

Exxon Valdez Oil Spill
Restoration Project Annual Report

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

Restoration Project 98306
Annual Report

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

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April 1999

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Ecology and Demographics of Pacific Sand Lance,
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Study History: The purpose of this study is to characterize the basic ecology, distribution, and demographics of sand lance in lower Cook Inlet. Recent declines of upper trophic level species in the northern Gulf of Alaska have been linked to decreasing availability of forage fishes. Sand lance is the most important forage fish in most nearshore areas of the northern Gulf. Despite its importance to commercial fish, seabirds, and marine mammals, little is known or published on the basic biology of this key prey species. Therefore, restoration project 98306 was established to work in coordination with restoration APEX project 98163M to help characterize the relationship between seabird population dynamics and forage fish abundance.

This annual report consists of the attached manuscript:

Robards, M.D., J.A. Anthony, G.A. Rose, and J.F. Piatt. 1999. Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) relative to maturity, season, and location. (submitted to Journal of Experimental Marine Biology and Ecology.)

The following manuscript was submitted in last year's annual report, and is now in press:

Robards, M.D., J.F. Piatt, and G.A. Rose. 1999. Maturation, Fecundity, and Intertidal Spawning of Pacific Sand Lance (*Ammodytes hexapterus*) in the Northern Gulf of Alaska. Journal of Fish Biology 54: 000-000. (in press)

The following manuscripts are submitted and in review:

Robards, M.R. and J.F. Piatt. 1999. Biology of the Genus *Ammodytes* – The Sand Lances. U.S. Forest Service Technical Report Series. (Accepted, under revision.)

Willson, M.F., R.H. Armstrong, M.D. Robards, and J.F. Piatt. 1999. Sand lance as cornerstone species for predator populations. U.S. Forest Service Technical Report Series. (Accepted, under revision.)

Willson, M.F., R.H. Armstrong, M.D. Robards, and J.F. Piatt. 1999. An annotated bibliography of sand lance. U.S. Forest Service Technical Report Series. (Accepted, under revision.)

Other manuscripts in preparation are:

Robards, M.D. G.A. Rose, and J.F. Piatt. 1999. Somatic growth and otolith development of Pacific sand lance (*Ammodytes hexapterus*) under different oceanographic regimes. (Undergoing final revision for submission to Fisheries Oceanography).

Other products in preparation are:

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

Abstract: We report here on changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) relative to maturity, season, and location. We collected sand lance from the nearshore (using beach seines and digging in intertidal substrates) and offshore (using mid-water trawls and halibut) during the past three years from Kachemak Bay, Chisik Island, and the Barren Islands. Proximate composition analyses showed that the body condition and energy density of adult sand lance cycle seasonally. Mean dry-weight energy values peaked in spring and early summer (20.9 kJ/g for males, 21.1 kJ/g for females), and subsequently declined by about 25% during late summer and fall. Declines in energy density paralleled gonadal development. Adult sand lance spawn in October and subsequently enter the water column with close to their minimum whole body energy content. The energy content of juvenile sand lance remains fairly constant until they reach about 80 mm in length, and is higher than adults during summer. The value of sand lance to predators varies markedly among geographic areas and within seasons. However, maximum energy value coincides with important feeding periods for marine mammals, birds and fish.

Keywords: *Ammodytes hexapterus*; bioenergetics; condition index; Pacific sand lance; proximate composition; seasonal variation

Project Data: (will be addressed in Final Report of 2000)

Citation: Robards, M.D. and J.F. Piatt. 1999. Ecology and demographics of Pacific sand lance, *Ammodytes hexapterus* Pallas, in Lower Cook Inlet, Alaska. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 98306), U.S. Geological Survey, Anchorage, Alaska.

Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) relative to maturity, season, and location.

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Running Head: Proximate Composition of Sand Lance

Abstract

The body condition and energy density of adult Pacific sand lance (*Ammodytes hexapterus*) 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 and subsequently enter 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 about 80 mm fork length. Above this length, relative proportions of protein remained constant while proportion of lipids increased significantly. Dry weight energy densities of juveniles thus 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 value of adult sand lance to predators varies markedly among geographic areas and within seasons. However, maximum energetic value to predators coincides with important feeding periods for marine mammals, fish, and seabirds. Juvenile sand lance rapidly increase in energetic value and would be most valuable to predators in early winter.

