ECOLOGY AND DEMOGRAPHICS OF PACIFIC SAND LANCE, *Ammodytes hexapterus* PALLAS, IN LOWER COOK INLET, ALASKA

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

By

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Abstract

Distinct sand lance populations occur within the relatively small geographic area of Lower Cook Inlet, Alaska. Marked meso-scale differences in abundance, growth, and mortality existed as a consequence of differing oceanographic regimes. Growth rate within populations (between years) was positively correlated with temperature. However, this did not extend to inter-population comparisons where differing growth rates were better correlated to marine productivity. Opaque otoliths form in juvenile sand lance during their first summer coinciding with their period of rapid growth. Subsequent opaque zones are deposited during spring, in conjunction with rapidly increasing water temperatures. Areal rather than radial descriptors of otolith size provide the best relation to sand lance length. A single linear regression was insufficient to describe this relationship with separate linear regressions needed for both juveniles and adults. No sexual dimorphism was observed for sand lance in length-at-weight (gonad-free) or length-at-age. Most sand lance reached maturity in their second year. Field observations and indices of maturity, gonad development, and ova-size distribution all indicated that sand lance spawn once each year. Males mature earlier in the season than females, but females (31 %) attain a higher gonadosomatic index than males (21 %). Sand lance spawned intertidally in late September and October on fine gravel/sandy beaches soon after the seasonal peak in water temperatures. Fecundity of females (93-199 mm) was proportional to length, ranging from 1,468 to 16,081 ova. Spawned eggs were 1.02 ± 0.08 mm in diameter, demersal, slightly adhesive, and deposited in the intertidal just below the waterline. Sand lance embryos developed over 67 days through periods of intertidal exposure and sub-freezing air temperatures. Mean dry-weight energy value of sand lance cycles seasonally, peaking in spring and early summer (20.91 kJg^{-1} for males, 21.08 kJg^{-1} for females), and subsequently declining by about 25 % during late summer and fall (15.91 kJg^{-1} for males, 15.74 kJg^{-1} for females). Declines in energy density during late summer paralleled gonadal development, sand lance entering the winter with close to their minimum whole body energy content. Dry weight energy densities of juveniles increased from a minimum 16.67 kJg^{-1} to a maximum of 19.68 kJg^{-1} and are higher than adults in late summer.

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After the Sand lance digging

My long wood-handled shovel's sticking from the gravel
towards heaven still,
And there's a bucket that I didn't fill
beside it, and there may be two or three
empty bags lay upon my bow.
But I am done with sand lance-digging now.
Essence of winter sleep is on the night,
The scent of sand lance: I am drowsing off.
I cannot rub the strangeness from my sight
I got from staring at a silvery fish
I dug this morning from the exposed earth
And held before the world of shifting sands.
It wiggled, and I let it fall and escape.
But I was well
Upon my way to sleep before it fell,
And I could tell
What form my dreaming was about to take.
Magnified sand lance appear and disappear,
Head end and tail end,
And every plicae of silver showing clear.
My hand not only keeps the ache,

It keeps the pressure of the shovel-round.

I can feel the surf sway as the tide shifts.

And I can hear from within the sand

The squiggling sound

Of school on school of sand lance digging in.

For I have had too much

of sand lance-digging: I am overtired

Of the great harvest that I myself desired.

There were ten thousand thousand fish to touch,

cherish in hand, and then bag, but not let fall.

For any that struck the sand,

No matter if not not fast or slow,

Sank surely back into hiding.

As if never caught.

One can see what will trouble

This sleep of mine, whatever sleep it is.

Were he not gone,

The brown bear could say whether it's like his

Long sleep, as I describe it's coming on,

or just some human sleep.

(Apologies to Robert Frost)

Chapter 1

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

Published as:

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1.1 Abstract

We investigated seasonal maturation and spawning of Pacific sand lance in Kachemak Bay, Alaska, between May 1996 and October 1997. No sexual dimorphism was observed in length-at-weight (gonad-free) or length-at-age. Most sand lance reached maturity in their second year. Field observations and indices of maturity, gonad development, and ova-size distribution all indicated that sand lance spawned once each year. Males matured earlier in the season than females, but females (31 %) attained a higher gonadosomatic index than males (21 %). Sand lance spawned intertidally in late September and October on fine gravel or sandy beaches soon after the seasonal peak in water temperatures. Sand lance collected from elsewhere in Cook Inlet and Prince William Sound displayed similar maturation schedules. Schools were dominated 2:1 by males as they approached the intertidal zone at a site where spawning has taken place for decades. Sand lance spawned vigorously in dense formations, leaving scoured pits in beach sediments. Fecundity of females (size range: 93-199 mm) was proportional to length, ranging from 1,468 to 16,081 ova per female. About half of the overall spawning school fecundity was derived from age-group-1 female sand lance, which made up 55 % of the school by number. Spawned eggs were 1.02 ± 0.08 mm in diameter, demersal, slightly adhesive, and deposited in the intertidal just below the waterline. Sand lance embryos developed over 67 days through periods of intertidal exposure and sub-freezing air temperatures.

1.2 Introduction

Sand lance (genus *Ammodytes*) are zooplanktivorous, semi-demersal, schooling perciforms, ubiquitous in boreo-arctic regions of the North Atlantic and North Pacific oceans. Several species of *Ammodytes* have been described, but only *A. hexapterus* is known to occur in the northeastern Pacific. *A. hexapterus* dominates nearshore Gulf of Alaska and Bering Sea fish communities and comprises the principal forage fish for many marine birds and mammals (Blackburn and Anderson, 1997; Piatt and Anderson, 1996; Springer, 1991). Despite their importance in the marine ecosystem, little is known about the annual life cycle of Pacific sand lance.

Sand lance are closely linked with specific benthic habitats, alternately lying buried in the substrate and swimming pelagically in well-formed schools. Hence, nearshore aggregations are typically associated with fine gravel and sandy substrates up to and including the intertidal zone (O'Connell and Fives, 1995). Sand lance are highly selective in their use of burrowing habitat (e.g., Pinto *et al.*, 1984), but spawning habitat and substrates remain undescribed. We are aware of no year-round studies of maturation phenology for *A. hexapterus*. Most estimates of spawning phenology are based on back-calculation from the occurrence of early-stage larvae (Field, 1988). Larval surveys conducted around Kodiak Island (Alaska) suggested that sand lance spawn February-March (Rogers *et al.*,1979; Kendall *et al.*,1980). McGurk and Warburton (1992) calculated that *A. hexapterus* in the Port Moller estuary (Alaska Peninsula) spawned between mid-January and late April. Captive *A. hexapterus* collected from the Strait of

Juan de Fuca (Washington) also indicated late winter (March) spawning (Pinto, 1984). In contrast, the only direct observations of spawning condition *A. hexapterus* were made off Kodiak Island (Dick and Warner, 1982) and Cook Inlet (Blackburn and Anderson, 1997) during August to October.

To address this lack of information on Pacific sand lance reproductive biology, we initiated a year-round study in Kachemak Bay, Cook Inlet (Fig. 1-1). Local residents indicated that spawning sand lance had used some beaches in this area for decades. In this paper we provide the first estimates of maturation phenology and fecundity for Pacific sand lance based on year-round observations, and describe the spawning behavior of this species in coastal waters.

1.3 Materials and Methods

Kachemak Bay (Fig. 1-1) is near the southern tip of the Kenai Peninsula in Alaska (59.617N, 151.450W). The bay is about 38 km wide at its entrance from Cook Inlet and 62 km long. Most of the bay is relatively shallow, ranging from about 35 to 90 m, with deeper depths on the southern side. Most water entering the bay originates from the Gulf of Alaska, passing north of the Barren Islands (Burbank, 1977).

Sand lance were collected at many beaches throughout Kachemak Bay, but spawning was observed only at one site in Seldovia Bay (Raby's spit; 59.413N, 151.718W) at the southern entrance to Kachemak Bay. We also collected adult sand lance during summer

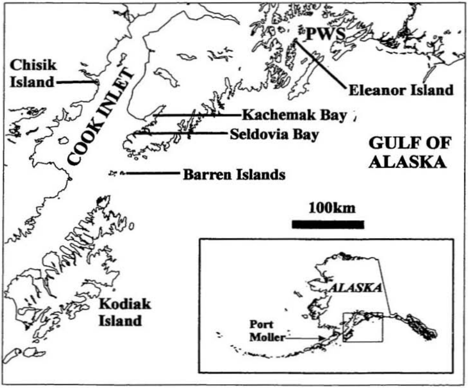

Figure 1-1: Location of sand lance collections within Cook Inlet and Prince William Sound (PWS). Spawning occurred at Raby's spit (not visible at this scale), located on the west side of Seldovia Bay.

at Chisik Island (60.142N, 152.596W) and from Eleanor Island in central Prince William Sound (60.533N, 147.600W; Fig 1-1). Water temperatures were measured at 10 minute intervals with temperature loggers (Optic StowAway version 2.02, Onset Computer Corporation) placed at 3m depth below low water (0 m) 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 with beach seines or by digging in intertidal substrates. Knotless seine nets were 44 m long and had 4 m deep, 3 mm nylon stretch mesh (sm) in the middle 15.3 m, tapering to 2.3 m deep with 13 mm sm wings. The net was set parallel to shore at a distance of 25m as described by Caillet *et al.* (1986). Samples were collected about every two weeks from May to September and once per month through the winter during 1996 and 1997. Spawning schools were caught by setting the beach seine tangent to the beach and closing the open end when sand lance swam into the net. About once a month, sand lance were collected by digging in exposed intertidal substrates during negative tides. No samples were collected in January.

Approximately 150,000 sand lance were caught in Kachemak Bay during 1996 and 1997, but only 19,000 of these were adults. A subsample of 3,189 adults was analyzed for age and sexual status. No adults were caught in seines during winter (November to March); these fish being found only in intertidal sediments. Subsampled sand lance were immediately measured (fork length in mm), blotted dry, weighed (±0.01g), individually bagged, and frozen. Gonads were excised from partially thawed individuals to prevent rupturing, particularly in later developmental stages. Gonads were identified as ovaries or testes using a dissecting microscope, weighed (±0.001g), and further classified 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 5 mm size classes from 90 to 200 mm) samples of stage-II ovaries ($n = 51$) collected in August and September. Ovaries were removed and preserved (hardened) in 5 % formalin. Before counting, ovaries were placed in small tubes and vigorously shaken with boiling water to free eggs from ovarian tissue. All eggs from both ovaries were counted individually on a partitioned petri-dish under a dissecting microscope. We also collected samples of 150 eggs from ripe (stage-III) females ($n = 30$). Spawned eggs were collected from a spawning pit on Raby's Spit (10/12/96; $n = 100$), and on subsequent visits to the spawning site (10/24/96, 11/25/96, and 12/9/96; $n = 78$). These were kept moist in seawater to prevent desiccation and analyzed immediately. Eggs were measured using an ocular micrometer at 40x magnification. Embryo development in spawned eggs was classified into six stages as described by Smigielski *et al.* (1984).

We aged a sub-sample ($n = 2,800$) of sand lance collected in Kachemak Bay and all fish from Chisik Island and Prince William Sound. Sagital otoliths were removed from the saculus after making a transverse incision behind the skull. Fibrous material was removed from otoliths; they 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 readings were inconsistent were omitted from the dataset ($n = 4$). Age designations are based on a 1 January hatch date with first year fish designated as age-0 and second year fish as age 1, up to seventh year fish as age-6.

About 3 kg of substrate containing spawned eggs was collected from each of three spawn sites on Raby's Spit. Samples were dried at 65°C to constant mass. Each sample was sieved through 16 mm, 8 mm, 4 mm, 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm 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 corresponds 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 sexual maturity on individuals of stage I - VI. All immature (stage-0) fish were omitted from this analysis. The GSI was calculated as: GSI= (gonad weight/gonad-free body weight) x 100 (Nikolsky, 1963).

To compare the length/weight relationships between sexes, we tested for differences in slope and y-intercept of linear regressions 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 50:50 sex ratio.

