

Climatic Influence Linking Copepod Production with Strong Year-Classes in Sablefish, *Anoplopoma fimbria*

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Stomach contents from first-feeding larval sablefish (*Anoplopoma fimbria*) comprised mainly calanoid copepods. Along the west coast of Vancouver Island, these copepods were the dominant zooplankton at the depth that sablefish larvae developed. We propose that strong year-classes in sablefish populations occur when there is exceptional production of copepods. The periods of exceptional copepod production appear to be correlated with climate and ocean conditions.

On a observé que les contenus stomacaux de larves de morue charbonnière (*Anoplopoma fimbria*) en début d'alimentation comprenaient principalement des copépodes calanoïdes. Le long de la côte ouest de l'île de Vancouver, ces copépodes composaient la plus grande partie du zooplancton à la profondeur à laquelle ces larves de morue charbonnière se développaient. Nous pensons qu'il y a production de fortes classes d'âge dans les populations de morue charbonnière quand il y a abondance de copépodes. Le climat et les conditions océaniques semblent être responsables des périodes de production exceptionnelle de copépodes.

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Understanding the factors that control recruitment is the most important problem in fisheries science. The extensive literature published on this topic since Hjort's (1914) original hypothesis that year-class strength was determined early in the life history is evidence that the population dynamics process remains poorly understood. A major advance was made when Ricker (1954) and Beverton and Holt (1957) proposed that recruitment could be predicted from stock size. Rothschild (1986) pointed out, however, that the stock–recruitment relationship is a paradox: although the relationship of recruitment to parent stock appears to be critical to population stability, there are little supporting data for the existence of such a relationship. One difficulty with stock–recruitment theory is that the relevance of environmental factors is not well understood. By studying the relationship of environmental variation and recruitment, we attempted to gain a better comprehension of the importance of environmental variation to the stock–recruitment relationship.

In an earlier paper, we examined the relationships between the environment and recruitment of sablefish (*Anoplopoma fimbria*) (McFarlane and Beamish 1986). There, we excluded the possibility of the physical movement of larvae into more productive onshore areas because oceanographic events that were correlated with year-class strength occurred before most larval fish reached the surface waters. We hypothesized that favourable oceanographic conditions increased the amount of food available for sablefish larvae at depth. We believed that this increased production of food would coincide with the initiation of larval feeding, possibly as early as the half yolk sac utilization stage. In this study, we provide evidence to support our hypothesis.

Methods

Study Area

The study area included the La Perouse Bank area and associated slope waters off the southwest coast of Vancouver

Island (Fig. 1). Two transect lines, approximately 36 km apart, were laid out approximately perpendicular to the bottom contours. Each line extended from 8 to 200 km from shore, with sampling stations 10–20 km apart.

Sampling Procedures

Discrete depth samples were taken at each station using a 1-m² Tucker trawl that opened and closed at depth. Each trawl unit consisted of three nets. When deploying this gear, the bottom net was open with the middle and top net closed. At the desired depth, the middle net was opened and the top and bottom net closed for a tow duration of approximately 15 min. During retrieval the top net was open.

Nets were constructed of 335- μ m black nitex mesh with a ridged codend equipped with a 335- μ m screen. A flowmeter installed in the mouth of each net recorded the volume of water filtered. Samples were collected during January, February, and March 1987 and February and March 1988 at stations along the transect lines. Samples were collected at <200, 300, 500, and 700 m. In addition, Tucker trawl and surface samples were collected in April of both years from selected stations to examine the distribution and stomach contents of larval sablefish.

Surface samples were taken at night using a modified Sameoto sampler — a neuston sampler equipped with a flowmeter (Sameoto and Jaroszynski 1969). The sampler was 45 cm high \times 45 cm wide with a 500- μ m mesh Nitex net. The codend was PVC with a 351- μ m stainless steel mesh window. Each tow was 15 min long at a speed of 3 knots.

The recovered nets were thoroughly washed down and the catch preserved in 5% buffered seawater formaldehyde. In the laboratory, zooplankton were identified and a subsample enumerated. Copepods from the subsample were identified to genus with the exception of calanoid copepods which were identified to species. Relative abundance estimates (numbers per cubic metre) were made for total plankton per station and for cope-

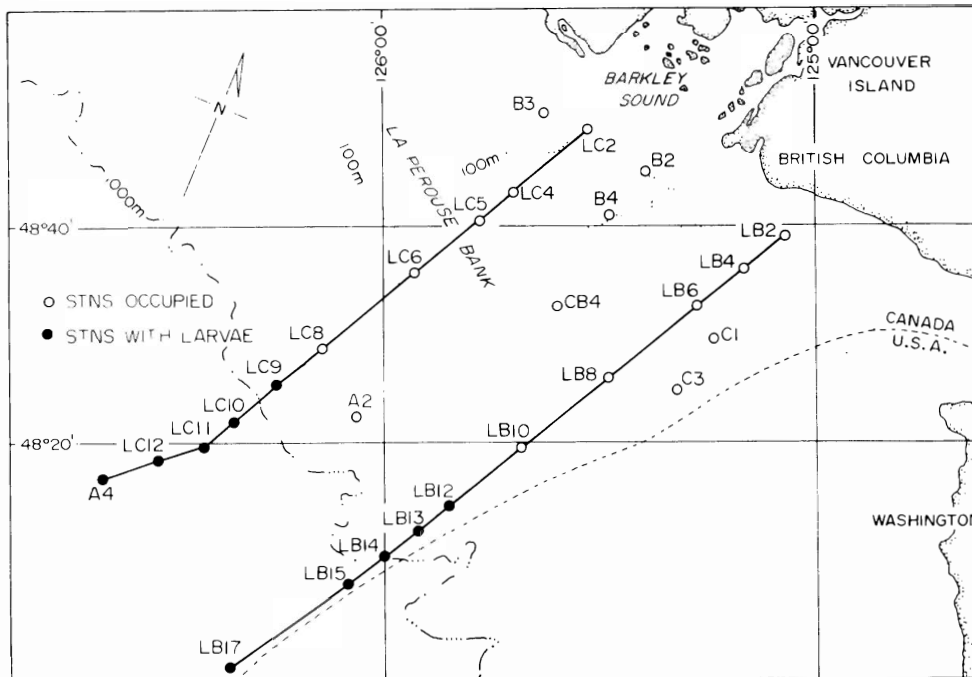


FIG. 1. La Perouse Bank survey lines and sampling stations.

Pods per station. All fish larvae were identified to species and enumerated. All sablefish larvae were measured, developmental stage determined, and stomach contents identified.

