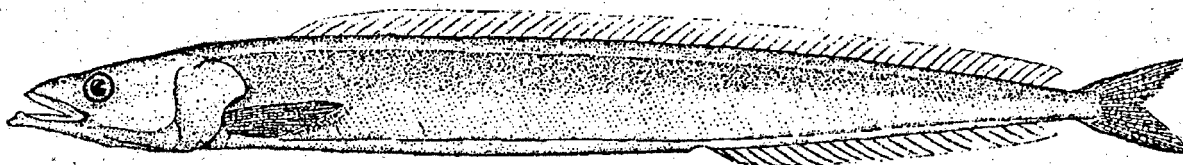
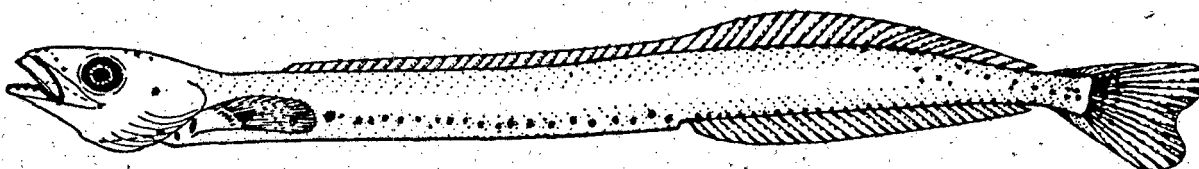
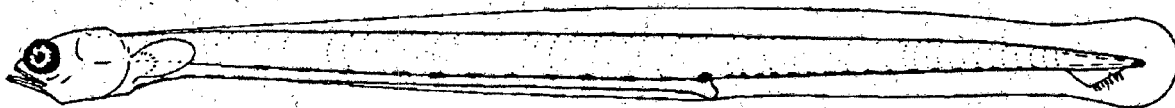


Fisheries Oceanography of the Southeast Bering Sea:

OCS Study
MMS 92-0019

Relationships of Growth,
Dispersion and Mortality
of Sand Lance Larvae to
Environmental Conditions
in the Port Moller Estuary



MMS

U.S. Department of the Interior
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Relationships of Growth, Dispersion and Mortality of Sand Lance Larvae to Environmental Conditions in the Port Moller Estuary

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ABSTRACT

Three waves of spawning Pacific sand lance, *Ammodytes hexapterus*, entered the Port Moller estuary on the northern shore of the Alaska Peninsula from mid-January to late May, 1990. They laid their eggs on sand in lower Moller Bay. The center of egg distribution was about 12 km south of the boundary of the estuary. Peak spawning occurred on January 14, March 15 and April 30. Eggs incubated for a period of 45 to 94 d. The number of days of incubation decreased as water temperatures rose in spring and early summer. Peak hatch dates for the three cohorts were April 18, May 23 and June 14. Hatching occurred over an extended period of time, ranging from 41 to 63 d.

Mean length of larvae at hatch was 5.8 mm, and mean length at absorption of the yolk was 7.6 mm. Larvae grew slowly over the first 49 d of life at an average rate of 0.06 to 0.19 mm·d⁻¹. Growth rate rose to 0.26 mm·d⁻¹ in larvae 50 to 100 d old. Weight-specific growth rate rose from about 1 %·d⁻¹ in larvae <50 d old to 3 to 6 %·d⁻¹ in older larvae. Slow growth was directly responsible for the reduced number of cohorts and the long time periods between peak hatch dates compared to other demersally-spawning fish such as herring or capelin because first-feeding sand lance larvae took longer to vacate their feeding niches.

Sand lance fed primarily during the day on a diet of copepod eggs and nauplii, copepodites and small adults copepods. This type of prey and its average length and width were similar to that of herring larvae, indicating that the larvae of these two species shared the same food resource.

Almost all larvae were found above the thermocline in the upper 30 m of the water column. The smallest larvae were found near the surface and larval length increased with increasing depth. Density (number·m⁻³) of larvae was maximal at 10 m and decreased with increasing depth. There was no diurnal pattern of vertical distribution. If it existed, it most likely followed a type II pattern - migration to the surface at dawn followed by sinking at dusk.

Newly-hatched larvae from all three cohorts were advected at an average rate of 0.277 km·d⁻¹ from lower Moller Bay to the head of nearby Herendeen Bay in the same estuary. Larvae diffused from the centroid of each cohort at a rate that decreased inversely with age. The rate of transport of larvae that initially diffused into upper Moller Bay was reduced by an anti-seaward surface current in upper Moller Bay that was caused by upwelling at the junction of upper and lower Moller Bays.

Total loss rate of sand lance larvae in lower Moller Bay and Herendeen Bays was 0.166 d⁻¹, of which 0.133 d⁻¹ was due to natural mortality and 0.033 d⁻¹ was due to offshore transport. The rates of loss and mortality of sand lance in upper Moller Bay were higher due to different physical conditions south of the upwelling zone, but the proportion of dispersal loss to mortality loss was similar to that in the rest of the estuary.

We conclude that the stock of sand lance that spawns in Port Moller belongs to a class of stocks that have an entirely estuarine or coastal early life history, in contrast to some stocks of sand lance whose larvae disperse offshore from inshore spawning sites. This life history strategy may have evolved in response to the unique physical conditions of the Port Moller estuary - a shallow, well-mixed site with sandy substrate that is suitable for incubation of demersal eggs next to a deep, stable fjord with a rich zooplankton community that is suitable for rearing of larval and juvenile sand lance.

One consequence of this life history strategy is that annual variation in recruitment is causally linked to variation in physical factors, particularly the factors that affect dispersal of larvae: storm events, local wind-forced surface currents, baroclinic surface currents, and regional downwelling events at the boundary of the estuary.

One consequence of the small scale of larval dispersal in this stock is that density-dependent factors such as competition for food between sand lance, between sand lance and other planktivorous fish larvae such as herring, and between sand lance and invertebrate planktivores such as chaetognaths may play as important a role as density-independent physical factors.

Another consequence of the small scale of dispersal in this stock is that any industrial development of the Port Moller estuary such as dredging of its narrow channels or release of toxic chemicals into its water will have a greater impact on this stock than if it followed a strategy of dispersing offshore. The fate of the Port Moller sand lance stock depends on the maintenance of undisturbed spawning areas in lower Moller Bay and a productive zooplankton community in upper Herendeen Bay.

INTRODUCTION

This is the final report of our investigations into the early life history of Pacific sand lance, *Ammodytes hexapterus*, in the Port Moller estuary of Alaska. This report is the third in a series of four that is devoted to the fisheries oceanography of the southeastern Bering Sea. The first report by McGurk (1989b, 1991) described the growth, mortality and dispersion of Pacific herring, *Clupea pallasii*, larvae in Port Moller in early June, 1989, based on a 2 week long reconnaissance of the estuary. The second report by McGurk et al. (1991a, 1991b) described the physical oceanography of the estuary and the population dynamics of Pacific herring larvae in the estuary for May to July, 1990, based on an intensive 4 month study of the estuary. The fourth report in this series (McGurk et al. 1992) will describe simulation modelling of dispersal of both herring and sand lance larvae in Port Moller in 1990.

This program of fisheries oceanography is supported by the U.S. Minerals Management Service. The purpose of the program is to collect original scientific information on the early life history of forage fishes in the southeastern Bering Sea that will be used to assess the impact of oil and gas development in the Bering Sea on these fishes. Early life history was targeted for three reasons: fish larvae are more sensitive to hydrocarbons than juveniles or adults (Rice et al. 1987); they are less able to avoid pollutants than adults because of their limited sensory and motor capabilities; and events in the egg and larval stages are considered to be crucial for the establishment of year-class strength in fishes (Cushing 1975, 1990).

This report focuses exclusively on the growth, feeding, dispersal and mortality of three cohorts of Pacific sand lance larvae that hatched in the Port Moller estuary. We do not describe the physical oceanography or the zooplankton community of the area, except when they impinge directly on the population dynamics of sand lance, because physical oceanography and zooplankton community was described in detail by McGurk et al. (1991a, 1991b). Neither do we discuss the nutritional status of sand lance larvae, as measured by RNA-DNA ratios, because that subject was described by McGurk et al. (1992).

Ecological importance of sand lances

Sand lances are small, slender fishes that live in the pelagic zone of temperate seas. They are distinguished from other pelagic fishes such as herring by their elongate eel-like body and by their remarkable habit of burying themselves in sand and gravel at night to avoid predators.

In North America sand lance has been occasionally caught for bait (Auster and Stewart 1986). In the North Sea sand lance are fished for meal, oil and bait; the fishery was relatively small until the mid-1970s (Reay 1970; Sherman et al. 1981). In Japan sand lance are caught for food; it is one of the most important commercial species, for example it accounted for about 22% of the total fisheries catch in the Seto Inland Sea from 1975 to 1984 (Fujiwara et al. 1990).

Sand lances are very important forage fishes in temperate seas (Sherman et al. 1981, 1984). Their abundance, their relatively small size compared to salmonids and groundfishes, and their pelagic life history means that they are an important link in the food chain between zooplankton

and larger animals of commercial, ecological and cultural importance. Sand lances are prey for many species of fish in the North Pacific (Outram and Haegele 1972; Westrheim and Harling 1983) as well as the North Atlantic (Scott 1968; Kelley 1987). They are also prey for marine mammals (Nemoto 1959; Overholtz and Nicolas 1979; Payne et al. 1986; Payne and Selzer 1989; Pierce et al. 1990) and for sea birds (Sealy 1975; Furness 1984, 1990; Vermeer and Westrheim 1984; Harris and Wanless 1990).

Sand lances may also be significant predators on the eggs and larvae of other commercially important species. For example, Rankine and Morrison (1989) reported that the adults of two species of sand lance (*Ammodytes marinus* and *Hyperoplus lanceolatus*) in the Firth of Clyde, Scotland, bury themselves in the gravel that is used as spawning substrate by Atlantic herring. These sand lance feed on herring eggs and newly-hatched larvae when they are available.

The ecological importance of sand lances extends throughout their life history. Large biomasses of sand lance produce large numbers of pelagic larvae over fall, winter and spring. Sand lance larvae are common and abundant in late winter and early spring in the North Sea, on the continental shelf of the Northeast Atlantic, and on the continental shelf of the northeastern and northwestern Pacific ocean. Sand lance larvae have been captured often in ichthyoplankton surveys of temperate seas. Much of the literature on sand lance larvae consists of data reports of ichthyoplankton surveys.

The ecological importance of sand lances has grown over the last three decades, at least in the North Sea and in the northeastern Atlantic, as their biomasses have grown. This recent increase in sand lance biomass appears to be the result of a decrease in the biomass of their predators and competitors caused by excessive fishing pressure (Sherman et al. 1981).

Previous research on Pacific sand lance larvae

Little research effort has been directed towards the early life history of sand lances because commercial fisheries for sand lance are less valuable than those of herring and other fishes. Research has also been obstructed by the difficulty of identifying sand lances to the species level. All species are similar in external appearance, so fisheries scientists have resorted to counting meristic characters, especially the number of vertebrae (Einarsson 1951; Kobayashi 1961; Hashimoto 1984; Winters and Dalley 1986; Dalley and Winters 1987; Nizinski and Collette 1990), or to characterizing proteins with electrophoresis (Okamoto 1989). This has led to some confusion in the scientific literature about species names and geographic ranges (Stevens et al. 1984). Fortunately for this study, *A. hexapterus* does not share its range of distribution with any other species of sand lance except the Japanese sand eel, *A. personatus*, and that species is apparently restricted to waters south and west of Hokkaido Island, the northernmost island in the Japanese archipelago (Okamoto 1989).

Since there has never been a commercial fishery for *A. hexapterus*, less is known about its early life history than most other species of sand lance. Natural spawning has never been observed, but it is suspected to occur during late

fall or winter because newly-hatched larvae are found in the water column in late winter and early spring. Like all sand lances, the eggs of *A. hexapterus* are demersal and are deposited on sand and fine gravel. Spatial distribution of eggs and density of eggs on spawning substrate has never been measured. Pinto (1984) artificially spawned *A. hexapterus* eggs taken from adults captured off the coast of Washington and described the developing egg and the newly-hatched larva. However, his experiment was carried out at only one temperature (9 °C), so we know little about the effects of temperature on egg incubation time, duration of hatching, hatching success and size of larvae at hatch. *A. hexapterus* larvae have never been raised in the laboratory so we know little about the relationships between larval growth, temperature and prey concentration.

Ichthyoplankton surveys have found wild *A. hexapterus* larvae from the northeastern tip of Japan through the Okhotsk and Bering Seas (Kobayashi 1961), and on the continental shelf off southcentral Alaska (Rogers et al. 1980; McGurk et al. 1990), British Columbia (LeBrasseur 1970; Barraclough 1967a, 1967b, 1967c; Barraclough and Fulton 1967, 1968; Barraclough et al. 1968; Robinson 1969a, 1969b; Robinson et al. 1968a, 1968b), and the states of Washington (Day 1971; Waldron 1972) and Oregon (Mitsano 1977; Richardson and Percy 1977). Sand lance larvae were incidental catches in all of these reports, except Kobayashi (1961), so there is little material available to estimate rates of larval growth and mortality. Vertical distribution of large larvae at night was described by Richardson and Percy (1977). The data reports authored by Barraclough and Richardson include much information on the gut contents of larval and juvenile sand lance. This data was summarized by Pearre (1986). Juvenile sand lances have been occasionally captured as part of nearshore surveys by beach seines (Gordon and Levings 1984; Orsi and Landingham 1985).

Study site

The Port Moller estuary is the largest embayment on the northern shore of the Alaska Peninsula (Fig. 1). It exchanges water with Bristol Bay, the southeastern part of the Bering Sea. The estuary has a total area of 876 km² enclosed in four bays: Mud Bay, Nelson lagoon, Herendeen Bay and Moller Bay. At low tides Mud Bay and Nelson Lagoon are dewatered and the rest of the estuary can only be navigated through three narrow channels.

The estuary contains two distinctly different physical and biological environments: Moller Bay and the northern two thirds of Herendeen Bay are shallow and turbulent with narrow tidal channels running down their centers, but the southern third of Herendeen Bay is a deep (>100 m), fjord-like basin with a stratified water column.

Moller Bay contains extensive mud flats which are dewatered at low tides, a shelf region that is rarely dewatered, and a narrow channel that is never deeper than about 30 m. In this report, we have arbitrarily divided Moller Bay into an upper, southern bay and a lower, northern bay. The dividing line is at Harbor Point. The northern two thirds of Herendeen Bay also contain mud flats, a shelf region and two narrow channels: Hague and Johnston Channels. The water in Moller Bay and northern Herendeen Bay is well-

mixed due to strong tidal flushing and frequent storm events and there is little or no vertical stratification. The sediments in this area are predominantly sand and gravel (Sharma 1974).

Upper Herendeen Bay, the region extending south of Shingle Point, contains a deep basin which may have been carved out of sediment by glaciers from the surrounding mountains. This basin has the lowest flushing rate of any part of the estuary, and it is the only part of the estuary that has significant vertical stratification, with a thermocline at about 30 m depth. Concentration of prey for sand lance larvae is higher in the basin than in any other part of the estuary (McGurk et al. 1991a, 1991b).

Numerical modelling of the hydrodynamics of Port Moller has shown the presence of two convergences of surface currents (McGurk et al. 1991b). Both convergences are caused by the collision of an anti-seaward current from the north with a baroclinic seaward current from the south. The strongest convergence is located south of Harbor Point in upper Moller Bay. Its anti-seaward current is produced by strong, persistent upwelling at Harbor Point. The weaker convergence is located at the northern tip of the deep basin in Herendeen Bay. The cause of its anti-seaward current may be residual tidal currents.

MATERIALS AND METHODS

Twenty three plankton stations were established in the estuary and occupied at least once each week from April 28 to July 30, 1990 (Fig. 1). Methods of collecting plankton were described by McGurk et al. (1991a).

Cohort identification and growth

Sand lance larvae were sorted from the formalin-preserved samples of ichthyoplankton captured with the 333, 505 and 1000 µm mesh nets. All sand lance larvae were removed and counted except for those samples containing >1,000 fish larvae, which were split to a manageable size with a Folsom splitter. Between 15 and 30 larvae were randomly chosen from each sample; their standard lengths were measured to the nearest 0.1 mm and the presence or absence of a yolk sac recorded. Mean lengths (±1 SD) of each cohort were estimated from the length frequency distributions for the pooled data of each of the 13 surveys using a PC-version of NORMSEP (Tomlinson 1971), a computer program that separates mixtures of normal distributions.

Otolith analyses

Six extra samples of ichthyoplankton containing several hundred sand lance larvae were taken at station 36 during May and June and preserved in 35% isopropyl alcohol for otolith examination. A dissecting microscope with a polarized light source and polarized filters was used to illuminate the otoliths in the intact heads of sand lance larvae, and to follow the otoliths as they were teased out of the heads with jeweller's probes. The otoliths were fixed to microscope slides with clear nail polish. A compound microscope with

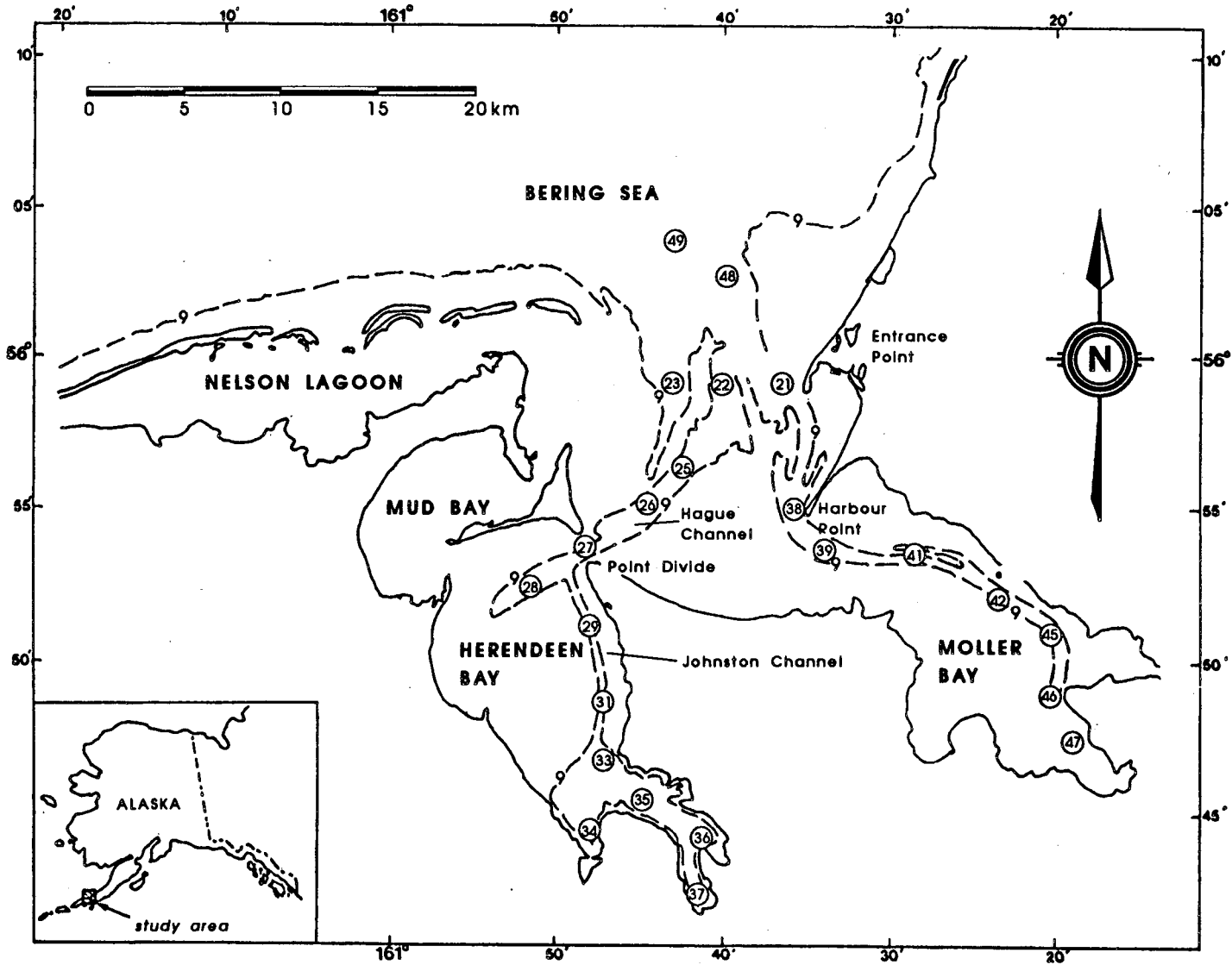


FIGURE 1
Map of Port Moller Estuary Showing the 5 Fathom Depth Contour
Circled numbers are plankton stations

a 1000X oil immersion lens was used to image the otoliths. The image was enlarged and enhanced using a video camera attached to the microscope.