1.4 Results

Physical Environment:

Sea surface temperatures (SST) in Kachemak Bay during 1996 increased steadily from less than 2°C in March, plateaued at about 11°C in August, and then after a mid-September 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 about 13°C in August (Fig. 1-2). We did not observe any difference between SST's in Kachemak Bay and those at the spawning site in Seldovia Bay.

Air temperatures steadily increased from a low in January, and by April were generally above freezing. Air temperatures were usually highest in August, and declined rapidly during September (Fig. 1-2). Beginning in October, sub-freezing temperatures were common and during most of November and December, temperatures never rose above freezing.

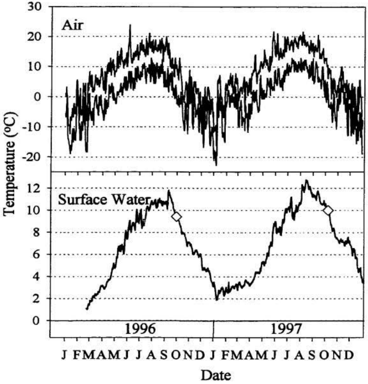

Figure 1-2: Seasonal variation in maximum and minimum air temperatures and sea surface temperatures (SSTs) at Kachemak Bay in 1996 and 1997. Diamonds on SST plots indicate onset of sand lance spawning.

Reproductive Characteristics:

Male and female lengths-at-age (Fig. 1-3) did not differ significantly for any age prior to gonadal development (May/June), during sexual maturation (July/August), or at spawning (September/October; Mann-Whitney rank sum test; all $P>0.05$). Chow tests indicated no significant differences between male and female length/somatic weight relationships during pre-gonad development, gonad development, or at spawning stages (Fig 1-4; $F^* = 0.851$, $P>0.05$; $F^* = 0.000$, $P>0.05$; $F^* = 0.067$, $P>0.05$ respectively).

No age 0 fish ($n = 419$) showed signs of developing gonads, although 11 fish (3 %) had passed from the stage-0 to stage-I phase in October. Gonads of some of the age-1 through -4 fish did not appear to develop and remained 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 age-1 (88 mm and 113 mm, respectively). The oldest maturing fish were a male and female of age-6 (163 mm and 173 mm, respectively). In September, most age-1 sand lance were developing or ripe (72 %, $n = 234$), and the proportion increased during spawning in October (97 %, $n = 230$). Some of these fish (15 %) were also spent.

These results indicate that sand lance mature at an age of about 21 months. Age-1 (50 %) and age-2 (31 %) sand lance dominated spawning schools. Ages-3, -4, -5, and -6 made up 14 %, 4 %, 1 %, and <1 %, respectively, of the overall school composition.

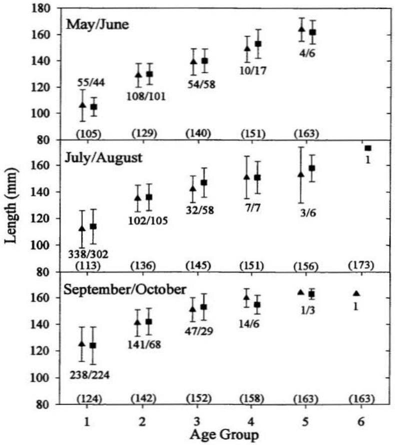

Figure 1-3: Lengths-at-age (±1 sd) of adult male (▲) and female (■) sand lance collected before gonad development (May and June), during sexual maturation (July and August), and while ripe and spawning (September and October) in Kachemak Bay. Numbers are samples sizes (M/F) and numbers in parentheses are overall mean lengths for sexes combined.

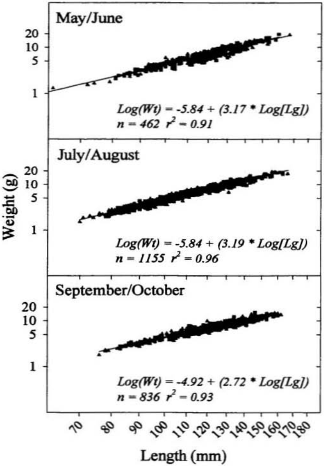

Figure 1-4: Regression plots of length (mm) against gonad-free body weight (g; Log_{10} transformed data) for male (▲) and female (■) sand lance. Sand lance were collected before gonad development (May and June; $n = 236$ male, 226 female), during development (July and August; $n = 580$ male, 575 female), and while ripe and spawning (September and October; $n = 475$ male, 361 female). Regression equations are for sexes combined.

From February to May, most sand lance were in the resting phase, and a few fish were still recovering from spawning (Table 1-1). Gonadal recrudescence began in June and July, when a small proportion (6-9 %) of fish displayed developing gonads. Gonadal development increased rapidly (Fig. 1-5) in August as sea surface temperature reached maximal levels (Fig. 1-2). Spawning-condition gonads developed as SST's declined from seasonal peaks and spawning occurred when these SST's reached approximately10°C. Gonadosomatic indices (GSI) indicated that males developed earlier than females, but ultimately attained a lower index at spawning (21 % males, 31 % females). GSI's differed significantly among sexes in both 1996 and 1997 (Mann-Whitney rank sum tests; all $P< 0.01$). Maximum GSI for individual males and females were 47 % and 55 % respectively. Overall GSI for males and females from spawning schools (Table 1-2) were similar in 1996 and 1997, with no significant difference detected for either sex between years (Mann-Whitney rank sum tests; $P>0.5$).

By the end of November, 67 % of sand lance collected ($n = 24$) were in post-spawning condition (spent, recovering, or resting). No fish in spawning condition were found after this time (Table 1-1). All sizes of adult sand lance were grouped for analysis based on no significant relationship existing between GSI and body length of ripe fish collected in October (Fig. 1-6).

Table 1-1. Percentage of *A. hexapterus* classified into maturity stages by month for fish collected in Kachemak Bay during 1996/1997. Maturity stages were I=resting, II=developing, III=ripe, IV=running, V=spent, VI=recovering.

Month	Sex	Maturity Stage						Total No.
		I	II	III	IV	V	VI	
Feb	Male	95	-	-	-	-	5	21
	Female	75	-	-	-	-	25	12
Mar	Male	100	-	-	-	-	-	8
	Female	100	-	-	-	-	-	8
Apr	Male	92	-	-	-	-	8	24
	Female	95	-	-	-	-	5	21
May	Male	100	-	-	-	-	-	69
	Female	99	-	-	-	-	1	81
Jun	Male	93	7	-	-	-	-	173
	Female	93	7	-	-	-	-	160
Jul	Male	91	9	-	-	-	-	210
	Female	94	6	-	-	-	-	239
Aug	Male	39	57	4	-	-	-	301
	Female	59	41	-	-	-	-	287
Sep	Male	14	45	39	2	-	-	167
	Female	26	67	7	-	-	-	163
Oct	Male	1	7	44	41	7	-	310
	Female	1	4	47	43	5	-	195
Nov	Male	20	-	27	27	-	27	15
	Female	-	-	11	11	22	56	9
Dec	Male	-	-	-	-	-	100	1
	Female	-	-	-	-	-	100	2

Table 1-2. Mean gonadosomatic index (±95 %CI) for male and female sand lance collected in October of 1996 and 1997 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)

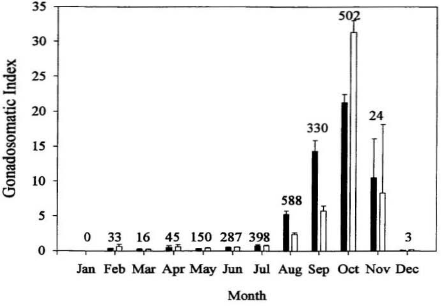

Figure 1-5: Seasonal changes in male (■) and female (□) gonadosomatic indices (±95 % confidence intervals) for sand lance collected in Kachemak Bay between May 1996 and October 1997. Numbers are sample sizes for each month.

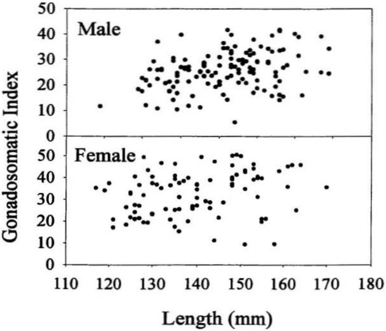

Figure 1-6: Scatter plot of male ($n = 131$) and female ($n = 91$) GSI's against body length for ripe (stage-III) sand lance collected during October from spawning schools in Kachemak Bay during 1996 and 1997.

Indices of maturity revealed (Table1-3) that fish collected from Eleanor and Chisik Islands were maturing at time of capture (July and August respectively). Based on a mean resting GSI (calculated from stage-I fish collected during April through 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; all $P<0.01$). These results were similar to those found for the Kachemak Bay population (Table 1-1, Fig. 1-5).

During the resting and developing stages (Stage-I and -II) in spring and summer, sex ratios were relatively even. During the spawning period however, ripe and spawning males predominated (Table 1-4). 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 ranged from 1,468 to 16,081 ova per female for sand lance ranging from 93 to 199 mm fork length (Fig. 1-7). Fecundity was significantly correlated with body length ($P<0.01$). About half of the overall spawning school fecundity was derived from age-group-1 fish, which made up 55 % of the school by number (Table 1-5). Ages 1-3 accounted for 95 % of the total fecundity. Ova diameter exhibited a unimodal distribution in each of the 30 females investigated, and overall (Fig. 1-8). Each egg typically contained a single bright yellow oil globule (in 2 females about 5 % of ova contained two oil globules).

Table 1-3. Maturation status of *A. hexapterus* at two collection areas in southcentral Alaska.

Location	Dates Collected	Sex	*n*	Stage	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 1-4. Sex ratios of sand lance collected in Kachemak Bay at different maturity stages during 1996 and 1997.

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

Table 1-5. Percent contribution to the overall spawning school fecundity derived from females of the different age groups present in October 1996 and 1997 (*n*=165).

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

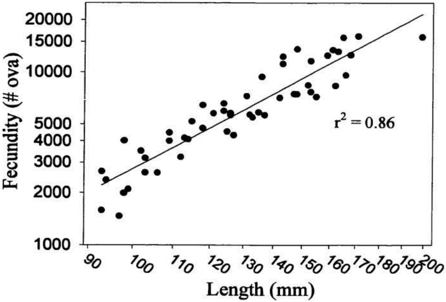

Figure 1-7: Regression of fecundity on body length (mm; $\log_{10}$ transformed data) for pre-spawning (stage-II) female sand lance collected from Kachemak Bay ($n = 51$, $r^2 = 0.86$, $P < 0.01$; $\log_{10}$fecundity = -2.54 + (2.99 • $\log_{10}$length).

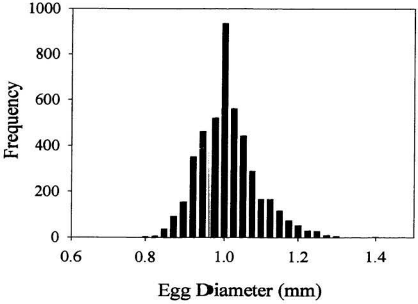

Figure 1-8: Size distribution of eggs found in ovaries of 30 ripe female sand lance collected from spawning schools in Kachemak Bay during 1996 and 1997 ($n = 4500$, mean = 1.01 mm, SD = 0.08 mm).

Spawning Habitat and Timing:

Spawning occurred in a shallow open bay on the southern, sheltered side of Raby's spit, within 100m of routinely used sand lance burrowing habitat. Local residents indicated that sand lance (local name: "needlefish") had spawned at this site during the month of October for at least the past 20 years. No spawning was observed on the outer exposed side of the spit in 1996 or 1997. The substrate of the spawning area consisted of coarse sand and gravel (Fig. 1-9) of which about 20 % was shell fragments.

