Exxon Valdez Oil Spill
Restoration Project Annual Report

Ecology and Demographics of Pacific Sand Lance, *Ammodytes hexapterus* Pallas, in Lower Cook Inlet, Alaska

Restoration Project 97306
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Study History: The purpose of this study is to characterize the basic ecology, distribution, and demographics of sand lance in lower Cook Inlet. Recent declines of upper trophic level species in the Northern Gulf of Alaska have been linked to decreasing availability of forage fishes. Sand lance is the most important forage fish in most nearshore areas of the northern Gulf. Despite its importance to commercial fish, seabirds, and marine mammals, little is know or published on the basic biology of this key prey species. Therefore, restoration project 97306 was established to work in coordination with restoration project 96163M to help characterize the relationship between seabird population dynamics and forage fish abundance. This project has benefited greatly from the logistic assistance of the USGS Alaska Biological Science Center, the USFWS Alaska Maritime National Wildlife Refuge, and the University of Alaska, Fairbanks. A journal article regarding the project has been prepared and awaits final internal review.

The following manuscripts are in preparation:

Robards, M.D. and J. F. Piatt. 1998. Maturation, fecundity, and intertidal spawning of Pacific Sand Lance (*Ammodytes hexapterus*) in the Northern Gulf of Alaska. This manuscript is being submitted to the Journal of Marine Biology pending final revisions, and is submitted here as a report to the EVOS Trustee Council.

Martin D. Robards, George A. Rose, and John F. Piatt. Spatial Variation in Abundance and Growth of Pacific Sand Lance (*Ammodytes hexapterus*) in the Gulf of Alaska. *Internal review before submitting to Trans. Am. Fish. Soc.*

Martin D. Robards, John F. Piatt, Jill Anthony, Daniel Roby, and George Rose. Proximate Composition of Pacific sand lance (*Ammodytes hexapterus*) in lower Cook Inlet, Alaska – A case of feast and famine? *In prep for J. Fish. Biol.*

Another product in preparation is:

Electronic sand lance bibliography in ProCite format (submitted to EVOS Trustee Council in January 1998). This will be appended in the final report pending changes or additions by Willson and Armstrong.

Abstract: We collected sand lance (*Ammodytes hexapterus*) from the nearshore (using beach seines and digging in intertidal substrates) and offshore (using mid-water trawls and halibut) throughout the year from Kachemak Bay, Chisik Island, and the Barren

Islands. Sand lance were analyzed for maturity status, weighed, and measured. We collected otoliths from over 2000 fish to establish age structure of the different populations. On a subsample, we measured length and areas of these otoliths and their annuli. Samples of sand lance have been sent for proximate analysis to Oregon State University. We investigated the physical structure of sand lance habitat at the three study sites using sieve analysis.

Keywords: *Ammodytes hexapterus*; sand lance; maturation; spawning, fecundity; gonadosomatic index; intertidal; Alaska

Project Data: (will be addressed in final report)

Citation: Robards, M.D. and J.F. Piatt. 1998. Ecology and demographics of Pacific sand lance, *Ammodytes hexapterus* Pallas, in Lower Cook Inlet, Alaska, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 97306), U.S. Geological Survey, Biological Resources Division, Anchorage, Alaska.

Maturation, Fecundity, and Intertidal Spawning of Pacific Sand Lance (Ammodytes hexapterus) in the Northern Gulf of Alaska.

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Running Head: Maturation and Spawning of Sand Lance

Keywords: Ammodytes hexapterus; sand lance; maturation; spawning; fecundity; gonadosomatic index; intertidal; Alaska

Abstract: We investigated the seasonal maturity and spawning of Pacific sand lance (Ammodytes hexapterus) in Kachemak Bay, Alaska between May 1996 and October 1997. No significant sexual dimorphism was observed based on length/gonad-free body weight or length-at-age relationships. Sand lance typically reached maturity in their second year, although a few individuals remained immature for longer periods. Indices such as maturity stage, gonadosomatic index, ova-size distribution, as well as field observations indicate that these fish spawn once each year. Males mature earlier in the season than females. However, females attain a higher gonadosomatic index of 31% compared to 21% for males. Spawning occurred in late September and October on fine gravel/sandy beaches soon after the summer water temperatures began to decline. Shoals dominated in number (2:1) by males approached the intertidal zone at a site where spawning has taken place for decades. Spawning occurred in dense formations that scoured pits in intertidal beach sediments. Sand lance collected from elsewhere in Cook Inlet and Prince William Sound displayed similar maturation schedules. Fecundity of females was proportional (after $\log_{10}$ transformation) to length ranging from 1,468 to 16,081 ova per female (size range: 93-199mm). Spawned eggs averaged 1.02mm in diameter, were demersal, slightly adhesive, and deposited in the intertidal just below the waterline. Sand lance embryos were observed to develop over 67 days through periods of intertidal exposure and sub-freezing temperatures.

Introduction:

Sand lance (genus Ammodytes) are zooplanktivorous, semi-demersal, schooling perciforms. They are ubiquitous in the boreo-arctic regions of the North Atlantic and North Pacific oceans and are often abundant in coastal regions. Several species of Ammodytes have been described in the North Atlantic and North Pacific. However, Ammodytes hexapterus is the only species known to occur in the northeastern Pacific. A. hexapterus is the dominant species in many nearshore fish communities in the Gulf of Alaska and comprises the principle forage fish for many marine birds and mammals (Thomson, 1987; Field, 1988). Despite their importance in the marine ecosystem, little information is available pertaining to the annual life cycle of Pacific sand lance. In particular, reports on adult maturation schedules, time of spawning, habitat selection, fecundity, eggs, and larval development are few and often conflicting.

Sand lance exhibit the rather unusual habit of alternating between lying buried in the substrate and swimming pelagically in well-formed schools. Hence, they are typically associated with fine gravel and sandy substrates up to and including the intertidal zone (O'Connell and Fives, 1995). Although sand lance appear to be selective in their use of burrowing habitat (e.g., Pinto *et al.*, 1984), the extent to which spawning substrates or specific areas are selected is unknown.

Sand lance spawning and reproductive characteristics in the northeastern Pacific are poorly-known and contradictory. Most estimates of spawning phenology are based on back-calculation from the occurrence of early stage larvae (Field, 1988). Larval surveys in the Kodiak region suggested late winter (February-March) spawning (Rogers *et al.*, 1979; Kendall *et al.*, 1980). Similarly, McGurk and Warburton (1992) calculated that A. hexapterus in the Port Moller estuary (Alaska Peninsula) spawned between mid-January and late April. Observations by Pinto (1984) for captive A. hexapterus collected from the Strait of Juan de Fuca (Washington State, USA) area also indicated late winter (March) spawning. However, direct observations of spawning condition A. hexapterus in Alaska have suggested the existance of fall spawning (August to October) in the vicinity of Kodiak Island (Dick and Warner, 1982) and in Cook Inlet (Blackburn and Anderson, 1998).

To address the lack of information on Pacific sand lance reproductive and spawning characteristics, and to provide specific estimates of maturation and fecundity, a year-round study was initiated in the Kachemak Bay area of Cook Inlet of the Gulf of Alaska (Fig. 1). Local residents indicated this area had been key sand lance habitat for decades. In this paper we provide the first available estimates of maturation phenology and fecundity for Pacific sand lance based on year-round observations, and provide descriptions of spawning behavior of this species in coastal waters.

Materials and Methods:

Kachemak Bay (Fig. 1) is situated at the southern tip of the Kenai Peninsula in Alaska (59.617N, 151.450W). The bay is approximately 38km wide at its entrance and 62km long. Depths in the bay are relatively shallow ranging from about 35 to 90m, with depths generally deeper on the southern side of the bay. Water entering the bay is largely oceanic, originating from the Gulf of Alaska via the Kennedy entrance at the southern end of the Kenai Peninsula. Observations of spawning occurred at Raby's Spit (59.413N, 151.718W) located in Seldovia Bay at the southern entrance to Kachemak Bay.

We made two comparative collections of adult sand lance during the summer at Chisik Island (60.142N, 152.596W) located approximately 90km northwest in Cook Inlet, and from Eleanor Island located in central Prince William Sound (60.533N, 147.600W).