Weight-length

Larvae were measured for standard length, rinsed with freshwater, and sealed in numbered foil packets which were then dried at 60°C for 24 h. The packets were stored in a desiccator for 24 h before being weighed to the nearest 1 µg on an electrobalance.

Specific growth rate

Instantaneous daily specific growth in dry weight of sand lance larvae was calculated as:

$$(1) \quad G_w = (100/t) \ln[W_t/W_0]$$

where G_w = specific growth (%·d⁻¹) in dry weight, W_0 = dry weight (µg) at hatch = 64 µg, and W_t = dry weight (µg) at age t (d). Mean dry weights were calculated from mean lengths greater than 7.4 using a weight-length regression. Larvae less than 7.4 mm long were assumed to be yolked and have a mean dry weight of 64 µg.

Gut analysis

Larvae were chosen randomly from each sample chosen for gut analysis. Their standard length was measured with a dissecting microscope to the nearest 0.1 mm. The length of the maxillary bone, which makes up most of the upper jaw, was measured to the nearest 0.01 mm with an ocular micrometer. Maximum potential gape of mouth of larval fishes is assumed to be equal to $\sqrt{2}$ times maxillary length (Shirota 1970). Percent gut fullness was estimated visually. (The guts of sand lance larvae are transparent until the fish metamorphose into the juvenile stage.) The guts of larvae with non-zero gut contents were opened with dissecting needles. Prey were identified to the nearest taxon and counted, and their width and length was measured to the nearest 0.01 mm with an ocular micrometer. Length of copepodites and adult copepods was cephalothorax length, which is equal to total length minus the urosome. This measure of length was used because the urosome was often missing, having been broken off during capture.

Vertical distribution

Vertical distribution of sand lance larvae was measured with two types of gear: stacked bongo nets and open-closing Tucker trawls. Two sets of stacked bongo net tows was performed in daylight near station 36 in Herendeen Bay on May 7 to 8. Each set consisted of 8 tows performed over a 2.5 h period. For each tow, a bongo net frame with one 333 µm and one 505 µm net was lowered at 0.5 m·s⁻¹ to the desired depth, towed horizontally for 10 min at 1 m·s⁻¹, and then retrieved at 0.5 m·s⁻¹. The desired depth was 10 m on the first tow and it increased at 10 m intervals to 80 m on the eighth tow. Therefore, each 10 m stratum above the target stratum was sampled for a total of only 10 s, or 2% of the total time (600 s) spent by a net in the target stratum.

The measured density of larvae captured by the stacked

bongo nets was

$$(2a) \quad N_i = n_i [600 / (600 + 10j)] + [n_{i-10} + \dots + n_{i-10j}] [10 / (600 + 10j)]$$

where N_i = measured density (m⁻³) of a tow directed at a target depth i (m), n_i = actual density (m⁻³) at depth i , and j = number of 10 m-wide depth strata above target depth strata i . We assumed that there were no differences in extrusion or net avoidance between the two mesh sizes, so N_i was the total number of larvae captured in the two bongo nets divided by the total volume of water filtered by the two nets. Rearranging equation (2a), we obtain an expression for n_i :

$$(2b) \quad n_i = (1 + 0.017j)N_i - 0.017(n_{i-10} + \dots + n_{i-10j}).$$

This equation was used iteratively; for example, first it was used to calculate n_{20} , and then n_{10} and n_{20} were substituted into equation (2b) in order to calculate n_{30} . Densities were not corrected for net avoidance.

An open-closing Tucker trawl was used to measure vertical distribution of sand lance larvae at station 36 in Herendeen Bay and station 39 in Moller Bay at three dates: June 24 to 26, July 2 and July 24 to 25. The trawl sampled 10 m deep strata from the sea surface to the sea bottom every 6 h over a 24 h period. Eight strata were sampled at station 36, but only 3 strata at station 39. The Tucker trawl was lowered to the mid-point of a stratum, opened with a messenger, towed at a speed of about 1 m·s⁻¹ for 10 min, closed with a second messenger and then retrieved.

Horizontal dispersion

Density of sand lance larvae was calculated as number·m⁻² of sea surface by multiplying number·m⁻³ by the average depth of tow. Density was corrected for net avoidance with a regression model of night-day catch ratios (Appendix A).

To describe the dispersion of larvae we created a two-dimensional coordinate system for Moller and Herendeen Bays. Since sand lance larvae hatched in lower Moller and Herendeen Bays we set the origin of the system on the northern boundary of the estuary along the line formed by stations 21, 22 and 23 (Fig. 1), rather than at the heads of the estuary as was done for the population analysis of herring larvae (McGurk et al. 1991a). This was also the origin used in the three-dimensional hydrodynamics model (McGurk et al. 1991b: Appendix C, Table 3).

We treated the estuary as if it consisted of two channels whose ends joined at the boundary. The x-axis of the western channel passed from station 22 in the center of the boundary south through the center of Hague and Johnston Channels and through the center of the deep basin at the head of Herendeen Bay. The x-axis of the eastern channel passed from station 22 directly to station 38 and then around Harbor Point and through the center of the channel in upper Moller Bay. The x-axis continued offshore directly from station 22 to station 49; a negative x value was assigned to stations 48 and 49. The y-axis was at right angles to the x-axis. Since almost all sampling was conducted along the x-axis, only 5 of the 23 stations: numbers 21, 23, 28, 33 and 48, had a non-zero y-coordinate and of those five only station 21 had a positive y-value.

The x-coordinate of the centers of larval distribution along the x-axis, or centroids, for each cohort were:

$$(3) \quad x_t = \frac{\sum_i N_{it} x_i}{\sum_i N_{it}}$$

where x_i = distance (km) of a centroid from the origin, N_{it} = density (m^{-2}) of larvae at station i at age t (d), and x_i = distance (km) from station i to the origin. Centroids were calculated for each cohort for each of the 13 complete surveys of the estuary for which there were at least three densities measured at three different stations in a survey.

Y-coordinates of the centroids, y_t (km), could be calculated in a similar way, but the results were not useful because the y-axis was not adequately sampled. In the absence of any other information, the y-coordinate of the centroids was assumed to be zero at all ages.

Horizontal spatial variance of larval density in the x-axis, s_{xt}^2 (km^2), was calculated as

$$(4) \quad s_{xt}^2 = \frac{\sum_i N_{it} (x_i - x_t)^2}{\sum_i N_{it}}$$

s_{xt}^2 was calculated only for surveys that had at least three densities measured at three different stations.

Spatial variance along the y-axis, s_{yt}^2 (km^2), was calculated similarly, but because of poor sampling coverage a meaningful s_{yt}^2 could only be calculated for those surveys with three or more stations with non-negative y values.

Mortality

Calculation of larval mortality required correction of larval densities for transport of larvae into and out of the estuary. It was not possible to use the standard method of calculating numbers of larvae by multiplying larval density by the area around each station because we had almost no information about the density of sand lance larvae outside the boundary of the estuary.

Instead, we used a simple advection-diffusion population model (5a)

$$N_{it} = M \frac{\exp \left[-\frac{(x_i - x_t)^2}{s_{xt}^2} - \frac{(y_i - y_t)^2}{s_{yt}^2} - Zt \right]}{\pi (s_{xt}^2 s_{yt}^2)^{1/2}}$$

where N_{it} = larval density (m^{-2}) at distance x (m) from its origin and at age t (d), M = number of herring larvae released into the water at age 0 d, Z = mortality (d^{-1}), x_t and y_t were in units of m, and s_{xt}^2 and s_{yt}^2 were in units of m^2 . Equation (5a) was fit to the data by, first, converting all densities to numbers. This was done by rearranging equation (5a) so that all terms relating to dispersion were placed on the left-hand side (5b)

$$n_t = N_{it} \pi (s_{xt}^2 s_{yt}^2)^{1/2} \exp \left[\frac{(x_i - x_t)^2}{s_{xt}^2} + \frac{(y_i - y_t)^2}{s_{yt}^2} \right]$$

where n_t = number of sand lance larvae at age t . Then, n_t was regressed on age

$$(5c) \quad \ln(n_t) = \ln(M) - Zt$$

M is not a true estimate of the actual number of larvae that hatched into Port Moller because this model assumed radial

diffusion along both axes, an assumption that is clearly not appropriate for the enclosed area of Port Moller. We use equation (5) in this study only to obtain measures of dispersal and mortality.

Statistics

The minimum level of statistical significance was the 5% probability level. The r^2 of all regressions was adjusted for the number of degrees of freedom in the regression model. All regressions in which the dependent variable was a mean were weighted by the sample size of the mean divided by its variance. All regressions in which the dependent variable was a ratio were weighted by the sample size used to calculate the ratio.

RESULTS

Number of cohorts

Of 473 samples of ichthyoplankton collected in 1990, 421 (89.0%) contained at least one sand lance larva. Larvae were found in almost all samples between April 25 and June 30, but they were rarely found after July 7.

The lengths of 3,154 sand lance larvae were measured. Length frequency distributions pooled by survey showed that three cohorts of larvae hatched into the estuary between April and July (Fig. 2). They were labeled cohorts 1 to 3, with the earliest cohort being number 1. Mean (± 1 SD, n) length for each cohort for each survey was calculated by separating the length frequencies into three normal distributions.

The number of cohorts and their timing of entry into the water column is shown more clearly by a plot of the fraction of yolked larvae in a survey against day of year (DOY) from April 25 (DOY = 115) to July 14 (DOY = 188) (Fig. 3). Surveys number 12 and 13 in mid- to late-July did not capture any yolk sac larvae.

Three maxima occurred on April 27 (DOY = 117), May 27 (DOY = 147), and June 17 (DOY = 168).

Yolk sac dynamics

Presence of yolk sac larvae

Yolk sac larvae were common in the first 11 surveys; in three of those surveys more than 50% of the population was yolked. This finding does not support a statement originally made by Masterman (1895) and subsequently repeated by Reay (1970), Trumble (1973) and Macy et al. (1978) that sand lance larvae remain within the sand until their yolk is exhausted before swimming up into the water column. Almost every study of the distribution of sand lance larvae has reported the presence of yolked fish in the water column, often in large numbers (Einarsson 1951; Wheatland 1956; Covill 1959; Kobayashi 1961; Norcross et al. 1961; Percy and Richards 1962; Herman 1963; Macer 1965; Fives 1967; Inoue et al. 1967; Langham 1971; Scott 1972; Waldron 1972; Richards and Kendall 1973; Altukhov 1978; Rogers et al. 1980; Scott 1980; Yamashita et al. 1985a, 1985b; Monteleone and Peterson 1986; Dalley and Winter 1987; Potter and Lough 1987; Harris et al. 1988; Nakata 1988). Also, studies

FIGURE 2
Length Frequency Distributions for Sand Lance Larvae Captured During
12 Surveys of Port Moller Estuary in April-July, 1990.
 Mean (± 1 SD, n) lengths of three cohorts are shown.
 Broken lines connect mean lengths of each cohort between surveys.

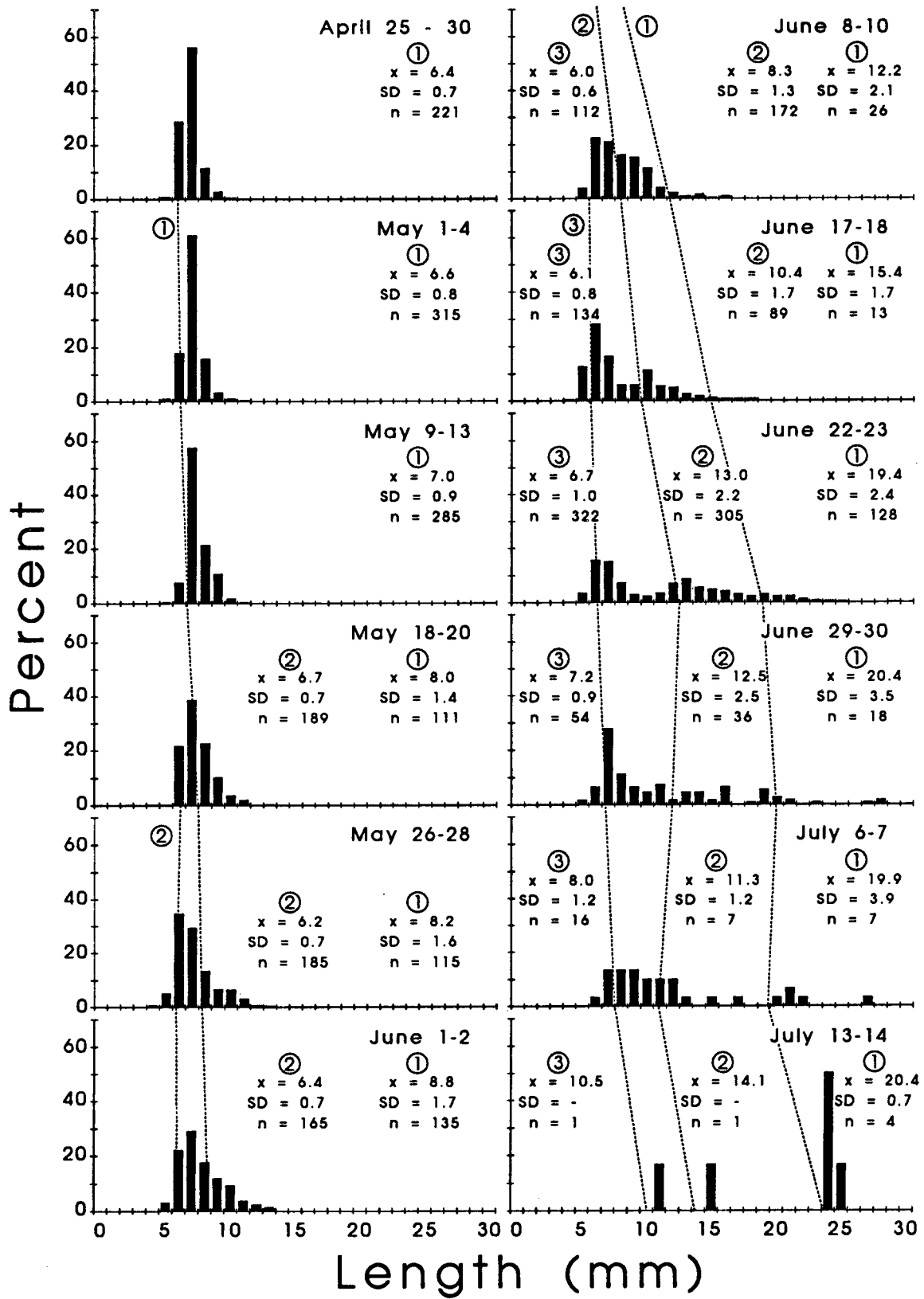
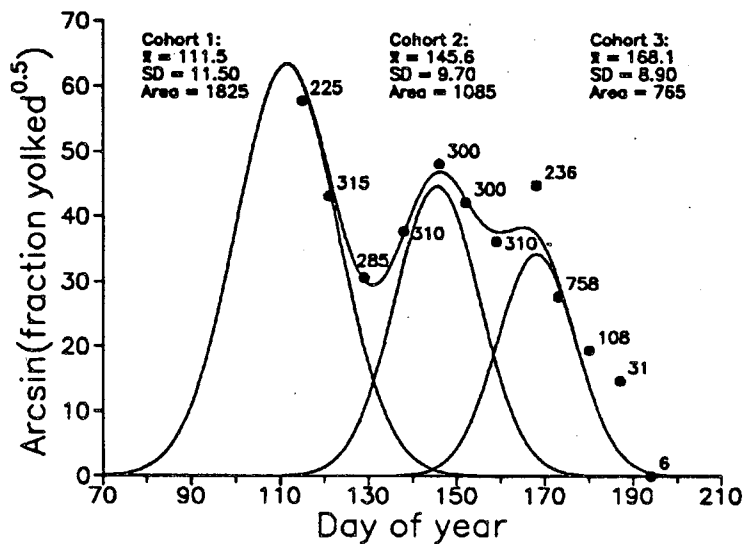


FIGURE 3
 Distribution of the fraction of yolked sand lance larvae in the Port Moller Estuary with day of year (mid-point of survey), separated into three normal distributions corresponding to three cohorts of larvae. Numbers next to symbols are total number of sand lance larvae captured in a survey.



of hatching of sand lance eggs in the laboratory have never reported the incubation of yolk sac larvae within sand (Inoue et al. 1967; Pinto 1984; Smigielski et al. 1984; Yamashita and Aoyama 1985). We conclude that sand lance larvae enter the water column immediately upon hatch, so the seasonal distribution of the fraction of yolk sac larvae contains information about the dates of hatch and the duration of hatch for each cohort.

Seasonal distribution of yolked larvae

In order to recover this information, three normal distributions corresponding to three cohorts of sand lance larvae were fit to the arcsin-transformed fractions of yolked larvae with least-squares techniques (Fig. 3). A mixture of three normal distributions explained 69% of the variance in the transformed fractions.

The parameters of the three distributions changed with time in such a regular pattern that they must have been related to the increase in mean water temperature of the upper 30 m of the Port Moller estuary over the April-July period. The three maxima of yolked larvae occurred at intervals of 22 to 34 d, with the interval decreasing in length over the April-July period. The relative number of yolked larvae in each cohort also decreased with time, as did the maximum fraction of yolked larvae, which fell from 0.798 in cohort 1 to 0.493 in cohort 2 and to 0.343 in cohort 3.

To back-calculate the distribution of hatching dates we required two pieces of information: estimates of the average winter-spring temperatures of the Port Moller estuary and the nearshore zone of Bristol Bay; and a relationship between temperature and the duration of the yolk sac stage in sand lance.

Mean water temperatures, January-July

The change in mean water temperature of the upper 30 m of Port Moller over the April-July period was well described by a linear regression of mean daily temperature on day of year (Fig. 4). We assumed that temperatures in the adjacent nearshore zone of Bristol Bay are very similar to those measured in Port Moller because the coastal domain of the Bering Sea resembles the estuary in being shallow, well-mixed and vertically homogenous (Coachman and Charnell 1977; Ingraham 1981; Cline et al. 1982; Kinder and Schumacher 1981; Greengrove 1991).

Information on water temperatures of the January-April period was taken from two sources. Ingraham (1981) estimated mean surface and bottom temperatures for the Bering Sea during winter (January-March) from data collected up to 1981 by Japanese and American (Northwest and Alaska Fisheries Center, Seattle, Wash.) fisheries researchers, as well as OCSEAP investigators, that is stored at the U.S. National Oceanic Data Center. Ingraham (1981) reported that mean monthly sur-

face and bottom temperatures of the coastal domain along the Alaska Peninsula during winter were all about 0°C. Cline et al. (1982) reported ranges of temperatures for the entire water column of the coastal domain, including Port Moller estuary, and the southern section of the middle shelf domain off the Alaska Peninsula for February and May 1981. In February, the temperature ranges were -1.7°C to 1.3°C for the coastal domain and 0°C to 4°C for the middle shelf domain. In May, temperature ranged from 4.4°C to 8.8°C for the coastal domain and 2.8°C to 7.8°C for the middle shelf domain. These ranges for May 1981 bracketed the mean temperatures we recorded in Port Moller in 1990. Based on this data, we assumed that the average winter water temperature of the coastal domain was 0°C in January, February and most of March 1990.

Based on analysis of dispersal of sand lance larvae within Port Moller (section 3.7.1 of this report), we assumed that sand lance eggs were laid on sand within the estuary and perhaps in the nearby coastal domain, which is about 50 km wide off Port Moller. We further assumed that the same linear rate of increase in mean temperature observed for May-July extended back from April 27 to March 27, which was the date at which the linear regression predicted 0°C.

