CONDITION AND FOOD AVAILABILITY TO PACIFIC SAND LANCE (AMMODYTES HEXAPTERUS) IN PRINCE WILLIAM SOUND, ALASKA

By

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THESIS

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By

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ABSTRACT

Pacific sand lance (*Ammodytes hexapterus*) is a common forage fish for seabirds in Prince William Sound, Alaska (PWS). The objectives of this study were to determine if condition of young-of-the-year (YOY) sand lance varies within PWS, and if variation in condition is related to temperature and food availability. Fish were collected in 1996, 1997, and 1998 and assayed for energy content. Zooplankton samples were collected concurrently. SeaWiFS ocean color satellite images and AVHRR temperature images were analyzed for chlorophyll biomass and temperature history. Standard lengths of YOY sand lance ranged from 47 to 97 mm, and their energy content ranged from 4490 to 5670 cal/g, with significant differences among stations. Sand lance in southern PWS were in better condition than those in other areas. Surface chlorophyll concentration and zooplankton abundance were not related to energy content; however, there was a positive and significant relationship between energy content and SST.

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INTRODUCTION

The condition of a fish is determined by its storage of energy reserves. A fish in good condition will cope with adverse environmental conditions better than a fish in poor condition. Consequently, condition affects survival and reproductive fitness by determining tolerance to food shortage (Smith et al. 1986, Thompson et al. 1991, Umino et al. 1991, Wicker and Johnson 1987), resistance to disease (Goede and Barton 1990), and is a useful measure of the relative fitness of a fish or a population of fish.

The condition of fish can be affected by biological as well as physical factors (Paloheimo and Dickie 1966). Biological factors include the availability of prey. Prey concentrations leading to food limitation and starvation affect the growth and survival of larval fish, juveniles, and adults (Eckmann and Rey 1987, Malloy and Targett 1994, McGurk et al. 1992, Smith et al. 1986). The physical factor that is most likely to have a significant effect on growth and condition of fish is temperature. Given an abundance of food, fish at higher temperatures (within tolerance limits) grow faster (Paloheimo and Dickie 1966). Mean length and year-class strength of young-of-the-year pikeperch are highly correlated with mean summer temperature (Buijse and Houthuijzen 1992). Differences in summer water temperature can cause annual growth to vary by a factor of two in walleye and yellow perch (Kitchell et al. 1977). As temperatures increase, so do metabolic demands (Paloheimo and Dickie 1966). Consequently, in order to grow at the same rate, fish at higher temperatures require higher food rations.

Many seabirds suffered high direct mortality from the Exxon Valdez Oil Spill (EVOS) in 1989. Some colonies continued to decline after the oil had left the

immediate surface of the water, and recovery for many colonies has been slow. This lack of recovery may be due to an alteration in abundance of forage fish prey (Piatt and Anderson 1996).

The dependence of seabird colony productivity on the availability and quality of forage fish has been demonstrated in different parts of the world (Bailey 1991, Bailey et al. 1991, Monaghan 1992, Montevecchi and Piatt 1984, Roby et al. 1996). Pacific sand lance (*Ammodytes hexapterus*) are prey to a variety of seabirds, including puffins, murres, cormorants, black-legged kittiwakes, and pigeon guillemots (Field 1988, Hatch and Sanger 1992). Sand lance have twice the energy content of walleye pollock, making them a preferred prey item of nesting sea birds (Anthony and Roby 1997). In PWS adult black-legged kittiwakes feed their chicks primarily herring and sand lance (Irons and Suryan 1996). The chicks grow better on sand lance or capelin than on leaner fish such as pollock (Piatt et al. 1997). This has been confirmed in captive breeding experiments with black-legged kittiwakes and tufted puffins (Romano et al. 1997). The recovery of a pigeon guillemot colony at an oiled site in PWS appears to be limited by the availability of sand lance (Roby et al. 1998). Sand lance availability may also affect the reproductive output of common murres (Piatt and Anderson 1996).

The Pacific sand lance is not commercially harvested in North America, and is poorly studied. No data are available on prey density requirements for optimum growth of sand lance. In the north Aleutians most prey consumption occurs in winter and spring when sand lance feed primarily on euphausiids. By late summer, copepods are the preferred prey (Craig 1987). The main growth period in the Aleutians is February to June (Craig 1987). In lower Cook Inlet, Alaska, 80-100 % of annual growth of sand lance occurs in spring and summer (Robards 1999). In PWS, sand lance have a varied diet in the summer, feeding on copepods, barnacle larvae, hyperid amphipods, and other zooplankton in the water column (Sturdevant and Hulbert, in review).

Sand lance depend on sand or sandy gravel bottoms throughout their life history for reproduction (Lemberg 1994), predator escape (Macer 1966), as well as nocturnal and winter burrowing substrate (Field 1988, Hobson 1986). The limited distribution of suitable habitat in PWS probably leads to limited movement of individual schools. High site-fidelity has been documented for sand lance in lower Cook Inlet, Alaska (Robards et al. 1999). This makes possible a comparison between schools from different areas, as the likelihood of schools moving out of their respective areas is low. The limited movement of sand lance subjects populations from individual sandy bottom areas to different prey and temperature conditions. This may lead to variation in growth and condition of young-of-the-year fish from different areas. A recent study, which based energy density calculations on proximate composition, found intraspecific variability in the condition of forage fish (Roby et al. 1998). Young-of-the-year walleye pollock from different areas in PWS have significantly different caloric values (Boldt 1996). This is also true for several species of euphausiids (Mooney 1999).

The objectives of this study were 1) to determine if the condition of sand lance varies within PWS, 2) to explore the relationship of several measures of condition, and 3) to determine if variations in condition can be related to physical and biological factors or to diet of sand lance.

METHODS

Field Methods

PWS is a large, complex, fjord-type estuarine system, with 180 m deep sills enclosing up to 700 m interior depths (Niebauer et al. 1994). Central PWS covers an area of approximately 60 by 90 km (Niebauer et al. 1994), with an extensive system of bays, islands, and passages surrounding it (Fig. 1).

Sand lance were collected in PWS during the summers of 1996, 1997, and 1998 using beach seines and fry purse seines (Figs. 1 and 2, Appendix A). The beach seine was 5 m deep at the center to 1.5 m deep at the wings and it is 37 m long. The center panel where fish are caught had a 10 mm stretched mesh. The fry purse seine was 5 m deep and 20 m long, and it had a 10 mm stretched mesh. In 1996, 1997, and 1998, 4, 4, and 13 samples of sand lance schools were collected, respectively. The northernmost (8N1) and southernmost (8S5) stations were approximately 150 km apart (Fig. 1). At each collection station the fork lengths of a subsample of approximately 200 individuals were measured to the nearest millimeter. The subsample was then frozen for lab analyses. In 1998, a separate random subsample of at least 10 fish was preserved in 10 % formalin for stomach content analysis.

In 1998, zooplankton were collected in three replicates at each station, or as close to it as feasible, with vertical hauls from a depth of 18 m using a ring net. The ring net had a mouth diameter of 0.5 m and a 243 μ m mesh with a 243 μ m codend. Plankton samples were preserved in 10 % formalin. Vertical tow collections were also made with a 20 cm Bongo net with 243 μ m mesh from 60 m depth (or 10 m above

bottom) in the north, central and south areas of PWS (Fig. 3, Appendix B). Samples were preserved in 5% buffered formalin.

In 1998, temperature, salinity, and chlorophyll were measured by CTD (Seacat model SBE 19-03 equipped with a WETstar Miniature Fluorometer model 9702008). The data acquisition software used was Seasoft version 4.225 (Sea-Bird Electronics, Inc. 1997). All sampling was conducted during daylight hours.

Laboratory Methods

PROCEDURES FOR FISH

In the lab, a random subsample of 50 fish per station was thawed and blotted dry before being weighed to the nearest milligram and measured (fork length and standard length) to the nearest millimeter. Stomachs were extracted and the contents removed, before being blotted and returned to the fish. Otoliths were removed and stored in glycerin. The otoliths were mounted on slides for age determination under a dissecting scope. The fish were dried at 60°C until a stable weight was reached (24-48 hours). Only young-of-the-year sand lance were used in the following analyses.

Individual fish were ground with mortar and pestle, and subsamples of approximately 0.150 g were pressed into pellets for combustion. To reduce bias in the weight of the pellets due to absorption of moisture in the air, pellets were weighed to the nearest 0.01 mg immediately after being pressed. The caloric value of each pellet was measured with a Parr semimicro bomb calorimeter. Methods for the bomb calorimetry are in the Parr Operating Instruction Manuals for the 1107 semimicro oxygen bomb in a 1425 semimicro bomb calorimeter (Parr 1991, 1992, 1993).

The fuse wire used in the combustion was an alloy (Parr No. 45C10) with a heat of combustion of 2.3 calories per centimeter. To correct for fuse wire combustion. residual fuse wire was measured after each sample and entered as a correction factor into the calculations of the caloric value of the sample. The formation of nitric acid during ignition, from air trapped in the bomb, releases additional heat that did not originate from the sample. As nitric acid formation should be relatively constant for all samples, besides probably being negligible in a 23 ml bomb, it was not corrected for. The oxidation of sulfur from the sample into sulfuric trioxide, which combines with water vapor to form sulfuric acid, also liberates additional heat. This was also not corrected for, which probably introduces a minimal error into the caloric value estimates of the samples. The formation of sulfuric acid is a factor of sample mass. Since this was held relatively constant $(0.150\pm0.01g)$, the error should be similar for all samples (excluding station 8S2, where fish under 0.15 g were combusted whole). The oxidation process of nitrogen releases energy that has no biological meaning, as it is not available to the food web (Kersting 1972). Available energy may be as much as 10% less than that determined in an oxygen bomb (Kersting 1972). However, since only fish of the same species were compared, nitrogen content is likely to be almost identical among individuals, and the error therefore consistent for all samples.

