Comparisons of early-life-history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido, Japan*

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Abstract.–Over the past several years researchers in Japan and the United States have independently been conducting extensive studies on the early life history of two discrete populations of walleye pollock *Theragra chalcogramma*, trying to understand recruitment variation. The population of interest to Japanese researchers spawns near Funka Bay, Hokkaido, Japan, while the population of interest to American researchers spawns in Shelikof Strait, Gulf of Alaska. This paper summarizes and compares characteristics of spawning and ecology of eggs, larvae, and early juveniles of the species in these two areas. Although the species has apparently adapted its early-life-history pattern to environmental differences in the two areas, some underlying similarities exist. The adults mainly spawn at a particular time of year following a spawning migration to a specific location so that the eggs and larvae can reach specific areas for subsequent development. In both areas oceanographic conditions are favorable for larval food production (copepod nauplii) when the walleye pollock larvae are present. Drift of the eggs into the bay, where copepod production is enhanced, seems important in Funka Bay, and drift of the larvae toward juvenile nursery grounds on the continental shelf as opposed to being swept offshore, seems important in Shelikof Strait. Interannual differences in larval drift and food production because of varying oceanographic conditions may contribute significantly to variations in year-class size.

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Walleye pollock *Theragra chalcogramma* is a dominant fish in the North Pacific Ocean and in the Bering Sea, both in terms of population size and importance to commercial fisheries. It is a major fishery resource in the Funka Bay area on the Pacific Ocean side of Hokkaido, Japan, and in Shelikof Strait, Gulf of Alaska. In both areas, most fishing is done just prior to and during the spawning season. In Funka Bay, walleye pollock are caught in bottom gillnets, while in Shelikof Strait midwater trawls are used. In Funka Bay the catch varied from about 4.3×10^4 metric tons (t) to about 10.7×10^4 t from 1976 to 1986. In Shelikof Strait, an intense fishery on the spawners existed from 1981 through 1988, although harvest has been severely restricted since 1986 because of reduced abundance of the population (Megrey 1989). The harvest in Shelikof Strait peaked in 1984 at about 31×10^4 t.

There is a growing interest in understanding recruitment in this species, and considerable work has been conducted independently by Japanese researchers in Funka Bay and by U.S. researchers in Shelikof Strait over the past several years. This paper compares the results of these studies (Table 1). While these studies reveal that the early-life-history strategy of walleye pollock allows this species to adapt to different environments, they also indicate that underlying similarities exist between populations. Although understanding causes of recruitment variation in either area is a distant goal, testable hypotheses have been developed in both areas. The comparisons presented in this paper may help researchers in both areas focus their studies toward an understanding of the recruitment process. They may also guide future studies of the species in other areas such as the Bering Sea.

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Environmental comparisons

Physical setting

Funka Bay is located in the southern part of Hokkaido, Japan, at about 42°N (Fig. 1). Depths within the bay are generally less than 80 m, although there is a small area of water deeper than 100 m in the center of the bay. Immediately outside the bay the bottom slopes evenly to 500 m within 45 km. The area of the bay is 2270 km^2.

Shelikof Strait is located in the northern Gulf of Alaska between the Alaska Peninsula and the Kodiak Archipelago at about 57°N (Fig. 1). Water depths within Shelikof Strait exceed 300 m in some areas. At the northeast and southwest ends of the strait there are sill depths of about 200 m. Depths of greater than 500 m are reached on the continental slope immediately beyond the southwestern sill. The southern part of the strait and waters to the south comprising about 12,450 km², are the areas occupied by eggs and larvae of walleye pollock originating in Shelikof Strait.

Table 1

Comparisons of early-life-history characteristics of walleye pollock *Theragra chalcogramma* and their spawning environments in Funka Bay, Japan, and Shelikof Strait, Gulf of Alaska.

	Funka Bay	Shelikof Strait
Latitude	45°50′–42°35′N	56°00′–59°00′N
Area	2270 km²	12,450 km²
Nominal annual catch	[a]70,000 t	[b]100,000 t
Spawning season	[c]Dec.–Mar.	[d]Early April
Spawning depth	[e]100–120 m	[d]200–300 m
Temperature at spawning depth	[e]2–6°C	[f]5.5°C
Depth of maximum egg concentrations	[e]0–40 m	[f]150–200 m
Egg specific gravity	[e]1.020–1.026 g/cm³	[f]1.024–1.031 g/cm³
Depth of maximum larval occurrence	[g]10–20 m	[h]15–50 m
Length of larvae when copepod nauplii are predominant components of diet	[e]<7–8 mm	[h]<11 mm
Larval growth rate	—	[h]0.21 mm/day

[a]Nakayama et al. 1987, [b]Megrey 1989, [c]Maeda et al. 1976, [d]Kendall and Picquelle 1990, [e]Nakatani 1988, [f]Kendall and Kim 1989, [g]Kamba 1977, [h]Kendall et al. 1987.