Relationship between duration of yolk and temperature

No studies have yet been done of the timing of yolk absorption in *A. hexapterus*. However, it has been measured for *A. americanus* by Smigielski et al. (1984) and for *A. personatus* by Yamashita and Aoyama (1985) (Table 1). Both studies show that the duration of the yolk sac stage in *Ammodytes* spp. is highly correlated with water temperature over the range of 2 to 10°C (Fig. 5A). Therefore, the percentage daily loss in yolk sac larvae was calculated as

$$Y = 100 / \text{predicted duration} = 5.18 \exp(0.133T)$$

where Y = percent daily loss in yolk sac, and T = temperature (°C).

Distribution of hatching dates

Using equation (6) and the daily mean water temperatures for the January-July period, we back-calculated each of the three distributions of fraction of yolked larvae. We assumed that these distributions were identical to the distributions of dates of hatch. Peak hatch occurred on April 18 (DOY = 108) for cohort 1, May 23 (DOY = 143) for cohort 2 and June 14 (DOY = 165) for cohort 3 (Table 2). Duration of hatch fell from 64 d for cohort 1 to 48 d for cohort 2 and 42 d for cohort 3. These durations are similar to those measured in the laboratory for *A. americanus* (Smigielski et al. 1984) and *A. personatus* (Yamashita and Aoyama 1985) (Fig. 5B).

FIGURE 4
Average winter-summer water temperatures for Port Moller and the coastal domain of Bristol Bay. Closed circles are mean observed temperature of the upper 30 m of the Port Moller estuary from April 27 to July 27, 1990

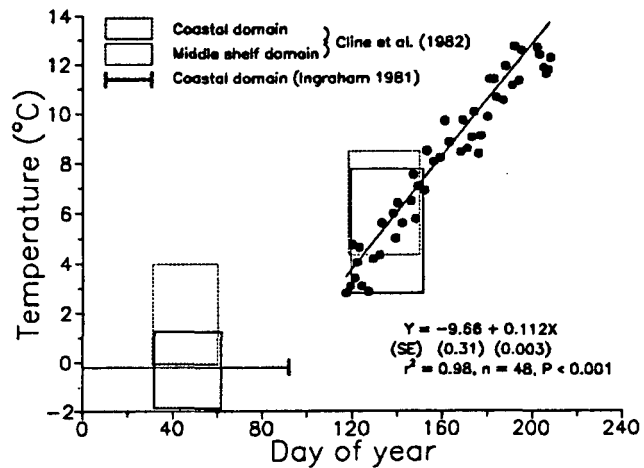


TABLE 1

Schedules of incubation, hatching and yolk absorption, plus lengths at hatching and yolk absorption, for three species of sand lance (*Ammodytes* spp.) incubated in the laboratory. Dashes indicate no data available.

Temperature (°C)	Duration of egg incubation (d)	Duration of hatch (d)	Mean length at hatch (mm)	Days to yolk absorption	Mean length at yolk absorption (mm)
<i>A. hexapterus</i> (Pinto 1984)					
9.0	24	-	5.3	-	-
<i>A. personatus</i> (Yamashita and Aoyama 1985)					
6.5	51	59	4.72	9	5.86
10.5	25	29	-	-	-
15.5	20	12	-	-	-
<i>A. Americanus</i> (Smigielski et al. 1984)					
2.0	82	74	6.24	14	7.22
4.0	67	65	6.34	12	7.37
7.0	48	43	5.71	7	7.20
10.0	30	30	6.06	5	7.41

Spawning dates

Pinto (1984) measured the egg incubation time of *A. hexapterus* at only one temperature, so a relationship between egg incubation time and temperature had to be developed by combining data from two other species of sand lance (Table 1). Fortunately, all three species of sand lance have remarkably similar incubation-temperature relationships (Fig. 5C). The percent daily egg development rate was calculated in the same way as the percent daily loss in yolk:

$$Y = 100 / \text{predicted incubation} = 1.01 \exp(0.12T)$$

where Y = egg development rate (%d⁻¹).

Equation (7) was used to back-calculate from the date of peak hatch to the date of peak spawning; cohort 1 was spawned on January 14, cohort 2 on March 15 and cohort 3 on April 30.

Length at hatch and at yolk absorption

Mean length of newly-hatched sand lance larvae was estimated by regressing mean length of individual samples against the fraction of larvae in those samples that carried yolk. The fraction of yolked larvae was normalized by the arcsin transformation. Only samples from the first three surveys (April 25-May 13) were used because most, if not all, of the larvae captured during these three surveys belonged to cohort 1. The regression predicted that length was 5.8 mm when all larvae were yolked (Fig. 6).

This mean length at hatch for a temperature range of 2.4 to 4.9°C is about 0.4 to 0.5 mm lower than that reported

by Smigielski et al. (1984) for live *A. americanus* incubated at 2 to 4°C (Table 1). A substantial part of this 6 to 8% difference in lengths may have been due to shrinkage of *A. hexapterus* during capture and additional shrinkage due to post-capture preservation in formalin.

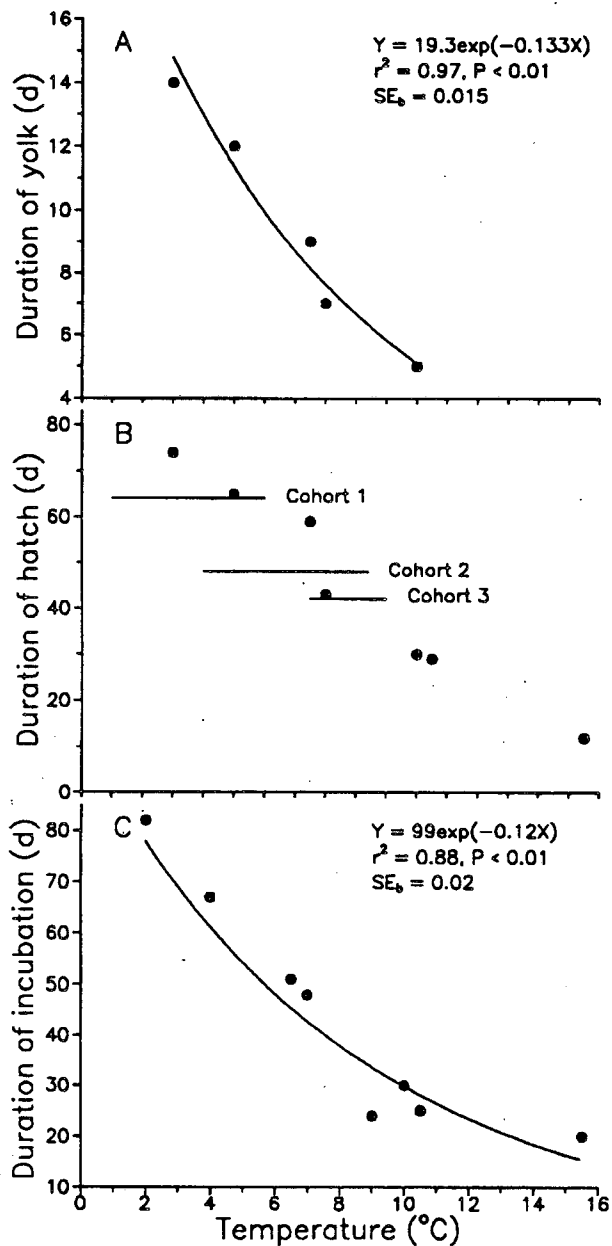
TABLE 2

Estimated day of year (DOY) of spawning of three cohorts of sand lance larvae from Port Moller, 1990

Cohort	DOY of spawn	DOY of hatch			Yolk duration (d)
		start	peak	end	
1	14	66	108	129	64
2	74	113	143	160	48
3	120	142	165	183	42

FIGURE 5

Temperature dependence of early life history of *Ammodytes* spp reared in laboratory aquaria. Data from Table 1: (A) regression of the duration of the yolk sac stage on temperature; (B) plot of duration of hatching period on temperature. Horizontal bars are ranges of water temperatures over the hatching periods of three cohorts of *A. hexapterus* from Port Moller; and (C) regression of egg incubation time on temperature

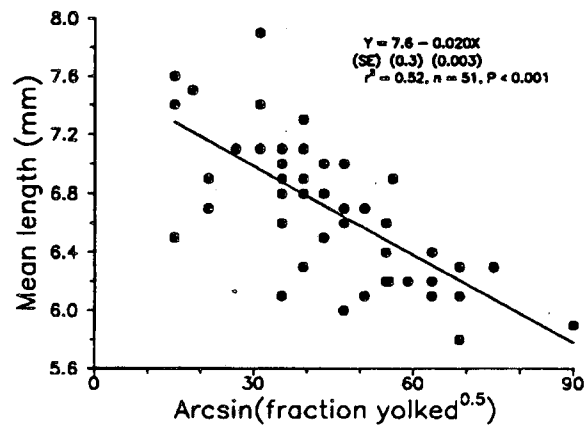


The regression shown in Fig. 6 also predicts that mean length at yolk absorption was 7.6 mm. This was 0.2 to 0.4 mm longer than the lengths at yolk absorption for live *A. americanus* incubated at 2 to 4°C (Smigielski et al. 1984). Fig. 6

However, this difference is probably not significant because it is smaller than the standard deviation of Smigielski et al.'s (1984) mean lengths.

FIGURE 6

Regression of mean length of sand lance on the fraction of yolked larvae. Only samples from the first three surveys (April 25 to May 13), consisting mainly of cohort 1 larvae, were used



Growth

Individual sand lance larvae could not be classified into cohorts because of the extensive overlap of length ranges of the cohorts due to the long duration of the hatching period. Therefore, an attempt was first made to age larvae from a length-age curve based on the number of daily increments in their otoliths.

Otolith analyses

After 2 wk of work by two technicians, otoliths were removed from only 8 of the several hundred alcohol-preserved sand lance larvae; one otolith was removed from each of 4 fish, two otoliths were removed from each of three fish, and three otoliths were removed from one fish, for a total of 13 otoliths (Table 3). The main obstacle to retrieving more otoliths was their very small size, 17 to 45 μm in diameter, which made locating and handling them a time-consuming task. Otoliths were present in all larvae and they had not been degraded by a build up of high acidity in the preservative fluid, a common problem in alcohol-preserved fish larvae. Large otoliths with clear ring patterns were easily recovered from pholid fishes preserved in the same samples as the sand lance.

Sand lance larvae from Port Moller have smaller otoliths for a given body length than herring larvae. A regression of otolith diameter on larval length showed that the average otolith diameter of a 10 mm long sand lance larvae is about 26 μm (Fig. 7), similar in size to that of a Pacific herring larvae of the same length from Auke Bay, Alaska (McGurk 1989a), and from Prince William Sound, Alaska (McGurk et al. 1990). However the average otolith diameter of a 20 mm long sand lance larvae is only 42 μm , about half of the average diameter of an otolith from a 20 mm long herring larvae from southeast and southcentral Alaska.

Only 6 of these otoliths showed a pattern of concentric rings. There were no significant correlations between ring number and fish length or date of capture. The mean number of rings

TABLE 3

Otoliths of sand lance larvae collected at station 36 in Port Moller in 1990. Dashes indicate no data available

Sample number	Date	Larval length (mm)	Sagitta number	Otolith diameter (μm)	Number of otolith rings
69	19-May	9.8	1	17	-
69	19-May	9.8	1	32	-
69	19-May	12.1	1	19	-
69	19-May	12.1	2	27	-
69	19-May	12.1	3	20	-
127	1-Jun	10.6	1	26	13
127	1-Jun	10.6	2	35	-
163	8-Jun	11.4	1	45	-
369	29-Jun	18.9	1	45	15
369	29-Jun	18.9	2	36	9
369	29-Jun	17.9	1	37	7
369	29-Jun	19.7	1	45	17
369	29-Jun	16.9	1	35	9

was 12 (SD = 4, range = 7 to 17, n = 6). Since larvae 16.9 to 19.7 mm long, which were 30 to 45 d old, had only 7 to 17 rings, the rings were deposited at a rate much less than 1 d^{-1} . This means that the number of rings could not be an accurate estimator of age for these fish, even if the otoliths were easy to extract.

The 6 otoliths with rings shared a common pattern. Moving from the center to the edge of each otolith, we first observed a check at the edge of the nucleus. This was usually surrounded by a clear band in which few or no rings were visible. Surrounding this band was an outer group of closely-bunched thin rings. We interpreted the check as marking the end of the yolk sac stage and the beginning of exogenous feeding; the empty band may have been caused by a initial period of slow growth after yolk absorption; and the thin outer rings may have marked a period of more rapid growth as the larvae learned to feed successfully.

This pattern may reflect the survival strategy of sand lance. Their larvae hatch in early spring in cold water before the spring bloom of copepod nauplii. Consequently, their initial rate of growth tends to be lower than that of other species such as herring that hatch later in the spring. They are also capable of surviving much longer periods of starvation than other fish larvae (Yamashita and Aoyama 1986; Buckley et al. 1987).

We decided to stop otolith investigations after 2 wk of work because the rate of otoliths recovery was not equal to the time and expense of the work, and because the otoliths we recovered were of little use in ageing larvae. Instead, we decided to age sand lance larvae from the progression of modes in their length frequencies.

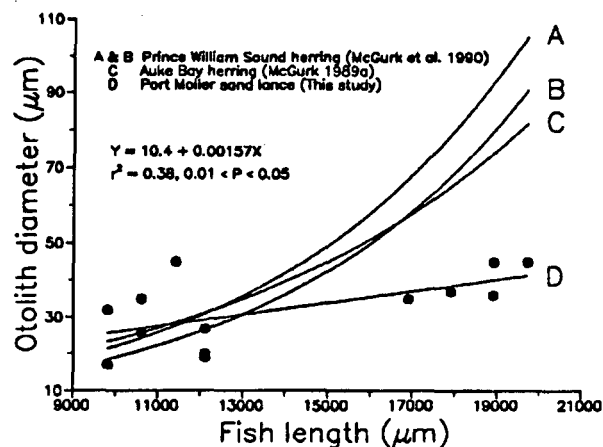
Growth from length frequency analysis

Plots of mean length against day of year for the three cohorts showed that growth during the first 51 d after hatch was low and approximately linear, but that it increased in an obviously non-linearly manner in older fish (Fig. 8). Non-linear regression was used to fit a Gompertz growth model to the mean lengths at age for the pooled data of the three cohorts.

Multiple linear regression with dummy variables for the three cohorts showed that the rate of growth over the first 50 d of age was significantly ($P < 0.001$) different between co-

FIGURE 7

Regression of otolith diameter on larval length for sand lance larvae from Port Moller, 1990, compared to regressions for herring larvae from other areas in Alaska



horts, ranging from 0.06 (SE = 0.01) $\text{mm} \cdot \text{d}^{-1}$ for cohort 1 to 0.19 (SE = 0.02) $\text{mm} \cdot \text{d}^{-1}$ for cohort 2 and 0.10 (SE = 0.04) $\text{mm} \cdot \text{d}^{-1}$ for cohort 3. The relatively low growth of cohort 1 larvae may have been due to lower water temperatures earlier in the season. However, temperature was not the only controlling variable because the second cohort had faster growth than the third cohort.

In cohort 1, the only cohort for which we have data for older larvae, the average rate of growth over the 50 to 100 d period, 0.26 (SE = 0.07) $\text{mm} \cdot \text{d}^{-1}$, was about four times higher than the initial growth rate.

These average growth rates are similar to those estimated from mean length-at-date data reported for other species of sand lance, including *A. hexapterus* from the Bering Sea (Table 4 and Fig. 9).

Yolked and non-yolked sand lance larvae had different weight-length relationships (Fig. 10). There was no significant regression of $\ln(\text{dry weight})$ on $\ln(\text{length})$ for yolked larvae, but there was a highly significant regression for larvae that had exhausted their yolk.

G_w increased with age in all three cohorts, rising from $\leq 1\% \text{ d}^{-1}$ in young larvae to between 3 and $6\% \text{ d}^{-1}$ in older larvae (Fig. 11). This was similar to the range of G_w 2 to $4\% \text{ d}^{-1}$, that was reported for 6 to 18 mm long wild *A. americanus* larvae collected from Long Island Sound by Monteleone and Peterson (1986). As expected from growth in length, the rise in G_w with age was greater in cohort 2 and 3 than in cohort 1. Fig. 11 shows that G_w of 20 to 50 d old larvae was less than the range predicted from *Ammodytes* spp. larvae reared in aquaria at high rations. This period of low growth was not caused by low temperatures. It was also not due to low prey concentrations because microzooplankton prey concentration was high over the study period (McGurk et al. 1992). It may have been caused by reduced foraging competence due to abnormalities, a lack of feeding experience due to age, or competition for food with other planktonic animals.

TABLE 4
Growth in length of wild sand lance larvae estimated from seasonal progressions in mean lengths

Data set	Area	Month	Mean length (mm)	Growth rate (mm-d ⁻¹)	Author
<i>Ammodytes hexapterus</i>					
1	Okhotsk Sea 45-50° N	Jun	25.9		Kobayashi (1961)
		Jul	32.6	0.22	
		Aug	50.5	0.60	
2	Okhotsk Sea 50-55°N	Jul	26.0		Kobayashi (1961)
		Aug	44.9	0.63	
3	Okhotsk Sea 55-60°N	Jul	26.3		Kobayashi (1961)
		Aug	30.0	0.12	
4	Bering Sea 50-55°N	Jun	35.4		Kobayashi (1961)
		Jul	41.0	0.19	
		Aug	48.9	0.26	
<i>Ammodytes americanus</i>					
5	Long Island Sound	Mar	11.5		Wheatland (1956)
		Apr	15.6	0.14	
6	Long Island Sound	Dec	7.0		Wheatland (1956)
		Jan	8.9	0.06	
		Feb	12.7	0.13	
		Mar	14.5	0.06	
		Apr	15.7	0.04	
7	Long Island Sound	Dec	6.4		Wheatland (1956)
		Jan	9.4	0.10	
		Feb	10.6	0.04	
		Mar	15.9	0.18	
8	Long Island Sound	Apr	18.0	0.07	Monteleone and Peterson (1986)
		Dec	5.7		
		Jan	8.3	0.09	
		Mar	12.3	0.07	
9	Chesapeake Bay	Apr	18.8	0.22	Norcross et al. (1961)
		Jan	11.5		
		Feb	12.4	0.03	
		Mar	12.8	0.01	
<i>Ammodytes dubius</i>					
10	Emerald Bank, SW Nova Scotia	Apr	17.0	0.14	Scott (1972)
		Feb	6.9		
		Mar	14.4	0.25	
		May	22.9	0.09	
<i>Ammodytes marinus</i>					
11	Humber area, S North Sea	Feb	6.7		Macer (1965)
		Mar	8.4	0.06	
		Apr	10.0	0.05	
12	N Scotland	Feb	5.0		Langham (1971)
		Mar	5.3	0.01	
		Apr	13.6	0.28	
		May	15.2	0.05	
		Jun	29.5	0.48	
<i>Ammodytes lancea</i>					
13	S North Sea	Nov	8.5		Macer (1965)
		Dec	9.8	0.04	
		Jan	17.1	0.24	
		Feb	22.5	0.18	
		Mar	30.8	0.28	
<i>Ammodytes lanceolatus</i>					
14	S North Sea	Jun	5.6		Macer (1965)
		Jul	6.0	0.01	
		Sep	12.3	0.11	
		Nov	33.8	0.36	
15	N Scotland	Jun	8.3		Langham (1971)
		Jul	9.7	0.05	
		Aug	11.2	0.05	
		Sep	17.5	0.21	
<i>Ammodytes immaculatus</i>					
16	N Scotland	May	12.8		Langham (1971)
		Jun	14.0	0.04	
		Jul	36.2	0.37	
<i>Gymnammodytes semisquamatus</i>					
17	S North Sea	Jun	4.7		Macer (1965)
		Jul	6.7	0.07	
		Sep	17.1	0.17	
		Nov	29.0	0.20	
18	N Scotland	Jun	11.7		Langham (1971)
		Jul	14.1	0.08	
		Aug	14.4	0.01	
		Sep	24.0	0.32	

FIGURE 8
Non-linear regression of mean length (± 1 SD) on age for three cohorts of sand lance larvae collected from Port Moller in 1990

