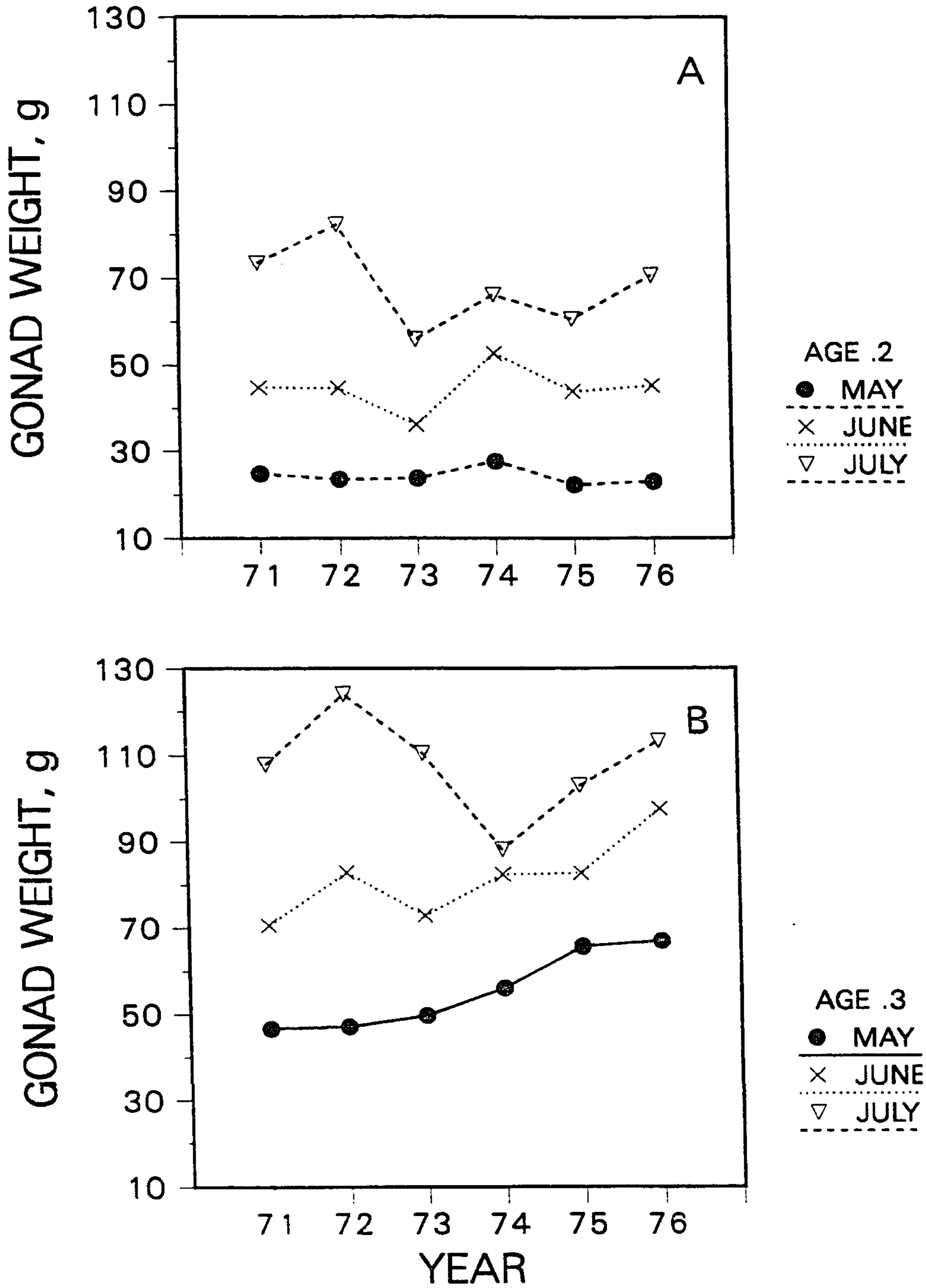

Figure 12. Monthly mean gonad weight for age .2 (A) and .3 (B) sockeye salmon, 1971-76.

Appendix Table A-6. In June and July, the GW_2 increased to 36-53 *g* and 56-82 *g*, respectively, about two and four times higher than the value in May. The variation between years was obvious in June and July. For June, the highest GW_2 was found in 1974, and the lowest in 1973. For July, the GW_2 was greatest in 1972, and lowest in 1973. The average monthly GW_2 during this study period was 24 *g* in May, 45 *g* in June, and 67.9 *g* in July.

The gonad weight of age .3 fish was 39-79 % greater than that of age .2 fish. Unlike the GW_2, the mean GW_3 showed an annual variance in May; the GW_3 was small in 1971-73, but increased steadily from 1974 (56 *g*) to 1976 (67 *g*). For June, the GW_3 showed an increasing trend from 71 *g* in 1971 to 98 *g* in 1976. For July, no increasing trend with year was observed. The minimum and maximum GW_3 were 88 *g* in 1974 and 124 *g* in 1972 with great annual variation. Relative to May, the GW_3 in June and July increased two and three times, respectively, except in 1974 during which time the mean GW_3 remained low. The average of the mean GW_3 during 1971-76 was 55 *g* in May, 81 *g* in June, and 108 *g* in July.

The largest increment of GW_2 during June-July (38 *g*) occurred in 1972 (Appendix Table A-7). The lowest increment of GW_2 was 12 *g* in May-June 1973. In age .3 fish, the largest increment (41 *g*) of GW_3 appeared in June-July 1972 and the lowest increment (6 *g*) occurred in June-July 1974.

Spatial change in gonad weight

Annual mean gonad weight for each 5° longitude differed between years and areas and with age of fish (Figures 13 & 14; Appendix Tables A-8 & A-9). The mean gonad weight varied from 21 to 107 *g* in age .2 (GW_2) fish and from 29 to 175 *g* in age .3 (GW_3) fish. The lowest GW_2 and GW_3 in May through July was generally found in the 160°E-165°E region, whereas the highest GW_2 and GW_3 was seen in the central region in 175°E-170°W. The GW_2 for May was consistent (18-28 *g*). The GW_3 was the same in 1971-73, but varied in 1974-76. The trend of GW_2 and GW_3 increased eastward in

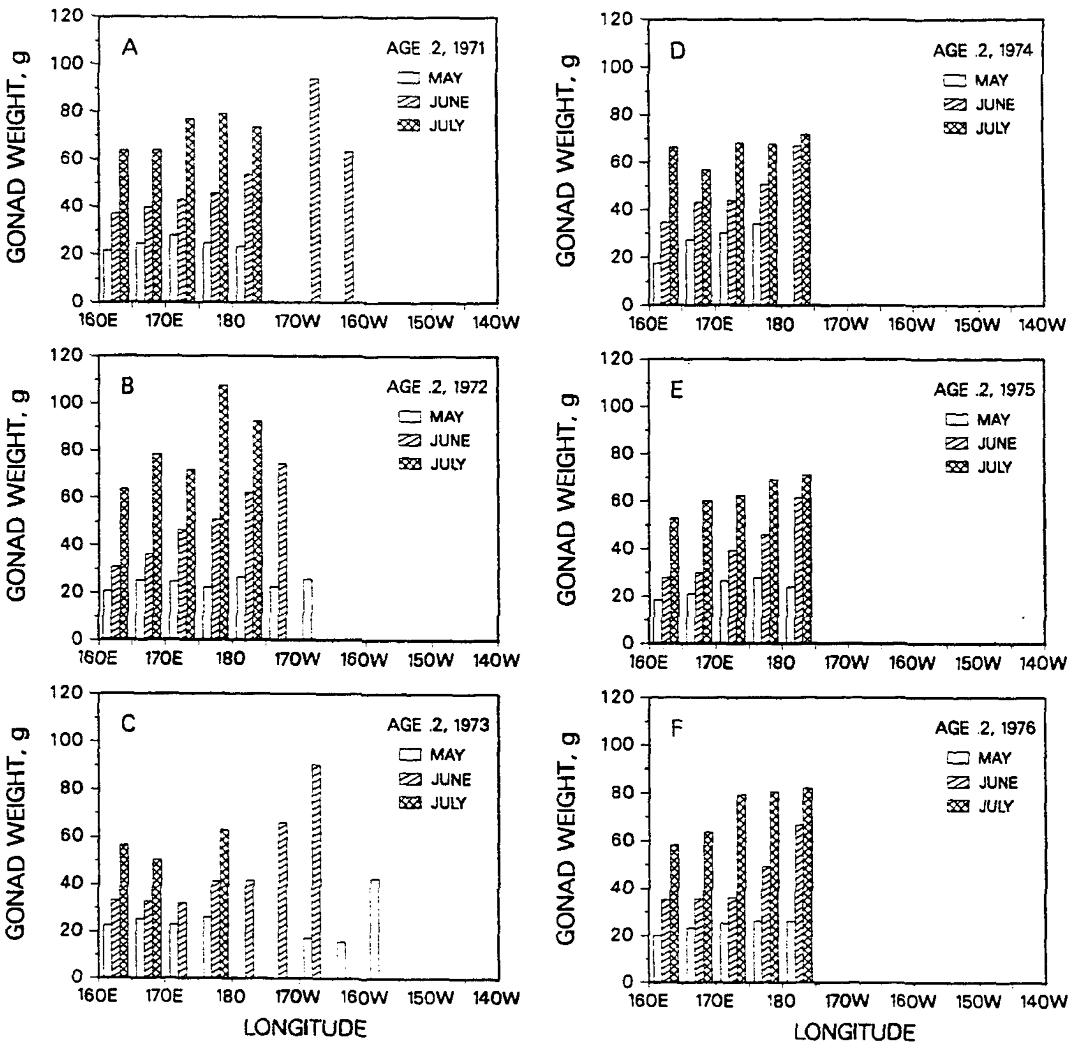

Figure 13. Mean gonad weight for May, June, and July of age .2 sockeye salmon for each 5^{o} long. in area 1, 1971-76.

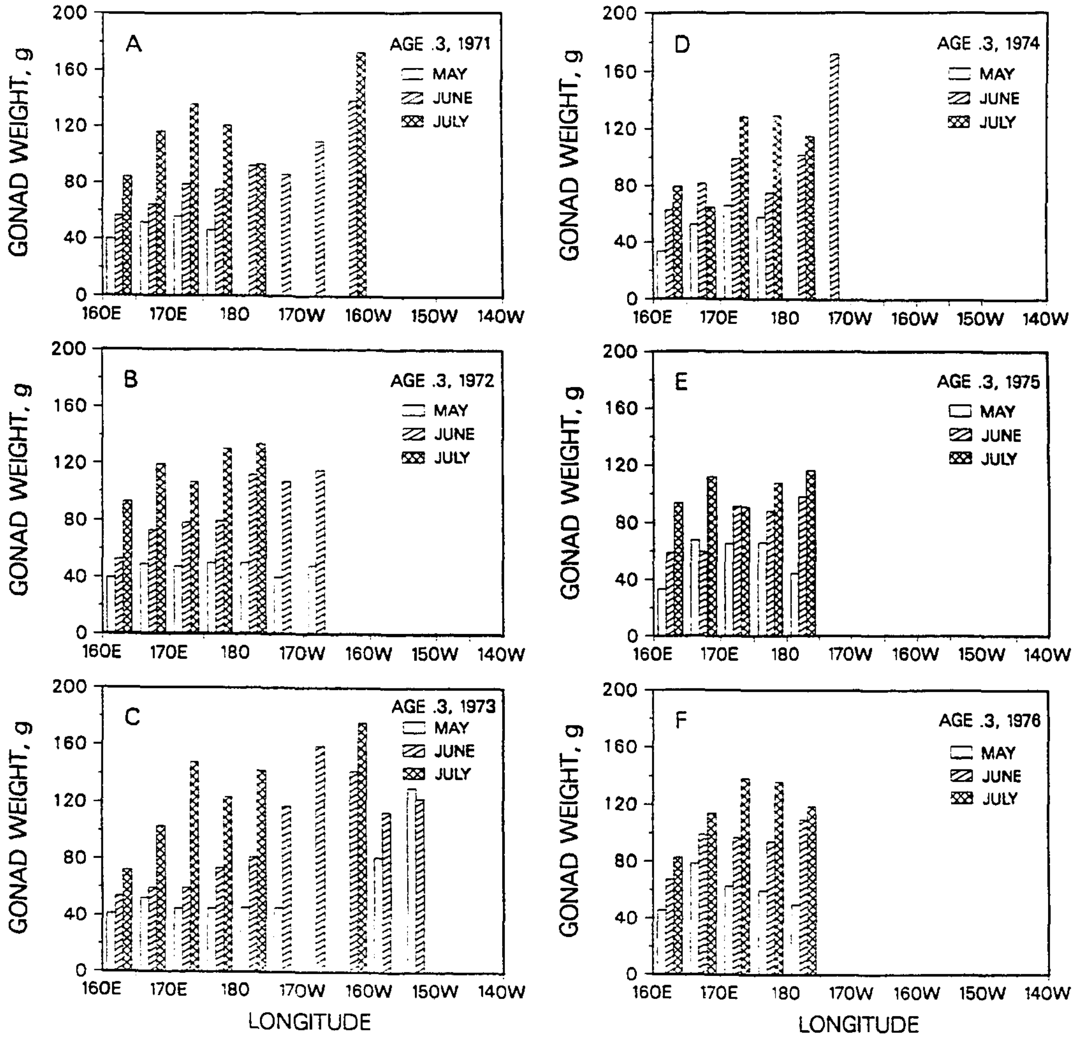

Figure 14. Mean gonad weight for May, June, and July of age .3 sockeye salmon for each 5° long. in area 1, 1971-76.

June. In July, the trend of GW_2 showed a general eastward increase, whereas GW_3 only increased longitudinally between 160°E and 170°E.

The general pattern of GW_2 and GW_3 (in logarithmic scale) increased with the increase of latitude during 1971-76 (Figures 15 & 16; Appendix Tables A-10 to A-15). This latitudinal increase pattern of gonad weight was evident in May and June, rather than in July. The range of GW_2 was between 1.244 and 2.070, and between 1.305 and 2.223 for GW_3. Annual differences of GW_2 and GW_3 were insignificant at low latitude and were significant at high latitude (P<.05). In age .2 fish, the annual difference of gonad weight was low between 44°N and 50°N in May, 54°N and 56°N in June, and 52°N and 54°N in July. Heavy gonad weight was found between 52°N and 54°N in May, 54°N and 56°N in June, and 54°N and 60°N in July. In age .3 fish, the annual difference of gonad weight was low in the 54°N-56°N quadrant in June, and in the 56°N-58°N quadrant in July, but this trend was not seen for both areas in May. Gonad weight between 46°N and 52°N in May 1975 and 1976 was higher than in the other four years. In June of these two years, the gonad weight between 50°N and 52°N was higher than in the previous four years, while no difference was observed for July during the same years.

DISCUSSION

Evidence indicates a 5-year cyclic fluctuation in abundance of Bristol Bay sockeye salmon during 1961-80. Mathisen and Poe (1981) described this 5-year cycle for Bristol Bay fish. The cyclic abundance fluctuation has been observed in other areas. Sockeye salmon in the Fraser, Adams, and Skeena Rivers in British Columbia, Canada, exhibit a 4- or 5-year cycle (Ricker, 1950; Godfrey, 1958; Ward and Larkin, 1964). In Kamchatka, the fluctuations in numbers of sockeye salmon has been inferred (Birman, 1970). Krogius (1978) found the abundance of Dal'neye Lake sockeye salmon exhibited a 4-year cycle. This observed cycle has been attributed to both biotic and abiotic factors. Ricker (1950), Godfrey (1958), and Ward and Larkin (1964) emphasized biotic factors, including the predation of sockeye salmon fry in freshwater. Johnson (1968) suggested self-regulation

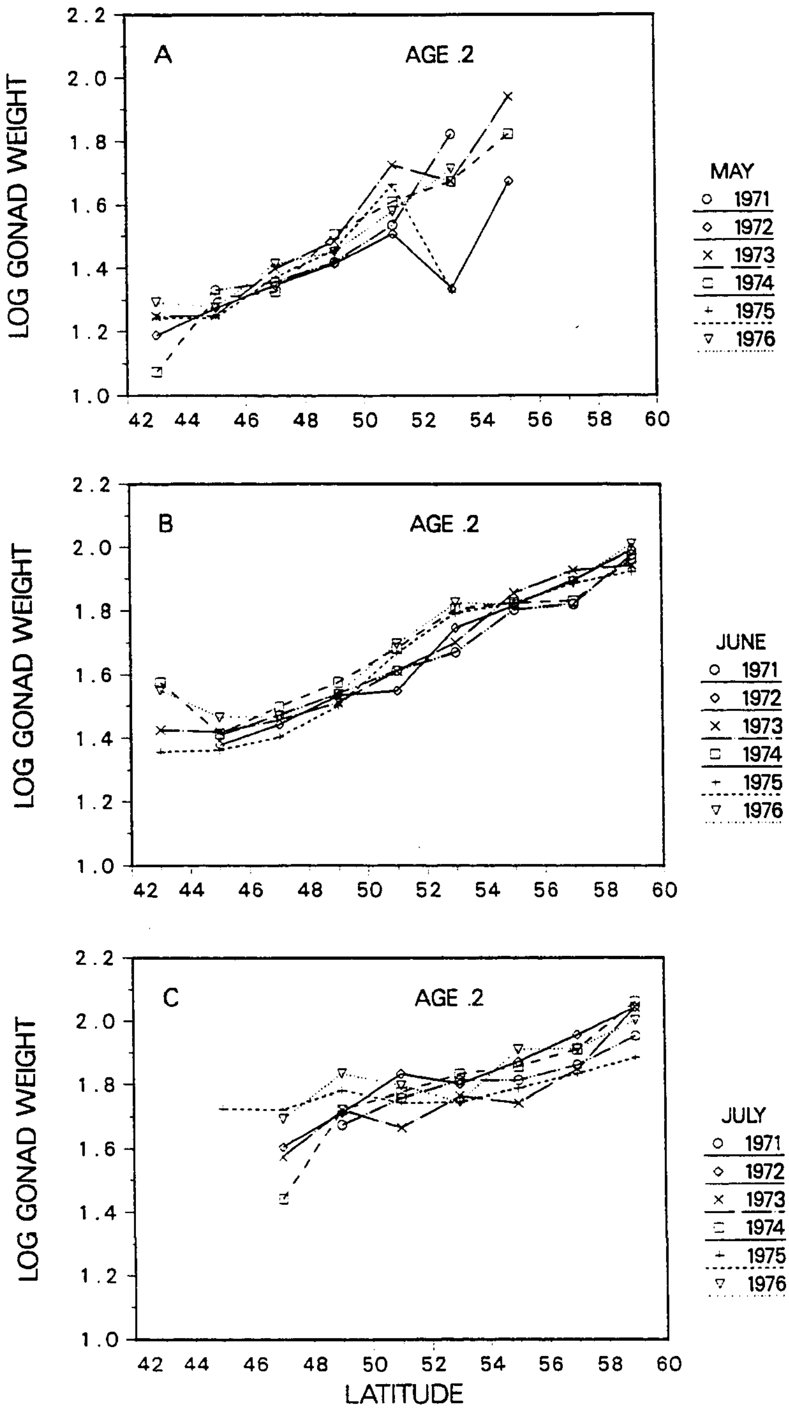

Figure 15. Mean gonad weight for May, June, and July of age .2 sockeye salmon for each 2^{o} lat. in area 1, 1971-76.

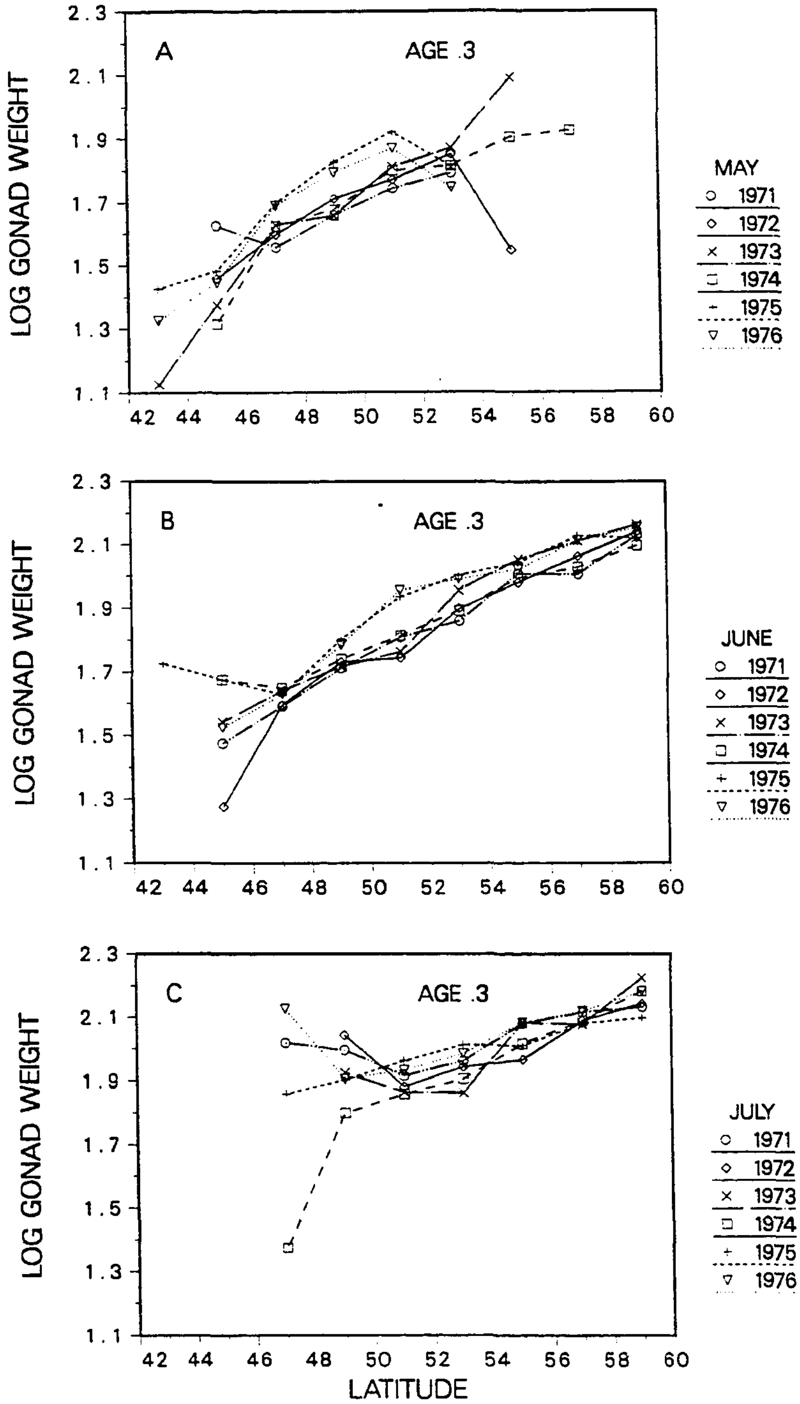

Figure 16. Mean gonad weight for May, June, and July of age .3 sockeye salmon for each 2° lat. in area 1, 1971-76.

or density-dependence factors. Mysak *et al.* (1982) found a correlation between the catch of sockeye salmon and sea surface temperature, salinity, and sea level pressure, whereas Birman (1973) ascribed the catch fluctuation of pink and chum salmon to the sun spot cycle, but not for sockeye salmon. Furthermore, Krogius (1978) found a 4-year cycle of biogenic matter discharging into the Dal'neye Lake, which coincided with a 4-year cyclic fluctuation in abundance of sockeye salmon in that lake.

An increase in oceanic landings of sockeye salmon has been apparent since 1978. Eggers *et al.* (1984) and Rogers (1984) suggested a favorable change in climate which might have increased the marine survival of sockeye salmon. They also ascribed part of the increase in landing to a decline of the Japanese high seas catch after 1957. In addition, increased escapement of spawners in recent years is an important factor which allows the production of a great number of offspring.

In contrast to the Bristol Bay area, there was a decline in the return of sockeye salmon to the Kamchatka area during 1958-83. Without considering the Dal'neye Lake, there is no apparent cycle in abundance of Kamchatka sockeye salmon . The cause of the decreasing return has been attributed to the Japanese high seas salmon fishery (Kurenkov, 1959; Birman, 1964). However, Krogius (1967) attributed this decline to the increase in the abundance of Kamchatka pink salmon, since both species compete for the same food organisms in the ocean.

Since 1978, the ocean abundance of sockeye salmon increased. Apparently, this increase was largely due to the presence of Bristol Bay sockeye salmon. The return of sockeye salmon to the Kamchatka area was high during 1958-62, and this is reflected on the ocean abundance in 1961 and 1962. Therefore, abundance of sockeye salmon can be used as an appropriate indicator for the return of the fish to their spawning area.

The present study indicates a monthly difference in CPUE of sockeye salmon. This is caused by Bristol Bay fish, since the return of Bristol Bay fish is much larger than that of Kamchatka fish.

The CPUE of age .2 and .3 sockeye salmon was lowest throughout three months in 1973. This lowest CPUE coincides with the record low return of Bristol Bay sockeye salmon in 1973.

Changes in gonad weight of sockeye salmon in time and space can be due to two factors. During the last year of ocean residence, maturing Bristol Bay sockeye salmon maintain an extensive east-west distribution north of 50°N until they begin their inshore migration in June (French *et al.*, 1976). Maturing Kamchatka sockeye salmon move southward and eastward in an area between 43°N-50°N and 150°E-177°W. Bristol Bay sockeye salmon in the eastern Gulf of Alaska migrate westward and enter into the Bering Sea through the Aleutian passes. The migration of mature Kamchatka sockeye salmon is northward and westward from the south of the Aleutian Islands toward the coast (Kondo *et al.*, 1965; Margolis *et al.*, 1966). Bristol Bay fish generally mature earlier in time and age than Kamchatka fish. Mature age .3 sockeye salmon, with heavy gonad weight, occurred in more southern water than mature age .3 sockeye salmon (Mishima, 1974; Shimazaki and Nakayama, 1975). Therefore, different age compositions and different origin of sockeye salmon cause the variations of gonad weight, such as northward increasing trend within a month.

The spatial and temporal changes in gonad weight may be caused by sea surface temperatures. Nishiyama (1980) found a positive relation between sea surface temperature and maturation condition of Bristol Bay sockeye salmon in early June to early July in the eastern Bering Sea. This relation suggests that gonad development is accelerated by warmer sea temperatures. Therefore, the variation in gonad weight of fish in area 1 during 1971-76 may be related to the variation of sea surface temperature in that area.

SUMMARY

Cyclic high return of Bristol Bay sockeye salmon was found every fifth year during 1960-80. Ocean age .2 fish played a major role in contributing to this cycle. The Kamchatka sockeye salmon were very low in abundance and exhibited no apparent cycle.

The relative ocean abundance of sockeye salmon decreased from 1971 to 1975, and then increased since 1976. The ocean abundance of mature and immature fish during 1971-76 was the lowest among the three periods, 1961-70, 1971-76, and 1977-85. In 1971-76, mature Kamchatka fish were 24 % more abundant than mature Bristol Bay fish, and there was no difference in immature fish abundance between the two populations.

Seasonal change in the relative abundance of sockeye salmon was observed during the 1971-76 period, whereas the age composition of fish was almost stable from May through July. The proportion of immature to mature fish varied by month and by year.

The gonad weight of age .2 and .3 sockeye salmon increased seasonally during 1971-76. Low gonad weight of age .2 and .3 fish occurred in May through July in area 1. High gonad weight, however, was seen in the central ocean between 175°E and 170°W, except for age .2 fish in 1971 and for .3 fish in 1971 and 1975. An eastward increasing trend of gonad weight prevailed throughout 1971-76. Gonad weight was greater in higher latitudes than those in lower latitudes. Monthly mean gonad weight was different from year to year and from area to area.

Chapter III: Abiotic Factors in Relation to Return, Ocean Abundance, and Maturity of Sockeye Salmon

INTRODUCTION

This chapter examines several oceanic and atmospheric conditions in the habitat of sockeye salmon. Three relations are analyzed: (1) atmospheric forcing (wind stress curl) is related with the total return, coastal catch and escapement, of Bristol Bay sockeye salmon, (2) mean sea surface temperature (SST) is related to the ocean abundance of sockeye salmon, and (3) oceanic and atmospheric variables, SST, sea level pressure (SLP), and cloudiness (CLD), are related with the maturity of sockeye salmon at sea.

The relationships between environmental factors and biological aspects of salmonids have been investigated at various life stages in different populations. Kostarev (1970) and Kayev (1983) analyzed the abundance fluctuation of chum salmon in the Okhotsk Sea area, and ascribed the low production of fish to effect of river runoff, water temperature, timing and duration of snowcover, and snowfall during the freshwater period of fish. In Prince William Sound, Alaska, Willette (1985) found that odd- and even-year pink salmon population sizes responded to odd-year ocean temperature anomalies. Ivankov (1985) reported that the annual changes in abundance of young pink salmon was positively related to the May-June coastal water temperature in the south Kuril Island.

Cyclic fluctuations in abundance of sockeye salmon appeared to be related to large scale oceanographic and meteorological events. Mysak *et al.* (1982) pointed out that in British Columbia, a 5- to 6-year period of coherent signal among SLP, SST, and salinity coincided with the annual sockeye salmon catch. Little study, however, has been conducted on the relationship between the ocean abundance of sockeye salmon and the SST in the northwestern North Pacific. Currently, no information is available on the relation between the meterological events such as wind stress curl and the total return of Bristol Bay sockeye salmon. In the central Bering Sea, the maturity (gonadsomatic index) of ocean age .2 sockeye salmon returning to Bristol Bay has been postively related to the SST in that area (Nishiyama, 1982). This temperature-maturity relation, however, is not examined for the northwestern North Pacific.

DATA SOURCES AND METHODS

Wind stress curl

Curl of the wind stress (τ) is a measure of the torque about a vertical axis exerted on a column by the surface winds (McLellan, 1965).

$$\text{curl}_z\ \vec{\tau} = \frac{\partial \tau_y}{\partial x} - \frac{\partial \tau_x}{\partial y} \tag{9}$$

where τ_x and τ_y are the x and y components of $\vec{\tau}$. Wind stress curl was calculated using monthly mean sea level atmospheric pressure from a $3^{\circ} \times 3^{\circ}$ grid in the North Pacific between equator and lat. 60°N, and between long. 130°E and 110°W. The data were adapted from Royer (1985). To eliminate the seasonal effect, the wind stress curl of each month was calculated as a 25-month running average. Both smoothed and unsmoothed curl were analyzed. Seasonal variation of unsmoothed wind curl was especially examined in the 1970-76 period. A power spectrum analysis (Box and Jenkins, 1976; Dixon *et al.*, 1985) was made to find the periodicity of the averaged wind stress curl. A cross correlation analysis was then applied to examine the relation between the annual mean wind curl and the total return of sockeye salmon. The annual mean wind curl and the total return of fish were transformed into logarithmic scales prior to performing cross correlation analysis.

Sea surface temperature and sea level pressure

The SST and SLP data were provided by the Scripps Institution of Oceanography, La Jolla, California, and the Fleet Numerical Oceanography Center, Monterey, California. Both SST and SLP data were recorded in Marsden squares on a $5^{\circ} \times 5^{\circ}$ grid for almost the entire North Pacific between the equator and lat. 60°N, and between long. 130°E and 110°W, based on ships of opportunity.

