Abstract.–Ichthyoplankton were sampled weekly in Auke Bay, southeastern Alaska, from March or early April through June, 1986–89. The spring primary production bloom occurred in April, and was followed in May by the annual maximum in herbivorous copepods. Each year, the five most-abundant fish larvae were osmerids, Pacific sandlance *Ammodytes hexapterus*, walleye pollock *Theragra chalcogramma*, flathead sole *Hippoglossoides elassodon*, and rock sole *Pleuronectes bilineatus*. Each species tended to occur at the same time every year, and could be categorized either as synchronous species that were present at the time copepod abundance was maximized, or early species that were most abundant before the spring phytoplankton bloom. Pacific sandlance and rock sole larvae always reached maximum abundance prior to the spring bloom, whereas larvae of walleye pollock, flathead sole, and osmerids were most abundant at the time of the copepod maximum. Physical and biotic conditions experienced by early and synchronous larvae differ markedly, suggesting that survival through early life history is determined by different processes in the two groups.

Abundance patterns of marine fish larvae during spring in a southeastern Alaskan bay

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Fluctuation in recruitment to exploited fish populations remains a central problem in marine fish management. There are indications that much of the variation in year-class abundance in marine fish populations results from processes and events in planktonic early-life-history stages (Houde 1987, Pepin & Myers 1991). Interannual variation in survival through egg and larval life stages is undoubtedly determined by multiple and interacting mechanisms; however, timing of reproduction has often been implicated as a factor contributing to the success or failure of year-classes. For example, Hjort's (1914) critical-period hypothesis and Cushing's (1975) match-mismatch hypothesis describe the importance of synchrony between production of larval fishes and their planktonic prey.

In subarctic regions, nearshore marine ecosystems display marked seasonal changes in physical and biotic conditions (Smetacek et al. 1984). In such systems, timing of reproduction may be extremely important, as conditions that result in high survival through planktonic life-history stages may be transitory. A dominant feature in the annual subarctic nearshore production cycle is the spring phytoplankton bloom, an event that contributes much of the annual production (Smetacek et al. 1984). The phytoplankton bloom is followed by the herbivorous copepod maximum (Smetecek et al. 1984), a period of 1–2 months that produces an annual optimum in foraging conditions for those larval fishes that feed on copepod nauplii. Water temperature and predator density may also determine survival of fish eggs and larvae (Houde 1987) and could constitute important constraints on timing of reproduction.

In this paper we report the results of a 4-year investigation of larval fishes in a coastal subarctic marine ecosystem. Our observations describe when larvae of some northeast Pacific Ocean fish species occur relative to the spring production cycle. The study was part of an interdisciplinary project (APPRISE, Association of Primary Production and Recruitment in a Subarctic Ecosystem) that provided a detailed description of the physical and biotic environment present during the period from late winter through early summer.

Study area

The study was conducted in Auke Bay (lat. 58° 22'N, long. 134° 40'W), southeast Alaska. (Fig. 1). The 16 km² Bay varies in depth from 40 to 60 m. Physical conditions in Auke Bay are typical of nearshore subarctic marine