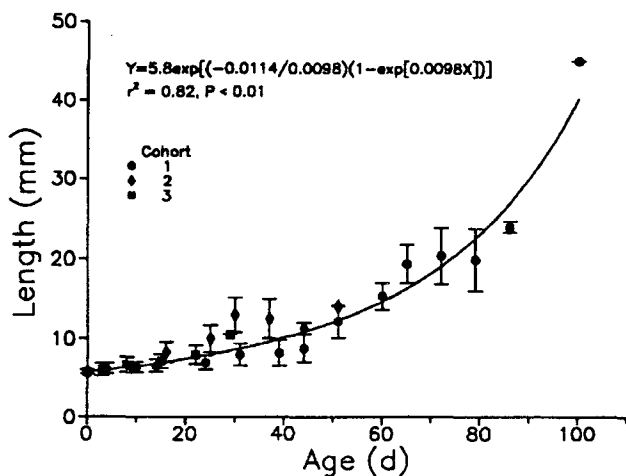


FIGURE 10
Regression of dry weight on length for sand larvae from Port Moller

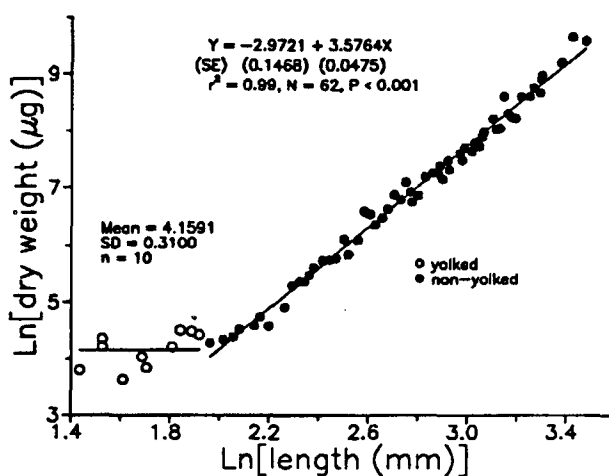


FIGURE 9
Linear growth in length of wild sand lance larvae from Port Moller plotted against the mid-point of the length range. The horizontal bars indicate the range of lengths from which they were calculated. Symbols indicate growth of other *Ammodytes* spp. larvae. Data from Table 4

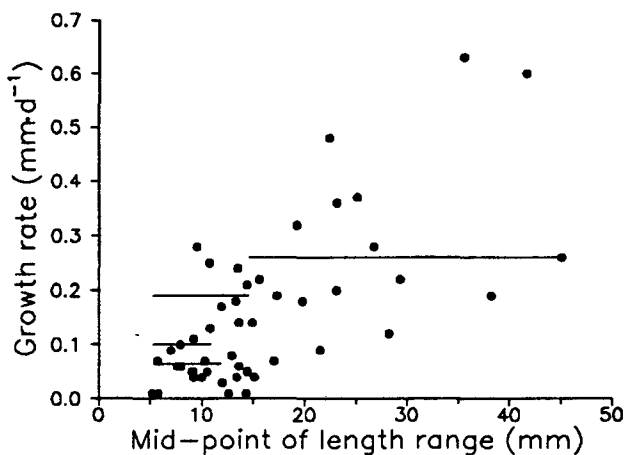
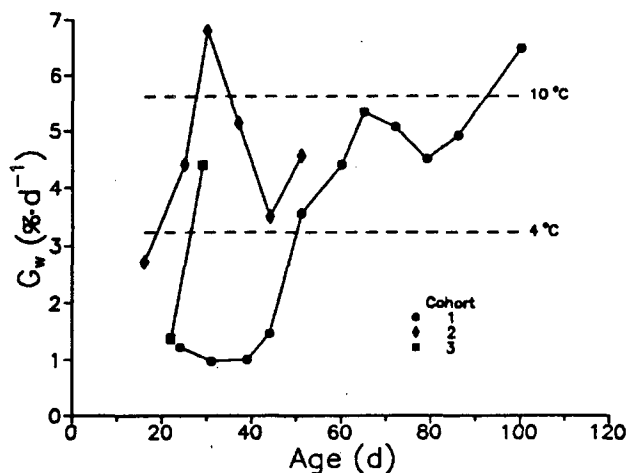


FIGURE 11
Specific growth in dry weight of three cohorts of *A. hexapterus* larvae from Port Moller in 1990. Broken lines are the ranges of G_w of *Ammodytes* spp. larvae reared in laboratory aquaria (Smigielski et al. 1984); Yamashita and Aoyama 1985, 1986; Buckley et al. 1987).



Vertical distribution

Vertical distribution of larval length

A separate two-way ANOVA of larval length on depth and day of year was performed for each of the four series of vertical catches. A single ANOVA with "series" as a third factor was not possible because of differences in gear type and depth range between the series. The only meaningful result was the finding of a highly significant ($P < 0.001$) increase in mean length with depth for the Tucker trawl catches taken at station 36 on June 25 to 26 (Table 5). There was no significant variation in mean length with depth for

the other three vertical series. Neither was there significant variation in larval length with time of day or with the interaction of depth and time of day for any of the four vertical series.

Vertical distribution of larval density

Stacked bongo net tows

In both sets of stacked tows density was highest at 10 m and decreased exponentially with depth (Table 6). Non-zero densities for depths of 50 to 80 m are almost certainly artifacts of the estimation procedure because the open-closing Tucker trawls never captured sand lance larvae

TABLE 5
 Mean lengths of sand lance larvae captured in Port Moller with stacked bongo nets in May and with open-closing Tucker trawls in June-July, 1990. Dashes indicate no data available

Depth (m)		Day	Late twilight	Night	Early twilight	Pooled
May 7-8 - station 36						
10 - 80	mean	7.3	-	-	-	7.3
	SD	1.0	-	-	-	1.0
	n	525	-	-	-	525
June 25-26 - station 36						
5	mean	13.3	12.5	14.6	14.5	13.6
	SD	3.8	2.7	3.4	2.8	3.3
	n	30	20	15	13	78
15	mean	17.7	15.0	15.9	15.0	16.3
	SD	4.7	3.8	3.5	2.8	4.1
	n	30	12	15	15	72
25	mean	19.1	-	18.6	15.5	17.3
	SD	2.2	-	5.6	4.6	5.1
	n	3	-	15	15	33
35	mean	20.9	-	-	19.9	20.7
	SD	2.3	-	-	9.4	4.1
	n	6	-	-	2	8
July 2 - station 39						
5	mean	-	18.5	11.8	5.9	12.0
	SD	-	-	6.6	-	6.5
	n	-	1	3	1	5
15	mean	9.3	-	6.1	9.2	8.7
	SD	5.7	-	-	1.3	3.0
	n	2	-	1	3	6
25	mean	23.6	-	-	16.8	19.1
	SD	-	-	-	14.3	10.9
	n	1	-	-	2	3
July 24-25 - station 36						
5	mean	-	-	17.9	-	17.9
	SD	-	-	-	-	-
	n	-	-	1	-	1
15	mean	-	-	27.1	-	27.1
	SD	-	-	-	-	-
	n	-	-	1	-	1
25	mean	-	-	35.1	-	35.1
	SD	-	-	4.0	-	4.0
	n	-	-	2	-	2
35	mean	-	-	-	-	-
	SD	-	-	-	-	-
	n	-	-	-	-	-
45	mean	-	-	30.6	-	30.6
	SD	-	-	-	-	-
	n	-	-	1	-	1

Notes: day = 0800-1600; late twilight = 1600-2000; night = 2000-0400; early twilight = 0400-0800.

TABLE 6
Density (number·m⁻³) at depth near station 36 in Herendeen Bay on May 7-8 as measured by stacked bongo net tows. Depth of maximum density is underlined. Z_{cm} is center of mass.

Depth (m)	Mean hour of vertical series	
	1415	0915
L = 3.0 - 8.9 mm		
10	23.500	36.759
20	9.211	12.934
30	0.822	5.571
40	0.104	3.455
50	-0.049	3.754
60	0.010	3.377
70	1.901	5.149
80	0.365	1.996
Z_{cm}	17	25
L = 9.0 - 14.9 mm		
10	1.382	2.626
20	0.263	2.587
30	0.022	0.000
40	0.000	0.115
50	-0.003	0.268
60	0.000	0.000
70	0.088	0.368
80	0.027	0.143
Z_{cm}	13	22

below 50 m. The center of gravity ranged from 13 to 25 m with a mean of 19 m (SD = 5, n = 4). This is an underestimate of the true Z_{cm} because no surface tows were taken.

A three-factor ANOVA of ln(density) on day (May 7 and May 8), depth (10 to 40 m and 50 to 80 m), and length (3.0 to 8.9 and 8.0 to 14.9 mm), found that ln(density) was significantly ($P = 0.011$) higher on May 8 than on May 7 and that it decreased significantly ($P = 0.033$) with depth and length class ($P = 0.004$). There were no significant interactions of day, depth and length.

Tucker trawls

All sand lance larvae captured by the Tucker trawls were found in the upper 50 m, with most concentrated in the upper 30 m (Tables 7 to 9).

On June 25 to 26 at station 36, sand lance larvae were concentrated in the upper 20 m of the water column. The depth of maximum larval density was in the 0 to 10 m stratum for 11 of the 15 possible combinations of depth and time of day. Although Z_{cm} ranged from 5 to 24 m, 8 of the 15 values were ≤ 10 m. A three factor ANOVA of ln(density) on time of day (night and day-twilight), depth (0 to 10 m and 20 to 40 m), and larval length (3.0 to 14.9 mm and ≥ 15.0 mm) found that density decreased significantly ($P = 0.004$) with depth and increased significantly ($P < 0.001$) with larval length, but that there was no significant effect of time of day and no significant interactions of time of day, depth or larval length. The mean Z_{cm} was 11 m (SD = 5, n = 15).

Sand lance larvae were found in both day and night samples on July 2, but in much fewer numbers than in May or June. Larvae were only caught at night on July 24 to 25. The decrease in capture success was due to increasing net avoidance by large larvae as they increased in size from May to July.

On July 2, Z_{cm} ranged from 5 to 25 m with a mean of 15 m (SD = 7, n = 9). There were insufficient numbers of sand lance larvae caught in July to permit analysis of variance of densities.

Summary

Almost all sand lance larvae of the Port Moller estuary were found in the upper 30 m of the water column, above the thermocline. The smallest larvae were found near the surface and larval size increased with depth. Density was highest in the upper 10 m and decreased with depth. We did not observe any night-day differences in this pattern, nor did we observe any changes in the pattern with larval size. There were too few sand lance larvae caught in July to permit comparisons in vertical distribution between the stratified water column of station 36 and the well-mixed water column of station 39.

These observations suggest that *A. hexapterus* in Port Moller follows a type II pattern of diel vertical migration, as defined by Neilson and Perry (1990), if only because larvae are found close to the surface during the day. The type II pattern has larvae move towards the surface during the day and towards deep water at night. It is opposite to the type I pattern observed for herring in Port Moller; the larvae of that species migrate to the surface during the night and then move deeper during the day.

The type II pattern is the dominant pattern for sand lances; it has been reported by Yamashita et al. (1985a, 1985b) for *A. personatus*, by Ryland (1964) for *A. marinus*, by Richards and Kendall (1973) for *A. americanus*, and by Potter and Lough (1987) for small *Ammodytes* spp. larvae.

We did not detect night-day differences in the vertical distribution of sand lance larvae in Port Moller because migration was restricted to a narrow range of depths. This may have been due to three factors. First, much of the estuary is shallow. Second, diel vertical migration may have been inhibited by strong tidally-induced turbulence. Third, abundant prey may have reduced the need for diel vertical migration (Neilson and Perry 1990).

The length-at-depth data for June 24 to 26 suggest that larger larvae tend to occupy deeper water than small larvae. There was no evidence for ontogenetic change in vertical migration in the larval density data. This was probably due to net avoidance. Although night-day correction factors were developed for the Tucker trawl catches, they cannot be used to correct zero catches, and most of the cells in the July 24-25 Tucker trawl series contained zero catches.

Feeding

Sand lance larvae from two sets of samples were examined for incidence of gut contents and size of prey: stacked bongo net samples taken near station 36 on May 7 to 8, and Tucker

TABLE 7

Density (number·m⁻³) at depth for sand lance larvae captured at station 36 in Herendeen Bay on June 25-26 with open-closing Tucker trawls.

Depth of maximum density is underlined. Z_{cm} is center of mass. Only depths with non-zero densities are shown.

Depth (m)	Mean hour of vertical series				
	1224	0053	0625	1216	1900
L = 3.0-8.9 mm					
5	0.044	0.024	0.000	0.043	0.066
15	0.025	0.000	0.001	0.000	0.009
25	0.000	0.018	0.013	0.000	0.000
Z_{cm}	9	14	24	5	6
L = 9.0-14.9 mm					
5	0.122	0.147	0.170	0.092	0.142
15	0.038	0.074	0.004	0.045	0.008
25	0.000	0.036	0.038	0.000	0.000
35	0.000	0.000	0.009	0.000	0.000
Z_{cm}	5	11	10	8	5
L > 15.0					
5	0.131	0.194	0.259	0.437	0.359
15	0.590	0.147	0.018	0.812	0.121
25	0.018	0.212	0.234	0.019	0.000
35	0.123	0.000	0.044	0.000	0.000
Z_{cm}	16	15	16	12	7

TABLE 8

Density (number·m⁻³) at depth for sand lance larvae captured at station 39 in Moller Bay on July 2 with open-closing Tucker trawls.

Depth of maximum density is underlined. Z_{cm} is center of gravity.

Only times with non-zero densities are shown. Dashes indicate no data available or calculable.

Depth (m)	Mean hour of vertical series						
	0017	0051	0555	0628	1208	1244	1816
L = 3.0-8.9 mm							
5	0.030	0.000	0.000	0.038	0.000	0.000	0.000
15	0.058	0.000	0.000	0.022	0.000	0.011	0.000
25	0.000	0.000	0.042	0.000	0.000	0.000	0.000
Z_{cm}	12	-	25	9	-	15	-
L = 9.0-14.9 mm							
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000
15	0.000	0.000	0.000	0.120	0.040	0.000	0.000
25	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Z_{cm}	-	-	-	15	15	-	-
L > 15 mm							
5	0.000	0.000	0.000	0.000	0.000	0.000	0.039
15	0.000	0.050	0.000	0.000	0.000	0.000	0.000
25	0.000	0.000	0.047	0.000	0.000	0.000	0.000
Z_{cm}	-	15	25	-	-	-	5

trawl samples taken at station 39 on July 2 and at station 36 on June 25 to 26. The bongo net samples contained mostly small newly-hatched larvae and the Tucker trawl samples contained mostly mid-size and large larvae.

Percent gut fullness

Of 644 sand lance larvae examined from the stacked bongo net catches only 1 (0.2%) had any gut contents, but of 533

TABLE 9

Density (number·m⁻³) at depth for sand lance larvae captured at station 36 in Herendeen Bay on July 24-25 with open-closing Tucker trawls.

Depth of maximum density is underlined.

Z_{cm} is center of gravity. Only depths and times with non-zero densities are shown.

Depth (m)	Mean hour of vertical series
	0130
L > 15.0	
5	0.004
15	0.004
25	0.008
35	0.000
45	0.003
Z_{cm}	22

sand lance larvae examined from the Tucker trawl catches 114 (21.4%) had gut contents. Therefore, our analysis of feeding schedule and predator-prey relationships was based on the Tucker trawl catches.

Average percent gut fullness increased from zero in larvae <10.0 mm long to about 12% in larvae 20.0 to 24.9 mm long and then it declined to zero in larvae 35.0 to 39.9 mm long (Fig. 12). The absence of food in small larvae indicates that they were either not feeding or that they voided their guts upon capture. We cannot determine the relative importance of these two factors, but the increase in percentage gut contents with length suggests that voiding decreased with increasing length. The absence of food in larvae >25.0 mm long can only be explained if we assume that healthy feeding large larvae avoided the net. If correct, larvae >25 mm long represented only the portion of the population that was in poor condition and not feeding.

Previous studies of gut fullness of wild *Ammodytes* spp. larvae generally support a link between net avoidance and decreasing percent gut fullness in large larvae. Ryland (1964), a series of data reports written by Barraclough, Fulton and Robinson [Barraclough 1967a, 1967b, 1967c;

Barraclough and Fulton 1967, 1968; Barraclough et al. 1968; Robinson 1969a, 1969b; Robinson et al. 1968a, 1968b, hereafter called the BFR data set], Last (1980), and Monteleone and Peterson (1986) all reported a steady increase in gut fullness with larval length up to lengths >20 mm. Ryland (1964) and Last (1980) used high-speed (about 5 knots) plankton nets, the BFR data was collected with two-boat surface trawls and Isaacs-Kidd midwater trawls, and

Monteleone and Peterson (1986) used ring nets towed at 2 to 3 knots. In contrast, Covill (1959) reported an increase in gut fullness up to a length of 16.0 mm and then a decrease in gut fullness with lengths >16.0 mm. Covill (1959) used Clarke-Bumpus nets; he did not report the tow speed, but it was likely less than 2 knots because this type of net is usually used to sample small invertebrate plankton, which are not known for their ability to evade towed plankton nets.

Average percent gut content was maximal at depth strata of 15 and 25 m, much lower at depth strata of 5 and 35 m, and zero at depths below 35 m (Fig. 12B). This suggests that sand lance larvae were concentrated in the upper 30 m of the water column because that is where their food is concentrated. To the best of our knowledge, this is the first report to describe the depth distribution of feeding in *Ammodytes* spp. larvae.

Average percent gut content was highest at night (2000 to 0400) and lowest during early twilight (0400 to 0800), and it reached a second maximum during daylight hours (Fig. 12C). To interpret this finding, we must remember that there is a time lag between the cessation of feeding and the complete emptying of a gut. The only authors to measure the time rate of gut emptying in *Ammodytes* spp. larvae was Yamashita et al. (1985a). They reported that after 9 hours of starvation at 6°C, gut fullness of *A. personatus* larvae fell from about 60% to about 10%. Therefore, we conclude that the absence of food in larvae captured in early twilight supports the standard model of daytime feeding by *A. hexapterus* larvae; larvae ceased feeding at late twilight, fasted over the night, and resumed feeding during the next day.

Our findings support other studies that show that *Ammodytes* spp. larvae feed primarily during the day. The highest values of gut fullness or number of prey items per gut usually reaches a maximum at midday and decreases continuously to a minimum near dawn (Covill 1959; Ryland 1964; Last 1980; Yamashita et al. 1985a).

Since 521 (97.7%) of the 533 larvae came from station 36 and only 12 (2.3%) came from station 39, we were not able to examine the effect of station on percent gut fullness.

A three-way ANOVA of percent gut fullness on larval length (four groups: 5.0 to 9.9, 10.0 to 14.9, 15.0 to 19.9 and 20.0 to 39.9 mm), water depth (three groups: 5, 15 and 25-65 m), and time of day [two groups: day (0600 to 1800) and night (1800 to 0600)] showed that all three factors were highly significant (Table 10).

The interaction of length x depth was highly significant because large larvae tended to be found at deeper depths than small larvae (Table 11). Since large larvae had higher percent gut contents than small larvae, the depth of maximal percent gut contents decreased from 5 m in larvae 5.0 to 9.9 mm long to 15 m or deeper in larvae >10.0 mm long.