During 1996, sand lance were first observed spawning at 18:45 on 30 September (1.5 hours after high tide, 3 days after spring tides, and 3 days prior to the next neap tide) when SSTs were 9.4°C. Initially, we observed laterally compressed schools (about 1-8 m in length and up to 1 m across) of adult sand lance at high tide moving back and forth along the length of the beach, within 5 m of shore, and in less than 1 m of water. Spawning was preceded immediately by sand lance moving back and forth along a 20m stretch of beach (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 adopted this formation. Sand lance were again observed spawning at 18:25 (0.5 h after high tide) on 1 October, at 18:30 (2.5 h after low tide [neap]) on 5 October, and at 08:20 (2.5 h before high tide) on 6 October. Demersal eggs were found intertidally in shallow (< 50 mm) depressions ("pits") up to 0.4m in diameter from about 2 –5 m above the low tide line. The pits were formed at the time of spawning by sand lance as they

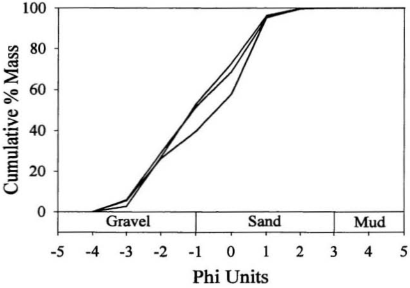

Figure 1-9: Graphical representation of sand lance spawning substrate in Seldovia Bay (median particle diameter = 1.9 mm). Phi units = -$\log_2$ particle diameter (mm).

schooled near the bottom. Sand lance continued to spawn in these shallows, and new pits containing eggs were observed through 12 November (spring tide). During morning low tides we periodically found egg-filled pits that had not been noted the previous evening, indicating that sand lance also spawn at night.

We first observed spawning in 1997 during the neap tide series on 8 October at 16:00 (2.5 h after low tide) when SSTs were about 10.0°C. Spawning was observed again on 9 October from 17:00 to 20:00 (mid-flood tide), 10 October at 08:30 (1.5 h before high tide), and 11 October 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 and they were not caught in beach seines until the following spring.

Sand lance eggs are cryptic and blend in well with small fragments of shell and gravel. This prevented us from making an accurate assessment of egg distribution over the entire beach. Eggs were observed on the sand surface of spawning pits at a density of up to 7 cm^{-2} and within the substrate to a depth of about 30 mm. Eggs were demersal, slightly adhesive, translucent, and almost spherical in shape (mean diameter 1.02 mm, SD= 0.08 mm, 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 (<2 d old; Smigielski *et al.*, 1984) were collected on 12 October, 1996 from a freshly formed spawning pit. An incomplete blastodermal cap characterized these eggs. Yolk cloudiness was not observed at this or subsequent stages. At the same pit on 24 October, eggs were at stage 3 and no blastodermal cap was evident. By 25 November, egg density at this pit had declined dramatically, and only nine eggs were 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 3.8 mm in length. Eyes were pigmented (0.18 mm diameter), myomeres were visible along most of the embryo's length, a beating heart was observed, and a developing alimentary canal was visible. On 9 December 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 this spawning pit were all part of the 12 October spawning, development over the observed 58 days (until 9 December, when stage-6 embryos were observed) occurred in an average sea and air temperature of 6.4°C and -2.5°C, respectively.

1.5 Discussion

Second year spawning is common among other species of sand lance, occurring in *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 our study, only a single age-group-0 fish (immature) was observed within the spawning schools, although exclusively age-0 schools were caught elsewhere in the bay at the same time. The maximum life-span for *A. hexapterus* was 7 years, which is also the upper age found for *A. tobianus* (O'Connell and Fives, 1995). For fish populations such as those studied here, wherein a single cohort at age-1 contributes 50 % of the population fecundity, any large variations in recruitment are, in turn, likely to have large and immediate effects on population size.

Gonadal development was initially slow and differed between the sexes. No sexual dimorphism was observed for mature sand lance, either in their length-to-weight ratios or length-at-age relationship. We can therefore attribute gender differences in the GSI to variable rates of gonadal development independent of differences in body size between sexes. Gonads maturated rapidly in August as adult sand lance leave the nearshore zone (Robards *et al.*, unpubl. data). During August and September, mean GSIs for males are higher, indicating that males mature more quickly and earlier during the reproductive season. Initial maturation in *A. dubius* is also quite slow (Winters, 1983), and *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 differential rates of maturation between males and females. While testes of *A. hexapterus* peaked in development earlier, ovaries eventually attained a greater relative weight. Gonad maturation time for *A. hexapterus* was comparable to that found for fall-spawning Atlantic sand lance (*ca.* 3 months). In contrast, winter- and spring-spawning Atlantic sand lance require from 5-7 months to reach maturity (Reay, 1970).

Our data (maturity stages, GSI) indicate that *A. hexapterus* spawns only once per year in late fall. The presence of a few recovering fish as late as May (Table 1-1) indicates that some individuals may spawn later in the winter (as in *A. dubius*, Winters, 1983). However, we found no evidence for different spawning groups within the population, i.e., one that also spawns during the spring (as in *A. tobianus*; O'Connell and Fives, 1995). *A. hexapterus* from Chisik Island and Prince William Sound (PWS) also appear to spawn during the fall.

Sand lance (*A. hexapterus*) spawned in Kachemak Bay during a 1-3 week period in October of 1996 and 1997. In the northwest Atlantic, *A.dubius* and *A. americanus* spawn over a period of about 3 months in late fall and early winter (Winters, 1989). In Japan *A. personatus* spawns over a 1.5 month period (Okamoto *et al.*, 1989). Although our observations indicate a shorter window of spawning within Kachemak Bay, spawning may occur over a longer period throughout the entire Gulf of Alaska region.

Male sand lance outnumbered females by about 2:1 in the nearshore zone during spawning, but not during earlier stages of development. This has also been observed for *A. marinus* (Macer, 1966; Gauld and Hutcheon, 1990). A higher ratio of males at spawning may indicate that they remain in the spawning area over a longer period [similar to capelin (*Mallotus villosus*; Templeman, 1948)]. Meanwhile, slower-developing females that are not fully mature probably remain buried in sediments until ready to spawn.

We found a unimodal size distribution of ova in the developing ovaries of Pacific sand lance. Unimodal size distributions of ova in *A. hexapterus* (Pinto, 1984), *A. dubius* (Scott, 1972a), and *A. marinus* (Macer, 1966) are suggestive of single-batch, once yearly spawning in these species. Egg diameters for *A. hexapterus* in Kachemak Bay were comparable with other observations for this species [e.g., about 1 mm for Murman sand lance (Andriyashev, 1954) and a mean of 1 mm for sand lance in the Pacific Northwest (Pinto, 1984; Penttila, 1995)]. Williams *et al.* (1964) and Pinto (1984) both observed that eggs contained one oil globule. However, we occasionally observed multiple oil globules, which does occur infrequently in this genus (Garrison and Miller, 1982).

Fecundity of *A. hexapterus* from Kachemak Bay ranged from 1500-16,000 ova. This is similar to fecundity observed in most other sand lance species and populations: Japanese *A. hexapterus* (Hashimoto, 1984); *A. americanus* (Westin *et al.*, 1979); *A. marinus* (Macer, 1966); and *A. tobianus* (O'Connell and Fives, 1995). However, Nelson (1990) reported lower values for *A. dubius* and Hashimoto (1984) greater values for *A. personatus.*

Pits formed in the substrate during spawning probably result from females boring through loose gravel, and whilst doing so discharging eggs into the surrounding medium as reported for *A. tobianus* (McIntosh and Masterman, 1897). We observed no significant clumping (Smigielski *et al.*, 1984) or cloudiness (Pinto, 1984) of spawned sand lance eggs as reported in laboratory studies. Although slightly adhesive, the eggs did not appear to remain on the beach in large numbers over the course of incubation. Perhaps loose adherence to gravel over time allows eggs to be dispersed by tidal action both interstitially and within the water column. Adherence of eggs to gravel and fine substrates would help prevent desiccation when they are exposed to air at low tides.

The egg development time demonstrated in this study is longer than total incubation times reported for other species of sand lance at similar water temperatures. Smigielski *et al.* (1984) and Inoue *et al.* (1967) reported maturation times of 39 days at 7°C for *A. americanus*, and 33 days at 6.2°C for *A. personatus*, respectively. Judging from a mid-stage 6 development, Kachemak Bay sand lance were at 88 % development on 9 December; suggesting a 67 day total incubation period. Thus, hatching should have occurred on or around December 17. Our total incubation times were similar to the 62 days incubation period reported for *A. americanus* eggs at 2°C (Smigielski *et al.*, 1984). We suspect that the long incubation period observed in Kachemak Bay results from exposure of eggs to very cold air temperatures during the approximately 12 hours of intertidal exposure each day (Fig. 1-2). McGurk and Warburton (1992) reported comparable results for *A. hexapterus* in the Port Moller estuary on the Alaskan Peninsula (45-94 days of 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 surf smelt (*Hypomesus pretiosus*; Loosanoff, 1937), and to increased oxygenation for Pacific herring (*Clupea pallasi;* Jones, 1972).

During the spawning period, sand lance appeared to spawn with little regard for tidal stage or time of day. However, spawning may occur more frequently at high tide as evidenced by the high position of spawning pits on the beach. Penttila (1995) observed a similar vertical spread of intertidal spawning pits, i.e., within a few meters of the high water line with egg deposition in the top 30 mm of gravel.

We found no indication that sand lance move above the high waterline as described for grunions (*Leuresthes spp.*, Thompson, 1919) and capelin (Templeman, 1948). Reports of sand lance found above the waterline in the intertidal zone (e.g., Dick and Warner, 1982) may result from sand lance being stranded on low angled beaches by 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 (e.g., Beston, 1928).

Spawning of *A. hexapterus* occurred on fine gravel and sandy beaches as is typical of this species (Penttila, 1995). Results of our 2-year study and long-term observations of local residents suggest that sand lance use the same sites for spawning year after year for decades. Penttila (1995) also documented repeated use of spawning sites. Perennial use of the same beaches has direct implications for the conservation of this species and for the predators that rely on sand lance. Sand lance may be particularly vulnerable to pollution of coastal areas and development of beach-front habitats. It would be useful to establish a quantitative library of beach substrates to help identify potential spawning habitat for this key species.

Our study did not allow us to determine if Pacific sand lance are obligate intertidal spawners. Penttila (1995) collected subtidal samples in the vicinity of fresh intertidal sand lance spawn and did not find any evidence for coincident subtidal spawn deposition. We found no published references to offshore spawning by *A. hexapterus*, unlike for capelin that 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). Our results corroborate with Reay (1970) who suggested sand lance spawn within their normal range, rather than migrating to special spawning areas. *A. tobianus* is the only other sand lance species known to spawn intertidally (McIntosh and Masterman, 1897). *A.marinus* (Reay, 1970), *A. americanus* (Westin *et al.*, 1979), *A. dubius* (Winters, 1983), and *A. personatus* (Kimura *et al.*, 1992) all spawn subtidally in nearshore areas and/or on shallow offshore banks.

Late fall spawning in the intertidal is unusual. Eggs and larvae are exposed to harsh winter conditions leading to prolonged incubation and hatch periods. Pelagic sand lance larvae appear in late March and April (Haldorson *et al.*, 1993), well in advance of the spring phytoplankton bloom or the herbivorous copepod maximum. This is unlike many other fish larvae which occur much later (May) in approximate synchrony with maximum zooplankton densities (Haldorson *et al.*, 1993). The ecological significance of this timing is thought to be adaptive in situations where prey availability is unpredictable (Haldorson *et al.*, 1993). However, other factors of ecological significance may be to 1) utilize the full period of prey abundance, 2) avoid inter-specific competition, and 3) develop at a time of low predator abundance (Wright and Bailey, 1996). Hence, adaptations such as delayed and variable egg development, larval feeding before absorption of yolk sac (Yamashita and Aoyama, 1985), reduced metabolism at cold temperatures (Haldorson *et al.*, 1993), and resultant reduction in caloric requirements (Buckley *et al.*, 1984) all appear to increase the survivorship and chance of sand lance larvae being able to fully-capitalize on the spring plankton bloom.