Physical oceanography

The water of Funka Bay originates from the seasonal influx of two water masses: The Tsugaru Warm Water and the Oyashio Water. Tsugaru Warm Water enters the Bay in late-summer when surface waters exceed 15°C and there is a strong thermocline in the upper 20 m (Nakatani 1988). Autumnal cooling produces isothermal conditions and cooling to about 4°C (Winter Funka Bay Water: Ohtani and Kido 1980). In late-winter or early-spring, the cold (<2°C), less saline (<33.0‰) Oyashio Water usually intrudes into the Bay above the Winter Funka Bay Water, producing a stratified condition with a temperature inversion. In late-spring and early-summer, seasonal warming of surface waters occurs and a thermocline develops. Throughout the year, bottom temperatures remain at 3–6°C.

Shelikof Strait has an estuarine type circulation, with less seasonal variation than Funka Bay. In its upper layers, the Alaska Coastal Current (ACC) flows to the southwest and is particularly pronounced on the Alaska Peninsula side of the Strait. During runoff seasons (late-spring to early-fall), substantial amounts of freshwater enter the strait, primarily from Cook Inlet, and flow along the Peninsula until thoroughly mixed with the ACC. From approximately 150 m to the bottom, more saline water flows into the strait over the sill to the southwest (Kim 1987). During April and May (when walleye pollock eggs and larvae are present), near-surface water temperatures in the ACC are generally 0–4°C, warming to 7°C by late May, while the deeper waters are generally 4–5.5°C. Salinity varies from about 31 to 33.5‰.

In Funka Bay there is considerable interannual variation in the date when the Oyashio Water intrudes and in the length of time that surface temperatures remain cold (<3°C). In Shelikof Strait, interannual variation in the frequency, intensity, and track of storms affects water properties and transport.

Biological comparisons

Spawning

In Funka Bay, adult walleye pollock mature and spawn from November to March, with peak spawning activity occurring in January and February (Maeda et al. 1976 and 1981, Yoon 1981), whereas in Shelikof Strait most fish mature in February and March and spawning peaks in early April (Kim 1989, Kendall and Picquelle 1990). Pelagic eggs are present in Funka Bay from December until March, and in Shelikof Strait eggs are present mainly in April. There is some interannual variation in time of spawning in Funka Bay, and eggs have even been collected in November and April (Maeda et al. 1980). Thus the spawning season seems to occur earlier in the year and lasts longer in Funka Bay than in Shelikof Strait. Spawning occurs mainly at depths of 100–120 m near the entrance of Funka Bay (Maeda et al. 1976, Nakatani 1988, Nakatani and Maeda 1989). In Shelikof Strait, spawning is concen-