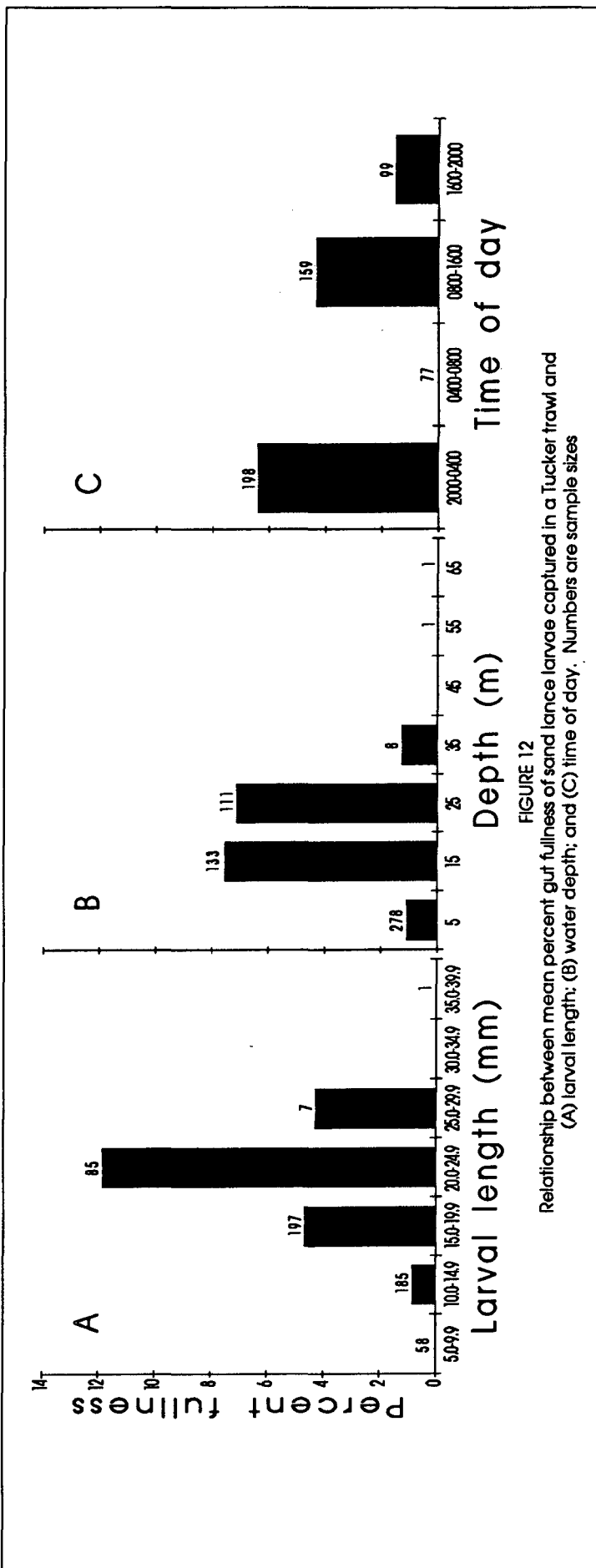


FIGURE 12 Relationship between mean percent gut fullness of sand lance larvae captured in a Tucker trawl and (A) larval length; (B) water depth; and (C) time of day. Numbers are sample sizes

TABLE 10

Analysis of variance of percent gut fullness of sand lance larvae captured at discrete depths with a Tucker trawl

Source	df	F	P
larval length	3	22.201	<0.001
water depth	2	13.894	<0.001
time of day	1	12.419	<0.001
length x depth	6	5.445	<0.001
length x time	3	1.229	0.299
depth x time	2	8.101	<0.001
length x depth x time	6	0.778	0.587
explained	23	9.755	<0.001
residual	509		
total	532		

TABLE 11

Mean percent gut fullness of sand lance larvae captured in Port Moller in 1990 with a Tucker trawl for four classes of larval length and three classes of water depth

Length (mm)	Depth (m)	Percent gut fullness		
		mean	SD	n
5.0-9.9	pooled	0.034	0.263	58
	5	0.057	0.338	35
	15	0.000	0.000	15
	25-65	0.000	0.000	8
10.0-14.9	pooled	0.784	3.544	185
	5	0.688	3.684	138
	15	1.000	3.051	30
	25-65	1.176	3.321	17
15.0-19.9	pooled	4.660	9.120	197
	5	2.050	6.439	100
	15	7.160	11.173	50
	25-65	6.553	10.101	47
20.0-39.9	pooled	11.150	13.993	93
	5	0.000	0.000	5
	15	16.105	16.271	38
	25-65	8.500	11.350	50

The interaction of depth x time was highly significant because percent gut fullness was greater during the day than during the night (Table 12). The difference between day and night varied with larval length; it appeared to increase steadily with length, reaching a maximum for length class 15.0 to 19.9 mm, but then it decreased for length class 20.0 to 39.9 mm. This decrease was probably the result of avoidance of the plankton net by large larvae during the daytime.

TABLE 12

Mean percent gut fullness of sand lance larvae captured with a Tucker trawl for four classes of larval length and two classes of time of day

Length (mm)	Time *	Percent of gut fullness		
		mean	SD	n
5.0-9.9	pooled	0.034	0.263	58
	day	0.080	0.400	25
	night	0.000	0.000	33
10.0-14.9	pooled	0.783	3.544	185
	day	1.190	4.468	105
	night	0.250	1.571	80
15.0-19.9	pooled	4.660	9.120	197
	day	6.214	9.897	117
	night	2.387	7.330	80
20.0-39.9	pooled	11.150	13.993	93
	day	11.200	13.231	50
	night	11.093	14.989	43

* day = 0600-1800; night = 1800-0600

Predator-prey relationship

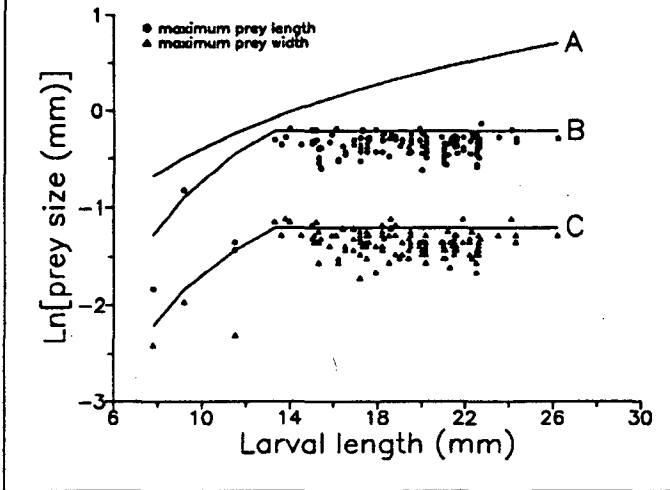
Mean length and mean width of prey for sand lance increased over the length range of 7.8 to 13.3 mm, and then remained constant at a mean length of 0.71 mm (SD = 0.06, n = 146) and a mean width of 0.26 mm (SD = 0.03, n = 145) over the larval length range of 13 to 26 mm (Fig. 13). Prey width, the most important dimension for determining suitable prey because larval fish swallow prey end-on (Pearre 1980), was always at least one quarter of the maximum potential mouth gape. For the larval length range of 13 to 26 mm the mean maximum prey length was 0.81 mm (SD = 0.04, n = 16) and the mean maximum prey width was 0.30 mm (SD = 0.02, n = 16). For larvae <13 mm long, we calculated mean length (mean = 0.28, SD = 0.12, n = 4) and width (mean = 0.11, SD = 0.02, n = 4), and then interpolated between these two means over the larval length range of 7.0 to 13.0 mm.

These ranges of prey lengths and widths are similar to those reported for other populations of *Ammodytes* spp. larvae in the scientific literature. However, they differ in that prey length and weight are usually reported as increasing continuously with larval length, not reaching an asymptote as they did in this study. Last (1980) reported that mean prey width of *A. marinus* larvae of the North Sea increased from 0.12 mm in larvae 6.0 to 6.9 mm long to 0.26 mm in larvae 12.0 to 12.9 mm long. In Pearre's (1986) analysis of the BFR data set, geometric mean prey length increased steadily from 0.43 mm at a larval length of 8 mm to 0.78 mm at a larval length of 25 mm. This is almost identical to the predator-prey length relationship observed in this study.

These ranges of prey lengths and widths are also similar to those for herring larvae. For example, analysis of gut contents of Pacific herring of the BFR data set showed that maximum prey length increased from 0.2 mm in herring larvae 6 mm long to 0.9 in herring larvae 20 mm long (McGurk 1989). Checkley (1982) reported that maximum width of prey of Atlantic herring larvae rose from 0.15 mm in larvae 12 mm long to 0.31 in larvae 20 mm long.

FIGURE 13

Plot of prey length and width on length of sand lance larvae. Line A is the regression of maximum potential mouth gape of sand lance larvae on larval length: $Y = 0.04837X^{1.145}$, $r^2 = 0.741$, $n = 113$, $P < 0.001$.



We conclude that sand lance larvae, like herring larvae, behave as invertebrate predators rather than as vertebrate predators (Checkley 1982) - they select for many small prey rather than a few large prey.

Types of prey

Over 99% of the 153 prey items found in the guts of sand lance larvae were various life history stages of copepods (Table 13). In fact, the only non-copepod prey was a single gastropod veliger. Small (<15 mm long) sand lance larvae selected gastropod veligers, copepod nauplii, and small adult calanoid copepods of the genus *Eurytemora*. Larger sand lance larvae selected copepodites, *Eurytemora* and other adult copepods including *Centropages abdominalis*.

TABLE 13
Number and type of prey of sand lance larvae from Port Moller, 1990

	Larval length (mm)							Total
	5.0 9.9	10.0 14.9	15.0 19.9	20.0 24.9	25.0 29.9	30.0 34.5	35.0 39.9	
Sand lance:								
with prey	2	6	43	37	1	0	0	89
empty	56	179	154	48	6	0	1	444
total	58	185	197	85	7	0	1	533
Prey type:								
Gastropod larvae	1							1
Copepod nauplii	1	2						3
Copepodite		3						3
Calanoid (unident.)		3	33	25	1			62
Calanoid (<i>Eurytemora</i>)		1	34	48				83
<i>Centropages abdominalis</i>				1				1
total prey	2	6	70	74	1	0	0	153

These results agree with those reported for other populations of *A. hexapterus* (BFR data set) and, with one exception, other species of sand lance (Covill 1959; Ryland 1964; Last 1980; Monteleone and Peterson 1986). Table 14 shows an analysis of the BFR data set. First-feeding sand lance fed on phytoplankton and copepod nauplii. As the larvae grew in size, copepodites and small adult copepods replaced phytoplankton and copepod nauplii. In turn, these organisms were gradually replaced by larger prey items such as large adult copepods, e.g. *Calanus pacificus*, and fish eggs and larvae. The exception to this diet is *A. marinus* of the North Sea, which preys heavily on the appendicularian *Oikopeura doica* (Ryland 1964; Last 1980).

These prey items are also the same as those generally chosen by herring larvae (Checkley 1982).

We conclude on the basis of size and type of prey that sand lance and herring larvae compete for substantially the same prey resource. Therefore, all investigations of sand lance biology in this study that involve prey concentration, for example McGurk et al. (1992), used the same schedule of prey concentrations that was developed for herring larvae.

Dispersion and mortality

Densities of sand lance larvae were always highest in lower Moller Bay and Herendeen Bay (Fig. 14). Densities decreased with day of year in upper Moller Bay and increased with day of year in upper Herendeen Bay, indicating transport of larvae out of lower Moller Bay and into Herendeen Bay.

Assigning larval density to cohorts

To estimate dispersal and mortality of the three cohorts of sand lance larvae, we divided the densities of each sample into densities of each of the three cohorts. This was done by, first, dividing avoidance-corrected larval density (number m^{-2}) of a sample among 1 mm-wide length bins according to the length distribution of that sample. Then, a proportion of the density in each length bin was assigned to one of the three cohorts using the proportions of larvae of each cohort in that length bin for each of the 13 surveys. Proportions were calculated using the normal distributions of length calculated from the parameters shown in Fig. 2. Finally, total density for each cohort for each sample was calculated by summing across lengths.

Advection

X-coordinates of centroids were first calculated for Moller and Herendeen Bay samples separately because the movement of larvae was different in each bay; centroids in Moller Bay moved towards the boundary of the estuary whereas centroids in Herendeen Bay moved away from the boundary and towards the head of Herendeen Bay (Fig. 15A, 15B). Regression

TABLE 14
Percent of sand lance larvae from Strait of Georgia
containing prey type. Data from the BFR series of data reports

Prey type	Sand lance length (mm)						
	5.0	10.0	15.0	20.0	25.0	30.0	35.0
	9.9	14.9	19.9	24.9	29.9	34.9	39.9
empty	33.3	24.4	18.6	12.5	15.7	11.3	4.0
phytoplankton	13.1	0.0	0.0	0.0	0.0	1.3	0.0
copepod eggs	0.0	7.3	5.7	5.6	9.3	20.0	21.8
copepod nauplii	53.3	61.0	34.3	27.8	16.7	8.0	7.3
copepodites	0.0	2.4	5.7	6.9	11.1	4.7	4.8
copepods (unidentified)	0.0	2.4	27.1	22.2	35.2	36.0	37.9
Microcalanus spp.	0.0	2.4	1.4	1.4	0.0	0.7	0.8
pseudocalanus minutus	0.0	0.0	4.3	13.9	10.2	12.7	12.9
Acartia longiremis	0.0	0.0	2.9	4.2	0.0	0.0	0.0
Calanus pacificus	0.0	0.0	0.0	0.0	0.0	0.7	1.6
cladocerans (Podon)	0.0	0.0	0.0	0.0	0.0	0.7	1.6
ostracods (Corycaeus)	0.0	0.0	0.0	0.0	0.0	0.0	2.4
oikopleura	0.0	0.0	0.0	2.8	0.0	2.0	0.8
fish eggs	0.0	0.0	0.0	0.0	1.9	0.7	0.8
fish larvae	0.0	0.0	0.0	0.0	0.0	0.0	1.6
cirripedia	0.0	0.0	0.0	0.0	0.0	0.0	0.8
eiphausiid eggs	0.0	0.0	0.0	0.0	0.0	0.0	0.8
total no. sand lance	15	41	70	72	108	150	124

analysis showed that there were no significant differences in advection rate between cohorts in either bay. Anti-seaward advection along the x-axis in Herendeen Bay (from the boundary to station 37 along Hague and Johnston Channels), $0.276 \text{ km} \cdot \text{d}^{-1}$ (SE = 0.033), was almost twice as great as seaward advection, $0.157 \text{ km} \cdot \text{d}^{-1}$ (SE = 0.040), in Moller Bay (station 47 to the boundary).

This finding indicates that larvae that hatched into lower Moller Bay were advected in at least two directions; larvae that hatched close to Hague and Johnston Channels were advected into Herendeen Bay whereas larvae that had initially diffused into upper Moller Bay from the hatch sites in lower Moller Bay eventually advected back towards lower Moller Bay. We do not know if Moller Bay larvae continued to be advected across the boundary or whether they joined the anti-seaward flow into Herendeen Bay after entering lower Moller Bay. However, it is more reasonable to assume that most larvae were advected into Herendeen Bay than to assume a complicated bi-directional flow with some larvae transported offshore while others were transported inshore.

We note that the x-coordinate of the centroid for Moller Bay never crossed the strong upwelling zone near Harbor Point that separates lower and upper Moller Bays. At present, we have no good explanation for this observation, other than to suggest that most sand lance larvae actively avoided this zone. The lower advection rate of sand lance larvae in upper Moller Bay compared to the rest of the estuary is undoubtedly due to anti-seaward flow caused by this upwelling.

If larvae captured in upper Moller Bay were transported there by diffusion from lower Moller Bay, then the true advection rate for the entire population was closer to the Herendeen Bay rate than the Moller Bay rate. We calculated this rate, $0.277 \text{ km} \cdot \text{d}^{-1}$ (SE = 0.036), for the pooled data of both bays (Fig. 15).

Hatch sites

At hatching all three cohorts in Moller Bay had an average x-coordinate of 12.0 km. This is approximately the distance from the boundary to a point midway between stations 26 and 27 in Hague Channel and to station 39 in the eastern Moller Bay channel. Therefore, sand lance larvae hatched from a broad area in lower Moller Bay with a center between Point Divide and Harbor Point. We cannot calculate a total area for the spawning bed because we do not know how far this patch of eggs extended in the seaward direction. In the absence of any other information, we conclude that sand lance eggs were laid on the extensive beds of sand in lower Moller Bay (Sharma 1974).

Spatial variance

s_x^2 was calculated using the centroid for the entire estuary, not the centroids for separate bays. Regression analysis with dummy variables for cohorts showed that s_x^2 was constant at 117.782 km^2 (SD = 48.624, n = 24) over all ages and cohorts. s_y^2 was constant at 10.839 km^2 (SD = 0.643, n = 20) over all ages and cohorts.

Loss and mortality

Regression analysis with dummy variables for cohorts and bays showed that the avoidance-corrected density of all three cohorts in Herendeen Bay decreased at an exponential rate of 0.166 d^{-1} (SE = 0.006) (Fig. 16), but that density in Moller Bay decreased at a significantly ($P < 0.001$) higher rate of 0.253 d^{-1} (SE = 0.012). There were no significant differences in loss rate between cohorts in either bay.

These loss rates included both mortality and dispersal of larvae out of the study area. We interpret the higher rate of loss in Moller Bay than in Herendeen Bay as a result of the movement of larvae from Moller Bay into Herendeen Bay.

To separate these two sources of loss, larval densities were converted to larval numbers using equation (5b). x_i for all stations and ages was estimated from the regression of x_i on age for the entire estuary. y_i was assumed to be zero at all times and places. s_x^2 was assumed to be constant at 117.782 km^2 and s_y^2 was assumed to be constant at 10.839 km^2 . The numbers of larvae were then regressed on age using equation (5c); dummy variables were inserted to test for differences between cohorts and bays in intercepts and slopes.

Mortality was estimated to be 0.133 d^{-1} (SE = 0.006) in Herendeen Bay and 0.192 d^{-1} (SE = 0.010) in Moller Bay (Fig. 16B), a difference that was highly significant ($P < 0.001$). Cohort 2 in Moller Bay had a mortality rate that was even higher: 0.282 d^{-1} (SE = 0.022). Therefore, the average rate of loss due to dispersal out of the study area (= loss - mortality) was 0.033 d^{-1} for all cohorts in Herendeen Bay, 0.061 d^{-1} for cohorts 1 and 3 in Moller Bay, and 0.029 d^{-1} for cohort 2 in Moller Bay.