Figure 1

Auke Bay study area in southeast Alaska, and location of the Auke Bay Monitor (ABM) station.
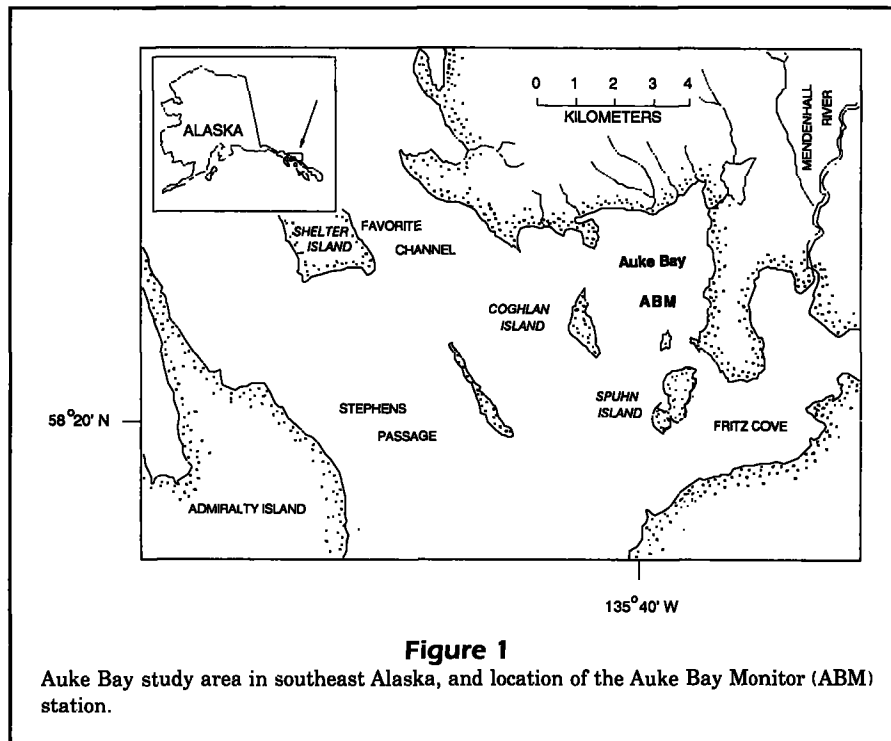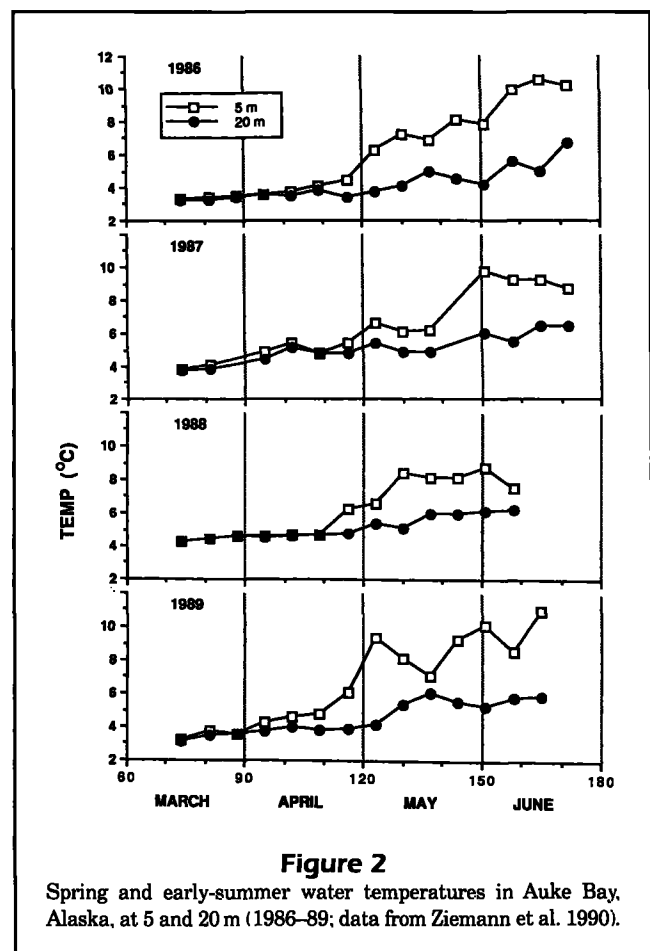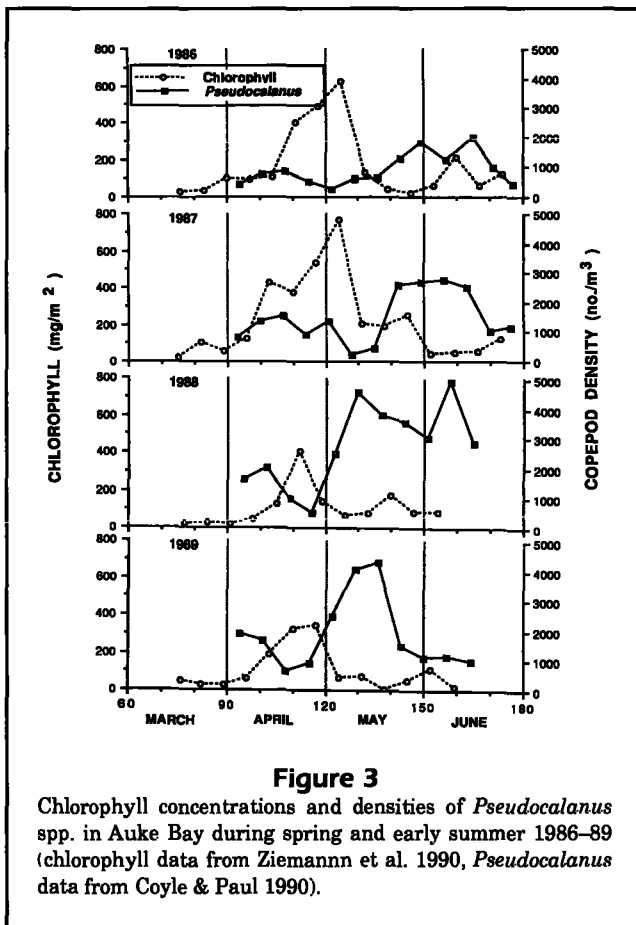
Materials and methods