Water temperatures were measured using remote temperature loggers (Optic StowAway version 2.02, Onset Computer Corporation). The loggers were programmed to read water temperature every 10 minutes and placed at 3m depth (below low low water) on the south side of Kachemak Bay (permanent placement) and at Raby's Spit (only during spawning/incubation period of 1996). Air temperatures were collected in Homer by the Alaska Climate Center.

Fish were collected primarily by beach seines, or by digging in intertidal substrates. Beach seining utilized a 44m long variable mesh beach seine. The net had 4m deep, 3mm knotless nylon stretch mesh (sm) for the middle 15.3m and tapered to 2.3m deep with 13mm knotless nylon sm wings. Thirty meters of rope were attached to each end of the seine for use in deployment. The net was set parallel to shore at a distance of 25m as described by Caillet *et al.* (1986). Samples were collected approximately every two weeks from May to September and once per month through the winter during during 1996 and 1997. Spawning schools were caught by setting the beach seine at a tangent from the beach and closing the open end when sand lance swam into the net. Sand lance collections made by digging in exposed intertidal substrates during negative tides (below chart datum) occurred approximately once per month through the year. No samples were collected in January due to field conditions.

A total of 3,189 sand lance were collected in Kachemak Bay. No adult sand lance were caught by beach seine in the winter (November to March), these fish only being found in exposed intertidal sediments. Sand lance were immediately measured to fork length (mm), blotted dry, weighed (±0.01g), individually bagged, and frozen. Gonads were excised from only partially thawed individuals preventing their rupture, particularly in later developmental stages. Gonads were identified as ovaries or testes using a dissecting microscope, weighed (±0.001g), and further classified microscopically as stage 0- immature, stage I- resting (based on Nelson and Ross, 1991), or stage II- developing, stage III- ripe, stage IV- running, stage V- spent, and stage VI- recovering (based on Macer, 1966).

Fecundity was calculated using stratified (by 5mm size classes from 90 to 200mm) samples of 51 stage-II ovaries collected in August and September. Ovaries were carefully removed from fresh fish and preserved in 5% formalin which hardened ova. Before counting, ovaries were placed in small tubes and vigorously shaken with boiling water which resulted in the freeing of eggs from ovarian tissue. All eggs from both ovaries were individually counted on a partitioned petri-dish using a dissecting microscope. We also collected 150 eggs from each of 30 ripe (stage-III) females, 100 eggs from a spawning pit on Raby's Spit (10/12/96), and 78 eggs on subsequent visits to the spawning site (10/24/96, 11/25/96, and 12/9/96). These were analyzed immediately while being kept moist in seawater to prevent desiccation. Eggs were measured using an ocular micrometer at 40x magnification. Embryo development was based on the classification into six stages as outlined by Smigielski *et al.* (1984).

We aged a sub-sample (2,800) of the fish collected in Kachemak Bay and all fish from the two comparative sites. Sagital otoliths were removed from the saculus using fine forceps after making a transverse incision behind the skull. Fibrous material was removed from otoliths which were then cleared and bonded to microscope slides using crystalbond thermal resin. We determined ages on two separate occasions using the methodology of Macer (1966) and Scott (1973). Otoliths with poorly defined annuli that could not be confirmed using the second otolith or where disagreement occurred between readings were omitted from the dataset. Age designations are based on a 1 January hatch date with first year fish designated as age group-0 and second year fish as age group 1, up to seventh year fish being classified as age group-6.

Approximately 3kg of substrate was collected from each of three spawn sites on Raby's Spit. Samples were dried at 65°C until no change in mass was observed. The sample for each site was sieved through 16mm, 8mm, 4mm, 2mm, 1mm, 0.5mm, 0.25mm, 0.125mm, and 0.063mm sieves. Percent mass of substrate retained by each sieve was calculated. Particle sizes were classified according to the Wentworth scale in phi (ϕ) units, where $\phi = -\log_2$ diameter (mm). Median particle diameter is the diameter corresponding to the 50% mark on the cumulative curve using a probability transformed Y-axis (Brown and McLachlan, 1990).

A modified gonadosomatic index (GSI) was used to quantify seasonality of reproduction on sexed individuals of stages-I through VI. All immature (stage-0) fish were omitted from this calculation. The GSI was calculated as: GSI = (gonad weight/gonad-free body weight) x 100 (Nikolsky, 1963; Cuellar *et al.*, 1996).

To compare the length/weight relationships between sexes, we compared the slope and intersect of linear regressions statistically using the Chow test (Salvanes and Stockley, 1996). Mann-Whitney rank sum tests were used to evaluate differences between length at age for the different sexes and between different groups of GSI values. A chi-square (χ^2) test was used to assess deviation from a hypothetical 50:50 sex ratio.

Results:

Physical Environment:

In Kachemak Bay, 1996 sea surface temperatures (SST) increased steadily from less than 2°C in March to about 11°C in August, plateaued at 11°C until mid-September and then after a late summer peak of 12°C declined steadily to about 2°C in January 1997. Temperatures in 1997 followed a similar pattern with a slightly higher peak temperature of approximately 13°C in August (Fig. 2). We did not observe any difference between the permanent temperature logger values in Kachemak Bay to the local SST's at Raby's spit (Fig. 2).

Air temperatures steadily increased from a low in January, and by April were generally above freezing. Air temperatures were generally highest in August, and declined rapidly during September (Fig. 2). Sub-freezing temperatures were common starting in October with many days in November and December never passing above freezing.

Reproductive Characteristics:

Male and female lengths-at-age did not differ significantly for any age group during pre-gonad development (May/June), gonad development (July/August), or at spawning (September/October; Mann-Whitney rank sum test; P's from 0.069 to 0.659; Fig. 3).

Length and weight were significantly correlated (Fig. 4). No significant differences were noted between male and female length/somatic weight relationships during pre-gonad development, gonad development, or at spawning stages (P's >0.05).

No age group-0 fish showed signs of developing gonads (N=419) although 11 fish (3%) had passed from the stage-0 to stage-I phase in October. Gonads of some of the age group-1 through -4 fish did not appear to develop, remaining at the immature, stage-0 phase (19% of 1310, 3% of 697, 0.3% of 287, 2% of 62 respectively).

The smallest ripe male and female fish were both age group-1 (88mm and 113mm respectively). The oldest maturing fish were a male and female, both of age group-6 (163mm and 173mm respectively).

Gonads from the age group-1 fish collected in September were predominantly developing or ripe (72% n=234) which increased at spawning in October with some of these fish also spent (97% n=230). These results indicate that sand lance mature in their second year, at an age of approximately 21 months. Spawning schools were dominated by age group-1 and -2 fish with these two groups representing over 80% of the fish (50% and 31% respectively). Age group-3, -4, -5, and -6 made up only 14%, 4%, 1%, and <1% respectively of the overall spawning school structure.

Sexual development was followed from May of 1996 to October of 1997. Seasonality of reproduction was indicated by monthly changes in maturation stage (Table 1) and gonadosomatic indices (GSI; Fig. 5) in adults (age groups -1 to -6). From February to May, most fish were in the resting phase with a few fish still recovering from spawning. The gradual onset of gonad recrudescence began in June and July, indicated by a small proportion of the fish displaying developing gonads (6-9%; Table 1). A rapid increase in gonadal development began in August apparently in accordance with the peak in SST (Fig. 2). Subsequent development of spawning condition gonads occurred during declining fall SSTs (Fig. 2) until spawning occurred at approximately 10°C. Although mean GSI's indicated an earlier development for males, females ultimately attained a higher index at spawning (31%, compared to 21% for males) which differed significantly from that of males in both 1996 and 1997 (Mann-Whitney rank sum tests; P's <0.01) . Maximum GSI for individual males and females were 47% and 55% respectively. Overall spawning school GSI for males and females (Table 2) were strikingly similar between 1996 and 1997 with no significant differences detected between sexes in either period (Mann-Whitney rank sum tests; P's >0.5). By the end of November, although samples were small, 67% of sand lance collected were in the post spawning condition (spent, recovering, or resting). No spawning condition fish were found after this time (Table 1).