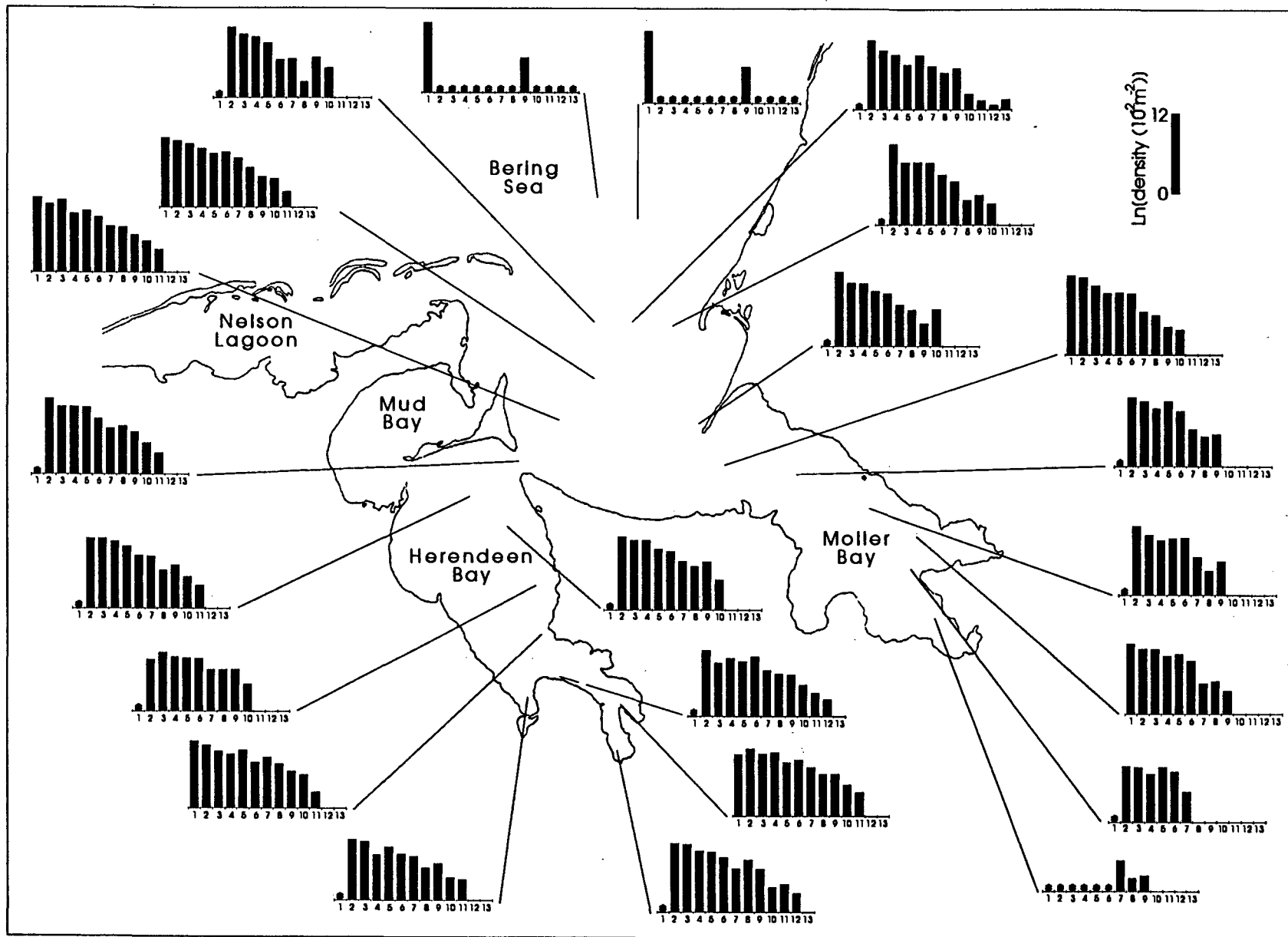
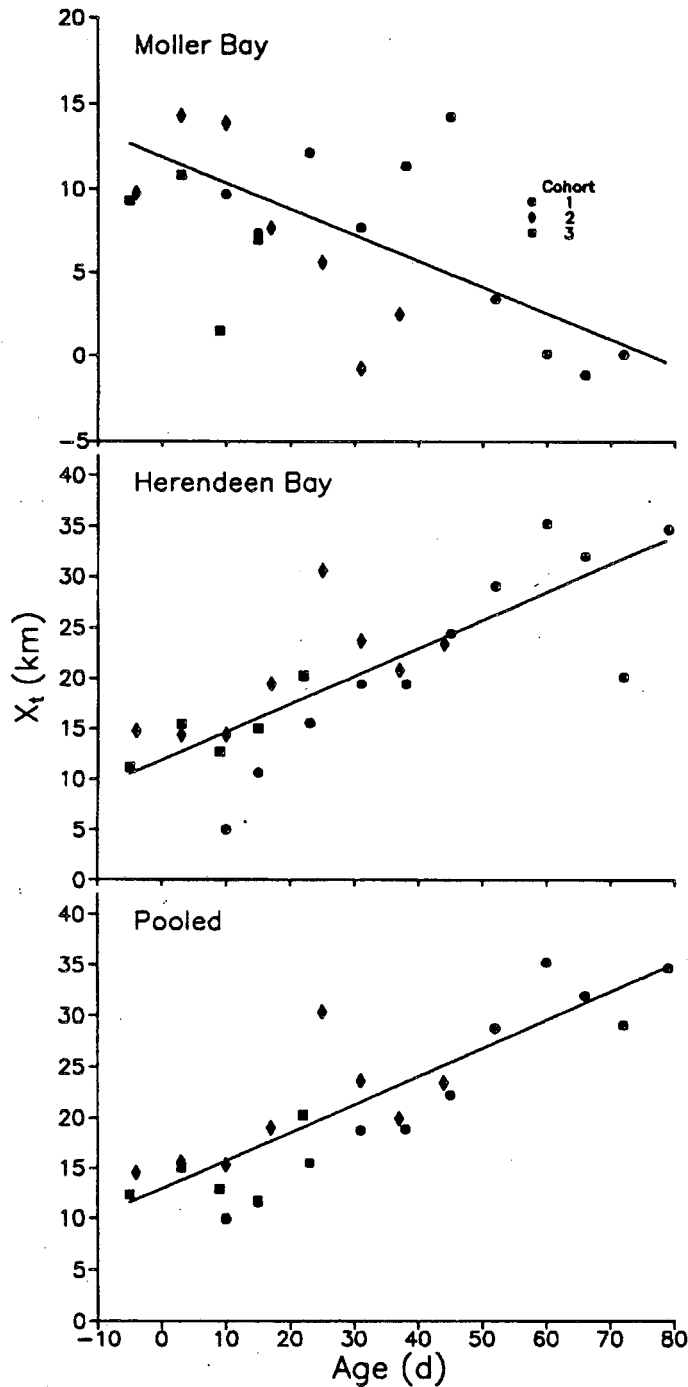


FIGURE 14
 Map of Port Moller showing densities of sand lance larvae captured at each of 13 surveys.
 Densities were not corrected for net avoidance.

FIGURE 15

X-coordinates of centroids of three cohorts of sand lance larvae plotted against age for Moller and Herendeen Bays separately and for the entire estuary combined. Regression for separate bays: $x_t = 11.903 + 0.276\text{Age} - 0.433 g_1$, $n = 45$, $r^2 = 0.74$, $P < 0.001$, where $g_1 = 1$ for Moller Bay and 0 for Herendeen Bay.

Regression for pooled data:
 $x_t = 12.944 + 0.277\text{Age}$, $n = 24$, $r^2 = 0.71$, $P < 0.001$.

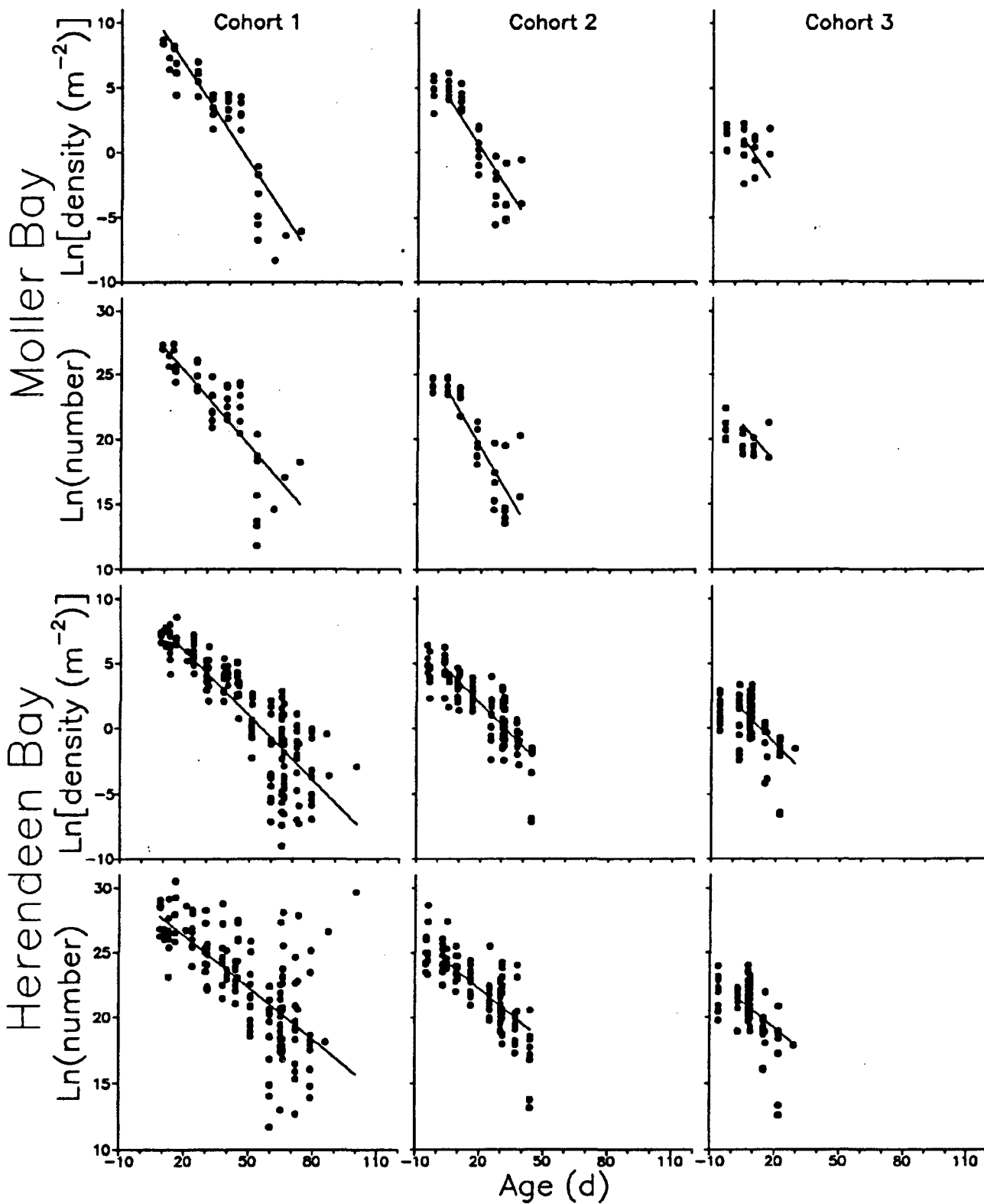


The difference in mortality rates between bays was an artifact due to movement of larvae out of upper Moller Bay and into lower Moller Bay and Herendeen Bay. Since dispersal of larvae south of the upwelling zone was lower than that of larvae in other parts of the estuary, their population number was not accurately estimated by a single advection rate or a single s_x^2 for the entire estuary. Based on this reasoning, the average rate of loss of larvae from the entire estuary was close to $3\% \cdot d^{-1}$.

The intercept of the regression of numbers on age is not an accurate measure of true abundance of sand lance larvae because our estimate of s_x^2 is almost certainly an underestimate due to our limited sampling in the y-axis, and because our simple population model could not accurately estimate numbers of larvae in Moller Bay because its advective-diffusive dispersal was lower than that of Herendeen Bay. However, the relative numbers of the three cohorts are not affected by these problems, so we conclude that 98.26% of all larvae hatched in cohort 1, 1.66% hatched in cohort 2 and 0.08% hatched in cohort 3.

FIGURE 16

(A) Regression of density of sand larvae on age for three cohorts:
 $Y = 2.1170 - 0.1633\text{Age} + 7.1515g_2 + 3.0950g_3 - 0.0870g_1\text{Age} + 2.4298g_1g_2$, $n = 470$, $r^2 = 0.711$, $P < 0.001$,
 where $g_1 = 1$ for Moller Bay and 0 for Herendeen Bay, $g_2 = 1$ for cohort 1 and 0 for other cohorts, and
 $g_3 = 1$ for cohort 2 and 0 for other cohorts. Only positive ages were used in the regression.
 (B) Regression of number of sand lance larvae on age:
 $Y = 21.8629 - 0.1332\text{Age} + 7.1138g_2 + 3.0308g_3 - 0.0587g_1\text{Age} - 0.0899g_1g_2$, $n = 470$, $r^2 = 0.550$, $P < 0.001$.



DISCUSSION

Spawning time and location

Sand lance began spawning in Port Moller in mid-January 1990 and continued until the end of May. This is the first estimate of the natural spawning period for this species. It confirms Pinto's (1984) observation of *A. hexapterus* spawning in mid-March in laboratory tanks in Sequim, Washington.

This report is the first evidence of sand lance spawning inside the Port Moller estuary. It is not surprising that this spawning event has never been reported before. All winter spawning would be hidden under ice and all spring spawning would be over before aerial surveys for herring biomass began in early June. Sand lance is not an important subsistence fish for Alaskan natives, so it is unlikely that they direct much attention to it.

Number and timing of cohorts

Three cohorts of sand lance eggs were laid in the lower Port Moller estuary during winter and spring of 1990. This is the first report of cohort structure in *A. hexapterus*. To the best of our knowledge, only Dalley and Winters (1987) have shown evidence of cohort structure in another species of *Ammodytes*. They reported at least three cohorts in *A. dubius* larvae captured in June in Fortune Bay, southern Newfoundland.

Time intervals of 46 to 60 d separated the dates of peak spawning of the three Port Moller cohorts. Rising water temperatures in late winter and early spring meant that these time intervals shrank to 22 to 35 d separating peak hatching dates. These are still longer than the time intervals that usually separate herring cohorts (Lambert 1984; Lambert and Ware 1984).

The relatively low number of cohorts and long time intervals between cohorts compared to other pelagic species of fish, is a consequence of their strategy of winter spawning. Lambert and Ware (1984) reported that the time interval between hatching of cohorts of Atlantic herring and capelin, *Mallotus villosus*, decreased with increasing larval growth according to the regression $Y = 1.71X^{-1.56}$, where Y = time interval (d) between cohorts and X = rate of growth in length ($\text{mm}\cdot\text{d}^{-1}$). They argued that this strategy enhanced survival of larvae by preventing competition for food between cohorts. The faster a cohort grew, the more rapidly it grew out of a size range of prey, thus allowing another cohort to exploit that size range of prey. Herring and capelin typically have growth rates ranging from 0.2 to 0.4 $\text{mm}\cdot\text{d}^{-1}$, which means that the time interval between their cohorts is only 7 to 25 d. Thus, they can produce as many as eight cohorts over a spawning season without overlap of cohort feeding ranges.

However, in 1990 the average growth rate of sand lance in Port Moller was $<0.1 \text{ mm}\cdot\text{d}^{-1}$ over the first 30 d after hatch and rose to $0.26 \text{ mm}\cdot\text{d}^{-1}$ over the following 70 d. Therefore, according to Lambert and Ware's (1984) equation the time interval between cohorts should have ranged from 15 to 65 d, which brackets our observed range of 22 to 35 d. Since the time interval between sand lance cohorts was about twice as great as that for herring and capelin, the number of sand lance cohorts is only half that of herring and capelin.

The agreement between our results and those predicted by Lambert and Ware's (1984) regression is less important than the fact that there are ecological reasons for sand lance to have fewer cohorts and longer time intervals between cohorts than other pelagic fish that lay demersal eggs. The ultimate cause of these differences between sand lance and other pelagic fish is its strategy of reproducing in winter and early spring when water is cold and food is dilute.

Nature of spawning waves

The three waves of sand lance spawning in Port Moller may have been conducted by different age classes of one stock. Three lines of evidence support this argument. First, the eggs could not have been produced by the same adults spawning repeatedly over winter and spring because all studies of the seasonal cycle of sexual maturity in Pacific sand lances (Inoue et al. 1967) and Atlantic sand lances (Reay 1970; Smigielski et al. 1984) indicate that individuals spawn only once each year.

Second, the spawning waves were unlikely to have represented three different stocks because the three episodes of spawning occurred at the same location and their larvae grew and fed at the same location. Fish stocks are usually geographically separate during their spawning and early life history stages.

Third, this phenomenon is observed in other short-lived, small-bodied pelagic fishes that spawn demersally, for example both Pacific and Atlantic herring, and capelin (Hay 1985; Lambert 1984, 1987; Lambert and Ware 1984). This is the strongest argument in favor of spawning of sand lance by age classes. Since the underlying characteristics of the early life history of sand lance can be explained with reference to other pelagic life fishes, it is reasonable to suspect that they share this characteristic as well.

If correct, this hypothesis predicts that there are at least three groups of breeding age classes in populations of *A. hexapterus* in the Bering Sea. This is the case for most other species of sand lance. For example, *A. personatus* matures after its first or second year of growth, and rarely lives to be older than 4 yr old (Inoue et al. 1967). Species of sand lance from the Atlantic may live to an age of 9 yr, but the majority of the biomass is concentrated in the 1 to 3 yr age classes (Reay 1970; Auster and Stewart 1986; Winters 1989; Nelson and Ross 1991).

We use the term "groups of breeding age classes" because the three waves of sand lance spawners that entered Port Moller in the winter and spring of 1990 could not have been individual age classes. If we assume that the fraction of total newly-hatched larvae in each cohort was proportional to the biomass of adults in each spawning wave, and that the oldest adults spawn first, then the first spawning wave must have consisted of most adult age classes and the second and third waves must have been newly-recruiting age classes.

Growth

Growth in length of sand lance larvae from Port Moller in 1990 fell within the range estimated from length frequencies reported by other authors. The wide range of growth rates shown in Table 4 and Fig. 9 is due in part to the wide range

of temperatures expected from a comparison between sites stretching from the Okhotsk Sea to Chesapeake Bay. Part of the variance in may also be due to variation in feeding conditions between sites.

Can growth of sand lance larvae from Port Moller in 1990 be used to infer their feeding success? In theory, there is no obstacle as long as there are controlled rearing experiments available for comparison. However, the results of the three rearing experiments performed to date do not support each other.

Two studies support the conclusion that a range of G_w of 4 to 6 %d⁻¹ at temperatures of 6 to 10°C indicates that sand lance larvae are growing very nearly at their maximum rate, or at least feeding in very high prey concentrations. Yamashita and Aoyama (1985, 1986) reported a G_w of 4.2 %d⁻¹ for *A. personatus* larvae 4.7 to 7.6 mm long reared at 6.5°C and fed rotifers and natural microzooplankton at concentrations of 5,000 L⁻¹. Initial stocking density of sand lance larvae was 40 larvae in a 3 L aquaria or 13 L⁻¹.

Smigielski et al. (1984) reported G_w of 2.40 %d⁻¹ at 2°C, 3.23 %d⁻¹ at 4°C, 4.75 %d⁻¹ at 7°C and 5.62 %d⁻¹ at 10°C for *A. americanus* larvae 5.7 to 32.0 mm long that were fed rotifers, natural zooplankton and cultured brine shrimp nauplii at concentrations of 2,000 L⁻¹. Buckley et al. (1984) reports that the initial stocking densities of sand lance larvae for those experiments was 300 larvae in 38 L aquaria or 8 L⁻¹.

In contrast, a third study reports that a range of G_w of 4 to 6 %d⁻¹ indicates that sand lance are feeding at prey concentrations of only 10 to 50 plankters·L⁻¹, an order of magnitude lower than the concentration of prey inferred from the other two experiments. Buckley et al. (1987) reported that G_w of *A. americanus* rose from 3 to 6 %d⁻¹ over a range of prey concentrations of 5 to 50 plankters·L⁻¹. Larvae were reared at 6 to 8°C and fed on natural zooplankton. Initial stocking densities were 200 sand lance larvae in a 200 L aquaria or 1 L⁻¹.

We have no explanation for these conflicting results, except to suggest that if stocking density and tank volume are as important as temperature and prey density in controlling growth of sand lance, then the growth of laboratory-reared larvae can not be compared to the growth of wild larvae. This is a subject that deserves closer study, if only because there is data available on growth of wild sand lance larvae that may be used to generate a model of temperature-dependent growth in the wild.

Pseudo-type I vertical distribution

At least three studies: Johansen (1925), Richardson and Percy (1977), and Potter and Lough (1987), reported type I pattern of vertical migration for large *Ammodytes* spp. larvae. Neilson and Perry (1990) interpreted this as support for the idea that fish are flexible in their adoption of strategies of vertical migration. Such flexibility would allow fish to respond to temporal variation in their environment. We agree with this idea, but we suggest that for the particular case of sand lance larvae reports of type I vertical migration are probably artifacts resulting from avoidance of sampling gear by large larvae. We call these artifacts "pseudo-type I".

The defining characteristic of the pseudo-type I pattern is that it is only observed in populations of late-stage larvae or juveniles - fish large enough that significant numbers of them are capable of avoiding plankton nets. Net avoidance has the paradoxical effect of reversing the true pattern of vertical distribution for these large larvae.

The best example of pseudo-type I was a study reported by Potter and Lough (1987) on *Ammodytes* spp. larvae of Georges Bank. Although small larvae exhibited a type II pattern, larger larvae and juveniles appeared to follow a type I pattern - large larvae were caught in greater numbers at night than during the day, and in greater numbers in deep strata than in shallow strata. This appeared to be a case in which large larvae were migrating off the sea floor into the upper water column at night. To their credit, Potter and Lough (1987) concluded that they were unable to make firm conclusions about the migration pattern of large sand lance larvae because their catches of large fish were biased by avoidance of their sampling gear, the Multiple Open-Closing Net and Environmental Sensing System or MOCNESS. [Brander and Thompson (1989) showed that MOCNESS is less effective in catching herring larvae than high-speed plankton nets or the Longhurst-Hardy plankton recorder because of greater net avoidance.]

Richardson and Percy (1977) provided another example; they reported that large (range = 17 to 37 mm long) *A. hexapterus* larvae caught at night off Yaquina Bay, Oregon, were found over the depth range of 0 to 150 m, but were concentrated mainly in the 0 to 10 m strata. This appears to be an example of a type I migration pattern. However, this result could just as easily have been produced if large sand lance completely avoided the 70 cm diameter bongo nets. Then only the smallest larvae, which would tend to occupy the uppermost layers of the water column at any time of day, would be captured. Strong support for the existence of a high degree of net avoidance is Richardson and Percy's (1977) observation that they never caught any sand lance larvae during the day.