To determine whether an increase in calories per gram with increasing standard length might be due to stations with smaller fish also being in poorer condition, or to a

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general trend in sand lance, length stratified sampling was used at one station with a wide size distribution (Station 8S2). For this station, four to five fish were combusted from each 5 mm length interval between 48 mm and 98 mm standard length, a total of 49 fish. In order to separate the size effect from the condition assessment, 10 fish from a size interval that was present at all stations (75-85 mm standard length) were used for the bomb calorimetry.

PROCEDURES FOR PLANKTON AND STOMACH CONTENTS

Each of the three plankton samples per station was rinsed with water and sorted whole for large or unusual items, before being split with a Folsom plankton splitter. Samples were split up to a subsample of 1/64 to yield approximately 200 items for sorting. Plankton samples were sorted to categories (e.g. small calanoid copepod, larvacean, etc.), except for the seven most abundant copepod genera, which were identified when possible (Table 1). The actual count was then multiplied by the fraction of the original sample that was used for the actual count to estimate the true concentration in the sample. Thirty-eight samples were sorted in this fashion. The Bongo samples were sorted to categories and species (by Jennifer Purcell) in the same fashion.

Stomach contents were obtained from the formalin-preserved fish. The stomach contents of 130 fish (10 for each of the 13 stations collected in 1998) were analyzed. Fish were stored in 70 % ethanol for at least one month before stomachs were removed. Each fish was blotted dry, weighed to the nearest milligram, and standard and fork lengths were measured to the nearest millimeter. After extracting the stomach, it was blotted dry, weighed to the nearest milligram, and contents were removed and stored in 70 % ethanol. The empty stomach was blotted dry and weighed to the nearest milligram. The weight of the stomach content was calculated as full stomach weight minus empty stomach weight. Stomach contents were counted whole using the same categories as for the plankton samples.

Methods for Satellite Data

Data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), which is integrated into the SeaStar spacecraft, were obtained from the Goddard Distributive Active Archive Center. The data obtained was unprocessed instrument data at full resolution, time referenced, and annotated with ancillary information (Level 1A images). For Local Area Coverage, nominal ground resolution (full resolution directly underneath the satellite) is 1.13 km. When the area of interest is not directly under the satellite, resolution may decrease to as much as 4 km on the edges of a path. The resolution, or pixel size, is therefore not constant between or within images. Global Area Coverage images, which have a nominal ground resolution of 4.5 km, were not used.

The level 1A images were processed with the SeaWiFS Data Analysis System (SeaDAS), a program developed by NASA specifically to process SeaWiFS data. Chlorophyll-a is calculated in SeaDAS with the following algorithm:

Chlor-a = $-0.040+10^{(0.341-3.001X+2.811X^2-2.041X^3)}$

where $X = \log_{10}[R_{rs}(490)/R_{rs}(555)]$ and $R_{rs}(\lambda) =$ reflectance of band λ .

The ancillary data were used in the processing of the raw data to correct for meteorological and atmospheric conditions such as wind and ozone. Meteorological data were collected every six hours, ozone data every 24 hours. For each image, the two meteorological data files that bracket the image file in time were used, as was the ozone file closest to the image in time.

There are numerous conditions during which chlorophyll cannot be calculated for a particular satellite pixel, clouds and land being the most obvious. The chlorophyll algorithm also fails when chlorophyll levels in the water are very high. Out of approximately 250 SeaWiFS satellite passes in the vicinity of Prince William Sound, for the time period from March to July, only seventeen images could be used for the estimation of chlorophyll. These images, spanning the time from March 8 to July 13, 1998, were used in the data analysis.

The processed images were projected using an Albers Conic Projection, with the center located at latitude 60.5 and longitude -147. Standard parallels for the projection were at latitude 59.0 and 61.0. The same projection was used for the temperature images.

Advanced Very High Resolution Radiometer (AVHRR) temperature data from the NOAA-14 and NOAA-12 satellite were obtained from the Fairbanks High Resolution Picture Transmission (HRPT) receiving station. Images were processed with the TeraScan® HRPT Antenna Server program. The following is an abbreviated version of methods published by McClain et al. (1985). After extraction from the recording tapes, images were navigated visually by lining up the coastline with the image. The image data were then calibrated with the ancillary calibration data to produce a dataset that is radiometrically calibrated in percent albedo and degrees Celsius. Subsequently the data were subjected to a variety of sequential tests to identify and eliminate cloudy areas. If a pixel fails to pass any one of the tests, it is flagged as cloudy and appears black in the image. A value of 2 °C was set as the maximum temperature change between adjacent pixels. A rapid temperature change usually indicates cloud contamination, as clouds can appear several degrees colder. Pixels were flagged if temperature changes exceeded this value. This screened out some frontal regions, but not in the areas of interest. To eliminate cloudy pixels from nighttime images, a value of -5 was assigned as the maximum difference between channels 3 and 4. This measures the difference between cloud and seasurface emissivity. All other parameters were left at their default values. As the tests were designed for temperate and tropical environments, the two adjustments were necessary. The parameter values were chosen by browsing all images using different values, and determining which gave the best tradeoff of excluding good data to possibly including bad (i.e. cloud contaminated) data. None of these tests affect the actual sea surface temperature (SST) calculations, but only eliminate pixels from being assigned a SST value.

Data Analysis

The hypothesis that physical or biological characteristics of the environment affect the energy content of sand lance was tested in several stages. First, I assessed

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whether there was a difference in length and condition among stations and years. Next, physical and biological measurements were tested for differences among stations, or for geographical trends. Finally, the relationships among environmental characteristics and energy content of sand lance were investigated. All analyses were performed in Microsoft®Excel 97 and StatView for Windows, version 5.0.

Before and after fitting a straight-line regression model, normality, variance, independence, and linearity were assessed in the data. The data were transformed if any one of these assumptions were not met. Unless stated otherwise, assumptions were met. Kruskal-Wallis tests were employed in place of Analyses of Variance when assumptions of equal variance were violated.

To test the hypothesis that standard lengths differed among stations and years, ANOVA was performed on years, and on stations within years. A Sheffe's test was employed to determine which stations or years were different. Length frequencies were unimodal after fish older than young-of-the-year (as determined by otoliths) had been removed (Appendix C).

Wet and dry weights were regressed on standard length to test whether lengthweight relationships differed among stations and years. Weights had to be transformed using logarithms in order to meet the assumption of linearity for straight-line regression. The data still had outliers and unequal variance. The outliers were distributed relatively evenly among stations, and were present on both ends of the distributions. They did not have an obvious effect on the slopes. Robust regression could not be used, as there is no method of comparing more than two slopes non-parametrically. Straight-line regressions were used as the only available tool. These were calculated for each station and year. Analysis of covariance (ANCOVA) was performed to compare the slopes of the regressions. A Tukey test was used to determine which slopes were different. It should be noted that the results might be questionable due to violations of assumptions.

To test the hypothesis that energy content was related to fish size, energy content was regressed on standard length for station 8S2. A scatterplot of the untransformed data suggested that the relationship could best be described by two separate regressions. The data were therefore divided at 70 mm standard length. An exponential model ($Y = ae^{bX}$) on undivided data was explored as an alternative.

ANOVA was used to test for differences in energy content among stations and years. To determine which stations were different, a Sheffe's test was performed. As other measures of condition, percent water (1-(dry weight/wet weight)*100) and Fulton's K index (K=(dry weight/length³)*100000) were calculated for each station. Cal/g dry weight was regressed on Fulton's K and on percent water to determine the reliability of these two alternative condition indices. Fulton's K and percent water are less time consuming and less costly to perform, and would be a welcome alternative if they prove to be reliable. Cal/g dry weight was also plotted against the standard length – dry weight regression slopes, but no confirmatory statistics were performed, as the relationship was non-linear, and the data too scarce to fit a curve.

To test for differences in ring net zooplankton abundance and in stomach content among stations, Kruskal-Wallis tests were performed on three plankton (and stomach content) categories: total plankton (or stomach content), small copepods, and cladocerans. Tukey-type non-parametric post-hoc comparisons (Zar 1984) were performed on the three categories. A Kruskal-Wallis test was also performed on the three areas (north, central, and south) from the Bongo net zooplankton. Post-hoc comparisons were performed as above. Plankton abundances are expressed as numbers per meter squared of water surface. Plankton per m^2 in a sample is equal to the sample count divided by the area of the ring net, 0.196 m².

Regression analysis was used to test the hypothesis that greater plankton abundance resulted in more items in the stomach. Station mean stomach content categories were regressed on station mean zooplankton categories (copepods, cladocerans, and total plankton).

To test the hypothesis that greater energy content was related to greater zooplankton abundance or stomach content, station mean energy content was regressed on station mean zooplankton abundance and stomach content. Preliminary scatterplots clearly showed the non-linearity and absence of trends in the ring net plankton and stomach content data, however, regression lines with r^2 values are included to show any possible trend.