We found no disproportionate development of gonads in relation to size, as no significant relationship was found between GSI and length for ripe fish collected in October (P<0.01; Fig. 6).

Maturity stages of fish collected from Eleanor and Chisik Islands indicated gonad development was occurring (Table 3) at time of capture (July and August respectively). Based on a mean resting GSI (calculated from stage-1 fish collected in April to June from Kachemak Bay) of 0.46, sand lance from Chisik and Eleanor islands displayed significant gonad recrudescence over GSI's observed at resting (Mann-Whitney rank sum tests; P's <0.01). These results were comparable to those found for the Kachemak Bay population (Table 1, Fig. 5).

In the spring and summer during the resting and developing stages (Stage-I and II), sex ratios were relatively even. However, during the spawning period, ripe and spawning males predominated (Table 4). Males were the predominant sex in all age classes (with the exception of age class-5 in which only 3 fish were collected) during this period.

Fecundity estimates ranged from 1,468 to 16,081 ova per female for sand lance ranging from 93 to 199mm fork length (Fig. 7). Fecundity was significantly related to total length after $\log_{10}$ transformation of the data ($P<0.05$). Approximately half of the overall spawning school fecundity was derived from age-group-1 fish which made up 55% of the school by number (Table 5). Ages 1-3 accounted for 95% of the total fecundity.

Ova diameter exhibited a unimodal distribution in all of the 30 females investigated. The overall distribution of the 4500 eggs measured is depicted in Fig. 8. Each egg typically contained a single bright yellow oil globule (in 2 females approximately 5% of ova contained two oil globules).

Spawning Hábitat and Timing:

Spawning occurred in a shallow open bay on the southern, sheltered side of Raby's spit within 100m of a refuge burrowing habitat observed to be frequently used by sand lance. Local residents indicated that sand lance (local name - needlefish) had spawned at this site during October for at least 20 years. No spawning was observed on the outer, exposed side of the spit in 1996 or 1997. Although spawning in 1996 and 1997 was observed on the beach in the area of a freshwater seep, local knowledge suggested that spawning had taken place historically up to 100m east of the seep. The substrate of the spawning area consisted of coarse sand/gravel of which approximately 20% was shell fragments (Fig. 9).

During 1996, sand lance were first observed spawning at 18:45 on September 30 (1.5 hours after high tide, 3 days after spring tides, and 3 days prior to the next neap tide) at a SST of 9.4°C. Initially, we observed laterally compressed schools (approximately one to eight meters in length and up to one meter across) of adult sand lance at high tide moving back and forth along the length of the beach, within 5 meters of shore, and in less than 1 meter of water. Spawning was immediately preceded by sand lance moving back and fourth along a 20m stretch of beach (the area where all spawning was observed), then the school moved to the tide line and compressed into a tight spherical formation just above the bottom (with the fish moving rapidly within this formation). Milt was observed in the water soon after the school adapted this formation. Sand lance were again observed spawning at 18:25 (0.5 hours after high tide) on October 1, at 18:30 (2.5 hours after low tide [neap]) on October 5, and at 08:20 (2.5 hours before high tide) on October 6. Demersal eggs were found intertidally in shallow (less than 50mm) depressions up to 0.4m in diameter from approximately 2.5-5.0m above low low tide. The depressions or pits appeared to be formed at the time of spawning by sand lance as they school close to the bottom. Sand lance continued to spawn in these shallows, and new depressions containing eggs were observed through November 12 (spring tide). During morning low tides we periodically found egg-filled depressions that had not been noted the previous evening, indicating the occurrence of night spawning.

In 1997, we first observed spawning during the neap tide series on October 8 at 16:00 (2.5 hours after low tide) at a similar SST to 1996 of 10.0°C. Subsequent spawning was observed on October 9 from 17:00 to 20:00 (mid-flood tide), October 10 at 08:30 (1.5 hours before high tide), and October 11 at 09:00 (high tide). High winds and snow prevented observations after this, although no spawning pits were observed on any subsequent low tides. After spawning, adult sand lance were not observed swimming in the nearshore, or caught by beach seine until the following spring.

The highly cryptic nature of sand lance eggs and their blending with small fragments of shell gravel prevented accurate assessment of egg distribution over the entire beach. Nevertheless, eggs were observed on the sand surface of the spawning depressions at a density of up to $7cm^{-2}$, and within the substrate to a depth of about 30mm. Eggs were demersal, slightly adhesive, translucent, and almost spherical in shape (mean diameter 1.02mm, sd=0.08mm, n =100). Some eggs were adhered to sand grains or each other, but many others were found individually and unattached within the gravel.

Stage 1 eggs (not more than two days old) were collected on October 12, 1996 in a freshly formed spawning depression. These eggs were characterized by an incomplete blastodermal cap. Yolk cloudiness was not observed at either this or subsequent stages. At the same pit on October 24, eggs were at stage 3 with no blastodermal cap evident. By November 25, egg density at this pit had declined dramatically with only nine eggs observed. Only one of these nine eggs was adhered to the lightly-frozen gravel particles. Each of the nine eggs contained a stage 5 embryo between 3.75 and 3.8mm in length. Eyes were pigmented (0.18mm diameter), myomeres were visible along most of the embryo's length, a beating heart was observed, and a developing alimentary canal visible. On December 9 a final sample of 3 eggs was found at this spawning pit. All three eggs contained a stage 6 embryo which exhibited convulsive movements at frequent intervals (every 10-15 seconds). Assuming the eggs from the same spawning pit location were all part of the October 12th. spawning, development over the observed 58 days (until

December 12 when stage-6 embryos were observed) occurred in an average sea temperature of 6.4°C in conjunction with a mean air temperature of -2.5°C.

Discussion:

Our data indicate that sand lance in Cook Inlet matured in their second year. Maturation in the second year is common amongst other species of sand lance and has been observed for A. personatus (Kitaguchi, 1979), A. americanus (Richards, 1982), and A. tobianus (O'Connell and Fives, 1995). In contrast, A. dubius (Scott, 1968; Winters, 1983) and A. marinus (Reay, 1970) can mature as second-year fish, but often mature at later ages. In the present study, only a single age-group-0 fish (immature) was observed within the spawning schools, although exclusively age group-0 schools were caught elsewhere in the bay at the same time. A. hexapterus developed gonads up to age-group-6 which is also the upper age found for A. tobianus (O'Connell and Fives, 1995). It is evident that for fish populations such as that studied here, wherein a single cohort (age group-1) contributes 50% of the population fecundity that recruitment is likely to propogate through time with a two year lag.

Our data also show that gonadal development was initially slow and differed between the sexes. No sexual dimorphism was observed for mature sand lance, either in their length/somatic weight or length at age relationship. Therefore, we can attribute gender differences in the GSI to gonad development independent of fundamental differences in body size between sexes. Winters (1983) noted that initial maturation was also slow in A. dubius. Rapid gonad maturation occurred in August at the same time that sand lance appear to leave the nearshore (Robards and Piatt, 1997). During August and September, mean GSIs for males are higher, indicating males mature quicker and earlier during the reproductive season. A. dubius (Nelson and Ross 1991), A. tobianus (O'Connell and Fives, 1995), A. marinus (Reay 1970), and A. personatus (Okamoto *et al.*, 1989) all display this differential rate of maturation between males and females. While testes of A. hexapterus reached peak development earlier, ovaries eventually attained a greater relative weight as found in A. dubius (Nelson 1990). Gonad maturation time for A. hexapterus was comparable to that found for fall spawning Atlantic sand lance, lasting about 3 months as opposed to winter and spring spawning Atlantic sand lance which take from five to seven months to mature (Reay 1970). Maturity stages indicating spawning condition and GSI's only peaked once during the fall (indicating once-per-year spawning). These indices were similar in 1996 and 1997 at the time of spawning.

The presence of a few spent fish as late as May (Table 1) indicates that some individuals may spawn later in the winter as suggested for A. dubius (Winters, 1983). However, based on our results, we found no evidence that different spawning groups exist within the population which spawn during the spring as for A. tobianus (O'Connell and Fives, 1995).