Laboratory Studies on Larval Development

In a laboratory study, sablefish were reared from egg to full yolk sac resorption (McFarlane and Nagata 1988). Information on egg and larval density relative to seawater was collected throughout the study by estimating salinity of neutral buoyancy (SNB) (Alderdice et al. 1988; G. A. McFarlane and J. O. T. Jensen, unpubl. data). Using this information, plus developmental times (McFarlane and Nagata 1988) and oceanographic data (McFarlane et al. 1991), it was possible to estimate the location of eggs and larvae by developmental stage in the water column as a function of the difference in density from that of the surrounding water (Alderdice et al. 1988; McFarlane et al. 1991). The rate of ascent or descent was calculated using Stokes' equation (Alderdice and Forrester 1971):

$$W = \frac{2}{9} g \frac{(p_1 - p_2)}{u} r^2$$

where W = vertical egg velocity (centimetres per second), g = 980.621, p_1 = egg density (grams per cubic centimetre), p_2 = density of the surrounding water (grams per cubic centimetre), u = 0.0150 (dynamic viscosity of seawater estimated at 35‰ and averaged for 5–10°C (Sverdrup et al. 1946), and r = radius of the egg (centimetres).

Schnute's (1981) general growth model was used to obtain empirical models to (1) estimate changes in egg density in relation to ambient temperature and (2) describe changes in salinity and temperature in relation to depth. This allowed calculation of water density (Millero and Poisson 1981) in the ocean water column to depths of 1000 m.

To calculate the location of eggs and larvae in the water column, these relationships were incorporated into an interactive model that, given an initial spawning depth, calculated egg density (dependent on temperature and time from fertilization).

This density value was put into the Stokes' equation to determine the vertical egg velocity at a given time and depth. The model then calculated, first at 12 h followed by 24-h intervals, the egg's new location in the water column. At this new location the water temperature and salinity were recalculated, based on the modelled STD data.

Then, the mean temperature exposure was determined and the corresponding egg development rate was calculated so that the SNB of the egg could be determined. The new SNB was again input into the Stokes' equation to calculate a new vertical egg velocity. This process was repeated until 510 h (21.5 d) past hatching.

Data Sources

The method for ageing sablefish was first developed in 1977 (Beamish and Chilton 1982). The method has since been validated (Beamish et al. 1983) and it is now known that the interpretation of annuli can be difficult for older fish. This reduced level of precision makes it difficult to identify the exact year in which previous strong year-classes were produced.

If it is assumed that total mortality has been relatively constant since the inception of the fishery and that the fishery did not target on any particular year-class, then it is possible to reconstruct relative cohort strength and develop a year-class index. Initially (McFarlane and Beamish 1983a), we reconstructed cohort strength for age frequencies of females from age composition data in 1980 and 1981 corrected for natural mortality (m) of 0.1 to identify strong year-classes in the 1950's and 1960's. This was done for the 1960–82 year-classes by standardizing the sample size for each year to 1000 individuals. The numbers of individuals in each age group were adjusted to estimate year-class strength using a natural mortality rate of 0.1. Estimates of year-class strength for year-classes from 1960 to 1975 were determined using age composition data from samples collected from 1980 to 1983. Estimates of year-class strength for year-classes from 1976 to 1982 were determined using age composition data from samples collected from 1984

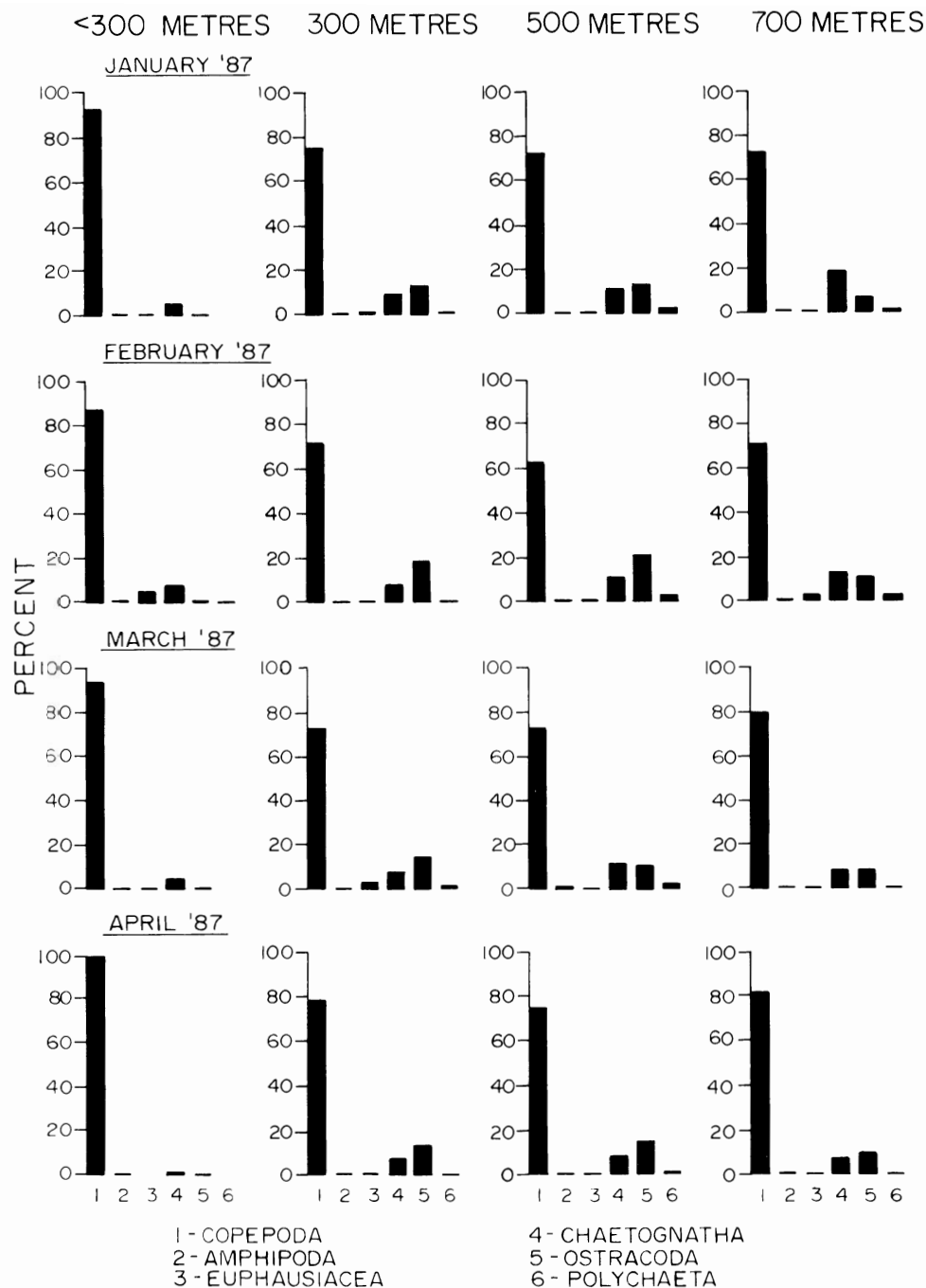


FIG. 2. Major components of zooplankton by depth, month, and year. (Fig. 2 concluded next page)

to 1989. The estimates of year-class strength were then averaged to produce a relative year-class index. The relative year-class index of year-classes in the early 1960's (1960-65) is poorly estimated because of the small numbers of observations.