Chapter 2

Changes in proximate composition and somatic energy content for Pacific sand lance relative to maturity, season, and location

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2.1 Abstract

The body condition and energy density of adult Pacific sand lance cycles seasonally. Mean dry-weight energy value peaked in spring and early summer (20.91 kJg^{-1} for males, 21.08 kJg^{-1} for females), and subsequently declined by about 25 % during late summer and fall (15.91 kJg^{-1} for males, 15.74 kJg^{-1} for females). Declines in energy density during late summer paralleled gonadal development. Gender differences in energy density (males < females) were only apparent from August to October. Adult sand lance spawn in October entering the winter with close to their minimum whole body energy content. Juvenile sand lance exhibited a relatively constant protein to lipid ratio until they reached 80 mm fork length. Thereafter, relative proportions of protein remained constant while lipid proportions increased significantly. Dry weight energy densities of juveniles increased from a minimum 16.67 kJg^{-1} to a maximum of 19.68 kJg^{-1} and are higher than adults in late summer. The food value of adult sand lance to predators varies markedly within seasons. However, maximum energetic value to predators coincides with important feeding periods for marine mammals, fish, and seabirds.

2.2 Introduction

Pacific sand lance *(Ammodytes hexapterus)* are common in many nearshore areas of the Gulf of Alaska and Bering Sea and are a principle prey for many marine birds, commercial fish, and marine mammals (Field, 1988; Springer, 1991; Piatt and Anderson, 1996; Blackburn and Anderson, 1997; Robards *et al.*, 1999c). Despite the food web importance of sand lance for higher-trophic level predators, seasonal or geographic variability in their nutritional value is poorly known. Such knowledge is critical for a better understanding of trophic interactions in the North Pacific environment.

Adult sand lance have been considered as a high-quality forage fish (Anthony and Roby, 1997; Van Pelt *et al.*, 1997). However, the value of sand lance as prey changes as a function of their size and energy density (kJg^{-1} wet mass) which is determined primarily by lipid content (percent dry mass; Anthony and Roby, 1997). Lipid content varies with season, location, gender, age, feeding rate, and activity level (Soofiani and Hawkins, 1985; Anthony and Roby, 1997). Marked seasonal variation in lipid content has been documented for other forage fish including an Atlantic sand lance (*A. marinus;* Hislop *et al.*, 1991), capelin, (*Mallotus villosus;* Jangaard, 1974), herring (*Clupea harengus*; Paul *et al.*, 1998) and several freshwater species (Bryan *et al.*, 1996). Seasonal energy storage is typically related to environmental production cycles (Dygert, 1990), as a consequence of intense feeding during secondary production blooms. With sand lance, however, these cycles of energy storage may be out of phase and lead physiological processes such as spawning, which occurs about four months after the strong spring primary production bloom (Damkaer, 1977; Dick and Warner, 1982).

In this paper we examine energy storage in relation to sexual development and winter dormancy of adults, plus energetic changes during development in juveniles.

2.3 Methods

Sand lance were sampled from Kachemak Bay in Lower Cook Inlet, Alaska (Fig. 2-1) where we were concurrently studying breeding seabirds. We collected sand lance from intertidal substrates (by random digging at known habitat beaches on extreme low tides) and by beach seine (Robards *et al.*, 1999c). Adult sand lance were collected in February, and then monthly from June to November in Kachemak Bay. We confirmed adults collected in October were in pre-spawning condition by the appearance of gonads and field observations.

Sand lance were measured (fork length, mm), blotted dry, weighed (±0.01 g), individually bagged, and frozen. Gonads were excised from partially-thawed individuals to prevent rupture. Ovaries and testes were identified using a dissecting microscope and weighed (±0.001 g). Gonads were retained with the rest of the body for proximate analysis.

Figure 2-1. Location of Kachemak Bay and Lower Cook Inlet, Alaska.

Sagittal otoliths were collected ventrally to the spinal column and anterior to a transverse incision made at the skull's posterior margin of the skull (visible through the skin). Otoliths were cleaned of fibrous tissue, and stored dry in Epindorf tubes for later analysis. The left otolith was mounted on a microscope slide in the sagittal plane using CrystalBond thermal resin. Age determinations were based on the otolith interpretations of Macer (1966) and Scott (1973). Based on January 1 hatch date (Dick and Warner, 1982), first year sand lance were designated as age group-0, second-year sand lance as age group-1, up to the seventh-year as age group-6. These age groups were divided into juveniles (group-0; sexually immature) and adults (groups 1-6; sexually mature; Robards *et al.*, 1999a).

Adult sand lance were processed individually for proximate composition, whereas juveniles were analyzed in batches of 10 (5 mm size classes) because of their small size. Two replicates were made for each size class. Sand lance were dried at 60 °C to constant mass and reweighed to determine water content. Lipid content of dry samples was determined by solvent extraction using a soxhlet apparatus and a solvent system of 7:2 hexane/isopropyl alcohol (Radin, 1981). Lean dry samples were ashed in a muffle furnace to determine ash-free lean dry mass (AFLDM). AFLDM is 94 % protein (Montevecchi *et al.*, 1984), and hereafter referred to as protein. Energy density (kJg^{-1} dry mass) and energy content (kJ/fish) were calculated from proximate composition (water, lipid, ash-free lean dry matter, and ash), using published energy equivalents (lipid = 39.3 kJg^{-1}, protein = 17.8 kJg^{-1}; Schmidt-Nielsen, 1997). In response to frequent calls for standardization of results (e.g., Montevecchi and Piatt, 1984; Hislop *et al.*, 1991; Van Pelt *et al.*, 1997) we report results as kJg^{-1} dry mass. All dry mass: wet mass relationships passed through the origin. We include slope parameters to allow calculation of kJg^{-1} wet mass in Table 2-1.

Table 2-1. Regression parameters for the fresh wet weight-dry weight relationship of adult and juvenile sand lance collected in Lower Cook Inlet during 1996.

Stage	*N*	r^2	Slope
Adult	243	0.87	0.25
Juvenile	14	0.99	0.25

A modified monthly gonadosomatic index (GSI; Nikolsky, 1963) was used to quantify seasonality of reproduction for stages 1 through 6 where GSI = (gonad weight/gonad-free body weight) x 100. Condition of sand lance in relation to wet, dry, lipid, and protein mass were calculated using a modified Fulton condition factor (K') proposed by Bagenal and Tesch (1978) where $K' = \text{mass} \times 10^7/(\text{length})^3$. We used the Student t-test to compare energetic values between sexes, time periods, and regions.

2.4 Results

Seasonal Variation:

Sand lance collected in February were emaciated with no visible fat reserves. By June and July, sand lance had observable mesenteric fat, which then declined until spawning when no mesenteric fat was observed. Proximate composition analyses confirmed these visual observations. Lipid content declined from July through November and February

(Table 2-2). As expected (Van Pelt *et al.*, 1997) energy density (kJg^{-1}), was inversely correlated with water content (water content = 59.9 – [0.54 x total energy density], r^2= 0.81, P<0.01, n = 267).

Energy densities for individual adults ranged from a high of 22.79 kJg^{-1} dry mass in June to a low of 14.23 kJg^{-1} dry mass in February. Mean energy densities declined by about 25 % from a peak in July (20.91 kJg^{-1} males, 21.08 kJg^{-1} females) through to November, with lowest values observed in February (15.91 kJg^{-1} males, 15.74 kJg^{-1} females). Energy density declined significantly (P<0.001), 13.1 % for females and 16.4 % for males between July and October, as gonadal development (GSI) increased (Fig. 2-2), in preparation for spawning. Energy densities for females were significantly (P<0.001) higher than for males in August, September, and October. Energy densities were further reduced by 8.6 % in females and 4.7 % in males in October; corresponding to the onset of spawning.

Pooled samples from June and July (no significant difference between months, sexes, or stage of development; P's > 0.05) only exhibited a weak positive relationship between fish length and energy density (r^2= 0.13, slope = 0.05). The percent of water content remained relatively stable from June to October then declined precipitously during spawning for both sexes (Fig. 2-3). Dry mass remained relatively constant during early summer before declining in August (males) and September (females). Protein biomass increased slowly during summer, but declined markedly to about 60 % of peak levels

Table 2-2. Mean (SD) monthly proximate composition for adult male and female sand lance collected in Lower Cook Inlet during 1996.

Month	Sex	N	Age (yrs)	Length (mm)	GSI (%)	Dry Mass (g)	% Water[†]	% Lipid[‡]	% Protein[‡]	% Ash[‡]	Energy Density (kJg^{-1})[‡]
February	M	13	2.2	127 (7.7)	0.4 (0.2)	1.06 (0.24)	79.6 (1.8)	6.7 (4.8)	74.5 (3.5)	14.2 (1.9)	15.91(1.35)
	F	9	2.2	125 (8.6)	0.6 (0.5)	1.02 (0.25)	79.5 (2.1)	6.8 (6.1)	73.5 (5.8)	15.4 (2.4)	15.74 (1.47)
June	M	21	2.3	137 (6.0)	0.3(0.2)	2.44 (0.55)	73.6 (1.5)	24.6 (4.2)	62.0 (3.6)	9.1 (1.1)	20.70 (1.05)
	F	21	2.3	138 (4.9)	0.6 (0.2)	2.49 (0.33)	73.1 (1.4)	24.9 (4.1)	61.3 (3.7)	9.3 (2.0)	20.69 (1.07)
July	M	9	2.2	140 (9.8)	0.6 (0.4)	2.84 (0.90)	73.4 (1.7)	25.5 (2.8)	61.2 (4.1)	8.6 (0.84)	20.91 (0.44)
	F	9	2.2	140 (6.9)	0.9 (0.3)	2.89 (0.46)	72.7 (1.2)	27.2 (1.8)	58.4 (3.3)	8.1 (0.64)	21.08 (0.34)
August	M	22	1.9	142 (11.5)	10.6 (3.5)	2.79 (0.77)	74.2 (0.8)	19.3 (2.5)	67.3 (2.4)	9.4 (0.46)	19.56 (0.66)
	F	21	2.0	144 (10.6)	5.4 (1.7)	3.05 (0.83)	72.0 (0.9)	22.8 (2.1)	65.4 (2.5)	8.6 (0.35)	20.60 (0.49)
September	M	27	1.9	132 (9.9)	25.1 (5.4)	2.08 (0.46)	75.7 (0.8)	16.6 (3.1)	69.3 (3.1)	10.7 (0.60)	18.87 (0.77)
	F	19	1.9	140 (11.0)	10.5 (5.1)	2.89 (0.73)	73.0 (1.0)	20.4 (3.4)	67.0 (3.3)	9.1 (0.60)	19.95 (0.80)
October	M	27	2.1	144 (13.9)	26.4 (7.5)	2.47 (0.75)	78.9 (1.0)	10.2 (2.3)	75.8 (2.7)	12.1 (1.8)	17.49 (0.60)
	F	32	1.9	138 (14.2)	30.9 (10.1)	2.44 (0.81)	77.7 (1.9)	12.8 (2.9)	74.7 (2.3)	10.3 (0.98)	18.32 (0.79)
November	M	6	1.2	119 (12.2)	5.4 (8.2)	1.02 (0.35)	80.5 (1.5)	9.9 (2.6)	71.0(1.7)	13.5 (1.7)	16.51 (0.74)
	F	7	1.7	129 (10.4)	6.6 (15.2)	1.32 (0.26)	79.9 (1.4)	10.3 (3.8)	70.1 (3.1)	14.9 (3.6)	16.51 (1.26)

[†] Of fresh wet mass

[‡] Of dry mass (wet values = dry value x [1-proportion of water])

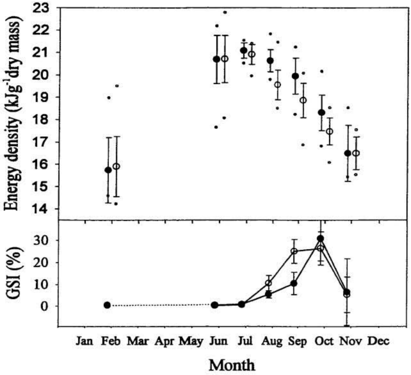

Figure 2-2. Monthly energy density (kJg^{-1} dry mass) and gonadosomatic index (GSI) for adult male (○) and female (●) sand lance collected in Kachemak Bay. Error bars are means ± standard deviation; small circles are range of data.