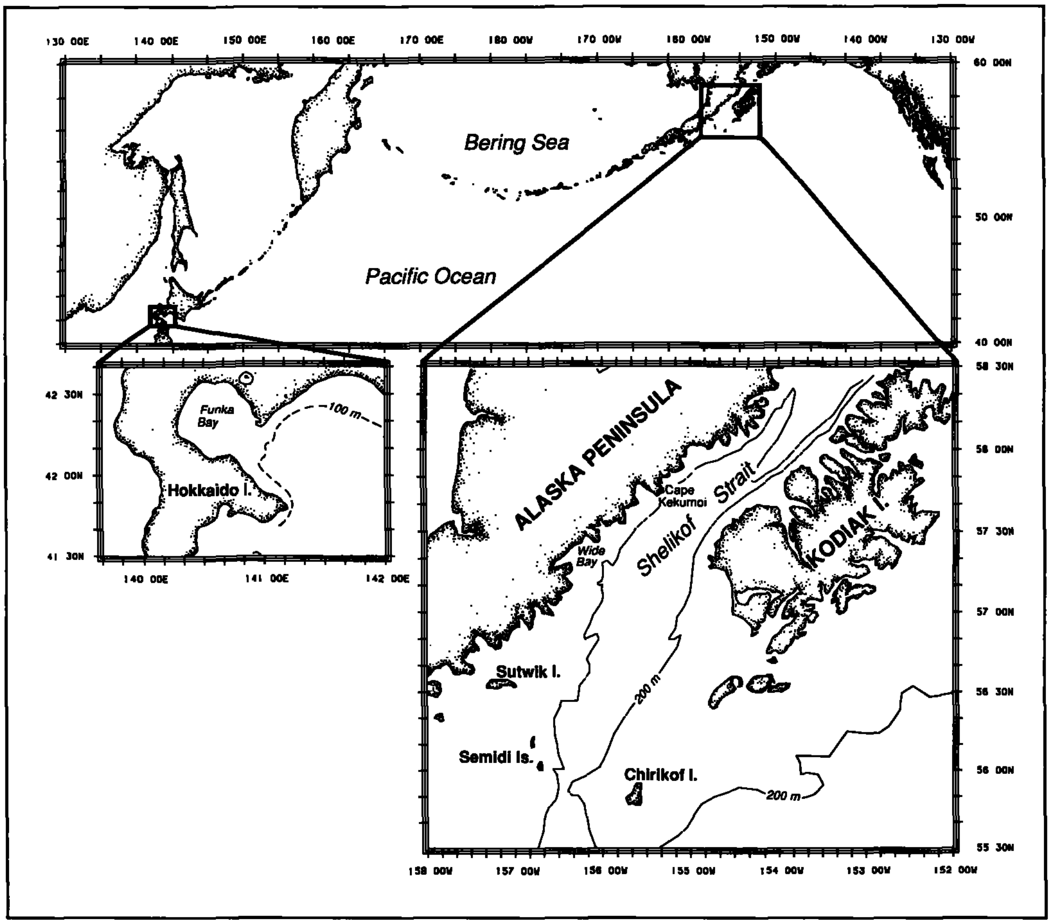

Figure 1
Location of Funka Bay, Japan, and Shelikof Strait, Gulf of Alaska. Insets are enlargements of the areas with pertinent bathymetry.

trated in a small area of deep water (>250 m) near Cape Kekurnoi (Fig. 1) (Kendall and Picquelle 1990).

Field surveys of adult walleye pollock in Funka Bay and Shelikof Strait show that fish congregate and migrate to a particular part of their range just prior to the spawning season. Final migration to a restricted spawning area takes place quickly. In Shelikof Strait, hydroacoustic surveys show that the fish separate into vertical strata, presumably by sex (females below males) and readiness to spawn (Muigwa 1989).

Although the fish move to the spawning area as a large group, spawning itself is by pairs. Behavior of spawning walleye pollock has been investigated using captive fish from Funka Bay (Sakurai 1982, 1989), as well as from Puget Sound, Washington (Baird and Olla 1991). The shallow tanks used by Sakurai (1989) may have prevented some of the vertical aspects of spawning behavior observed by Baird and Olla (1991). Although no such studies have been conducted on fish from Shelikof Strait, similarities between the behavior of fish from near the eastern (Puget Sound) and western (Funka Bay) extremes of the species distribution may indicate that spawning behavior varies little geographically. In experimental tanks, the fish form loose aggregations near the surface. Males frequently follow other males and females. Sakurai (1989) related male–male interaction to the agonistic behaviors associated with dominance; Baird and Olla (1991) considered the male's following behavior as a searching behavior for potential mates. Sakurai (1989) also observed courtship displays by males toward prospective mates. At the onset of a spawning, a female would swim down with a male following her. The male then made contact with her by rubbing his ventral surface first against her dorsum or side and then he swam beneath her, with their two vents in contact. Other males occasionally followed the pair closely and also made contact with the female. During vent-to-vent contact, the male rubbed his body rapidly against the female's abdomen, and presumably gametes were released at this time (they could not be seen in the water, but were found in the tank overflow within an hour). Most spawning took place in evening or morning twilight (Baird and Olla 1991).

Female walleye pollock characteristically spawn a number of batches of eggs over a fairly short period each year. The interval between batches is a few days. The number of eggs per batch and size of eggs decrease with successive batches. These patterns have been observed both in Funka Bay (Sakurai 1982) and Shelikof Strait (Hinckley 1990).

Fecundity

Miller et al. (1986) related fecundity of walleye pollock from Shelikof Strait to gutted weight and fork length, while Sakurai (1982) related fecundity of walleye pollock from Funka Bay to whole weight and body length. Conversions were applied here to the Funka Bay length and weight data so fecundity could be compared with Shelikof Strait values based on

$$Y = 0.7634X + 23.4472 \ (r^2\ 0.96628,\ N\ 40)$$

where X = body weight and Y = gutted weight (Y. Sakurai, unpubl.); and

$$Y = 1.0659X + 4.050 \ (r^2\ 0.9959,\ N\ 53)$$

where X = body length and Y = fork length (T. Maeda, unpubl.).

The relative fecundity of Funka Bay fish is represented by the relationship $F = 8.73 \times 10^{-6} L^{3.98}$ and $F = 106.2 W^{1.21}$, where L = body length in mm and W = body weight in grams (N 94) (Sakurai 1982); therefore a 300g (gutted weight) fish produces 129,000 eggs and a 1000g fish yields 589,000 eggs. In Shelikof Strait, the relationship was found to be $F = 1.2604 L^{3.2169}$ and $F = 387.4551 W^{1.0160}$ (N 60), where L = fork length in cm and W = gutted weight in grams; this yields 127,000 eggs for a 300g fish and 433,000 eggs for a 1000g fish (Miller et al. 1986). Thus small fish from Funka Bay have about the same number of eggs, but larger fish have more eggs than those from Shelikof Strait (Fig. 2).