Ocean Station P (50°N, 145°W) has yielded the longest time series of plankton abundance data in the central Northeast Pacific Ocean. Data for the winter months are available from 1965 to 1980, when the program was terminated. We developed an index of copepod abundance using Ocean Station P data for March-May 1965-80 (data from Fulton 1983). We chose March-May because this is the period of larval development of sablefish. A standard net haul was from 150 m to the surface at 1 m/s. Mean numbers for each month reflect the average of all vertical hauls made during daylight. In months

for which no data were available the mean number of copepods was estimated from the mean proportion of copepods captured in each month for the years 1965-80.

We needed to relate sablefish year-class strength and our copepod abundance index to an index of climate and/or ocean conditions. Because the strong 1977 year-class of sablefish occurred at the same time as strong year-classes for many other species along the west coast of North America (R. J. Beamish, unpubl. data), we believed that the environment was affecting fish production over an extremely large area. This indicated to us that the intensity of the Aleutian low pressure region, the major winter climate system in the central North Pacific Ocean, could be used as an index of climatic and oceanographic conditions. In particular, it would represent an index of wind

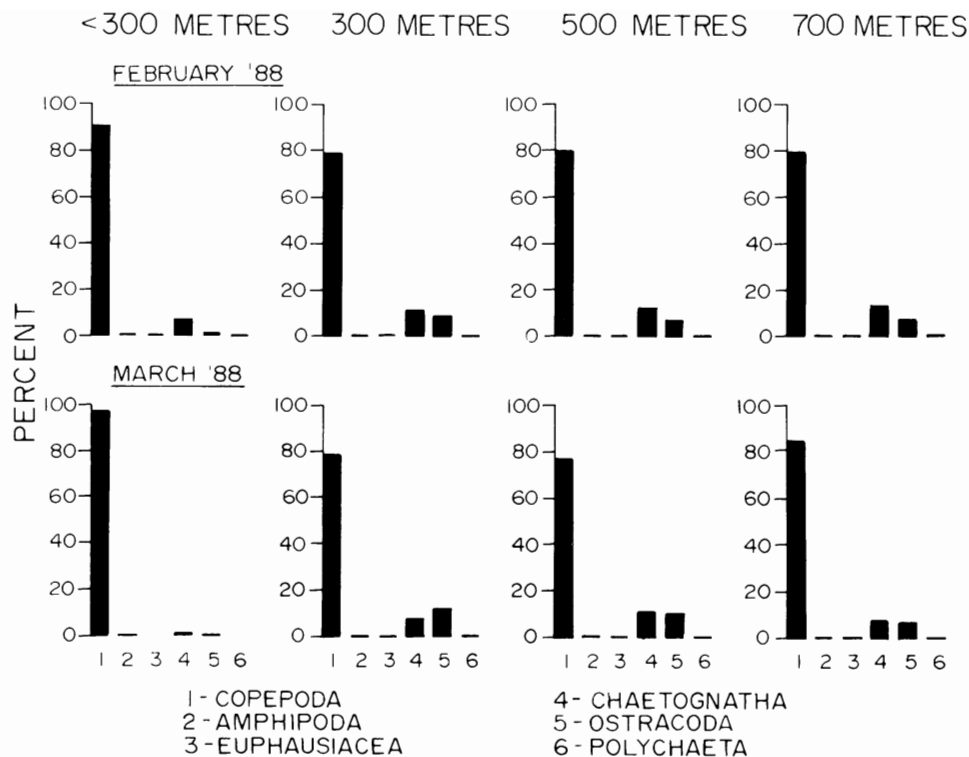


FIG. 2. (Concluded)

strength, current strength, midocean upwelling, coastal downwelling, and coastal sea surface temperature in the North Pacific Ocean.

Hamilton (1984) produced monthly estimates of the intensity of Aleutian lows in the North Pacific Ocean. We chose the 100-kPa isobar as the boundary of an intense Aleutian low. We developed an Aleutian low pressure index for winter months (December–February) for the years 1940–82 by estimating the area (square nautical miles) of the North Pacific Ocean with atmospheric pressures ≤ 100 kPa as indicated on atmospheric pressure maps (Hamilton 1984).

Results

Plankton

A total of 148 (444 samples) and 101 (303 samples) hauls were made in 1987 and 1988, respectively. In both years, copepods were the dominant zooplankton present at all depths and in all months (Fig. 2). In the upper layer (<300 m), copepods accounted for 88–98% of the plankton over all months sampled. At other depths, they accounted for 63–84%. The remaining zooplankton included representatives of Amphipoda, Euphausiacea, Chaetognatha, Ostracoda, and Polychaeta.

Copepod densities ranged from approximately 2.0 to 216.0 individuals/m³. There was large variation in the numbers of copepods per cubic metre among stations and depths (Fig. 3), with higher abundance in shallower waters (<200 m) over the continental shelf. At the stations and depths (Fig. 1) that sablefish larvae were captured (in waters >300 m over the shelf/slope break), copepods accounted for 65–92% of the plankton (Fig. 2). Calanoid copepods accounted for 85–100% of the copepods.

Larval sablefish were only captured in water deeper than 300 m in February and March of both years (Table 1). A total

of 147 sablefish larvae were captured at depth in February and March 1987 and 57 larvae in 1988. All larvae captured in February of both years were at an early developmental stage (6–8 mm; half yolk sac utilization stage or earlier). During March of both years, most (76 and 67%, respectively) larvae were captured at depths of 500 m or greater. These larvae were smaller, less pigmented, and at an earlier yolk utilization stage than those in shallower waters (<500 m). In April, no larvae were captured at depth and all larvae examined from the surface waters were >10 mm and had resorbed all yolk.

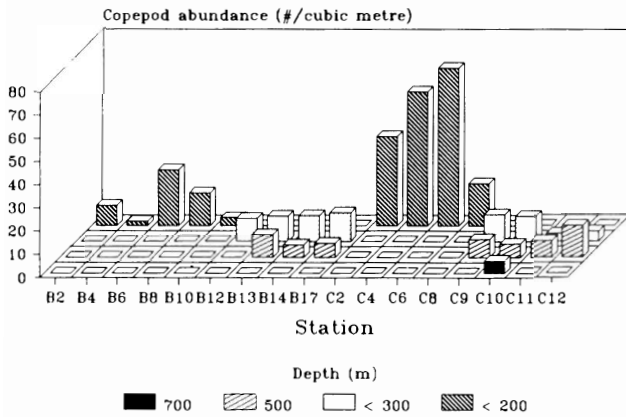
Larval Feeding

None of the larvae examined in February (Table 1) of either year contained food because they were in the early yolk utilization stage. At this stage the mouth is not functional (McFarlane and Nagata 1988). Of the 137 larvae examined from March 1987 collections, 70 (52%) contained food items. This percentage was almost identical for larvae examined from March 1988 collections (54%). In both years, sablefish larvae fed exclusively on copepod eggs and nauplii. In April, in each year, approximately 40 larvae captured in the surface waters (neuston samples) were examined for stomach contents: 85% in 1987 and 93% in 1988 contained food items. The majority (90–95%) were feeding almost exclusively on calanoid copepods (nauplii and adults).