Within area 1 (Figure 5), SST was separately averaged for the two areas, herein termed west habitat and east habitat (Figure 17). The west habitat is an area between

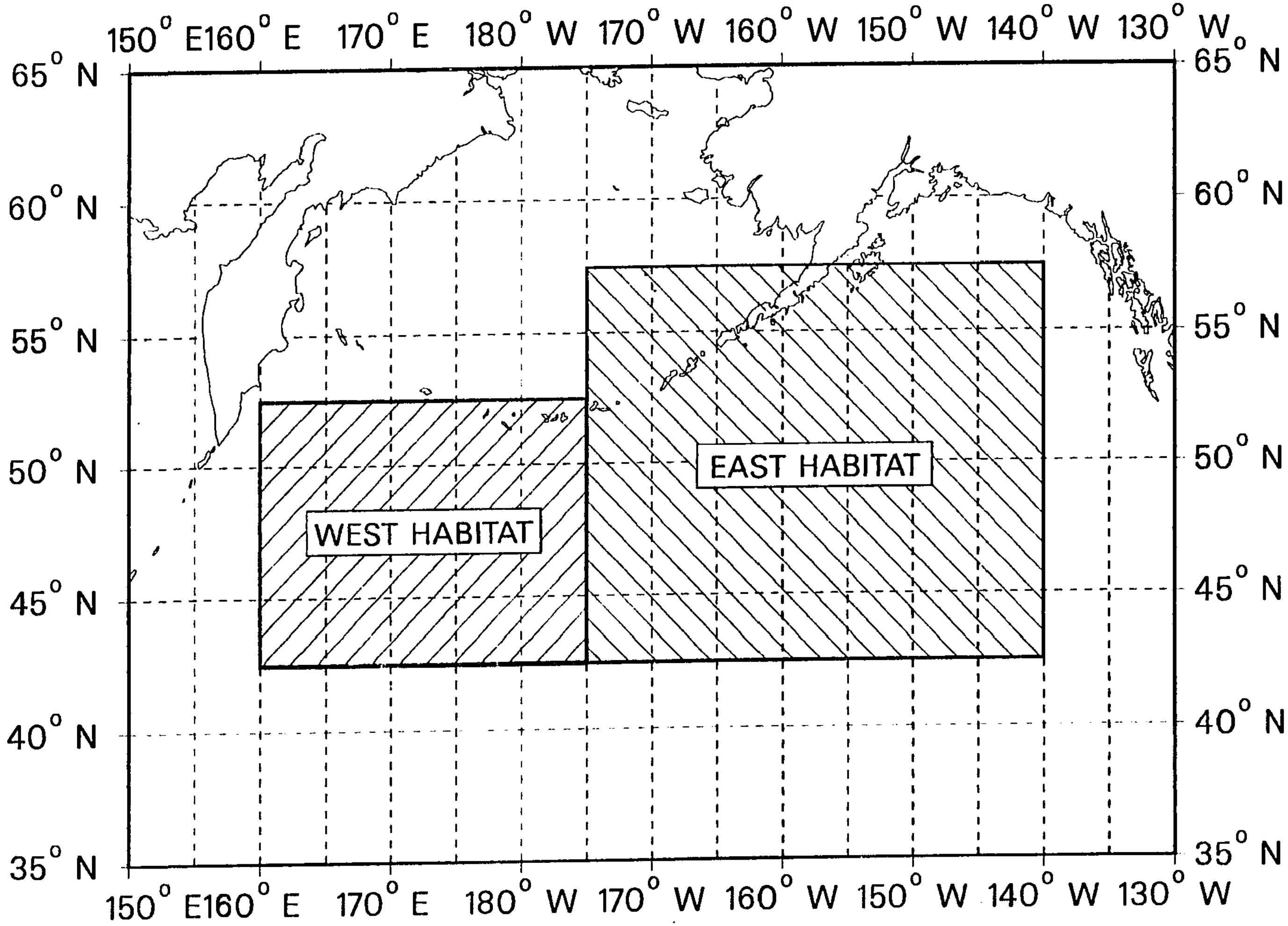

Figure 17. Major sockeye salmon habitats. West habitat (A), and east habitat (B).

$42^{\circ}30'$N-$52^{\circ}30'$N and 160°E-175°W, while the east habitat is an area between $42^{\circ}30'$N-$57^{\circ}30'$N and 175°W-140°W. Because sockeye salmon are distributed in these habitats mainly in May and June, the SST in each habitat was averaged for these two months. The relation between the deviation of the mean May-June SST and the deviation of the relative ocean abundance of sockeye salmon in the west habitat was determined by regression analysis (SAS Institute, 1985).

The monthly mean SST was then averaged for each 5° latitude quadrant in an area between 40°N-55°N and 160°E-175°W. The difference of monthly mean temperature at every 5° latitude was examined by the Tukey test, an analysis of variance with multiple comparison between sample means (Nie *et al.*, 1985). In addition, monthly mean SST and SLP were calculated for each 5° longitude quadrant in an area between 45°N-55°N and 160°E-140°W. Surface charts of monthly SLP based on $5^{\circ} \times 5^{\circ}$ grid were used to provide a synoptic view of the climatic conditions in the northern North Pacific.

Cloudiness

The CLD was used as one of the parameters of atmospheric environment. For this purpose, the daily mean cloudiness data (in *octa*) in the North Pacific were used as given by Sadler (1976). An *octa* is a measure of cloud coverage which is the sky divided into eight areas. These data were compiled from satellite images in a quadrant $2.5^{\circ} \times 2.5^{\circ}$ lat.-long. for the period of February 1965 to July 1973 between lat. 20°N and 60°N in the Pacific Ocean. The monthly CLD was calculated for each 5° longitude quadrant in the same area used for the calculation of monthly SST and SLP.

The correlation between $\log_{10}$ of sockeye salmon gonad weight and corresponding monthly SST, SLP, and CLD and preceding monthly SST_p, CLD_p, and SLP_p was made by Pearson correlation analysis (Nie *et al*). The correlation analyses were examined at different time intervals: (1) yearly; (2) monthly (May, June, and July, for a six-year period throughout 1971-76); and (3) during all three months combined (May-July) for the same six-year period. Because cloudiness data were available only for the years 1971-73, cloud analysis was limited to these years.

RESULTS

Abiotic factors

Wind stress curl

The signal of unsmoothed wind stress curl (*dynes* $cm^{-3} \times 10^{-9}$) was noisy with an amplitude between -14.4 and 41.4 (Figure 18). The running average of the monthly curl was the lowest (2.9) in April 1966, and was the highest, about 4 times higher than the lowest reading, in November 1983 (10.3).

Seasonal variations of unsmoothed wind stress curl during 1970-76 were nearly the same in 1970-71 and 1971-72 (Figure 19). The general pattern of the wind curl was a gradual increase from fall to next late spring or early summer and a steady decrease throughout the rest of the season. The average wind curl varied from -6.29 to 25.3 in the six-year study period.

The annual mean wind stress curl during 1955-85 is illustrated in Figure 20A. The lowest mean curl in *dynes* $cm^{-3} \times 10^{-10}$ was 36.2 in 1966, and the highest curl was 93.2 in 1976, about three times higher than the lowest mean curl. Power spectrum analysis of the monthly curl exhibited a major peak at 5.3-year and a second peak at 3.1-year (Figure 20B).

Sea surface temperature

Mean May-June temperature

The mean May-June temperature in the two major areas, *i.e.*, west and east habitats of sockeye salmon during 1960-84, is given in Figures 21A & 21B. Apparently, the long term fluctuation of SST differed between the two habitats. The temperature range was 6.3-8.3^{o}C in the east habitat, and 5.2-6.8^{o}C in the west habitat. In the east habitat, the SST was higher during the periods 1960-68 and 1979-84 than the long-term average. The low SST occurred during the period of 1969-76. In the west habitat, a warm period

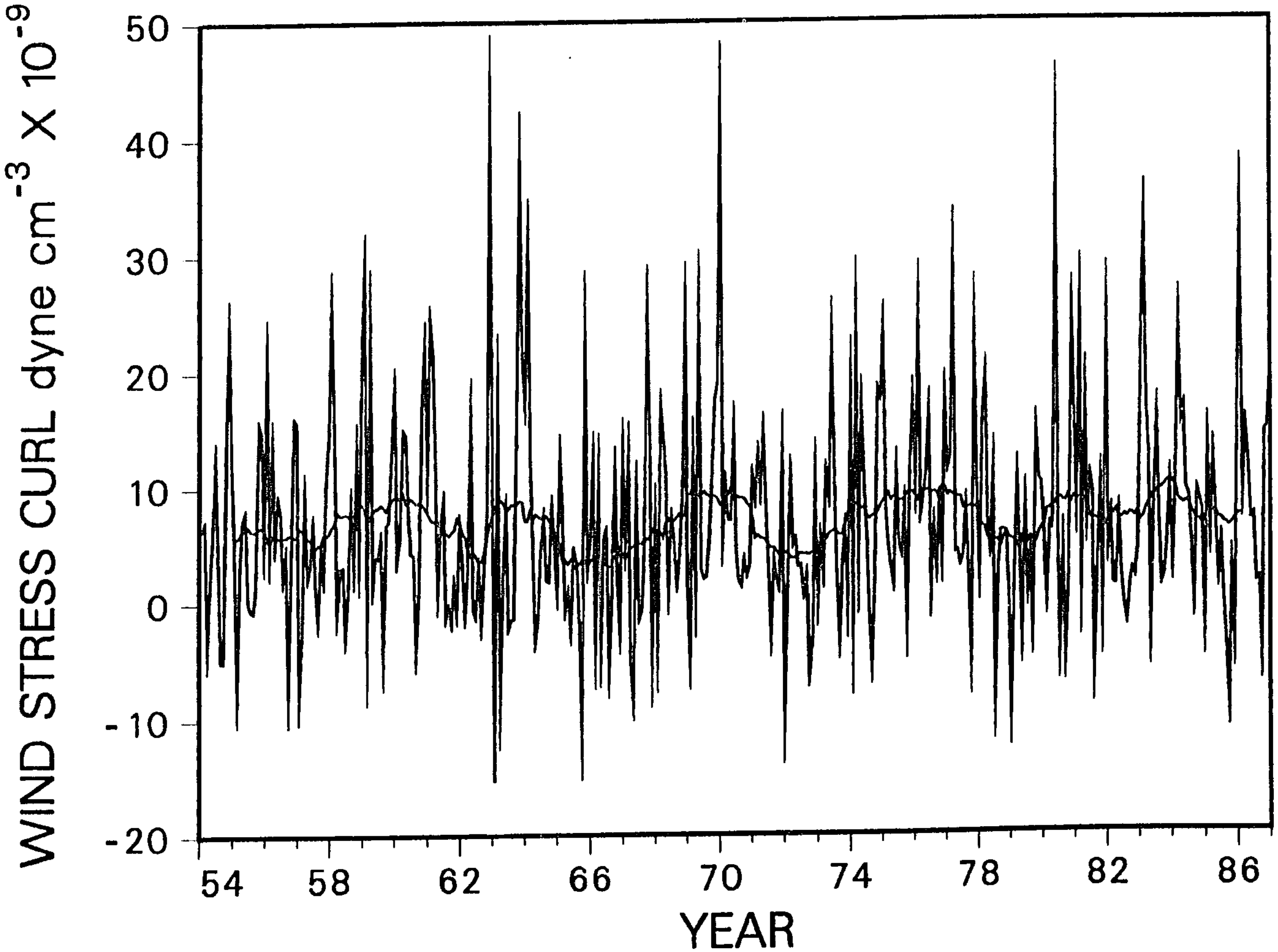

Figure 18. Unsmoothed monthly wind stress curl in the Gulf of Alaska during 1954-86, and smoothed wind stress curl based on a 25-month running average.

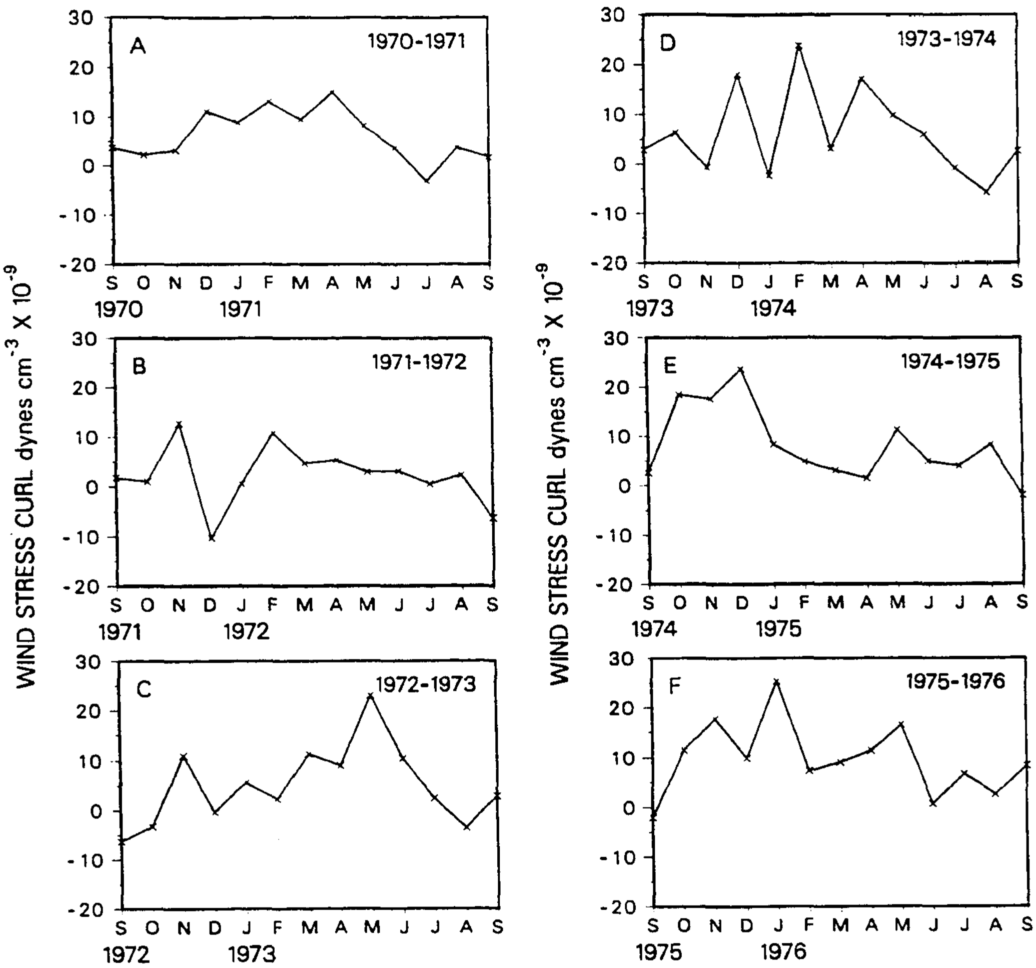

Figure 19. Unsmoothed monthly wind stress curl in the Gulf of Alaska (year begining in September) for 1970-71 (A); 1971-72 (B); 1972-73 (C); 1973-74 (D); 1974-75 (E); and 1975-76 (F).

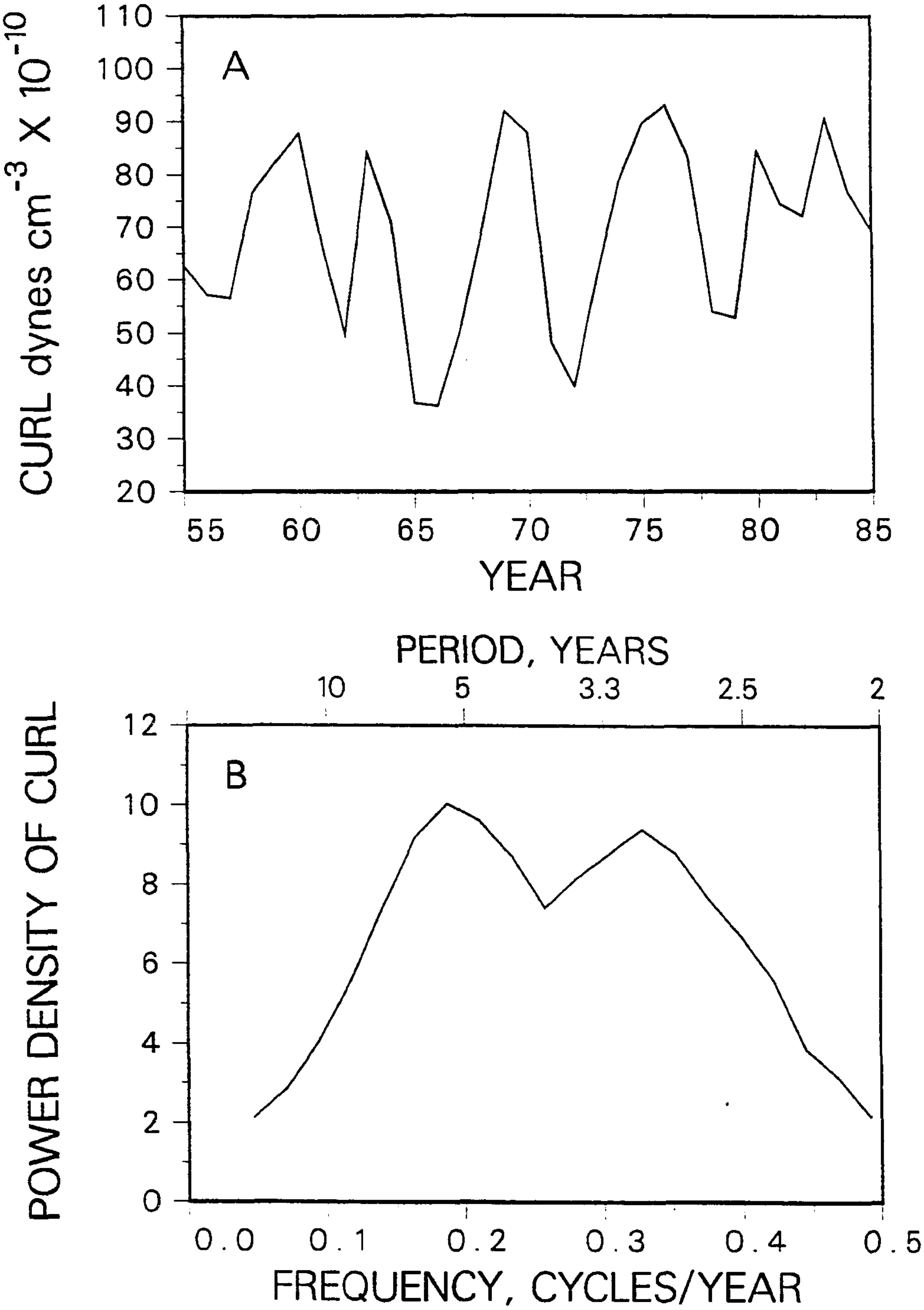

Figure 20. Annual mean wind stress curl in the Gulf of Alaska during 1955-85 (A) and power spectrum (B).

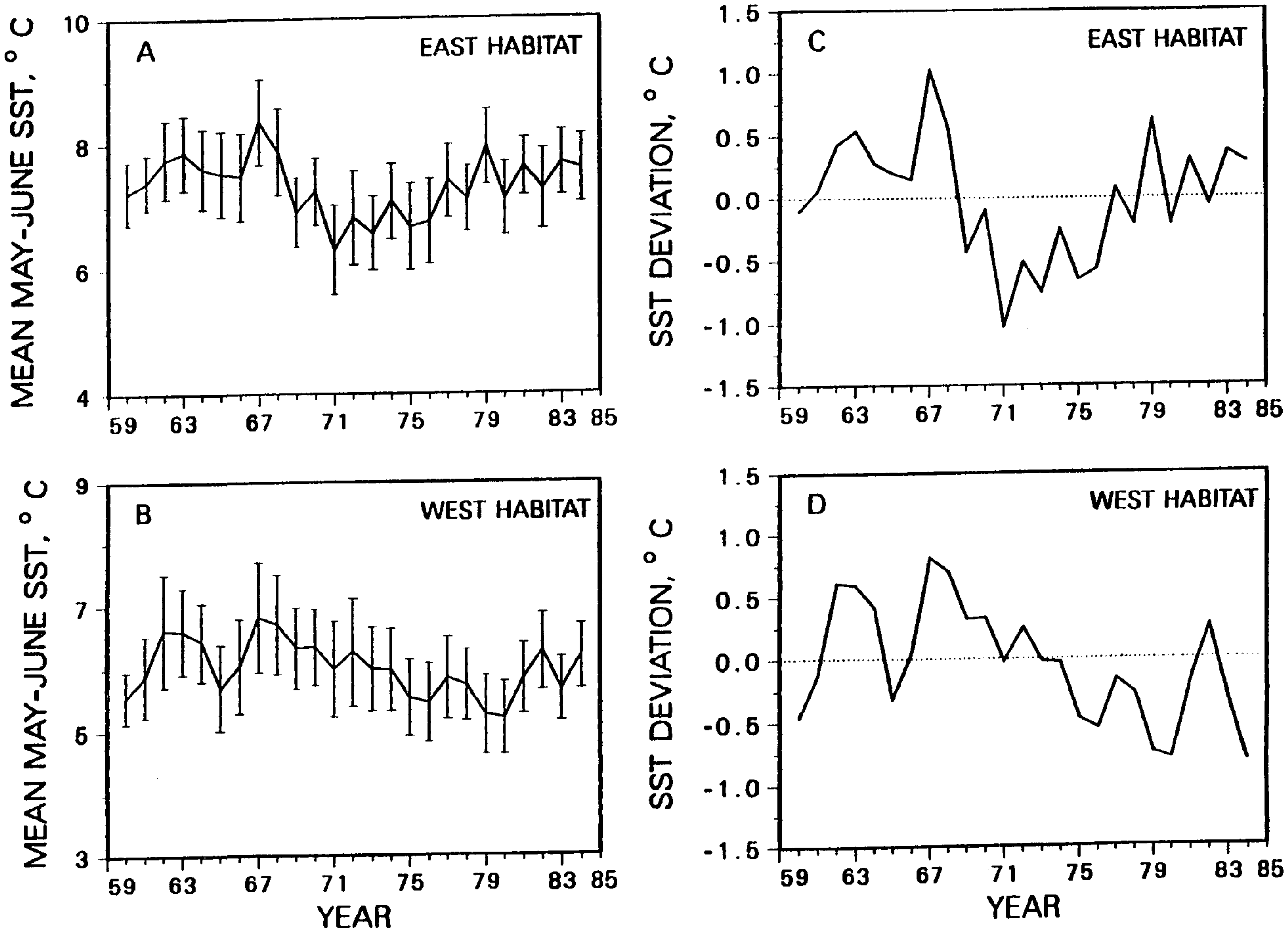

Figure 21. May-June mean SST for the west habitat (A) and east habitat (B). Also SST deviations for the two habitats (C & D).

extended from 1960 to 1972, except in 1965, and low SST persisted during the years 1973-80.

The average SST during 1960-84 was 6.0°C in the west habitat and 7.3°C in the east habitat. The deviation of SST for the 30-year mean is shown in Figures 21C and 21D. In the east habitat, prior to 1971, the SST showed a decreasing trend. From 1972 through 1985, a steadily increasing trend of SST is seen in the east habitat. In the west habitat the trend decreased until 1980, and then increased after 1981. Most notably, the temperature in the east habitat dropped drastically from 1967 to 1971 with a difference of 2°C and recovered in 1972. In contrast, the cooling trend was slower and longer from 1967 to 1980 in the west habitat. Thus, during 1971-80 the east and west habitats displayed reversed trends.

Spatial and seasonal change in temperature

Monthly mean temperature decreased with latitude in an area between 40°N-55°N and increased with season (Figure 22; Apendix Table B-1). The temperature range was 2.5-11.5°C in April, 3.2-12.9°C in May, 4.7-12.9°C in June, and 6.5-17.9°C in July. In April, the temperature between 45°N and 55°N was relatively lower in 1973 and 1976 than in the other four years. In May, the temperature between 45°N and 50°N was comparatively lower in 1975 and 1976 than in 1971 through 1974. Relatively higher variation of temperature (1.1-1.4°C) was observed at 45°N. No apparent difference of temperature at the same latitude existed in April during the six-year period. With the advance of season, significant difference ($P<.01$) of temperature became more evident from May to July.

Figure 23 shows the longitudinal distribution of SST for the six-year study period. In general, a trend existed with SST increasing from west to east, though this trend varied with year. The lowest SST was consistently found in the western region of area 1, 160°E-165°E, coinciding with the position of the Subarctic Gyre, whereas the highest SST was

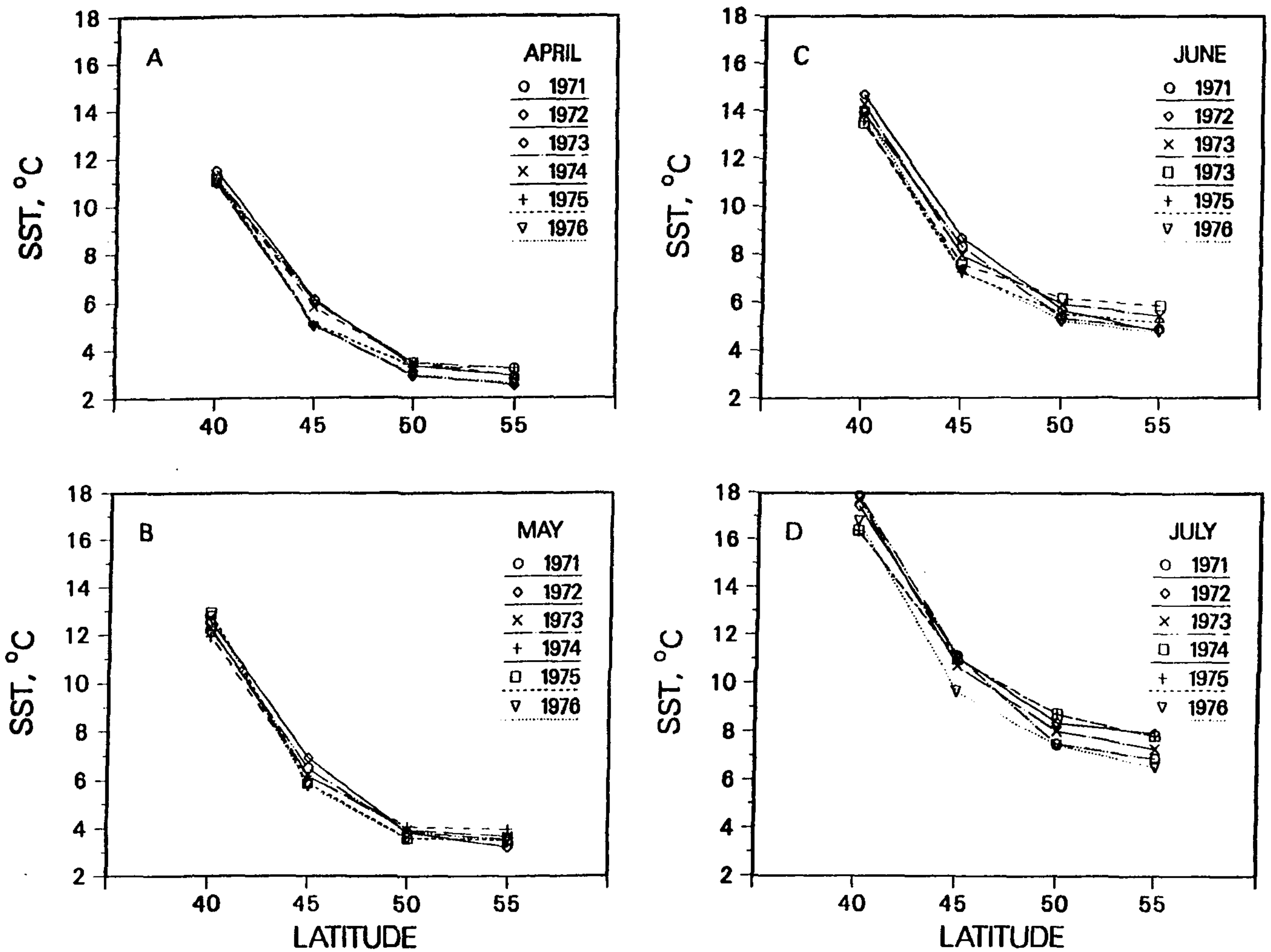

Figure 22. Mean SST for each 5° lat. in area 1 for April (A); May (B); June (C); and July (D), 1971-76.

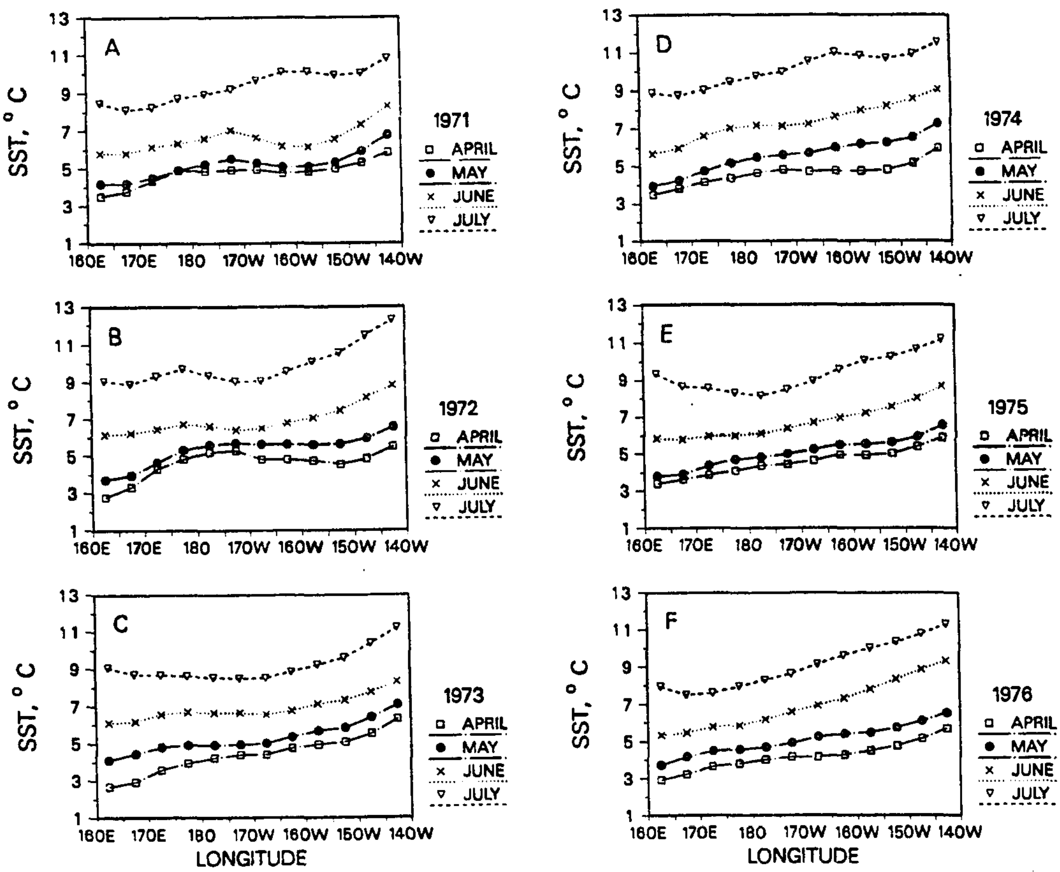

Figure 23. Mean SST for each 5° long. in area 1, for April-July, 1971-76.

seen in the Gulf of Alaska, 140°W-145°W. Evidently, the temperature and its longitudinal fluctuation were low between April and May and high between June and July. The temperature range for each 5° longitude was 2.7-6.0°C in April, 2.7-7.3°C in May, 5.4-9.3°C in June, and 7.6-12.3°C in July (Appendix Table B-2).

The monthly mean SST within the entire study area were similar with season and increased all years except 1971, regardless of the mean values (Figure 24). The SST increment was smallest in April-May in 1971 (0.4°C), and highest in June-July in 1972 (2.9°C). The SST in April and May was consistently between 4.2°C and 4.8°C and 5.1-5.5°C, respectively, throughout the six-year period. The SST in June showed a slightly eastward increasing trend from 1971 to 1976 ranging from 6.6°C to 7.4°C. In July, the SST varied from 9.1°C to 10.1°C, but did not show any annual trend.

Sea level pressure

The SLP generally varied by month (April-July) and year (1971-76) depending upon the position and duration of major prevailing pressure systems, including the Okhotsk Low and Siberia High and the Aleutian Low and Pacific High (Figure 25). An intense low was observed in April and May 1971, May 1973, and April 1974, north of 50°N between 140°W and 165°W. The range of SLP for every 5° longitude (in *mb*) was between 1005.6 and 1021.4 in April-July (Appendix Table B-3).

The annual difference of monthly change in mean pressure during 1971-76 varied between years (Figure 26) and was greatest in April, followed by July, while it was smallest in May. In 1972, 1973, and 1975, pressure decreased rapidly from April to May, then steadily increased in June and July. The pressure in April was very low in 1971 and 1974, but very high in 1972 and 1975. In 1976, the pressure was the same in April and May, increased in June, and then decreased in July.