Fish larvae were collected in Auke Bay at a station designated ABM (Fig. 1) from mid-March or early April through mid-June, 1986–89. The ABM station was selected because it had been used in previous studies (summarized in Coyle & Shirley 1990). Samples were collected on the same day each week between 0800 and 1300, with the exception on the second week of April 1986 (Fig. 4). Each week five replicate samples were collected with a $1\,m^2$ Tucker trawl constructed of $505\,\mu$ mesh and fitted with a digital flowmeter in the middle of the net opening. Each replicate was collected at the ABM station by towing the net in a double-oblique trajectory to a depth of 30–35 m. The vessel

systems. The water column is isothermal until April, when surface warming and increased freshwater runoff contribute to formation of a pycnocline (Bruce et al. 1977, Ziemann et al. 1991). In the 4 years of this study water temperature prior to stratification varied from 3° to 5°C, was colder in 1986 and 1989, and warmer in 1988 (Fig. 2; data from Ziemann et al. 1990). Stratification, indicated by diverging temperatures at 5 and 20 m, began in April (Fig. 2; data from Ziemann et al. 1990).

Auke Bay exhibits a typical subarctic annual production cycle (Williamson 1978, Ziemann et al. 1991). The spring phytoplankton bloom began in early April, 1986–89 (Fig. 3; data from Ziemann et al. 1990), in response to several consecutive days of relatively high light levels (Ziemann et al. 1991). Chlorophyll biomass peaked in late April or early May each year, with a subsequent decline resulting from nutrient limitation (Ziemann et al. 1991). The herbivorous copepod maximum began 2–4 weeks after the spring phytoplankton bloom (Fig. 3; data from Coyle & Paul 1990), with *Pseudocalanus* spp. copepods dominant in every year (Coyle et al. 1990). Copepod nauplii in the size-ranges consumed by larval fishes were typically in low density prior to the herbivorous copepod maximum and reached maximum density in May, although there was considerable interannual variation in nauplii density during the period of peak abundance (Paul et al. 1991).

Figure 2

Spring and early-summer water temperatures in Auke Bay, Alaska, at 5 and 20 m (1986–89; data from Ziemann et al. 1990).

Figure 3

Chlorophyll concentrations and densities of *Pseudocalanus* spp. in Auke Bay during spring and early summer 1986–89 (chlorophyll data from Ziemannn et al. 1990, *Pseudocalanus* data from Coyle & Paul 1990).

Figure 4

Mean densities of all fish larvae, excluding osmerids, in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

speed was about 1.5 kn. Each tow lasted 7–8 min, and volume filtered was typically around 300 m³. Volume filtered per tow was very similar among years. Tows were collected on reciprocal compass courses set at 90° to the wind direction.

Fish larvae were removed from each replicate and enumerated by species, with the exception of osmerids, agonids, cottids, and cyclopterids, which were identified only to family. Osmerids were not identified to species because larvae of eulachon *Thaleichthys pacificus* and capelin *Mallotus villosus*, the two species common in the Auke Bay area, are very similar. The other three families (Agonidae, Cottidae, and Cyclopteridae) lack comprehensive identification guides to the species level. Mean densities of each taxon were calculated as the number/m² of surface.

Results

Total number of larvae collected annually ranged from 6087 in 1988 to 18,655 in 1986 (Table 1). Most of the interannual variation was due to differences in catches
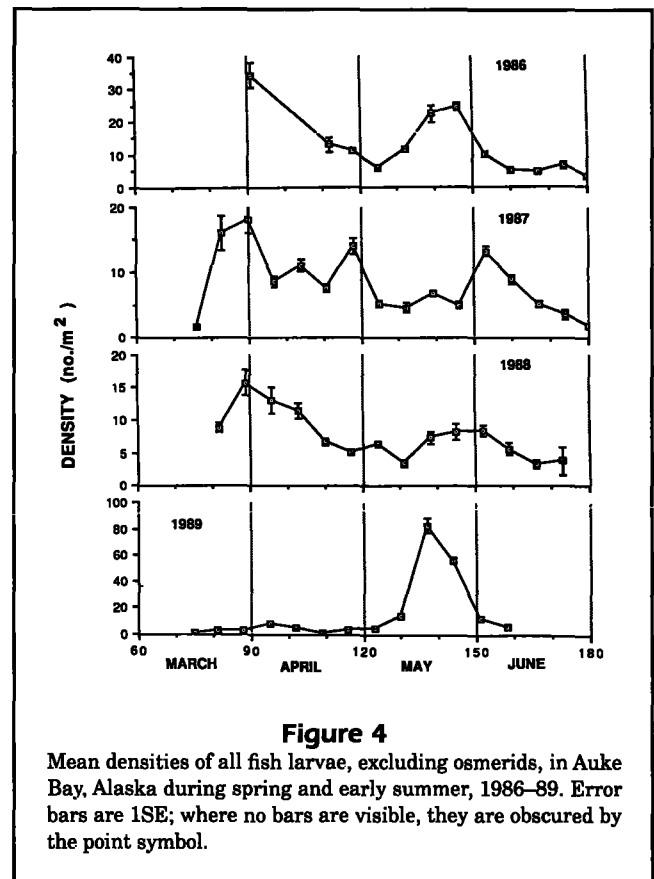
of osmerids. The five most-abundant taxa in all years were osmerids, Pacific sandlance *Ammodytes hexapterus*, walleye pollock *Theragra chalcogramma*, flathead sole *Hippoglossoides elassodon*, and rock sole *Pleuronectes bilineatus*. We did not include cottids in this summary, as they include at least eight species, none of which was exceptionally abundant; whereas the osmerids were very abundant, and included two species.