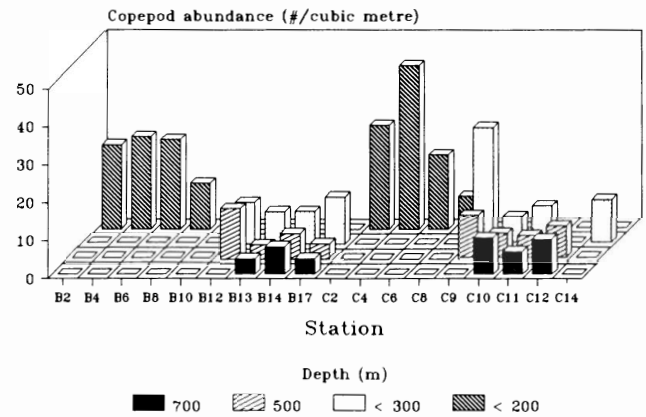
Larval Development from Laboratory Studies

Sablefish were reared from egg to full yolk sac resorption (McFarlane and Nagata 1988). Although it was difficult to make accurate SNB measurements on late-stage yolk sac larvae, visual observations of these larvae in the incubators indicate that after half yolk sac utilization, they were able to maintain themselves in the water column and would routinely move towards the surface. Incorporating the information on larval develop-

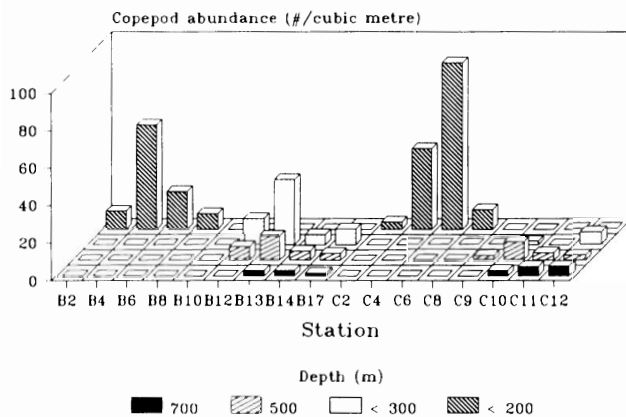
January 1987



February 1987



March 1987



April 1987

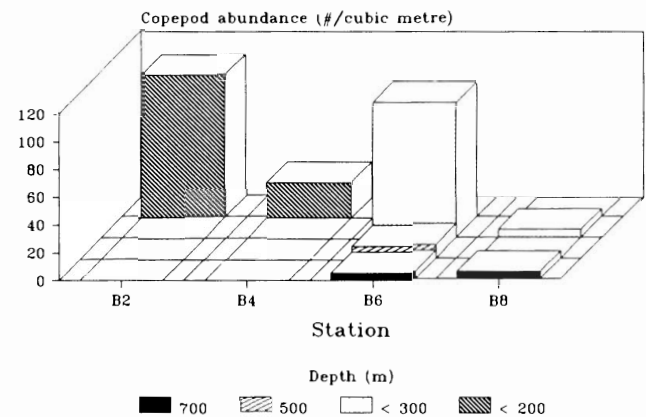


FIG. 3. Copepod abundance by month, station, and depth from 1987 and 1988. (Fig. 3 concluded next page)

ment (McFarlane and Nagata 1988), SNB, and ocean temperature at depth (McFarlane et al. 1991) into an interactive model, we can estimate development time at depth in the open ocean (Fig. 4). Assuming a spawning depth of approximately 300–500 m, the eggs rise to between 200 and 300 m immediately after fertilization (McFarlane and Nagata 1988). They remain suspended at this depth until approximately 24 h prior to hatching (12 d at 6°C). At this time, egg density increases and the eggs begin to sink. The newly hatched larvae become denser and continue sinking in the water column during early development (approximately 6 or 7 d), reaching a maximum depth of between 1000 and 1200 m. At this time, the eyes become pigmented. They remain at this depth until the half yolk sac utilization stage (approximately 14–17 d after hatching). During this time the alimentary canal, head, and body become pigmented. At approximately half yolk sac utilization, the mouth becomes functional and the larvae begin swimming movements. Larvae begin to show prey capture movements and ingest small food organisms within 2–3 d (approximately 20 d after hatching). Larvae begin to rise in the water column, presumably following copepod nauplii, and by full yolk sac utilization (approximately 40 d after hatching) are near the surface waters.

Strong Year-Classes

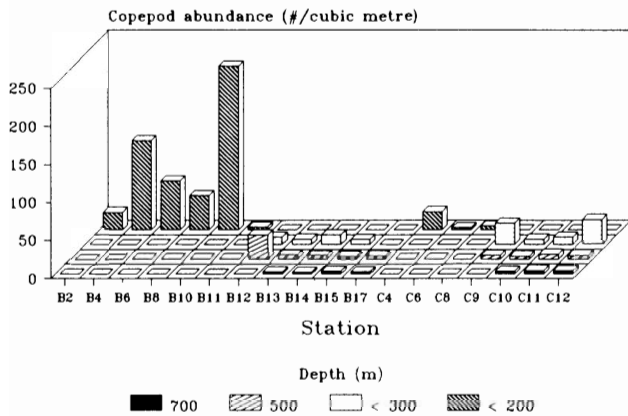
Variability in year-class survival is an important feature of sablefish populations (McFarlane and Beamish 1983a). Unfor-

tunately, age estimates needed to identify year-class strength or to reconstruct stock age compositions were not available until 1978 when the method for age determination of sablefish was first developed (Beamish and Chilton 1982). We used catch information from the commercial fishery and research cruises to identify the approximate year of strong year-classes in the 1940's, 1950's, and 1960's.