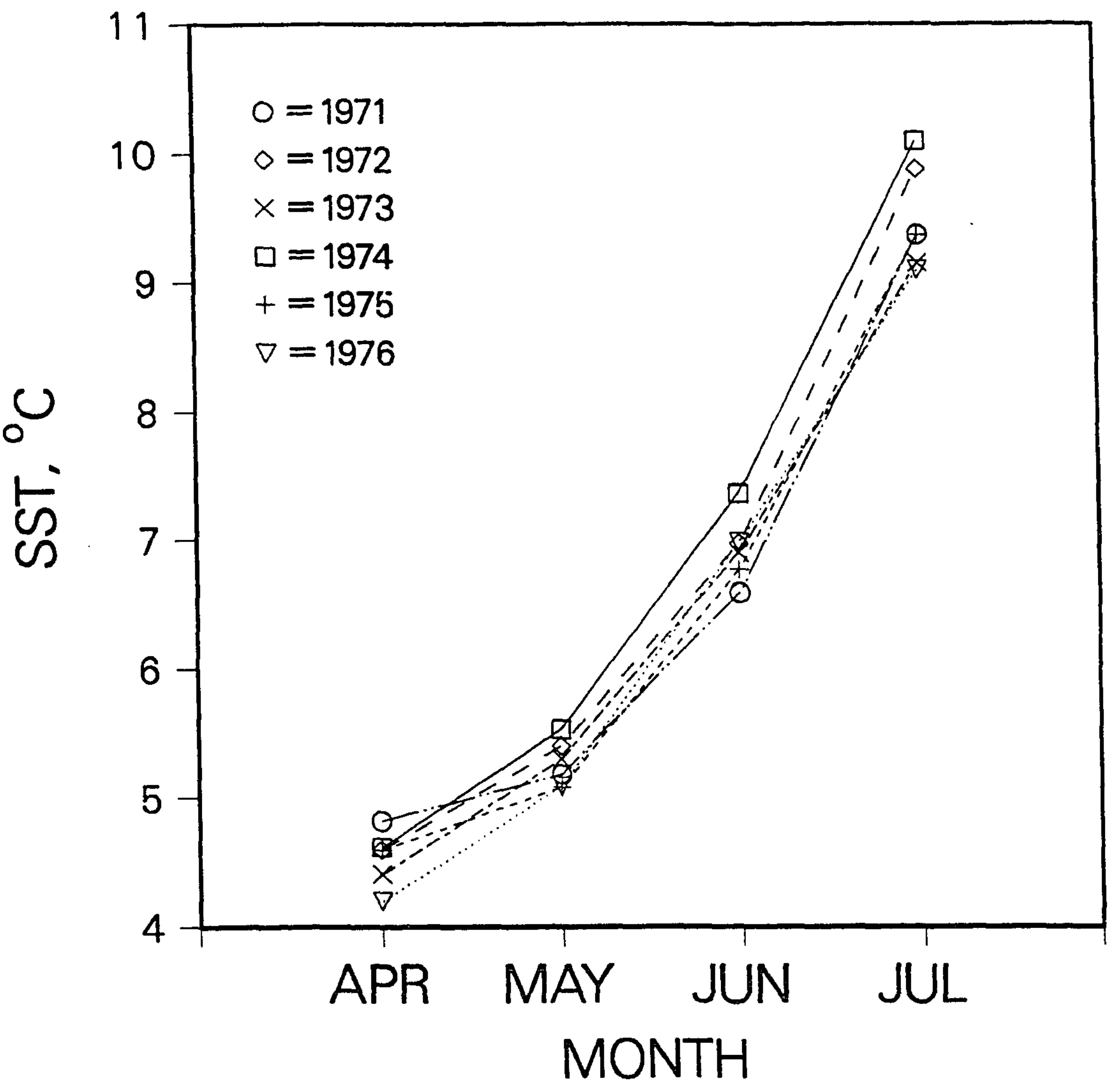

Figure 24. Monthly mean SST in area 1, 1971-76.

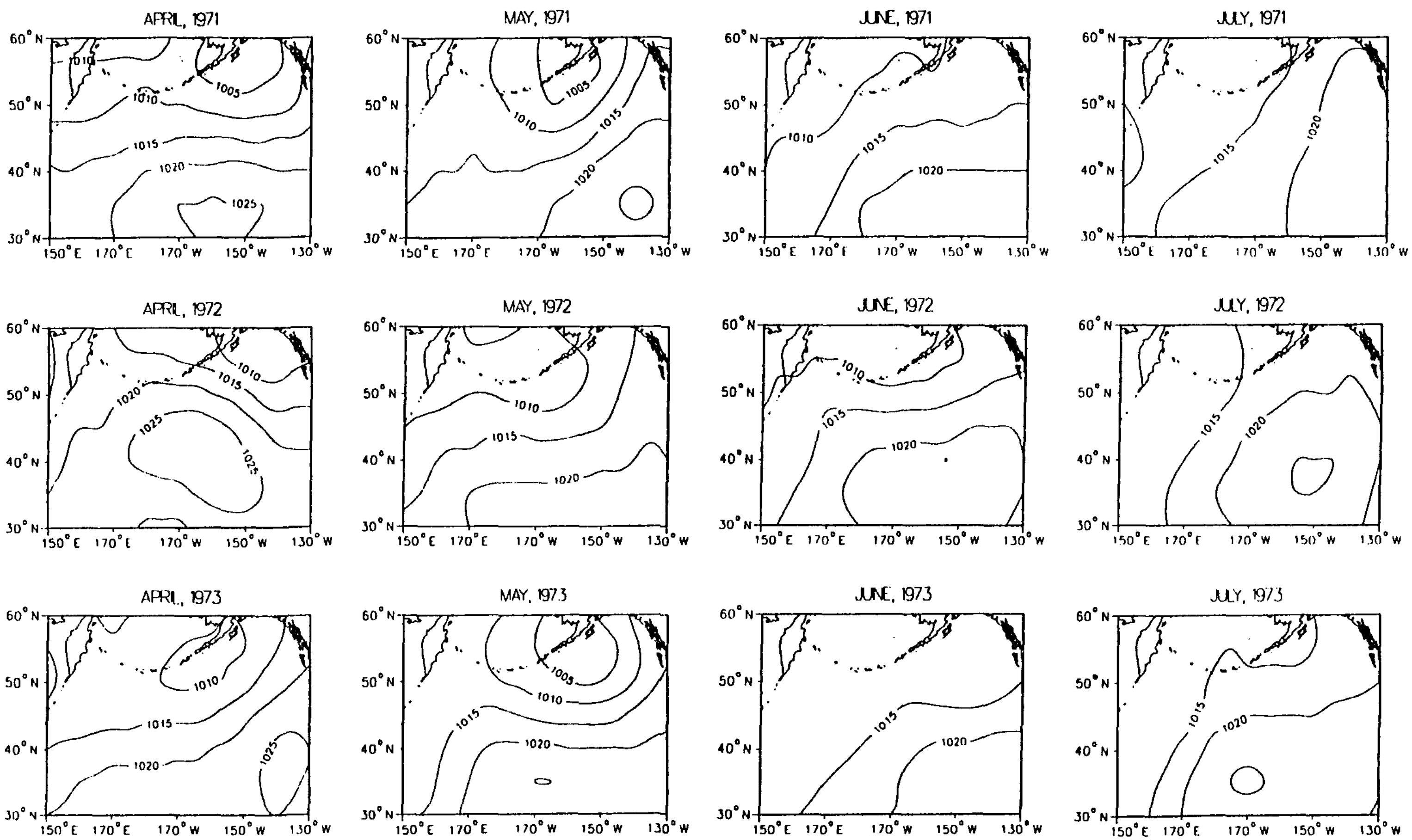

Figure 25A. Mean sea level pressure charts for April-July, 1971-73.

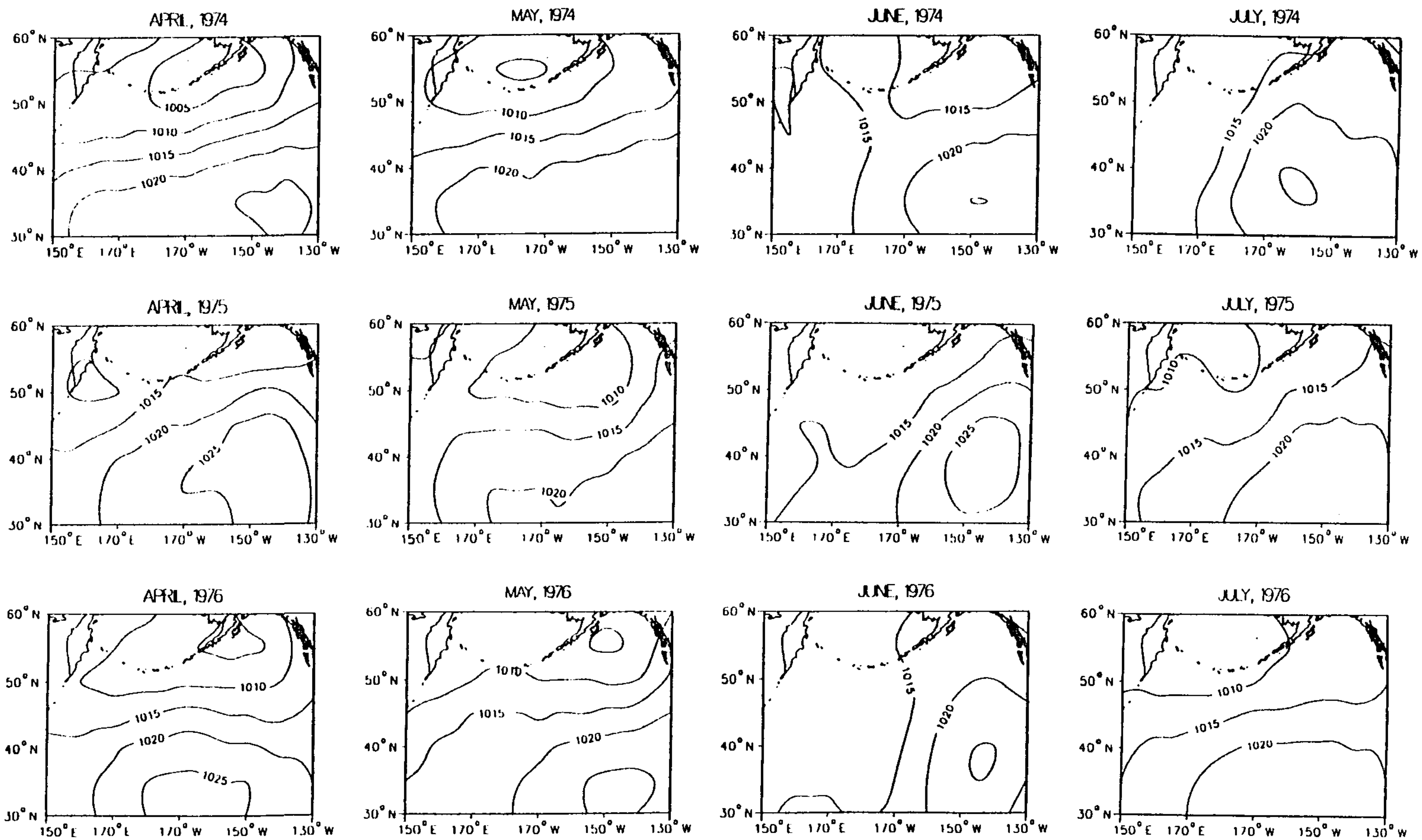

Figure 25B. Mean sea level pressure charts for April-July, 1974-76.

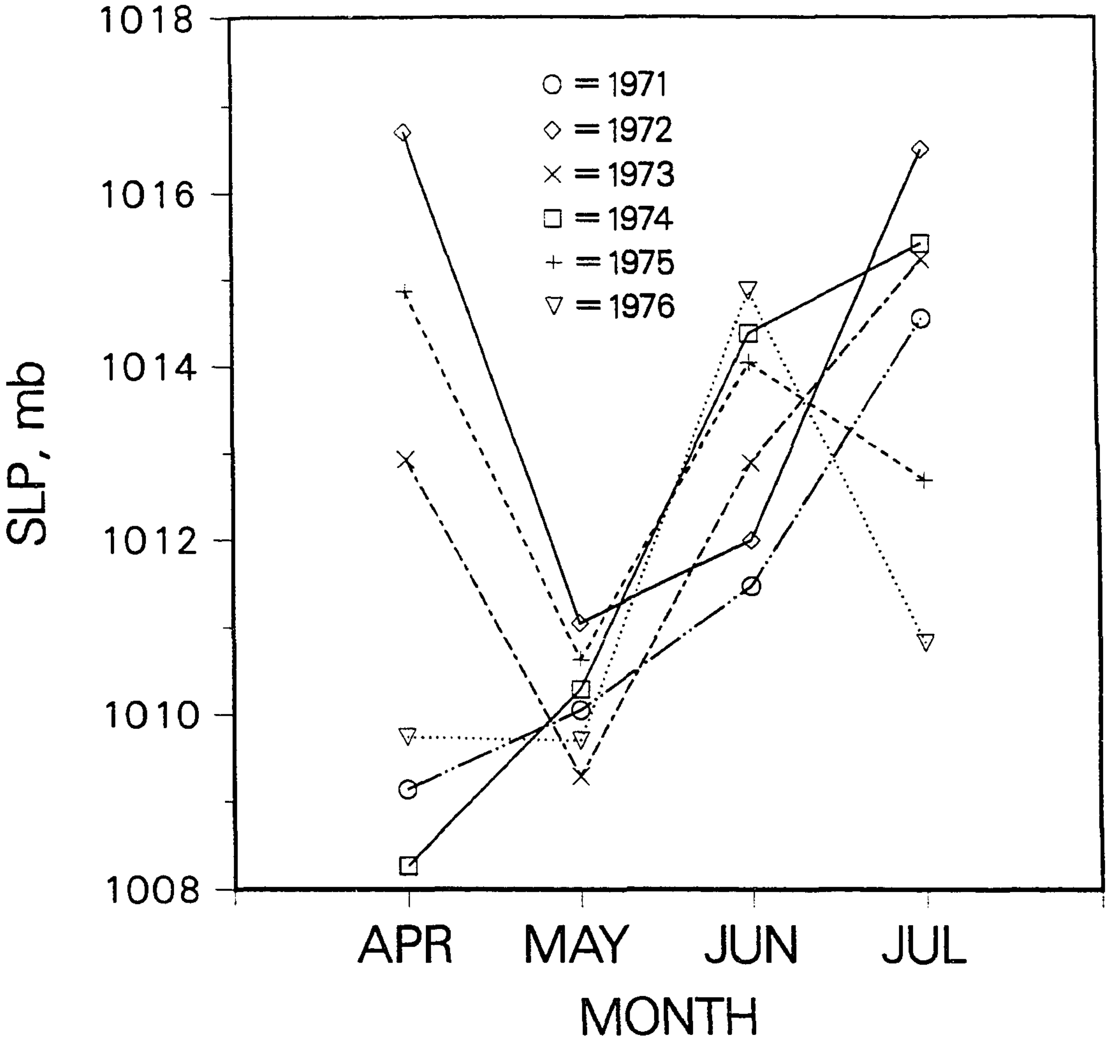

Figure 26. Monthly mean sea level pressure in area 1, 1971-76.

Cloudiness

The longitudinal mean CLD in 1971 to 1973 varied slightly with a little systematic fluctuation in area 1 (Figure 27). The mean CLD during these three years was at or around 6 *octa* (Appendix Table B-4).

Figure 28 shows the annual mean monthly CLD of the entire area 1 during 1971-73. The lowest CLD was in April 1971 (5.5). The CLD systematically increased in May, June, and July, except in 1971 when there was a slight decrease from June to July. The CLD during the entire 1971-73 period was always greater than 5.5 in the monthly mean, indicating that about 60 % of the sky in the study area was covered by clouds.

Abiotic factors in relation to return, abundance, and gonad weight of sockeye salmon

Return and wind stress curl

The cross-correlation analysis between the return of Bristol Bay sockeye salmon and the annual mean wind stress curl showed that return of fish of most age groups was significantly ($P<.10$) correlated with curl (Figure 29; Table 3). For age .2, return of age 1.2 fish yielded a 0-year lag (the year of spawning migration) to wind curl (Figure 29A), whereas return of age 2.2 fish revealed a 0- and 5-year lag (the year of spawning migration) to wind curl (Figure 29B). For age .3, return of age 1.3 fish showed a 0- (the year of spawning migration) and 1-year (the first year of lake residence) with wind curl (Figure 29C), and return of age 2.3 fish yielded a 1- (the first year of lake residence), 6- (the year of spawning migration), and 7-year (the first year of lake residence) lag with wind curl (Figure 29D).

Although the results indicated return leads curl, it would be impractical to attempt to interpret this fact simply because it is unlikely that fish influence atmospheric forcing.

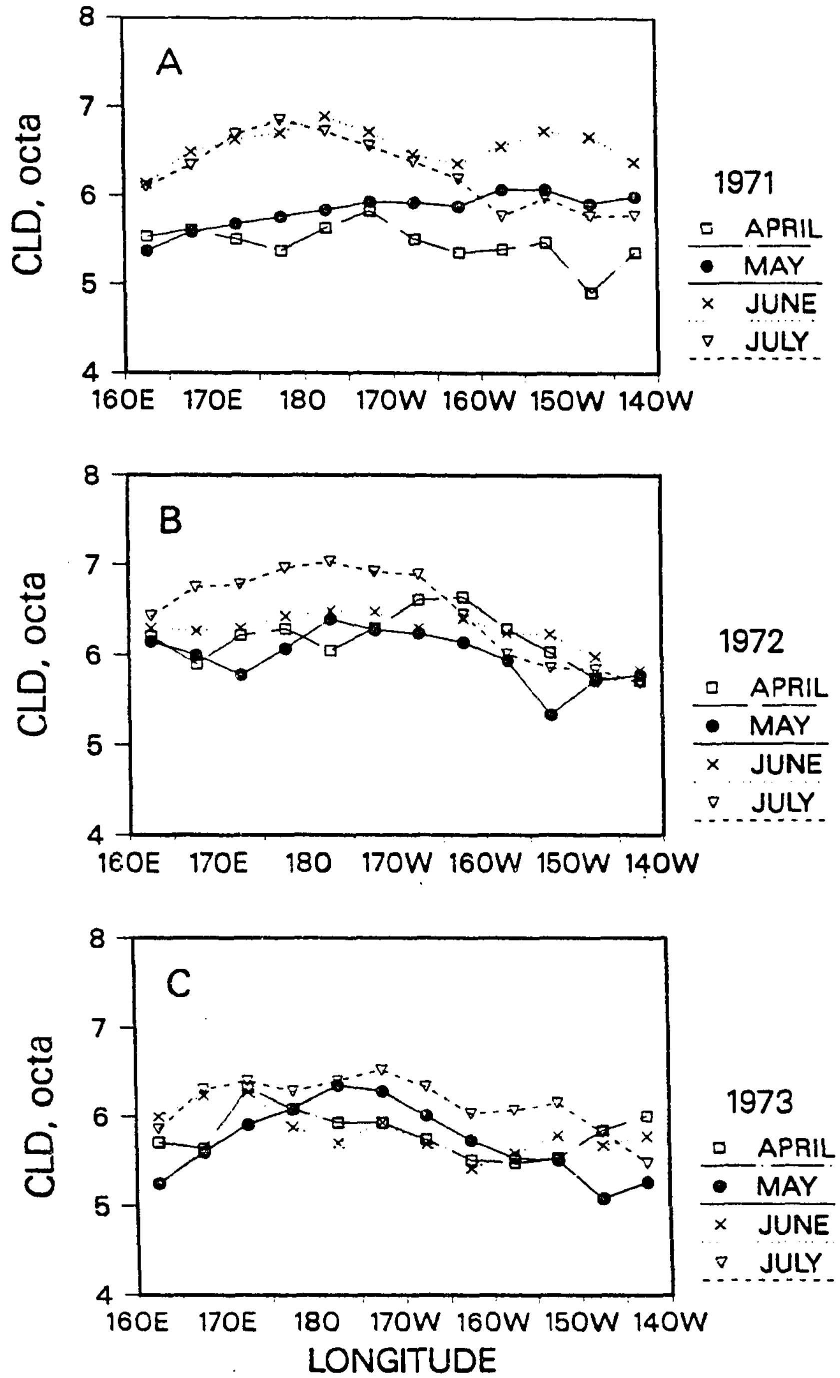

Figure 27. Mean cloudiness for each 5° long. in area 1 for April-July 1971-73.

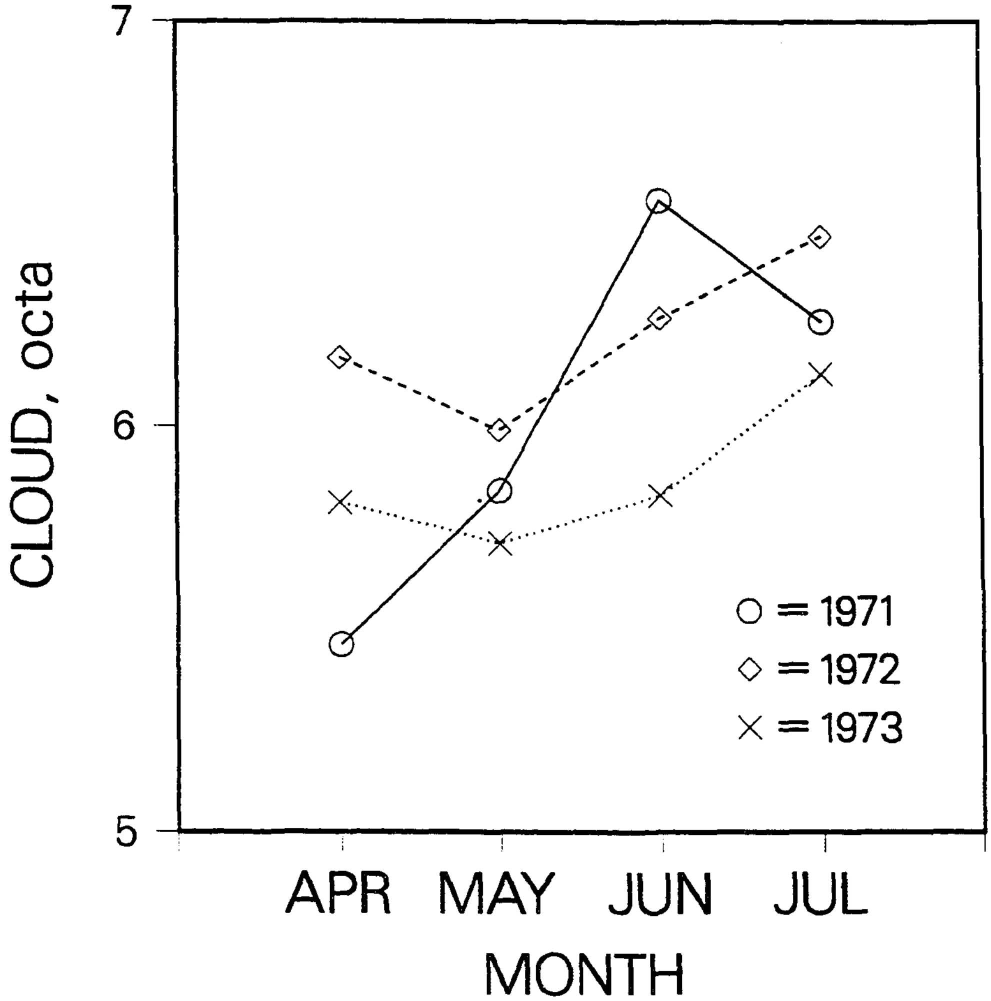

Figure 28. Mothly mean cloudiness in area 1, 1971-73.

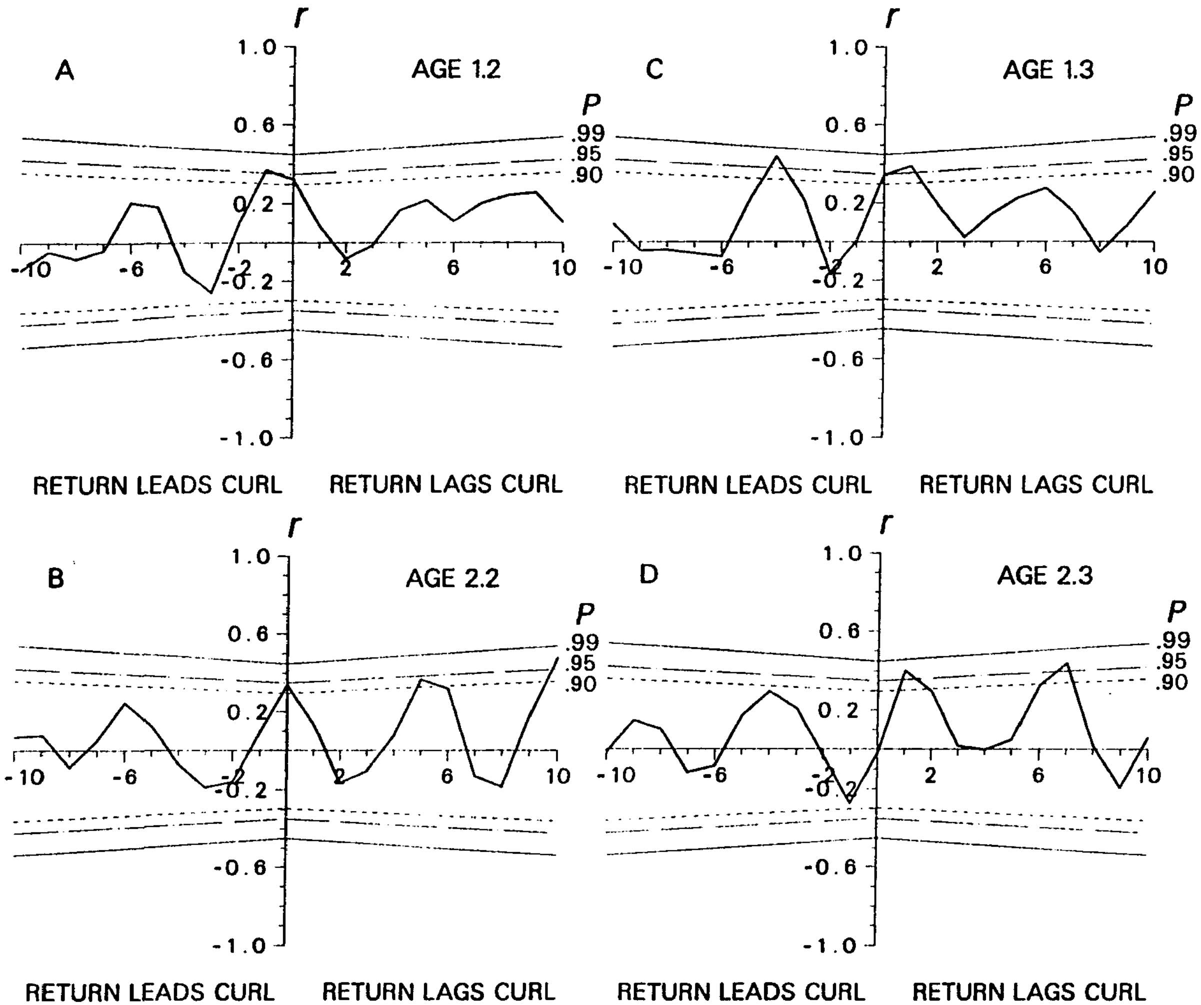

Figure 29. Cross correlation between wind stress curl and return of Bristol Bay sockeye salmon for age 1.2 (A); 2.2 (B); 1.3 (C); and 2.3 (D) fish, 1956-85.

Table 3. Cross correlation of wind stress curl tc the total return of Bristol Bay sockeye salmon for 30-year sample. ** and * denote the significant level <.05 and <.01, respectively.

AGE	TIME LAG YEAR	*r*	*P*	EFFECT YEAR	EFFECT ENVIRONMENT
1.2	0	.323	.075*	0	ocean
2.2	0	.335	.066*	0	ocean
	5	.369	.055*	0	ocean
1.3	0	.343	.075*	0	ocean
	1	.390	.028**	1	lake
2.3	1	.296	.100*	1	lake
	6	.325	.098*	0	ocean
	7	.441	.026**	1	lake

*: significant level < .10

**: significant level < .05

Abundance and temperature

There were no consistent relationships between the relative abundance of Kamchatka and Bristol Bay sockeye salmon and the current year and previous year SST during 1961-85 (Figures 30 & 31; Tables 4 & 5). There was no relation between immature Kamchatka fish and SST (Figures 30A & 31A; r=.01, P<.600). In contrast, there was a significant relation between the immature Bristol Bay fish and current- (r=.48, P<.001) and previous- (r=.56, P<.001) year's SST (Figures 30C & 31C). Significant relationships were also found between mature Kamchatka fish and current-year SST (r=.66, P<.001) and previous-year SST (r=.56, P<.001), respectively (Figures 30B & 31B). Similarly, significant relationships were seen between mature Bristol Bay fish and same-year SST (r=.52, P<.01). However, there was no relation between mature Bristol Bay fish and the previous-year SST (Figures 30D & 31D; r=.26, P<.30).

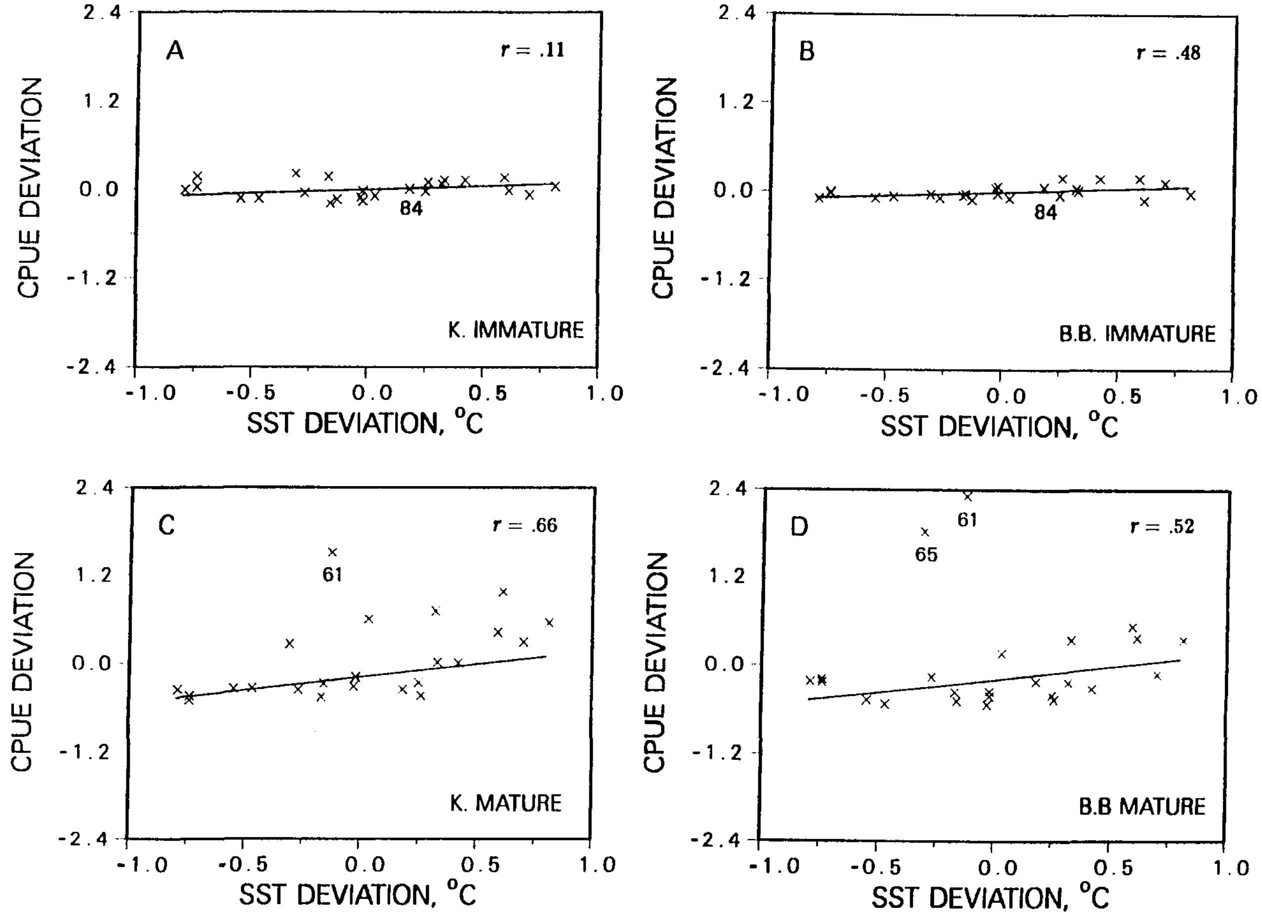

Figure 30. Linear relation between the mean May-June SST deviation and the deviation of CPUE of immature sockeye salmon in Kamchatka (A) and in Bristol Bay area (B). Linear relation between the mean May-June SST deviation and the deviation of CPUE of mature sockeye salmon in Kamchatka (C) and in Bristol Bay area (D).