Total abundance of all larvae, excluding osmerids, peaked in March or early April of 1986–88 and in May 1989 (Fig. 4). Osmerids were excluded from total abundance estimates because in 1986 and 1987 their abundance obscured patterns associated with seasonal cycles of other species. In all years, osmerid abundance peaked from late May through June (Fig. 5). Such consistency in time of appearance in Auke Bay was typical of most species.

Larvae present in late March or early April were well in advance of either the spring phytoplankton bloom or the herbivorous copepod maximum. These early peaks in abundance were due primarily to high numbers of Pacific sandlance and rock sole (Figs. 6,

Table 1
Taxa of larval fishes collected in Auke Bay, Alaska in the spring, 1986–89, with total number collected (and rank order, in parentheses) of the five most frequently collected taxa in each year. The number of weekly samples, each consisting of five replicates, is indicated below each year.

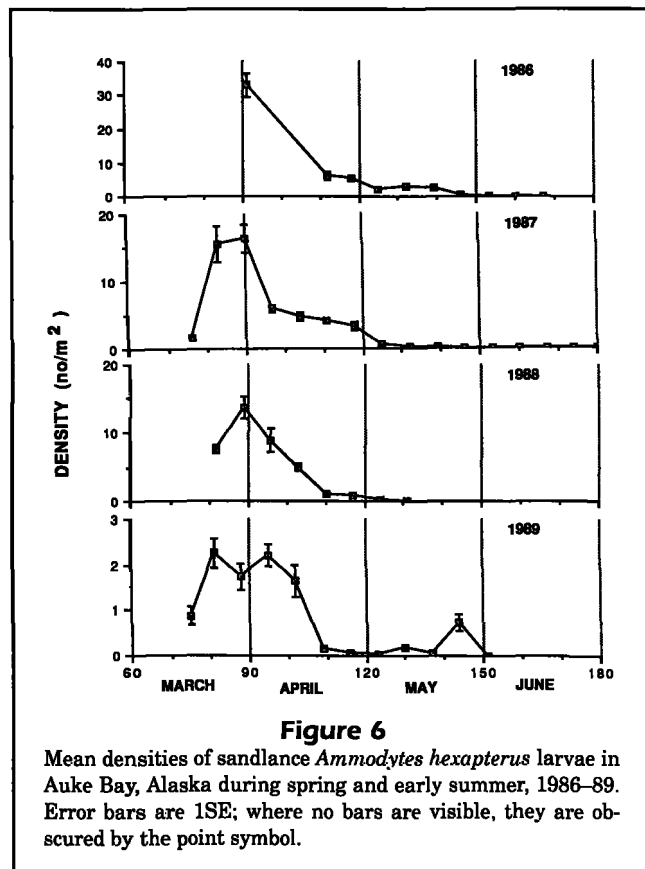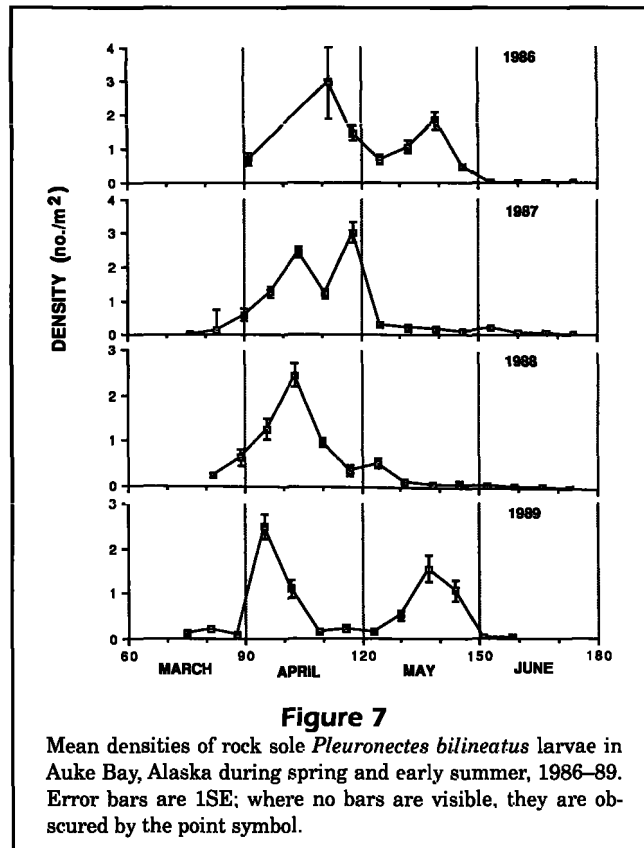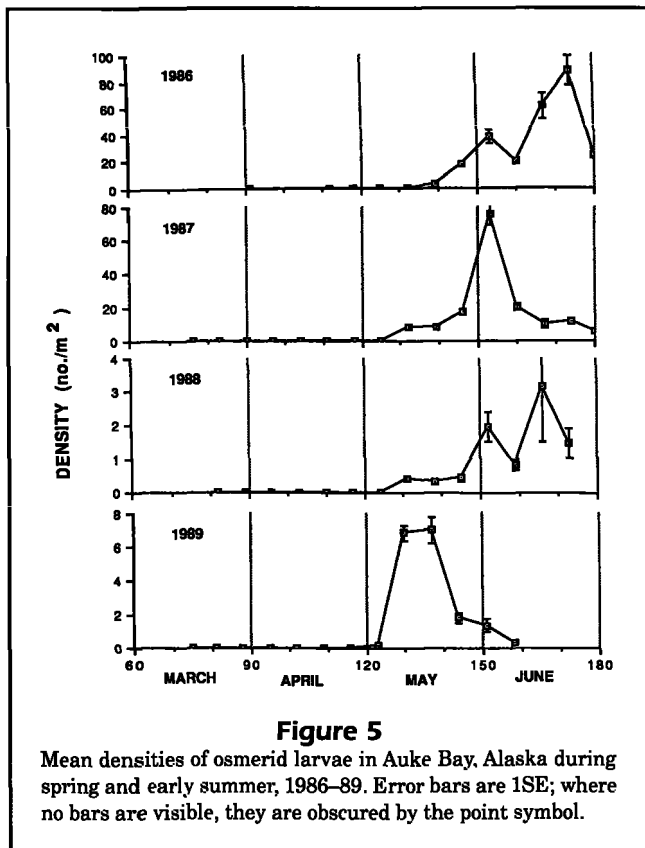|	1986 12		1987 16		1988 14		1989 13	
Clupeidae								
Clupea harengus	67		125		128		283	
Osmeridae	11975	(1)	9704	(1)	336	(4)	1006	(3)
Ammodytidae								
Ammodytes hexapterus	1926	(2)	2829	(2)	2295	(1)	611	(4)
Bathylagidae								
Leuroglossus schmidti	121		401		155		326	
Gadidae								
Theragra chalcogramma	1696	(3)	856	(3)	1453	(2)	4618	(1)
Gadus macrocephalus	0		4		2		0	
Stichaeidae								
Anoplarchus insignis	221		108		103		114	
Lumpenella longirostris	108		63		110		210	
Lumpenus sagitta	175		178		75		150	
Ptilichthyidae								
Ptilichthys goodei	5		3		7		6	
Cryptacanthodidae	17		35		7		18	
Cottidae*	541		531		306		860	
Agonidae	396		404		216		334	
Cyclopteridae	26		34		14		31	
Pleuronectidae								
Hippoglossoides elassodon	474	(4)	428	(5)	303	(5)	2741	(2)