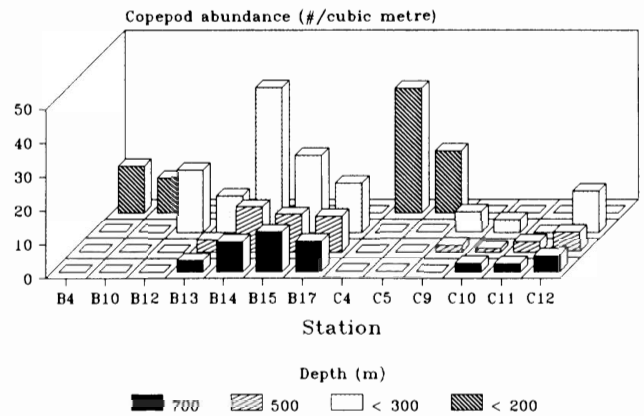
The Strong 1941 Year-Class

Exploratory groundfish research cruises started on the west coast of Vancouver Island in the mid-1940's (Forester 1946). An exploratory sunken gillnet fishery in Barkley Sound (Fig. 1) from 1944 to 1946 showed a dramatic decline in abundance of sablefish in July and August 1945 and 1946 from catches in 1944. Although no length data were available from catches in the 1940's, we believe that the method, area, and depth of capture indicate that the large numbers of sablefish caught in 1944 were juveniles. The decline in catch-per-unit-effort (CUPE) from 82.9 to 1.0 fish·net⁻¹·24 h⁻¹ in 1945 and 0.4 fish·net⁻¹·24 h⁻¹ in 1946 indicates a movement of juveniles out of this area. A similar movement of juveniles of the 1977 year-class out of shallow water occurred in the Canadian zone in 1980 (McFarlane and Beamish 1983b). If the juveniles in Barkley Sound in 1944 behaved in a similar manner, they would be age 3+ when movement occurred which suggests the 1941

February 1988



March 1988



April 1988

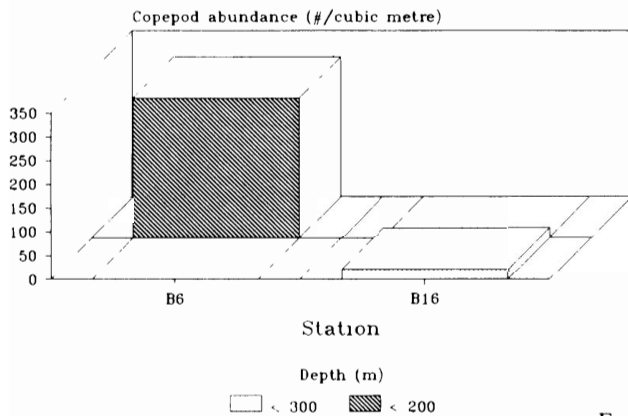


FIG. 3. (Concluded)

year-class was exceptionally strong. Another indication that large numbers of juveniles occurred in shallow waters in the mid-1940's was the introduction of a size limit in 1945 to restrict the number of small sablefish that were being caught in shallow water (Ketchen 1956). A decline in CPUE also occurred in the fisheries off Alaska between 1945 and 1947, suggesting to us that juveniles were very abundant in shallow waters prior to this time and that a strong 1941 year-class occurred over a relatively large area.

The 1953, 1958, 1967, and 1977 Year-Classes

Because sablefish live up to 70 yr (Beamish and Chilton 1982; Beamish and McFarlane 1987) the age composition of a population provides an index of relative year-class strength. We interpreted the relative year-class strength to indicate that strong year-classes occurred in the early 1950's (1953), the late 1950's (1958), and possibly the late 1960's (1967). Our initial reconstruction of relative year-class strength (McFarlane and Beamish 1983a) indicated that the 1958 year-class was exceptionally strong. We believe that this year-class was an important component of the large foreign fishery that occurred off Canada during 1968–76 (McFarlane and Beamish 1983c).

Small sablefish were abundant in the trawl fishery catches in 1969 and 1970. The large catches of small fish resulted in an attempt to develop a market for these fish during 1970

(McFarlane and Beamish 1983c). Again, assuming that these fish were approximately 3 yr old, they would be from the 1967 year-class. The most recent strong year-class occurred in 1977 (Fig. 5; Table 2). The initial indication of the strength of this year-class was the high abundance of juveniles in the inside waters throughout the range of sablefish in 1978 and 1979 (McFarlane and Beamish 1983b; Umeda et al. 1983; Fujioka 1985; Sasaki 1985). After this year-class moved out of the inside waters in 1980–81 (McFarlane and Beamish 1983b), there has been no indication of another strong year-class. The 1977 year-class was dominant in the fishery through the early to mid-1980's (Saunders et al. 1987). Although no year-classes of comparable size to 1977 have been identified since, survival of some year-classes has been above average (Francis 1985; Fujioka 1985, Saunders et al. 1987). Our relative year-class index also indicates that year-classes after 1977 were reasonably strong.

Climate, Oceanography, and Copepod Production

Strong year-classes occurred after extended periods of below-average sea surface temperatures in coastal waters which occurred off Vancouver Island during 1936–39, 1945–52, 1954–57, and 1968–76 and a moderate cooling during 1964–66 (Fig. 6). All strong year-classes followed immediately after the cooling period in coastal waters changed to a period of

TABLE 1. Sablefish larvae captured by Tucker trawl, February and March 1987 and 1988. Numbers in parentheses indicate larvae with copepods in gut.

Stn. No.	Depth strata (m)			Depth strata (m)		
	300	500	700	300	500	700
February 1987						
LB12	1	4		4	4	
LB13			1		13	10
LB14		1		3	3	1
LB17	1		1	1	5	5
LC9		1		6	4	
LC10				8	13	14
LC11				5	4	5
A4				6	5	9
Total	2 (0) ^a	6 (0) ^a	2 (0) ^a	33 (24) ^b	51 (27) ^c	53 (19) ^d
February 1988						
LB12				3		
LB13				5	3	4
LB14	1			1		2
LB15				4	1	1
LB17					2	4
LC9					5	
LC10	2	1		4	1	5
LC11				1	4	
LC12				1		3
A4			1			
Total	3 (0) ^a	1 (0) ^a	1 (0) ^a	17 (12) ^b	16 (7) ^c	19 (9) ^d

^aAll larvae at half yolk sac utilization stage or earlier.

^bMost larvae nearing full yolk sac utilization stage.

^cMost larvae at three quarters yolk sac utilization stage or later.

^dMost larvae at half yolk sac utilization stage or later.

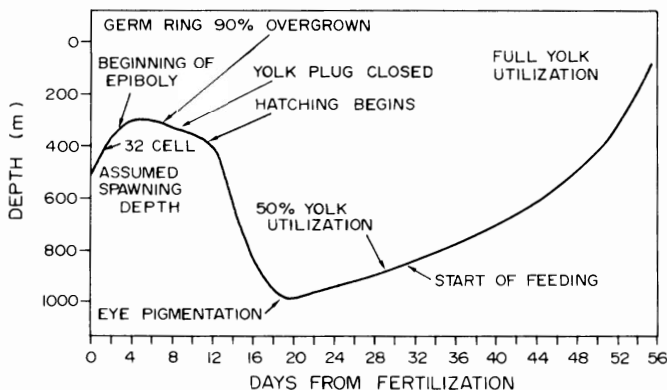


FIG. 4. Probable depth distribution by developmental stage of sablefish eggs and larvae in the study area.

above-average sea surface temperatures. There was no such period of change that did not produce a strong year-class, and no strong year-class was produced during other periods. The warming event in coastal waters following the period of change was characterized by more intense Aleutian lows in the North Pacific Ocean (Fig. 7).