Keywords: *Ammodytes hexapterus*; bioenergetics; condition index; Pacific sand lance; proximate composition; seasonal variation

Introduction

Pacific sand lance (*Ammodytes hexapterus*) dominate nearshore fish communities in many areas of the Gulf of Alaska and Bering Sea and comprise the 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.*, 1999a). Despite the importance of sand lance for upper-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, their value 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 can vary with season, location, gender, and age, as well as 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 primary and secondary production blooms. With sand lance, however, these cycles of energy storage may be out of phase with and lead physiological processes such as spawning, which occurs about four months after the single secondary production bloom (Damkaer, 1977; Dick and Warner, 1982).

In this paper we examine energy storage in relation to sexual development and subsequent winter dormancy of adult male and female sand lance. We also evaluate the energetics of growth and development in juvenile sand lance. Finally, we consider how variations in energy content might affect predators of sand lance.

Methods

Sand lance were sampled at three areas in Lower Cook Inlet: Kachemak Bay, Chisik Island, and the Barren Islands (Fig. 1). These areas were chosen because we were concurrently conducting studies on seabirds that breed in each area. We collected sand lance from intertidal substrates and by beach seine (Robards *et al.*, 1999a).

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. Adults were collected from Chisik Island and the Barren Islands during July. Juvenile sand lance were collected only from Kachemak Bay.

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 their 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.

Sagittal otoliths were collected ventrally to the spinal column and anterior to a transverse incision made at the posterior margin of the skull (visible through the skin). Otoliths were cleaned of fibrous tissue, and stored dry in Eppendorf 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 & 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.*, 1999b).

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 I.

A modified monthly gonadosomatic index (GSI; Nikolsky, 1963) was used to quantify seasonality of reproduction for stages 1 through 6 where $\text{GSI} = (\text{gonad weight/gonad-free body weight}) \times 100$. 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.

Results

Seasonal Variation

Sand lance collected in February were emaciated with no visible fat reserves. By June and July, sand lance had clearly 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 II). As expected (Van Pelt *et al.*, 1997) energy density (kJg^{-1}), was inversely correlated with water content (water content = $59.9 - [0.54 \times \text{total energy density}]$, $r^2 = 0.81$, $P < 0.01$, $n = 267$).

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), in preparation for spawning in October. 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 in sand lance remained relatively stable from June to October then declined

precipitously during spawning for both sexes (Fig. 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 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), and for both events, males preceded females by about one month.

Geographic Variation

Mean energy values were similar (Student t-test; $P=0.588$) among sand lance from the Chisik and Barren Islands (Table II). However, mean energy values for sand lance at both sites were significantly lower (by about 10%) than Kachemak Bay sand lance in July (Table II; $P<0.001$). Although lipid content was lower at both Chisik and the Barren Island sites, protein condition at Chisik was not significantly different from Kachemak Bay ($P=0.89$). Protein condition at Chisik Island and Kachemak Bay was significantly greater than at the Barren Islands ($P's<0.01$).

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 85-89mm (Table III). 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 = $67.8 - (0.64 \times \text{total energy density})$, $r^2=0.92$, $P<0.01$, $n=14$). Relative energetic content of sand lance between 55 and 80mm indicated similar contributions from lipid and protein (Fig. 4). Relative protein content steadily increased between 55 and 80 mm (Fig. 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.

Discussion

Adult sand lance display a seasonal cycle of energy accumulation that results in a 31% increase in energy density (kJg^{-1} dry mass) between February and June. Peak energy values reported here were similar to those reported for Atlantic species of sand lance (e.g., Hislop *et al.*, 1991; Mårtensson *et al.*, 1996). The seasonal increase may be largely attributed to a short period of intense feeding during the spring plankton bloom in April and May (Larrance *et al.*, 1977), as for another Alaskan species, yellowfin sole (*Pleuronectes asper*; Paul *et al.*, 1993). Lipid content of other species of sand lance 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 ($r^2_{\text{adj}} = 0.35$, or less; Lawson *et al.*, 1998).

Female sand lance, as in many other fish species expend more energy than males in reproduction due to the production and loss of eggs, which requires greater accumulation of reserves in the feeding season (Love, 1980). Energy densities of males and female adult sand lance declined through the summer as lipid reserves were directed to the development of gonads. In laboratory experiments, Pinto (1984) also observed significant loss of lipid prior to spawning by sand lance. Many other species (such as cod) lose about 30% of their energy during, rather than prior to spawning (Smith *et al.*, 1990). Whereas gonad production may be one contributor to the energetic loss observed through the summer, sand lance also reduce time spent feeding, as evidenced by late summer declines in catch-per-unit-effort and frequency-of-capture (Winslade 1974; Robards *et al.*, 1999a). As noted for Japanese sand lance (*A. personatus*; summarized in Field, 1988) adult sand lance may compete 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 (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. Adult sand lance have developed the ability to endure long periods of reduced food intake. In experimental situations, *A. personatus* survived for over two months in starvation (Inoue *et al.*, 1967).

