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ABSTRACT: In 1991 the major cohorts of walleye pollock Theragra chalcogramma larvae in Resurrection Bay, Alaska, initiated feeding when the copepod nauplii population was still at low winter density levels. First-feeding walleye pollock larvae were most abundant between 16 April and 14 May; thereafter, there were very few recently hatched larvae in the plankton. Copepod nauplii did not begin their annual increase in abundance until mid June. Throughout the spring and summer few walleye pollock larger than the first-feeding stage were observed, suggesting that low prey abundance was limiting larval growth. In 1991 the small late-hatching cohorts had the best feeding conditions in the bay.

INTRODUCTION

Walleye pollock Theragra chalcogramma compose a major food web link (Springer 1992), and fishery oceanographers are currently trying to understand recruitment processes of this species (Schumacher and Kendall 1995). Pollock support some of the world’s largest single-species fisheries and are prey for many commercially harvested fishes, as well as sea birds and marine mammals. Our study site, Resurrection Bay in Alaska’s Kenai Peninsula (Figure 1), is one of the many nursery grounds for walleye pollock in the northern Gulf of Alaska (Smith et al. 1991; Muter and Norcross 1994). Recruitment from planktonic marine fish larvae is controlled largely through variations in growth rates and predation pressure (Ware 1975; Brodeur and Merati 1993). Growth rates of larval pollock are related to the availability of copepod nauplii, their predominant prey (Dagg et al. 1984; Haldorson et al. 1989; Hillgruber et al. 1995).

This study examined the timing of occurrence and spring and early summer length frequency profiles for pollock larvae in Resurrection Bay. The relative abundance of larvae that had grown beyond the first-feeding stage was estimated from the length data. Copepod nauplii were concurrently sampled to monitor the post-winter copepod population increase and to describe how the different hatching cohorts of pollock larvae were timed to that increase.

METHODS

Study Site

All work was done at the head of the University of Alaska’s line of oceanographic stations known as the Seward Line that begins in Resurrection Bay (Figure 1). The fiord is 30 km long, 6–8 km wide, and opens directly into the Gulf of Alaska. Generally, beginning in April, temperature and salinity stratifications in the upper water column are caused by spring warming, snowmelt, and freshwater runoff (Muter 1992), much of which comes from glaciers and permanent snowfields. By the end of May a strong pycnocline occurs at depths of 20–25 m (Heggie et al. 1977). Mountains surround the bay creating a short fetch from any direction and wave height typically is <1 m. Water temperature (Figure 2) was measured daily at the sea surface and at a depth of 70 m near station RES 1.
Copepod Nauplii

Prey samples were taken weekly at 10 m with a 10-L water bottle at stations RES 1, RES 2.5, and RES 4 from 2 April to 9 July 1991. We selected the 10-m depth for monitoring the timing of the spring prey increase because walleye pollock larvae have been commonly found during daylight hours at this depth (Dagg et al. 1984; Haldorson et al. 1993; Muter and Norcross 1994). Nauplii sampling was not done to determine prey abundance estimates for Resurrection Bay but rather to identify the timing of the spring copepod bloom. Previous surveys (Paul et al. 1991; Smith et al. 1991) have shown that the spring increase in copepods can be observed throughout the upper 20 m of the water, so sampling at 10 m is appropriate for establishing the bloom timing. A single bottle sample was taken weekly between 1000 and 1400 hours at each of the 3 stations. Ambient light at depth was not measured. Water from the bottle was passed through a 64-µm bag net and the retained organisms preserved for microscopic analysis. Measured with an ocular micrometer, nauplii were divided into 2 length groups (<150 µm and 150–350 µm body lengths, exclusive of caudal spines) and for each group the number per liter was determined by counting the whole sample. Nauplii of crustaceans other than copepods were not enumerated.