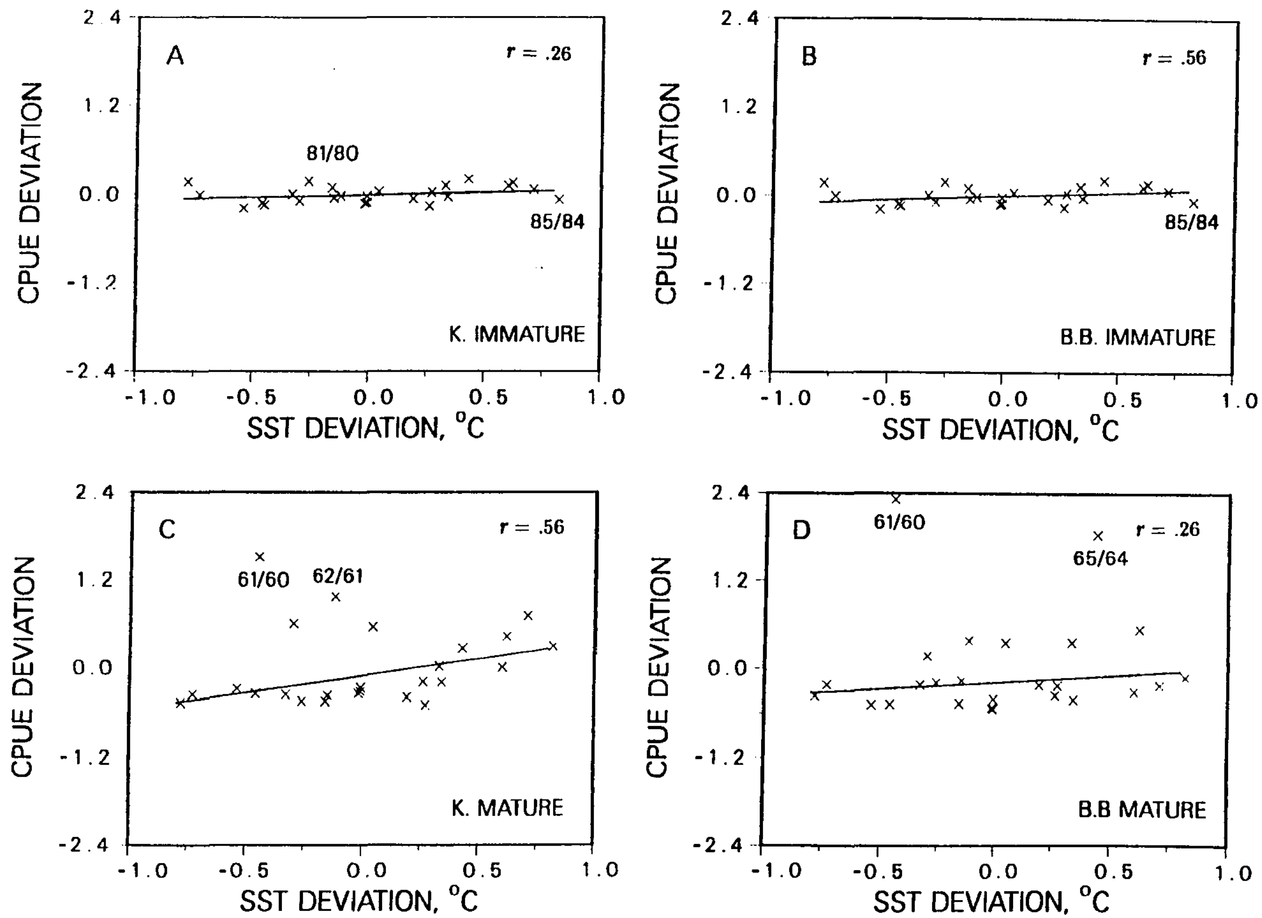

Figure 31. Linear relation between the mean May-June SST deviation for preceding years and the devation of CPUE of immature sockeye salmon in Kamchatka (A) and in Bristol Bay area (B). Linear relation between the mean May-June SST deviation for preceding years and the deviation of CPUE of mature sockeye salmon in Kamchatka (C) and in Bristol Bay area (D).

Table 4. Coefficients of linear regression between the ocean abundance (A) of sockeye salmon by maturity and the mean May-June SST from the current year in the western North Pacific, 1961-84 ($A = a + b \times SST$). N is sample size in years. ** denotes the significant level < .001.

POPULATION	N	a	b	r	F	P
Kamchatka Mature	24[1)]	-.0544	.616	.662	6.332	.001**
Kamchatka Immature	24[2)]	-.0020	.228	.114	.287	.597
Bristol Bay Mature	23[3)]	-.2800	.357	.522	7.472	.001**
Bristol Bay Immature	24[2)]	-.0002	.094	.482	6.635	.001**

1) 1961 excluded

2) 1984 and 1985 excluded

3) 1961 and 1965 excluded

Table 5. Coefficients of linear regression between the ocean abundance (A) of sockeye salmon by maturity and the mean May-June SST from the previous year in the western North Pacific, 1961-84 ($A = a + b \times SST$). N is sample size in years. ** denotes the significant level < .001.

POPULATION	N	a	b	r	F	P
Kamchatka Mature	23[1)]	-.100	.452	.560	9.169	.001**
Kamchatka Immature	25[2)]	-.003	.065	.259	1.577	.222
Bristol Bay Mature	23[3)]	-.177	.176	.255	1.577	.254
Bristol Bay Immature	25[4)]	.002	.107	.557	9.865	.001**

1) 1961 and 1962 excluded

2) 1981 and 1985 excluded

3) 1961 and 1965 excluded

4) 1985 excluded

Gonad weight of sockeye salmon in relation to abiotic factors

The relationships between the GW of age .2 and .3 fish and SST and SST_p were consistently high (*P*<.01) during the six-year study period (Figures 32 & 33; Appendix tables B-5 to B-10). However, there was no consistent relationship of GW_2 and GW_3 to SLP, SLP_p, CLD, and CLD_p. A positive and negative relation of GW_2 and GW_3 to SLP was found in 1972 and 1975, respectively. GW_2 and GW_3 were inversely related to SLP_p in 1972 and 1973, whereas only GW_2 was positively related to SLP_p in 1976. From 1971 to 1973, GW_2 and GW_3 were positively related to CLD in 1971 and 1972, but not in 1973. GW_2 and GW_3, however, showed a positive relation with CLD_p in 1971.

When the data of 1971 to 1973 were combined (Appendix Table B-11), only GW_2 showed an inverse relation to SLP, among the six abiotic factors in May. From 1974 to 1976, GW_2 in May showed a positive relation to SST and SST_p (Appendix Table B-12), while no correlation was found between GW_3 and any of the abiotic variables. When all the years from 1971 to 1976 were combined, no significant relation was found between GW_3 and the other abiotic factors (Appendix Table B-12). An inverse relation was seen between GW_2 and SLP, and a positive relation between GW_2 and SST and between GW_2 and SST_p.

In June 1971-73, GW_2 and GW_3 were inversely related to SLP_p and positively related to ST_p (Appendix Table B-14). For the 1974-76 period, GW_2 and GW_3 were positively related to SST_p, while only GW_2 was positively related to SST (Appendix Table B-15). When the six-year data were combined, GW_2 and GW_3 were positively related to SST_p and inversely related to SLP_p (Appendix Table B-16), whereas only GW_2 was positively related to SST.

The outcomes in July were somewhat different from May and June. From 1971 to 1973, only GW_2 and GW_3 were related to CLD (Appendix Table B-17). No relation was found between GW_2 and GW_3 and the three abiotic variables in 1974 to 1976 (Appendix

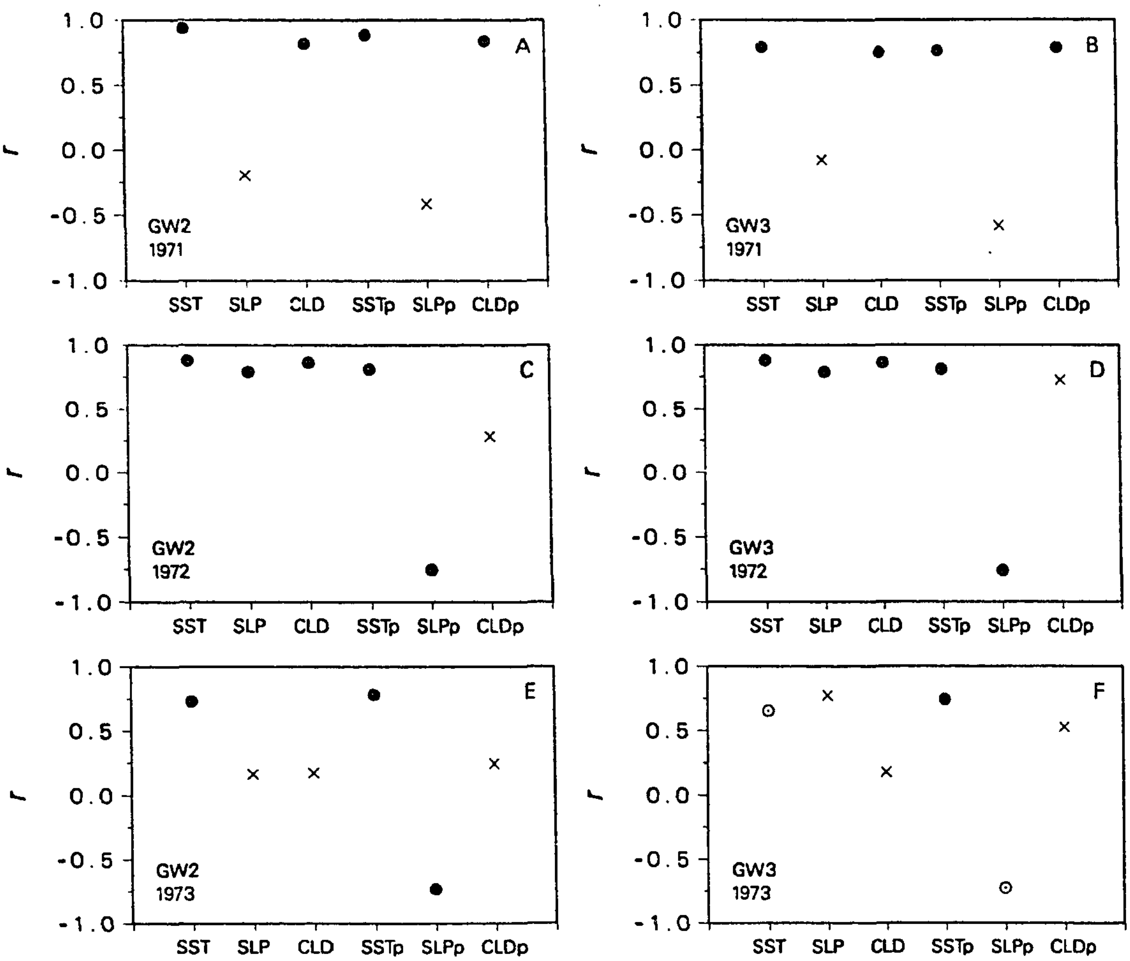

Figure 32. Correlation coefficient of abiotic factors to gonad weight of ocean age .2 (GW_2) and .3 (GW_3) sockeye salmon in 1971 (A & D); 1972 (B & E); and 1973 (C & F). Current and preceding month sea surface temperature (SST & SST_p), sea level pressure (SLP & SLP_p), and cloudiness (CLD & CLD_p). (Symbols: ● ,$P < 0.001$; ⊙ , $P < 0.01$; × , not significant).

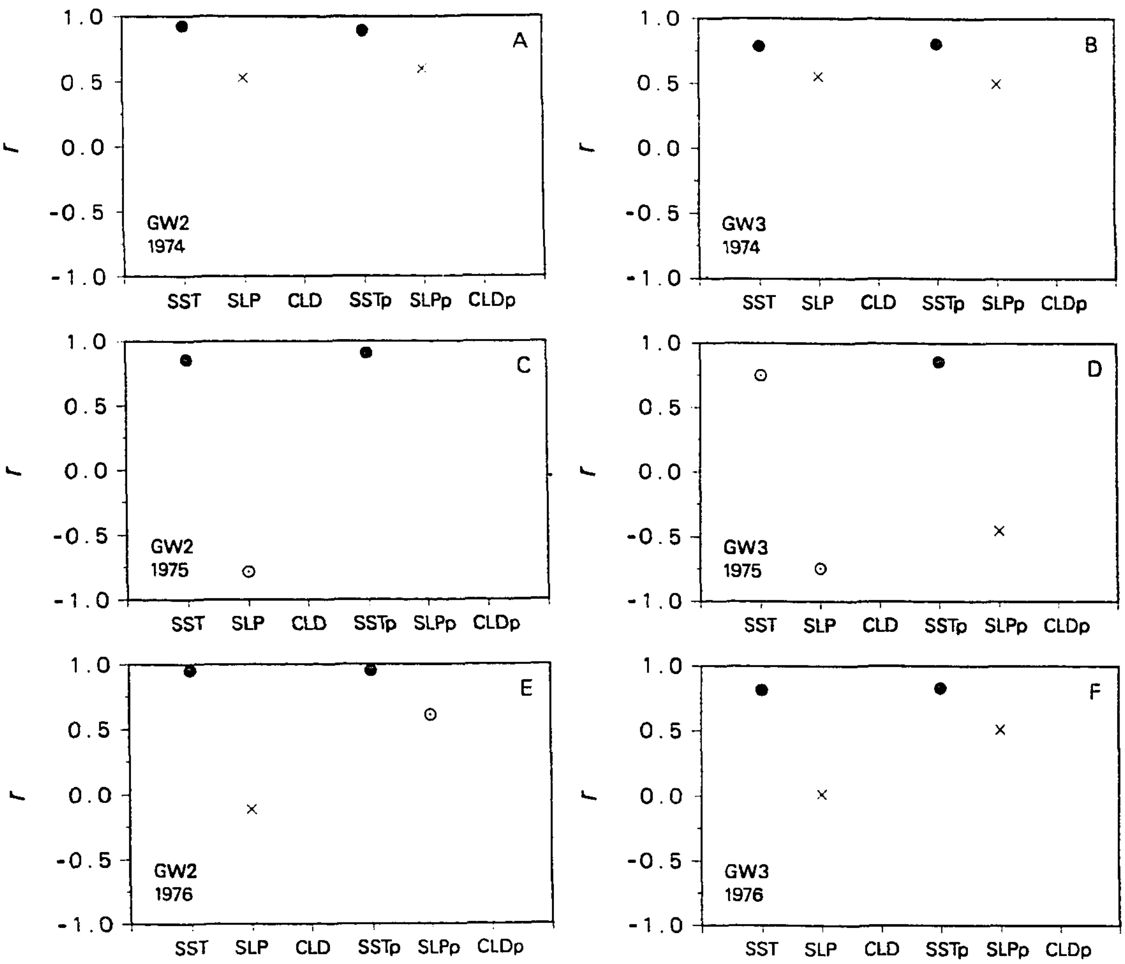

Figure 33. Correlation coefficient of abiotic factors to gonad weight of ocean age .2 (GW_2) and .3 (GW_3) sockeye salmon in 1974 (A & D); 1975 (B & E); and 1976 (C & F). Current and preceding month sea surface temperature (SST & SST_p), sea level pressure (SLP & SLP_p), and cloudiness (CLD & CLD_p). (see Figure 32 for symbol definitions).

TableB-18). The results for the six-year period showed no significant relation ($P<.01$) of GW_2 and GW_3 to the abiotic factors (Appendix Table B-19).

In 1971-73, GW_2 and GW_3 were significantly related ($P<.01$) to all the abiotic factors (Figures 34A & 34B; Appendix Table B-20). An inverse relation was found between GW_2 and SLP_p (r=-.61), and between GW_3 and SLP_p (r=-.64). GW_2 and GW_3 were positively correlated with CLD and CLD_p, but not with SLP. GW_2 and GW_3 were to a high degree related to SST_p. During 1974-76, GW_2 and GW_3 only yielded a positive relation with SST and SST_p (Figures 34C & 34D; Appendix Table B-21). In the 1971-76 period, GW_2 and GW_3 showed a positive relation with SST and SST_p (Figures 34E &34F; Appendix Table B-22). An inverse relation was found between GW_2 and GW_3 and SLP_p.

DISCUSSION

The fluctuation of wind stress curl in the northeastern North Pacific showed 3.1 and 5.3-year cycles, and the latter cycle coincided with a 5-year cycle in abundance of sockeye salmon in the Bristol Bay area. Further, cross-correlation analysis revealed that the returns of the four major age groups were in most instances significantly correlated with the curl mostly at 0-year lag. In the northeastern North Pacific, wind curl (cyclonic wind) tends to spiral the ocean counterclockwise, causing upwelling in the oceanic region and downwelling along the coastal boundaries (Royer, 1985). Since upwelling carries nutrients from the lower layer, primary production is likely to increase. Subsequently, the abundance of zooplankton and other food organisms will increase. However, since nutrient concentrations are never limited in the Gulf of Alaska (Frost, 1983), other mechanisms may be involved in causing high zooplankton abundance. According to Parsons and LeBrasseur (1968), there is an inverse relationship between the zooplankton growth rate and depth of the mixed layer in April at Ocean Station P, which implies that the wind stress curl inducing mixing of the upper water layer may indirectly affect the zooplankton abundance. Under circumstances of increased food abundance, growth and fecundity of sockeye salmon may be increased, and increased fecundity will produce a larger number

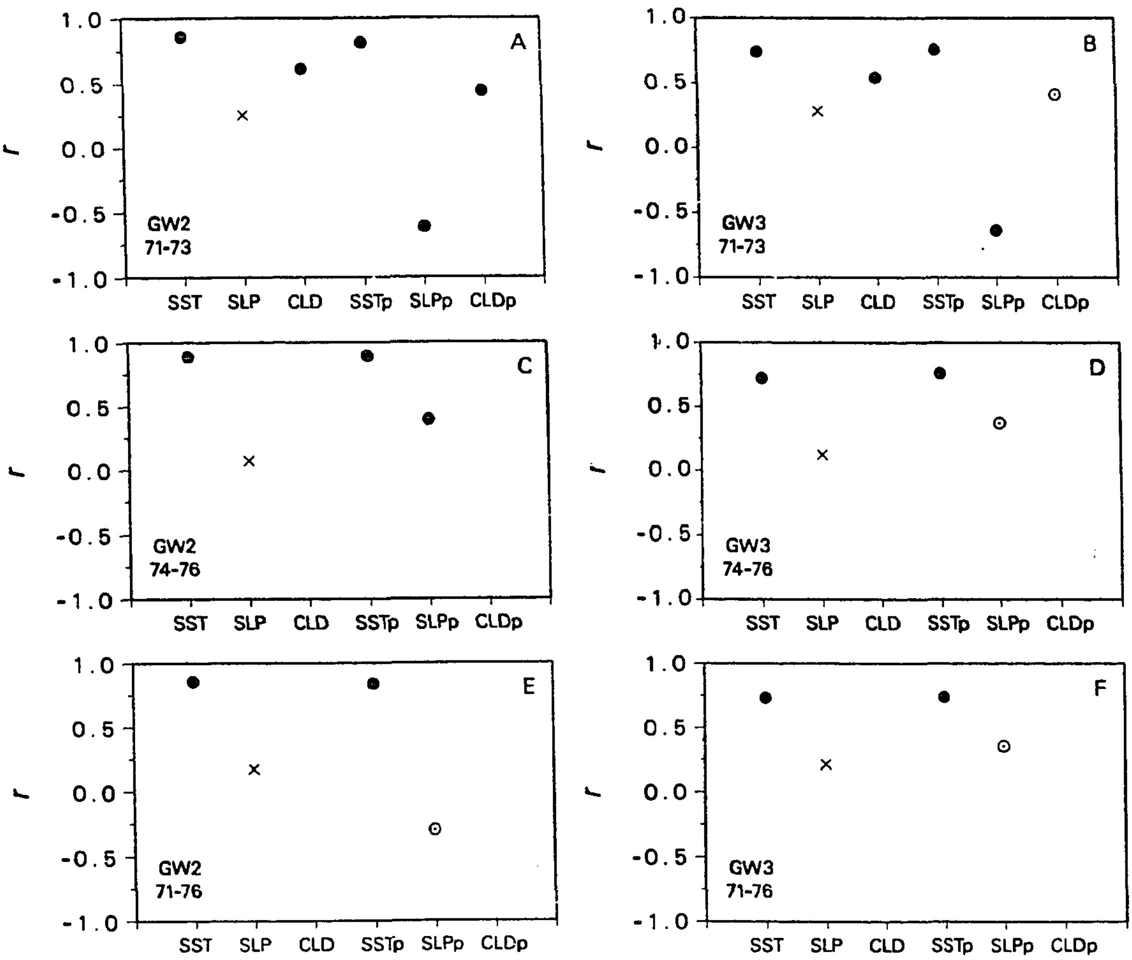

Figure 34. Correlation coefficient of abiotic factors to gonad weight of ocean age .2 (GW_2) and .3 (GW_3) sockeye salmon in 1971-73 (A & D); 1974-76 (B & E); and 1971-76 (C & F). Current and preceding month sea surface temperature (SST & SST_p), sea level pressure (SLP & SLP_p), and cloudiness (CLD & CLD_p). (see Figure 32 for symbol definitions).

of offspring, resulting in a high return of sockeye salmon five years later. Figure 35 is the proposed model based on the above discussion.

The cyclic dominance of Bristol Bay sockeye salmon appears to be more related to their earlier life stage in the freshwater system. High spawner returns increase primary production through the biogenic processes generated from the spawner's carcasses (Donaldson, 1967; Mathisen, 1972; Richey *et al.*, 1975). Since sockeye salmon die immediately after spawning, the cyclic return of Bristol Bay sockeye salmon every fifth year will increase nutrients in the lake, and thus increase the primary production one year after their return, provided that this one-year lag is necessary for the processes of biogenic nutrients from the decomposed spawner carcasses. Primary production calculated from the chlorophyll α concentration in the Iliamna Lake, Alaska, showed a peak every five years, one year after the peak return of the spawner (Poe, 1980), which supports the above assumption. Since zooplankton abundance in the Iliamna Lake is increased by primary production, the chances for survival of sockeye salmon fry will increase. The increased number of fry will reflect the number of spawners two to three years after the smolt move to the sea.

The mean May-June SST in the west habitat is positively related to the ocean abundance of mature sockeye salmon. In analysis of temperature deviations, the current year versus CPUE indicated that 1961 was an exceptional year for Kamchatka fish, and 1961 and 1965 were exceptional years for Bristol Bay fish. Likewise, the values between the temperature deviations of the previous year and CPUE, were extreme in 1961 and 1962 for Kamchatka fish, and in 1961 and 1965 for Bristol Bay fish.

During the 1968-80 period, the temperature in the west habitat showed a declining trend. This decline coincides with a decreased trend of the ocean abundance of mature Kamchatka sockeye salmon. In this period, the abundance of Kamchatka fish was higher than Bristol Bay fish. This suggests that the decrease of the ocean abundance of Kamchatka fish is related to the decrease of water temperature within the habitat.

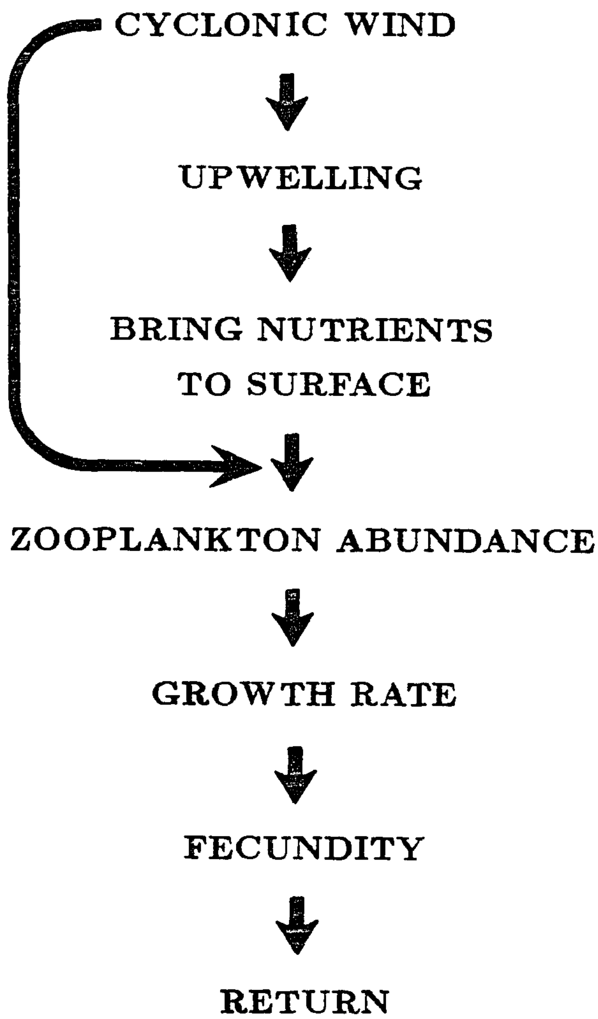

Figure 35. Model on the interrelation of wind stress curl in the Gulf of Alaska to the high return of Bristol Bay sockeye salmon.

The low CPUE of Bristol Bay sockeye salmon during 1971-77 appears to be coincidental with the decrease of the SST in the west habitat. Thus, low temperature in the west habitat might delimit the westward distribution of Bristol Bay fish. In contrast, the high CPUE of Bristol Bay fish after 1978 is in agreement with the increase of the SST in the east habitat.

Because mature fish (age .2 and .3) were immature in the preceding year (age .1 and .2), the relation between the preceding year's temperature and the CPUE of mature sockeye salmon from both populations appears to contradict the relation between the same year's temperature and the CPUE of immature sockeye salmon. However, since the Japanese high seas fishery targeted mainly adult fish, and the immature fish were taken incidentally in the gillnet operation, it is impratical to interpret the relation between the temperature and the CPUE of immature fish. Insignificant correlation found between the preceding year's temperature and the current year's CPUE of Bristol Bay sockeye salmon might be due to either the relatively lower ocean abundance of this fish, or lower water temperatures in the west habitat.

During 1971-76, monthly SST showed an increase trend from east to west and from north to south in area 1. The difference of temperature at the same latitude between years was small in April and May, but was large in June and July. Higher variation of temperature was mostly seen at 45°N. Similar results have been reported by Dodimead *et al.* (1963) and Favorite *et al.* (1976). In the Subarctic Pacific, the Subarctic Boundary separates the cold diluted Subarctic waters from the warm and saline Subtropic waters (Favorite *et al.*, 1979). This boundary is often associated with the thermal front, which occurs near 45°N and causes great difference of temperature at either side (Uda, 1963; Kitano, 1966). The Polar Front is given as a transition belt characterized by salinity and temperature structures between 42°N and 47°N (Uda, 1963). The relation between the position of this thermal front and the southernmost distribution of sockeye salmon is discussed in next chapter.

SST showed the most significant positive relation to the gonad weight of fish. This relationship suggests that the gonad weight of sockeye salmon increases with the increase of water temperatures. Therefore, sockeye salmon mature faster in warm water than in cold water. The gonad weight of sockeye salmon increased with the increasing latitude within same month, but same month SST decreased latitudinally. This is caused by the difference in geographic distribution of sockeye salmon of different stages of maturity, *i.e.* elder fish with heavy gonad weights live in more northern waters than younger or less mature fish.

SLP and CLD exhibited less significant relationships to the gonad weight of sockeye salmon. In the Northern hemisphere, low pressure piles up water at its center causing upwelling, whereas high pressure expells water from its center toward the periphery, bringing downwelling (Royer, 1985). Normally, low pressure is accompanied by cloudy conditions and strong wind cooling the water at its periphery (Lockwood, 1985). Conversely, high pressure is associated with clear days and mild winds resulting in surface waters warming. Low pressure may slower the maturity of sockeye salmon by causing lower water temperatures. High pressure occurring in summer in the North Pacific creates clear sky conditions over the ocean which allows more light to penetrate into waters. With enough light and nutrients, photosynthesis is accelerated (Parsons *et al.*, 1984). Thus, areas with high photosynthesis attract zooplankton in the ocean. In this case, sockeye salmon may have a better chance of increasing their growth and fecundity.

The correlation between gonad weight of sockeye salmon and cloudiness was insignificant. Possibly, the spatial and time scales used in this study were too broad. Further study must be made employing smaller spatial and time scales.

In conclusion, one can state from above observations and analysis that there is a close relation of the wind stress curl to return of sockeye salmon, and relationship of SST to ocean abundance and gonad weight of sockeye salmon.

SUMMARY

Spectral analysis of the fluctuation of mean wind stress curl (calculated on a 25-month running average) for a 30-year period exhibited 3.1- and 5.3-year peaks, and the latter peak coincides with the 5-year peak return of Bristol Bay sockeye salmon. Cross-correlation analysis revealed that wind stress curl generally leads return at 0- and 1-year lag, which signify the year of spawning migration and the first year of freshwater residence of sockeye salmon.

Mean May-June SST in the west habitat was positively correlated to the ocean abundance of sockeye salmon, and explained 56-66 % of the variation of immature and mature fish from the Kamchatka area, and 56 % of mature fish from the Bristol Bay area.

During 1971-76, monthly SST showed an eastward increasing trend in area 1. The annual difference of temperature at the same latitude was small in April and May, and became great in June and July. Higher variance of temperature was observed at 45°N. Monthly SLP fluctuated depending upon the position and duration of major prevailing high and low pressure systems. The monthly mean CLD was about 6 *octa*, and did not show any obvious trend during this period.

During the six-year study period, the gonad weight of age .2 and .3 sockeye salmon was highly correlated to SST and SST_p.

Chapter IV: Distribution of Sockeye in Relation to Sea Surface and Subsurface Hydrography

INTRODUCTION

The findings in the previous chapters revealed that the relative ocean abundance of sockeye salmon varied widely during the 1961-85 period, with the lowest abundance occurring in 1971-76. Further, deviations in ocean abundance of sockeye salmon were related to deviations in mean May-June SST in the west habitat. The low ocean abundance of sockeye salmon in 1971-76 is likely related to the change of sea water temperature in the west habitat. In addition to water temperature, the subsurface hydrostructures may also have affected the distribution of sockeye salmon during 1971-76. Thus, this chapter attempts to analyze (1) the hydrographic structures of the upper water column; (2) the water temperature condition in the upper 50 *m* water layer; (3) the distribution pattern of sockeye salmon at sea; and (4) the relation between the geographical and seasonal shift of surface isotherms to the oceanic distribution of sockeye salmon.

The distribution and migration of fish are known to be related of influenced by oceanographic features, water temperature being the most easily observed (Laevastu and Hayes, 1981). Therefore, many studies have been conducted which relate the occurrence and behavior of fish with sea water temperature and its fluctuation.

Variations in water temperature have been shown to influence the distribution and movement of sockeye salmon at sea (French *et al.*, 1976). Sockeye salmon inhabit the upper 50 *m* water layer (Manzer *et al.*, 1964; Machidori, 1966; Kikuchi and Tsujita, 1977) but are confined by the thermocline in the Gulf of Alaska. Favorite (1967) found a relationship between their distribution in the northeastern Pacific and the temperature-minimum stratum (< 4°C) at 150 *m* depth. The southern and eastern limits for sockeye salmon lay between 6°C and 7°C surface isotherms (Fisheries Research Board of Canada, 1966). Seasonally, mature fish occur in waters at a temperature of 2-3°C in winter, and 4-6°C in June, but immature fish inhabit waters at 5-6°C in winter, and at 7-11°C in

August (French *et al.*, 1976). The southern limit of sockeye salmon corresponds to areas with temperatures of 7-8°C in winter and 12-13°C in summer.

For Kamchatka sockeye salmon, young fish were mainly found at the 12°C surface isotherm in coastal region (Birman, 1962). In April, adult fish were distributed in waters with temperatures of 1.5-6.0°C (Birman, 1964). Adults were located at the 6°C surface isotherm in early May.

DATA SOURCES AND METHODS

To examine the relationship between the occurrence of sockeye salmon and temperature and salinity distribution, data were obtained for three years, two cold (1971 and 1973) and one warm (1982) years, and two transects. Sockeye salmon catch data and water temperature data were obtained from Japanese records (Fishery Agency of Japan, 1971 to 1976). The study area in this chapter is the region between 40°N-52°N and 160°E-170°W, and is designated as area 3 (Figure 5). Temperature and salinity data were obtained from data records of oceanographic observations (Hokkaido University, 1971; 1982) made along 180° transect, and also from Mishima (1974) for the 167°30'E transect.

The relative ocean abundance of sockeye salmon at each station was calculated from

$$\bar{C} = \sum_{i=1}^{4} n_i \times c_i / N \tag{10}$$

where $\bar{C}$ is the mean CPUE at each station, n is the number of *tan* of gillnet mesh size i (one of four meshes; 100, 106, 115, and 121 *mm* in stretched measure), c is the CPUE by mesh size i, and N is the total number of net in tan. c_i was calculated from

$$c_i = t_i / f_i \tag{11}$$

where t is the number of fish caught by mesh size i, and f is the number of nets with mesh size i.