After spawning, sand lance enter the winter season in poor condition. Without plentiful food supplies to replenish energy (Damkaer, 1977) and little reserves to cover

basic metabolic function, sand lance remain dormant in nearshore substrates through the winter (Robards, *pers. obs.*). Sand lance are adapted for winter dormancy with the ability to reduce metabolism (Quinn and Schneider, 1991) and prolong gut evacuation times (Ciannelli, 1997). Sand lance are also regarded as a high protein fish, as protein generally constitutes greater than 15% of wet mass (Stansby, 1976). The proportionally high amount of protein may provide a buffer against reduced food intake prior to spawning and during winter. Neither male nor female sand lance appeared to rely on lipid stores during spawning. Lipids comprise only 20% (dry weight) of sand lance ovaries (Tocher and Sargent, 1984) and protein rather than lipid is the principle energy source for gonadal development (Love, 1970). Protein content varied seasonally by over 14% (dry mass) in adult sand lance from Kachemak Bay. During early winter, remaining lipids are presumably mobilized in response to low food availability (Love, 1980), prior to utilization of protein reserves for metabolic needs (Maddock and Burton, 1994).

Accounting for this seasonal variability in energy content is critical when comparing relative values between species, 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.

Up to a fork-length of about 80mm, juvenile sand lance appear to channel lipid reserves into somatic growth. Rapid growth and good condition likely lead to increased survival (as for salmon fry) because larger fish are 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). Juvenile energy density is relatively low (about 17 kJg⁻¹ dry mass) during early somatic growth, but increases rapidly with accumulated lipid reserves to nearly 20 kJg⁻¹ dry mass by late summer, exceeding energy densities of adult males and matching that 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.

Adult sand lance from Chisik Island and the Barren Islands had lower energy densities (kJg⁻¹) than those collected in Kachemak Bay. Although sand lance collected at these sites were smaller than those in Kachemak Bay, size of adult sand lance did not appear to be strongly related to energy density. Chisik Island is on the west side of Cook Inlet where waters are estuarine and loaded with glacial sediments (Larrance *et al.*, 1977). This area supports only 10% of the primary productivity observed in Kachemak Bay, and peak zooplankton biomass occurs later and at reduced levels (Larrance *et al.*, 1977; Damkaer, 1977). This may preclude accumulation of large

early-season energy stores as in Kachemak Bay. In contrast, the Barren Islands are supported by highly productive, upwelled, oceanic waters (Burbank, 1977).

However, little sheltered habitat is available at this site, particularly during winter, and this reduces the likelihood that sand lance can maintain large resident populations at the Barren Islands. Adult sand lance were caught in only 3 % of seines and accounted for < 1% of the entire sand lance catch (compared to 19% and 10%, respectively in Kachemak Bay; Robards *et al.*, 1999a). Poor body condition of adult sand lance from the Barren Islands during mid-summer indicates unfavorable environmental conditions or a lack of suitable food during spring and early summer.

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 when compared to sand lance. For example, adult capelin and herring are seasonal feeders that build up fat stores to sustain them when food is scarce 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 and subsequent summer resources, maximizing their growth and energy storage potential for the year. 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.*, 1999a) 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 during June and July. Further nutritional benefit is likely from the high protein content present in sand lance. In fact, during early summer sand lance may well be a quintessential forage fish (Springer and Speckman, 1997). Other important Gulf of Alaska forage species such as capelin which lose 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, reprovisioning

capelin and herring would provide a much greater energy return to predators, particularly prior and during winter whilst sand lance is both energetically poor and dormant for long periods. Although whole fish energy values for pelagically caught sand lance in July indicate juveniles are relatively poor prey compared to adults (by a factor of 18:1; Table IV), 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 therefore, also be a significant early-winter food source for predators.

In conclusion, our results concur with Mårtensson *et al.* (1996) who showed marked seasonal variation in proximate composition exists for several forage species as a consequence of seasonality in primary production. Significant seasonal and spatial variability in composition and energetic value emphasizes the need for care in attributing gross numbers in modeling trophic energy flow. Furthermore, the need for energy density estimates of prey species, for specific seasons, prey sizes/age classes, and regions of interest are vital for a full understanding of a predator's foraging requirements.