The comparative populations sampled at Chisik and Eleanor Island indicated that fall-spawning occurs elsewhere for A. hexapterus within the northern Gulf of Alaska. These fish also showed similar stages of gonad development to the sand lance of Kachemak Bay. Males also exhibited greater GSIs during early stages of maturation in these populations.

Male sand lance outnumbered females in the nearshore zone during spawning, but not during earlier stages of development. This tendancy (male: female ratio of 2:1) has also been observed for A. marinus (Macer, 1966; Gauld and Hutcheon, 1990). A higher ratio of males present at spawning than prior to may indicate: 1) that they remain in the spawning area over a longer period [similar to capelin (Mallotus villosus; Templeman 1948)], or 2) slower-developing females that have not fully attained ripe gonads, remain buried in their refuge habitat until fully ready to spawn. Our data do not allow us to differentiate between these two possibilities.

We found a unimodal size distribution of ova in the developing ovaries of Pacific sand lance suggesting single batch spawning. Unimodal size distributions of ova in A. hexapterus (Pinto 1984), A. dubius (Scott 1972), and A. marinus (Macer 1966) are given as evidence of once-yearly spawning in these species.

Egg sizes for A. hexapterus in Kachemak Bay were comparable with other observations for this species. Andriyashev (1954) reported approximately 1mm for Murman (former USSR) sand lance, Pinto (1984) 0.88 to 1.20mm (mean 1.00mm), and Penttila (1995) approximately 1mm for the Washington State coast sand lance. Williams *et al.* (1964) and Pinto (1984) both observed each egg contained one oil globule. However, our observations indicate the rare occurrence of multiple oil globules which was noted by Garrison and Miller (1982) to occur in this genus.

Our data indicate that fecundity in A. hexapterus ranges from 1500-16,000 ova, and is a function of size. Fecundity of most other sand lance species and populations fell within the range of our data: Japanese A. hexapterus (Hashimoto, 1984); A. americanus (Westin *et al.*, 1979); A. marinus (Macer, 1966); A. tobianus (O'Connell and Fives, 1995). However, two species fell outside of this range; Nelson (1990) reported lower values for A. dubius and Hashimoto (1984) greater values for A. personatus.

Our data indicate that sand lance (A. hexapterus) spawned in Kachemak Bay during a 1-3 week period in October in 1996 and 1997. Spawning over a period of approximately 3 months in the late fall-early winter period was found for A.dubius and A. americanus in the Northwestern Atlantic (Winters, 1989) and over 1.5 months for A. personatus off Japan (Okamoto *et al.*, 1989). Although our observations indicated a shorter (approximately 2 week) window of spawning within Kachemak Bay, these results reflect one spawning site rather than the cumulative reults of an entire region.

During the spawning period, our data suggest that sand lance spawn without regard to tidal state or time of day. However, there is some evidence that spawning occurred more frequently at high tide. This is from the generally high position of spawning pits we located on the beach. Penttila (1995) observed a similar vertical spread of intertidal spawning pits from 1.5m to mean higher high water line with egg deposition in the top 30mm of gravel. Based on our results, we suggest that temperature and/or photoperiod may be cues for the onset of spawning. It was not clear if eggs were deliberately buried by burrowing sand lance or covered by tidal action.

Sand lance spawning occurred on fine gravel/sandy beaches (Fig. 9) in accordance with the findings of Penttila (1995). We feel it is important to establish a quantitative library of the structure of these beach substrates to help identify critical spawning habitat of this key species. Our results in conjunction with the long-term observations of local residents suggest that sand lance use the same sites for spawning year after year for decades. Spawning may occur preferentially on spits such as the site we observed based on observations by Penttila (1995) who also documented repeated use of spawning sites. Perennial use of the same beaches has direct implications to the conservation of this species and others (fish, mammals, birds) that prey on sand lance. This result points to the potential effects of coastal pollution such as oil-spills or beach-front developments that could impact sand lance productivity.

We found no indication that sand lance attempt to move above the high waterline as well known for grunions (Leuresthes spp., Thompson, 1919) and capelin (Templeman, 1948). Reports of sand lance found above water in the intertidal zone (Dick and Warner 1982) may result from sand lance being stranded on low angled beaches under rapidly retreating tides. Stranding may also be the result of predators (intentionally or inadvertently) herding sand lance into the shallows where they may be swept above waterline by the surf (Beston, 1928).

Flocks of glaucous-wing gulls (Larus glaucescens), surf scoters (Melanitta perspicillata), and red-breasted mergansers (Mergus serrator) were present at high tide throughout the spawning period, and were observed to prey on sand lance. Large sculpins were also observed preying on sand lance in the nearshore throughout the spawning period.

The scope of our study did not allow us to establish whether Pacific sand lance are obligate intertidal spawners. However, subtidal samples in the vicinity of fresh intertidal sand lance spawn collected by Penttila (1995) did not find any evidence of coincident subtidal spawn deposition. Capelin (Mallotus villosus) spawn intertidally as well as in deeper offshore waters (Templeman 1948). The intertidal spawning of pelagic species such as capelin appears to be optional (Taylor 1990). Atlantic sand lance are known to spawn subtidally on the offshore banks (Reay 1970) where they prefer the colder, less saline waters (Bye 1990). We found no published reports of intertidal spawning for Atlantic sand lance which may indicate a fundamental biological difference between the Pacific and Atlantic representatives of this genus.

During spawning, we observed no significant clumping (Smigielski et al. 1984) or cloudiness (Pinto, 1984) of spawned sand lance eggs as reported in experimental research. The eggs, although slightly adhesive, did not appear to remain on the beach in large numbers over the course of incubation. Only loose adherence to gravel over time allows eggs to be dispersed by tidal action both interstitially and within the water column. Eggs adhered to gravel and fine substrates would help prevent desiccation while exposed in the intertidal.

The egg development time demonstrated in this study is clearly slower than total incubation times for other species of sand lance at similar water temperatures; Smigielski *et al.* (1984) and Inoue *et al.* (1967) reported 39 days at 7°C for A. americanus and 33 days at 6.2°C for A. personatus respectively. Based on a mid-stage 6 development, Seldovia Bay sand lance on 9 December were at 88% development which would lead to a 67 day total incubation; for this incubation period, hatching occurred on or around December 17. Our total incubation times are a little higher than the 62 days incubation period at 2°C for A. americanus eggs (Smigielski et al. 1984). We suspect that the long incubation observed is probably a result of exposure to much colder temperatures during the approximately 12 hours of intertidal exposure each day (Fig. 2). McGurk and Warburton (1992) report comparable results for A. hexapterus in the Port Moller estuary on the Alaskan Peninsula of 45 to 94 days incubation with a hatching period of 41-63 days.

The location of deposited eggs within the intertidal has a substantial influence on development and survival rates. Similar to Taylor (1984) we found that A. hexapterus eggs deposited in the intertidal developed slower than for other sand lance species that lay eggs immersed in the sub-tidal. Increased egg survival in the intertidal compared to the subtidal has been attributed to lower temperatures for other sand lance species (A.personatus; Yamashita and Aoyama, 1985) and surf smelt (Hypomesus pretiosus pretiosus; Loosanoff, 1937) and to increased oxygenation for Pacific herring (Clupea pallasi; Jones 1972).

The ecological significance of fall-intertidal spawning, and winter egg development may be related to increased development times and extended hatch periods, which could enhance survival in the variable environments of northern oceans. We would also expect less predation during winter due to reduced predatory fish abundance in the nearshore

(Piatt *et al.*, 1997). The timing of hatch may be critical to larval sand lance survival in relation to the onset of spring plankton bloom (Wright and Bailey, 1996). Delayed and variable egg development coupled with further adaptations including larval feeding before absorption of yolk sac (Yamashita and Aoyama, 1985), and reduced metabolism at cold temperatures (Haldorson et al., 1993) all increase the chance of some proportion of larval fish being able to capitalize on the spring plankton bloom.

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Figure 1: Area map. *In prep.*

Figure 2: Seasonal variation in 1996/1997 maximum and minimum air temperatures and sea-surface temperatures (3 m below low low tide level) at Kachemak Bay. Diamonds on sea-surface temperature plot indicate onset of spawning. The plot for Raby's spit SSTs underlies the values for extended plot shown.