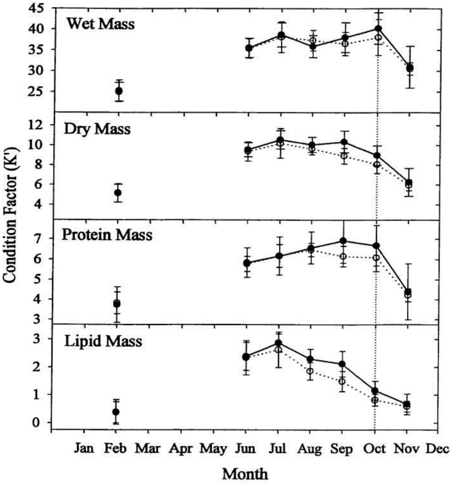

Figure 2-3. Seasonal condition factor (K') for male (···○···) and female (—●—) sand lance collected in Kachemak Bay. Error bars are means ± one standard deviation. Vertical dashed line indicates time of spawning (Robards *et al.* 1999a).

during spawning. Lipid reserves peaked in July and gradually declined to minimal levels by November. Lipid content declined more rapidly for males than females. Lipid declines paralleled gonad development (Fig. 2-2), and for both events, males preceded females by about one month.

Juvenile Sand Lance:

Energy density of juvenile sand lance ranged from 16.67 kJg^{-1} at 55-59 mm to 19.68 kJg^{-1} at 85-89 mm (Table 2-3). The largest juveniles collected in August were similar in energy density (per g) to adult sand lance, although approximately one sixth the dry mass. Juvenile energy densities were inversely correlated with water content (water content = 67.8 – (0.64 x total energy density), r^2=0.92, P<0.01, n=14). Relative energetic content of sand lance between 55 and 80 mm indicated similar contributions from lipid and protein (Fig. 2-4). Relative protein content steadily increased between 55 and 80 mm (Fig. 2-5). Further growth was not associated with proportional increases in protein, but with relative lipid content, which increased by over 100 % between fork-lengths of 80 and 90 mm.

2.5 Discussion

Adult sand lance display a seasonal cycle of energy accumulation with a 31 % increase in energy density between February and June. Peak energy values reported here were similar to those for Atlantic sand lance (e.g., Hislop *et al.*, 1991; Mårtensson *et al.*, 1996). The seasonal increase corresponds to the spring plankton bloom in April and May

Table 2-3. Mean proximate composition for juvenile sand lance collected in Lower Cook Inlet during 1996.

Size Gp. (mm)	Rep.[†]	Length		Dry Mass (g)	% Water[‡]	% Lipid[††]	% Protein[††]	% Ash[††]	Energy Density (kJg^{-1})[††]
		mm	S.D.						
55-59	1	56.7	0.5	1.15	79.6	5.9	80.6	14.3	16.67
	2	57.7	0.5	1.25	79.1	7.0	79.9	14.0	16.99
60-64	1	61.8	0.4	1.52	79.4	8.5	78.3	14.4	17.28
	2	62.9	0.4	1.52	79.7	7.2	78.8	15.1	16.85
65-69	1	67.8	0.3	2.05	78.9	6.3	80.3	14.3	16.78
	2	67.1	0.4	2.01	78.9	7.8	78.9	14.5	17.10
70-74	1	72.7	0.4	2.51	78.3	8.3	78.8	14.1	17.28
	2	71.8	0.4	2.42	78.8	7.3	79.6	14.2	17.03
75-79	1	77.7	0.4	3.22	78.0	7.6	79.5	13.9	17.15
	2	76.8	0.3	3.13	78.1	8.7	78.6	13.9	17.40
80-84	1	82.2	0.5	3.89	76.9	11.2	76.9	13.4	18.09
	2	82.5	0.4	4.26	75.8	14.7	74.2	13.0	19.00
85-89	1	86.8	0.5	4.98	76.0	15.7	73.4	13.0	19.23
	2	86.9	0.3	4.95	75.3	17.5	71.9	12.9	19.68

[†] Each replicate consists of a pooled sample of 10 fish.

[‡] Fresh wet mass

[††] Dry mass (wet values = dry value x [1-proportion of water])

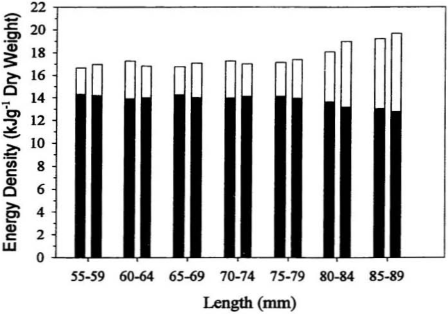

Figure 2-4. Total energy densities (kJg^{-1} dry mass) of juvenile sand lance collected monthly in Kachemak Bay. Two bars are shown for each month sampled; replicates 1 and 2. Relative energy contributions of protein (black bar) and lipid (white bar) are shown.

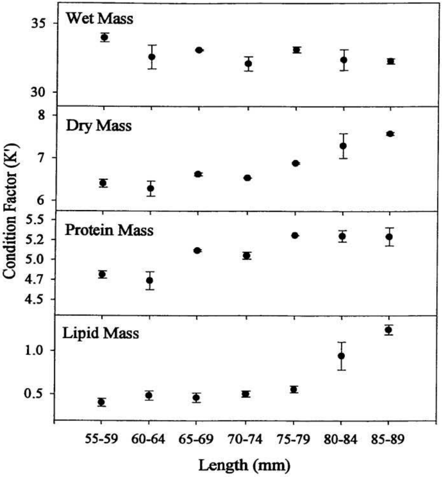

Figure 2-5. Relationship between size and condition factor (K') for juvenile sand lance collected in Kachemak Bay. Error bars are mean and range of the two samples for each size-class.

(Larrance *et al.*, 1977), like another Alaskan species, yellowfin sole (*Pleuronectes asper*; Paul *et al.*, 1993). Lipid content of other sand lance species also increases rapidly prior to summer (e.g., *A. personatus*, Sekiguchi, 1977; and *A. marinus*, Hislop *et al.*, 1991). Energy density was not significantly related to fish length although a weak positive relationship was observed (r^2=0.13). This appears normal for many marine prey species where the relationship is generally weak ($r^2_{adj} = 0.35$, or less; Lawson *et al.*, 1998).

Female sand lance expend more energy than males in reproduction due to the production of eggs, which requires greater accumulation of reserves in the feeding season (Love, 1980). In the laboratory, Pinto (1984) observed significant loss of lipid prior to spawning by sand lance. Many other species (such as cod) loose about 30 % of their energy during, rather than prior to spawning (Smith *et al.*, 1990). Whereas gonad production may contribute to the summer energetic loss, sand lance also reduce their feeding, spending more time buried as evidenced by late summer declines in catch-per-unit-effort and frequency-of-capture (Winslade 1974; Robards *et al.*, 1999c). As noted for Japanese sand lance (*A. personatus*; summarized in Field, 1988) adult sand lance may also compete for the same zooplankton prey species with recruiting juveniles in the nearshore. Feeding may be further reduced during the final stages of maturation due to sheer volume of gonads within the body cavity, reducing the potential volume of the gut (as observed in gadids [Love, 1980] and herring [*Clupea harengus*; Bradford, 1993]). Prior to spawning, *A. hexapterus* gonads were turgid and completely filled the body cavity. Captive *A.*

personatus survived for over two months unfed indicating adult sand lance can endure long fasts (Inoue et al., 1967).

Greater rates of lipid loss were not observed for either sex at spawning compared to the prior three months. However, protein content declined markedly. Lipids comprise only 20 % (dry weight) of sand lance ovaries (Tocher and Sargent, 1984) and protein is the principle energy source for gonadal development (Love, 1970). After spawning, sand lance enter the winter season in poor condition. In cooler temperatures, without plentiful food supplies (Damkaer, 1977), and little reserves for metabolism, sand lance remain dormant in nearshore substrates through the winter (Robards, *pers. obs.*). During winter dormancy metabolism is reduced (Quinn and Schneider, 1991) and gut evacuation times are greatly prolonged (Ciannelli, 1997). During early winter, remaining lipids are presumably mobilized in response to the low food availability (Love, 1980), prior to utilization of protein reserves for metabolic needs (Maddock and Burton, 1994). Sand lance are regarded as a high protein fish, as protein generally constitutes greater than 15 % of wet mass (Stansby, 1976). The proportionally high protein content may be an adaptation to low food intake periods. Utilization of some of this protein (Maddock and Burton, 1994) would provide an additional buffer to cover metabolic needs during fasting. Protein content varied seasonally by over 14 % (dry mass) in adult sand lance from Kachemak Bay.

Accounting for this seasonal variability in energy content is critical when comparing relative food values, and modeling trophic energy flow. Excluding *Myctophidae* which have unusually high lipid content, the seasonal variation we observed was as profound as the inter-specific variation described by Van Pelt *et al.* (1997) for 12 different forage species and described by Anthony and Roby (1997) for 11 species. Consequently, sand lance over the period of about 4-5 months span the range from a relatively high to comparatively low value forage fish.

Juvenile sand lance less than 80 mm in length apparently channel lipid reserves into somatic growth. Larger fish are probably less susceptible to predation (Parker, 1971). Subsequently, juveniles rapidly develop lipid reserves in lieu of somatic growth as observed for *A. personatus* (Sekiguchi, 1977), although this species makes the transition at a shorter length (45-50 mm). Therefore, although energy density of juveniles is initially relatively low, by late summer values exceed those of adult males and match those of adult females. Juveniles have far less protein to buffer against starvation than adults, and late-summer accumulation of lipid reserves may therefore be critical for winter survival.

Dramatic seasonal variations in proximate composition has also been documented in various other forage species e.g., herring, Pacific cod (*Gadus macrocephalus*) and capelin (Montevecchi and Piatt, 1984; Smith *et al.*, 1990; Mårtensson *et al.*, 1996; Lawson *et al.*, 1998). However, contrasting interspecific life histories result in markedly different cycles of energy content. For example, adult capelin and herring are seasonal feeders that build up fat stores to sustain them during winter months. Energetic values peak during winter and fall for capelin and herring, respectively, frequently reaching values twice that found during the summer (Montevecchi and Piatt, 1984; Lawson *et al.*, 1998; Paul *et al.*, 1998). A prime reason for this difference is that sand lance are fall-spawners, whereas capelin and herring spawn in the spring, having overwintered with developing gonads. Ecologically, fall spawning and winter hatch (Dick and Warner, 1982) is adaptive to producing larvae prior to the spring plankton blooms. Consequently, juveniles can feed when planktonic prey are most abundant and thus grow rapidly to minimize the suite of predators that can catch them while storing energy for the less productive summer. Overwintering first-year sand lance may need this advantage, to allow enough growth to facilitate a storage medium for lipid reserves. This is in contrast to juvenile herring for which fall energy content in the neighboring Prince William Sound is markedly higher (5.7 kJg^{-1} wet mass; Paul *et al.*, 1998), despite metamorphosing much later compared to sand lance (July vs. March-May, respectively; Smigielski *et al.*, 1984). Juveniles were the only age-class of sand lance caught pelagically during winter months (in low numbers) during 1996 and 1997 in Kachemak Bay (*Robards et al.*, 1999c) or in the North Sea (Macer, 1966) indicating that at least some individuals continue foraging during this period.

The multitude of summer predators for which sand lance are an important prey species such as breeding seabirds, migratory whales, and commercial fish (Field, 1988) all gain maximum energetic returns from sand lance during June and July. Other important Gulf of Alaska forage species such as herring and capelin which loose up to 80 % of their fat during spring spawning (Jangaard, 1974) provide only about two-thirds the energetic return compared to sand lance in early summer (Anthony and Roby, 1997). However, as energy content of sand lance declines during the fall and winter, reprovisioning with capelin and herring would provide a much greater energy return to predators, particularly during winter whilst sand lance is dormant for long periods. Although in July, juveniles are relatively poor prey compared to adults (by a factor of 18:1; Table 2-4), by August due to accumulated lipid reserves they only differ by a factor of 6:1. Large schools of juveniles that dominate the nearshore during September and October when adults are scarce (Blackburn and Anderson, 1977; Robards *pers. obs.*) may be a significant early-winter prey.

Table 2-4. Energy value (kJ/fish) based on mean adult and juvenile fish sizes collected by beach seine[1] in Lower Cook Inlet during 1996.