Pleuronectes bilineatus	409	(5)	522	(4)	406	(3)	449	(5)
Pleuronectes asper	146		104		1		5	
Pleuronectes vetulus	84		131		24		2	
Platichthys stellatus	171		142		85		427	
Psettichthys melanostictus	71		93		22		122	
Unidentified	26		33		41		47	
Total	18655		16724		6087		12360	

*Not ranked; included at least 8 species.

7). Two less abundant species—longsnout prickleback *Lumpenella longirostris* and slender cockscomb *Anoplarchus insignis*—also appeared early in 1987 and 1988, but had maximum density in May of 1989.

Two of the most abundant species, walleye pollock and flathead sole, consistently appeared in May (Figs. 8, 9) and were well synchronized with maximum density of copepods. Less common larvae that also tended to reach maximum density in May were starry flounder *Platichthys stellatus* and poachers (agonids) (Figs. 10, 11).

Discussion

It has been observed that many fish larvae occur in approximate synchrony with maximum zooplankton densities (Sherman et al. 1981 and 1984, Townsend 1984, Jenkins 1986). The strategy of synchronizing production of larvae to high abundance of prey has obvious adaptive value, and is the prerequisite of high recruitment in Cushing's (1975) match-mismatch hypothsis. Fishes with this strategy were termed "synchronous" by Sherman et al. (1984). An alternate

Figure 5

Mean densities of osmerid larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

Figure 7

Mean densities of rock sole *Pleuronectes bilineatus* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

Figure 6

Mean densities of sandlance *Ammodytes hexapterus* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

strategy, characterized by prolonged production of larvae, has been termed "bet-hedging" (Lambert & Ware 1984) or "ubiquitous" (Sherman et al. 1984). This strategy is described as adaptive in situations where prey availability is unpredictable.