The CPUE was given as the number of fish per 100 *tan* (equal to $\bar{C}$ times 100) and transformed into logarithmic value as C_t.

$$C_t = \log(\bar{C} \times 100 + 1) \tag{12}$$

The frequency distribution of C_t was used to examine the seasonal variation in abundance of sockeye salmon for the months May through July. To represent relative abundance, each value of CPUE of was grouped into one of four categories: (1) $C_t>2.004$; (2) $2.004 \geq C_t > 1.041$; (3) $1.041 \geq C_t > 0$; and (4) $C_t=0$ [This corresponds to (1) $\bar{C}>1.0$; (2) $1.0 \geq \bar{C} > .1$; (3) $.1 \geq \bar{C} > 0$; and (4) $\bar{C}=0$, respectively]. In this chapter $C_t>2.004$ was used as index of where the major abundance of sockeye salmon occurred.

Sockeye salmon mainly inhabit the upper 50 *m* water layer in the northwestern North Pacific (Kikuchi and Tsujita, 1977). Thus, the sea water temperature mean and range in area 3 were calculated for 0, 10, 20, 30, and 50 *m* depth layers to compare monthly and annual differences where the fish might occur. Water temperatures at high CPUE ($C_t>2.004$) were used to examine the relation between temperature and high abundance of fish.

The contouring of isothermal distribution of SST was conducted using the Universal Kriging (UK) method (Davis, 1986). The UK method, commonly used in geostatistics, is designed so that scattered data points of SST generate a regular grid point with no error estimation. Therefore, this method is appropriate for the data type used here since the position of the salmon research vessels varied monthly.

Every 0.5°C interval was calculated using the semivariagram estimation and UK program (Skrivan and Karlinger, 1980). The grid point generated by UK was then contoured with a Surf II contouring subroutine (Sampson, 1986), the surface isotherms in unsampled areas estimated. The C_t distributions were overlapped on the temperature contour map.

RESULTS

Subsurface features in the Subarctic Pacific

The vertical profiles of temperature above 200 *m* depth along 167°30'E were different for the years 1971-73 (Figure 36). In 1971 the Subarctic Boundary, as defined by 34°/oo isohaline (Dodimead *et al.*, 1963), was at 42°N, where the 5-10°C isotherms occurred (Figure 36A). In 1972, the front was bounded by 6-10°C temperature isotherms, which occurred above 100 *m* depth layer at 43°N (Figure 36B). In 1973, a sharp temperature gradient (4-9°C) formed the front between the surface and 150 *m* near 42°N (Figure 36C). Warm water (> 11°C), was located above 150 *m* depth south of 41°N in 1971, above 50 *m* depth near 42°N in 1972, and near surface at 41°N in 1973. Cold water in the upper layer (< 3°C) was seen north of 46°N in 1971, north of 47°N in 1972, and north of 45°N in 1973. In 1972, water < 2°C prevailed in the upper 150 *m* near 47°N-49°N, whereas in 1971 this cold water was not present. In 1973, water < 2°C appeared above 150 *m* between 49°N and 50°N.

Along the 180° transect, the Subarctic Boundary was located near 45°N in July 1971 where the 12.5-14.5°C isotherms occurred (Figure 37), and in June 1982 at 41°N-42°N where isotherms of 9-11°C occurred (Figure 38). Warm water (> 11°C) at the surface extended as far north as approximately 48°N in 1971, and around 43°N in 1982. Cold water (< 3°C) occurred below 150 *m* depth north of 48°N in July 1971, but was seen near 47°N below 100 *m* depth in 1982.

Water temperature of the upper 50 *m* layer

The May mean temperature and range was small throughout the upper 50 *m* depth in area 3 (Figure 39; Appendix Table C-1). The mean temperature at all depths was 3.5-4.6°C during 1971-73, 5.5°C in 1974, and 4.5°C in 1975 and 1976. The temperature range varied from 5.5 to 9°C, and was narrowest in 1971 (Figure 39A) and widest in 1974

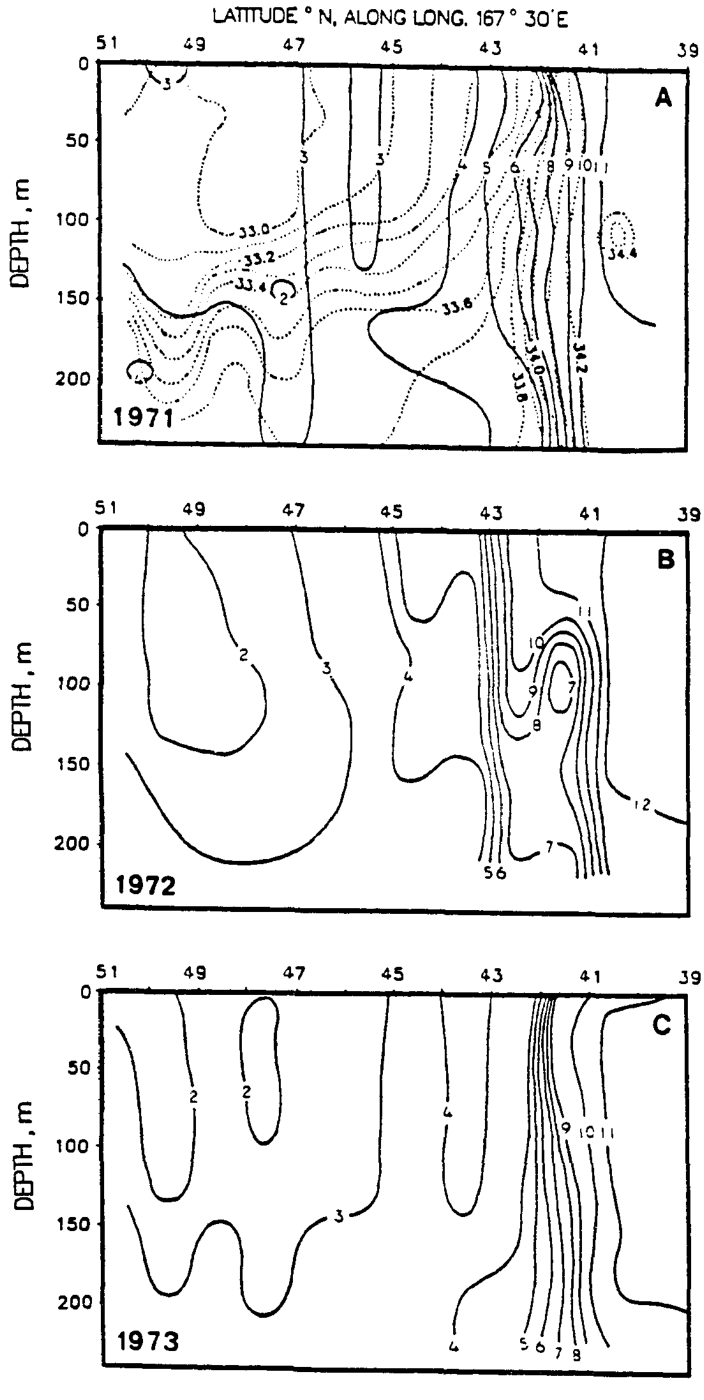

Figure 36. Vertical profiles of temperature and salinity along long. 167°30'E in April 1971 (A); 1972 (B); and 1973 (C) (from Mishima, 1974).

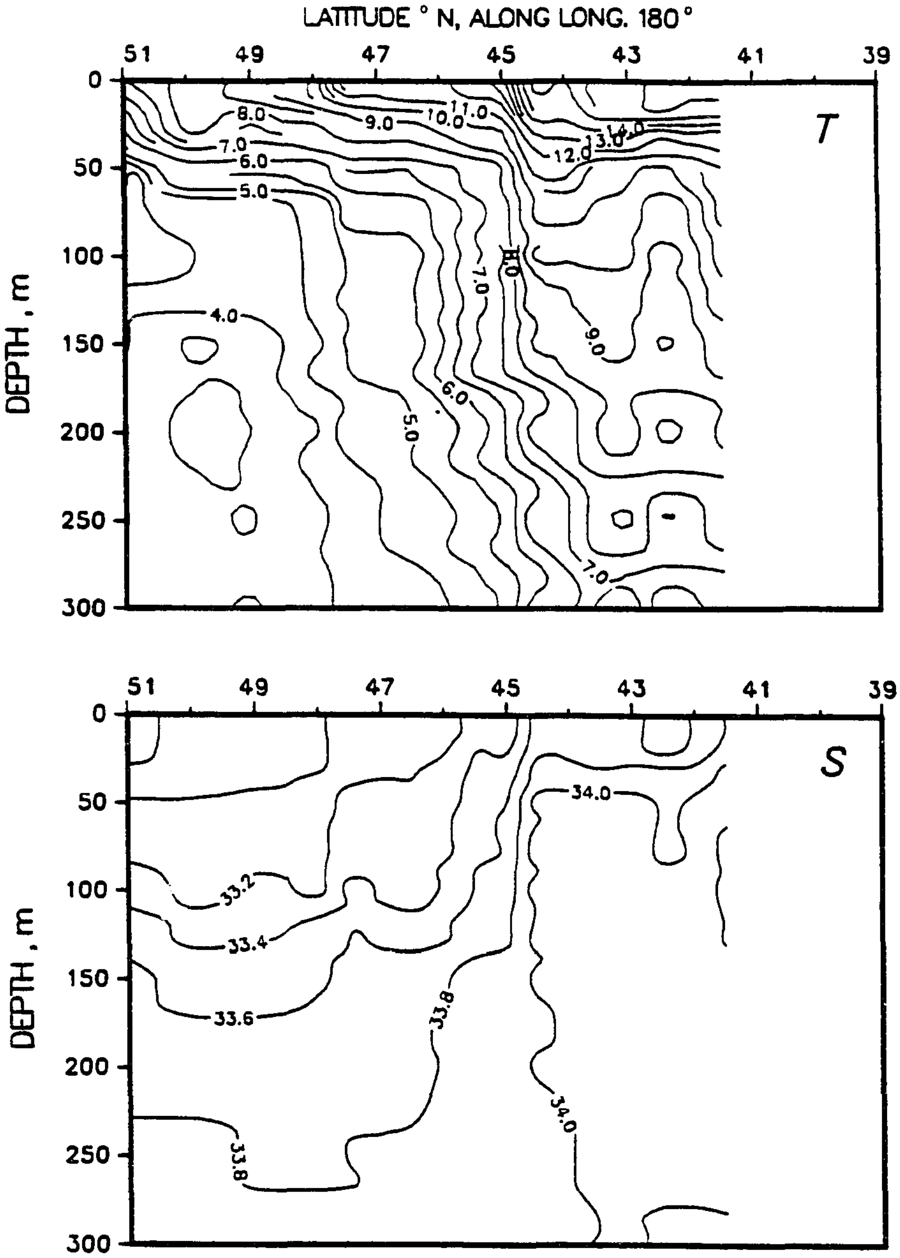

Figure 37. Vertical profiles of temperature and salinity along long. 180°, July 1971.

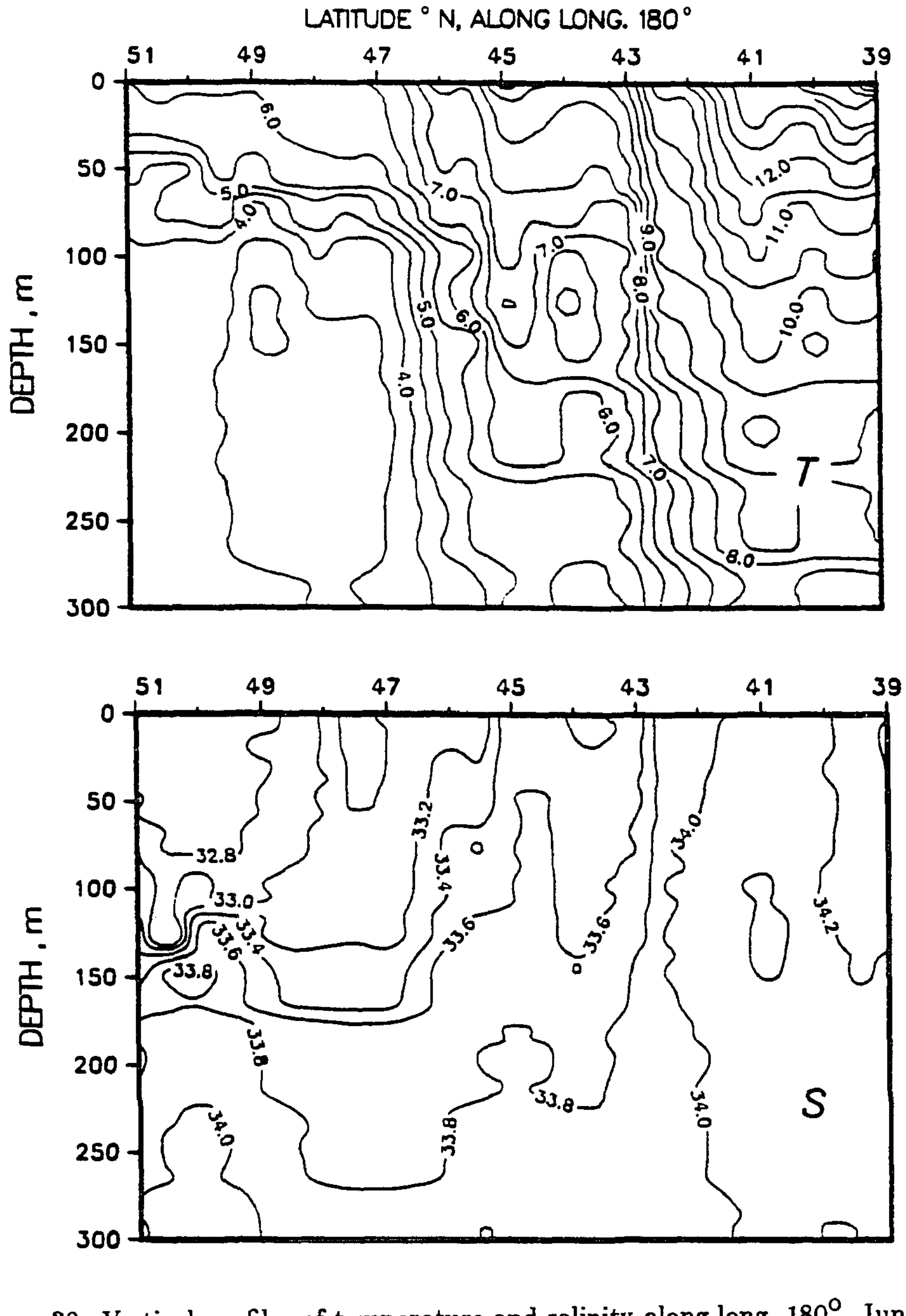

Figure 38. Vertical profiles of temperature and salinity along long. 180°, June 1982.

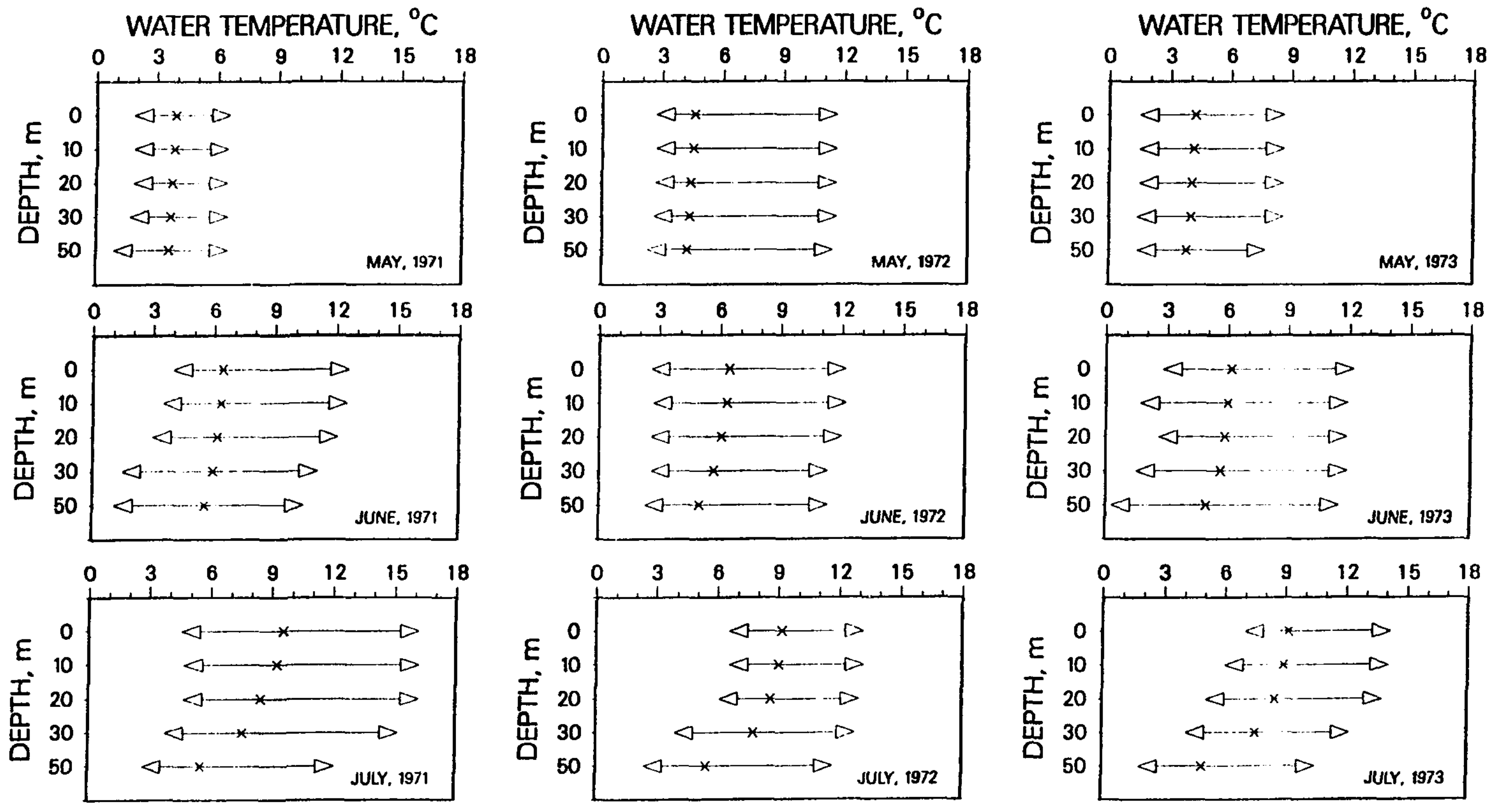

Figure 39A. Water temperature in the upper 50 m layer of area 3 for May-July, 1971-73

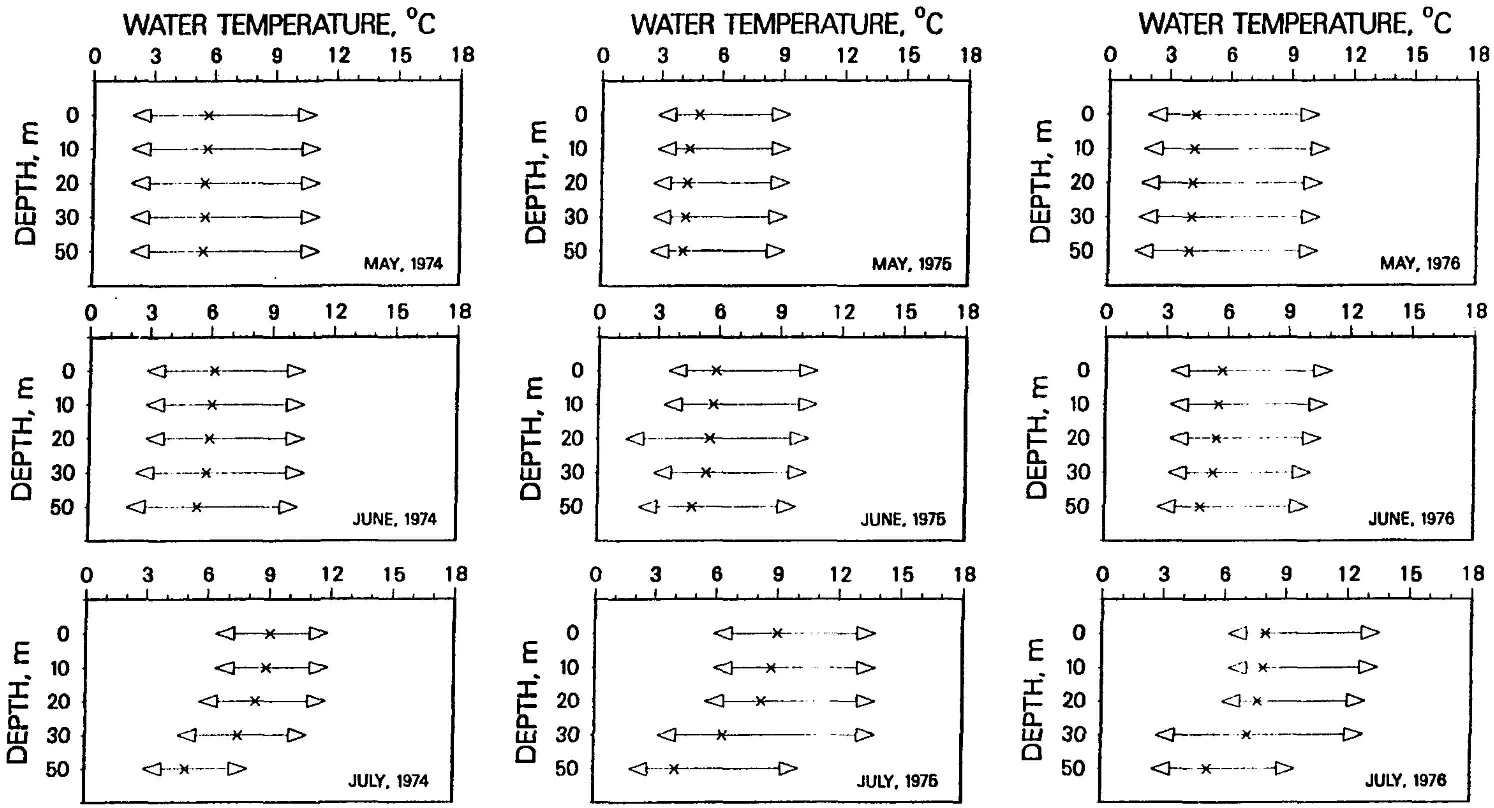

Figure 39B. Water temperature in the upper 50 m layer of area 3 for May-July, 1974-76.

(Figure 39B). In June and July a thermocline established between 20-30 *m* depth above which were relatively high temperatures.

Abundance of sockeye salmon in relation to sea water temperature

Sockeye salmon CPUE (C_t) varied from 1.19 to 1.78 in May-July 1971-76 and indicated a decline in abundance with season, except in 1974 (Figure 40). In 1974, the abundance of sockeye salmon was higher in June than in May.

Throughout the upper 50 *m*, the mean (3.7°C-4.4°C)and range (1.8-7.8°C) of temperature with a high CPUE of fish in May was vertically similar (Figure 41; Appendix Table C-2). In June and July, the temperature where a high CPUE occurred was above 30 *m*. The temperature range was narrower at all depths in June and July than in May, the narrowest occurred in 1974.

Distribution of sockeye salmon in relation to surface isothermal distribution

The percentage of stations with catches of sockeye salmon decreased with season (Table 6), indicating fish catch decreased with advanced season which can not be easily seen in Figures 42-47. There was a sharp temperature gradient of surface isotherms during May-July 1971-76 in area 3 (Figures 42-47). This temperature gradient was located in the southern region in May and shifted northward during June and July. Most of the stations with the highest CPUE (circles in Figures 42-47) are found near the 3-6°C isotherms between 44°N-46°N and 160°E-170°E in May, except in 1971, where a high CPUE occurred north of 46°N. Except in 1976, no fish were taken south of 43°N. In June, mean CPUE spread widely north of 44°N along 4-6°C isotherms. No fish were caught south of 44°N, except in 1974 and 1975. In July, mean CPUE occurred along the 7-8.5°C surface isotherms north of 50°N. No fish were caught north of 44°N where temperatures were greater than 9°C, except in 1971 and 1972.

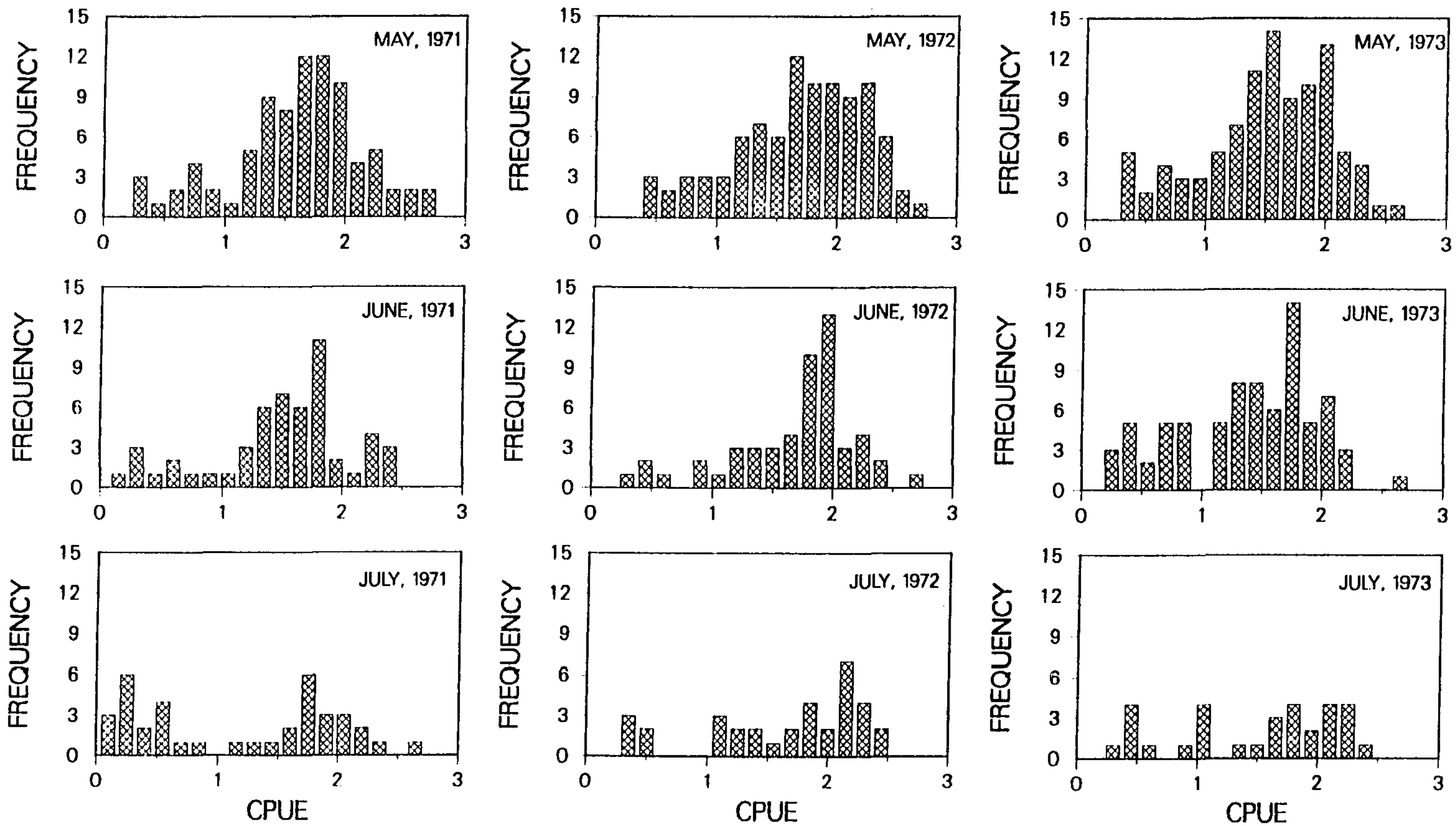

Figure 40A. CPUE (C_t) of sockeye salmon as frequency of occurrence in area 3 for May-July, 1971-73.

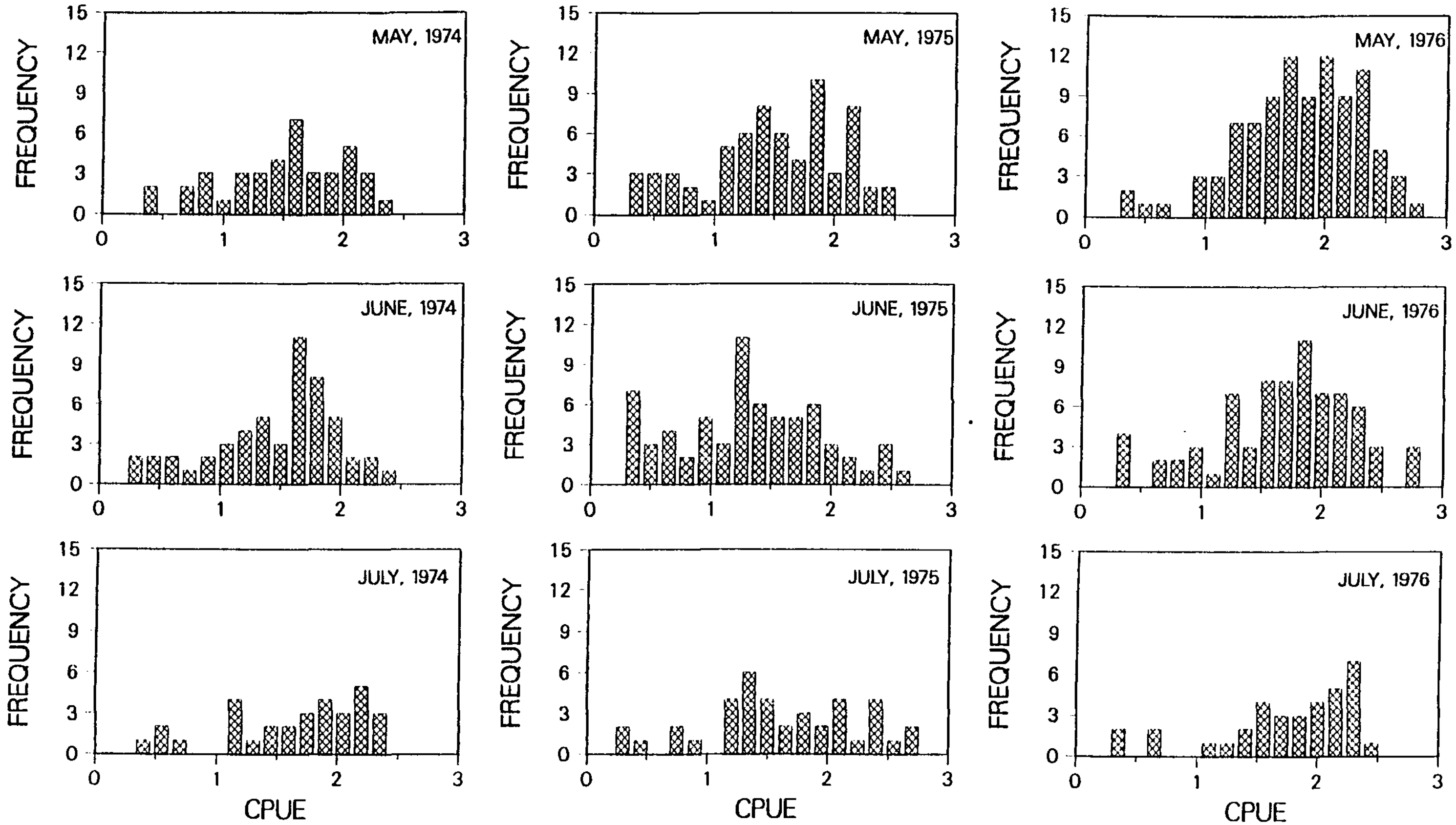

Figure 40B. CPUE (C_t) of sockeye salmon as frequency of occurrence in area 3 for May-July, 1974-76.