Diurnal patterns in zooplankton abundance and stomach content were not assessed statistically. To check for possible trends visually, they were plotted against time.

The relationship between energy content and local temperature and chlorophyll levels was explored with correlations. The high variability and scarcity of energy content-CTD temperature and energy content-CTD chlorophyll data makes the use of parametric techniques questionable, as the assumptions cannot be satisfactorily assessed. Results of the regressions of energy content on CTD temperature and CTD chlorophyll are included primarily to show a possible trend in the data that may not be apparent to the naked eye.

To test the hypothesis that energy content of sand lance is related to either temperature or chlorophyll history, a mean was calculated for each AVHRR and SeaWiFS image. Values for each station were expressed in mean deviations from the image means. Mean energy content was then regressed on the mean deviations.

From the SeaWiFS images, a 15 by 15 computer pixel (one pixel represents 0.3573 km on each side) array was extracted around each station. These arrays contained data from between 0 and 17 non-flagged satellite pixels. The means of each array were log+1 transformed. For each image, a mean of all stations was calculated. For each station, the deviation from this image mean was then calculated. The mean of the deviations at each station was used for the confirmatory statistics.

From the AVHRR images a 3 by 3 array of pixels was extracted around each station (stations 8C1 and 8C2 were considered one station, because of their proximity to each other). The image was projected so that each pixel represented the maximum satellite resolution of 1.1 km. The arrays contained between 0 and 9 non-flagged pixels. Means and deviations were calculated as for the SeaWiFS data, but transformations were not necessary. Only images later than April 10, 1998 were included in the temperature analysis. This date was set as the first likely date during which postmetamorphosis sand lance may have been exposed to a temperature regime at a given

station. Mean energy content was regressed on mean deviations from mean temperature.

To test for coincidence between CTD-chlorophyll and SeaWiFS chlorophyll measurements, mean chlorophyll of the upper 2 m from the CTD data (collected on July 16 to 27) was regressed against mean chlorophyll from the last two SeaWiFS images (July 12 and 13). This test could not be performed for temperature measurements, as the last available AVHRR image data was collected on June 22, one month before the CTD casts.

RESULTS

Fish

Standard lengths of random subsamples of approximately 50 fish per station ranged from 52-102 mm, 53-110 mm, and 47-97 mm in 96, 97, and 98, respectively (Fig. 4, Appendix D). Length varied significantly within years (p < 0.001 for all years) as well as among years (p < 0.001). Standard lengths in 1997 (mean = 79.3 mm) were significantly higher than in 1996 (mean = 76.7 mm) or 1998 (mean = 76.2 mm; p =0.033 and p < 0.001 respectively). In 1998 station 8N2 and 8C6 had significantly lower standard lengths than most other stations, and station 8S4 had significantly higher standard length than most other stations (Appendix E). In 1998, the only year in which they can be compared, standard lengths from all three areas were significantly different, with the North being the lowest, the Central intermediate, and the South the highest. In 1997, all four stations were significantly different from each other except stations 7C2 and 7S1, the two stations of intermediate standard lengths. In1996, station 6N2 had significantly greater standard length than all other stations.

There was no significant difference between the standard length – wet weight or the standard length – dry weight regressions slopes among years (Fig. 5, Tables 2 and 3).

Standard length – wet weight regression slopes differed significantly among stations in 1998 (ANCOVA, p < 0.001). This difference is due to two stations, 8N1 and 8C2, which were the stations with the lowest and the highest slope, respectively (Tukey test). Standard length – dry weight regression slopes differed significantly among stations (ANCOVA, p = 0.01), due to station 8N1, the lowest slope, being significantly different from the highest slopes (stations 8S3 and 8S5; Tukey test).

At station 8S2 calories/g increased with increasing standard length; however, this trend did not appear until sand lance reached approximately 70 mm in length. Smaller fish did not increase in caloric content with increasing length (Fig. 6). The regression of energy content on standard length for sand lance > 70mm is significant (p < 0.001, $r^2 = 0.496$). The exponential model (Cal/g = 3850.386*e^{0.004*Standard length}) may be used as an alternative. However, although the fit is significant (p < 0.001), in a residual calories vs. standard length plot, positive residuals were decreasing in value up to 65 mm and were notably absent between 65 and 72 mm, suggesting a poor fit.

Although fish for caloric analyses were subsampled within a narrow size range, the mean length of those subsamples differed significantly among stations. Stations 8N2 and 8S5 were significantly shorter (mean = 77.5 and 77.5 mm) than stations 8S4 and 8S1 (mean = 82.3 and 81.7 mm, ANOVA and Tukey test).

Energy content ranged from 4760 to 5610 cal/g in 1996, from 4630 to 5670 cal/g in 1997, and from 4490 to 5670 cal/g in 1998 (Appendix F). Energy content among years and among stations within years were significantly different.

Energy content in 1998 was significantly lower than in either 1996 or 1997 (mean = 5055 cal/g vs. 5257 and 5240 cal/g respectively, p < 0.001). There was no difference between energy contents in 1996 and 1997.

In 1998, the two stations highest in energy content (8S1 and 8S4) were significantly different from the three stations with lowest energy content (8N1, 8C3, and 8C5; ANOVA, Appendix G). Although not consistently significant, stations south of Naked Island generally had higher energy content than other stations (Fig. 7). A notable exception to this is station 8S5 in 1998, the southernmost station, which had low energy density. In 1998, the South area had significantly higher energy content (5212 cal/g) than the North (4904 cal/g), and Central (4971 cal/g) areas (ANOVA with Scheffe's, p < 0.001).

In 1998, stations with longer fish had higher energy content, even though there was a 75-85 mm range of the calorimetry subsample (Fig. 8). This does not appear to be true for other years, although it cannot be assessed by regression due to the lack of sufficient data. In 1996 and 1997 the southern stations (7S1, 7S2, and 6S1) have high energy content with low or intermediate standard lengths (Fig. 4 and 7).

Fulton's K index is a poor predictor of energy content. Although the regression is highly significant (p < 0.001), the relationship is quite variable ($r^2 = 0.211$; Fig. 9). The percent water – energy content regression is also significant (p < 0.001). The relationship strengthens with increasing size of fish (Fig. 10). Percent water predicts energy content with greater accuracy ($r^2 = 0.639$) than Fulton's K ($r^2 = 0.211$).

The slopes of the standard length – dry weight regressions for all years were positively correlated with energy content (Fig. 11). However, the relationship was non-linear, with the highest slopes not exhibiting a corresponding increase in calories/g.

Temperature and Chlorophyll

Mean temperature measured by CTD over 2-10 m depth ranged from 11.8 °C (Station 8S3 on 7/25/98) to 13.7 °C (Station 8N2 on 7/22/98). The northeastern stations had the highest temperatures. Mean chlorophyll measured by CTD over 2-11 m depth ranged from 38.7 μ g/L (Station 8S3, 7/25/98) to 96.4 μ g/L (Station 8C3, 7/17/98). Energy content of sand lance was unrelated to CTD temperature as well as chlorophyll (p = 0.349, r² = 0.080 and p = 0.255, r² = 0.116; Figs. 12 and 13 respectively).

Temperatures from the AVHRR images ranged from 2.8 °C to 11.2 °C for individual pixels within the arrays. Image means ranged from 4.6 °C to 11.0 °C for the period from March 21 to June 22, 1998 (Fig. 14, Appendix H). Station means over the entire period ranged from 6.0 °C (8C1&2) to 7.1 °C (8S2). There was a clear geographic trend in mean deviations from mean temperatures at each station (Fig. 15). Stations north and west of Naked Island (8N1, 8C1&2, 3, and 4) had negative deviations, stations east and south of Naked Island (8C5 and 6, 8S1, 2, and 3) had positive deviations. The maximum difference between mean station deviations was 0.84 °C. The regression of energy content on mean temperature deviation was significant ($r^2 = 0.455$, p = 0.032; Fig. 16). Energy content was higher at stations with higher temperatures.

Chlorophyll as estimated by SeaWiFS images ranged from < 0.1 μ g/L to > 64 μ g/L for individual pixels within the arrays (Fig. 17, Appendix I). Image means ranged from 0.9 μ g/L to 14 μ g/L for the period from March 8 to July 13,1998. Station means over the entire period ranged from 5.2 μ g/L (station 8S3) to 1.6 μ g/L (station 8S2). Stations 8N2 and 8S3 had the greatest positive mean deviations from the mean. Stations 8C1, 8C5 and 8C6 had the greatest negative deviations (Fig. 18). No geographic trend was apparent in the distribution of surface chlorophyll. Energy content of sand lance was unrelated to chlorophyll as estimated by SeaWiFS images (r² = 0.064, p = 0.403). There was no relationship between chlorophyll estimates from the CTD and from SeaWiFS images (r² = 0.242, p = 0.088).