In Auke Bay, fish species reproducing in the spring appear to follow two strategies: One group, typified by walleye pollock and flathead sole, is clearly synchronous, in the sense described above; whereas Pacific sandlance and rock sole are examples of species that could be termed "early." The early group can be defined as those species that produce their larvae prior to the peak in the spring phytoplankton bloom (before mid-April in Auke Bay). It is possible that early species in Auke Bay are following the "bet hedging" strategy discussed above, as they could have been producing larvae throughout the winter. In that case our sampling would have coincided with the end of their production period.

From mid-March through June, conditions in Auke Bay are rapidly changing as the system passes through two of the production phases—spring phytoplankton bloom and herbivorous copepod maximum—that typify nearshore subarctic marine environments (Smetacek et al. 1984). In the pre-bloom period, the water column
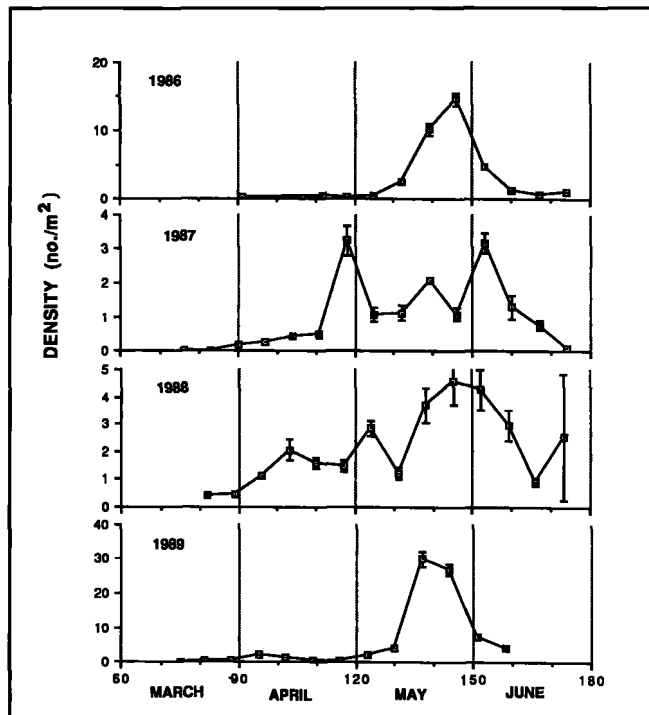
Figure 8

Mean densities of walleye pollock *Theragra chalcogramma* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.
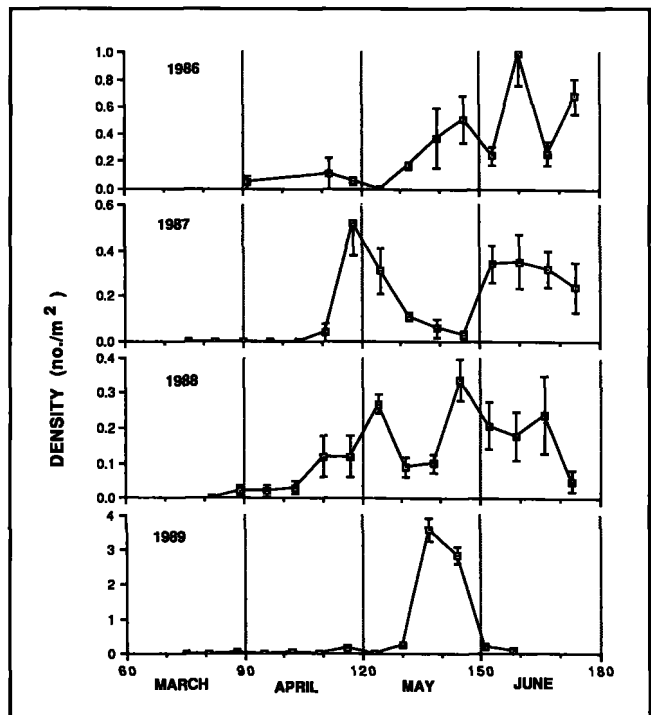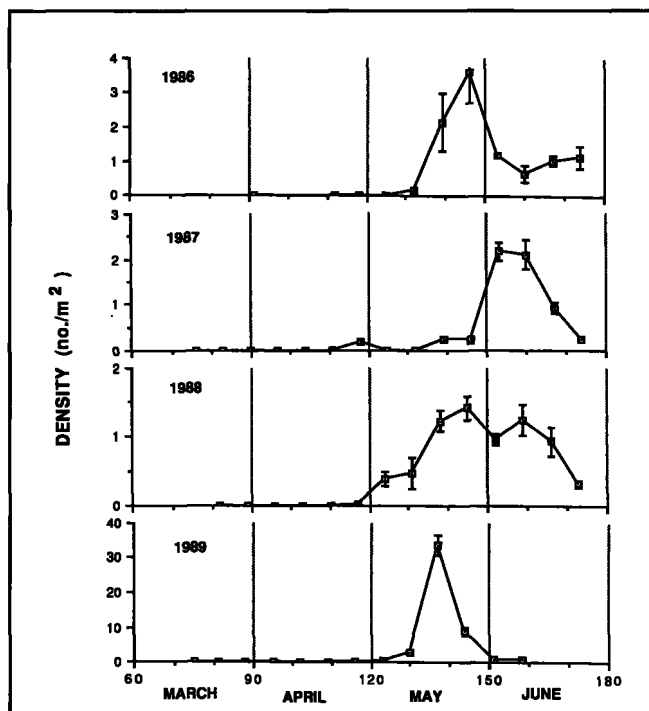
Figure 10