The Aleutian low-pressure region is the dominant feature of the climate and ocean circulation (Fig. 8) in the northern North Pacific Ocean (Wilson and Overland 1987). Aleutian lows begin to form about the time of the fall transition in October and persist until approximately April of the following year.

Aleutian lows are caused by intense storms that frequent the area. These storms transfer momentum to surface waters increasing wave and current activity. Strong Aleutian lows intensify the strength of the eastward flowing subarctic current, the westwind drift, and the Alaska current that flows poleward (Emery and Hamilton 1985). This leads to a stronger than normal poleward advection of warm coastal water along the west coast of North America. Surface temperature patterns off British Columbia clearly show these warming trends (Fig. 6). During the winter of 1977, the Aleutian low was the strongest since 1940 (Fig. 7) and coastal sea surface temperatures were the highest since 1968. Other periods of intense Aleutian lows coincided with each of the strong year-classes identified except for the intense Aleutian lows of the early 1960's and 1970 which were not coincident with a period of below-average sea surface temperatures.

Copepods dominate the zooplankton biomass of the North-east Pacific Ocean. Two large calanoid copepods, *Neocalanus plumchrus* and *N. cristatus*, make up 75% of the total zooplankton biomass (Miller et al. 1984). Although annual variations in copepod biomass in the Northeast Pacific Ocean are not well documented, relative abundance indices developed from Ocean Station P data (Table 3) suggest considerable variation. Despite this variation, it is apparent that biomass of copepods increased in 1976 and 1977. Copepod production was also above average in 1967.

As part of our study of sablefish year-class production, we wanted to examine the relationship among the Aleutian low index, copepod abundance, and sablefish year-class strength. Proper analysis of these data required a time series approach. Using a transfer function noise (TFN) model (Noakes et al. 1987), we found that the time series of copepod abundance (Table 3) was positively related ($r^2 = 0.63$; $p < 0.001$) to the time series of the Aleutian low index (Fig. 7). As suggested by this analysis, these two time series were sufficiently correlated that only one of them was required to adequately explain the time series of sablefish year-class relative abundance; thus, using the TFN process, we found that the Aleutian low index bore a closer statistical relationship to the sablefish year-class index ($r^2 = 0.53$; $p \leq 0.001$) than did copepod abundance ($r^2 = 0.45$; $p \leq 0.001$). These analyses demonstrated a positive relationship between sablefish year-class strength and both copepod abundance and the intensity of the Aleutian lows, with stronger year-classes tending to occur during years of more intensive Aleutian lows and higher copepod abundance.

Discussion

Theory

Strong year-classes are an important feature of sablefish population dynamics. We propose that strong year-classes are associated with large-scale increases in copepod abundance, which occur during major climate events in the North Pacific Ocean. We propose that cooling of the central North Pacific Ocean increases nutrient supply to the surface waters, improving primary productivity. The intense Aleutian low that follows this period of cooling transports nutrients and plankton into coastal waters by increasing wind-driven transport of surface waters. The intensification of the Aleutian low also increases the intensity of the northward flowing coastal current (Alaska current) and increases coastal sea surface temperature. Exceptionally strong year-classes are produced at the beginning of a cycle when coastal waters change from below-average to above-average sea surface temperatures. At the same time the

TABLE 2. Year-class index (YCI) for sablefish (1960–82) developed from the numbers in each age group of age composition samples collected from 1980 to 1989 (standardized to 1000 and adjusted using a natural mortality rate of 0.1).

Year-class	Year										YCI
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	
1960	165	142	50	65							105
1961	156	114	88	70							107
1962	146	132	77	74							107
1963	162	117	70	82							108
1964	178	130	92	75							119
1965	134	136	70	60							100
1966	135	137	87	80							110
1967	181	167	145	98							148
1968	128	104	95	85							103
1969	97	122	107	74							100
1970	62	71	91	50							69
1971	54	63	105	64							72
1972	44	45	64	31							46
1973	38	32	77	57							51
1974	31	59	62	36							47
1975	20	51	53	34							40
1976		84	104	77							80
1977			228	272	333	214					262
1978				94	194	228	202				179
1979				144	201	186	192				181
1980					127	150	192	222			173
1981						112	112	190	183		149
1982							46	111	112	66	84

intense Aleutian low increases upwelling in the central North Pacific Ocean, further increasing transport of nutrients into surface waters. The advection of increased amounts of nutrients and plankton to and along the coast increases the survival of copepod nauplii, increasing the food supply for larval sablefish. In the following discussion, we provide evidence to support our theory.

1. Importance of spawning biology and egg and larval development

Sablefish spawn from January to March along the continental slope at depths exceeding 300 m. Peak spawning occurs in mid- to late February. Sablefish spawn almost simultaneously in all areas over the Canadian continental slope (Mason et al. 1983). Tagging studies (Beamish and McFarlane 1983, 1988; Dark 1983) indicate little movement of adult sablefish. For example, 81% of the fish tagged from February to September 1977–80 were captured in spawning condition within 100 km of the capture and release location (Mason et al. 1983), indicating no extensive spawning migration.

Eggs hatch in deep water in approximately 12 d and larvae sink to approximately 1000 m and remain there until initiation of feeding (about 20 d after hatching). Sablefish spawning is synchronous with the spawning of two of the most abundant copepods in the Northeast Pacific Ocean, *N. plumchrus* and *N. cristatus*, which constitute 75% of the zooplankton (Miller et al. 1984). We found that calanoid copepods represented 85–100% of the copepod biomass at the depths that sablefish larvae were captured. In both years the captured larvae were feeding exclusively on copepod eggs and nauplii. Therefore, it appears that larval sablefish survival is closely linked to calanoid copepod production, and a dramatic increase in copepod abundance would be expected to improve sablefish survival.

2. Importance of copepod biology

The biology and spawning behaviour of calanoid copepods are critical to our theory for the regulation of sablefish popu-

lation size. *Neocalanus plumchrus* can graze on a wide range of phytoplankton (Parsons et al. 1969) and is one of the few copepods that spawn at depths over 1000 m (Miller et al. 1984). After grazing in the surface waters during May–August, *N. plumchrus* stores lipids in preparation for overwintering. This storage of lipids during the seasonal phytoplankton production cycle not only ensures survival over the winter, but the volume of lipids is directly related to fecundity (Cooney 1987). At Ocean Station P during 1980 and 1981, Miller et al. (1984) reported that the two *Neocalanus* sp. spawned below 250 m and as deep as 1200 m during the entire year. Most spawning occurred from August through February, resulting in the production of large numbers of eggs and nauplii. After hatching, nauplii moved to the surface and copepodite stages were present in greatest abundance from April to July (Miller et al. 1984). The reproductive cycle of these two species, as determined at Ocean Station P, coincides with the spawning cycle and early development of larval sablefish. Prior to our study, there was no information on copepod reproductive behaviour or egg and nauplii development along the continental shelf or slope off the west coast of Canada. Our observations confirm the Ocean Station P observations and indicate that large numbers of copepods spawn over the Canadian continental slope at depths of at least the maximum depth sampled (700 m).