Acknowledgments

Major financial and logistic support for the Cook Inlet Seabird and Forage Fish Study

(CISeaFFS) was provided by the Exxon Valdez Oil Spill (EVOS) Trustee Council (Restoration Project 98306), U. S. Geological Survey, and the Alaska Department of Fish and Game. The findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the EVOS Trustee council. We gratefully acknowledge the assistance of Mike and Phyllis Balough for their dedicated help with observations and collections in Seldovia Bay. Special thanks go to David Black, Lilly Goodman, Arthur Kettle, Kali Mangel, April Nielsen, and Stephanie Zuniga for long hours of help in the field. We are grateful to Mike Geagel (University of Alaska, Fairbanks) and Tom Van Pelt for logistical help, Dr. Dan Roby for laboratory support, and Alexander Kitaysky, Nancy Tileston, and Kathy Turco for technical help during analysis and writing. All sand lance were collected under Alaska Department of Fish and Game permits.

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Table 1. Regression parameters for fresh wet weight:dry weight relationship.

Area	Stage	<i>N</i>	<i>r</i> ²	Slope
Kachemak Bay	Adult	243	0.87	0.25
	Juvenile	14	0.99	0.25
Chisik Island	Adult	12	0.97	0.27
Barren Islands	Adult	12	0.93	0.25

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Table II. Mean monthly proximate composition for adult male and female sand lance collected in Lower Cook Inlet during 1996

Area	Month	Sex	N	Age (yrs)	Length		GSI (%)	Dry Mass	% Water [†]	% Lipid [‡]	% Protein [‡]	% Ash [‡]	Energy Density [‡]	
					mm	S.E.							kJg ⁻¹	S.E.
Kachemak Bay	February	M	13	2.2	127	2.1	0.4	1.06	79.6	6.7	74.5	14.2	15.91	0.37
		F	9	2.2	125	2.9	0.6	1.02	79.5	6.8	73.5	15.4	15.74	0.49
	June	M	21	2.3	137	1.3	0.3	2.44	73.6	24.6	62.0	9.1	20.70	0.23
		F	21	2.3	138	1.1	0.6	2.49	73.1	24.9	61.3	9.3	20.69	0.23
	July	M	9	2.2	140	3.3	0.6	2.84	73.4	25.5	61.2	8.6	20.91	0.15
		F	9	2.2	140	2.3	0.9	2.89	72.7	27.2	58.4	8.1	21.08	0.11
	August	M	22	1.9	142	2.5	10.6	2.79	74.2	19.3	67.3	9.4	19.56	0.14
		F	21	2.0	144	2.3	5.4	3.05	72.0	22.8	65.4	8.6	20.60	0.11
	September	M	27	1.9	132	1.9	25.1	2.08	75.7	16.6	69.3	10.7	18.87	0.15
		F	19	1.9	140	2.9	10.5	2.89	73.0	20.4	67.0	9.1	19.95	0.18
	October	M	27	2.1	144	2.7	26.4	2.47	78.9	10.2	75.8	12.1	17.49	0.12
		F	32	1.9	138	2.5	30.9	2.44	77.7	12.8	74.7	10.3	18.32	0.14
	November	M	6	1.2	119	5.0	5.4	1.02	80.5	9.9	71.0	13.5	16.51	0.30
		F	7	1.7	129	3.9	6.6	1.32	79.9	10.3	70.1	14.9	16.51	0.48
Chisik Island	July	M/F ^{††}	12	2.7	117	3.4	--	1.49	79.7	17.2	66.9	12.8	18.65	0.28
Barren Islands	July	M/F ^{††}	12	1.0	104	1.3	--	0.93	80.5	18.9	64.7	11.0	18.92	0.39

[†]Fresh wet mass

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

^{††}Numbers of male and female sand lance respectively at Chisik Island (6,6) and the Barren Islands (5,7)

Table III. Mean proximate composition for juvenile sand lance collected in Kachemak Bay 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])

Table IV. Energy value (kJ/fish) based on mean adult and juvenile fish sizes collected by beach seine in each area¹

Location	July				August			
	N	Wet Wt (g)	Length (mm)	Energy per Fish (kJ)	N	Wet Wt (g)	Length (mm)	Energy per Fish (kJ)
Chisik Island	209	3.78	102	19.03	-	-	-	-
Kachemak Bay - Adult	300	6.89	120	36.16	1095	7.45	121	36.47
Kachemak Bay - Juvenile	54	0.51	55	2.15	114	1.38	73	5.92
Barren Islands	27	3.59	102	16.98	-	-	-	-