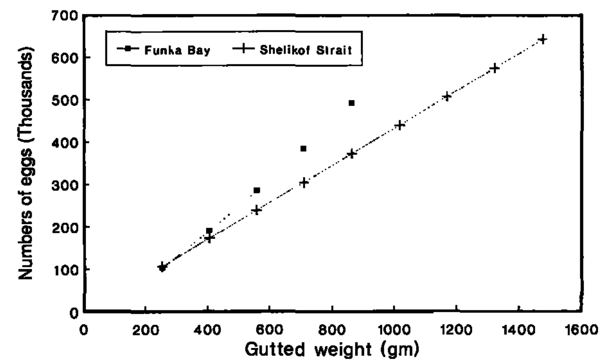

Figure 2
Fecundity-weight relationship for walleye pollock in Funka Bay, Japan (based on Sakurai 1982), and Shelikof Strait, Gulf of Alaska (based on Miller et al. 1986).

Eggs

Development Eggs from Funka Bay are more variable in size and slightly larger than those from Shelikof Strait. In Funka Bay, eggs are 1.15–1.68mm ($\bar{x}$ 1.46mm) in diameter (Nakatani and Maeda 1984, T. Nakatani, unpubl.). In Shelikof Strait, egg diameter ranges from 1.30 to 1.41mm, and egg size has been shown to vary interannually and decrease during the spawning season (Hinckley 1990).

Eggs from Funka Bay develop at a rate dependent on temperature according to the relationship

$$D = 31.70 \exp(-0.12T),$$

where D is days to 50% hatch and T is temperature (°C). Thus 50% hatch times are 22.1 days at 3°C, 17.4 days at 5°C, and 15.4 days at 6°C (Nakatani and Maeda 1984). No measurements of incubation time are available for eggs from Shelikof Strait; however, reared eggs from Auke Bay in southeast Alaska (58°20′N) required 19.2 days at 3°C, 14.1 days at 5°C, and 12.2 days at 6°C for 50% hatch (Haynes and Ignell 1983). Thus eggs from southeast Alaska developed to hatching more quickly, by about 2–3 days, than those from Funka Bay (Fig. 3).

Vertical distribution The vertical distribution and buoyancy of eggs have been investigated in both Funka Bay and Shelikof Strait. In Funka Bay, eggs rise in the water column as they develop. Stage-1 (fertilization to morula) eggs were found at a depth of roughly 30m (10–40m), whereas Stage-5 (embryo more than three-fourths yolk circumference) eggs were mainly at depths of 10–20m (Nakatani 1988). The specific gravity of Funka Bay eggs throughout development was within a range of 1.020–1.025g/cm³ ($\bar{x}$ 1.0226g/cm³). This resulted in an upward velocity of 4.9m/h in ambient water through the homogenized water column early in the spawning season (σ^t 26.41–27.17), and is consistent with field observations of shallower depths for older eggs compared with those recently spawned (Nakatani and Maeda 1984, Nakatani 1988).

In Shelikof Strait, the vertical distribution of eggs changes during development in response to their changing specific gravity. Newly spawned eggs are positively buoyant, and thus rise from the deep locations where they are spawned. In middle stages of development, the eggs become heavier and sink until just before hatching when they again rise toward the surface (Kendall and Kim 1989). The specific gravity

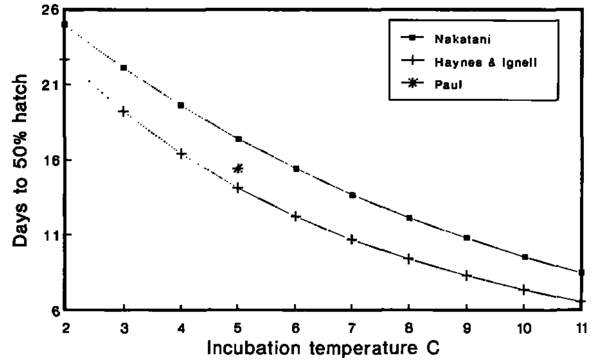

Figure 3
Incubation period of walleye pollock eggs from Funka Bay, Japan (based on Nakatani 1988); Resurrection Bay (based on A.J. Paul, Univ. Alaska, Seward, pers. commun.) and Auke Bay, Alaska (based on Haynes and Ignell 1983).

of eggs from Shelikof Strait varied from 1.0243 to 1.031 g/cm^3, whereas the water density varied from 1.0256 to 1.0259 g/cm^3 (in 1985). Less than 20% of eggs of all ages occurred above 162 m in Shelikof Strait. Over 80% of early- (fertilization to morula) and late-stage eggs (embryo more than one-half circumference of yolk to hatching) occurred between 216 and 277 m (near bottom), while over 60% of middle-stage eggs (gastrula) occurred between 162 and 216 m (Kendall and Kim 1989). Thus eggs in Shelikof Strait are heavier and occur deeper than those in Funka Bay.