Plankton and Stomach Content

Plankton consisted primarily of small copepods (mostly *Pseudocalanus* sp. and *Acartia* sp.), cladocerans (*Evadne* sp. and *Podon* sp.), larvaceans (*Oikopleura* sp.), and mollusks (bivalve and gastropod larvae and juveniles) (Fig. 19a). Total ring net plankton abundance ranged from 15,180 items per m² at station 8C6 to 142,906 items

per m² at station 8C2 (Table 4). Abundances of small copepods, cladocerans, and total zooplankton differed significantly among stations (p < 0.01 for all). For total ring net plankton, station 8C6 was significantly lower than stations 8C2 and 8C4; for copepods, station 8S2 was significantly higher than stations 8C6 and 8S5; for cladocerans, station 8C4 was significantly higher than station 8S3 (Tukey-type test). There was no geographic trend in ring net plankton distribution (Fig. 19b).

Bongo net plankton was predominantly small copepods (Fig. 20a). The south area had significantly more total plankton than the north and central areas (Kruskal-Wallis with Tukey type post-hoc; Fig. 20b), as well as a higher proportion of copepods (Fig. 20a).

Stomach content also consisted of mostly small copepods, cladocerans, and mollusks. Larvaceans were not as abundant in the stomachs as they were in the plankton (Table 5). Total stomach content counts ranged from 0 to 2296 items per stomach. The stomach content weights ranged from 0 g to 0.125 g. The stomach content weight – stomach content count regression was significant (p < 0.001, $r^2 = 0.704$, n = 130).

Stomach contents differed significantly among stations for all categories (p < 0.001 for all categories; Appendix J). For all categories, stations 8S2 and 8S3 were lower than most other stations. Both of these stations had very low stomach content counts, with several empty or almost empty stomachs. Total stomach content was unrelated to mean total plankton (p = 0.305, $r^2 = 0.095$, Fig. 21).

Energy content of sand lance (mean calories/g) was unrelated to stomach content weight (p = 0.258, $r^2 = 0.115$, Fig. 22) or stomach content as percent of body weight (p = 0.245, $r^2 = 0.121$; Fig. 23). There was no significant relationship between the station means of any of the categories (for plankton or stomach contents) and mean energy content (p > 0.15 for all categories; Fig. 24). No trends were apparent in the data. Time of day at which samples were collected had no apparent effect on zooplankton abundance or stomach content abundance (Fig. 25 and 26).

DISCUSSION

The link between seabird productivity and sand lance availability has been documented in the Atlantic (Bailey et al. 1991, Lock 1987, Monaghan 1992) and in the Pacific (Bertram and Kaiser 1993, Roby et al. 1998). The high energy content of sand lance species explains their importance as forage fish, especially to nesting seabirds. Sand lance rank fourth (out of 18 forage fish species) in mean energy content (per wet mass) after lanternfish, eulachon, and herring (Anthony et al., in review). For some seabirds, sand lance abundance may be the key factor in reproductive success, especially for species such as horned puffins, whose diet in the northern Gulf of Alaska consisted of 85 % sand lance in 1985-87 (Hatch and Sanger 1992).

Energy content of sand lance varied among stations in PWS. Variations in condition have also been reported for herring and walleye pollock in PWS (Boldt 1996, Paul and Paul 1999), indicating areas in PWS vary in quality of habitat for planktivorous fishes. Calories per gram dry weight of YOY sand lance ranged from 4490 to 5670. This is close to the range of values for YOY *Ammodytes* spp. (75-85 mm) elsewhere (5255 cal/g, Hislop et al. 1991; 4060-4540 cal/g, Robards 1999). Sand lance in the south had higher energy content than sand lance in the north or central PWS in 1998. This was true for 1996 and 1997 as well, although the sample size in those years was smaller.

Energy content was considered the best indicator of fish condition. Percent water was more highly correlated with energy content than Fulton's K condition index. Using water content as a quick method for estimating energy content has been suggested for other families of fish (Hartman and Brandt 1995), as well as for *Ammodytes marinus* (Hislop et al.1991). The relationships between energy content and water content for *A. marinus* ($r^2 = 0.89$, Hislop et al. 1991) and *A. hexapterus* in lower Cook Inlet (Robards 1999, $r^2 = 0.92$), in addition to that found for sand lance in PWS ($r^2 = 0.64$) clearly show that water content may be a welcome alternative to energy content analysis.

Slopes of the standard length – dry weight regressions were positively correlated with energy content. The relationship was non-linear, and the low number of data points precluded development of a curve to describe the relationship. However, standard length – dry weight regression slopes may be a good indicator of condition for slopes less than 0.025.

Standard lengths of YOY sand lance ranged from 47 mm to 97 mm in 1998, with the smallest fish still having clear tails at the time of catch in July, indicating they had recently metamorphosed from the larval stage. Energy content was assessed only for fish between 75 and 85 mm standard length. For some schools, this represents only the oldest fish in the school. For others, the size interval samples only the most recent recruits, as timing of recruitment varies among schools. The source of sand lance larvae, ocean currents, may also be the source of some of the variations in other biological and physical factors. It is therefore difficult to distinguish between the effects of water body properties and age of sand lance, since time of metamorphosis could not be determined. Therefore, while eliminating the comparison of condition of fish of unequal lengths, choosing a size interval for sampling introduces the potential bias of unequal age. This may explain why sand lance from schools with greater mean fork length, which were probably older, also had greater energy content.

The variability in chlorophyll and temperature in PWS make clear that PWS is not a homogeneous body of water. A portion of the Alaska Coastal Current enters PWS through Hinchinbrook Entrance and exits through Montague Straight (Niebauer et al. 1994). Some of this water sets up a cyclonic circulation pattern in the eastern part of PWS. Variability in inflow/outflow, watermass residence time, and great variability in depth (Niebauer et al. 1994) may lead to different oceanographic conditions among areas of PWS, including temperatures, salinity, and plankton.

The SeaWiFS chlorophyll images and the CTD fluorometer casts revealed no trend in chlorophyll distribution within PWS. CTD casts were cut off at a depth of 11 m because there were no data available for deeper depths at several stations due to problems with the CTD. For the five stations for which data were available to 20 m depth, the top 11 m contained the majority of the chlorophyll in the watercolumn at

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three stations. The differences between the means of 11m depths and 20 m depths were within 2 μ g/L.

Chlorophyll a biomass measurements have been used extensively as a proxy for primary productivity (Platt and Sathyendranath 1988). This, in turn, is a good indicator of the energy that is available to the food web. Productivity is the rate at which carbon is fixed. Measuring the standing stock of chlorophyll does not take into account the turnover rate of phytoplankton, which depends on several factors, including zooplankton grazing rates, temperature, nutrient availability, and phytoplankton species. PWS proved to be variable in temperature, and nutrients in the water are likely to have differed among areas with varying amounts of runoff. Surface chlorophyll may therefore only moderately correlate with productivity, as was the case on the northwest Atlantic continental shelf (Campbell and O'Reilly, 1988).

Station 8S3, located off Green Island, stands out among the remotely sensed chlorophyll measurements for its high positive mean deviation. The deviation is a result of high chlorophyll values throughout the time of measurements, and not caused by a single high data point. This station is also second highest in the temperature deviations, and therefore not likely to be an area of local upwelling and consequent high productivity.

The inconsistency between the results of the fluorometer and the satellite image that was closest to the CTD cast in time may be attributed to the time difference of 3 to 14 days between the two types of measurements. It may also be due to the degree of error associated with remotely sensed chlorophyll biomass (Pinkerton and Aiken 1999). The fluorometer takes one measurement for every meter in depth, while the satellite sensor only receives the light that is returned from the surface of the ocean. Satellite images, which give good coverage in time, do not show how chlorophyll is distributed in the water column. Deeper maxima will be undersampled due to the light attenuation. Phytoplankton species also affect satellite chlorophyll estimates, so that different species assemblages may require the use of different algorithms to calculate chlorophyll biomass (Chavez 1995). The fluorometer, which takes a more accurate measurement of chlorophyll in the water column was employed only once at each station.

In addition to the uncertainty of the chlorophyll measurements and the difficulty of predicting primary productivity from chlorophyll, predicting production of secondary or tertiary consumers, such as sand lance, from it becomes a difficult task at best. This may explain why fisheries applications of remotely sensed chlorophyll biomass are rare. In the southern Benguela Current system ocean color measurements were used in combination with ship observations and available data on primary productivity to assess food limitation of pelagic fish stocks (Shannon and Field 1985). Without the local productivity to biomass ratios, however, chlorophyll standing stock may not be a very useful measurement.

The reliability of AVHRR sea surface temperature (SST) measurements is well established (Bernstein 1982), and due to the extensive scale in time and space, provide a good picture of the temperature history that sand lance in PWS experienced in 1998. Between the end of March and the end of June 1998, mean SST increased from approximately 5 °C to 11 °C. The clear separation between colder SST in the north and

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west, and warmer waters in the east and south, may be due to the glacial runoff in the north and northwest of PWS and the separation between east and west by the Naked and Knight Island Groups. CTD temperatures, which are based on a single observation at each station, did not coincide with satellite data.

The Bongo net plankton samples had significantly more small copepods and total plankton in the south region of PWS, than in the north and central area. There was no trend in the distribution of ring net zooplankton, which is probably due to the small sample sizes and only one time sampling. The Bongo net samples provide a better representation of zooplankton present in an area, because they were taken at night and over deeper waters. Vertically migrating zooplankton would not have been captured in the ring net samples.

The lack of relationship between stomach content, ring net plankton abundance, and energy density is not surprising, as the samples were collected at a single point in time. There are no obvious reasons why two stations (8S2 and 8S3) had many empty or almost empty stomachs. All samples were collected long after sunrise, when, presumably, sand lance begin to feed.