¹Robards (unpubl. Data)

Table II. Mean monthly proximate composition for adult male and female sand lance collected in Lower Cook Inlet during 1996

Area	Month	Sex	N	Age (yrs)	Length		GSI (%)	Dry Mass	% Water [†]	% Lipid [‡]	% Protein [‡]	% Ash [‡]	Energy Density [‡]	
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Table III. Mean proximate composition for juvenile sand lance collected in Kachemak Bay during 1996

Size Gp. (mm)	Rep. [†]	Length		Dry Mass (g)	% Water [‡]	% Lipid ^{††}	% Protein ^{††}	% Ash ^{††}	Energy Density (kJg ⁻¹) ^{††}
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¹Robards (unpubl. Data)

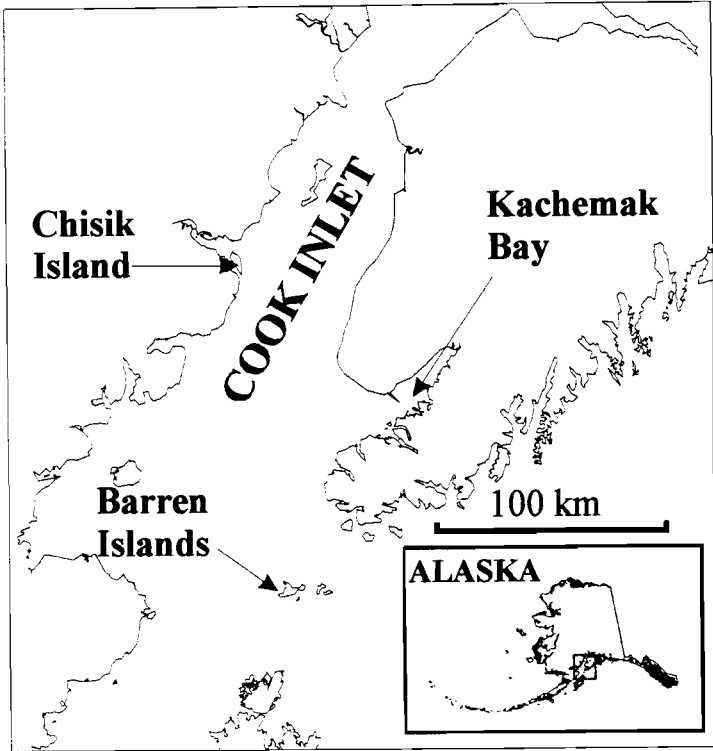
Figure 1. Sampling locations in Lower Cook Inlet, Alaska.

Figure 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 \pm standard error.

Figure 3. Seasonal condition factor (K') for male (⋯○⋯) and female (—●—) sand lance collected in Kachemak Bay. Error bars are means \pm one standard error. Vertical dashed line indicates time of spawning (Robards *et al.* 1999b).

Figure 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) as well as water contents (circles) are shown.

Figure 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.