Figure 1. Location of sample stations for walleye pollock larvae and copepod nauplii in Resurrection Bay, Gulf of Alaska, during the spring of 1991.
Figure 2. Resurrection Bay mean monthly water temperatures at the surface (upper) and at the 70-m depth (lower) for March, April, May, and June 1984–1994, the months that *Theragra chalcogramma* larvae are usually present.
Figure 3. Total number of copepod nauplii with body lengths $<150 \mu m$ (upper) and with body lengths of 150–350 $\mu m$ (lower) collected at a depth of 10 m from 3 stations in Resurrection Bay during 1991.
Walleye Pollock Larvae

Larval walleye pollock were collected to determine the temporal occurrence for major cohorts and trends in growth based on changes in length frequency. The sampling was not designed to produce a population estimate. From 2 April to 9 July 1991 larvae were collected weekly between 1000 and 1400 hours using a 1-m Tucker trawl (NIO net) towed down to 80 m and back up to the surface. It had a 505-µm mesh and included depth and flow meters. Preserved in 10% formalin, samples were collected at stations RES 1 and RES 4, but no sample was taken at RES 4 on 21 May. Sample counts of walleye pollock larvae were converted to numbers per 100 m³ at each station. Larval lengths were measured to the nearest 0.1 mm using a microscope and ocular micrometer. Standard length was used because the tail is poorly developed in the larvae and the caudal peduncle is prominent. The larval length categories were as follows: ≤ 5.5, 5.6–6.5, 6.6–7.5, 7.6–8.5, and > 8.5 mm standard length.

For the weekly samples, the hatching period and prevalence of the pre- (≤ 5.5 mm) and first-feeding stages (5.6–6.5 mm) were estimated. Larvae 5.6–6.5 mm were considered to be the most susceptible to poor feeding conditions because they had exhausted their yoke supply and had to learn how to capture prey to survive. This transition period from living on yolk to feeding is a critical period in the recruitment process of pollock larvae (Ware 1975; Bailey et al. 1995). Pollock larvae > 7.5 mm long were considered to have passed the first-feeding stage because their survival and growth to that size proved they were successfully capturing prey.

RESULTS

Copepod Nauplii

During April and the first 2 weeks of May copepod nauplii (150–350 µm length) were present at < 4 nauplii·L⁻¹ (Figure 3). In the last week of May, samples contained > 10 nauplii·L⁻¹ and by mid June, > 20 nauplii·L⁻¹. Nauplii < 150 µm long, which would grow to sizes and stages eaten by pollock larvae or fry, were present in numbers similar to the 150–350-µm group (Figure 3). Nauplii abundance generally increased over time, but in some samples counts were low even into July.

Figure 4. Abundance of recently hatched and first-feeding (≤ 6.5 mm standard length) and larger (> 6.5 mm) walleye pollock larvae at stations RES 1 (upper) and RES 4 (lower) in Resurrection Bay during the spring 1991.

Figure 5. Average abundance and timing of occurrence for walleye pollock larvae ≤ 6.6 mm and copepod nauplii with body lengths of 150–350 µm at all stations sampled in Resurrection Bay during 1991.
Figure 6. Length frequencies of larval walleye pollock at station RES 1 (upper) and RES 4 (lower) in Resurrection Bay during the spring of 1991. The number of larvae measured appears at the top of the size-frequency bars.
**Walleye Pollock Larvae**

The average amount of water filtered per net sample for all samples was 170 m³ (SD = 38). Pollock larvae < 6.5 mm were most abundant from 9 April to 14 May at station RES 4, whereas at RES 1 the peak was restricted to mid April (Figure 4). Pollock larvae > 6.5 mm did not exceed 1–2 individuals per 100 m³ at the inshore station, except on 4 June. At the seaward station, RES 4, a pulse of larvae > 6.5 mm occurred on 7 May, and abundance was above average the following week (Figure 4). Pollock larvae < 6.6 mm were most abundant in samples from mid April to mid May, whereas copepod nauplii 150–350 µm long became abundant in mid June (Figure 5). Apparently, in 1991 most newly hatched and first-feeding pollock larvae occurred when the copepod nauplii population was still at winter density levels. Size-frequency data in Figure 6 show that during the first 5 weeks of sampling relatively few larvae had grown past the first-feeding stage (> 6.5 mm). Larvae past the first-feeding stage became common beginning 14 May, and most larvae > 8.5 mm were captured after 1 June.