Life-Stage	July				August			
	N	Wet Wt (g)	Length (mm)	Energy per Fish (kJ)	N	Wet Wt. (g)	Length (mm)	Energy per Fish (kJ)
Adult	300	6.89	120	36.16	1095	7.45	121	36.47
Juvenile	54	0.51	55	2.15	114	1.38	73	5.92

[1] Robards (unpubl. Data)

Chapter 3

Growth and abundance of Pacific sand lance under differing oceanographic regimes

3.1 Abstract

Dramatic changes in seabird and marine mammal populations in the Gulf of Alaska have been linked to shifts in abundance and composition of forage fish stocks over the past 20 years. The relative value of specific forage fish stocks to predators under temporally changing oceanographic regimes is also expected to vary. We inferred potential temporal responses in condition, growth, and abundance of a key forage fish, sand lance by studying across spatially different oceanographic regimes. Marked meso-scale differences in abundance, growth, and mortality existed as a consequence of these differing regimes. Growth rate within populations (between years) was positively correlated with temperature. However, this did not extend to inter-population comparisons where differing growth rates were better correlated to marine productivity. Sand lance were least abundant and grew slowest at the warmest site (Chisik Island), an area of limited habitat and low food abundance. Abundance and growth were highest at the coolest site (Barren Islands), an area of highly productive upwelled waters. However, these sand lance were predominantly juvenile due to lack of sheltered winter habitat. Sand lance at two sites located oceanographically between the Barren Islands and Chisik Island (inner- and outer-Kachemak Bay) displayed correspondingly intermediate abundance and growth. Resident predators at these sites are presented with markedly different numbers and quality of this key prey species. Our results suggest that at the decadal scale, Gulf of Alaska forage fish such as sand lance are probably more profoundly affected by changes in abundance and quality of their planktonic food, than by temperature alone.

3.2 Introduction

Pelagic fishes are often subject to large-scale fluctuations in productivity thought to relate to oceanographic variability (Dragesund *et al.*, 1997; Francis *et al.*, 1998). Causal links between oceanic processes and fish are often difficult to disentangle. Most studies have used correlation between time series of population states in attempts to link physical processes with fish productivity (Francis *et al.*, 1998). An alternative strategy is to study biological processes across physical regimes, which may vary spatially. Lower Cook Inlet in the Gulf of Alaska (Fig. 3-1) provides the opportunity to study a key semi-pelagic fish, sand lance (genus *Ammodytes*), under very different oceanographic conditions (Trasky *et al.*, 1977).

Sand lance are ubiquitous in boreo-arctic coastal regions of the North Atlantic and North Pacific. Within this area sand lance constitute a key prey species for many vertebrate predators including seabirds, fishes, and marine mammals (Field, 1988; Willson *et al.*, 1999). *Ammodytes hexapterus* is the only sand lance species known to occur in the northeastern Pacific (Field, 1988). However, despite their importance in the food web and the growing interest in modeling ecological processes (Chambers and Miller, 1995), little is known about *A. hexapterus* age structure, growth, relative abundance, or how environmental processes influence these parameters. Differences in quality, size, and abundance of sand lance in different areas would present predators with markedly different returns. This may be particularly important for species such as seabirds that carry a limited number of prey items back to their nestlings.

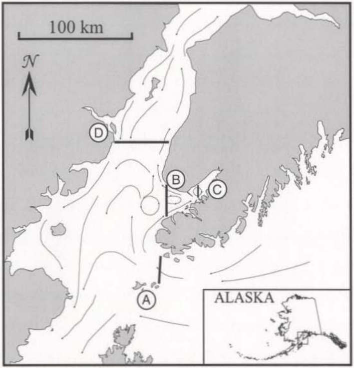

Figure 3-1. Location of study sites in Lower Cook Inlet showing the prevailing currents (based on Trasky *et al.*, 1977). Study sites are A - Barren Islands, B - outer-Kachemak Bay, C – inner-Kachemak Bay, D - Chisik Island. CTD transects are shown as dark lines.

Growth is dependent on both abiotic and biotic factors such as temperature, food availability, competition, and predation (Nelson and Ross, 1991). As a result, populations inhabiting different oceanographic regimes may exhibit differing growth and survival rates. In this paper, we investigate the relative importance to growth and survival of an abiotic factor (temperature) in comparison to a biotic factor (food availability).

Growth comparisons between different sand lance populations at a standard age were made using back-calculations from sand lance otoliths. Otoliths are also found in guts, scats, and regurgitations of marine piscivores and are often used to identify both species and size of prey items (e.g., Lidster *et al.*, 1994). In this paper we contribute the first published relation between otolith size and *A. hexapterus* length, and provide validation for timing of annulus formation. We investigate age and regional differences in the somatic-otolith relationship in relation to local oceanographic regimes, and discuss the degree of potential error for trophic studies that assign single regressions covering several distinct populations.

3.3 Oceanographic Setting

The Alaska Coastal Current passes north of the Barren Islands, leading to intense upwelling of cold, nutrient-rich waters onto the shallow shelf of southeast Cook Inlet (Burbank, 1977; Fig 3-1). The well-mixed nutrient-rich water passes into outer-Kachemak Bay and subsequently past the 7 km Homer Spit into the more estuarine inner-

Kachemak Bay interrupted by two semipermanent gyres (Trasky *et al.*, 1977; Fig. 3-1). The gyre system acts to increase the residence time of water in outer-Kachemak Bay and contributes to the early development of a large spring and summer plankton population (Feder and Jewett, 1987). Water exits along the north side of Kachemak Bay before circulating in a counter clockwise direction within Cook Inlet and past Chisik Island (Fig. 3-1). Waters are warmest and most estuarine around Chisik Island, having received significant glacier-fed freshwater input from large rivers at the head of Cook Inlet (Burbank, 1977; Feely and Massoth, 1982) and from the adjacent glacially-fed bay to the west (Fig. 3-1).

The highly turbid estuarine water around Chisik Island supports low chlorophyll-a concentrations, resulting in a restricted primary productivity of approximately one tenth the amount found at the other sites (Larrance *et al.*, 1977; Feder and Jewett, 1987). Secondary production peaks in May in Kachemak Bay, then declines throughout the summer. Waters around Chisik and the Barren Islands show a steady rise in productivity through the summer peaking in the fall (lower peak compared to Kachemak Bay) with lowest secondary productivity at Chisik Island (Damkaer, 1977).

3.4 Materials and Methods

Oceanographic Parameters:

The most detailed descriptions of local oceanography (Larrance et al., 1977) and productivity (Damkaer, 1977; Feder and Jewett, 1987) were published over a decade ago. Although we were unable to conduct a concurrent multi-year seasonal investigation of oceanography at all sites, we collected sea-surface-temperatures (SSTs) and conductivity, temperature, and density (CTD) profiles to establish if the previously described patterns of oceanography within Cook Inlet were consistent with current conditions. Nearshore water temperatures were measured at 10-minute intervals with temperature loggers (Optic StowAway version 2.02, Onset Computer Corporation). Loggers were placed at 3 m below low water (0 m) in inner-Kachemak Bay (permanent placement) and at outer-Kachemak Bay, Chisik Island, and the Barren Islands (July only). A (CTD) recorder (Seabird Electronics Inc, SBE-19 SEACAT profiler) was used to collect vertical temperature and salinity profiles along a transect adjacent to each study site (Fig. 3-1) during July, 1997.

Sand Lance Sampling Strategy:

Fish were collected by beach seine and random digging in intertidal substrates. Beach seines utilized a 44m long, knotless nylon stretch-mesh net. Dimensions were 4 m deep, 3 mm mesh for the middle 15.3 m, tapered to 2.3 m deep with 13 mm mesh in the wings. The net was set parallel to shore at a distance of 25 m as described by Cailliet *et al.* (1986). Inner-Kachemak Bay was sampled approximately every two weeks from May to

September and once per month through the winter during 1996 and 1997. The other Cook Inlet sites were sampled approximately every two weeks from late June until September during 1996 and 1997.

An 8-liter sample of sand lance was collected from each seine catch. Sand lance collected from exposed substrates were less numerous, therefore, all individuals were retained for measuring. Stratified samples (5-mm size classes, 15 fish per class) were collected each month to develop seasonal age/length keys. Based on our small size classes and reasonable sample size this method was expected to produce reliable length estimates (Macdonald, 1987; Devries and Frie, 1996). However, adult sand lance are only sporadically caught in seines (Robards *et al.*, 1999c) and are only available in intertidal substrates on infrequent negative-tides. This precluded the comparison of size-at-age between populations for specific time periods. Therefore, to allow inter-area comparisons, we calculated size at end of the annual growing season via otolith interpretations. Samples of sand lance otoliths were collected between July and September, 1997 (post-annulus formation; see otolith validation) from all sites to allow length-at-age and growth curves to be calculated. All sand lance were immediately measured to fork length (mm), blotted dry, weighed (±0.01 g), individually bagged, and frozen. No significant gender differences exist for mean length at age of *A. hexapterus* (Robards *et al.*, 1999a) or *A. dubius* (North Atlantic; Nelson and Ross, 1991), thus age data for each sex were combined for growth analyses.

Otolith Protocol:

In response to frequent requests for validation of otolith methodology (e.g., Devries and Frie, 1996) we have included these results within our methods. Otoliths were removed, cleaned of fibrous material, bonded to microscope slides using crystalbond thermal resin, and aged on two separate occasions. Otoliths from all age classes of sand lance had clearly defined bands and only 12 of the 3909 otoliths (<1 %) provided inconsistent readings or were unreadable due to indistinct ring formation. Age designations are based on a 1 January hatch date (Dick and Warner, 1982, Robards *et al.*, 1999a), with first year sand lance designated as group-0, second year as group-1, up to seventh year (group-6). The terms juvenile and adult are used to describe group-0, and group-1 or older respectively.

Total and within-annulus areas, as well as annular diameters were measured using a video imaging system (Optimas) connected to a Nikon Optiphot-2 stereo microscope using 40x magnification. A consistent measurement precision (evaluated by measuring all rings on the same age-3 otolith 30 times) of ± 0.006 mm^2 was found using this system. No significant difference was found between left and right otolith area on an initial random sample of 100 fish (paired t-test; P=0.94). However, left otoliths were recorded throughout the investigation for consistency. More of the variation between sand lance fork-length and otolith size was accounted for by the regressions using otolith area, rather than for diameter (Table 3-1). We therefore used the areal measure of otolith size for analysis at all sites.

Table 3-1. Relationship between root otolith area and fork-length for sand lance collected in lower Cook Inlet. Relationship is expressed as: Fork length = (a•root otolith area) + b.

Location	Age	n	a	b	r^2	r^2 for otolith diameter: fork length relationship
Chisik Island	Juvenile	74	82.16	10.46	0.77	-
Chisik Island	Adult	205	85.26	5.86	0.90	-
Kachemak Bay	Juvenile	168	73.95	21.80	0.92	0.87
inner-Kachemak	Adult	362	110.6	-14.30	0.88	0.84
outer-Kachemak	Adult	481	103.7	-6.36	0.83	0.74
Barren Islands	Juvenile	101	89.40	15.90	0.87	-
Barren Islands	Adult	67	68.90	24.90	0.48	-

Morrow (1979) and Scott (1973) have described sand lance otoliths in detail. Their basic descriptions correspond with our findings. Otoliths are basically almond shaped, the long axis is nearly straight, sulcus opens at the extreme tip and doesn't exceed 70 % of the otolith length, the excisura major is present, and the excisura minor absent. However, otoliths were highly variable in finer scale details. Differing degrees to which otoliths were elongated or laterally compressed was the most obvious form of variation and probably relates to why area rather than diameter better described the otolith size/body size relationship. Other common differences included missing, wide, augmented, or forked rostrums, and a greater or lesser degree of scalloping along the otolith periphery.

In 11 sand lance, one of the two otoliths appeared decalcified with a ragged periphery and semi-translucent appearance. In none of these cases were both otoliths in this state.