Sand lance fed on all zooplankton that was available to them, primarily small copepods. The only discrepancy between plankton samples and stomach contents was for larvaceans, which were underrepresented in the stomachs. Sturdevant and Hulbert (in review) also reported a slight negative selection for larvaceans. This could be due to either lower consumption rates of larvaceans, which are possibly invisible to sand lance in the water, or to quicker digestion rates of these soft bodied organisms.

The two sand lance schools sampled in the north in 1998 both were mixed schools with herring. Mixed schools of sand lance and herring are not uncommon (Richards 1976, Sturdevant and Hulbert, in review), but the reason for schooling together has not been studied. It may be related to the lack of conspecifics in the area. Although not apparent from this study, sand lance reportedly shift their diet and feed less when schooling with herring (Sturdevant and Hulbert, in review). If that was the case for these schools, there was no significant decrease in condition in response compared to the schools from the central area, in spite of the relatively small size of the northern sand lance.

The relationship I observed between length and condition has been observed in sand lance and other species. Larval anchovy in the Southern California Bight exhibit an exponential relationship between length and lipid content (Håkanson 1989). A shift in energy allocation from protein growth to lipid storage with attainment of a larger size has been suggested for young-of-the-year gulf menhaden (Deegan 1986). Larger *Ammodytes marinus* (lesser sandeel) tend to have higher caloric values than smaller ones (Hislop et al. 1991). Robards (1999) found that juvenile sand lance in lower Cook Inlet increased lipid growth relative to protein growth at a standard length of approximately 80 mm, a size similar to the threshold for change in energy content observed in this study (70 mm). The initial growth phase, an increase in length without the gain in energy content, may decrease the vulnerability to predators. Not only does escape speed increase with increasing length (Folkvord and Hunter 1986, Williams and
Brown 1992), the prey may also outgrow some of their predators' gape size (Werner et al. 1983).

Sand lance in 1998 had the lowest energy content of all three years studied. Although the sample distribution was unbalanced among areas in those years, which may lead to biased results, the significant decline in energy content in 1998 may be a result of the oceanographic conditions of that year. The El Niño event in the winter of 1997/98 was one of the strongest recorded in the northern Pacific ocean (Barnston et al. 1999). The low productivity of forage fish that results from El Niño is well documented for the northeast Pacific (Bailey et al. 1995). It is possible, therefore, that the lower productivity associated with El Niño carried into PWS with the Gulf of Alaska waters, and led to lower condition of sand lance in 1998. However, there is no indication that 1998 temperatures differed from those in 1996 and 1997 in PWS (Haldorson et al. 1999). El Niño conditions may have been responsible for the decline in energy content of sand lance in 1998, but no change in temperature was detected. It is possible that the difference in energy content among years is solely due to the biased sample distribution.

Energy content of YOY sand lance positively correlated with temperature history. The warmer, southern areas of PWS had high zooplankton abundance, and were harboring fish of better condition. Several euphausiid species in PWS exhibited a similar trend in energy content, with individuals from the south being in better condition than those from the north (Mooney 1999). This may indicate high primary productivity in that area, with no food shortage for either zooplankton or sand lance. In lower Cook Inlet, sand lance from colder sites grew faster than those from warmer sites (Robards

1999). This may be due to the interrelationship of temperature and prey availability. Higher water temperatures and the associated higher metabolism and feeding rates (Paloheimo and Dickie 1966) would lead to higher growth rates only if food was abundant. This may have been the case in PWS, particularly in the south. In times of food shortage, colder temperatures and hence lower metabolic rates would be of advantage to the fish, which may have been the case in lower Cook Inlet (Robards 1999). Sand lance in lower Cook Inlet were in poorer condition than those in PWS, with a mean energy content of 4706 cal/g for sand lance of 85-89 mm standard length (Robards 1999).

Sand lance were not sampled quantitatively. However, in spite of great effort, we were not able to get samples of more than two schools in north PWS in 1998. These are sites where sand lance had been caught in previous years. A comprehensive study of fish biomass in PWS reported no sand lance in the north in 1998 (Haldorson et al. 1999). This coincides with a decline in the proportion of sand lance in black-legged kittiwake diets in that area (Roby et al. 1999). YOY sand lance dominated the diet of kittiwakes (Irons et al. 1999) at Eleanor Island, just south of Naked Island where sand lance were abundant.

1998 was a poor year for black-legged kittiwakes and pigeon guillemots (Roby et al. 1999), as it was for sand lance with respect to condition. Availability and quality of prey items may have been the limiting factor, possibly brought on by El Niño conditions (Irons et al. 1999). Kittiwake colonies in the central and south PWS were more successful in 1998 than the colony in the north (Irons et al. 1999). Energy provisioning rates to Pigeon Guillemot nestlings were almost twice as high in the southern colony, Jackpot Island, than in the Naked Island colony (Roby et al. 1999). This is in agreement with the results of my study. The greater breeding success and higher energy provisioning rates to bird colonies in southern PWS (Irons et al. 1999, Roby et al. 1999) may be due to greater productivity in that area, a hypothesis supported by high plankton abundance and greater energy content of sand lance in the south.

SUMMARY

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Energy content of YOY sand lance varied among years and areas of PWS. Sand lance in the south were in better condition than those in the central and north areas of PWS. Energy content was lower in 1998 than in 1997 and 1996. Energy content was related to standard length of the schools from which the samples originated, regardless of the limitation of 75-85 mm for calorific analyses. Energy content increased with increasing standard length only after sand lance had reached approximately 70 mm. There was no geographic trend in chlorophyll distribution in PWS. SST was lower in the north and west than in the south, separated by the Naked and Knight Island groups. Energy content of sand lance was positively correlated with SST. There was no trend in ring net plankton or stomach content abundance. Bongo net plankton was significantly more abundant in the south than in the north and central areas. This agrees with the higher SST and greater energy content of sand lance in the south, indicating higher productivity in that area.

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Fig. 1 Map of Prince William Sound, Alaska, with the 1998 collection stations.







Fig. 3 Map of Bongo net zooplankton collection areas.



Fig. 4 Mean standard lengths of sand lance in 1998 (a), 1997 (b), and 1996 (c). Error bars are \pm one standard error.



Fig. 5 Log(wet weight) regressed on log(standard length) for 1996, 1997, and 1998 combined. N = 1039



Fig. 6 Calories per gram dry weight regressed on standard length (mm) for station 8S2. The data were split at 70 mm. N = 49



Fig. 7 Mean calories per gram dry weight of sand lance for 1998 (a), 1997 (b), and 1996 (c). All values are for sand lance of 75-85 mm standard length. Error bars are \pm one standard error.



Fig. 8 Mean calories per gram dry weight from the 10 fish subsample (75-85 mm standard length) regressed on mean fork length (mm) measured in the field for at least 200 sand lance per station. N = 13



Fig. 9 Calories per gram dry weight regressed on Fulton's K condition index for 1998. N = 130



Fig. 10 Calories per gram dry weight regressed on percent water for 1998 sand lance. N = 130



Fig. 11 Mean calories per gram dry weight plotted against the standard length – dry weight regression slopes. N = 21



Fig. 12 Mean calories per gram dry weight regressed on mean temperature (°C) over the depth of 2-10 m measured by CTD. N = 13



Fig. 13 Mean calories per gram dry weight regressed on total chlorophyll (μ g/L) over the depth of 2-11 m measured by fluorometer on CTD. N = 13



Fig. 14 Satellite AVHRR sea surface temperature images. The scale ranges from 0 to 13 °C. Numbers indicate julian dates of 1998.

Fig. 10 Mean calories per gram dry weight regressed on mean deviation from mean temperature (°C) measured by AVHRR. Deviations are averaged for days 103 to 173 1968. N = 10, p = 0 tr331







Fig. 16 Mean calories per gram dry weight regressed on mean deviation from mean temperature (°C) measured by AVHRR. Deviations are averaged for days 103 to 173, 1998. N = 10, p = 0.0323



Fig. 17 Examples of satellite SeaWiFS chlorophyll a images. Images were taken on julian days 113 (a) and 168 (b), 1998. The scale is from 0.01 to $64 \mu g/L$.



Fig. 18 Mean deviation from mean log(chlorophyll+1) measured by SeaWiFS at each station for March 8 to July 13, 1998.



Fig. 19 a) Percent composition of ring net plankton at each station in 1998. b) Mean number of items per square meter of ring net plankton. c) Mean number of items per stomach at the same stations. Error bars are ± 1 standard error.



Fig. 20 a) Percent composition of Bongo net plankton samples. b) Mean number of total zooplankton per square meter. Error bars are ± 1 standard error.

Central Areas

South

a)

50

0

North



Fig. 21 Mean total stomach content regressed on mean total ring net plankton/m². N = 13; regression is not significant.



Fig. 22 Mean calories per gram dry weight regressed on mean stomach content weight (g). N = 13; regression is not significant.



Fig. 23 Mean calories per gram dry weight regressed on mean stomach content weight as percent of body weight. N = 13; regression is not significant.



Fig. 24 1998 mean calories/g regressed on mean copepods in plankton (a) and stomach (b); mean cladocerans in plankton (c) and stomach (d); mean total plankton (e) and total stomach content (f). All regressions are not significant.



Fig. 25 Mean zooplankton abundance at the collection times for each sample. Error bars are ± 1 standard error. N = 3 for each station.