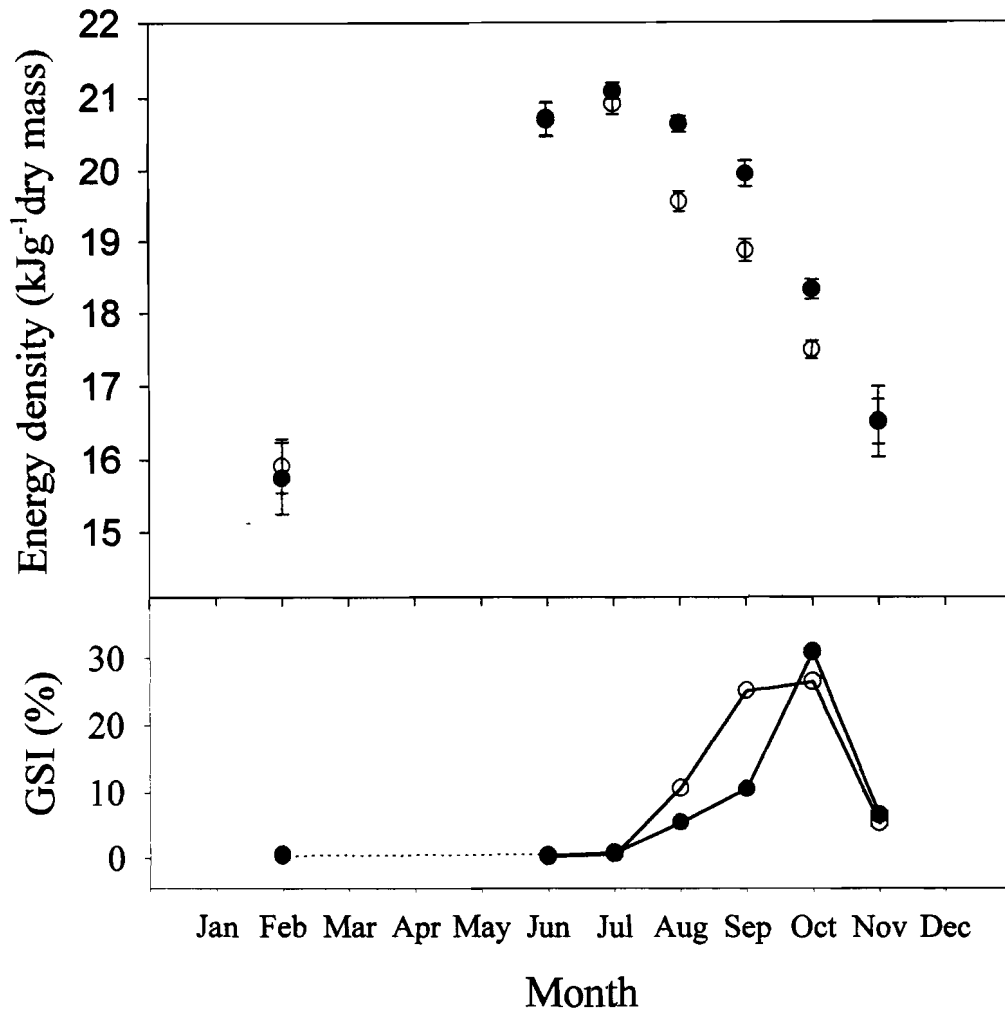
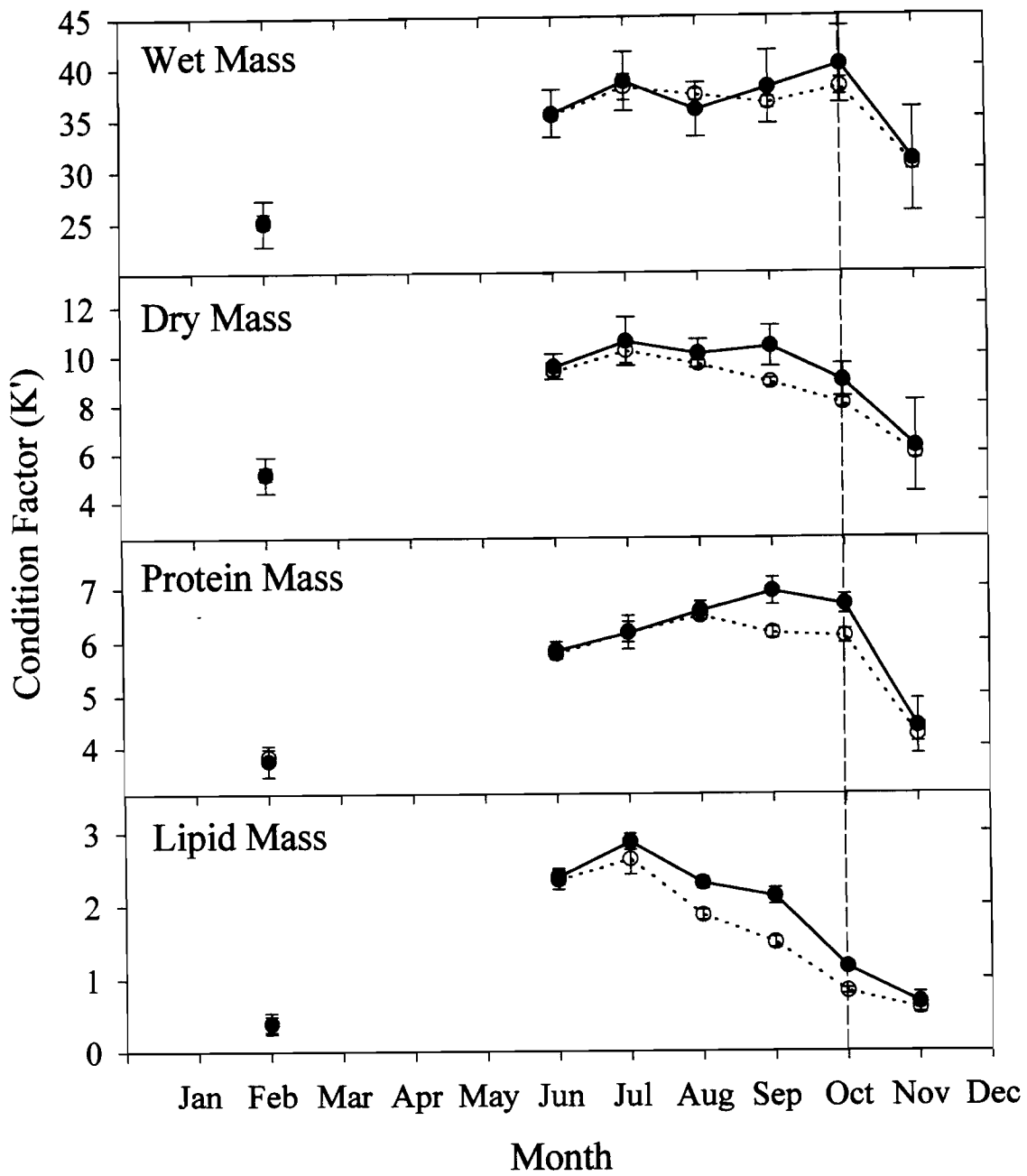