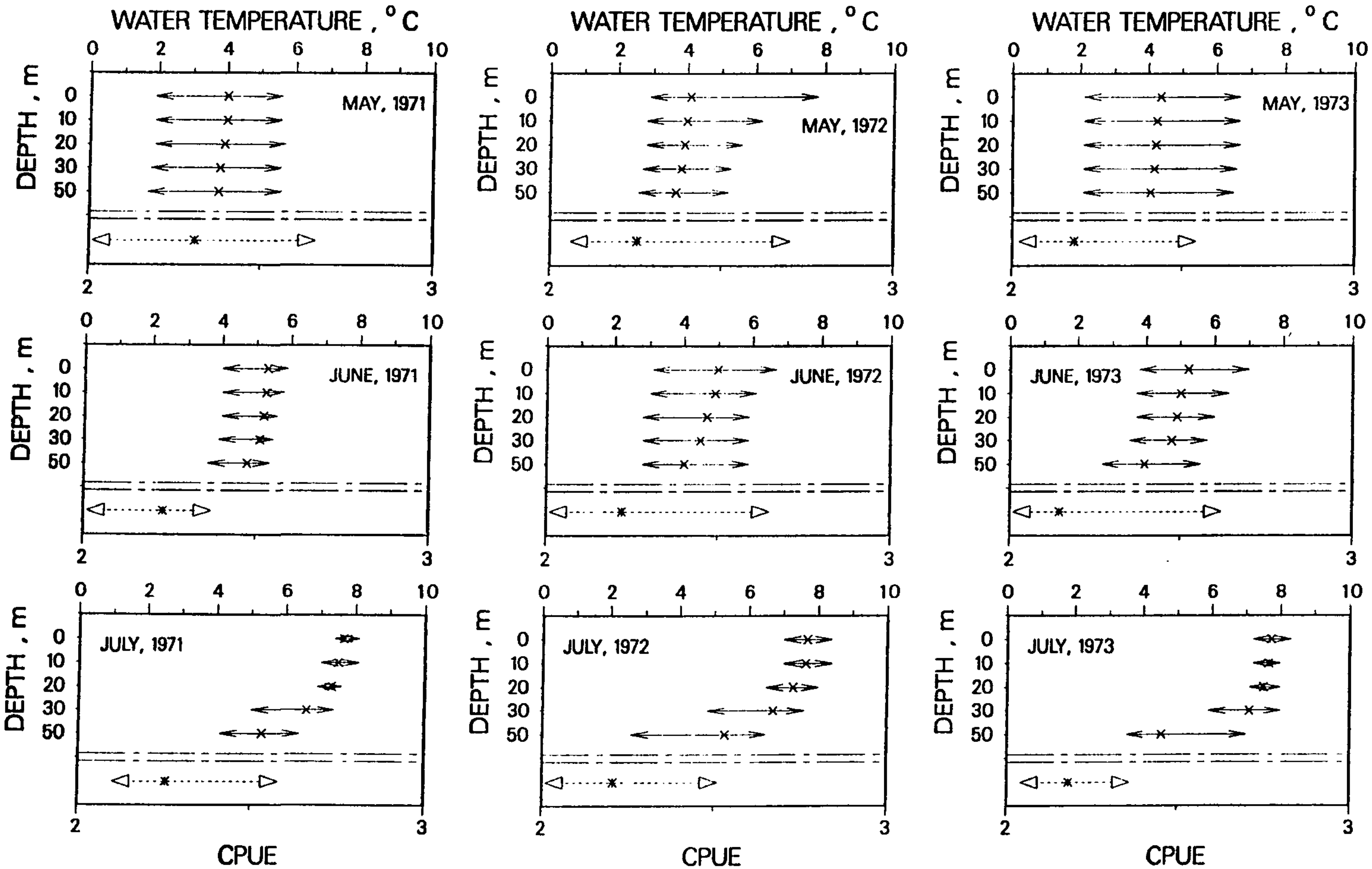

Figure 41A. Water temperature in the upper 50 m layer with CPUE (C_t>2) of sockeye salmon in area 3 for May-July, 1971-73. Upper portion of each figure is temperature and lower portion is CPUE.

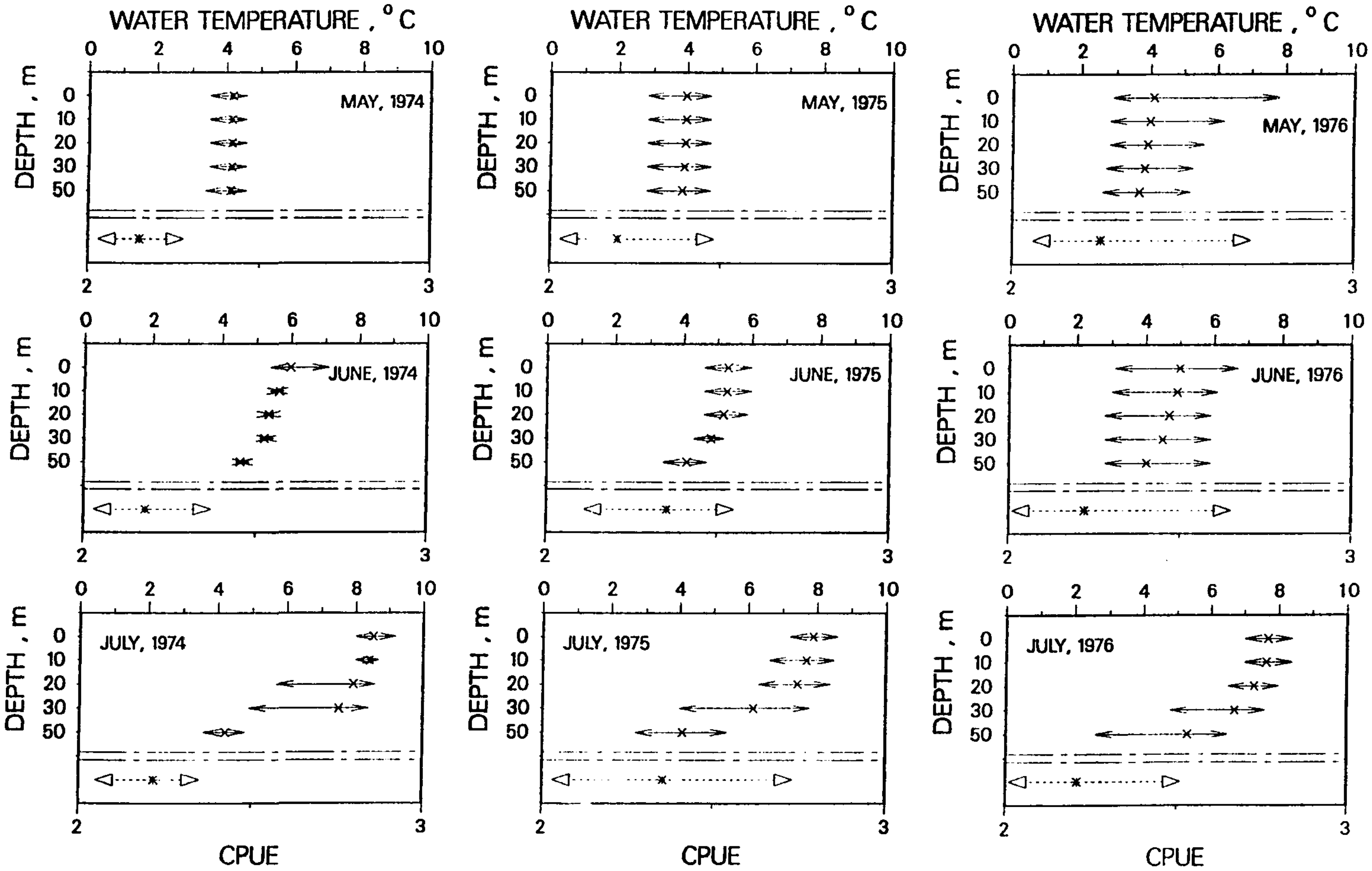

Figure 41B. Water temperature in the upper 50 m layer with CPUE ($C_t > 2$) of sockeye salmon in area 3 for May-July, 1974-76. Upper portion of each figure is temperature and lower portion is CPUE.

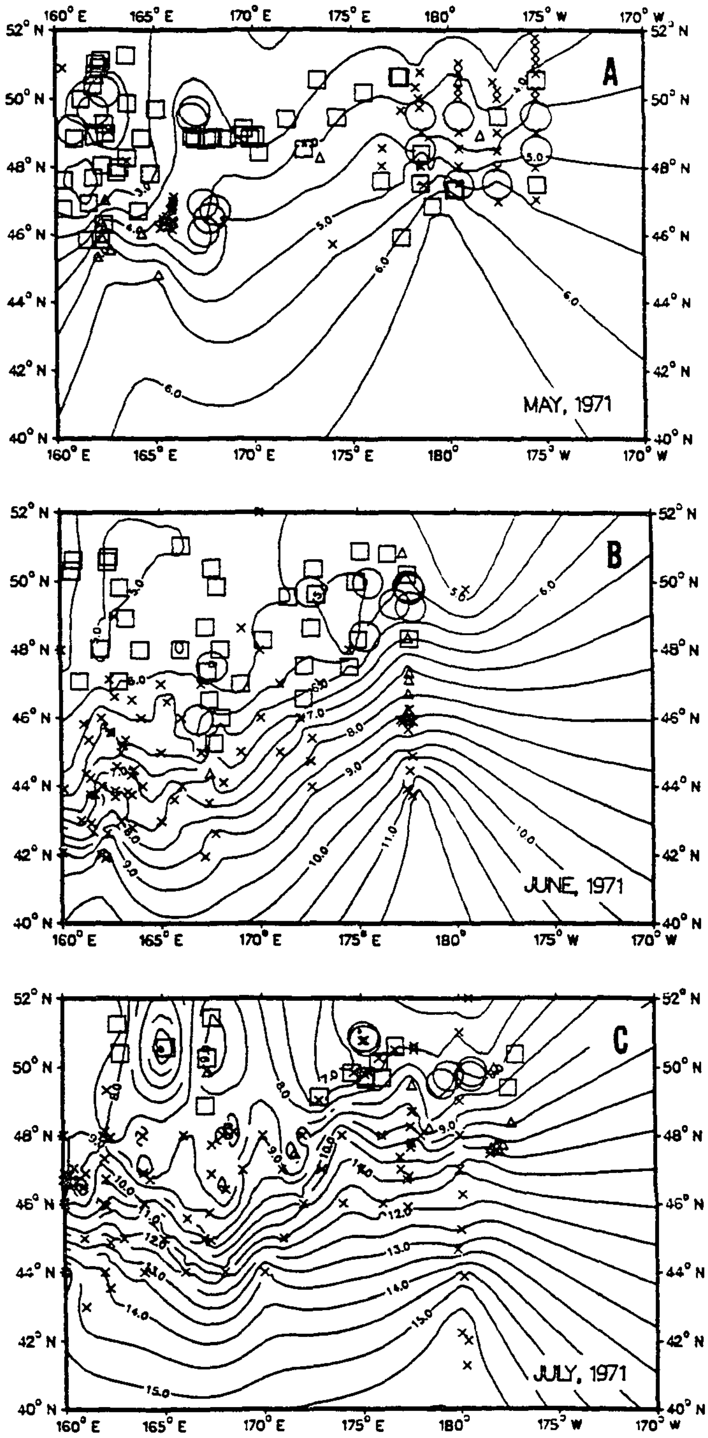

Figure 42. Surface isothermal distribution and mean CPUE (C_t) of sockeye salmon in area 3 for May (A); June (B); and July (C), 1971. (Symbols: ○, C_t>2.004; □, 2.004>C_t>1.041; △, 1.041>C_t>0; ×, C_t=0).

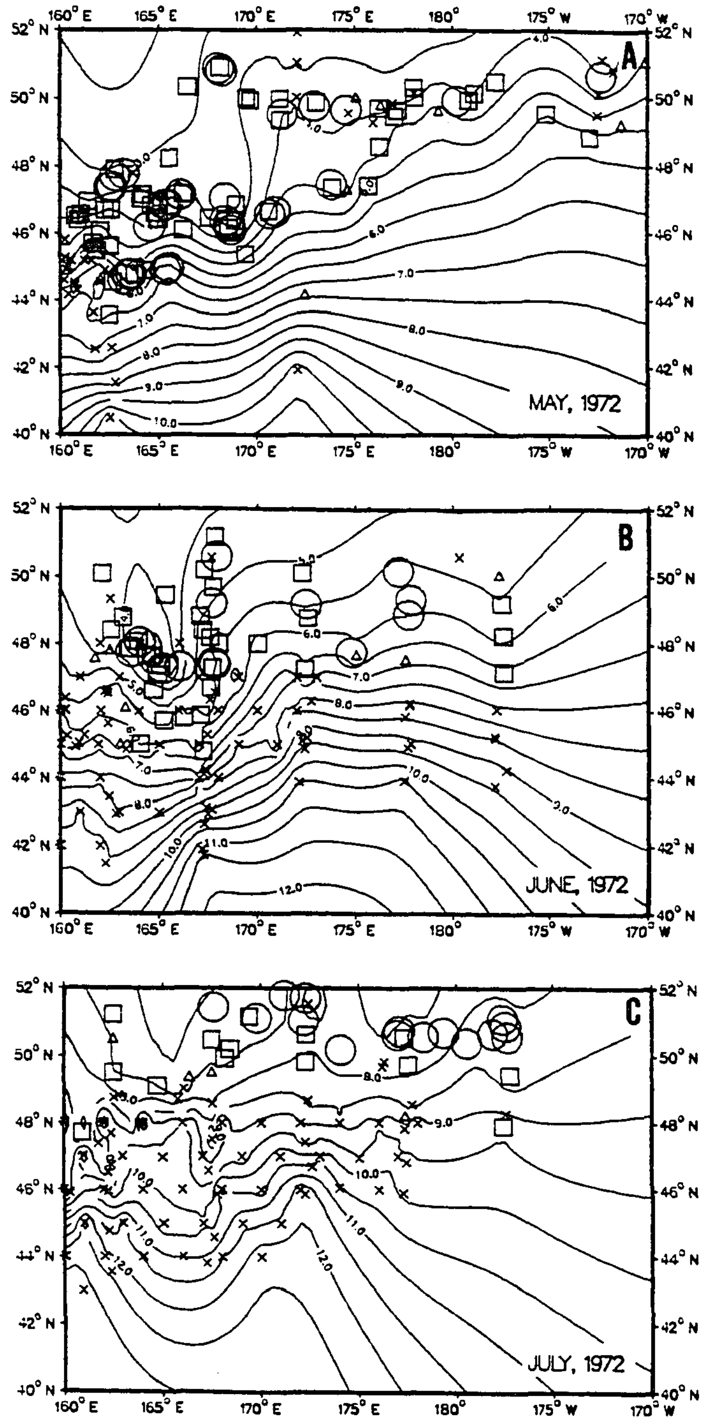

Figure 43. Surface isothermal distribution and mean CPUE (C_t) of sockeye salmon in area 3 for May (A); June (B); and July (C), 1972. (see Figure 42 for symbol definitions).

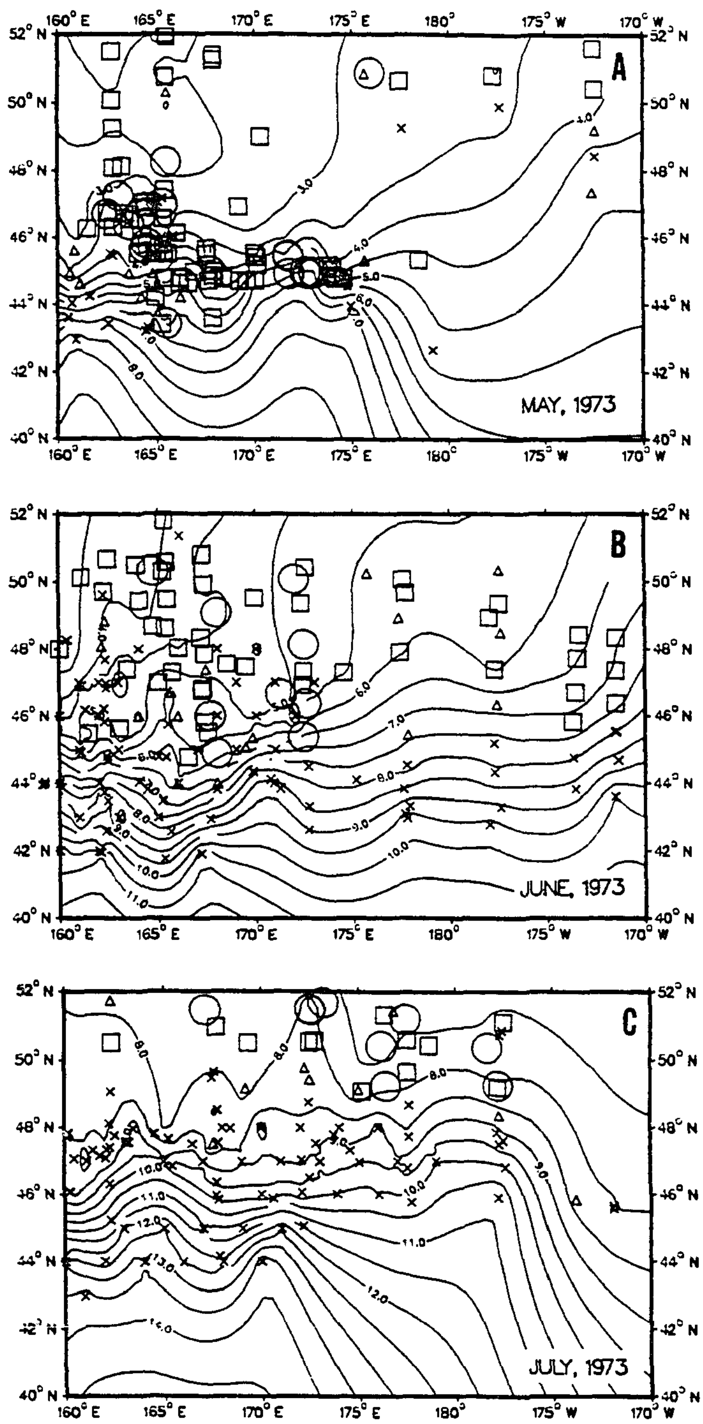

Figure 44. Surface isothermal distribution and mean CPUE (C_t) of sockeye salmon in area 3 for May (A); June (B); and July (C), 1973. (see Figure 42 for symbol definitions).

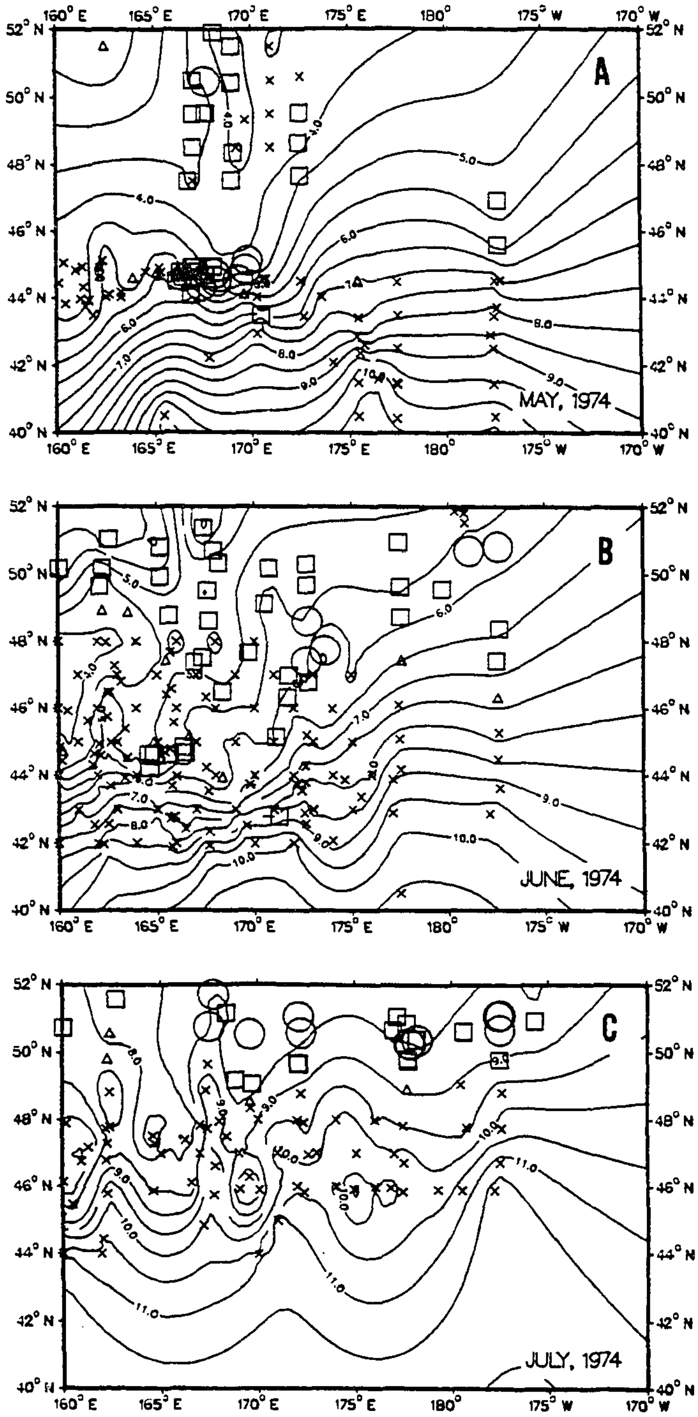

Figure 45. Surface isothermal distribution and mean CPUE (C_t) of sockeye salmon in area 3 for May (A); June (B); and July (C), 1974. (see Figure 42 for symbol definitions).

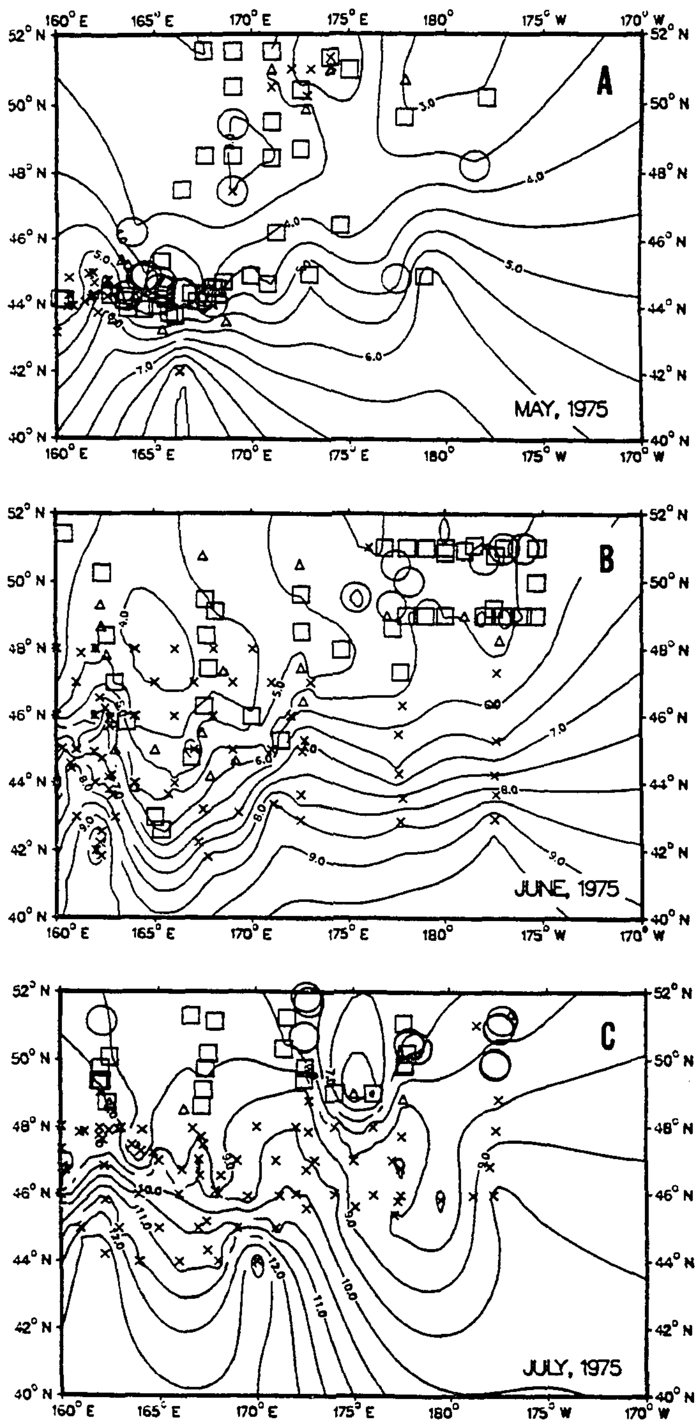

Figure 46. Surface isothermal distribution and mean CPUE (C_t) of sockeye salmon in area 3 for May (A); June (B); and July (C), 1975. (see Figure 45 for symbol definitions).

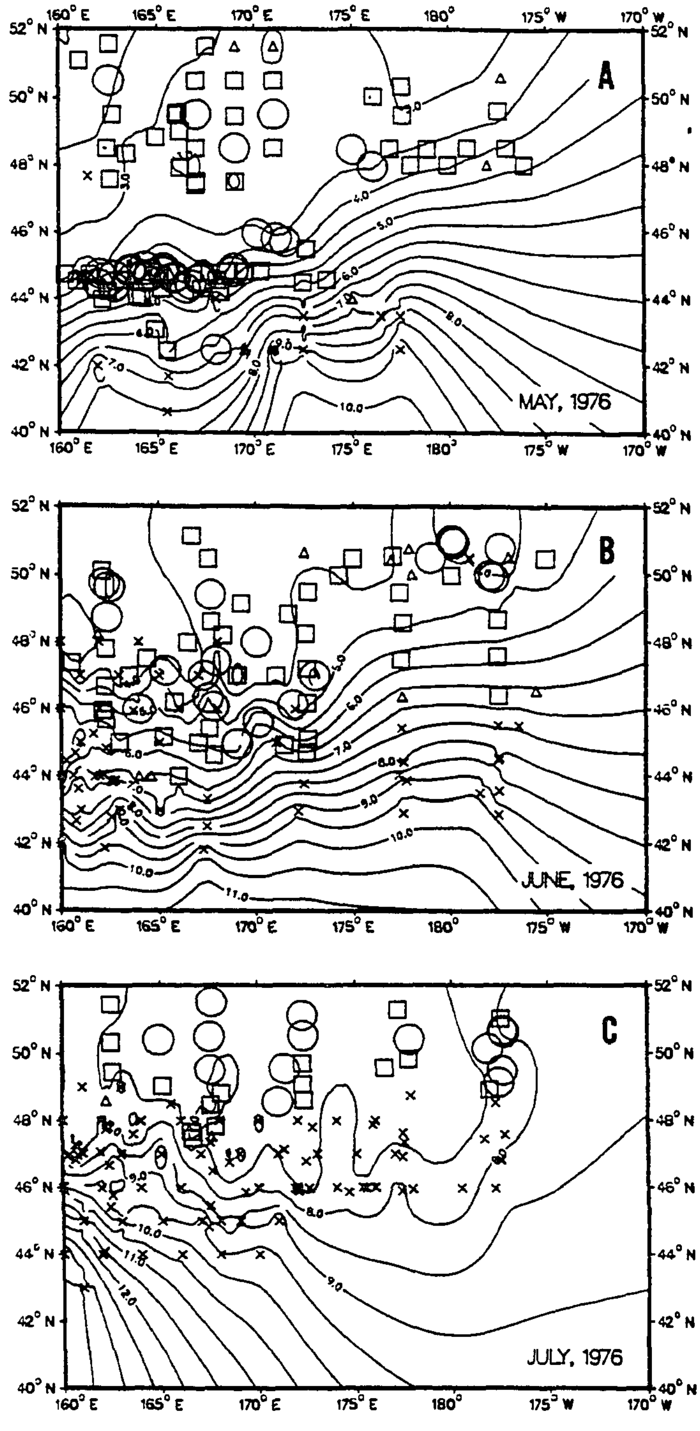

Figure 47. Surface isothermal distribution and mean CPUE (C_t) of sockeye salmon in area 3 for May (A); June (B); and July (C), 1976. (see Figure 42 for symbol definitions).

Table 6. The percentage (%) of stations with catches of sockeye salmon (POS) from area 3 for May-July, 1971-76. N is the number of sampled stations.

MONTH		1971	1972	1973	1974	1975	1976
MAY	N	141	128	114	103	90	109
	POS	84	96	97	40	66	95
	%	60	75	85	39	73	87
JUNE	N	127	129	153	167	133	130
	POS	54	53	71	53	67	75
	%	43	41	50	32	50	58
JULY	N	130	105	112	96	115	121
	POS	38	34	31	31	39	35
	%	29	32	26	32	34	29

DISCUSSION

The distribution of sockeye salmon is related to subsurface hydrostructures in the Subarctic Pacific. The Subarctic Front is a narrow and meandering area of convergence and relatively strong vertical mixing which occurs near 42°N (Roden, 1972; 1977; Bowman and Esaias, 1978). In the northwestern North Pacific, sockeye salmon appeared along 167°30'E in April 1971-73 in an area between 43°N and 48°N where temperatures were between 3-9°C (Mishima, 1974). Therefore, in 1972 and 1973 sockeye salmon avoided the areas north of 47°N-51°N where water $<$ 2°C prevailed. In contrast, in 1971 cold water was located further north and Mishima (1974) found that the fish occurred at 51°N. Immature fish appeared in the southern part and mature fish were dominant in the northern part of the transect 167°30'E. Shimazaki and Nakayama (1975) found similar results where they observed sockeye salmon restricted in winter 1970-73 between 44°N-47°N and 165°E-168°E where the thermal front (4-7°C) occurred.

Ohtani (1965) found that mature sockeye salmon occurred north of 49°N between 160°E-175°W in the northwestern North Pacific in June 1958-64. In the present study, in June 1982 sockeye salmon were taken north of 47°N along the 180° transect where temperatures were less than 7°C. The extent of the latitudinal distribution of sockeye salmon is not known for 1971 because no gillnet fishing took place. However, the distribution of sockeye salmon in relation to isothermal distribution suggests that the fish in 1971 would have been near 49°N where the 7-8°C isotherms were located. Evidence indicates that the position of thermal front in July 1971 was 2° farther northward than that in July 1982. Since there is a one month difference between sampling in these two years, it is impractical to compare the the distribution of sockeye salmon relating to the hydrographic structure between 1971 and 1982.

Water temperatures above the 50 *m* depth layer in area 3 exhibited monthly and annual differences throughout the 1971-76 period. In the North Pacific, water temperature is affected by the wind mixed layer depth (MLD), which is determined by the thickness of the turbulent and homogeneous surface layers (Laevastu and Hayes, 1980; Bathen, 1972). The MLD undergoes a strong seasonal change with increasing latitude in response to summer heating. A shallow MLD begins during the spring in the central western North Pacific, expands across mid-latitudes by early summer, and extends to high latitude by midsummer (Bathen, 1972). In other words, the water temperature in the northwestern North Pacific gradually increases from May to July, because of the shallow thermocline in mid- and late-summer which also forms a shallow MLD. The shallow thermocline in summer in the Gulf of Alaska has been shown to the depth to which the fish descend and confines the vertical distribution of sockeye salmon in that area (Manzer *et al.*, 1964).

It has been inferred that sockeye salmon abundance will increase where there is a sharp temperature gradient (Maeda, 1959, Ohtani, 1965; Takagi, 1967). I have shown this to occur in the northwestern North Pacific for area 3 where the fish tend to be associated with sharp temperature gradients in May during 1971-76. The fish were distributed widely in June, and moved northward in July in response to the surface warming in this area. Additionally, this is the time in which the fish begin their spawning migration (Hartman, 1971). This northward movement has been mentioned by Margolis *et al.* (1966) and French *et al.* (1976). This northward movement with increasing season may also explain why the decreasing frequency of CPUE and the percentage of stations with decreased catches from May to July. In May this sharp temperature gradient area where high CPUE occurs is also an area where there is high primary productivity and biomass (Hobson, 1980; Taniguchi, 1981; Tsujita, 1981).

I conclude that the Subarctic Front in the northwestern North Pacific limits the southernmost distribution of sockeye salmon in early summer. Later in the season, they respond to the water warming and perform spawning migration and gradually move northward.

SUMMARY

The subsurface features were different along three transects in the western and middle parts of the Subarctic Pacific. Along the 167°30'E transect, the thermal front was near 41°N-43°N. The front was near 43°N-45°N along the 180° transect.

Surface warming prevailed in the upper 50 *m* water layer in area 3 during summer in 1971-76. The monthly temperature change was largest at the surface and smallest at the 50 *m* depth layer. The majority of sockeye salmon underwent a seasonal change in depth; as the water warmed, they were found higher in the water column.

The distribution of sockeye salmon in relation to the surface isothermal distribution in May indicated that they tended to be associated with 3-6°C isotherms near 44°N-46°N. In June, they spread widely, but were more abundant at the 4-6°C isotherms north of 44°N. In July, sockeye salmon were seen north of 48°N at the 7.0-8.5°C isotherms. The frequency distribution of CPUE of sockeye salmon during the six-year period indicated a decrease in abundance with advanced season.

The southern limit of sockeye salmon in May was usually seen at 43°N. In June, most fish occurred north of 44°N. In July, sockeye salmon were not found south of 48°N.

Chapter V: General Discussion

The time series records in return abundance of Bristol Bay sockeye salmon during 1956-86 show a 5-year cycle. The wind stress curl in the Gulf of Alaska during 1955-1986 shows a 5.3-year clcle. There is also a 5-year cycle in the ocean-to-atmosphere total heat transfer (Figure 48) during 1950-79 in the Kuroshio area (Zhao and McBean, 1986). The fluctuation in wind stress curl was correlated with the peak return of Bristol Bay sockeye salmon at no lag (spawning) and 1-year lag (first-year lake residence). Similary, one should expect a relation between the sea-air total heat transfer and the return abundance of Bristol Bay sockeye salmon. These relationships suggest that physical factors are important in the biology of Bristol Bay sockeye salmon. However, the mechanisms that determine these relationships are unknown.