Fig. 26 Mean stomach content counts at the times of collection for each sample. Error bars are ± 1 standard error. N = 10 for each station.

Table 1 List of items in zooplankton and stomach content samples and corresponding categories.

Item	Category
Calanoid, unidentified small (< 2.5 mm) Calanoid, <i>Acartia</i> sp. Calanoid, <i>Centropages abdominalis</i> Calanoid, <i>Eurytemora pacifica</i> Calanoid, <i>Pseudocalanus</i> sp. Calanoid, <i>Metridia</i> sp. Cyclopoid, <i>Oithona</i> sp. Calanoid, unidentified large (> 2.5 mm) Calanoid, <i>Calanus</i> sp. Harpacticoid, unidentified	Copepod
Calanoid, unidentified nauplius	Copepod nauplius
Larvacea, Oikopleura sp.	Larvacean
Gelatinous zooplankton, unidentified Ctenophore, general	Gelatinous
Cladoceran, <i>Evadne</i> sp. Cladoceran, <i>Podon</i> sp.	Cladoceran
Shrimp, general unknown large crustacean (usually eyes only) Decapod zoea, unidentified	Large crustacean
Gastropoda, unidentified juvenile snail Gastropoda, Pteropod, unidentified Bivalve, unidentified juvenile Gastropod, unidentified veliger	Mollusk
Invertebrate egg Ostracod, unidentified Eggmass, unidentified Unidentified item Unidentified "worm" Barnacle, cyprid Barnacle adult molt (cirri & moutharea) Barnacle, nauplius	Other

Table 2 Standard length - dry weight regression coefficients for sand lance collected in 1996, 1997, and 1998. All regressions are significant.

Station	Slope	Intercept	r ²
6N1	0.023	-1.286	0.892
6N2	0.049	-3.568	0.855
6N3	0.018	-0.961	0.911
6S1	0.021	-1.151	0.945
7C1	0.021	-1.172	0.818
7C2	0.017	-0.924	0.821
7S1	0.033	-2.184	0.904
7S2	0.050	-2 .270	0.938
8 N1	0.014	-0.679	0.826
8N2	0.013	-0.573	0.909
8C1	0.022	-1.249	0.875
8C2	0.020	-1.100	0.936
8C3	0.01 8	-0.951	0.931
8C4	0.019	-1.021	0.817
8C5	0.017	-0. 8 70	0.939
8C6	0.013	-0.651	0.927
8S1	0.025	-1.432	0.857
8S2	0.019	-0.958	0.914
8S3	0.019	-1.014	0.866
8S4	0.029	-1. 8 45	0.926
8S5	0.019	-1.082	0.899

Table 3 Regression coefficients for the standard length (mm) - wet weight (g) regressions for 1998. Regressions follow the formula

wet weight = aL^b ,

where a is the intercept, b is the slope, and L is the standard length in mm. All regressions are significant.

Station	а	b	r ²
8N1	-4.894	2.731	0. 8 59
8N2	-5.589	3.112	0.926
8C1	-5.122	2. 8 93	0.908
8C2	-6.175	3. 4 3 8	0.967
8C3	-5.283	2.971	0.942
8C4	-5.257	2.963	0. 8 80
8C5	-5.706	3.197	0.975
8C6	-5.732	3.1 8 2	0.979
8S1	-5.449	3.062	0.914
8S2	-5.701	3.179	0.9 8 9
8 S3	-5.699	3.170	0.96 8
8S4	-5.937	3.307	0.934
8S5	-5.638	3.13 8	0.944

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Table 4 Mean ring net zooplankton abundance and standard errors at each station in 1998.

14.

STATIONS:	8N1	se	<u>8N2</u>	Se	8 C1	se	8 C2	Se	8C3	Se	8 C4	se	8C5	se
copepods	4794	491.3	6404	686.3	7851	1258.9	8725	1631.8	4144	528.0	8262	1126.1	6886	1253.4
cop. naup.	448	169.3	928	231.5	960	133.2	2112	205.7	752	48.0	4096	352.5	208	75.6
larvacean	267	64.9	427	21.3	939	166.6	1301	182.3	576	288.0	1899	56.4	1130	266.2
gelatinou s	17	3.8	208	130.8	420	95.2	551	116.1	21	20.5	279	39.0	204	43.9
cladocer.	3403	2114.0	4277	584.9	4011	351.2	6229	1703.1	3440	80.0	5739	565.6	491	74.3
lg. crust.	143	98.3	195	96.9	322	97.7	87	57.5	18	17.5	411	138.6	67	40.4
mollusks	2848	1532.2	7552	758.2	3328	288.9	7425	2273.4	2529	159.5	4569	833.6	460	105.1
other	356	65.4	960	98.0	747	237.6	1579	272.4	44 9	31.0	491	56.5	789	64.9
TOTAL	12275	4317.1	20951	1574.3	18577	1554.3	28010	5829.1	11928	791.5	25745	2702.0	10236	1660.2
total/m^2	62628		106891		94781		142906		60855		131350		52223	

STATIONS:	8C6	se	8S1	se	8 S2	se	8 S 3	Se	8S4	se	8S5	Se
copepods	463	94.2	6129	804.3	13720	1389.9	6070	343.1	3885	174.1	1643	254.6
cop. naup.	300	26.0	368	162.4	384	64.0	128	18.5	533	111.4	981	46.5
larvacean	684	162.3	880	82.1	1173	129.8	1877	117.3	363	101.8	2581	76.9
gelatinous	29	10.2	194	47.4	119	74.6	534	84.6	48	16.8	671	58.7
cladocer.	301	28.2	1387	460.2	1685	106.7	224	18.5	1472	32.0	2059	272.4
lg. crust.	2	1.2	113	24.4	172	21.0	22	21.5	11	10.7	43	10.7
mollusks	282	10.1	1446	361.8	1239	174.7	267	21.5	5302	419.2	1612	385.0
other	915	125.9	576	104.9	363	42.8	171	91.1	533	125.8	705	157.6
TOTAL	2975	247.6	11092	1643.8	18855	1371.6	9293	389.1	12147	691.9	10295	601.7
total/m^2	15180		56594		96201		47413		61976		52526	

STATIONS:	8N1	se	8N2	se	8C1	se	8C2	se	8C3	se	8 C4	se	8C5	se
copepods	249	25.7	196	10.6	407	49.4	116	48.2	87	29.0	380	46.8	765.3	197.7
cop. naup.	10	1.3	54	6.2	21	2.9	15	5.3	8	2.8	48	11.6	29.2	6.5
larvacean	6	0.9	7	1.4	9	1.5	1	0.4	9	2.5	13	1.8	21.6	3.9
cladocer.	109	6.8	340	32.9	148	28.9	80	34.8	78	26.6	370	45.6	52	9.7
la. crust.	3	0.8	3	1.1	4	0.8	1	0.4	0	0.1	3	0.9	2	0.6
mollusks	24	5.8	184	38.7	42	8.6	66	21.3	53	23.4	90	20.8	27.7	7.2
other	20	5.5	72	13.5	24	3.0	13	3.6	19	6.7	71	12.1	52	11.6

291 110.8

253 84.8

Table 5 Mean stomach content abundance and standard errors at each station in 1998.

855 77.9

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TOTAL

420 28.4

STATIONS:	8 C6	se	8S1	se	8S2	se	8 S3	se	8 S4	se	8 S5	se
copepods	145	52.1	483	73.8	29	11.7	24	9.6	185	52.2	168	40.7
cop. naup.	4.3	1.6	12	1.8	2	1.3	1	0.4	8	1.3	46	4.2
larvacean	8.6	2.2	12	1.9	7	2.2	7	3.5	4	1.7	47	10.7
cladocer.	16	5.0	44	4.8	2	0.9	1	0.5	36	8.0	43	7.5
lg. crust.	2	0.9	10	1.6	0	0.1	0	0.2	1	0.4	2	0.7
mollusks	16	4.3	. 11	1.9	3	1.5	1	0.6	80	19.7	58	11.6
other	34	7.2	12	3.1	2	1.0	2	0.6	100	16.7	50	10.1
TOTAL	225	68.0	5 8 5	84.3	45	16.9	37	13.8	413	81.5	414	74.0

655 85.5

71

976 121.7

950 218.0

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Appendix A

Sand lance and ring net zooplankton collection stations.