Figure 3: Length-at-age for male (▲) and female (■) sand lance collected before gonad development (May and June), during development (July and August), and whilst ripe and spawning (September and October).

Figure 4: Regression plots of length against gonad-free body weight (Log_{10} transformed data) for male (▲) and female (■) sand lance collected before gonad development (May and June), during development (July and August), and whilst ripe and spawning (September and October). Chow tests indicated no significant differences between males and females in any of the three time periods ($F^* = 0.851$, $P>0.05$; $F^* = 0.000$, $P>0.05$; $F^* = 0.067$, $P>0.05$ respectively).

Figure 5: Seasonal changes in male (■) and female (□) monthly gonadosomatic indices (+95% confidence intervals) for sand lance collected in Kachemak Bay between May 1996 and October 1997 (Numbers are sample sizes for each month).

Figure 6: Scatter plot of male and female GSI's against length for ripe (stage-III) fish collected from spawning schools in Kachemak Bay during 1996 and 1997.

Figure 7: Regression of fecundity on body length ($\log_{10}$ transformed data) for pre-spawning (stage-II) female sand lance collected from Kachemak Bay.

Figure 8: Size distribution of eggs found in ovaries of 30 ripe female sand lance collected from spawning schools in Kachemak Bay during 1996 and 1997.

Figure 9: Graphical representation of spawning substrate composition in Seldovia Bay.

Table 1. Percentages of *Ammodytes hexapterus* classified into maturity stages by month for fish collected in Kachemak Bay. Maturity stages were I=resting, II=developing, III=ripe, IV=running, V=spent, VI=recovering.

Month	Sex	Maturity Stage						
		I	II	III	IV	V	VI	Total No.
February	Male	95	-	-	-	-	5	21
	Female	75	-	-	-	-	25	12
March	Male	100	-	-	-	-	-	8
	Female	100	-	-	-	-	-	8
April	Male	92	-	-	-	-	8	24
	Female	95	-	-	-	-	5	21
May	Male	100	-	-	-	-	-	69
	Female	99	-	-	-	-	1	81
June	Male	93	7	-	-	-	-	173
	Female	93	7	-	-	-	-	160
July	Male	91	9	-	-	-	-	210
	Female	94	6	-	-	-	-	239
August	Male	39	57	4	-	-	-	301
	Female	59	41	-	-	-	-	287
September	Male	14	45	39	2	-	-	167
	Female	26	67	7	-	-	-	163
October	Male	1	7	44	41	7	-	310
	Female	1	4	47	43	5	-	195
November	Male	20	-	27	27	-	27	15
	Female	-	-	11	11	22	56	9
December	Male	-	-	-	-	-	100	1
	Female	-	-	-	-	-	100	2

Table 2. Mean gonadosomatic index (±95%CI) for male and female sand lance collected from spawning schools in Seldovia Bay. Numbers in parentheses are sample sizes.

	1996	1997
Male	21.12 ± 1.65 (141)	21.57 ± 1.59 (164)
Female	31.27 ± 2.66 (89)	31.81 ± 2.09 (103)

Table 3. Comparison of maturation status at two other collection areas in southcentral Alaska.

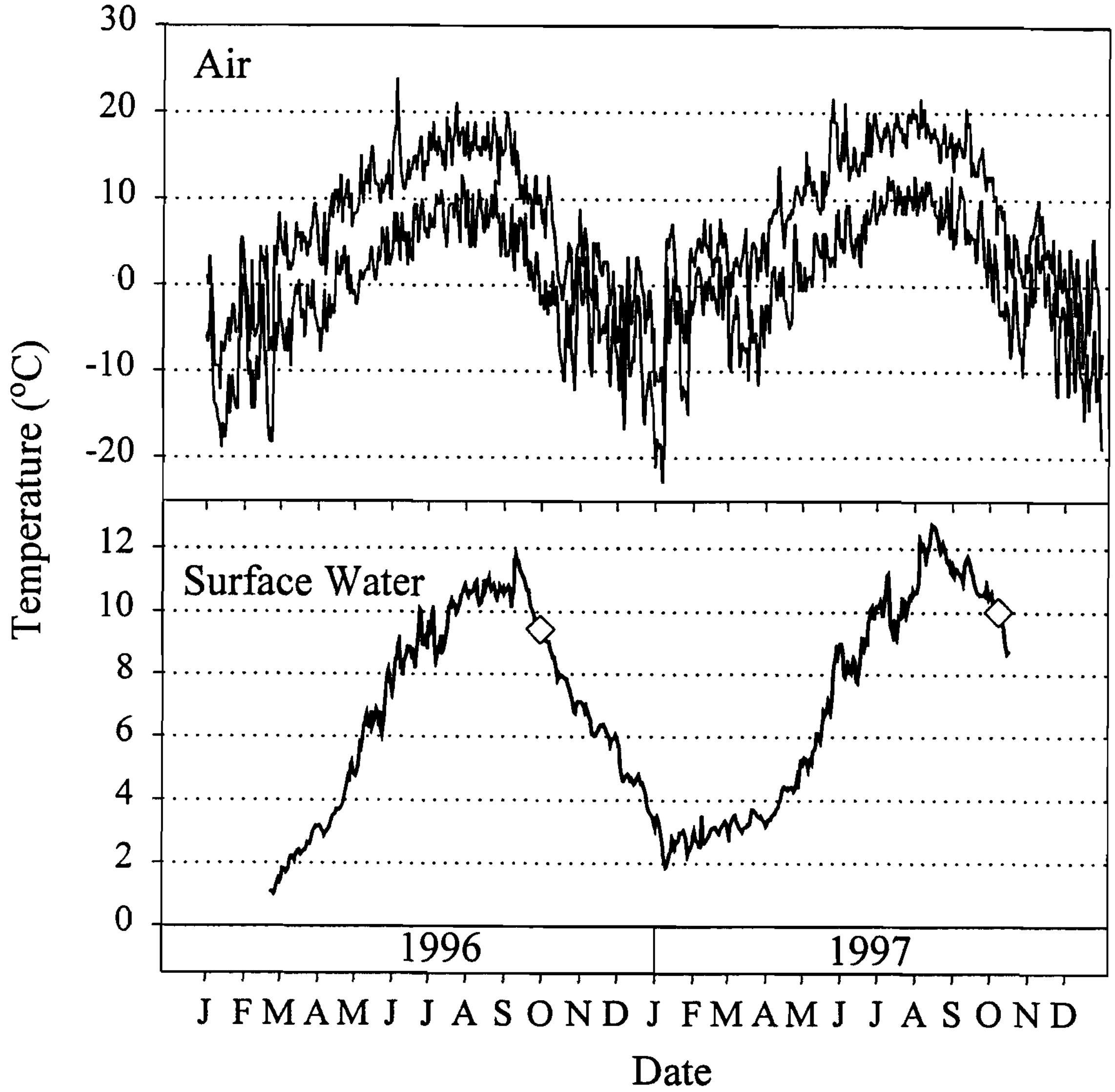
Location	Dates Collected	Sex	N	Index	GSI (±95% CI)
Chisik Island	August 1996/97	M	22	I-III	4.69 ± 1.60
		F	23	I-II	2.81 ± 0.76
		Overall	45	I-III	3.64 ± 1.06
Eleanor Island	July 1997	M	18	I-II	5.81 ± 1.32
		F	24	I-II	3.11 ± 0.53
		Overall	42	I-II	4.27 ± 0.75

Table 4. Sex ratios for sand lance collected at different maturity stages during 1996 and 1997 from Kachemak Bay. Sample sizes, Chi-square statistic, and probability of significant differences from a hypothetical 50:50 sex ratio are given.