**DISCUSSION**

Muter and Norcross (1994) reported that fish larvae and their planktonic prey in Resurrection Bay represent a community whose horizontal distribution is determined by upper layer water flow. The bay’s upper water column is affected by the Alaska Coastal Current, water inflow along the fiord’s east side and outflow along the west shore. Thus, it was unlikely that larvae and nauplii sampled each week were the same groups sampled throughout the study; they more likely represented a population spread over a much larger geographical region than Resurrection Bay. Observations on the health of pollock larvae in Shelikof Strait, to the west of Resurrection Bay, support this premise; i.e., this major spawning area was not a good pollock nursery that year. Through histological examination, Theilacker and Porter (1995) found that 40% of the Shelikof Strait larvae were poorly nourished in 1991, and the survivors had low growth rates (Bailey et al. 1995). Likewise, in April 1991 only a few pollock larvae in our Resurrection Bay samples had grown past the first-feeding stage.

Generally, fish have better survival rates if hatched when copepod nauplii are most abundant, an idea referred to as the “match-mismatch hypothesis” by Cushing (1975). Prey availability was low during 1991 in Shelikof Strait (Bailey et al. 1995), and our survey suggests similar conditions in Resurrection Bay. Our sampling at just 10 m was not adequate to describe generalized prey abundance, but it did identify that timing of the spring copepod increase occurred well after the time that most numerous cohorts of pollock larvae started to feed. In contrast, Smith et al. (1991) found the major 1988 cohort of pollock larvae appeared in the fiord when copepod nauplii numbered ≥ 20–50 · L⁻¹ (Figure 7), relatively high values for nauplii abundance (Dagg et al. 1984; Paul et al. 1991; Bailey et al. 1995). Sea temperatures were warmer in 1988 than in 1991 (Bailey et al. 1995; Figure 2), presumably favoring more rapid growth of the larvae. In the northern Gulf of Alaska the 1988 year class had good recruitment, whereas the 1991 year class did not (Kendall et al. 1996).

Over the southeastern Bering Sea shelf, in Auke Bay, Shelikof Strait, and Resurrection Bay, *Pseudocalanus* is a predominant copepod nauplii eaten by pollock larvae. Abundance of *Pseudocalanus* nauplii when pollock hatch is primarily a function of the number of adult female copepods present when the spring phytoplankton bloom occurs (Dagg et al. 1984; Paul et al. 1990). Water temperature and energy intake regulate growth rates of copepods. Female abundance, temperature, and food are probably key factors

![Figure 7. Mean abundance and timing of occurrence for larval walleye pollock and copepod nauplii with body lengths of 150–350 µm in Resurrection Bay, Gulf of Alaska, during the spring of 1988; data from Smith et al. (1991).](image-url)
in the recruitment of all copepod species eaten by pollock larvae. In recent years the major spawning events by pollock in the northern Gulf of Alaska has consistently occurred during the third week of April to the first week of May (Muter and Norcross 1994), but the clues initiating spawning have not been described. The disparate appearance in 1991 of the major cohort of pollock larvae and copepod nauplii suggests that production processes for copepods and pollock are not similarly linked to the same factors.

Pollock larvae typically grow at about 1.2 mm/week at 4–5°C (Muter and Norcross 1994), but there are no published values for growth at lower temperatures. Most of the pollock larvae collected for the first 4 weeks of sampling in 1991 were <6.5 mm in length; few were beyond the first-feeding stage. This poor growth rate leaves the larvae susceptible to predation on their prey begin their spring proliferation (Paul et al. 1990). In May, when water temperatures were 4–5°C (Figure 2) and patches of prey (>10 nauplii ·L⁻¹) existed at 10-m depths, pollock larvae >6.6 mm started to appear in Resurrection Bay, indicating that some of them had passed the first-feeding stage. Some new recruits to the first-feeding size category were even present in the plankton after 11 June, when nauplii >20 nauplii ·L⁻¹ were present, a prey concentration sufficient to support rapid growth rates in pollock larvae (Haldorson et al. 1989).

In 1991 the small, late-hatching cohorts had the best feeding conditions in Resurrection Bay, whereas the majority of the larvae from the major spawning events in April failed to grow beyond the first-feeding stage. In the Gulf of Alaska pollock have a protracted spawning period with peak spawning in April or May, but some larvae are present in the plankton from March to the end of June (Haldorson et al. 1992). Protracted spawning ensures that at least some larvae hatch after their prey begin their spring proliferation (Paul et al. 1991). Our study demonstrates the survival value of the protracted spawning of walleye pollock.

LITERATURE CITED


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