						Bottom Depth	Gear Depth
Station	Date	Time	Location	Lat.	Long.	(m)	(m)
6N1	24/07	9:50	S. Bligh Island	60 49.78	146 48.89		
6N2	24/07		Port Fidalgo	60 46.72	146 25.40		
6N3	25/07	14:30	Knowles Head	60 41.40	146 32.00		
6S1			Swansen Bay	60 01.08	148 12.00	20	2

						Bottom	Gear
						Depth	Depth
Station	Date	Time	Location	Lat.	Long.	(m)	(m)
7C1	24/07	11:00	W. Naked Island	60 38.75	147 29.71	5	5
7C2	02/08	13:00	Cabin Bay	60 40.15	147 26.77	18	
7S1	04/08	13:45	Shelter Bay	60 07.70	147 56.67	16	
7S2	19/07	14:15	Bainbridge Passage	60 8.94	148 9.46	50	3

						Bottom	Gear
						Depth	Depth
Station	Date	Time	Location	Lat.	Long.	(m)	(m)
8N1	22/7	1150	Valdez Arm	60 57.78	146 45.31	61	5
8N2	21/7	1730	Reef Island	60 51.36	146 48.63	6	5
8C1	23/7	850	N. Naked Island	60 41.27	147 27.66	3	5
8C2	23/7	1000	NW Naked Island	60 41.18	147 28.87	3	5
8C3	17/7	1245	W. Naked Island	60 41.**	147 33.**	2	2
8C4	23/7	1235	Outside Bay	60 39.**	147 36.39	5	5
8C5	23/7	1400	Outside Bay	60 37.91	147 27.73	6	5
8C6	16/7	1545	E. Naked Island	60 39.15	147 19.11	12	5
8S1	24/7	1400	NE Ingot Island	60 31.50	147 37.19	5	5
8S2	24/7	1745	Bay of Isles	60 25.06	147 37.62	3	3
8S3	25/7	1400	Green Island	60 14.77	147 26,06	4	3
8S5	26/7	1530	NE Elrington Island	59 58.48	148 10.51	4	3
8S4	27/7	1215	N. Evans Island	60 07.15	147 53.43	4	3
Appendix B

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Bongo net zooplankton collection locations. All samples were collected in 1998.

Data	Time	Location	Lot In	Longin	Bottom	Gear
Dale	1 11116	Location	Lat. In	Long m.	depth (m)	depth (m)
14/7	23:27	North	60 41.873	146 14.372	146	60
15/7	0:35	North	60 40.722	146 17.962	132	60
15/7	4:05	North	60 42.167	146 19.883	56	55
15/7	22:42	North	60 43.976	146 19.777	25	22
15/7	23:27	North	60 41.622	146 23.026	41	35
16/7	0:10	North	60 39.117	146 22.336	118	60
16/7	1:46	North	60 38.908	146 27.075	43	40
16/7	3:18	North	60 39.639	146 35.287	37	30
16/7	22:52	Central	60 37.829	147 17.273	105	60
16/7	23:43	Central	60 38.03	147 15.495	173	60
17/7	0:11	Central	60 39.773	147 14.837	140	60
17/7	1:23	Central	60 41.161	147 14.620	161	60
17/7	2:39	Central	60 43.29	147 15.446	170	60
17/7	22:55	Central	60 43.92	147 33.803	592	60
18/7	0:13	Central	60 40.816	147 33.253	>275	60
18/7	1:25	Central	60 38.787	147 36.651	560	60
18/7	2:35	Central	60 36.791	147 36.734	585	60
18/7	22:34	South	60 16.808	148 11.346	151	60
18/7	23:25	South	60 18.934	148 10.219	181	60
19/7	0:35	South	60 17.184	148 7.824	94	60
19/7	1:52	South	60 13.362	148 9.920	108	60
19/7	22:35	South	60 11.759	148 5.482	238	60
19/7	23:45	South	60 15.604	148 3.635	485	60
20/7	0:50	South	60 14.925	147 58.993	640	60
20/7	2:19	South	60 9.296	147 59.507	256	60

Appendix C















Appendix D

Standard length data for random subsamples from all years.

1996							
Station	Mean	Max	Min	Median	SD	SE	n
6N1	72.8	94	52	70	11.531	1.771	51
6N2	88.7	102	71	89	5.832	1.152	52
6N3	71.3	90	59	70	5.982	0.830	52
6S1	73.8	86	65	72	5.277	0.746	50

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1997

Station	Mean	Max	Min	Median	SD	SE	n
7C1	81.3	85	75	82	2.849	0.475	36
7C2	78.5	90	65	78	5.987	0.847	50
7S1	92.6	110	75	92	8.471	1.198	50
7S2	65.5	80	51	66	6.698	0.947	50

1998

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Station	Mean	Max	Min	Median	SD	SE	n
8N1	70.0	87	55	69	7.382	1.044	50
8N2	63.2	82	53	62	6.995	0.989	50
8C1	81.9	90	72	81.5	4.104	0.580	50
8C2	76.6	86	63	76	5.830	0.825	50
8C3	76.3	89	64	77	5.690	0.797	51
8C4	78.6	93	68	79.5	5.341	0.755	50
8C5	71.8	85	55	72.5	7.245	1.025	50
8C6	66.7	81	53	67	6.320	0.903	49
8S1	83.5	92	72	83	4.372	0.569	59
8S2	77.3	93	48	78	9.970	1.410	50
8S3	82.3	91	47	84	7.364	1.041	50
8S4	87.2	97	73	87	4.674	0.668	49
8S5	74.4	87	65	74	4.911	0.695	50

Appendix E

Significant differences in standard length according to Sheffe's test. Significance is indicated by the p-value.

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1998

Station	8S2	8S3	8S5	8S4	8C6	8C3	8N2	8N1	8C1	8C2	8C4	8C5
8S1	0.014		<0.01		<0.01	<0.01	<0.01	< 0.01		<0.01		<0.01
8S2	*			<0.01	<0.01		<0.01	< 0.01				
8S3		*	<0.01		<0.01	0.032	<0.01	< 0.01				<0.01
8S5			*	<0.01	<0.01		<0.01		< 0.01			
8S4				*	<0.01	<0.01	<0.01	<0.01		<0.01	<0.01	<0.01
8C6					*	<0.01			<0.01	<0.01	<0.01	< 0.01
8C3						*	<0.01	0.018				
8N2							*	<0.01	<0.01	<0.01	<0.01	<0.01
8N1								*	<0.01	<0.01	<0.01	
8C1									*			<0.01
8C2										*		
8C4											*	< 0.01

1997

Station	7S2	7C1	7 S 1
7C2	<0.01	<0.01	
7S2	*	< 0.01	<0.01
7C1		*	<0.01

1996

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Station	6N1	6N2	6N3
6S1 [<0.01	
6N1 [*	<0.01	
6N2 [*	<0.01

Appendix F

Calories per gram dry weight for 75-85 mm subsample (n=10 for each station) from all years. Mean standard length of the subsample is given for comparison.

1996							
Station	Mean	Max	Min	Median	SD	SE	Mean SL (combusted)
6N1	5184.1	5547.3	4907.5	5162.8	41641.9	64.531	81.3
6N2	5343.6	5521.4	5184.8	5344.2	13824.8	37.182	83.3
6N3	5104.5	5277.2	4762.7	5115.7	29281.1	54.112	79.3
6S1	5394.7	5610.5	5234.9	5379.5	18383.4	42.876	79.0

1997

Station	Mean	Max	Min	Median	SD	SE	Mean SL (combusted)
7C1	5128.2	5261.2	5052.0	5129.7	3713.6	19.271	80.9
7C2	4979.2	5177.7	4629.7	5009.4	26756.0	51.726	78.7
7S1	5342.3	5663.8	5013.3	5318.5	4909 0.4	70.065	81.6
7S2	5508.2	5665.9	5400.3	5498.5	6049.0	24.595	78.0

1998

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Station	Mean	Max	Min	Median	SD	SE	Mean SL (combusted)
0N11	A946.6	52474	4400.0	4055.2	67050 1	92 427	
	4040.0	5547.4	4400.9	4000.0	07909.1	02.431	/ 0.0
8N2 _	4962.4	5211.2	4577.1	4931.4	37911.7	61.573	77.5
8C1	5063.2	5456.9	4837.1	5037.1	45780.3	67.661	81.3
8C2	5003.1	5287.7	4712.4	5027.9	31927.7	56.505	79.3
8C3	4819.2	5020.5	4494.6	4863.6	29167.7	54.007	80.1
8C4	49 9 0.4	5345.9	4494.3	5017.0	52078.9	72.166	80.3
8C5	4849.6	5313.3	4642.1	4793.3	47273.3	68.756	78.5
8C6	5103.2	5459.2	4657.0	5057.4	65501.7	80.933	79.9
8S1	5322.3	5669.5	4989.8	5354.4	50613.2	71.143	81.7
8S2	5176.0	5456.8	4761.6	5228.7	76269.2	87.332	80.2
8S3	5269.5	5667.6	4863.3	5288.8	72780.3	85.311	81.1
8S4	5359.3	5617.7	5127.5	5315.7	22665.6	47.608	82.3
8S5	4961.1	5212.6	4605.1	4907.3	36888.2	60.736	77.5

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Appedix G

Significant differences in calories/g among stations. "s" indicates Tukey/Kramer test, p-value indicates Sheffe's test.

1998

Station	8C6	8C3	8N2	8N1	8C1	8C2	8C4	8C5	8S1	8S2	8S3	8S5	8S4
8C6	*												
8C3		*							0.02				0.01
8N2			*										
8N1				*					0.05				0.02
8C1					*								
8C2						*							
8C4							*						
8C5								*	0.04				0.02
8S1		S	S	S				S	*				
8S2		S								*			
8S3		S		S				S			*		
8S5									S			*	
8S4		S	S	S		S	S	S				S	*

1997

Station	7S2	7C1	7C2	7S1
7S2	*	0.000	0.000	
7C1	S	*		0.023
7C2	S		*	0.000
7S1		S	S	*

1996

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Station	6N1	6N2	6N3	6S1
6N1	*			0.050
6N2		*	0.020	
6N3		s	*	0.003
6S1	S		S	*

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Appendix H

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AVHRR temperature (in degrees Celsius) means and standard errors for each station and image.

na = not sufficient data to calculate se, nd = no data.