Horizontal distribution The horizontal distribution pattern of eggs in Funka Bay was fairly consistent among the 3 years (1977, 1978, and 1987) for which data are presented (Nakatani 1988, Nakatani and Maeda 1981 and 1989). Younger eggs are mainly found just outside the entrance to the bay and older eggs are found inside the bay, indicating that spawning occurs outside the bay and the eggs drift into the bay as they develop. During the period 24 January to 11 February 1978, egg abundance reached 13,424 Stage-4 eggs/m^2 at a station just south of the entrance to the bay where large numbers of Stage 2–5 eggs were also present, producing a total of 23,817 eggs/m^2.

The egg distribution pattern in Shelikof Strait was most intensively examined in 1981; however, sampling in other years (1978–86) indicates similar patterns. The first appearance of low numbers of eggs occurs in March and early April, mainly in the southern part of the strait (Kendall and Picquelle 1990). The highest concentrations of eggs occur off Cape Kekurnoi in early April, where abundances of Stage-2 and -3 eggs exceeded 1000/m^2 in 1981. The combined abundance for all stages was 350,000 eggs/m^2 in the area of maximum concentration; about 15 times the maximum abundance observed in Funka Bay. By late April, egg abundance is reduced as eggs are spread more evenly throughout the southern two-thirds of the strait and the area immediately to the southwest of the strait. By late May, egg abundance is further reduced, but the area of occurrence is still similar to that seen in late April. As opposed to Funka Bay, there is little evidence of drift of eggs in Shelikof Strait. It appears that the adults spawn some eggs in the southwestern part of the strait as they move toward the main spawning area off Cape Kekurnoi. Later spawning in late April and May seems to be dispersed throughout the strait and occurs at a much reduced level. Measurements of currents in Shelikof Strait also indicate that little drift would be expected in the deep waters (>150 m) where most eggs occur (Kendall and Kim 1989).

Larvae*

Vertical distribution The ecology of walleye pollock larvae has been investigated in both Funka Bay and Shelikof Strait. In both areas most larvae occur above 50 m in the water column and exhibit limited diel vertical migration (Kamba 1977, Kendall et al. 1987). Few larvae are collected at the surface, but some larvae move up to 10–20 m depth in the evening. At night they are fairly evenly distributed throughout the upper 50 m, and in the early morning they are again concentrated above 20 m. During midday they are most abundant at 20 m and deeper to 50 m. The larvae sampled by Kendall et al. (1987) in Shelikof Strait averaged 11.0 mm (SD 1.7 mm), while those in Funka Bay sampled by Kamba (1977) had a wide range of lengths from 4.6 to 26.4 mm, although most were 4.6–12.8 mm. Kamba (1977) indicated that larger larvae (>13.7 mm) were more often collected in shallow tows at night and in deep tows during the day, suggesting that either the larger larvae migrated more than the smaller ones or that the larger larvae were more successful at avoiding the shallow nets during the day. No large larvae were collected by Kendall et al. (1987). Kamba (1977) concluded that the diel vertical movements of pollock larvae in Funka Bay corresponded to those of their zooplankton prey. Both Kamba (1977) and Kendall et al. (1987) found a diel pattern in gut fullness, with little food found in guts at night and most food found in guts during the day.

* Lengths of larvae and juveniles are reported here as standard length (SL, from the tip of the snout to the end of the notochord or base of the hypural plate), although in the Japanese literature they were given as total length (TL). Conversion from TL to SL is based on our paired measurements of 1048 fish (4.2–103 mm SL) which resulted in the relationship: SL(mm) = 0.108 + 0.907 TL(mm).

Horizontal distribution In the Funka Bay region, walleye pollock larvae are generally concentrated inside the bay from late January through early April (Nakatani 1988, Nakatani and Maeda 1989). Their abundance decreases during this time from >5000 larvae/m^2 in the area of maximum concentration in late January to 200–400 larvae/m^2 in early April. In many cases, surveys have disclosed more than one area of abundance within the bay. Their occurrence generally overlaps that of the Oyashio Water. For example, in 1980 the Tsugaru Warm Water remained in the bay longer than usual, and the Oyashio Water did not enter the bay until mid-March; before then, the larvae were concentrated at the mouth of the bay. It is possible that larvae entering the bay before the invasion of the Oyashio Water would experience low survival because of inadequate prey production.