Validation of Opaque Band Formation:

Adult sand lance deposit opaque material as a ring on their otoliths over a period of about 4 months in the spring (Fig. 3-2). Duration of opaque material deposition appears to coincide with the approximately 7 °C rise in water temperatures between February and June (Fig. 3-2). Timing is distinctly different to juveniles, which form an opaque otolith throughout their first summer (Fig. 3-2), which is subsequently referred to as the otolith core. A translucent periphery is then formed until first annulus formation the following spring. Therefore, although deposition of opaque material is an annual event, it does not precisely represent age. Core formation in juveniles (L_0), based on a January 1 hatch date (Dick and Warner, 1982; Robards *et al.*, 1999a) represents an age of 7.5 months. Opaque ring formation in adult fish ($\geq L_1$) indicates an age of $L_x + 0.25$ years where x represents age-group.

Relation of sand lance length to otolith size:

A statistically significant difference ($P<0.05$; Fig. 3-3) existed between slopes and intercepts of adult and juvenile regressions at all sites. The inner-Kachemak Bay sample had enough overlap in sizes between adults and juveniles to allow statistical comparison between adults and juveniles with the same sized otolith. Adult sand lance were significantly smaller in length ($P<0.01$) than juveniles with the same sized otolith.

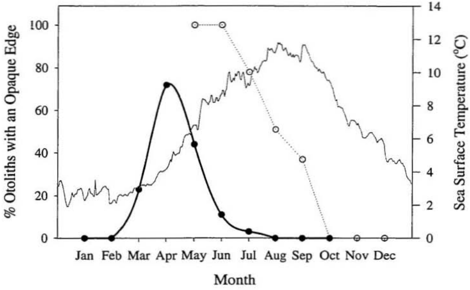

Figure 3-2. Seasonal proportions of otoliths with opaque edges for adult (—) and juvenile (····) sand lance. The gray line depicts mean daily sea-surface temperature (SST; 1996 and 1997).

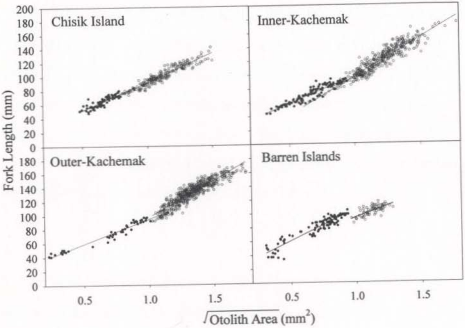

Figure 3-3. Relation between square root of otolith area and fork length (FL) for study sites within Lower Cook Inlet, Alaska (• = juvenile, ∘ = adult).

Therefore, we used two linear regressions, rather than a single quadratic relation to describe these populations. No significant difference in slope or intercept ($P<0.01$) was found between juvenile regressions at the inner- and outer- sites. Therefore, two separate regressions were produced for adults and only one for juveniles in Kachemak Bay (Table 3-1; Fig. 3-3). Otolith area and adult sand lance fork-length at the Barren Islands was only weakly related ($r^2 = 0.48$). Regressions for juveniles were significantly different ($P<0.01$) between the Barren Islands, Kachemak Bay (inner- and outer-bay combined), and Chisik Island. The adult relation was significantly different between all sites ($P<0.01$). Other researchers have also described uncoupling of somatic and otolith growth with age, and the consequent inadequacy of a single regression within the genus *Ammodytes* (e.g., Wright and Bailey, 1996; Winters, 1981).

Statistical Analysis:

Differences in the sea-surface temperature profiles for the different study areas were assessed using analysis of variance (ANOVA). Slopes and intersects of linear regressions were compared using analysis of covariance (ANCOVA). Back-calculated mean-length-at-age data for the different populations was derived using the Fraser-Lee model (using separate regressions for juveniles, adults, and the different study areas). From this data we calculated population growth curves using the Von Bertalanffy growth function (VBGF): $L_t = L_4 \cdot (1\text{-exp } (-k \cdot (t-t_0)))$ where L_t is the mean length at t years, L_4 is the asymptotic mean length, k is a constant determining the rate of change in length increments, and t_0 is the theoretical age at zero length (Ricker, 1975). Standard nonlinear optimized techniques of curve fitting were used to estimate the coefficients and their associated standard error. Due to the nonlinear formulation of the VBGF, a general linear model could not be used for analysis of covariance. Instead, an analysis of residual sum of squares was employed to compare VBGFs between areas (Chen *et al.*, 1992).

3.5 Results

Physical Environment:

July sea surface temperatures (SSTs) during 1996 and 1997 indicated significant differences between sites (ANOVA on ranks, $P<0.01$; Table 3-2). There is a distinct warming of waters as they upwell at the Barren Islands and pass around the inlet via outer- and inner- Kachemak and subsequently Chisik Island (Fig. 3-1). Sea surface temperatures in 1997 displayed a similar pattern between areas, but were all warmer than those measured in 1996.

Table 3-2. Mean July sea-surface-temperatures (SSTs) for 1996 and 1997 at Chisik Island, inner and outer Kachemak Bay, and the Barren Islands.

	1996		1997	
Location	Mean	sd	Mean	sd
Chisik Island	10.6	0.5	11.5	0.5
inner-Kachemak	9.7	0.7	10.1	0.5
outer-Kachemak	9.1	0.7	9.4	0.6
Barren Islands	8.5	0.6	8.6	1.1

CTD profiles indicated marked oceanographic differences between areas. Waters around the Barren Islands (north end of profile; Fig. 3-4) were cool and well mixed. Passing through Kachemak Bay waters become increasingly stratified before circulating around to Chisik Island (west end of profile; Fig. 3-4) where waters are warm, low salinity, and weakly stratified.

Catch:

Numbers of sand lance collected by different methods from the respective sites are summarized in Table 3-3. No adult sand lance were caught by beach seine during winter months (November to March) and were only found in exposed intertidal sediments during this time period. Juvenile sand lance were the dominant maturity stage in the nearshore from late June into winter (Robards *et al.*, 1999c). To assess relative abundance between areas, the catch statistics - frequency of capture, catch-per-unit-effort (CPUE), and median catch were calculated for July and August (Fig. 3-5). Sand lance at Chisik Island were caught about one third the frequency and in fewest numbers compared to the other sites. Frequency of juvenile capture and sand lance abundance were greater for inner-Kachemak Bay compared to the outer-bay. Catches at the Barren Islands were an order of magnitude greater than the other sites. However, most catches at this site were exclusively juveniles or mixed with low numbers of adults (Fig. 3-5).

Figure 3-4. Temperature and salinity profiles for transects in Lower Cook Inlet at the Barren Islands, inner- and outer- Kachemak Bay, and Chisik Island. Transect locations are depicted in Figure 1 with the compass direction given at the base of each profile.

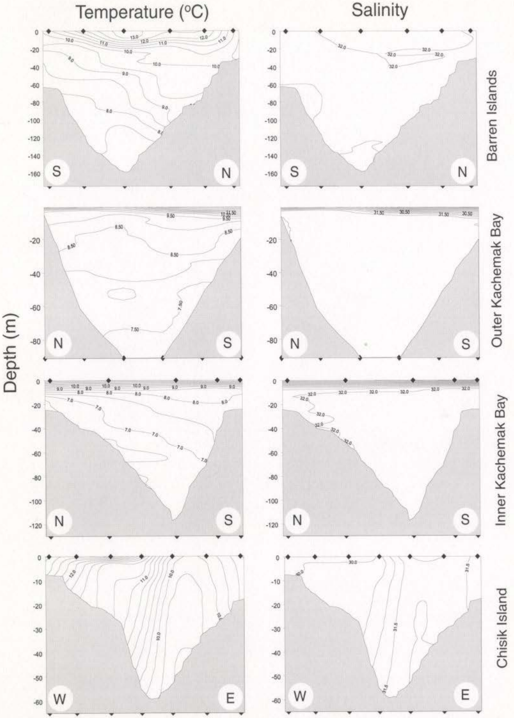
Temperature (°C)
Salinity
Depth (m)
Barren Islands
Outer Kachemak Bay
Inner Kachemak Bay
Chisik Island
S
N
W
E
0
-20
-40
-60
-80
-100
-120
-140
-160
-10
-30
-50
13.0
12.0
11.0
10.0
9.0
8.0
7.0
32.0
31.50
30.50
30.0
31.5
11.50
9.50
8.50
7.50

Table 3-3. Catch statistics for sand lance collected in Lower Cook Inlet during 1996 and 1997.

	Chisik Island (June-Sept)	Inner-Kachemak (June-Sept)	Inner-Kachemak (Oct-May)	Outer-Kachemak (June-Sept)	Barren Islands (June-Sept)
Number of beach seines	48	341	170	49	68
Sand Lance collected in seines	328	170,159	6,694	6,713	188,660
Number of digs	9	49	15	0	0
Sand lance collected in digs	359	2,483	875	0	0
Otoliths used for age/lg keys	284	1,622	1,183	669	151

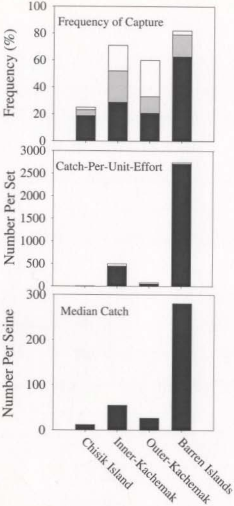

Figure 3-5. Indices of catch and abundance from beach seine data collected at Chisik Island, inner- and outer-Kachemak Bay, and the Barren Islands during June-September 1996 and 1997; ■ = juveniles, ▨ = mixed adults and juveniles, □ = adults. Median catches are for combined adult and juvenile data.

Inter-Seasonal Growth:

Slopes and intercepts of length-weight regressions ($\log_{10}$ transformed) were significantly different (ANCOVA; $P<0.01$) from zero (Table 3-4). Regression slopes and intercepts were also significantly different between areas ($P<0.01$). The regression slope was highest at the Barren Islands suggesting condition of juveniles was greatest at this area (greatest weight per unit length). A significant difference also existed between the spring and fall relation for sand lance in inner-Kachemak Bay, fall sand lance displaying greatest weight-per-unit-length.

Table 3-4. Relationship between length and weight for sand lance collected in lower Cook Inlet during 1996 and 1997. Two seasonally different regressions are given for inner-Kachemak. Relationship is expressed as: $\text{Log}_{10}(\text{Weight [g]}) = (\text{a}\cdot\text{Log}_{10}\text{Fork Length [mm]}) + \text{b}$.

Location	Season	n	a	b	r^2
Chisik Island	July/August	681	3.28	-6.02	0.99
inner-Kachemak	July/August	5,192	3.25	-5.95	0.99
inner-Kachemak	May/June	1,210	2.98	-5.50	0.99
outer-Kachemak	July/August	1,487	3.20	-5.87	0.99
Barren Islands	July/August	3,799	3.48	-6.40	0.98

A total of 3909 otoliths were used to produce age/length keys for the different sites (Table 3-3). Juvenile sand lance grow rapidly from at least May when they recruit to the nearshore until September (Fig. 3-6). During this period juveniles increased in size by 100 and 110 percent during 1996 and 1997, respectively. This corresponds to about 88 percent of total annual growth, in contrast to the 12 percent of annual growth observed in the subsequent 7 months. Adult sand lance grow over the same period, but to a lesser degree. Growth decreased with age during the May to September period, with an average 30 %, 8 %, and 3 % increase observed in age groups 1, 2, and 3, respectively. For age-group 3 adults, this constituted 100 percent of their annual growth for the 1996/1997-time period. Concurrent increases in variability of mean length with age due to small catches prevented accurate assessment for older age-classes.

Sufficient catches of juveniles from inner-Kachemak Bay and at the Barren Islands allowed us to produce time-series data for both 1996 and 1997. Growth in 1997 was slightly faster than 1996 for both sites based on regressions plotted between June and September (Fig. 3-6). After September, growth markedly slows. Size of sand lance in Kachemak Bay was more variable than the Barren Islands.