Mean densities of starry flounder *Platichthys stellatus* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.
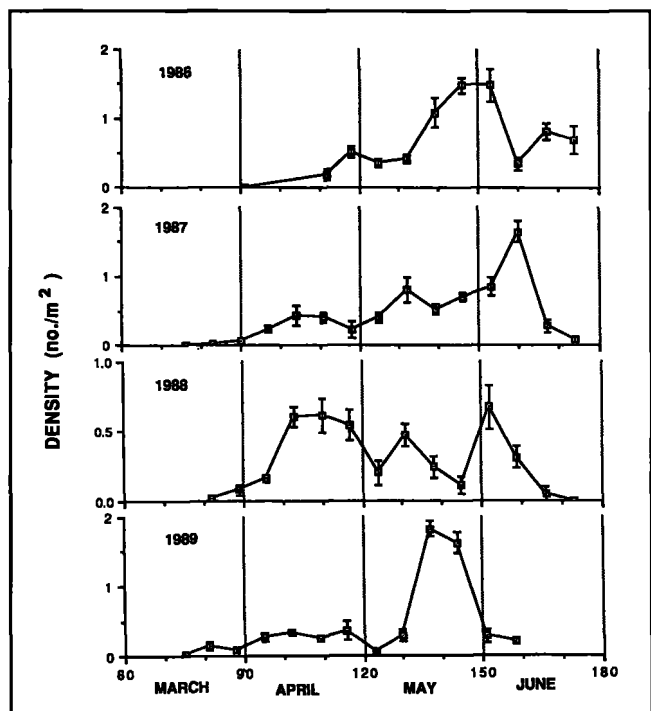
Figure 9

Mean densities of flathead sole *Hippoglossoides elassodon* larvae in Auke Bay, Alaska during spring and early summer, 1986-89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

Figure 11

Mean densities of agonid larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

is well mixed and uniformly cold, with mean temperature below 5°C. With onset of the phytoplankton bloom, the Bay stratifies, with rapid warming of the mixed layer to over 10°C by June (Bruce et al. 1977, Ziemann et al. 1991). Zooplankton are in low density until the end of the phytoplankton bloom, and are comprised of relatively large plankton such as overwintering copepedids and some meroplankton such as barnacle larvae (Wing & Reid 1972, Coyle & Paul 1990, Paul et al. 1991). The initiation of the herbivorous copepod maximum marks the start of a period with relatively high densities of smaller zooplankton, especially copepod nauplii in the size range (150–350 μ) utilized by synchronous species such as walleye pollock and flathead sole larvae (Fig. 12; data from Paul et al. 1991). It seems clear that fish larvae hatched prior to the phytoplankton bloom must be adapted to a very different set of conditions than those that occur synchronously with the herbivorous copepod maximum.
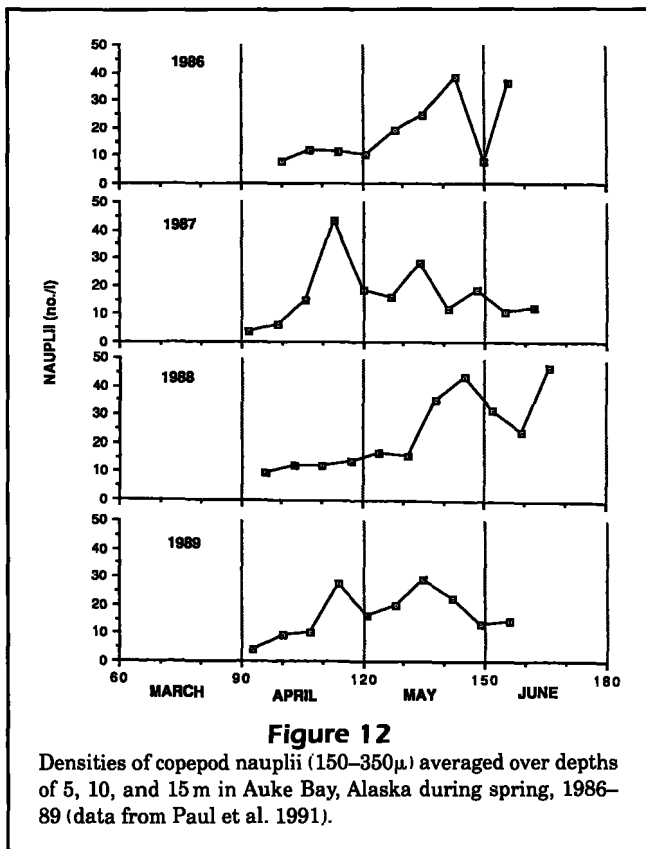
Larvae spawned in winter apparently employ various foraging strategies while utilizing similar energetic principles. Bailey (1982) concluded that Pacific hake larvae use energy slowly and grow slowly while passively hunting large prey. In Long Island Sound NY, larvae of American sandlance *Ammodytes americanus* hatched in winter are herbivores that sur-