In Shelikof Strait, most larvae are concentrated in one large patch that can be followed as it drifts to the southwest with the prevailing currents from April through May (Kendall et al. 1987). The velocity of drift may vary interannually and depend on weather patterns in the area as well as the strength of the ACC. In some years, it appears that most of the larvae drift out of the strait within 2–4 weeks after hatching, but in other years they remain for several more weeks because of the influence of nearshore eddies (Incze et al. 1989). There is considerable cross-strait shear in the current, so the drift of larvae is influenced by where they reach the surface layer from their deep incubation area (Kim and Kendall 1989). Larval abundances as high as 10,000/m^2 were observed in the patch in late April 1981, and by late May abundances of 2400/m^2 were present (Bates and Clark 1983).

Feeding Copepod nauplii, which were not identified to species, are the major prey item of first-feeding walleye pollock larvae (Kamba 1977, Kendall et al. 1987, Nakatani and Maeda 1983). Copepodids are the most important prey item in the diet of 11 mm larvae in Shelikof Strait and 8 mm larvae in Funka Bay. Copepod eggs were more prevalent in guts of larvae in Funka Bay than in Shelikof Strait (Nakatani and Maeda 1983, Kendall et al. 1987). Their digestibility and nutritional value for walleye pollock larvae are unknown. *Pseudocalanus* spp. was the most abundant copepod taxon in the water column in Shelikof Strait and Funka Bay when larvae were present (Kendall et al. 1987, Nakatani 1988). The nauplii in the guts of small larvae were probably mostly *Pseudocalanus* spp. and *Oithona* spp., and most of the copepodids in larger larvae were *Pseudocalanus* spp. Copepodids of *Pseudocalanus minutus* and *Oithona similis* were most abundant in larger larvae up to 30 mm in Funka Bay (Nakatani and Maeda 1983). The maximum prey size increases with growth of the larvae, but the minimum size remains fairly constant through fish up to about 73 mm (Kamba 1977).

Based on laboratory and field studies, naupliar abundances of about 10 per liter seem to be required to support growth of small (<8 mm) walleye pollock larvae (Paul 1983, Dagg et al. 1984). Prey densities above this threshold have been observed associated with the larval patch in Shelikof Strait before and during a storm (Incze et al. 1990). Naupliar abundances below this threshold were seen in Funka Bay throughout most of the larval period in 1987, but they were above 10 per liter in several other years (Nakatani and Maeda 1989). However, naupliar densities were probably underestimated, since they were collected on 100 μm sieves. Availability of smaller nauplii as larval food will require further observations.

Age and growth Daily growth increments on otoliths have been used to determine the age of larvae and early juveniles from both Shelikof Strait and Funka Bay. Based on a series of 109 larvae (6.0–14.6 mm SL) collected in Shelikof Strait in May 1983, the linear growth equation $SL = 4.29\,mm + 0.21\,d$ (r^2 0.75), where d = age in days, was fit (Kendall et al. 1987). Growth based on 357 larvae and early juveniles 3.9–30.0 mm SL from the Shelikof spawning collected May through July 1987 fit a Laird-Gompertz function: SL at age $t = 4.505\,(e^{7.854(1-e^{-0.004t})})$, where t = days after hatch (Yoklavich and Bailey 1989). The growth of larvae and juveniles from Funka Bay fit the function: $TL = 121.5/(1 + e^{-0.026(t-124.511)})$, with TL in mm (Nishimura and Yamada 1984). Thus larvae 50 days old from Funka Bay were about 14.0 mm SL (see footnote) while those from Shelikof Strait would range from 14.8 mm SL (Kendall et al. 1987) to 18.7 mm SL (Yoklavich and Bailey 1989) (Fig. 4).

Larval population length-frequency distributions depend on time of spawning, mortality of larvae, growth of larvae, and sampling bias. Except for sampling bias, these factors represent population processes occurring to the annual cohort of larvae. In Funka Bay, even though spawning takes place over a protracted period, larval survival appears low except during periods when adequate food is present. Mortality due to starvation is high for larvae that hatch before the spring increase of nauplii in Funka Bay (Nakatani and Maeda 1989, Nakatani 1991). Thus variations in size of larvae may depend more on differences in the birth dates of surviving larvae than on differences in growth rates.

In Shelikof Strait, spawning peaked during the first week of April in several years. By the end of April 1981, most larvae were about 4.8 mm. By the third week in May 1981, they were mostly 7–8 mm (Dunn et al. 1984), as they were in 1982 (Kendall et al. 1987).