Stage	Males	:	Females	N	χ^2	P<0.001
0	1.3	:	1.0	350	6.6	-
I	1.0	:	1.1	1319	5.5	-
II	1.1	:	1.0	563	2.7	-
III	2.1	:	1.0	321	38.4	Yes
IV	1.6	:	1.0	218	11.5	Yes
V	1.9	:	1.0	35	3.5	-
VI	1.0	:	1.5	20	0.8	-

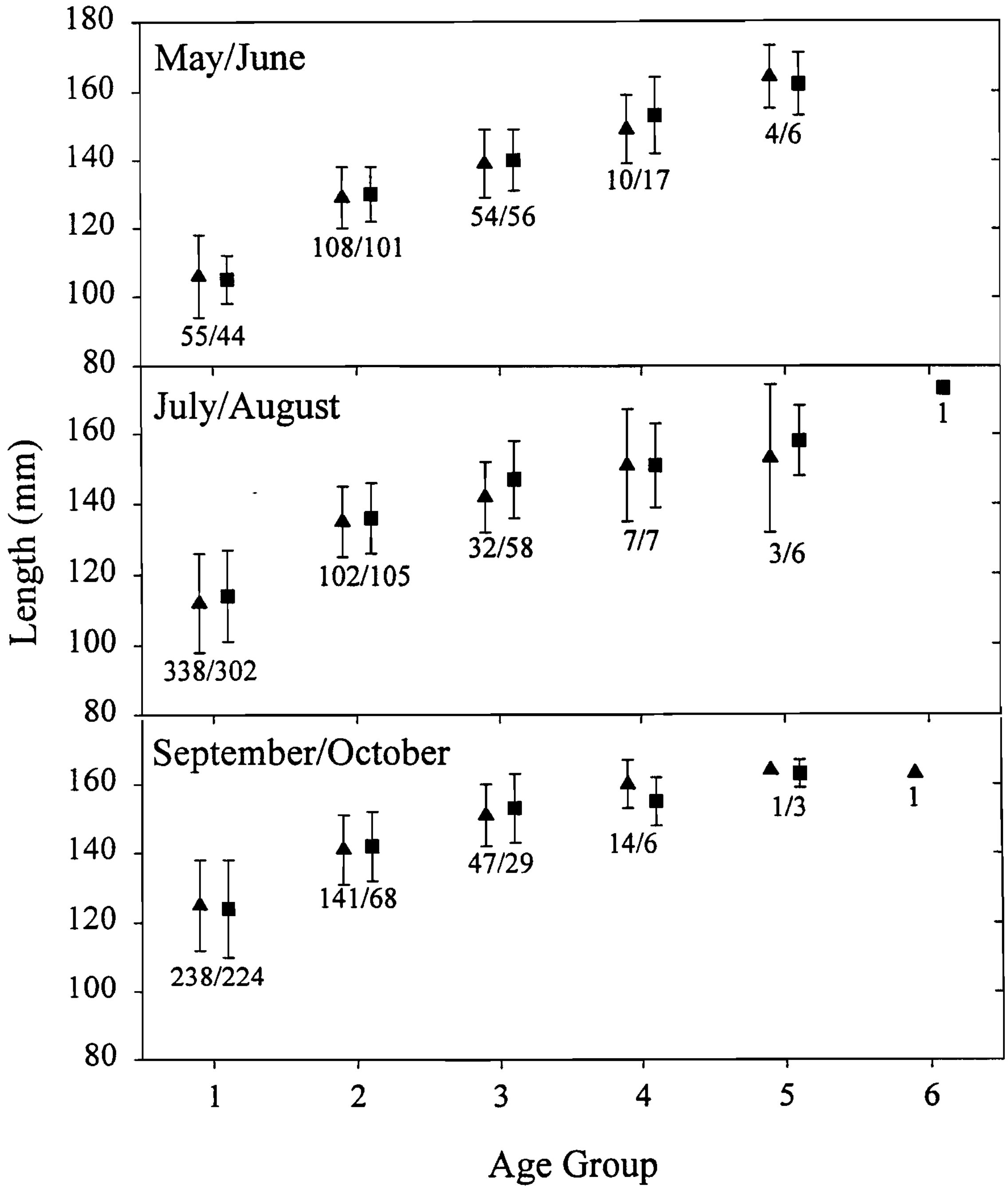
Table 5. Percent contribution to the overall spawning school fecundity derived from females of the different age groups present in 1996 and 1997 (N=165).

Age Group	Percent of Total Fish	Percent of Total Fecundity
0	0	0
1	55	48
2	26	28
3	15	19
4	3	4
5	1	1



Air
Surface Water
Temperature (°C)
30
20
10
0
-10
-20
12
10
8
6
4
2
0
1996
1997
J F M A M J J A S O N D J F M A M J J A S O N D
Date

Fig 2.



May/June
July/August
September/October
Length (mm)
Age Group
180
160
140
120
100
80
1
2
3
4
5
6
55/44
108/101
54/56
10/17
4/6
338/302
102/105
32/58
7/7
3/6
1
238/224
141/68
47/29
14/6
1/3
1

Fig 3

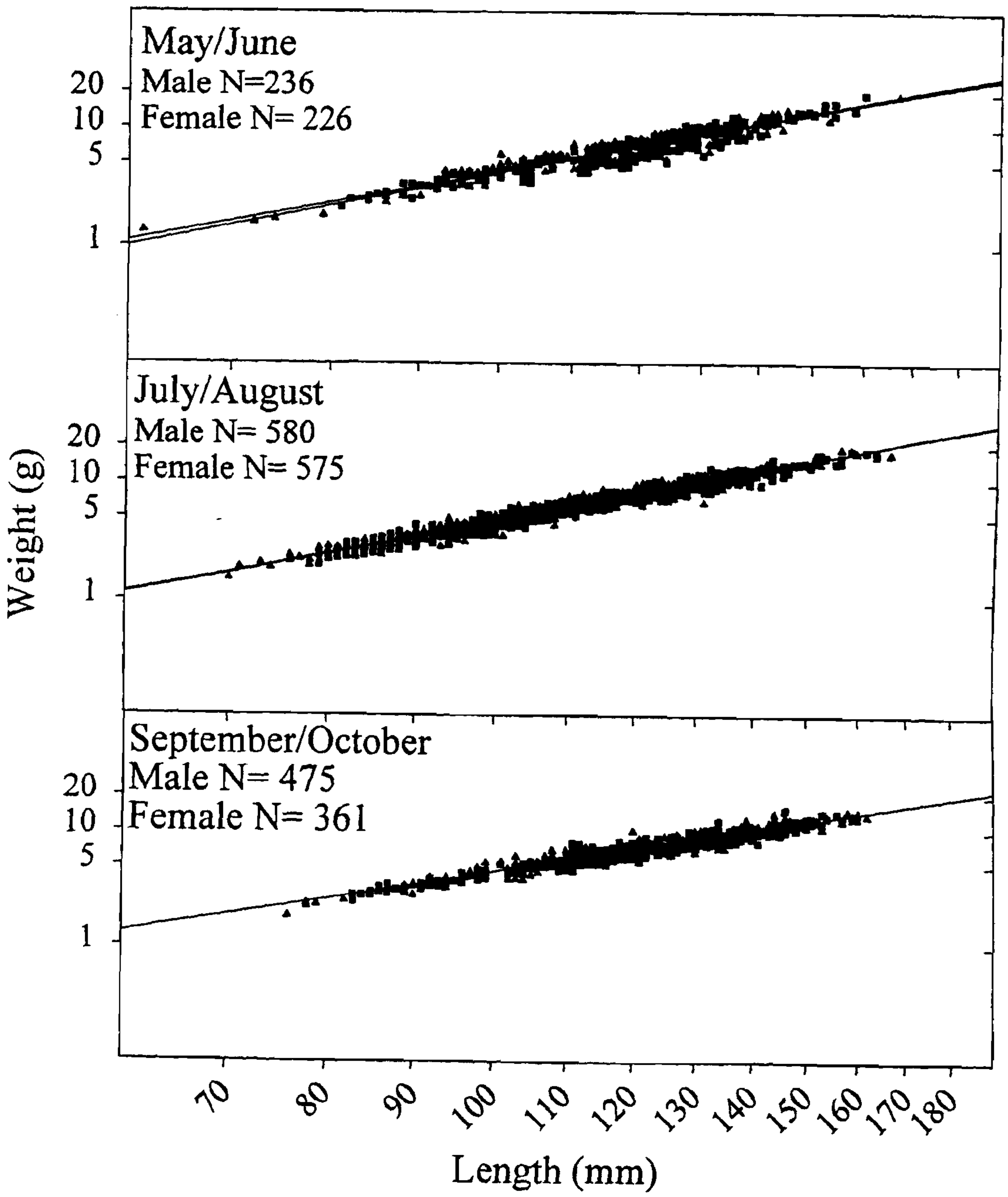

May/June
Male N=236
Female N= 226
20
10
5
1
July/August
Male N= 580
Female N= 575
20
10
5
1
September/October
Male N= 475
Female N= 361
20
10
5
1
Weight (g)
70
80
90
100
110
120
130
140
150
160
170
180
Length (mm)

Fig 4.