Interannual Growth:

No Von Bertalanffy growth function (VBGF) data was calculated for the Barren Islands as only two age-groups (0 and 1) were represented. Most variability was found for the inner-Kachemak sample (Table 3-5). Fish from the nearshore areas around Chisik Island

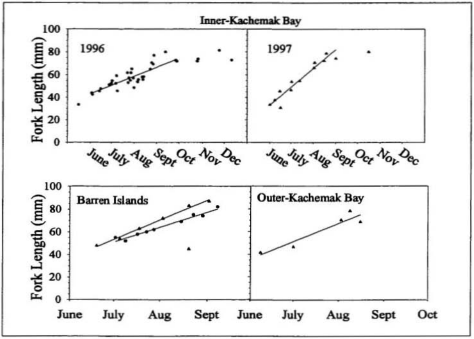

Figure 3-6. Seasonal growth of juvenile sand lance collected by seine from inner-Kachemak Bay and the Barren Islands during 1996 (•) and 1997 (▲), and outer-Kachemak Bay during 1997. Plots are derived from mean juvenile size in daily catches. Growth rates for the June to September period in 1996 and 1997 respectively of 0.43 and 0.57 mm/day at the Barren Islands, and 0.27 and 0.53 mm/day at inner-Kachemak Bay were observed. Growth rate for 1997 in outer-Kachemak Bay was 0.53 mm/day.

initially grow more slowly as evidenced by length at age-0, and ultimately reach a smaller size than for any other areas within the investigation (Fig. 3-7). Although sand lance from inner- and outer-Kachemak Bay were similar in size at the end of their first growing season, sand lance from the outer-bay subsequently grew faster than those from the inner bay. Significant differences (*P's*<0.01) were observed between Von Bertalanffy growth curves at Chisik Island and inner-Kachemak Bay (F = 222, df = 13,7), Chisik Island and outer-Kachemak Bay (F = 1,296, df = 13,7), and between inner- and outer-Kachemak Bay samples (F = 22, df = 14,8).

Table 3-5. Von Bertalanffy parameters and (standard error) for sand lance collected within Cook Inlet.

Parameter	Chisik Island	inner-Kachemak	outer-Kachemak
L_{inf}(mm)	135.61 (3.81)	235.74 (18.1)	166.33 (1.61)
K	0.3718 (0.04)	0.1528 (0.02)	0.4798 (0.02)
t_0	-1.7094 (0.17)	-2.8252 (0.30)	-1.5143 (0.07)

Assessment of Lee's Phenomenon:

Lee's phenomenon indicates selection against larger individuals in subsequent year classes. This was clearly apparent for the sand lance collected from around Chisik Island, but not for the Kachemak Bay sites (Fig. 3-8). As the same non-selective sampling strategy was used at all sites and Chisik Island sand lance were all collected from the same beach, we expect that this phenomenon is real as opposed to an artifact of the

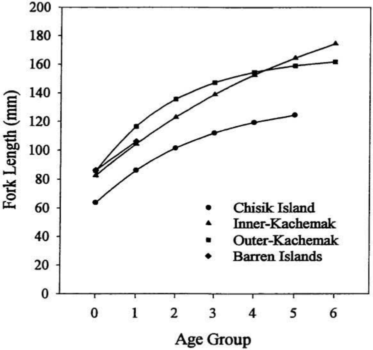

Figure 3-7. Von-Bertalanffy growth curves fitted to back-calculated length-at-age data for Chisik Island, inner-Kachemak, and outer-Kachemak. The growth curve for Barren Islands sand lance represents observed data due to only 2 age groups being present.

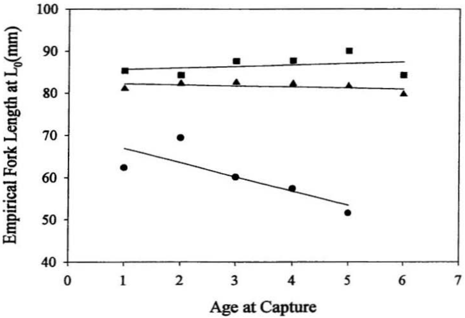

Figure 3-8. Graphical assessment of Lee's phenomenon using the relation between back-calculated length at the end of the first growing season (l_0) and age (■ = outer-Kachemak Bay, ▲ = inner-Kachemak Bay, ● = Chisik Island).

Fraser-Lee method of back-calculation. Only two age-classes at the Barren Islands prevented a relation being observed at this site.

3.6 Discussion

Local oceanographic regimes were reflected in profound differences in abundance, seasonal growth, size-at-age, and mortality between sites. These parameters directly impact the availability and quality of sand lance to the multitude of predators that rely on them for themselves and their progeny. Within populations (between years), *A. hexapterus* growth (as for *A. dubius;* Winters, 1981) was positively correlated with warmer temperatures. However, temperature regulation did not hold between different locations as Winters found for Atlantic sand lance. Sand lance from Chisik Island, where waters were warmest, were smallest and grew slowest. Juveniles from the Barren Islands, where waters were coldest grew fastest.

Ammodytes hexapterus appears typical of the genus (e.g., *A. marinus*, Brêthes *et al.*, 1992; *A. personatus*, Kitakata, 1957); growth is primarily associated with the spring and summer when 80 – 100 % of annual growth occurs. Warmer temperatures in Kachemak Bay and at the Barren Islands in 1997 compared to 1996 were reflected in faster growth of juvenile sand lance. However, these differences were not as profound as the growth differences observed between populations. Furthermore, differences between sites were negatively correlated with temperature. Our results suggest that food availability is the dominant factor regulating growth. Macer (1966) also suggested that differences in growth for *A. marinus* on different offshore banks were attributable to the presence of different current regimes supplying variable densities of food. Changes in food availability can be production-related or a result of density dependence. Unequivocal production differences between the sites are profound and can, alone be correlated with the differences in growth that we observed. Productivity at Chisik Island is considerably less than in Kachemak Bay (Damkaer, 1977; Larrance *et al.*, 1977; Drew[1], *Unpubl. Data*) and is reflected in poorest sand lance growth of all sites. Faster growth of adult sand lance in the cooler outer-Kachemak Bay compared to the inner-bay suggests food may be more limited in the inner-bay. Currents entering outer-Kachemak Bay are upwelled-highly productive oceanic waters, which subsequently become increasingly depleted as water passes around the inner-bay during the summer (Larrance *et al.*, 1977) supporting this observation. Furthermore, outer-Kachemak Bay supports the greatest epifaunal biomasses found in Cook Inlet corroborating with the high rates of production reported for this area (Feder and Jewett, 1987). The Barren Islands receive a less intense, but substantially more protracted bloom in secondary production than the other sites (Damkaer, 1977). This lengthened period of productivity suggests an extended period of food abundance for juveniles and is reflected in the fastest growth and highest condition for sand lance within the inlet.

Although production-related food availability can account for the growth differences in lower Cook Inlet, density dependence may exacerbate these effects at the two Kachemak

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[1] Dr. Gary Drew, U.S.G. S. Biological Resources Division. Unpublished Data.

Bay sites and Chisik Island. Damkaer (1977) described a small bloom in the Chisik area in late summer (July). In contrast a large spring (May) bloom exists in Kachemak Bay. Although sand lance at Chisik Island are at low abundance, the later bloom may increase intraspecific competition. Juveniles and adults that are largely segregated during the spring bloom in Kachemak Bay (pre-recruitment to nearshore; Robards *et al.*, 1999c), are present concurrently in nearshore Chisik Island waters and competing for similar prey during July (Field, 1988). Greater abundance of sand lance in inner-Kachemak Bay (particularly juveniles) compared to the outer-bay may also increase competition at this site. This may contribute to adults growing faster in the outer-bay, despite being of equal size at the end of their first season. Numerous density-dependent effects between maturity stages of sand lance have been reported for the Japanese sand lance (*A. personatus*), including increased mortality and reduced growth (Field, 1988).

Whereas temperature, production patterns, and density issues are correlated with sand lance growth, habitat is critical to abundance. Juvenile sand lance from the Barren Islands had the greatest condition index and grew fastest despite being in far greater numbers than at the other sites suggesting plentiful food. Therefore, low numbers of adults at the Barren Islands compared to the Kachemak Bay sites is probably attributable to habitat requirements rather than food or density issues. Although sandy beaches are evident around the islands, few of these beaches are sheltered, and all are subject to regular onshore wave action. The perpetual winter storms that plague the Barren Islands would result in constant disturbance of these substrates and preclude the normal sustained winter dormancy (Field, 1988) at a time of low food availability. In a similar fashion, outer-Kachemak Bay is much more exposed to onshore wave action than the inner-bay. This may explain the lower sand lance abundance in outer-Kachemak Bay. Sediment laden waters around Chisik Island (Feely and Massoth, 1982) render most nearshore areas muddy. This type of substrate is generally unsuitable for sand lance habitat (Pinto *et al.*, 1984), and probably accounts for the lowest abundance of sand lance in the inlet at this location.

In addition to the oceanographic consequences to growth and abundance of sand lance at Chisik Island, selection against larger individuals may also exist. The occurrence of Lee's Phenomenon suggests that there is either size selection within the sampling technique or that there is size selective mortality of larger fish within the population. As beach seines are regarded as non-size selective (Cailliet *et al.*, 1986), and we did not observe this phenomenon in Kachemak Bay, we conclude that larger fish within cohorts at Chisik Island are exposed to higher mortality, as opposed to this being a methodological aberration. This has also been described for sand lance (*A. dubius*) collected in the North Atlantic (Winters, 1981), and attributed to discriminatory mortality of the faster growing (earlier maturing) sand lance. The high energetic requirements required for gaining full maturation (Robards *et al.*, 1999b), poorer condition and the immediate onset of winter with limited food availability (Damkaer, 1977) might result in larger sand lance entering winter with insufficient reserves. Winters (1974) showed Lee's phenomenon for capelin (*Mallotus villosus*) and also suggested higher spawning mortality for larger, faster-growing individuals of this species. Otoliths in adult sand lance populations at Chisik Island were relatively large compared to similar sized individuals from Kachemak Bay. Relatively large otoliths within slow-growing individuals is quite common in fish populations such as at Chisik Island due to systematic variation in the somatic-otolith size relation with changes in somatic growth (Ralston, 1995).

Our site-specific results suggest that adult *A. hexapterus,* as for Atlantic sand lance (Scott, 1972b) exist in distinct populations with specific growth parameters, demonstrate site fidelity, and are generally limited in movement along coastlines. The ecological implications of site fidelity may be catastrophic if nearshore sand lance habitat is rendered unsuitable from anthropogenic perturbations such as oiling (Pinto et al., 1984). However, the occurrence of pelagic larvae allows for potential colonization of new areas as well as rehabilitation of damaged areas once they are rendered usable again.

Chisik Island sand lance are smaller at age than those in Kachemak Bay. This may be important to population fecundity and be partially responsible for the lower numbers of sand lance found at this site. Fecundity is directly proportional to size (Robards et al., 1999a) resulting in smaller fish containing lower number of eggs.

Implications to predators:

Each of the study areas supports important populations of marine piscivores such as cetaceans, pinnipeds, and seabirds. Perhaps the most important issue to these predators regarding sand lance is the large differences in abundance between sites. Predators are presented with a profoundly lower abundance of sand lance around Chisik Island. For some predators this may lead them to switch to a more abundant species (if available), and for others may lead to increased search time and range to acquire sufficient prey. Furthermore, the sand lance that they collect from around Chisik Island are likely to be of smaller size than in Kachemak Bay. This may be particularly important to certain species such as seabirds that are returning prey (sometimes singly) to their chicks.

Implications in trophic energy flow analysis:

The consequences of differing growth and otolith relationships between sites can have profound impacts to estimations of trophic energy flow. Otolith-somatic size regressions are frequently used to back-calculate size of prey in diet studies. Frequently, these calculations use a single regression (Campana, 1990). The potential error of using a single regression can be demonstrated using a single pooled Lower Cook Inlet otolith dataset. A 120 mm sand lance collected at Chisik would be estimated as approximately 5 mm larger than when back-calculated from a locally derived regression. Although only a four percent difference in length, this has a sizeable impact to trophic calculations. Based on our data, the difference would translate to an increase in mass of 0.9 g, equivalent to an energy density (ED) difference of as much as 5.7 kJ (14 %; ED value from Anthony and Roby, 1997). This discrepancy is similar to seasonal energy density adjustments used by Mårtensson et al. (1996), who indicated a 10-15 % difference in ED could amount to as much as 300,000 tonnes of prey during the feeding season for minke whales. As sand lance of the same species frequently show great disparity in growth between neighboring regions (e.g., Scott, 1973; Dick and Warner, 1982; this study) the significance of identifying geographical source of prey in feeding studies is obvious.

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