vive nonfeeding in cold temperatures until the spring phytoplankton bloom commences (Monteleone et al. 1987). In both of these strategies, larvae survive by relying on their ability to withstand long periods of low food availability, largely as a result of low metabolic rates at cold temperatures.

Sherman et al. (1984) identified the synchronous strategy as a major adaptive tactic for many northwest Atlantic Ocean fishes. In Auke Bay, several taxa including osmerids, walleye pollock, and flathead sole consistently appeared at about the time copepod abundance was maximized. Although prey is relatively plentiful during the herbivorous copepod maximum, the numbers of predatory invertebrates are rising (Smetacek et al. 1984, Coyle & Paul 1990); consequently, mortality rates of fish eggs and larvae are probably rising rapidly. Higher temperatures during this period may also limit the time available for larvae to encounter suitable conditions by causing high metabolic rates and more rapid depletion of energy reserves. These species are probably most sensitive to interannual variation in the production cycle and may demonstrate the type of recruitment fluctuation described by the match-mismatch hypothesis (Cushing 1975) or the critical-period hypothesis (Hjort 1914).

Patterns of abundance observed in Auke Bay could result from hatching of larvae in the Bay or from advective events that carried larvae into the Bay from other areas. Auke Bay has only one deep (>20 m) entrance, just east of Coghlan Island (Fig. 1). Water in the Bay is quite persistent, with an average replacement time of the water mass once a month or longer during the March–June period (Nebert 1990). In other studies of growth, length-frequencies were determined for walleye pollock and flathead sole larvae (Haldorson et al. 1989, 1990). Cohorts of both species first appeared in Auke Bay as small larvae comprising length-frequency modes that could be followed for several weeks. Over the 4 years of the study there were very few cases in which length-frequency modes occurred that could not be identified in preceding weeks. Consequently, we conclude that most of the larvae sampled in this study originated from hatching within or near the Bay, with possible exception of osmerids.

The osmerids in our study are most likely eulachon *Thaleichthys pacificus* and capelin *Mallotus villosus*. Eulachon is an anadromous species that spawns demersal, adhesive eggs in rivers. After hatching, the larvae are carried into nearby marine waters. The most likely source of eulachon larvae in Auke Bay is the Mendenhall River, a glacier-fed stream about 2 km east of Auke Bay. The fresh and turbid waters from the Mendenhall River form a surface lens that projects out into nearby Fritz Cove and often intrudes into the eastern edge of Auke Bay through a narrow passage

Figure 12

Densities of copepod nauplii (150–350μ) averaged over depths of 5, 10, and 15 m in Auke Bay, Alaska during spring, 1986–89 (data from Paul et al. 1991).

northeast of Spuhn Island (Fig. 1). In 1987 we studied the depth distribution of fish larvae in Auke Bay and found that osmerids were always concentrated above the pycnocline and moved to the surface at night (unpubl. data). Most other species were found at or below the pycnocline and tended to move deeper at night. Therefore, interannual and seasonal variation in osmerid abundance may reflect variation in the amounts of river water reaching Auke Bay.

Among the 4 years of the study, 1989 was distinguished by relatively high densities of larvae during May. Walleye pollock and flathead sole were markedly more abundant in 1989 than in the previous 3 years, as were less-common synchronous species such as starry flounder. This increase could have resulted from increased egg production in the bay or from exceptionally high survival of eggs and larvae. We have no data on density of fish eggs in Auke Bay; however, in 1989 invertebrate predators were present in the lowest abundance observed in the 4-year study (Coyle & Paul 1990). It seems possible that reduced predatory mortality contributed to the exceptionally high densities of fish larvae that occurred in May of 1989. However, 1986 also had relatively high abundances of fish larvae in May, and did not have reduced numbers of invertebrate predators (Coyle & Paul 1990).

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