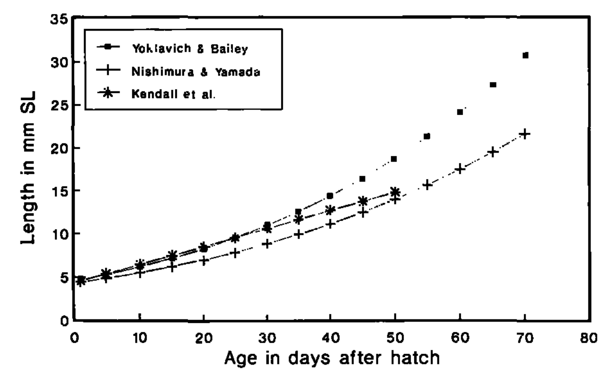

Figure 4
Growth of walleye pollock larvae and juveniles from Funka Bay, Japan (Nishimura and Yamada 1984), and larvae from Shelikof Strait, Gulf of Alaska (Kendall et al. 1987, Yoklavich and Bailey 1989).

However, in 1983 larvae averaged 11.23 mm in late May (Kendall et al. 1987). No interannual differences in larval growth rates were discerned for larvae collected in Shelikof Strait in late May 1983, 1985, 1986, or 1987. Because larvae were larger in late May 1983 than in 1985, 1986, or 1987, they may have been survivors of an earlier spawning than those observed in the other years (Yoklavich and Bailey 1989).

Early juveniles

Young-of-the-year juvenile walleye pollock (18–73 mm) have been sampled extensively in Funka Bay using midwater and bottom trawl nets (Nakatani and Maeda 1987). The juveniles are about 34 mm in late May, 36 mm in June, and 55–80 mm in late July. In June, juveniles (22–66 mm) are found mainly at 25–30 m at night and at 10–15 m during the day (Nakatani and Maeda 1987). The juveniles move deeper in the water column in May and June, and by late July most are on the bottom (Nakatani and Maeda 1987). In July, larger fish are caught in bottom trawls while smaller fish are still in the water column. As the juveniles grow and move toward deeper water and the bottom, they also move from inside the bay toward the entrance (in June) and to the shelf (100–300 m) just outside the bay (by August) (Nakatani and Maeda 1987).

Some variation in size-at-date of juveniles among years has been observed (Fukuchi 1976, Nakatani and Maeda 1987), which may be due to interannual differences in growth rates, or differences in hatch dates of surviving juveniles.

Food organisms changed during juvenile growth with *Neocalanus plumchrus* being most important in fish >27 mm long in midwater. Juveniles collected on the bottom fed on large-sized copepodids of *Neocalanus cristatus* and *Eucalanus bungii*, *Euphausia pacifica* (a euphausid), and *Parathemisto japonica* (an amphipod) (Nakatani and Maeda 1987).

Young-of-the-year juveniles from the Shelikof Strait spawning were sampled with a Methot midwater frame trawl (Methot 1986) in June and July 1987 (Hinckley et al. 1989), and by small-mesh midwater and bottom trawl surveys in late-summer of several years (Bailey and Spring, in review). Data from these studies have not yet been completely analyzed. However, in June and July the early juveniles (mainly 20–30 mm) were found on the shelf along the Alaska Peninsula. As with the eggs and larvae, they formed a large discrete patch surrounded by a large area with lower abundances. From their pattern of distribution, it appears that at this size and time of year they still inhabit midwater depths and are not schooling (Hinckley et al. 1989). Fish were found to feed mainly on various life stages of *Pseudocalanus* spp., smaller fish ate primarily nauplii and copepodids, while adults became more important in larger fish. Differences in diet between fish sampled at different locations indicated that the food organisms were patchily distributed (Grover 1990).

Sampling in late-summer has concentrated mainly on the bays around Kodiak Island and along the Alaska Peninsula. Considerable interannual variation in sampling and pattern of distribution of juveniles characterized these surveys. In 1987, when the sampling area in late-summer included the shelf west of the Shumagin Islands, a concentrated patch of juveniles was found that was likely the product of the Shelikof Strait spawning, i.e., the eggs and larvae that had been followed through the spring during their drift to the southwest from Shelikof Strait (Bailey and Spring, in review).

Year-class determinants

Studies of walleye pollock early life history in both Funka Bay and Shelikof Strait have been designed to determine causes of year-class fluctuations. The basic premise is that these fluctuations result from events during early life history and have little relation to the abundance or other characteristics of the spawning population. The influence of hydrography and its effect on larval food supply has been the most intensively studied factor in both areas, but predation has also been considered in Shelikof Strait research.