At least seven other studies have reported data of variable quality on vertical distribution of sand lance larvae, but firm conclusions about the type of migration cannot be made from these studies. Russell's (1926, 1928) investigations of *Ammodytes* spp. in the English Channel are difficult to interpret because there was great variation in the depth distribution of sand lance larvae. This was because he caught relatively few sand lance larvae and because he used an open net and did not correct for sampling of upper water layers during deployment and retrieval of the net. Norcross et al. (1961) compared the numbers of *A. americanus* larvae caught at the surface of outer Chesapeake Bay with the numbers caught at the sea bottom, but they did not sample at any depths between the two extremes so it is difficult to interpret the findings. Percy and Richards (1962) performed a similar kind of survey of *Ammodytes* larvae of the Mystic River, Connecticut estuary; not only did they not sample between the surface and the sea bottom, but they did not report separate day and night catches. Muller (1978) compared neuston catches made in Kiel Bay in the Baltic Sea with those made by oblique tows through the entire water column. Larvae were less abundant at the surface. He did not report day and night catches separately. Finally,

Monteleone and Peterson (1986) reported day catches of *A. americanus* at 1, 5 and 15 m depth in Long Island Sound. Larvae were concentrated at 5 m depth.

Adaptiveness of type II diel vertical migration strategy

There are at least three reasons why the type II pattern is more adaptive for sand lance larvae than the type I pattern. The first reason is that adult sand lance also follow a type II pattern of vertical migration; they feed throughout the water column during the day and bury themselves in sand at night to avoid predators. In the absence of strong evidence to the contrary, it is reasonable to conclude that there is continuity of the type of vertical migration throughout the species' life history. This assumption remains to be tested.

The second reason is that the advantage of locating dilute prey in a well-lit environment may outweigh the disadvantage of being vulnerable to visual predators. Sand lance larvae feed only during the day (Covill 1959; Ryland 1964; Yamashita et al. 1985a), so that during the day, all other factors being equal, they should occupy the upper water column where the highest concentrations of microzooplankton are found. At night, they should either remain in the upper water layers or slowly sink to lower depth strata as a result of lower activity levels. This argument is insufficient in itself to explain the choice of a type II migration pattern because larvae of other fish species such as herring also feed during daylight but exhibit a type I pattern of vertical migration. The difference between sand lance and other species is that sand lance hatch in winter and early spring before the spring bloom of zooplankton and before the hatch of most other species of spring spawners (Sherman et al. 1984). They hatch into a prey field with low densities compared to the prey fields of other species that hatch during the spring bloom. Although sand lance can survive and grow at very low prey densities, there must be selection pressure for this species to maximize the amount of time that they are in contact with whatever prey is available. This may have led to the strategy of migrating upwards to the well-lit surface layers at dawn, feeding throughout daylight as well as during early and late twilights, and then sinking at night to lower depths.

A third reason suggested by Yamashita et al. (1985a) is that migration to deeper water at night may reduce predation pressure because sand lance larvae may avoid vertebrate and invertebrate predators that follow a type I pattern of diel vertical migration. A reduction in activity of the larvae will reduce vibrations that may alert predators that hunt at low light levels.

Finally, there may be bioenergetic advantages to sinking at night and rising during the day (Neilson and Perry 1990). Higher temperatures in upper water layers may increase growth and lower water temperatures in deeper water may inhibit foraging by predators. However, bioenergetics probably have little importance to sand lance larvae in Port Moller because the estuary is well-mixed everywhere except in the southern end of Herendeen Bay, and even there sand lance larvae do not descend below the thermocline.

Advection

This study is the first to report dispersal and mortality parameters for *A. hexapterus* larvae. To the best of our knowledge, this study is only the second to report these parameters for any species of sand lance larvae. Fujiwara et al. (1990) estimated advection and mortality of *A. personatus* larvae within the Seto Inland Sea of Japan for the time period of 1981 to 1986.

An average advection rate of 0.321 cm s^{-1} towards the head of Herendeen Bay is higher than the average advection rate of 0.2 cm s^{-1} for *A. personatus* larvae in the Seto Sea reported by Fujiwara et al. (1990).

Nakata (1988) and Fujiwara et al. (1990) concluded that sand lance larvae in the Seto Sea were passively advected by water currents, and that the advection rate was controlled primarily by the speed and direction of winds. They based their reasoning on the fact that the average rate of wind-induced easterly flow of water within the Seto Sea during January and February was also close to 0.2 cm s^{-1} .

We do not believe that a similar situation occurs in the Port Moller estuary because 2 yr of oceanographic and meteorological observations have shown that the primary forcing mechanism in this estuary is the tide, not wind-induced surface currents (Greengrove 1991; McGurk et al. 1991a, 1991b). Superimposed on tidal effects are remote atmospheric forcing events, seaward surface currents due to baroclinic circulation caused by freshwater inflow into the heads of Moller and Herendeen Bays, and local topographically steered wind effects.

Remote atmospheric events are responsible for downwelling conditions at the boundary of the estuary (Greengrove 1991). From May to September, 1989, winds were primarily from the southeast with a few reversals from the northwest. This north-south pattern is a result of the north-south orientation of the mountain ranges surrounding the estuary. However, seaward outflow of water from the estuary was 180° out of phase with this time-series of winds. Greengrove (1991) hypothesized that this counter-intuitive result was due to a downwelling condition set up along the north coast of the Alaska Peninsula during a period of southeasterly winds. Thus, water flows into the estuary during periods of southeasterly winds and out of the estuary during periods of northwesterly winds.

From May to July, 1990, there was no consistent pattern of wind direction - it blew strongly from both directions and reversed as often as three times a week. Therefore, we do not at present know what magnitude was the downwelling at the estuary boundary.

The magnitude of baroclinic surface currents depends on the amount of freshwater flowing into the upper estuary. Precipitation in 1989 was much higher than in 1990, so baroclinic flow was greater in 1989 than in 1990 (McGurk et al. 1991b). The influence of local winds increases with distance from the boundary.

In summary, the mechanisms responsible for water movement in the Port Moller estuary, and their interaction with the movement of sand lance larvae, vary in space and time in a manner that is too complex to interpret without the assistance of a hydrodynamic model. This topic is the subject of the fourth report in this series.

Diffusion

This report provides the first estimate of spatial variance for any species of sand lance larvae. Although our estimates of s_y^2 were not reliable because the y-axis was not adequately sampled, our estimates of s_x^2 were reliable because the x-axis was well-sampled. Since $s_x^2 = 2K_x t$, where K_x = coefficient of Fickian diffusion (km^2d^{-1}) along the x-axis (Okubo 1980), K_x was $58.891 \text{ km}^2\text{d}^{-1}$ at age 1 d and decreased inversely with age. If sand lance larvae moved as passive particles, then K_x would increase with age as larger scale eddies were included in the area covered by the population. The fact that we obtained exactly the opposite result is strong evidence that sand lance larvae were not moving as passive particles, but instead were moving according to directed behavior.

Mortality

Mortality of sand lance larvae in Port Moller of 0.133 d^{-1} was about twice the value reported by Fujiwara et al. (1990) for *A. personatus* in the Seto Inland Sea. Both values fall within the range predicted for pelagic fish larvae from their dry weight range of 80 to 13,000 μg (Peterson and Wroblewski 1984; McGurk 1986).

The fact that mortality of sand lance larvae in Herendeen Bay was responsible for 80% of the total loss rate of 0.166 d^{-1} is strong evidence that transport of larvae outside of the estuary played a negligible role in their population dynamics.

Implications for resource management

The most important conclusion of this study is that there is a close association between the physical characteristics of the Port Moller estuary and the life history strategy followed by the local stock of sand lance. Lower Moller Bay is an incubation site for sand lance eggs and Herendeen Bay is a nursery area for sand lance larvae and post-larvae. Thus, we expect that the dynamics of the early life history stages of this stock, up to and including its annual rate of recruitment, may be causally related to variation in the physical oceanography of the estuary.

Our first point of discussion concerns the lack of offshore dispersal of larvae in this stock. This study shows conclusively that there exists a class of *A. hexapterus* stocks, such as the Port Moller stock, that are estuarine-dependent. A similar reproductive strategy may be followed by other species of sand lance because their larvae are often found in bays and inshore waters (Einarsson 1951; Wheatland 1956; Percy and Richards 1962; Herman 1963; Croker 1965; Inoue et al. 1967; Mitsuno 1977; Altukhov 1978; Scott 1980; Monteleone and Peterson 1986; Dalley and Winters 1987). At present the only other well-documented example of an "inshore" stock is the population of *A. personatus* larvae that spends its entire egg and larval stages within the Seto Inland Sea (Nakata 1988; Fujiwara et al. 1990).

On the other hand, sand lance larvae have also been found widely distributed over shallow continental shelves (Kobayashi 1961; Norcross et al. 1961; Macer 1965; LeBrasseur 1970; Day 1971; Langham 1971; Scott 1972; Waldron 1972; Richards and Kendall 1973). In fact, Sherman

et al. (1984) classified *Ammodytes* spp. larvae captured off the northeastern U.S. as "shelf-ubiquitous".

This evidence suggests that there are at least two life history strategies followed by sand lances. The estuarine/coastal strategy involves spawning in a shallow inshore area followed by directed transport of larvae into a nearby estuary or coastal embayment where the larvae feed and grow. The shelf strategy involves spawning in a shallow area of a continental shelf or in a coastal area followed by offshore dispersal of larvae.

At present we do not know whether the adoption of inshore or offshore rearing of sand lance larvae is species-specific or whether both strategies can occur in the same species under different physical conditions. It is not unreasonable to expect the latter situation because it has been shown to operate for at least one other species of pelagic marine fish.

The herring of the northeastern Atlantic exhibit both inshore and offshore rearing strategies depending on the oceanographic conditions near the hatching sites (Heath and Richardson 1989). In areas such as the central North Sea with nearby habitat for juvenile rearing, herring larvae do not disperse great distances from their hatch sites. They appear to obey Iles and Sinclair's (1982) retention zone hypothesis. However, in areas such as the west coast of Scotland with little nearby juvenile habitat, herring larvae are advected great distances from their hatch sites before encountering juvenile habitat. Stocks such as these do not have an identifiable larval retention zone, only a migration path.

By analogy with Atlantic herring, we propose that sand lances may also have a wide range of early life history strategies and that the strategy adopted by a stock is determined by the particular oceanographic features near its spawning grounds. In the case of the Port Moller estuary, we have the unique coincidence in space of a shallow, sandy and well-mixed spawning area (lower Moller Bay) next to a deep, stable fjord that supports a rich zooplankton community (deep basin of Herendeen Bay). Offshore dispersal is not necessary for sand lance larvae that hatch from lower Moller Bay - they can reach juvenile habitat by migrating towards the head of Herendeen Bay.

Since the early life history of the Port Moller stock of sand lance is restricted to the Port Moller estuary, recruitment variation in this stock is most likely causally related to annual variation in the physical and biological environment of the estuary. For reasons that have been discussed above, the hydrodynamics of this estuary are too complex to be investigated without a hydrodynamic model. In this discussion, we will only point out those aspects of the physical and biological environment that are considered important. Functional relationships between physical variables and larval dynamics will be investigated in the fourth report of this series.

The location and quality of habitat for sand lance egg incubation in the lower estuary is unlikely to be affected by any natural physical variable. However, these fish eggs are vulnerable to any industrial activity in the lower estuary because they are laid in shallow water close to the only navigable channels in the estuary. They could easily be vulnerable to dredging of the channels or to persistent release of toxic chemicals into the nearshore zone.

We recognize that it is highly unlikely that any development will occur in Port Moller estuary in this century, but the accidental release of hydrocarbons is conceivable if commercially valuable sources of oil and gas are ever discovered and developed in the southeastern Bering Sea.

In our opinion, the larval stage is the stage that will be most affected by variation in the physical environment because the timing and duration of the migration of larvae into their rearing area at the head of Herendeen Bay is dependent on physical processes. The speed of advection into Herendeen Bay will vary inversely with the strength of the baroclinic surface outflow. It will also vary directly or inversely with wind speed depending on whether the average wind direction is northwest or southeast. The extent of offshore transport of larvae by diffusion depends directly on the frequency and magnitude of storm events which add mixing energy to the outer estuary.

Physical variables are not the only factors that control larval population dynamics. Density of sand lance and the timing of their hatch in relation to the timing of the spring bloom of microzooplankton may be equally important factors because they control growth of larvae which indirectly controls survival. These density-independent factors, as opposed to the density-independent factors of the physical environment, may be more important in the Port Moller stock than they are in other stocks because of the small scale of their early life history (Heath and Richardson 1989).

We note that sand lance populations in the eastern and western Atlantic ocean have been shown to increase in response to overfishing of their competitors and their predators (Sherman et al. 1981). Therefore, we may expect a similar increase in sand lance biomass in southeastern Bering Sea in response to overfishing of herring and groundfish in the area. Such an increase would lead to increased importance of density-dependent mortality in Port Moller sand lance larvae.

Density-dependent factors also include competition for food with other planktivores and avoidance of predators. Since sand lance feed on the same resource as other abundant pelagic fish larvae such as herring, their feeding success will be affected by competition with those larvae. Sand lance larvae in Port Moller have minimized competition for food by spawning several months before most species of fish larvae. They also segregate themselves spatially. In 1990, maximum densities of herring larvae were found in upper Moller Bay (McGurk et al. 1991a), whereas the maximum densities of sand lance were found in Herendeen Bay.

CONCLUSIONS

1. This is the first report of the population dynamics of Pacific sand lance larvae from any site in North America, and the most detailed population analysis for any species of sand lance with the exception of the Japanese sand eel.
2. Due to a fortuitously early arrival of the study team in Port Moller in 1990, 89.0% of the 473 plankton samples collected during 13 surveys of the estuary from April to July, 1990, contained at least one sand lance larva.
3. Length frequencies constructed from measurement of 3,154 sand lance larvae were a mixture of three cohorts. This is the first report of cohort structure in Pacific sand lance. It is about half the number of cohorts found in a typical herring population, which confirms the prediction by Lambert and Ware (1984) that slow-growing pelagic larvae would be contained in fewer cohorts than faster-growing pelagic larvae.
4. Peak spawning for the three cohorts occurred on January 14, March 15 and April 30, and peak hatch occurred on April 18, May 23 and June 14. Spawning by this species has never been observed in Port Moller because the first and largest cohort of eggs were deposited under the inshore ice cover and the last cohort was spawned before aerial surveys of herring biomass began in early June.
5. By analogy with herring and capelin, we propose that each of the three waves of sand lance spawners were a group of age classes. Most older fish spawned in the first wave and newly-recruited adults spawned in the second and third waves.
6. Due to low water temperatures in winter and spring, the durations of the hatching periods for sand lance cohorts were several times longer than that of other demersal spawning fish such as herring. Durations fell from 64 d for cohort 1 to 42 d for cohort 3.
7. Mean length at hatch was 5.8 mm and mean length at yolk absorption was 7.6 mm.
8. Slow growth of young sand lance larvae meant that their otoliths were half the diameter of otoliths of herring larvae, and the increments in the otolith were thin and packed closely together. These two factors made it difficult to use otolith ring pattern for ageing sand lance larvae. Instead, larvae of each cohort were aged from their estimated dates of peak hatch.
9. Growth calculated from length frequency analysis rose from 0.06 to 0.19 mm·d⁻¹ in larvae 0 to 49 d old to 0.26 mm·d⁻¹ in larvae 50 to 100 d old. A Gompertz growth model best described growth over the entire larval period: $L = 5.8 \exp\{- (0.0114 / 0.0098) [1 - \exp(0.0098t)]\}$, where L = standard length (mm) and t = age (d).
10. Specific growth rate rose from ≤ 1 %·d⁻¹ in larvae <50 d old to 3 to 6 %·d⁻¹ in older larvae. The initial period of low growth was caused by low temperatures, low concentrations of microzooplankton prey, and, perhaps, by a lack of feeding experience in young larvae or by competition for prey with other plankters.
11. Almost all sand lance larvae were found above the thermocline in the upper 30 m of the water column. The smallest larvae were found near the surface and larval size increased with depth. Density (number·m⁻³) of larvae was highest in the upper 10 m and decreased with depth. There was no observable diurnal pattern in depth distribution. These observations suggest that sand lance followed a type II pattern of diel vertical migration - movement to the surface during the day followed by sinking at night.

12. Gut fullness of sand lance increased from zero in 10 mm long larvae to about 12% in 20.0 to 24.0 mm long larvae and then declined to zero in larvae ≥ 35 mm long. The absence of food in small larvae may have been caused by voiding of the gut upon capture in towed plankton nets. The absence of food in large larvae was due to avoidance of the net by large, healthy feeding larvae - only weak, poorly-feeding large larvae were captured.
13. Average percent gut content was maximal at 15 to 25 m depth.
14. Average percent gut content was highest at night and lowest during early twilight, with a second maximum during midday. After accounting for a time lag of about 9 h in passage of food through the gut, these results support the conclusion that sand lance feed primarily during daylight.
15. Over 99% of the 153 prey items found in sand lance guts were various life history stages of copepods, the same diet as herring larvae. Mean length and width of sand lance prey were similar to that of herring larvae. These findings indicate that sand lance larvae and herring larvae compete for the same food resource.
16. Larvae in Hague Channel, the western channel of the estuary, were transported into Herendeen Bay at an average rate of $0.277 \text{ km} \cdot \text{d}^{-1}$. Larvae in upper Moller Channel were transported to lower Moller Bay at an average rate of $0.157 \text{ km} \cdot \text{d}^{-1}$. Lower advection in Moller Bay than in Herendeen Bay was caused by an anti-seaward surface current formed by upwelling near the tip of Harbor Point.
17. Backcalculation of transport rates to age zero showed that sand lance larvae hatched from eggs laid on sand and fine gravel in lower Moller Bay. The offshore extent of the egg beds is not known.
18. As expected from the bathymetry of Port Moller and from the different directions of advection with the estuary, spatial variance of sand lance density was much greater in the along-channel axis ($s_x^2 = 177.782 \text{ km}^2$) than in the cross-channel axis ($s_y^2 = 10.839 \text{ km}^2$).
19. Total loss rate of sand lance larvae was 0.166 d^{-1} in Herendeen Bay, of which 0.133 d^{-1} was due to natural mortality and 0.033 d^{-1} due to dispersal out of the study area. This supports the idea that most Port Moller sand lance larvae migrate towards the head of Herendeen Bay rather than offshore into Bristol Bay.
20. The Port Moller stock of sand lance belongs to a class of sand lance stocks that have an entirely estuarine or coastal early life history. This may have evolved in response to the unique physical conditions of Port Moller - a shallow, well-mixed spawning site next to a deep, stable fjord with a rich zooplankton community. Under such a life history strategy, we expect that density-dependent processes of competition for prey and avoidance of predators will be more important than density-independent processes that control the timing and rate of transport from the hatching area to the juvenile rearing area.

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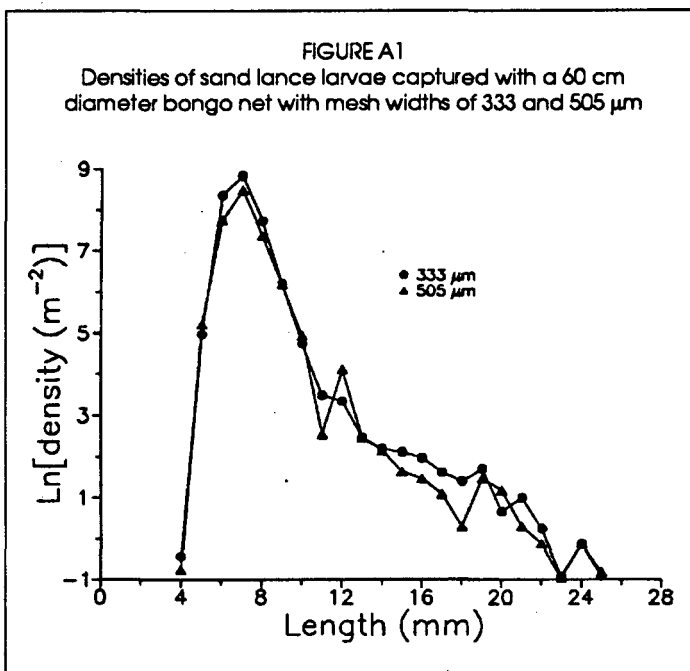
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APPENDIX A.