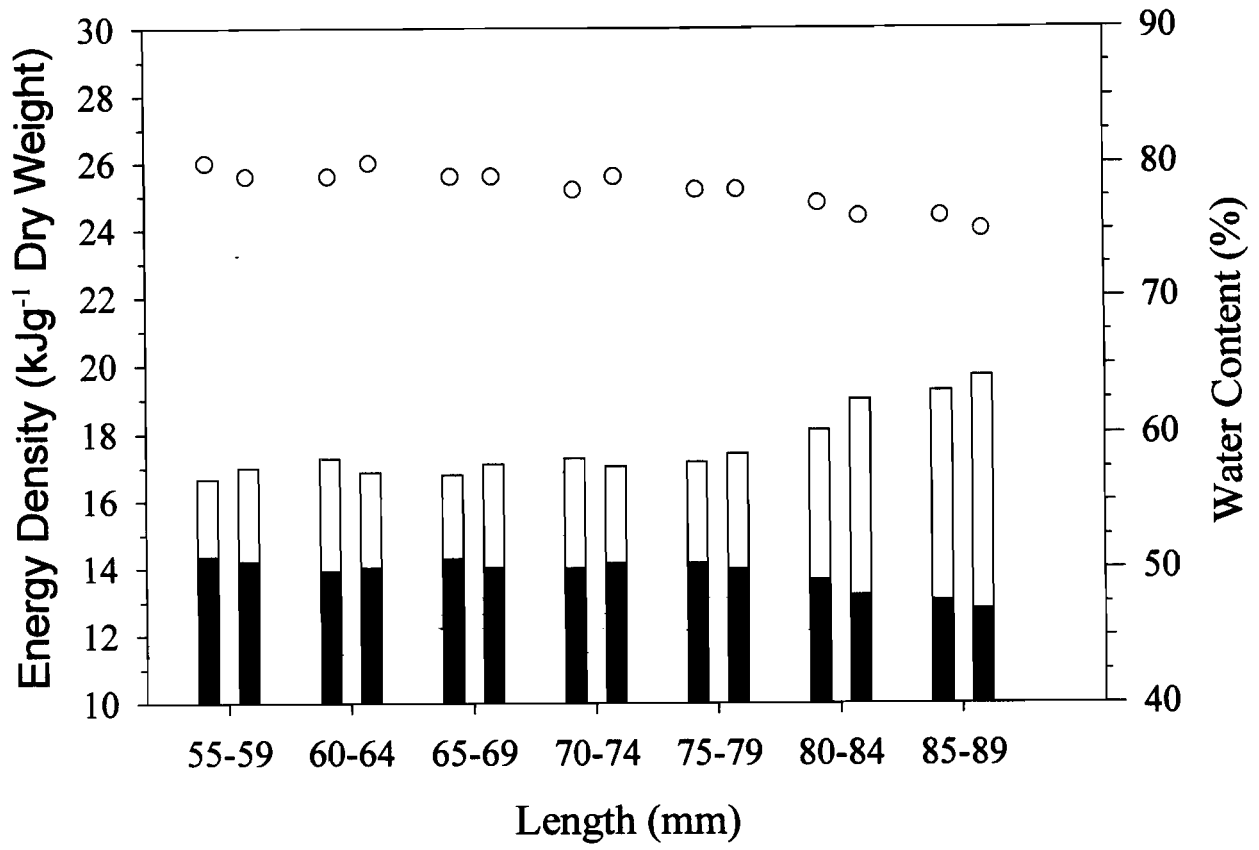