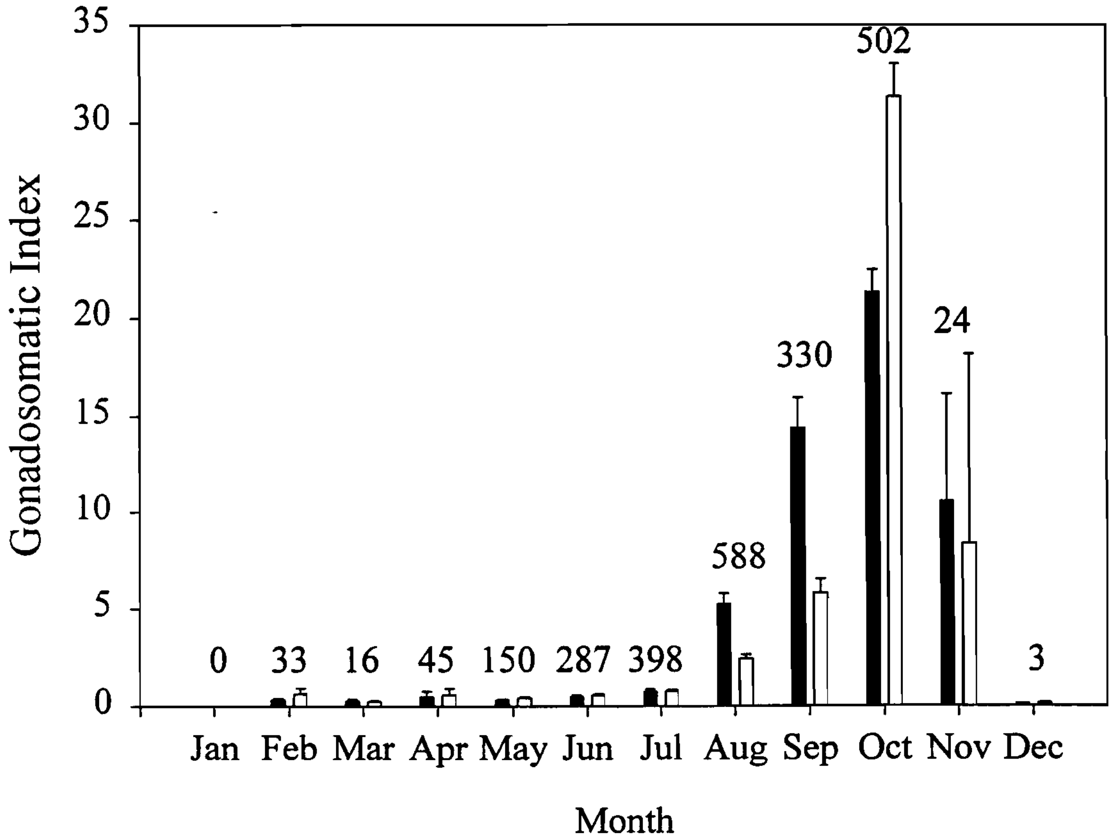
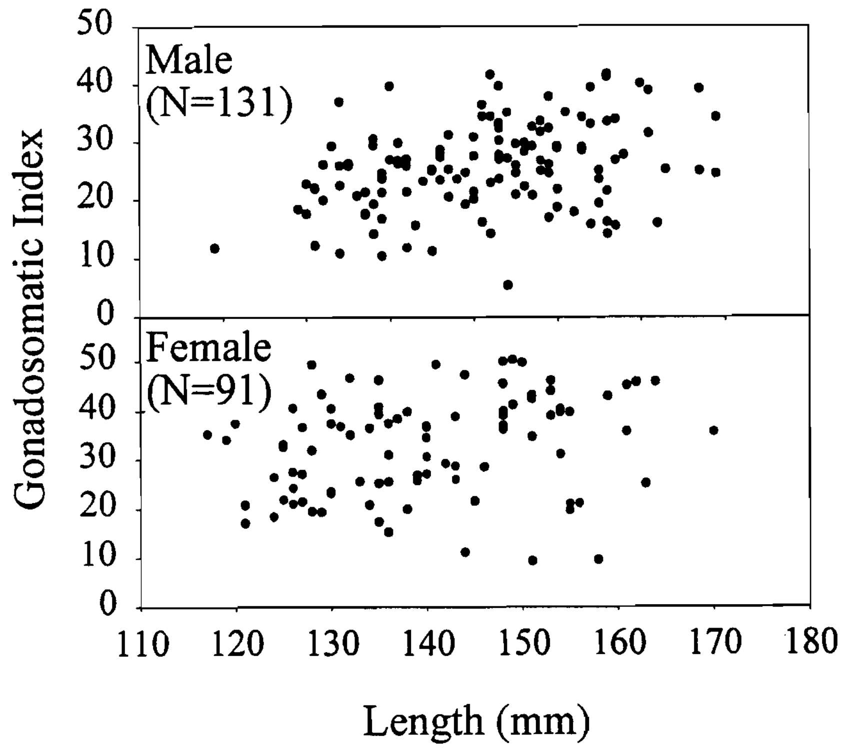
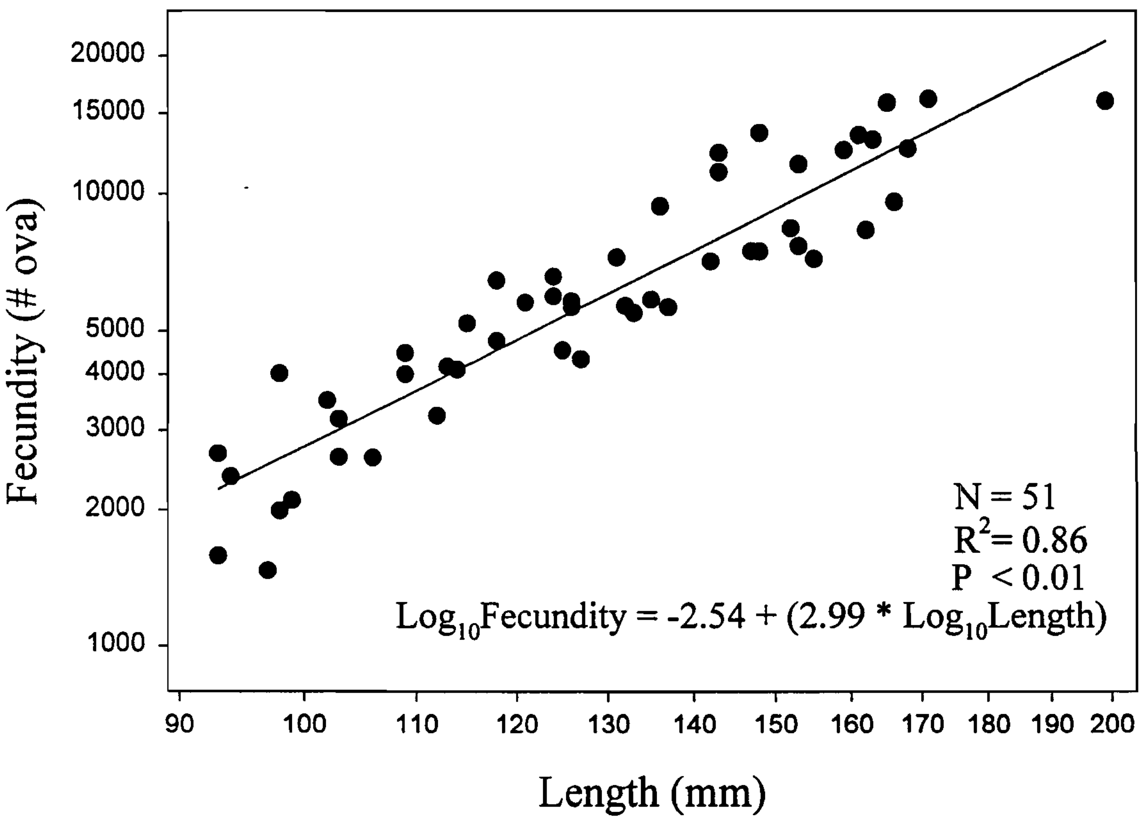

35
30
25
20
15
10
5
0
Gonadosomatic Index
0
33
16
45
150
287
398
588
330
502
24
3
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month

Fig 5.