The relationship between wind stress curl and SST is a complicated phenomenon and can be studied through air-sea interaction. Currently, it is not certain whether the atmosphere drives the ocean (Davis, 1978; Lanzante, 1984) or the ocean drives the atmosphere (Namias, 1976; Zhao and McBean, 1986) in the mid-latitude North Pacific. Royer (1985) has argued that the ocean and atmosphere are closely linked, therefore driving one another. It is generally agreed, however, that on a seasonal time scale, SST anomalies are maintained by anomalous wind-driven advections in the near-surface waters (Emery and Hamilton, 1985).

There is a positive relation between the mean May-June SST and ocean abundance of sockeye salmon in the west habitat during 1961-85. This suggests that a decrease or increase of SST in the west habitat reduces or increases the ocean abundance of sockeye salmon in that area. The proposed oceanic distribution of Bristol Bay sockeye salmon in relation to warm and cold water conditions in the west and east habitats is shown in Figure 49. Bristol Bay sockeye salmon will extend their distribution to the west habitat when warm water conditions prevail in both habitats (figure 49A). When warm water

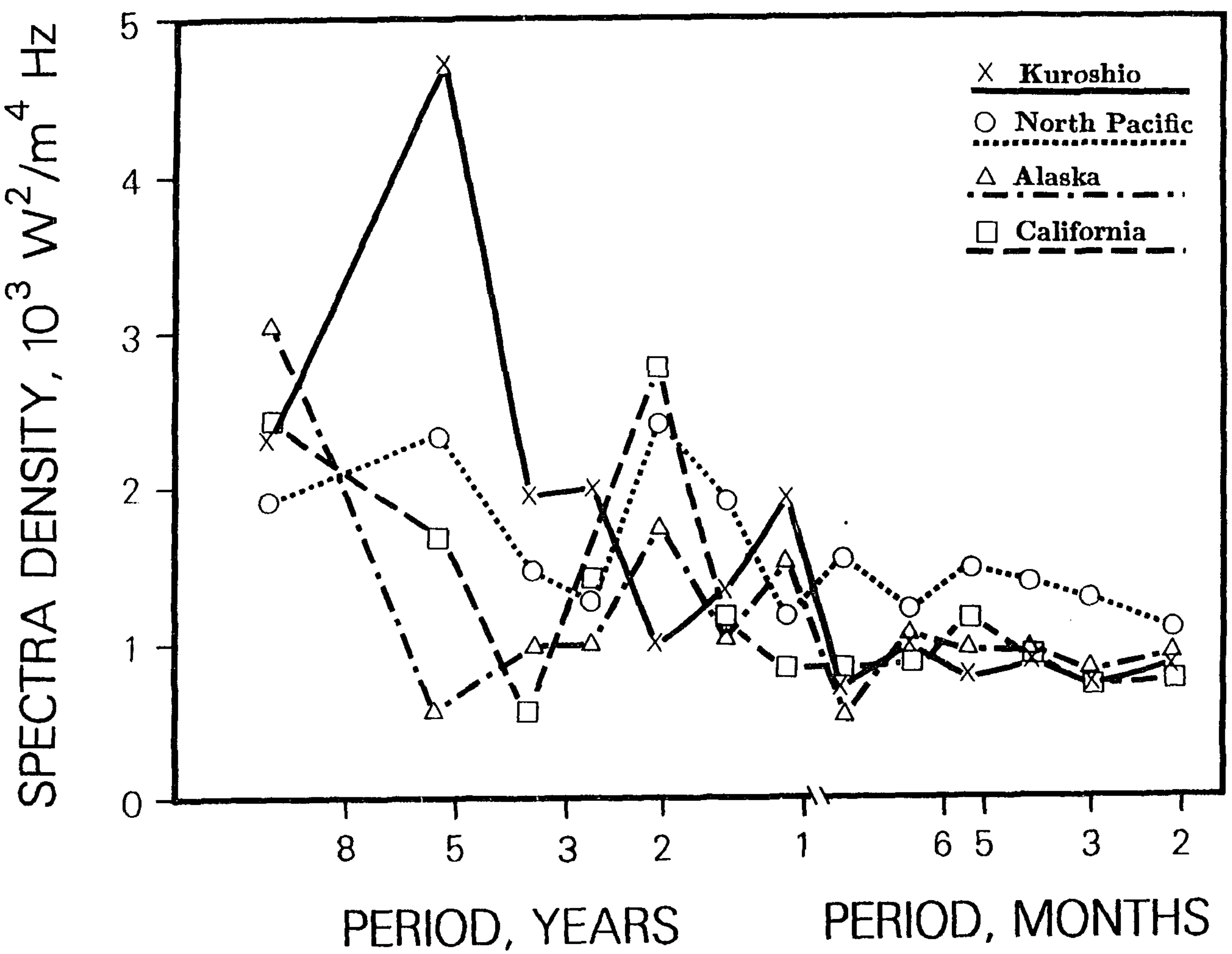

Figure 48. Spectra of the anomalies of total heat transfer from the 30-year mean annual cycle for the Kuroshio (×), North Pacific (○), Alaska (△), and California (□) areas. Note that frequency is in two frames, months (right) and years (left) (modified from Zhao and McBean, 1986).

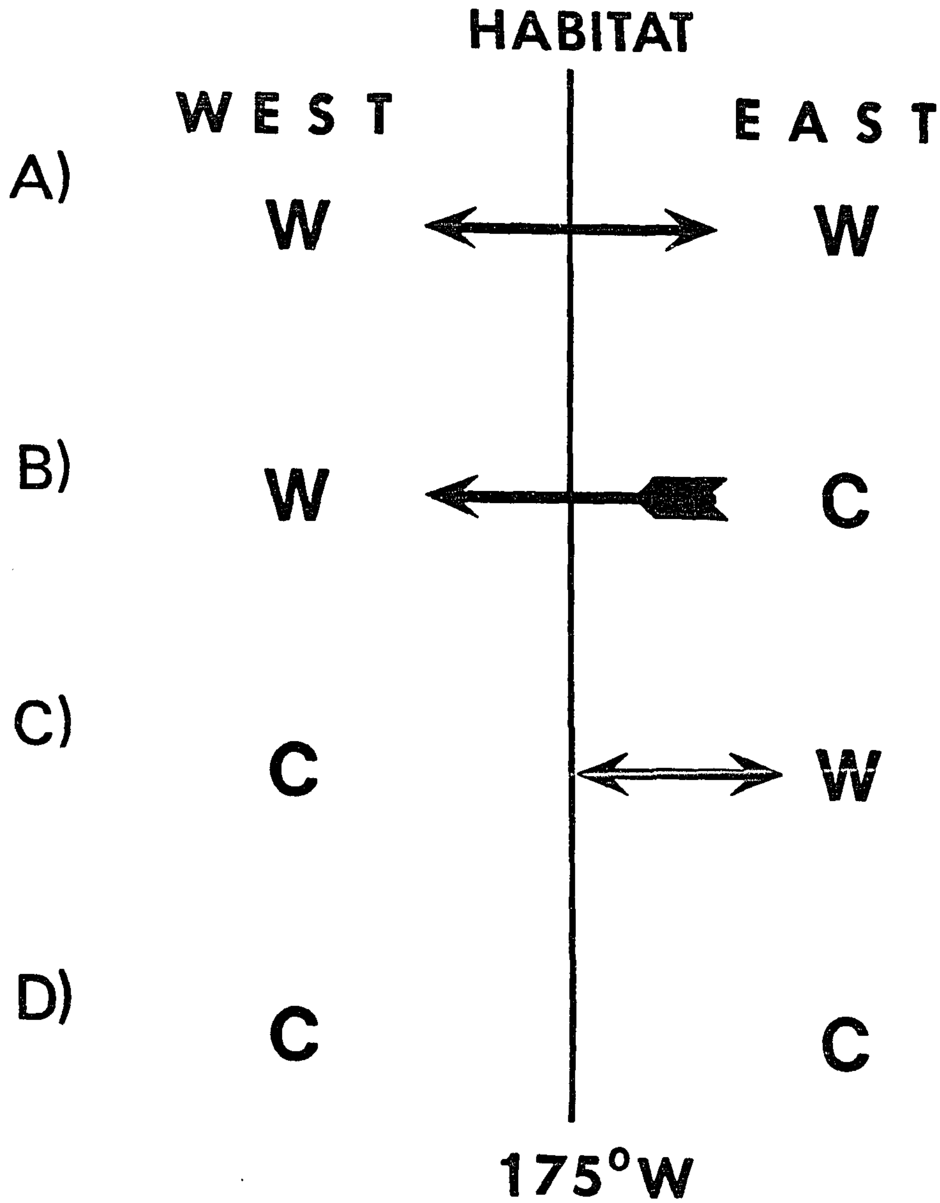

Figure 49. Oceanic distribution of Bristol Bay sockeye salmon in relation to warm (W) and cold (C) temperatures in the west and east habitat. The arrow indicates direction of fish movement and distribution.

occurs in the west habitat and cold water in the east habitat, they move to and are distributed within the west habitat (Figure 49B). In contrast, when there is cold water in the west habitat and warm water in the east habitat, most of them will remain within the east habitat (Figure 49C). When both habitats are cold, their ocean abundance tends to be low in both habitats (Figure 49D). This took place in the early 1970's when low abundance of sockeye salmon and cold water temperatures occured in the northern North Pacific

There is a positive relation between gonad weight of sockeye salmon and SST in the northern North Pacific. This indicates that the fish residing in warm water will mature earlier than those in cold water. Similarly, Nishiyama (1980) found the maturity of Bristol Bay sockeye salmon was positively related to the eastern Bering Sea SST.

Oceanic temperatures not only influence the ocean abundance and gonad weight of sockeye salmon, but may also affect the abundance of young fish in coastal regions, rivers, and lakes. Fujii *al.* (1974) suggests that the unusually low water temperatures in the eastern Bering Sea during 1971-73 would affect juvenile growth and survival rates during their migration along the northern of the Alaska Peninsula. In rivers, the cold winters of 1971-75 caused low water temperatures and resulted in a reduction in both number of fry produced from spawning streams and fry growth (Mathisen *et al.*, 1972; Mathisen *et al.*, 1974; Mathisen *et al.*, 1975). In turn, a reduction in fry numbers reduces numbers of smolt migrating to the ocean and results in a poor return of mature fish two or three years later.

Water temperature has been used to predict the peak return date of Bristol Bay sockeye salmon. Burgner (1978) found the air temprature and monthly SST deviations south of the Aleutian Peninsula and Adak Island were positively related to the peak return date of Bristol Bay sockeye salmon. By combining the water temperature and zooplankton biomass in the eastern Bering Sea, Nishiyama (1984) was able to predict the peak return date of sockeye salmon to the Kvichak River, Alaska.

I conclude that large-scale atmospheric and oceanic events affect the return, ocean abundance, and maturity of sockeye salmon. Research in this area is promising, but to what degree the results can be used in management of the species is still to be seen. A first approach might be to test the hypothesis that wind stress curl affects zooplankton abundance in the Gulf of Alaska (Chapter 3). Another approach, and more management oriented, would be to examine the relationship between total heat transfer and wind stress curl, and the return of major age groups of sockeye salmon to different stream-lake systems in Bristol Bay. Finally, another approach would be to determine the relation between sea surface temperatures and zooplankton abundance. This would lead to a better understanding of the relationship between temperature and ocean abundance of sockeye salmon found in this study.

Chapter VI: Summary

The primarily objective of this study was to examine the variations in return, ocean abundance, and maturity of sockeye salmon in relation to wind stress curl, sea surface temperature (SST), sea level pressure (SLP), and cloudiness (CLD). Historical records during two periods, 1971-76 and 1956-86, were the primary source of data used in this study.

Chapter 1 reviewed the literature on the life history and ocean distribution of sockeye salmon, climate and circulation in the Subarctic Pacific Ocean, and factors influencing fish growth, abundance, distribution, and migration.

Chapter 2 examined the fluctuation in abundance of sockeye salmon. During 1956-86, the abundance of Bristol Bay sockeye salmon fluctuated in a 5-year cycle. Age 2.2 and 1.3 fish showed an obvious 5-year cycle in abundance. Age .2 fish apparently contributed to most of the peak returns of sockeye salmon in that area during a 31-year period. In contrast, Kamchatka sockeye salmon showed no apparent cycle.

A continuous decline in ocean abundance of sockeye salmon was observed in the western Subarctic Pacific during 1957-77. Since 1978, however, oceanic abundance of sockeye salmon has increased. This increase was due to the presence of Bristol Bay fish in the western Subarctic Pacific. The abundance of mature and immature fish during 1971-76 was the lowest during the three periods: 1961-70, 1971-76, and 1977-85. The abundance of sockeye salmon changed with season, being lowest in May and June, and highest in July.

In 1971-76, mature Kamchatka sockeye salmon were 24 % more abundant than mature Bristol Bay sockeye salmon, though there was no difference between numbers of immature fish. Seasonal differences in age composition did not vary greatly but there was an annual difference of ocean age composition. In May 1975, age .3 fish outnumbered age .2 fish but was reversed in June and July. There was a yearly difference in immature-mature fish ratios in the same month.

The gonad weight of age .2 and .3 sockeye salmon increased from May to July in 1971-76. In age .2 fish, there was little variation in gonad weight for May between years. In contrast there was variation in June and July. In age .3 fish, gonad weight in May and June steadily increased from 1971 to 1976, but varied widely in July. The gonad weight in May through July was lowest in the 160°E-165°E region, except for age .3 fish in 1975, which was highest in the 175°E-170°W region. There was an eastward and northward trend of increasing gonad weight.

Chapter 3 examined the variations in wind stress curl, SST, SLP, and CLD, and the relationship to the biology of sockeye salmon. Spectra analysis of a 360-month period of mean wind stress curl in the Gulf of Alaska displayed 3.1- and 5.3-year peak cycles, the latter was similar to the 5-year cyclic dominance of Bristol Bay sockeye salmon. There was a correlation, using no lag and a 1-year lag (r=.32 to .44, P<.10), between wind stress curl and the return of four major age groups of sockeye salmon to Bristol Bay. Wind stress curl usually leads the return implying an environmental impact during the spawning phase, as well as during the first-year lake residence. Wind stress curl was correlated with the production of both age .2 and .3 fish. Additionally, there was a 5-year cycle of the sea-air total heat transfer in the Kuroshio area, which coincided with the 5.3-year cycle in wind stress curl and the 5-year cycle in return abundance of sockeye salmon. A simple model is proposed relating wind stress curl to the return of sockeye salmon abundance. Wind stress curl indirectly increases zooplankton abundance, which in turn increases growth rate and fecundity, resulting in a high return of sockeye salmon five years later (Figure 35). The processes and mechanisms that relate the total heat transfer and wind stress curl to the return of sockeye salmon are not known exactly.

During 1971-76, monthly SST pattern increased from east to west and from south to north. The latitudinal differences of temperature were small in April and May, but became larger in June and July. Variability in temperature was highest at 45°N. Monthly SLP fluctuated depending upon the position and duration of the high and low pressure systems. However, CLD did not show any obvious trend during this period. The mean cloudiness was mostly at or around 6 *octa*.

Mean May-June SST explained 56-66 % of the variation of mature and immature Kamchatka sockeye salmon abundance and 56 % of mature Bristol Bay sockeye salmon. The oceanic distribution of Bristol Bay sockeye salmon in the west and east habitats was closely related to the warm or cold SST in both habitats (Figure 49). SST explained 73 % of the variation in gonad weight of mature sockeye salmon during 1971-76. This indicated that sockeye salmon mature faster in warm water than in cold water.

Chapter 4 examined the subsurface hydrographic structures in the northern North Pacific and the surface isothermal distribution in relation to the ocean distribution of sockeye salmon. The Subarctic thermal front appeared near 41°N-43°N in the western Subarctic Pacific, and 43°N-45°N in the middle area.

In area 3, seasonal warming occurred in the upper 30 *m* depth layer. The monthly temperature change was largest at surface and smallest at the 50 *m* depth layer. During 1971-76, the seasonal difference in temperature was accompanied by a major concentration of sockeye salmon in the upper 50 m depth layer. In this layer, the temperature mean and range in May was similar in vertical direction (Figure 41). Relatively low temperature was seen in 1971 and 1973, but not in the other four years. A decrease of temperature with depth was obvious in June and July.

The frequency distribution of CPUE of sockeye salmon indicated a decrease in abundance from May to July. In the western Subarctic Pacific, the majority of sockeye salmon were found in the area with a greater temperature gradient. Sockeye salmon tended to be associated with 3-6°C surface isotherms near 44°N-46°N in May, and with 4-6°C isotherms north of 44°N in June. In July, the fish appeared further north above 48°N, with 7.0-8.5°C isotherms.

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Appendix Table A: Sockeye salmon ocean abundance, age composition, and gonad weight data

Abbreviations used in Appendix Table A and B;

GW_2: gonad weight of ocean age .2 sockeye salmon, and

GW_3: gonad weight of ocean age .3 sockeye salmon.

Table A-1. Annual mean of CPUE (no. of fish per *tan*) for both immature and mature sockeye salmon, Japanese motherships (M.S.), research vessels (R.V.), and the mean (MEAN) between them (from INPFC, 1979), 1971-76.

	1971		1972		1973		1974		1975		1976	
	N	CPUE	N	CPUE	N	CPUE	N	CPUE	N	CPUE	N	CPUE
M.S.	-	.608	-	.537	-	.448	-	.420	-	.385	-	.392
R.V.	176	.467	183	.370	205	.291	124	.250	172	.259	205	.444

Table A-2. Monthly mean CPUE of sockeye salmon based on the research vessels data, 1971-76.

	1971		1972		1973		1974		1975		1976	
MONTH	N	CPUE	N	CPUE	N	CPUE	N	CPUE	N	CPUE	N	CPUE
MAY	84	.522	96	.554	97	.410	40	.214	66	.283	95	.631
JUNE	54	.397	53	.277	77	.287	53	.226	67	.197	75	.445
JULY	38	.486	34	.370	31	.192	31	.293	39	.310	35	.284

Table A-3. Monthly mean of CPUE (no. of fish per 100 *tan*) of age .2 and .3 sockeye salmon, 1971-76.

MONTH	AGE	1971	1972	1973	1974	1975	1976
MAY	.2	1.69	2.93	2.22	2.23	1.15	6.91
	.3	3.58	3.22	4.37	2.78	1.43	5.84
JUNE	.2	5.37	2.85	3.09	1.84	3.78	4.01
	.3	6.98	4.02	6.81	3.99	2.25	3.54
JULY	.2	12.46	9.77	3.61	5.83	12.92	8.64
	.3	16.26	13.21	6.57	8.47	6.05	5.19

Table A-4. Percentage catch of age .2 and .3 sockeye salmon, 1971-76.

		AGE .2		AGE .3	
YEAR	MONTH	N	%	N	%
1971	MAY	1033	32.1	2181	67.9
	JUNE	1649	43.5	2145	56.5
	JULY	368	43.4	479	56.6
1972	MAY	1308	47.6	1440	52.4
	JUNE	1266	41.5	1787	58.5
	JULY	273	42.5	370	57.5
1973	MAY	1257	41.1	1803	58.9
	JUNE	1093	31.2	2411	68.8
	JULY	325	35.5	591	64.5
1974	MAY	684	29.2	1661	70.8
	JUNE	1225	31.5	2670	68.5
	JULY	278	40.8	404	59.2
1975	MAY	1178	44.5	1472	55.5
	JUNE	2225	62.7	1322	37.3
	JULY	631	68.1	296	31.9
1976	MAY	1659	54.2	1404	45.8
	JUNE	2235	53.1	1976	46.9
	JULY	881	62.5	528	37.5

Table A-5. Percentage catch of immature and mature sockeye salmon, 1971-76.

		IMMATURE		MATURE	
YEAR	MONTH	N	%	N	%
1971	MAY	7230	91.8	644	8.2
	JUNE	8049	72.6	3038	27.4
	JULY	3135	45.9	3699	50.1
1972	MAY	5903	89.7	680	10.3
	JUNE	7828	77.1	2326	22.9
	JULY	3814	43.4	4964	56.6
1973	MAY	5855	84.7	1056	15.3
	JUNE	7949	68.4	3664	31.6
	JULY	3785	49.0	3933	51.0
1974	MAY	4528	87.0	679	13.0
	JUNE	9181	81.5	2084	18.5
	JULY	4286	53.0	3805	47.0
1975	MAY	4878	89.7	562	10.3
	JUNE	7910	70.0	3384	30.0
	JULY	2936	39.9	4430	60.1
1976	MAY	6256	91.3	594	7.7
	JUNE	9855	77.4	2884	23.6
	JULY	4336	52.7	3892	47.3

Table A-6. Monthly mean of gonad weight of age .2 and .3 sockeye salmon, 1971-76.

		1971		1972		1973		1974		1975		1976	
MONTH	AGE	N	GW	N	GW	N	GW	N	GW	N	GW	N	GW
MAY	.2	1034	24.8	1303	23.5	1257	23.8	664	27.7	1179	22.3	1660	23.1
	.3	2181	46.6	1440	47.1	1804	49.7	1661	56.1	1476	65.7	1404	66.9
JUNE	.2	1647	44.8	1266	44.7	1099	36.2	1225	52.8	2225	44.0	2235	45.4
	.3	2155	70.6	1785	82.9	2461	72.9	2670	82.4	1322	82.7	1976	97.7
JULY	.2	368	73.5	272	82.3	324	56.0	278	66.3	631	60.7	881	70.8
	.3	479	107.9	366	124.0	591	110.5	404	88.2	296	103.0	528	113.

Table A-7. Monthly increment of GW of age .2 and .3 sockeye salmon, 1971-76.

MONTH	AGE	1971	1972	1973	1974	1975	1976
MAY-JUNE	.2	20.0	21.2	12.4	25.1	21.7	22.3
	.3	24.0	35.8	23.2	26.3	17.0	30.8
JUNE-JULY	.2	28.7	37.6	19.8	13.5	16.7	25.4
	.3	37.3	41.1	37.6	5.7	20.3	15.6

Table A-8. Monthly mean of gonad weight (g) of age .2 sockeye salmon, with sample numbers in bracket, 1971-76.

YEAR	MONTH	160E	165	170	175	180	175W	170	165	160	155
1971	MAY	21.5	24.5	27.8	24.7	23.3	-	-	-	-	-
		(112)	(589)	(211)	(100)	(22)	-	-	-	-	-
	JUNE	37.1	39.9	42.8	45.5	53.6	49.6	94.0	63.4	-	-
		(140)	(349)	(539)	(234)	(323)	(10)	(26)	(26)	-	-
	JULY	63.6	63.8	77.1	79.1	73.8	-	125.9	66.8	-	-
		(45)	(20)	(25)	(75)	(192)	-	(4)	(7)	-	-
1972	MAY	20.6	25.2	24.6	22.3	26.5	22.5	25.6	-	-	-
		(393)	(505)	(198)	(91)	(78)	(23)	(22)	-	-	-
	JUNE	30.8	36.1	46.4	51.1	62.2	74.5	67.6	-	-	-
		(114)	(419)	(231)	(256)	(195)	(34)	(19)	-	-	-
	JULY	63.7	78.5	71.8	107.4	92.4	63.1	-	-	-	-
		(58)	(38)	(30)	(46)	(98)	(2)	-	-	-	-
1973	MAY	22.4	25.2	22.9	25.9	100.0	16.3	17.0	15.4	42.5	77.5
		(300)	(427)	(360)	(53)	(2)	(7)	(20)	(44)	(37)	(7)
	JUNE	33.1	32.6	32.0	41.0	41.4	65.8	90.3	53.5	62.4	61.0
		(108)	(496)	(183)	(158)	(68)	(30)	(35)	(15)	(6)	(5)
	JULY	56.4	50.3	60.0	62.8	77.6	-	47.3	86.7	-	-
		(161)	(99)	(13)	(28)	(17)	-	(2)	(4)	-	-
1974	MAY	17.2	27.5	30.0	33.9	17.0	-	-	-	-	-
		(46)	(343)	(177)	(87)	(11)	-	-	-	-	-
	JUNE	34.5	43.0	43.6	50.8	67.0	80.0	-	-	-	-
		(15)	(282)	(165)	(310)	(446)	(7)	-	-	-	-
	JULY	66.3	56.8	68.1	67.5	71.9	-	-	-	-	-
		(104)	(44)	(26)	(35)	(69)	-	-	-	-	-
1975	MAY	18.3	20.8	26.3	27.6	23.8	-	-	-	-	-
		(236)	(467)	(324)	(117)	(34)	-	-	-	-	-
	JUNE	27.6	29.8	39.3	46.0	61.5	-	-	-	-	-
		(101)	(293)	(399)	(936)	(496)	-	-	-	-	-
	JULY	52.8	60.2	62.3	69.0	71.1	-	-	-	-	-
		(210)	(182)	(98)	(93)	(48)	-	-	-	-	-
1976	MAY	19.9	23.0	25.0	26.0	25.9	-	-	-	-	-
		(433)	(565)	(360)	(234)	(67)	-	-	-	-	-
	JUNE	35.0	35.5	35.9	49.0	66.5	-	-	-	-	-
		(168)	(575)	(326)	(606)	(560)	-	-	-	-	-
	JULY	58.0	63.5	79.3	80.5	82.1	-	-	-	-	-
		(243)	(155)	(95)	(166)	(222)	-	-	-	-	-

Table A-9. Monthly mean of gonad weight (g) of age .3 sockeye salmon, with sample numbers in bracket, 1971-76.

YEAR	MONTH	160E	165	170	175	180	175W	170	165	160	155
1971	MAY	39.8	51.6	55.8	46.1	28.9	-	-	-	-	-
		(852)	(997)	(228)	(90)	(14)	-	-	-	-	-
	JUNE	56.4	64.3	79.1	74.8	92.2	86.0	109.9	139.1	-	-
		(483)	(581)	(590)	(192)	(230)	(17)	(29)	(33)	-	-
	JULY	84.0	116.4	135.6	121.0	92.9	-	143.9	173.0	-	-
		(69)	(45)	(28)	(139)	(161)	-	(9)	(28)	-	-
1972	MAY	39.8	49.1	47.5	50.1	49.8	40.0	48.0	-	-	-
		(234)	(863)	(188)	(43)	(60)	(28)	(24)	-	-	-
	JUNE	52.6	73.1	78.3	79.3	111.9	106.7	114.9	-	-	-
		(56)	(430)	(363)	(518)	(336)	(52)	(30)	-	-	-
	JULY	93.1	119.0	106.5	130.3	133.5	33.5	-	167.9	-	-
		(35)	(48)	(22)	(108)	(153)	(1)	-	(3)	-	-
1973	MAY	41.4	52.2	44.6	44.7	45.4	45.4	-	33.5	81.0	130.0
		(304)	(960)	(279)	(120)	(22)	(26)	-	(5)	(60)	(28)
	JUNE	53.5	59.3	59.0	73.2	81.0	116.7	158.9	141.9	112.8	122.2
		(155)	(581)	(452)	(530)	(380)	(107)	(128)	(36)	(46)	(47)
	JULY	71.9	102.9	147.8	123.4	142.0	-	141.3	175.4	-	-
		(150)	(132)	(111)	(107)	(51)	-	(6)	(34)	-	-
1974	MAY	33.1	52.4	66.1	57.8	19.6	-	-	-	-	-
		(36)	(1056)	(428)	(135)	(6)	-	-	-	-	-
	JUNE	62.9	81.1	99.0	74.9	101.7	171.8	-	-	-	-
		(114)	(939)	(460)	(632)	(497)	(10)	-	-	-	-
	JULY	79.2	64.8	128.3	128.9	115.0	-	-	-	-	-
		(215)	(50)	(27)	(42)	(70)	-	-	-	-	-
1975	MAY	33.3	67.6	65.1	65.9	44.1	-	-	-	-	-
		(18)	(808)	(515)	(119)	(16)	-	-	-	-	-
	JUNE	58.7	59.3	90.8	87.5	97.6	-	-	-	-	-
		(82)	(189)	(391)	(497)	(163)	-	-	-	-	-
	JULY	93.4	111.7	90.2	107.3	116.1	-	-	-	-	-
		(99)	(84)	(30)	(40)	(43)	-	-	-	-	-
1976	MAY	45.6	78.5	62.8	59.4	49.4	-	-	-	-	-
		(172)	(728)	(297)	(170)	(37)	-	-	-	-	-
	JUNE	67.0	98.7	96.4	94.1	109.4	-	-	-	-	-
		(91)	(464)	(380)	(546)	(495)	-	-	-	-	-
	JULY	82.8	114.0	138.2	135.5	118.5	-	-	-	-	-
		(137)	(84)	(77)	(126)	(104)	-	-	-	-	-

Table A-10. Monthly mean of gonad weight for age .2 (GW_2) and .3 (GW_3) sockeye salmon in each 2^O latitude in 1971. N denotes the numbert of group, $\bar{X}$ is the average of group mean gonad weight, and SD, the standard deviation.

	MAY						JUNE						JULY					
	GW_2			GW_3			GW_2			GW_3			GW_2			GW_3		
LAT	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
60-58	-	-	-	-	-	-	3	1.975	0.181	2	2.129	0.198	4	1.952	0.208	4	2.131	0.172
58-56	-	-	-	-	-	-	7	1.821	0.183	7	2.007	0.207	6	1.861	0.181	6	2.115	0.224
56-54	-	-	-	-	-	-	6	1.804	0.186	6	2.008	0.203	3	1.813	0.164	3	2.079	0.166
54-52	1	1.825	-	1	1.790	-	5	1.670	0.188	5	1.861	0.195	3	1.813	0.164	2	1.961	0.152
52-50	4	1.536	0.207	4	1.741	0.226	5	1.612	0.190	5	1.809	0.196	4	1.758	0.161	4	1.915	0.137
50-48	5	1.419	0.176	5	1.657	0.208	5	1.538	0.181	5	1.712	0.195	4	1.675	0.115	4	1.995	0.175
48-46	5	1.356	0.151	5	1.556	0.194	4	1.472	0.157	3	1.592	0.184	-	-	-	1	2.018	-
46-44	2	1.331	-	1	1.625	-	2	1.408	-	1	1.475	-	-	-	-	-	-	-

Table A-11. Monthly mean of gonad weight for age .2 (GW_2) and .3 (GW_3) sockeye salmon in each 2^O latitude in 1972. N denotes the numbert of group, $\bar{X}$ is the average of group mean gonad weight, and SD, the standard deviation.

	MAY						JUNE						JULY					
	GW_2			GW_3			GW_2			GW_3			GW_2			GW_3		
LAT	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
60-58	-	-	-	-	-	-	4	1.992	0.228	5	2.140	0.185	4	2.043	0.182	4	2.142	0.192
58-56	-	-	-	-	-	-	6	1.895	0.215	6	2.063	0.188	6	1.956	0.211	6	2.089	0.183
56-54	1	1.675	-	1	1.546	-	5	1.816	0.199	5	1.981	0.187	2	1.871	0.172	2	1.965	0.017
54-52	2	1.336	0.089	2	1.849	0.114	6	1.747	0.188	6	1.899	0.229	3	1.802	0.152	3	1.942	0.139
52-50	5	1.509	0.211	6	1.768	0.236	5	1.548	0.173	5	1.744	0.213	5	1.833	0.111	6	1.882	0.095
50-48	7	1.414	0.180	7	1.709	0.228	5	1.533	0.163	5	1.731	0.199	2	1.713	0.142	1	2.042	-
48-46	3	1.346	0.168	3	1.596	0.210	4	1.442	0.130	4	1.596	0.170	1	1.605	-	-	-	-
46-44	3	1.274	0.120	2	1.458	0.158	2	1.377	0.190	1	1.275	-	-	-	-	-	-	-
44-42	1	1.188	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A-12. Monthly mean of gonad weight for age .2 (GW_2) and .3 (GW_3) sockeye salmon in each 2^{O} latitude in 1973. N denotes the numbert of group, $\bar{X}$ is the average of group mean gonad weight, and SD, the standard deviation.