3. Relationship with climate and oceanography

We have identified a significant relationship between larval survival, copepod abundance, and environmental conditions (Aleutian lows) for the years 1965–80. During the early 1970's, a period of weak Aleutian lows and below-average sea surface temperatures in coastal waters, the year-class index clearly shows a series of weak year-classes. The relationship between Aleutian lows and copepod abundance from 1965 to 1980 suggests that larval sablefish survival improves when there is an abundant supply of copepod eggs and nauplii. The intensive

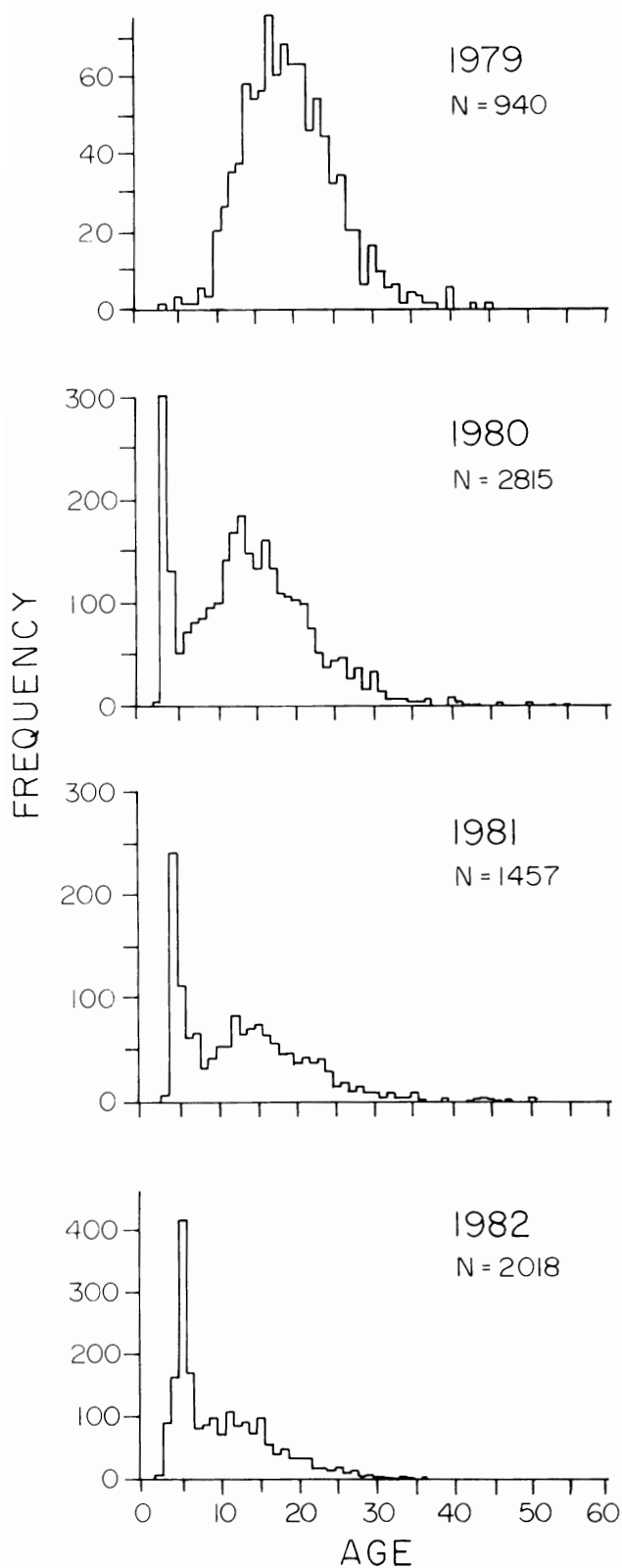


FIG. 5. Age composition of sablefish captured in the Canadian commercial fishery during 1979-82.

Aleutian lows in the early 1960's corresponded to above-average year-class strength; however, no exceptionally strong year-classes were identified. This could result because the year-class strength index was produced using age composition data from 1980 and 1981 and probably only approximates relative year-

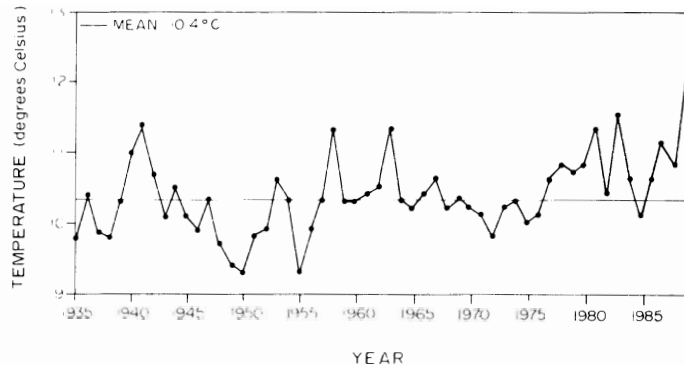


FIG. 6. Mean annual sea surface temperature at Amphitrite Point (southwest Vancouver Island) for 1935-89.

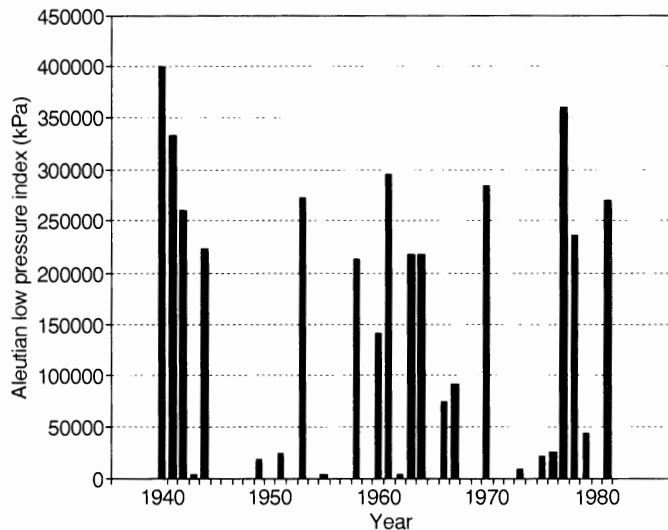


FIG. 7. Aleutian low pressure index for winter (December-February) 1940-82. The index reflects area (square nautical miles) of the North Pacific Ocean less than 100 kPa atmospheric pressure at sea surface.

class strength because of the small number of older fish in the samples. We suggest, however, that because the intense Aleutian lows in the early 1960's were not accompanied by a change from cool to warm surface temperatures in coastal waters at this time (temperatures were above average since 1958), no exceptionally strong year-classes were produced.