Station	8N1		8C1&2		8C3		8C4		8C5		8C6		8S1		852		8 S 3	
Day of year	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
80	5.8	0.03	5.3	0.03	5.3	0.04	5.3	0.04	5.3	0.03	5.2	0.02	5.3	0.01	6.2	0.03	5.9	0.03
81	6.5	na	nd	na	5.5	0.07	5.4	0.02	5.4	0.01	5.1	0.02	5.8	0.07	6.5	0.07	5.9	0.06
103	3.9	0.03	3.6	0.10	3.7	0.09	4.2	0.24	4.9	0.28	5.7	0.05	4.7	0.26	5.3	0.15	5.5	0.04
111	5.4	0.03	5.2	0.02	5.2	0.02	5.1	0.04	5.2	0.11	5.6	0.06	5.0	0.06	4.7	0.10	5.6	0.11
111 (2)	6.3	0.21	5.7	0.08	6.0	0.09	6.4	0.06	6.5	0.07	7.0	0.07	6.6	0.06	6.8	0.03	6.6	0.05
112	5.9	0.11	5.7	0.08	5.9	0.10	6.3	0.06	6.4	0.06	6.5	0.03	6.0	0.06	6.7	0.05	6.6	0.06
112 (2)	2.9	0.02	4.0	na	4.3	0.34	5.0	0.23	5.4	0.10	5.5	0.06	4.8	0.03	5.1	0.10	5.6	0.05
114	5.8	0.02	5.3	0.08	5.2	0.06	5.1	0.04	5.3	0.10	5.7	0.04	5.8	0.05	4.9	0.07	5.2	0.03
124	5.8	0.17	6.2	0.00	6.2	0.02	6.1	0.03	6.1	0.05	6.6	0.02	nd	na	nd	na	7.0	0.03
134	6.4	0.03	7.0	0.06	7.0	0.05	7.3	0.07	7.5	0.07	7.3	0.03	7.3	0.03	7.6	0.07	7.3	0.03
134 (2)	5.9	0.03	6.4	0.06	6.4	0.04	6.6	0.06	6.8	0.03	6.7	0.04	6.6	0.02	6.8	0.05	6.6	0.02
144	7.2	0.04	7.3	0.04	7.2	0.05	7.3	0.08	7.5	0.07	7.8	0.06	7.6	0.03	7.8	0.05	nd	na
154	8.6	0.06	7.7	0.45	7.5	0.21	7.3	0.14	7.4	0.22	9.2	0.10	9.6	0.10	10.4	0.04	9.0	0.14
165	8.9	0.23	9.0	0.09	9.1	0.08	9.2	0.05	9.1	0.05	9.2	0.05	9.1	0.09	10.2	0.04	9.9	0.04
173	10. 8	0.06	nd	na	nd	na	nd	na	nd	na	10.0	0.03	nd	na	11.0	0.06	nd	na
Mean at station	6.4		6.0		6.0		6.2		6.3		6.9		6.5		7.1		6.7	
Mean deviation																		
from mean (day	-0.371		-0.408		-0.357		-0.164		0.023		0.340		0.143		0.436		0.407	
103 to 173)																		

Appendix I

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SeaWiFS chlorophyll (in micrograms/L) means and standard errors for each station and image. na = not sufficient data to calculate se, nd = no data.

Station	8N1		8N2		8C1		8C2		8C3		8C4		8C5	
Day of year	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
67	0.86	0.19	1.04	0.23	1.18	0.33	1.23	0.23	1.18	0.20	0.93	0.06	0.72	0.07
85	0.76	n=1	1.70	0.40	0.83	0.06	0.90	0.06	0.99	0.04	0.99	0.03	0.85	0.03
102	2.97	1.36	2.51	0.83	1.34	0.29	1.37	0.14	1.28	0.12	0.94	0.02	0.94	0.06
110	0.63	0.26	1.32	n=1	0.77	0.06	0.77	0.06	0.84	0.06	0.93	0.07	0.77	na
110 (2)	1.03	0.07	1.75	0.18	0.67	0.16	0.72	0.11	0.76	0.09	0.96	0.04	0.86	0.03
111	1.27	0.16	2.02	0.18	0.66	0.08	0.81	0.07	0.86	0.06	0.90	0.02	0.70	0.03
113	58.64	6.12	35.03	9.58	2.29	0.69	8.45	5.67	10.57	5.49	12.04	4.01	10.39	9.07
115	4.62	2.27	8.58	2.54	12.20	10.52	11.87	6.99	11.16	5.17	9.60	4.33	1.64	0.25
133	0.76	0.04	1.34	0.07	0.92	0.03	0.99	0.05	1.04	0.07	1.28	0.07	1.74	0.58
134	0.84	0.09	1.20	0.11	0.85	0.10	0.90	0.10	1.17	0.07	1.68	0.06	1.52	0.12
143	0.80	na	1.06	0.11	0.83	0.14	1.06	0.12	1.13	0.08	1.25	0.07	1.17	0.05
166	1.52	0.11	1.64	0.14	2.89	0.27	2.61	0.08	2.25	0.21	1.81	0.08	3.05	0.39
168	1.18	0.10	1.49	0.11	1.55	0.14	1.55	0.09	1.49	0.09	1.33	0.03	1.41	0.15
193	1.28	0.01	1.20	0.05	1.41	0.05	1.42	0.06	1.48	0.05	1.51	0.05	1.42	0.05
194	1.20	0.09	nd	na	nd	na	nd	na	0.99	na	1.34	0.35	nd	na
Mean deviation from mean	0.002		0.073		-0.056		-0.015		-0.013		-0.007		-0.050	

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Station	8C6		8 S1		8 S2		8S3		8 S4		8S5		
													overall
			-										mean per
Day of year	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	day
67	0.99	0.21	0.53	na	0.54	0.11	nd	na	nd	na	nd	na	0.92
85	0.96	0.07	nd	na	1.20	0.14	1.32	0.1 0	3.87	0.34	1.05	0.09	1.29
102	0.74	0.13	nd	na	0.51	0.19	13.30	9.32	0.62	0.15	1.71	0.18	2.35
110	1.11	0.12	0.21	na	1.72	0.02	2.65	1.22	0.86	na	nd	na	1.05
110 (2)	nd	na	0.30	0.19	nd	na	4.95	2.43	0.71	0.16	0.65	0.06	1.22
111	1.02	0.12	1.29	0.71	2.65	0.69	nd	na	0.86	0.07	0.85	0.03	1.16
113	12.04	8.90	nd	na	1.78	0.18	5.79	2.43	8.75	5.79	2.70	0.94	14.04
115	1.70	0.50	1.75	na	nd	na	nd	na	nd	na	nd	na	7.01
133	1.23	0.14	1.14	na	2.35	0.46	4.45	1.61	1.49	0.10	1.29	0.16	1.54
134	1.56	0.10	1.33	na	1.87	1.32	3.36	1.36	2.16	1.24	3.34	2.34	1.68
143	0.99	0.27	nd	na	nd	na	nd	na	nd	na	nd	na	1.04
166	1.62	na	11.90	na	3.83	0.80	3.82	2.37	1.43	0.09	1.27	0.23	3.05
16 8	1.77	0.14	nd	na	1.05	0.06	1.97	1.28	2.07	0.25	1.42	0.03	1.52
193	1.15	0.56	2.61	na	0.94	0.40	10.76	3. 8 3	1.21	0.05	nd	na	2.20
194	0.77	0.14	nd	na	1.51	na	nd	na	2.27	0.61	5.24	0.30	1.90
Mean deviation	0.062		0.029		0.027		0.221		0.000		0.022		
from mean	-0.003		-0.028		-0.037		0.221		0.000		-0.023		

Appendix J

Post-hoc comparison results for stomach content categories (1998). "s" indicates significance according to the Tukey-test.

Total stomach contentStations8N28C5

	8N2	8C5	8C1	8S1	8N1	8S5	8S4	8C2	8C3	8C6	8S2	8S3
8C4							S	S	S	S	S	S
8N2	*							8	S	S	S	S
8C5		*						8	S	S	8	S
8C1			*					S	S	S	S	S
8S1				*							S	S
8N1					*						S	S
8S5						*					S	S
8\$4							*				S	S
8C2								*				
8C3									÷			
8C6										*		
8S2											*	

Copepods in stomach Stations 8N2 8C5

ns		8N2	8C5	8C1	8S1	8N1	8S5	8S4	8C2	8C3	8C6	8S2	8S3
	8C4								S	S	S	S	S
	8N2	*										S	S
	8C5		*				S	S	S	S	S	S	S
	8C1			*					S	S	S	S	S
	8S1				*		S		S	S	S	S	S
	8N1					*				S		S	S
	8S5						*						
	8S4							*				S	S
	8C2								*				
	8C3									*			
	8C6										*		
	8S2											*	

Cladocerans in stomach

Stations

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	8N2	8C5	8C1	8S1	8N1	8S5	8 S 4	8C2	8C3	8C6	8S2	8S3
8C4		8		S		S	S	8	S	S	S	S
8N2	*	S		S		S	S	S	S	S	S	S
8C5		*									S	8
8C1			*							S	S	S
8S1				*							S	S
8N1					*		S			S	8	S
8 \$5						*					8	S
8S4							*					
8C2								*			S	8
8C3									*		S	S
8C6										*		
8S2											*	