	MAY						JUNE						JULY					
	GW_2			GW_3			GW_2			GW_3			GW_2			GW_3		
LAT	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
60-58	-	-	-	-	-	-	1	1.942	-	2	2.163	0.176	4	2.043	0.101	4	2.223	0.150
58-56	-	-	-	-	-	-	6	1.926	0.151	7	2.112	0.201	8	1.848	0.211	7	2.077	0.180
56-54	2	1.940	0.142	2	2.089	0.136	7	1.855	0.198	7	2.053	0.201	3	1.742	0.149	3	2.082	0.226
54-52	2	1.675	0.188	3	1.869	0.198	8	1.701	0.170	8	1.957	0.189	3	1.765	0.152	2	1.862	0.153
52-50	6	1.726	0.209	7	1.808	0.223	5	1.611	0.203	5	1.763	0.200	5	1.666	0.124	4	1.864	0.138
50-48	4	1.485	0.173	6	1.656	0.225	7	1.511	0.157	5	1.717	0.193	3	1.722	0.146	4	1.925	0.125
48-46	7	1.399	0.153	6	1.627	0.159	5	1.456	0.155	4	1.641	0.179	1	1.575	-	-	-	-
46-44	6	1.251	0.147	5	1.374	0.238	5	1.419	0.137	1	1.542	-	-	-	-	-	-	-
44-42	1	1.248	-	1	1.125	-	2	1.425	0.136	-	-	-	-	-	-	-	-	-

Table A-13. Monthly mean of gonad weight for age .2 (GW_2) and .3 (GW_3) sockeye salmon in each 2^{O} latitude in 1974. N denotes the numbert of group, $\bar{X}$ is the average of group mean gonad weight, and SD, the standard deviation.

	MAY						JUNE						JULY					
	GW_2			GW_3			GW_2			GW_3			GW_2			GW_3		
LAT	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
60-58	-	-	-	-	-	-	3	1.962	0.216	3	2.097	0.200	3	2.060	0.223	3	2.182	0.216
58-56	-	-	-	1	1.925	-	5	1.830	0.229	6	2.029	0.215	3	1.911	0.182	5	2.088	0.157
56-54	1	1.825	-	1	1.903	-	4	1.824	0.187	4	1.995	0.222	2	1.856	0.181	2	2.016	0.146
54-52	4	1.675	0.171	4	1.813	0.204	4	1.806	0.173	4	1.894	0.200	3	1.833	0.134	3	1.905	0.138
52-50	3	1.610	0.201	4	1.797	0.207	5	1.682	0.199	5	1.814	0.188	5	1.776	0.163	4	1.858	0.160
50-48	3	1.508	0.199	4	1.676	0.196	5	1.574	0.174	5	1.740	0.192	5	1.723	0.167	5	1.798	0.050
48-46	3	1.326	0.163	3	1.587	0.191	3	1.498	0.154	3	1.649	0.207	1	1.442	-	1	1.375	-
46-44	2	1.305	0.173	2	1.315	0.245	2	1.413	0.106	1	1.675	-	-	-	-	-	-	-
44-42	2	1.075	-	-	-	-	1	1.575	-	-	-	-	-	-	-	-	-	-

Table A-14. Monthly mean of gonad weight for age .2 (GW_2) and .3 (GW_3) sockeye salmon in each 2^O latitude in 1975. N denotes the numbert of group, $\bar{X}$ is the average of group mean gonad weight, and SD, the standard deviation.

	MAY						JUNE						JULY					
	GW_2			GW_3			GW_2			GW_3			GW_2			GW_3		
LAT	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
60-58	-	-	-	-	-	-	2	1.923	0.235	1	2.121	-	4	1.884	0.244	4	2.097	0.220
58-56	-	-	-	-	-	-	4	1.885	0.222	3	2.128	0.162	4	1.834	0.216	4	2.080	0.195
56-54	-	-	-	-	-	-	3	1.823	0.196	3	2.043	0.229	2	1.788	0.230	2	2.009	0.204
54-52	2	1.325	0.071	1	1.811	-	5	1.795	0.184	5	2.003	0.214	2	1.746	0.139	2	2.012	0.206
52-50	4	1.664	0.183	4	1.919	0.185	5	1.667	0.189	5	1.936	0.192	5	1.744	0.156	5	1.961	0.175
50-48	4	1.457	0.196	4	1.824	0.217	5	1.500	0.138	5	1.802	0.189	5	1.782	0.113	4	1.903	0.184
48-46	4	1.371	0.136	4	1.695	0.217	5	1.402	0.120	5	1.629	0.233	4	1.723	0.146	2	1.858	0.047
46-44	3	1.244	0.110	4	1.482	0.232	2	1.362	0.102	2	1.675	0.000	1	1.725	-	-	-	-
44-42	2	1.242	0.085	2	1.425	0.036	2	1.356	0.134	1	1.725	-	-	-	-	-	-	-

Table A-15. Monthly mean of gonad weight for age .2 (GW_2) and .3 (GW_3) sockeye salmon in each 2^O latitude in 1976. N denotes the numbert of group, $\bar{X}$ is the average of group mean gonad weight, and SD, the standard deviation.

	MAY						JUNE						JULY					
	GW_2			GW_3			GW_2			GW_3			GW_2			GW_3		
LAT	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
60-58	-	-	-	-	-	-	3	2.010	0.272	3	2.154	0.146	4	2.001	0.173	4	2.181	0.144
58-56	-	-	-	-	-	-	5	1.890	0.231	5	2.113	0.163	5	1.913	0.197	5	2.118	0.158
56-54	-	-	-	-	-	-	3	1.819	0.189	3	2.022	0.185	3	1.910	0.162	3	2.082	0.159
54-52	1	1.715	-	2	1.744	0.243	4	1.824	0.175	4	1.991	0.174	3	1.746	0.130	4	1.984	0.195
52-50	4	1.580	0.244	5	1.867	0.206	5	1.696	0.183	5	1.956	0.194	5	1.797	0.132	4	1.932	0.172
50-48	5	1.451	0.179	5	1.792	0.220	5	1.539	0.157	5	1.785	0.197	5	1.835	0.126	5	1.906	0.152
48-46	4	1.414	0.143	4	1.688	0.215	5	1.468	0.154	4	1.629	0.213	3	1.693	0.087	3	2.125	0.000
46-44	3	1.277	0.154	3	1.444	0.263	4	1.465	0.158	2	1.525	0.142	-	-	-	-	-	-
44-42	2	1.292	0.164	1	1.325	-	1	1.550	-	-	-	-	-	-	-	-	-	-

Appendix Table B: Abiotic factors data

1. Abbreviation in this Appendix;

   SST: current month sea surface temperature,

   SST_p: previous month sea surface temperature,

   SLP: current month sea level pressure,

   SLP_p: previous month sea level pressure,

   CLD: current month cloudiness, and

   CLD_p: previous month cloudiness.

2. Symbols in this Appendix;

   *: $P < 0.01$, and

   **: $P < 0.001$.

Table B-1. Mean SST for each 2^{o} lat. quadrant in area 1, 1971-76.

	APRIL			MAY			JUNE			JULY				APRIL			MAY			JUNE			JULY		
LAT	N	$\bar{T}$	SD	N	$\bar{T}$	SD	N	$\bar{T}$	SD	N	$\bar{T}$	SD	LAT	N	$\bar{T}$	SD	N	$\bar{T}$	SD	N	$\bar{T}$	SD	N	$\bar{T}$	SD
1971													1974												
55	5	3.2	0.18	5	3.5	0.44	5	4.9	0.75	5	6.9	0.17	55	5	2.9	0.26	5	4.0	0.46	5	5.8	0.38	5	7.8	0.20
50	6	3.5	0.54	6	3.8	0.41	6	5.3	0.57	6	7.5	0.35	50	6	3.5	0.67	6	4.1	0.74	6	6.1	0.80	6	8.7	0.37
45	6	6.0	1.50	6	6.5	1.10	6	8.3	0.81	6	11.1	0.91	45	6	5.8	1.19	6	6.2	1.10	6	7.6	1.08	6	11.0	1.25
40	6	11.2	0.51	6	12.2	0.26	6	13.9	0.36	6	17.9	0.53	40	6	11.1	0.86	6	11.9	0.33	6	13.5	0.32	6	16.4	0.80
1972													1975												
55	5	2.9	1.09	5	3.2	0.53	5	4.8	0.34	5	7.9	0.30	55	5	3.2	0.19	5	3.5	0.32	5	5.2	0.25	5	7.4	0.52
50	6	3.3	0.99	6	3.8	0.89	6	5.6	0.53	6	8.4	0.23	50	6	3.3	0.50	6	3.6	0.52	6	5.5	0.26	6	8.0	0.51
45	6	6.1	1.67	6	6.9	1.50	6	8.6	0.89	6	11.1	0.64	45	6	5.1	0.82	6	5.9	0.88	6	7.2	0.55	6	10.3	0.61
40	6	11.5	0.65	6	12.6	0.35	6	14.7	0.34	6	17.5	0.26	40	6	11.1	0.29	6	12.9	0.23	6	13.6	0.53	6	16.4	0.37
1973													1976												
55	5	2.5	0.97	5	3.7	0.37	5	5.4	0.24	5	7.3	0.38	55	5	2.6	0.44	5	3.6	0.23	5	4.7	0.43	5	6.5	0.36
50	6	2.9	0.68	6	3.9	0.73	6	5.9	0.43	6	8.0	0.11	50	6	3.0	0.61	6	3.6	0.53	6	5.2	0.51	6	7.4	0.41
45	6	5.0	0.95	6	6.2	0.72	6	7.9	0.56	6	10.7	0.21	45	6	5.0	0.83	6	5.8	0.87	6	7.3	0.66	6	9.7	0.48
40	6	11.0	0.26	6	12.3	0.24	6	14.3	0.51	6	17.8	0.42	40	6	11.1	0.66	6	12.8	0.37	6	14.0	0.34	6	16.8	0.96

Table B-2. Mean SST for each 5^{o} long. quadrant in area 1, 1971-76.

YEAR	MON	160E	165	170	175	180	175W	170	165	160	155	150	145W
1971	APR	3.5	3.8	4.4	4.9	4.9	4.9	5.0	4.8	5.0	5.4	5.6	5.9
	MAY	4.2	4.2	4.5	4.9	5.2	5.5	5.3	5.1	5.1	5.3	5.9	6.8
	JUN	5.8	5.8	6.2	6.3	6.6	7.1	6.7	6.2	6.2	6.6	7.3	8.3
	JUL	8.5	8.1	8.3	8.7	9.0	9.2	9.7	10.1	10.1	9.9	10.0	10.8
1972	APR	2.8	3.3	4.3	4.9	5.2	5.3	4.8	4.8	4.8	4.6	4.9	5.5
	MAY	3.8	4.0	4.7	5.8	5.6	5.7	5.7	5.7	5.6	5.7	6.0	6.6
	JUN	6.2	6.3	6.5	6.8	6.6	6.4	6.5	6.8	7.1	7.5	8.2	8.9
	JUL	9.1	8.9	9.3	9.7	9.4	9.1	9.1	9.6	10.1	10.6	11.5	12.3
1973	APR	2.7	2.9	3.6	4.0	4.2	4.4	4.4	4.8	5.0	5.1	5.5	6.3
	MAY	4.1	4.5	4.8	4.9	4.9	5.0	5.0	5.4	5.7	5.8	6.4	7.1
	JUN	6.1	6.2	6.6	6.7	6.7	6.7	6.6	6.8	7.1	7.3	7.8	8.3
	JUL	9.1	8.7	8.7	8.6	8.5	8.5	8.5	8.9	9.2	9.6	10.4	11.2
1974	APR	3.5	3.8	4.2	4.4	4.6	4.8	4.7	4.8	4.8	4.8	5.2	6.0
	MAY	4.2	4.3	4.9	5.2	5.5	5.6	5.7	6.0	6.2	6.3	6.5	7.3
	JUN	5.7	6.0	6.6	7.0	7.2	7.1	7.3	7.6	8.0	8.2	8.6	9.1
	JUL	8.7	8.8	9.0	9.4	9.8	10.0	10.6	11.0	10.9	10.7	10.9	11.5
1975	APR	3.4	3.6	3.9	4.6	4.4	4.5	4.6	4.9	4.9	5.0	5.4	5.9
	MAY	3.8	3.9	4.4	4.7	4.8	5.0	5.2	5.5	5.5	5.6	5.9	6.6
	JUN	5.8	5.8	6.0	6.0	6.1	6.4	6.7	7.0	7.4	7.2	8.0	8.7
	JUL	9.3	8.7	8.6	8.3	8.1	8.5	9.0	9.8	10.1	10.3	10.7	11.2
1976	APR	2.9	3.2	3.7	3.8	4.0	4.2	4.2	4.3	4.5	4.8	5.2	5.7
	MAY	3.7	4.2	4.5	4.6	4.7	4.9	5.2	5.4	5.5	5.8	6.1	6.5
	JUN	5.4	5.5	5.8	5.9	6.2	6.6	6.9	7.3	7.8	8.3	8.9	9.3
	JUL	7.9	7.6	7.6	8.0	8.3	8.6	9.1	9.6	10.0	10.3	10.8	11.3

Table B-3. Mean SLP (mb) for each 5^{o} long. quadrant in area 1, 1971-76 (SLP have been subtracted from 900 to reduce the space).

YEAR	MON	160E	165	170	175	180	175W	170	165	160	155	150	145W
1971	APR	110.4	110.8	111.3	111.5	111.1	110.3	109.3	108.1	107.0	106.1	106.3	107.5
	MAY	113.8	113.1	112.1	110.8	109.1	107.5	106.3	106.0	106.9	108.9	111.6	114.5
	JUN	108.4	108.8	109.6	110.8	111.5	112.0	112.3	112.3	112.4	112.5	113.0	114.0
	JUL	110.3	110.5	111.0	111.6	112.3	113.0	114.3	115.6	116.8	118.1	120.0	121.4
1972	APR	117.0	117.5	118.1	118.6	119.0	119.0	118.8	118.0	116.5	114.5	112.4	111.1
	MAY	109.3	110.3	110.9	110.8	110.1	109.4	109.1	109.9	111.1	112.5	113.9	115.3
	JUN	111.0	111.9	112.3	111.9	111.1	110.6	110.6	111.0	111.8	112.9	114.0	114.9
	JUL	111.6	112.0	112.5	113.4	114.8	116.5	118.0	119.0	119.8	120.0	120.1	120.4
1973	APR	112.8	113.4	113.6	113.5	113.0	112.0	111.3	111.0	111.4	112.5	114.3	116.4
	MAY	112.5	112.8	112.5	111.8	110.5	108.9	107.3	106.1	105.6	106.0	107.5	110.0
	JUN	112.5	112.8	112.9	113.0	113.1	113.5	113.8	113.5	112.9	112.4	112.1	112.3
	JUL	112.1	112.8	113.4	114.4	115.3	115.6	115.8	115.9	116.0	116.4	117.3	118.1
1974	APR	110.1	109.9	109.3	108.5	107.3	106.3	106.3	106.6	107.1	107.9	109.0	111.0
	MAY	110.4	109.9	109.5	108.9	108.4	108.5	109.3	110.1	111.0	111.9	112.5	113.1
	JUN	113.9	114.4	115.0	115.4	115.6	115.1	114.4	114.0	113.6	113.5	113.6	114.3
	JUL	111.5	111.5	112.0	112.9	114.3	115.9	117.4	118.1	118.0	117.9	117.9	117.9
1975	APR	111.5	111.9	112.4	113.4	114.6	115.4	115.6	115.8	116.1	116.8	117.3	117.6
	MAY	113.5	112.9	112.3	111.6	110.8	109.8	108.8	108.3	108.4	108.8	110.0	112.4
	JUN	112.8	112.8	112.6	112.3	112.0	112.1	112.5	113.5	114.9	116.3	117.9	119.1
	JUL	110.6	111.3	111.1	110.6	110.3	110.9	112.1	113.6	114.9	115.3	115.6	116.1
1976	APR	111.6	111.1	110.6	110.4	110.0	109.8	109.5	109.0	108.4	108.3	108.6	109.6
	MAY	109.0	109.6	110.3	110.5	110.3	109.9	109.8	109.8	109.4	108.9	109.0	109.9
	JUN	112.5	112.8	112.9	112.9	112.9	113.5	114.5	115.6	116.6	117.4	118.3	118.8
	JUL	108.6	108.9	108.9	108.8	109.1	110.1	111.1	111.9	112.6	113.1	113.4	113.5

Table B-4. Mean cloudiness (*octa*) for each 5° long. quadrant in area 1, 1971-73.

YEAR	MON	160E	165	170	175	180	175W	170	165	160	155	150	145W
1971	APR	5.5	5.6	5.5	5.4	5.6	5.8	5.5	5.4	5.4	5.5	4.9	5.4
	MAY	5.4	5.6	5.7	5.8	5.8	5.9	5.9	5.9	6.1	6.1	5.9	6.0
	JUN	6.1	6.5	6.6	6.7	6.9	6.7	6.5	6.4	6.6	6.7	6.7	6.4
	JUL	6.1	6.3	6.7	6.9	6.7	6.6	6.4	6.2	5.8	6.0	5.8	5.8
1972	APR	6.2	5.9	6.2	6.3	6.1	6.3	6.6	6.6	6.3	6.0	5.8	5.7
	MAY	6.2	6.0	5.8	6.1	6.4	6.3	6.2	6.1	5.9	5.3	5.7	5.8
	JUN	6.3	6.3	6.3	6.4	6.5	6.5	6.3	6.4	6.2	6.2	6.0	5.8
	JUL	6.4	6.8	6.8	7.0	7.0	6.9	6.9	6.5	6.0	5.9	5.8	5.7
1973	APR	5.7	5.6	6.3	6.1	5.9	5.9	5.7	5.5	5.5	5.5	5.8	6.0
	MAY	5.3	5.6	5.9	6.1	6.4	6.3	6.0	5.7	5.5	5.5	5.1	5.2
	JUN	6.0	6.2	6.3	5.9	5.7	5.9	5.7	5.4	5.6	5.8	5.7	5.8
	JUL	5.9	6.3	6.4	6.3	6.4	6.5	6.3	6.0	6.1	6.2	5.8	5.4

Table B-5. Correlation coefficients of GW_2 and GW_3 to the abiotic factors in 1971.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	.821**	.754**	1.000					
SST	.941**	.796**	.725**	1.000				
SLP	-.194	.076	-.363	-.211	1.000			
CLD_p	.844**	.766**	.536	.899**	.154	1.000		
SST_p	.886**	.789**	.666*	.937**	.039	.901**	1.000	
SLP_p	-.413	-.581	-.079	-.272	-.448	-.327	-.355	1.000

Table B-6. Correlation coefficients of GW_2 and GW_3 to the abiotic factors in 1972.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	-.178	.182	1.000					
SST	.731*	.656*	.549	1.000				
SLP	.168	.176	.356	.238	1.000			
CLD_p	.248	-.286	.176	.264	.388	1.000		
SST_p	.783*	.744*	.549	.954*	.090	.284	1.000	
SLP_p	-.733*	-.726*	.254	-.152	-.088	.241*	-.225	1.000

Table B-7. Correlation coefficients of GW_2 and GW_3 to the abiotic factors in 1973.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	.864*	.831*	1.000					
SST	.861*	.855*	.879*	1.000				
SLP	.790*	.804*	.718*	.789*	1.000			
CLD_p	.285	.264	.411	.397	.063	1.000		
SST_p	.811*	.782*	.804*	.879*	.613*	.492	1.000	
SLP_p	-.757*	-.765*	-.548*	-.580*	-.632*	.068	-.372	1.000

Table B-8. Correlation coefficients of GW_2 and GW_3 to the abiotic factors in 1974.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.926**	.791**	1.000			
SLP	.532	.557	.402	1.000		
SST_p	.893**	.820**	.971**	.338	1.000	
SLP_p	.600	.499	.825**	-.004	.812**	1.000

Table B-9. Correlation coefficients of GW_2 and GW_3 to the abiotic factors in 1975.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.858**	.752*	1.000			
SLP	-.784*	-.744*	-.809*	1.000		
SST_p	.909**	.858**	.910**	-.945**	1.000	
SLP_p	-.352	-.450	.066	-.006	-.082	1.000

Table B-10. Correlation coefficients of GW_2 and GW_3 to the abiotic factors in 1976.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.952**	.816**	1.000			
SLP	-.117	-.016	-.272	1.000		
SST_p	.952**	.830**	.977**	-.249	1.000	
SLP_p	.608*	.511	.701*	-.793**	.695*	1.000

Table B-11. Correlation coefficients of GW_2 and GW_3 to abiotic factors in May, 1971-73.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	-.154	-.201	1.000					
SST	.388	.350	.487	1.000				
SLP	-.613*	-.516	-.384	-.536	1.000			
CLD_p	-.358	-.376	.741**	.368	.206	1.000		
SST_p	.397	.346	.471	.875**	-.509	.179	1.000	
SLP_p	-.256	-.249	.801*	.404	.382	.822**	.317	1.000

Table B-12. Correlation coefficients of GW_2 and GW_3 to abiotic factors in May, 1974-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.856**	.261	1.000			
SLP	-.191	.255	-.235	1.000		
SST_p	.761*	.259	.844**	.183	1.000	
SLP_p	-.307	.282	-.448	.678	-.085	1.000

Table B-13. Correlation coefficients of GW_2 and GW_3 to abiotic factors in May, 1971-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.494*	.118	1.000			
SLP	-.447*	-.251	-.393	1.000		
SST_p	.472*	.178	.868**	-.336	1.000	
SLP_p	-.185	-.313	.404	.078	.321	1.000

Table B-14. Correlation coefficients of GW_2 and GW_3 to abiotic factors in June, 1971-73.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	-.041	-.053	1.000					
SST	.479	.493	-.139	1.000				
SLP	.218	.349	-.553*	.678**	1.000			
CLD_p	.418	.511	-.153	.703**	.367	1.000		
SST_p	.712**	.665**	.197	.723**	.241	.543*	1.000	
SLP_p	-.774**	-.809**	.020	-.446	-.416	-.495	-.443	1.000

Table B-15. Correlation coefficients of GW_2 and GW_3 to abiotic factors in June, 1974-73.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.724*	.342	1.000			
SLP	.654	-.059	.760**	1.000		
SST_p	.843**	.669*	.880**	.552	1.000	
SLP_p	-.515	-.434	-.391	-.587	-.514	1.000

Table B-16. Correlation coefficients of GW_2 and GW_3 to abiotic factors in June, 1971-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.547*	.326	1.000			
SLP	.104	.250	.307	1.000		
SST_p	.763**	.616**	.781**	.116	1.000	
SLP_p	-.691**	-.714**	-.355	-.377	-.448*	1.000

Table B-17. Correlation coefficients of GW_2 and GW_3 to abiotic factors in July, 1971-73.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	.858**	.730*	1.000					
SST	.512	.003	.453	1.000				
SLP	.302	.358	.355	.610	1.000			
CLD_p	.503	.333	.659*	-.016	-.197	1.000		
SST_p	.567	.436	.616	.678*	.846**	.145	1.000	
SLP_p	-.093	.033	.055	.560	.717**	-.340	.647*	1.000

Table B-18. Correlation coefficients of GW_2 and GW_3 to abiotic factors in July, 1974-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	-.292	-.136	1.000			
SLP	-.096	-.069	.913**	1.000		
SST_p	.295	.370	.746**	.830**	1.000	
SLP_p	.028	.021	.729*	.794**	.763**	1.000

Table B-19. Correlation coefficients of GW_2 and GW_3 to abiotic factors in July, 1971-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.131	-.069	1.000			
SLP	.178	.114	.821**	1.000		
SST_p	.405	.382	.750**	.835**	1.000	
SLP_p	-.153	.040	.265	.204	.295	1.000

Table B-20. Correlation coefficients of GW_2 and GW_3 to abiotic factors, 1971-73.

	GW_2	GW_3	CLD	SST	SLP	CLD_p	SST_p	SLP_p
GW_2	1.000							
GW_3	-	1.000						
CLD	.613**	.545**	1.000					
SST	.856**	.774**	.657**	1.000				
SLP	.254	.286	-.008	.273	1.000			
CLD_p	.439**	.412*	.496**	.535**	.122	1.000		
SST_p	.813**	.759**	.646**	.907**	.171	.544*	1.000	
SLP_p	-.613**	-.638**	.105	-.348*	-.339*	.046	-.256	1.000

Table B-21. Correlation coefficients of GW_2 and GW_3 to abiotic factors, 1974-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.889**	.722**	1.000			
SLP	.074	.121	.076	1.000		
SST_p	.894**	.762**	.954**	.060	1.000	
SLP_p	.395*	.371*	.611**	-.136	.601**	1.000

Table B-22. Correlation coefficients of GW_2 and GW_3 to abiotic factors, 1971-76.

	GW_2	GW_3	SST	SLP	SST_p	SLP_p
GW_2	1.000					
GW_3	-	1.000				
SST	.857**	.732**	1.000			
SLP	.174	.213	.173	1.000		
SST_p	.839**	.739**	.928**	.117	1.000	
SLP_p	-.298*	-.354*	-.002	-.256*	.036	1.000

Appendix Table C: Water temperatures data

Table C-1. Monthly minimum, maximum, and mean of water temperature, at 0, 10, 30, and 50 *m* depth in area 3, 1971-76.

			0 *m*				10 *m*				20 *m*				30 *m*				50 *m*			
YEAR	MON	N	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD
1971	MAY	141	1.9	6.6	3.9	.99	1.9	6.5	3.9	.98	1.9	6.5	3.8	.99	1.7	6.5	3.7	1.01	0.9	6.5	3.6	1.03
	JUN	127	4.0	12.6	6.4	1.70	3.5	12.5	6.3	1.71	3.0	12.1	6.2	1.66	1.5	11.1	6.0	1.73	1.1	10.4	5.3	1.91
	JUL	130	4.6	16.2	9.6	2.24	4.7	16.2	9.3	2.24	4.7	16.2	8.5	2.01	3.8	15.2	7.6	1.75	2.7	12.1	5.5	1.71
1972	MAY	128	2.7	11.6	4.6	1.43	2.7	11.6	4.5	1.40	2.7	11.6	4.4	1.36	2.6	11.6	4.3	1.36	2.3	11.4	4.2	1.34
	JUN	129	2.6	12.2	6.4	2.02	2.7	12.2	6.3	2.01	2.6	12.0	6.1	2.03	2.6	11.3	5.7	1.97	2.3	11.3	5.0	1.87
	JUL	105	6.6	13.2	9.2	1.65	6.6	13.2	9.0	1.58	6.1	13.0	8.6	1.79	3.9	12.8	7.8	1.71	2.4	11.7	5.4	1.78
1973	MAY	114	1.5	8.6	4.2	1.39	1.5	8.6	4.1	1.14	1.5	8.6	4.1	1.32	1.4	8.5	4.0	1.30	1.4	7.7	3.8	1.19
	JUN	153	2.8	12.2	6.2	2.00	1.7	11.9	6.0	2.02	2.6	11.9	5.9	2.02	1.5	11.9	5.6	2.03	1.3	11.5	4.9	2.11
	JUL	112	7.0	14.2	9.2	1.62	6.0	14.1	8.9	1.60	5.1	13.8	8.5	1.66	4.1	12.2	7.5	1.81	1.8	10.5	4.8	1.54
1974	MAY	103	1.9	11.0	5.7	2.12	1.9	11.2	5.6	2.14	1.9	11.2	5.6	2.19	1.9	11.2	5.6	2.15	1.9	11.2	5.5	2.17
	JUN	167	2.8	10.6	6.1	1.69	2.8	10.6	6.1	1.68	2.8	10.6	5.9	1.92	2.3	10.6	5.8	1.79	1.0	10.3	5.4	1.93
	JUL	96	6.4	11.9	9.1	1.28	6.4	11.9	8.9	1.26	5.6	11.8	8.4	1.25	4.6	10.9	7.5	1.37	2.9	8.0	5.0	1.24
1975	MAY	90	2.8	9.3	4.9	1.22	2.8	9.3	4.4	1.19	2.6	9.3	4.3	1.71	2.6	9.2	4.2	1.15	2.5	9.2	4.1	1.11
	JUN	133	3.5	10.8	5.8	1.57	3.3	10.8	5.7	1.54	1.4	10.4	5.6	1.60	2.8	10.3	5.4	1.61	2.1	9.8	4.8	1.71
	JUL	115	5.9	13.8	9.0	1.33	5.9	13.8	8.7	1.36	5.5	13.8	8.2	1.49	3.2	13.8	6.4	1.57	1.8	10.1	4.1	1.46
1976	MAY	109	1.9	10.3	4.3	1.63	1.7	10.8	4.2	1.67	1.6	10.5	4.2	1.67	1.5	10.4	4.1	1.68	1.3	10.3	4.0	1.65
	JUN	130	3.2	11.1	5.7	1.78	3.2	10.9	5.7	1.76	3.2	10.6	5.5	1.75	3.1	10.1	5.3	1.69	2.6	10.0	4.7	1.53
	JUL	121	6.2	13.6	8.0	1.31	6.2	13.5	7.9	1.32	5.9	12.9	7.7	1.37	2.7	12.8	7.2	1.23	2.5	9.5	5.2	1.34

Table C-2. Monthly minimum, maximum, and mean of water temperature corresponding to $C_t > 2.004$ at 0, 10, 20, 30, and 50 *m* depth in the area 3, 1971-76.

			0 *m*				10 *m*				20 *m*				30 *m*				50 *m*			
YEAR	MON	N	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD	MIN	MAX	MEAN	SD
1971	MAY	16	1.9	5.6	4.0	1.10	1.9	5.6	4.0	1.09	1.9	5.7	3.9	1.10	1.8	5.6	3.8	1.10	1.7	5.6	3.8	1.11
	JUN	9	4.0	5.9	5.3	0.58	4.0	5.8	5.3	0.54	4.0	5.6	5.2	0.51	3.9	5.5	5.1	0.51	3.6	5.4	4.7	0.68
	JUL	6	7.4	8.1	7.7	0.26	7.0	8.1	7.5	0.37	6.9	7.6	7.3	0.30	5.0	7.4	6.6	1.09	4.1	6.4	5.3	0.99
1972	MAY	28	2.9	7.8	4.1	1.06	2.8	6.2	4.0	0.87	2.8	5.6	3.9	0.83	2.7	5.3	3.8	0.77	2.6	5.2	3.7	0.72
	JUN	13	3.1	6.7	5.0	1.16	3.0	6.1	4.9	1.13	2.8	5.9	4.7	1.07	2.8	5.9	4.5	1.13	2.8	5.9	4.0	1.02
	JUL	15	7.0	8.4	7.7	0.45	7.0	8.4	7.6	0.41	6.5	8.0	7.3	0.38	4.8	7.6	6.7	0.71	2.6	6.5	5.3	1.09
1973	MAY	16	2.1	6.7	4.4	1.45	2.1	6.7	4.3	1.40	2.1	6.7	4.2	1.40	2.1	6.6	4.2	1.37	2.1	6.5	4.1	1.32
	JUN	9	3.8	7.0	5.2	1.02	3.7	6.4	5.0	0.91	3.7	6.0	4.9	0.80	3.5	5.8	4.7	0.82	2.7	5.6	4.0	0.92
	JUL	9	7.2	8.3	7.7	0.37	7.2	8.0	7.7	0.32	7.1	8.0	7.5	0.33	5.9	8.0	7.1	0.62	3.5	7.0	4.5	1.05
1974	MAY	7	3.5	4.6	4.2	0.35	3.5	4.6	4.2	0.36	3.5	4.6	4.2	0.36	3.5	4.6	4.2	0.36	3.4	4.6	4.1	0.39
	JUN	5	5.4	7.1	6.0	0.65	5.4	5.8	5.7	0.17	5.2	5.5	5.4	0.13	5.1	5.5	5.2	0.17	4.4	4.8	4.5	0.17
	JUL	11	8.0	9.2	8.5	0.32	8.0	8.7	8.4	0.22	5.7	8.6	8.0	0.97	4.9	8.4	7.5	1.29	3.6	4.8	4.2	0.38
1975	MAY	13	2.8	4.7	4.0	0.73	2.8	4.7	4.0	0.73	2.8	4.7	4.0	0.71	2.8	4.7	3.9	0.71	2.8	4.7	3.9	0.70
	JUN	7	4.6	6.0	5.3	0.46	4.6	6.0	5.3	0.47	4.6	5.9	5.2	0.42	4.3	5.2	4.8	0.30	3.4	4.7	4.1	0.50
	JUL	12	7.2	8.6	7.9	0.40	6.6	8.5	7.7	0.66	6.3	8.4	7.4	0.62	4.0	7.8	6.2	0.98	2.7	5.4	4.1	0.71
1976	MAY	33	2.4	6.3	4.0	0.75	2.3	5.8	4.0	0.73	2.3	5.6	4.0	0.74	2.2	5.5	4.0	0.74	1.9	5.3	3.9	0.82
	JUN	22	3.6	6.6	4.9	0.77	3.5	6.0	4.6	0.74	3.3	5.9	4.5	0.74	3.1	5.9	4.3	0.80	2.6	5.6	3.8	0.76
	JUL	14	7.0	8.3	7.3	0.38	6.9	8.0	7.3	0.32	6.7	7.4	7.1	0.23	5.3	7.2	6.4	0.63	3.6	5.5	4.7	0.67