EXTRUSION AND AVOIDANCE OF SAND LANCE LARVAE

Extrusion

Extrusion of sand lance larvae through the meshes of plankton nets was assessed by comparing length frequencies of the catches of different meshes. Between April 27 to 30 and June 22 to 24, 45 oblique tows of a 60 cm diameter bongo net were made in which one side of the net was rigged with a 333 μm mesh net and the other with a 505 μm mesh net. Larvae were first captured at a length of 4.0 mm, but were not fully recruited to either mesh until they were at least 7 mm long (Fig. A1). The distribution of larval density was similar between meshes at most lengths; there is no evidence of greater extrusion of sand lance larvae through the 505 μm mesh than through the 333 μm mesh. Therefore, we did not make any corrections to larval density for extrusion.



Avoidance

Tucker trawl catches

In order to analyze night-day differences in avoidance of the Tucker trawl by sand lance larvae, we calculated average density of sand lance larvae over the entire water column at a particular time of day by dividing the total number of larvae captured in one set of vertical tows by the total volume of water filtered by those tows. Average depth-integrated density was then distributed into 5 mm-wide larval length intervals using the length frequency of the pooled samples for that station, date and time. Night densities were greater than day or twilight densities at all lengths except the 5 to 10 mm length interval for station 36 on June 25 to 26 (Fig. A2). Day and twilight densities were judged to be not different from each other because ratios of twilight to day densities did not consistently increase with

length, as would be expected if the ability of sand lance larvae to avoid a Tucker trawl was reduced during twilight as compared to day. Therefore, twilight densities were pooled into the day category.

The ratios of night to day densities varied significantly with length at station 36 on June 25-26, increasing from 0.9 at 7.5 mm to 6.1 at 22.5 mm (Fig. A3). In contrast, night-day ratios were constant with length at station 39 on July 2; the mean ratio was 1.5 (SD = 0.1, n = 2) over the length range of 7.5 to 17.5 mm. These results are similar to those reported for herring larvae from Port Moller (McGurk et al. 1991b).

There was another factor other than larval length which reduced net avoidance at station 39 compared to station 36. Following arguments presented in the analysis of the herring larval data (McGurk et al. 1991a), we assumed that this additional factor is turbidity caused by the high mixing energy in the water column of station 39. In the absence of a direct measure of turbidity, we assumed that it was directly proportional to root mean square water velocity over a tidal cycle, $U_{\text{rms}} \cdot U_{\text{rms}}$ at station 39 was 85 $\text{m} \cdot \text{s}^{-1/2}$ compared to only 2 $\text{m} \cdot \text{s}^{-1/2}$ at station 36.

There was insufficient data for a multiple regression of $\ln(\text{night-day ratio})$ on larval length, U_{rms} , and the interaction of length and U_{rms} , so we calculated a two-point regression to obtain:

$$(A1) \quad \ln(\text{ratio}) = -0.86 + 0.12L + 0.014U_{\text{rms}} - 0.014L \cdot U_{\text{rms}}$$

where L = larval length (mm).

Test of an ideal sampler - Methot trawl

Thirty pairs of a 60 cm diameter bongo net and a 1 m^2 diameter Methot mid-water trawl were conducted at the same sites and depths from June 22 to July 14, 1990. The Methot trawls were made to the same depth as the bongo nets and within 10 min of the bongo net tows. The bongo frames were fitted with either paired 333 and 505 μm mesh nets or tow 505 μm nets. Densities were not corrected for extrusion.

Larvae were recruited to the bongo nets at a length of 6 mm; they were not fully recruited to the Methot trawl until they were at least 13 mm long (Fig. A4). In order to test for differences in the slope of the right-hand limbs of the two catch curves, it was necessary to exclude all densities for larval lengths shorter than the length of full recruitment to the trawl. Regression analysis showed that there was no difference between gears in the slopes of their catch curves. It indicates that the Methot trawl was no more efficient at catching large larvae than the bongo net. A similar result was obtained for Methot trawl catches of herring.

Regression model of night-day catch ratios

In the absence of any other reliable method for correcting catches of sand lance larvae for net avoidance, we adopted the methods used to correct catches of herring larvae (McGurk 1992; McGurk et al. 1991b) - we constructed a regression model of night-day catch ratios. As with herring larvae, we assumed that the avoidance response of sand lances to towed plankton nets was similar between *Ammodytes* species, a reasonable assumption considering the morphological similarities between all *Ammodytes* spp. larvae.

FIGURE A2

Plot of densities of sand lance larvae against the mid-points of 5 mm-wide larval length intervals. Larvae were collected with an open-closing Tucker trawl at two stations in Port Moller, 1990

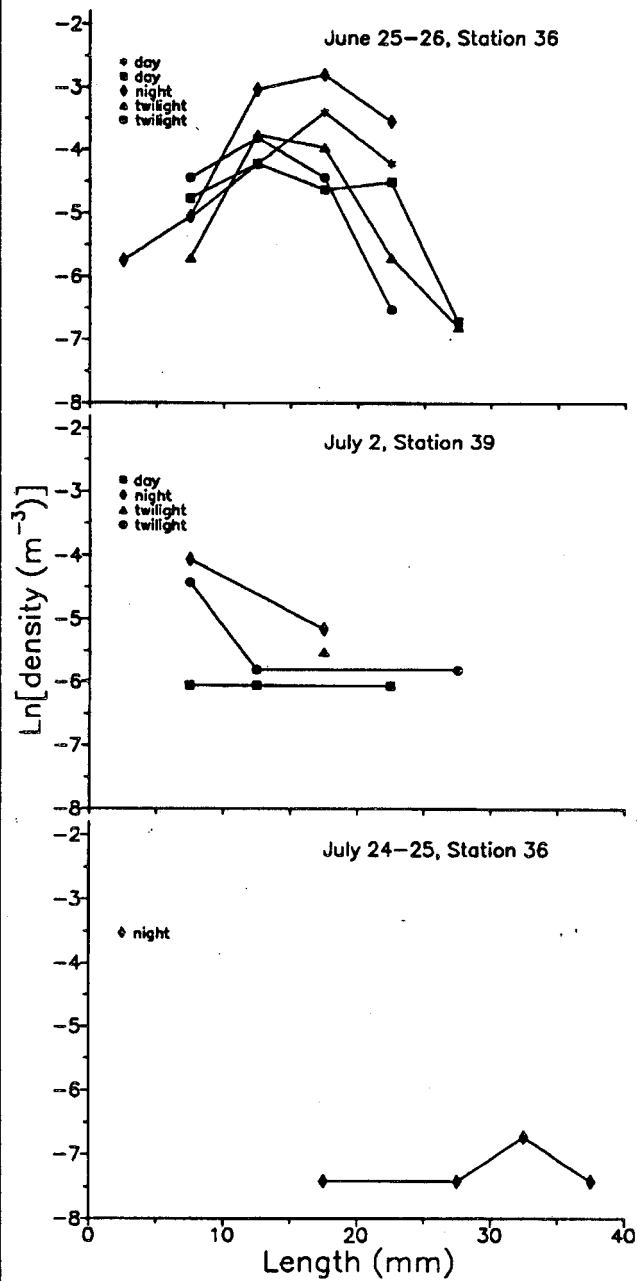


FIGURE A3

Regression of night-day catch ratios on the mid-points of 5 mm-wide larval length intervals. Larvae were collected with open-closing Tucker trawls. Only data from station 36 were used in the regression.

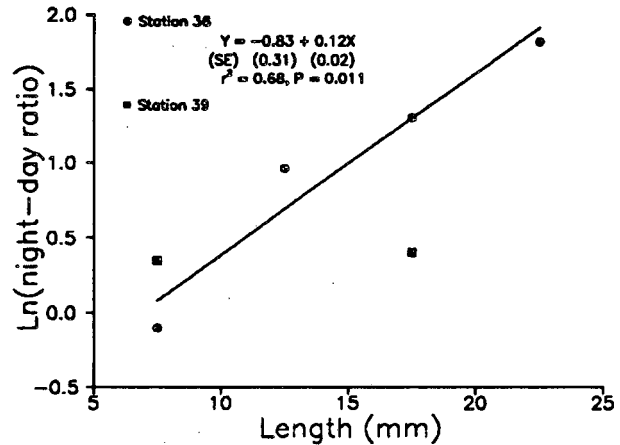
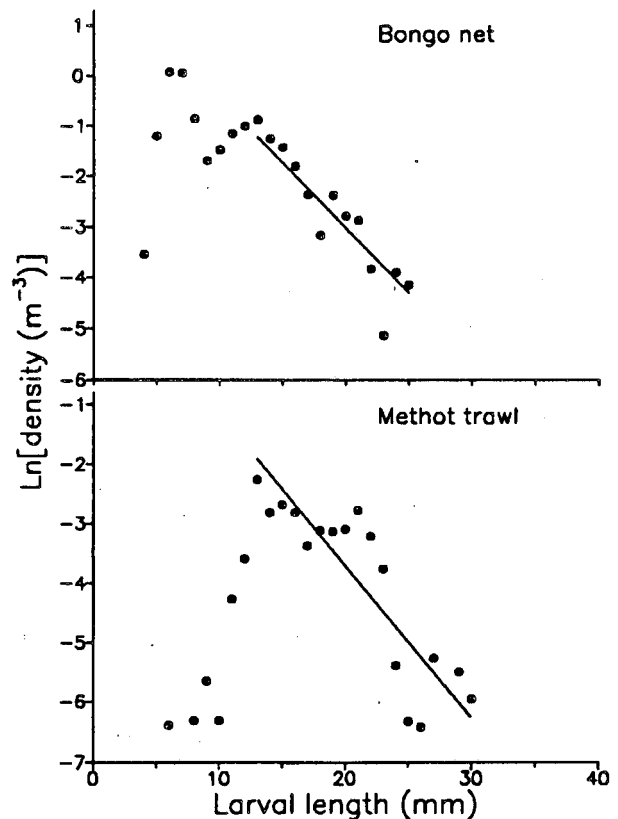


FIGURE A4

Regression of ln(larval density) on length for *A. hexapterus* larvae from Port Moller caught with bongo nets and Methot trawls: $Y = 1.4281 - 0.2568X + 0.6860g_1, n = 30, r^2 = 0.87, P < 0.001$, where $g_1 = 1$ for bongo net and 0 for Methot trawl.



Only two published studies contained useful data sets: Potter and Lough (1987) reported two sets of night-day ratios for *Ammodytes* spp. larvae collected from Georges Bank off the northeastern U.S. and Morse (1989) reported one data set for *Ammodytes* spp. larvae from the northeastern coast of the U.S. (Table A1). We added a fourth data set - the night-day catch ratios of *A. hexapterus* collected with a Tucker trawl at station 36 of Port Moller.

All other reports of night and day catches of sand lance larvae were rejected for different reasons. Several authors

did not sample at night (Herman 1963; Pearcy and Richards 1962; Mitsano 1977; Monteleone and Peterson 1986). At least one study reported night catches but no day catches due to net avoidance (Richardson and Pearcy 1977). Other authors may have collected both night and day catches, but reported only the pooled data (Wheatland 1956; Kobayashi 1961; Croker 1965; Macer 1965; LeBrasseur 1970; Langham 1971; Scott 1972; Muller 1978; Scott 1980), or they did not report larval densities in a form that was amenable to analysis (Russell 1926, 1928; Einarsson 1951; Ryland 1964; Fives 1967; Yamashita et al. 1985; Dalley and Winters 1987), or they did not report larval lengths (Day 1971; Waldron 1972), or they did not sample the entire water column so their results may have been biased by diel vertical migration (Norcross et al. 1961; Richards and Kendall 1973).

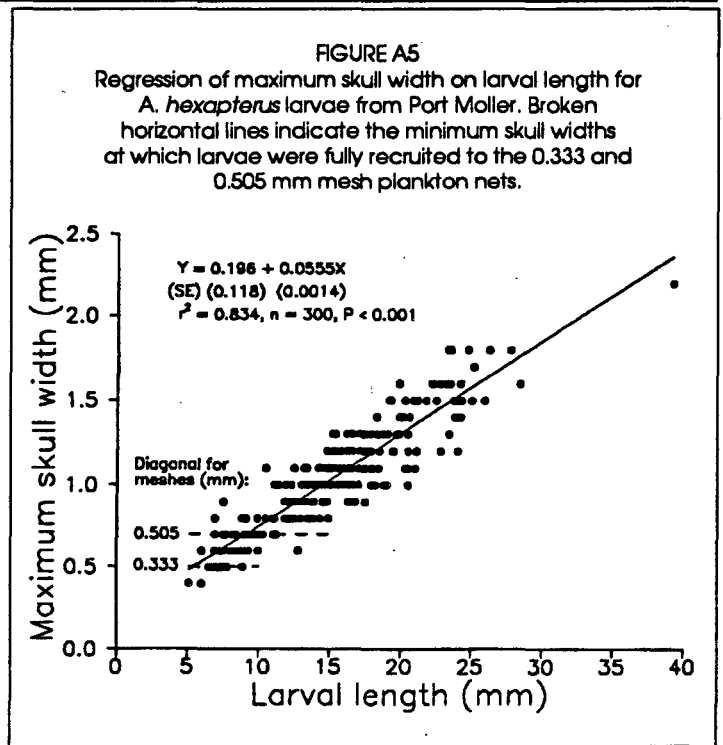
For each of the four data sets the mean night-day catch ratio was calculated for each 1 mm interval of sand lance standard length. Only those ratios for lengths that were fully retained by the mesh of the plankton net were used. Following Colton et al. (1980), we assumed that fish larvae are fully retained when the maximum width of their skulls, including the eyeballs, was greater than the diagonal across a mesh. Length and maximum skull width of 300 *A. hexapterus* larvae from Port Moller was measured to the nearest 0.1 mm. A plot of skull width against larval length shows that *A. hexapterus* larvae are fully recruited to a 0.333 mm mesh when their skull widths are 0.5 mm, which is equivalent to a mean length of about 5 mm (Fig. A5). They are fully recruited to a 0.505 mm mesh when their skull widths are 0.7 mm, which is equivalent to a mean length of about 10 mm.

TABLE A1
Specifications of towed plankton nets used to capture *Ammodytes* spp. larvae.

Data set	Gear	Mesh width (mm)	Net radius (mm)	Tow speed (mm s ⁻¹)	Author
1	Bongo net	0.333	305	1,806	Potter and Lough (1987)
2	MOCNESS	0.333	564	1,028	Potter and Lough (1987)
3	Bongo net	0.505	305	1,000	Morse (1989)
4	Tucker trawl	0.505	564	1,000	This study

Following Heath et al. (1987) day was defined as 8:00-16:00 local time, night as 20:00-4:00 local time, and twilight as two 4 h periods between night and day, 4:00-8:00 and 16:00-20:00. The distribution of night-day catch ratios was normalized by transformation with natural logarithms.

Night-day catch ratios ranged from 1.3 to 36.2 over a length range of 9 to 39 mm (Fig. A6). Three different types of towed plankton gear were used in the four data sets. Radii of nets ranged from 305 to 546 mm, mesh widths ranged from 0.33 to 0.505 mm, and tow speeds ranged from 1,000 to 1,806 mm s⁻¹. All three variables were significantly ($P < 0.001$) intercorrelated, with tow speed decreasing with increasing



net radius ($r = -0.5$), and mesh width decreasing with increasing tow speed ($r = -0.4$) and radius ($r = -0.5$).

These three variables were also confounded with each other and with larval length and gear type, which made it impossible to conduct standard analyses of variance of $\ln(\text{ratio})$. The data set is simply too small to allow a rigorous analysis of the contributions of all variables to night-day catch ratio. However, it is sufficiently large to allow us to estimate the length-dependence of the ratio for conditions in Port Moller.

To reduce the number of degrees of freedom in this problem, we first eliminated net radius by assuming that it was less important than speed in determining net avoidance (McGurk 1992). This meant that speed was the only variable that differed between data sets 1 and 2. To estimate the effect of speed on night-day catch ratio, we regressed $\ln(\text{ratio})$ on length, speed and the interaction of length and speed for the

$$(A2) \ln(\text{ratio}) = 2.3939 + 0.06104L - 0.001291v, \\ n = 42, r^2 = 0.75, P < 0.001$$

where v = speed (mm s⁻¹). The interaction of speed and length was not significant.

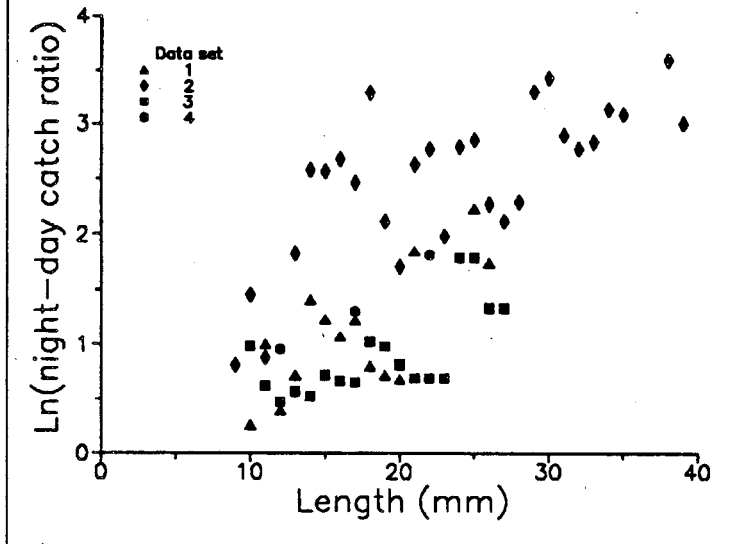
Equation (A2) allowed us to adjust the ratios of data sets 1 and 2 to a speed of 1,000 mm s⁻¹, the speed of nets in Port Moller, by adding 0.001291(speed-1,000) to their $\ln(\text{ratio})$. In doing so we eliminated speed as a variable in the problem.

This left larval length and mesh width as the only variables affecting night-day catch ratio. A regression of speed-adjusted $\ln(\text{ratio})$ on length, mesh width and their interaction for all four data sets was

$$(A3) \ln(\text{ratio}) = 3.5621 + 0.05926L - 7.2710W, \\ n = 63, r^2 = 0.77, P < 0.001$$

where W = mesh width (mm). The interaction term was not significant.

FIGURE A6
Plot of $\ln(\text{night-day catch ratio})$ against larval length
for *Ammodytes* spp. larvae. Data from Table A1.



Equation (A3) is still unsatisfactory for our purposes because it predicts a ratio for newly-hatched larvae caught with 0.333 mm mesh that is four times higher than the ratio for newly-hatched larvae caught with 0.505 mm mesh. This is not realistic, at least for the Port Moller situation, because we know that the densities-at-length were not significantly different between mesh sizes in paired bongo net catches (Fig. A1). It is also unrealistic to expect such large differences between mesh widths at a length when the night-day catch ratio should be close to 1.0. We suspect that the effect of mesh width is larger than it should be because it is confounded with the effects of speed, different types of gear, and perhaps net radius.

Therefore, we assumed that mesh width was not an important variable for Port Moller, but that the slope of the ratio with length was the same as that shown in equation (A3). To calculate an intercept, we assumed that the ratio was 1.0 at the length of hatch (= 5.8 mm). Thus, the ratio changed with length as

$$(A4) \quad \ln(\text{ratio}) = -0.3437 + 0.05926L.$$

Equation (A4) predicts that the percent of sand lance larvae captured by a bongo net in Port Moller fell from 100% at 6 mm to 78% at 10 mm and 24% at 30 mm.

Avoidance correction for Port Moller

From analyses of the Tucker trawl catches for both sand lance larvae and herring larvae, we expected variation in catchability of bongo nets due to variation in turbidity within the estuary. In the absence of any information on the relationship between the catchability of bongo nets and turbidity, we assumed that it was independent of gear type. We also assumed that turbidity was approximated by U_{ms} ($m \cdot s^{-1/2}$), the root mean square water velocity estimated from the three-

dimensional hydrodynamic model. This allowed us to include in equation (A4) the rate of decrease of the intercept and slope of the regression of $\ln(\text{night-day ratio})$ on length with U_{ms} that were measured for the Tucker trawl by equation (A1), i.e.

$$(A5) \quad N_L = N_{0L} \exp(-0.3437 + 0.05899L + 0.014U_{ms} - 1.4 \times 10^{-3}LU_{ms})$$

where N_L = corrected daytime density (number m^{-2}) of sand lance larvae in a length bin with a mid-point of length L (mm) and N_{0L} = measured daytime density.

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interest of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under U.S. Administration.