In Funka Bay, walleye pollock early life history seems to be closely tied to the timing and extent of the influx of Oyashio Water (Nakatani 1984). This cold, low-salinity water carries *Pseudocalanus minutus* into the bay where they produce nauplii, the primary diet of small larvae in nearsurface waters. Walleye pollock spawning seems to be timed and positioned to correspond to this influx. In years when this influx is delayed or absent, survival of larvae may be reduced (Nakatani and Maeda 1989). Years with an early invasion of the Oyashio Water have resulted in large year-classes of walleye pollock (Nakatani 1988). However, a strong year-class was also observed in 1980 when there was a late invasion (Nakatani and Maeda 1983, Nakayama et al. 1987). To predict population size fluctuations will require further studies on the causes of larval mortality.

Besides factors influencing larval food production in Shelikof Strait (Incze et al. 1990), the complex dynamics of the ACC as it exits the strait seem important in determining the rate of drift of the larval patch and its resultant position when the larvae are ready to settle (Reed et al. 1989). If the larvae are in the center of the ACC as it exits the strait, they may be carried quickly offshore through the sea valley between the Semidi Islands and Chirikof Island, as apparently happened in 1985 (Incze et al. 1989). Some of these larvae may remain offshore where larval feeding conditions are probably not ideal. The return of offshore larvae to the shelf for demersal settlement is also problematical. If the larvae are on the Alaska Peninsula side of the core of the ACC as it exits the strait, their drift will be slower, and they should remain in the coastal region where food production is probably enhanced. Their trajectory should carry them west along the Alaska Peninsula to shelf areas suitable for demersal settlement.

Storm winds blowing offshore from Wide Bay may displace the ACC as it exits the strait, and eddies have been observed in this area. The influence of such factors on the larval patch and larval food production may be important in determining the numbers of larvae reaching the juvenile stage.

Conclusions

It appears that within large areas of distribution, walleye pollock populations have evolved to spawn in very specific areas and during brief times of the year. Adults migrate to these areas annually for spawning. This spawning pattern produces concentrations of planktonic eggs and larvae that far exceed those reported for any other fish (>20,000 eggs/m^2; <5000 larvae/m^2). These spawnings are such that the eggs and larvae find themselves in areas where suitable food is abundant and where currents later carry larvae to suitable nursery areas. It appears that interannual variations in oceanographic conditions responsible for food production and larval drift impact larval survival, and hence year-class strength. Although there are marked differences in the geography and oceanography of Shelikof Strait and Funka Bay, walleye pollock have adapted to reproduce successfully in both areas. Adaptations in the early life history of walleye pollock to these differences in environment include timing and duration of the spawning season, specific gravity of the eggs, and differences in prey size in relation to larval size.

Time of spawning in both areas corresponds to seasonal transitions in hydrographic conditions (Nakatani 1988, Kim 1987). The spawning season is several months long in the lower-latitude Funka Bay area where there is considerable interannual variation in timing of the intrusion of the cold Oyashio Water, which increases copepod naupliar production. The Shelikof Strait area spawning is very peaked, taking place mainly over a few weeks and during the same time each year, early April. This is the time when currents are at an annual minimum due to reduced precipitation and weak winds. We do not know if low current strength is the seasonal signal that fish respond to, but presumably the signal is less variable than the intrusion of Oyashio Water.

Eggs are less dense in Funka Bay where water depths are only about one-third those of Shelikof Strait. In Funka Bay, the eggs rise in the water column after spawning and drift into the inner part of the bay. In Shelikof Strait, the eggs remain in the nearbottom water where they are spawned and show no appreciable drift. This difference in transport of eggs may relate to the desired location of hatching. Copepod production is enhanced when Oyashio Water enters Funka Bay and the egg drift pattern enables the eggs to hatch there. In Shelikof Strait, the upper layers of water during the spawning season are moving to the southwest at a rate that would flush eggs in surface waters out of the strait and into the offshore Alaska Stream in a few weeks. By remaining in the sluggish bottom waters, hatching is more likely to occur in southwest Shelikof Strait where larval prey may be more abundant. Interannual variations in storms in this area may effect copepod production and thereby larval condition.

In both areas, nauplii of species of small copepods, *Pseudocalanus* and *Oithona*, are dominant in the diet of first-feeding larvae. Eating small prey is energetically costly for larger larvae, so it may be critical for them to encounter more advanced stages of copepods (Incze et al. 1984). This may be more important in Shelikof Strait than in Funka Bay because larvae in Funka Bay start eating larger prey at a smaller size than do larvae in Shelikof Strait.

Drift of larvae to nursery grounds is more important in Shelikof Strait than it is in Funka Bay. It appears that most juveniles that result from spawning in Shelikof Strait inhabit shelf and nearshore areas 100–200 km from the spawning location by the age of 4 months

(Hinckley et al. 1989). Juveniles from the Funka Bay spawning are mostly found in waters just outside the bay during their first summer (Nakatani 1988). In the following winter, some of them remain in the center of the bay (T. Maeda and T. Nakatani, unpubl. data).

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