Climate can control ocean productivity by altering the heat storage in the surface waters above the mixing layer (Barber and Chavez 1983). A cold event is significant because during cold anomalies the thermocline is closer to the surface. This elevation brings the subsurface nutrient reservoir and surface light supply closer together, greatly increasing primary productivity (Barber and Chavez 1983). Venrick et al. (1987) identified a significant increase in primary productivity in the central North Pacific Ocean between the late 1960's/early 1970's and the early 1980's. An increase in winter winds (intense Aleutian lows) and a decrease in sea surface temperature in the central North Pacific Ocean were identified as the mechanisms responsible for this increased productivity and resulting increase in the carrying capacity. We suggest that a similar mechanism, accompanied by a change from below-average to above-average sea surface temperature in coastal waters, resulted in an increase in copepod abundance early in 1977. Conditions similar to 1977 occurred in 1940-41, 1952-53, and 1957-58 (Fig. 6, 7) and coincided with the production of the strong 1941, 1953, and 1958 year-classes of sablefish.

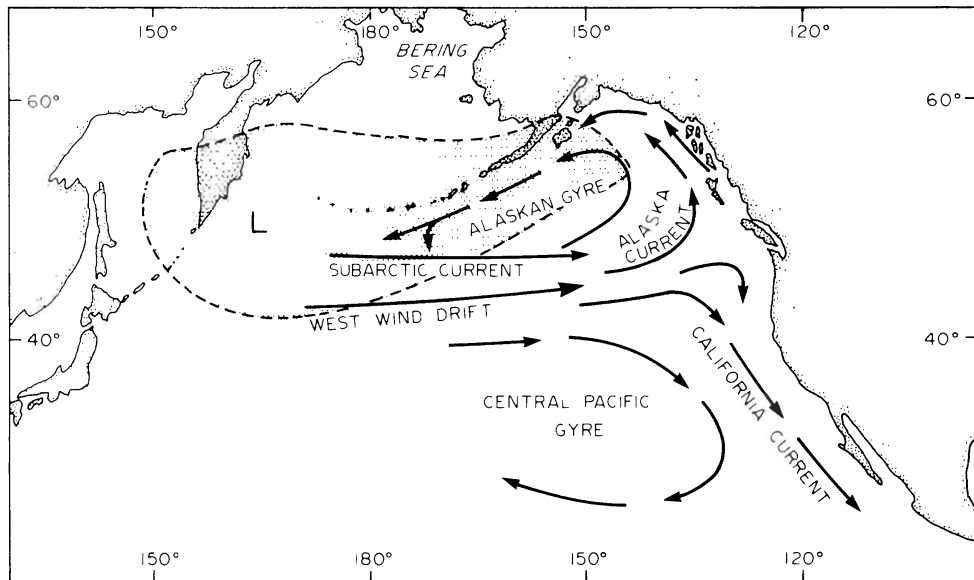


FIG. 8. Prevailing current directions and long-term mean (1940–82) Aleutian low pressure area in the North Pacific Ocean (from Hamilton 1984).

TABLE 3. Mean number of copepods per cubic metre at Ocean Station P (50°N, 145°W) in March, April, and May 1965–80.

Year	March	April	May	Average (weighted)
1965	26.5 ^a	50.8	61.4	46.2
1966	73.2	171.4	393.7	158.5
1967	81.1 ^a	98.7	246.0	141.6
1968	55.2	98.7	90.4	68.5
1969	19.7 ^a	39.8	46.8	35.4
1970	59.7	153.8	195.6	178.8
1971	4.8	14.9	25.2	15.4
1972	17.5	36.4	94.1	48.4
1973	71.2 ^a	121.3	180.2	124.2
1974	55.1	29.2 ^a	10.3	31.5
1975	44.1	84.6	105.4	92.7
1976	101.2	124.5 ^a	177.3	134.3
1977	143.2	256.2	263.4	236.3
1978	69.2	88.8	140.5	124.7
1979	44.6	41.1	231.4	106.4
1980	29.8	60.3	175.0	107.4

^aNo data available; estimated from the mean proportion of copepods caught in other months of the March–May period.

After 1977, sablefish year-classes had above-average survival (Francis 1985; Fujioka 1985; Saunders et al. 1987), but no exceptionally strong year-classes have been identified. These above-average year-classes appear to be a result of the increased productivity of the North Pacific Ocean in the late 1970's to mid-1980's identified by Venrick et al. (1987). Coastal sea surface temperatures have remained above average during this time. The absence of exceptionally strong year-classes corresponds with the absence of all ocean conditions similar to those that produced previous strong year-classes.

Many fish species exhibited exceptional production along the coast of North America from 1976 to 1978 (R. J. Beamish, unpubl. data). The increased survival of these species was also attributed to increased copepod production. Production of many of these stocks, particularly salmon, remained at a higher level in the 1980's. This increased fish production coupled with increased copepod abundance indicates that the increased sable-

fish production observed from the late 1970's to the early 1980's was part of an overall increased productivity in the North Pacific Ocean.

Frost et al. (1983) showed that calanoid copepods responded to increases in primary production by proportionally larger increases in feeding rate. An increase in feeding rate could result in increased growth, egg production, and survival in those species. Increased copepod abundance could occur as a result of improved fecundity, improved survival of copepod nauplii in coastal areas, or transport into these areas. It is apparent that the process responsible for improved copepod abundance requires further study. However, it appears that large-scale climate patterns are related to copepod abundance that in turn results in fluctuations in sablefish year-class strength.

Initially, we were concerned that our hypothesis would not explain why a relatively large population of sablefish occurred off California because *N. plumchrus* and *N. cristatus* are a minor component of the plankton in this region (Fulton and LeBrasseur 1985). Extensive surveys also have shown that larval sablefish are not found in this region (P. Smith, N.M.F.S., Southwest Fisheries Center, La Jolla, CA, pers. comm.), indicating that recruitment to this area must come from larval sablefish reared in more northern areas. Therefore, in all areas the distribution of sablefish larvae corresponds to the known distribution of *N. cristatus* and *N. plumchrus*.

Production of strong year-classes in long-lived fishes appears to be an adaptation to variations in ocean productivity or copepod production or both. Prior to the commercial fishery, sablefish probably responded to fluctuating food supplies by ensuring that there was always a minimal number of eggs produced. For sablefish and other long-lived species, this minimal number would be a function of fecundity, longevity, and population size. Over evolutionary time the length of less favourable environmental periods could select for the longevity of sablefish.

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