Male
(N=131)
Female
(N=91)
Gonadosomatic Index
Length (mm)
50
40
30
20
10
0
110
120
130
140
150
160
170
180

Fig 6.



Fecundity (# ova)
20000
15000
10000
5000
4000
3000
2000
1000
90
100
110
120
130
140
150
160
170
180
190
200
Length (mm)
N = 51
R^2= 0.86
P < 0.01
Log_{10}Fecundity = -2.54 + (2.99 * Log_{10}Length)

Fig 7.

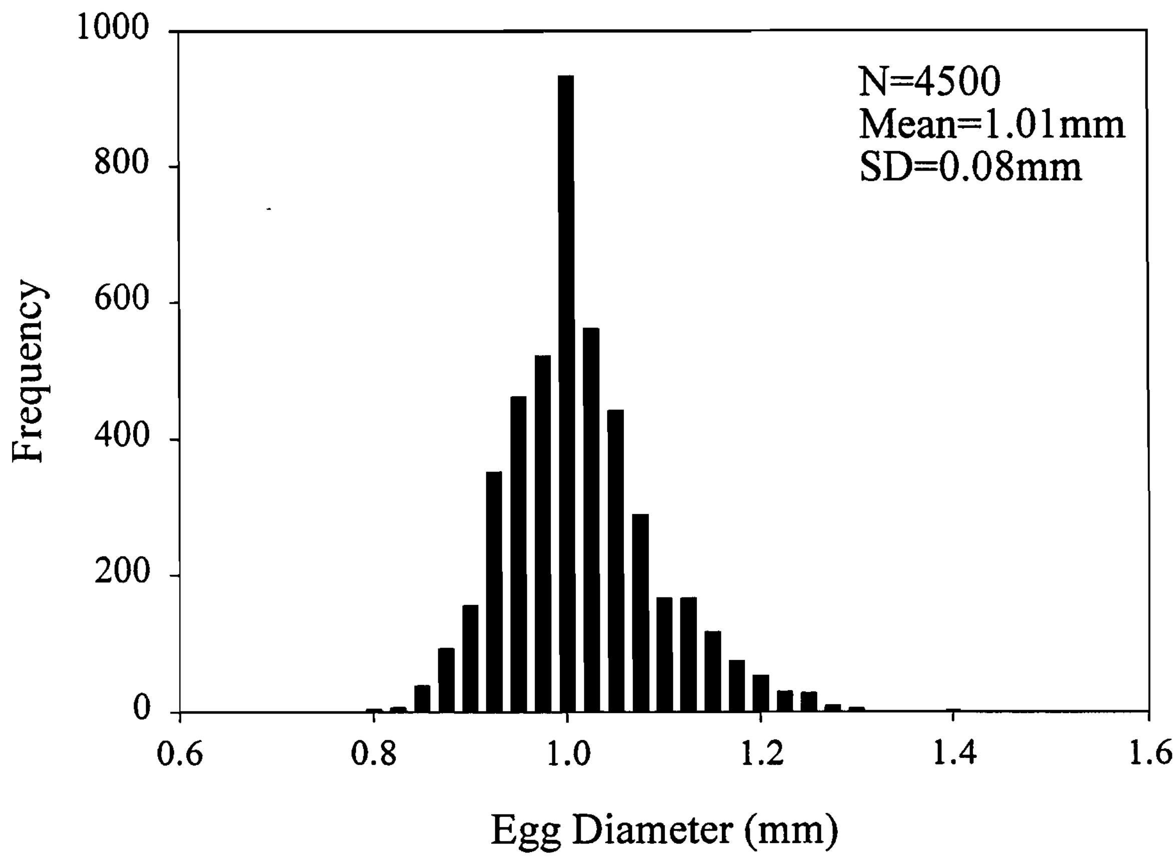

1000
800
600
400
200
0
Frequency
N=4500
Mean=1.01mm
SD=0.08mm
0.6
0.8
1.0
1.2
1.4
1.6
Egg Diameter (mm)

Fig 8.

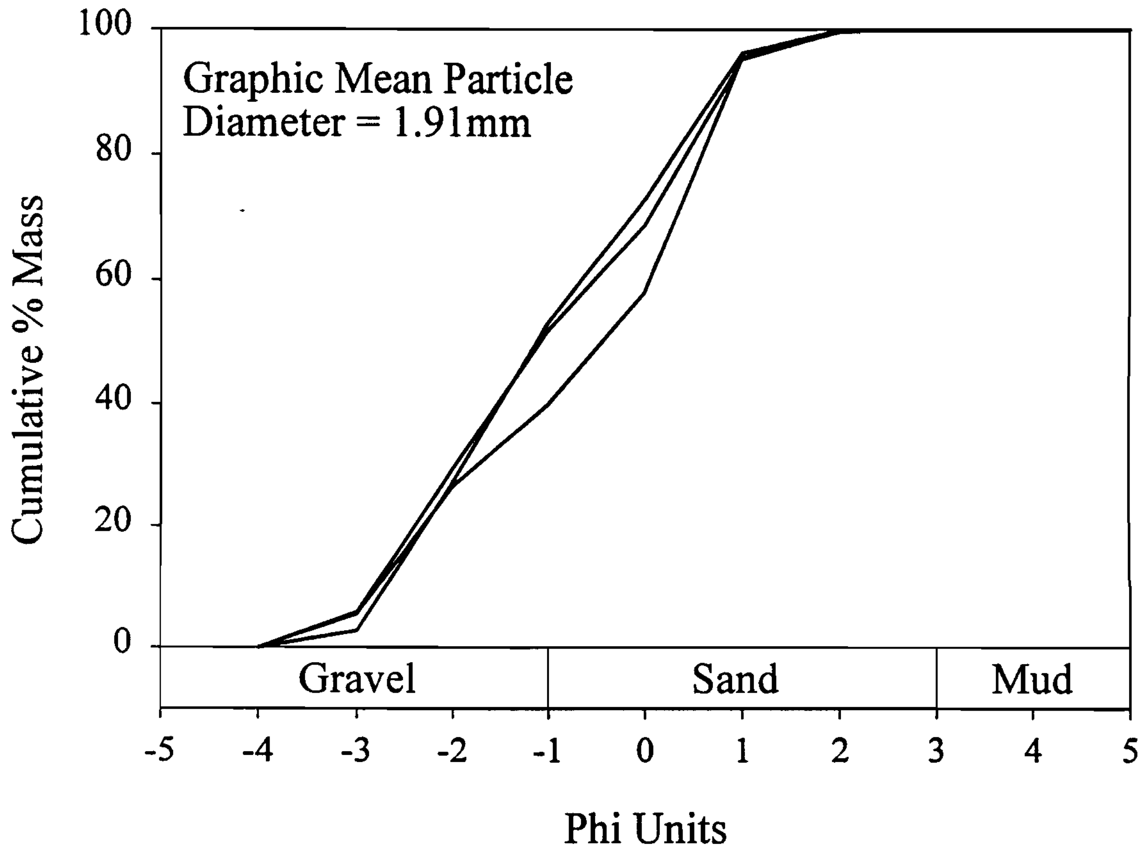

Graphic Mean Particle
Diameter = 1.91mm
Cumulative % Mass
0
20
40
60
80
100
Gravel
Sand
Mud
-5
-4
-3
-2
-1
0
1
2
3
4
5
Phi Units

Fig 9.