Fig. 2





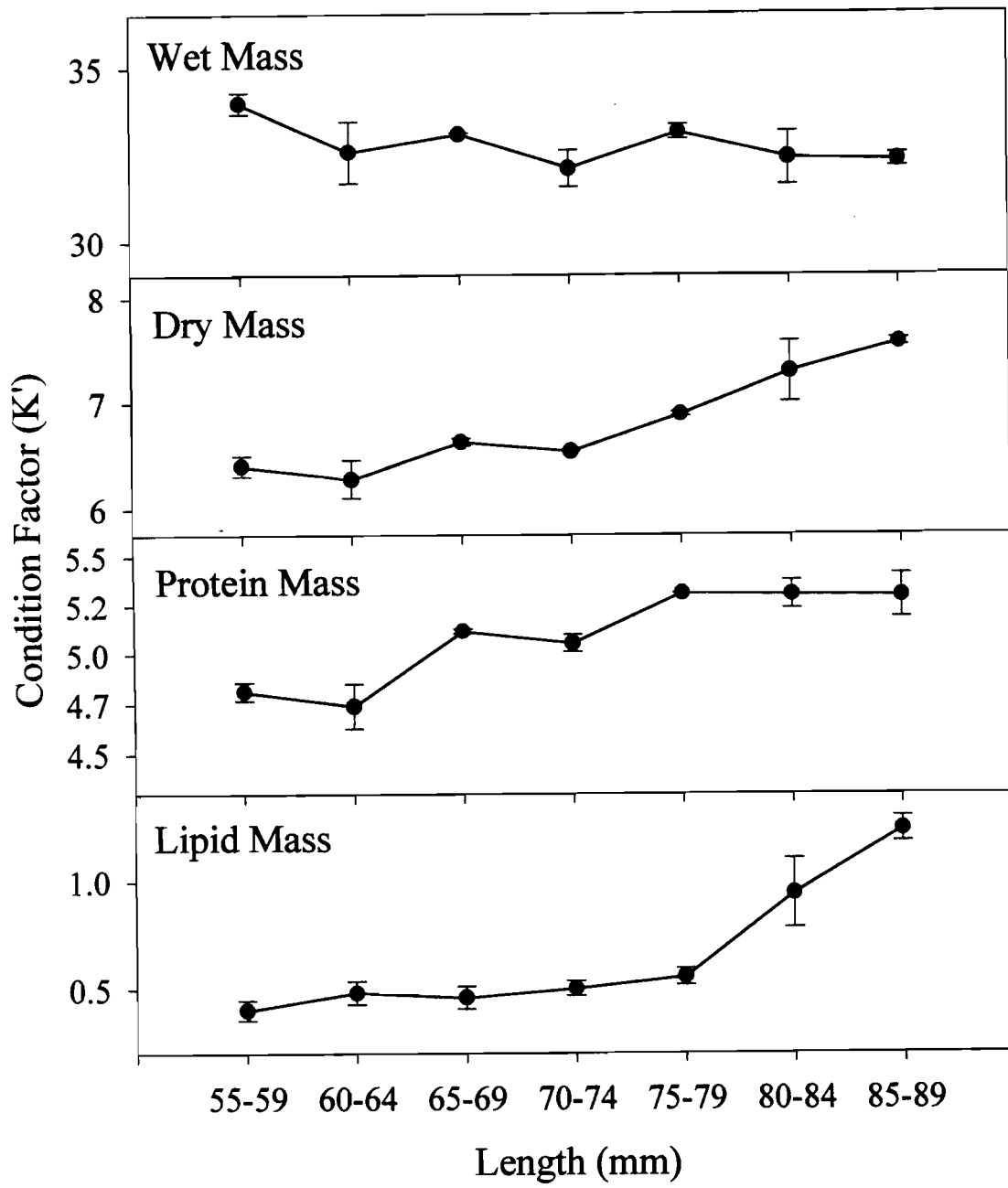


Fig. 5.