AN ABSTRACT OF THE THESIS OF

Michel A. Boudrias for the degree of Master of Science in Oceanography presented on July 26, 1985.

Title: Life History and Feeding Ecology of the Dominant Arctic Lysianassid Pseudalibrotus (= Onisimus) litoralis from the Inner Continental Shelf of the SW Beaufort Sea.

Abstract approved: Redacted for privacy

Andrew G. Carey Jr.

Research beneath landfast and floating pack ice in the Arctic and Antarctic has revealed abundant pennate diatoms, meiofaunal copepods and nematodes, and a macrofaunal community dominated by gammarid amphipods. On the inner continental shelf of the southwestern Beaufort Sea, the lysianassid Pseudalibrotus (= Onisimus) litoralis has a unique lifestyle as it is abundant in both the ice and sediment habitats during the spring. Its abundance and distribution have been studied but little is known on its life history or its feeding ecology. The following abstracts from each chapter address these processes.

Chapter II: Spatial and Temporal Variabiliy in Life History Patterns of Pseudalibrotus (= Onisimus) litoralis (Crustacea: Amphipoda) in Three Habitats of the Inner Continental Shelf of the SW Beaufort Sea.

The important life history traits of Pseudalibrotus (=Onisimus) litoralis from the ice, water column, and sediment habitats were measured in the laboratory. Length-frequency analyses resulted in a bimodal distribution which separated immatures from juveniles and adults. There were large temporal differences in the number and the size of immatures and adults associated with the ice undersurface. These temporal trends, the bimodal population structure, and the maturity of adults indicate that P. litoralis has a two year life cycle. The lack of spatial variability among the three habitats and the low abundance in the sediments during the spring suggest that there is a single population of this lysianassid species. The maximum growth rate in spring of adults and immatures, the peak in the percentage of mature and ovigerous females, and the decrease and stabilization of the sex ratio of females to males, all coincided with the spring maximum of primary production in the ice. The data, especially the presence of only one population of P. litoralis, suggest that this amphipod used the ice and its early spring carbon source as a temporary spawning and nursery ground for immatures and for juveniles preparing for fall breeding. Microspatial variability between dense amphipod aggregations and standard transect samples revealed a large difference in population structure within the ice habitat on a given date.

Chapter III: Feeding Ecology of Pseudalibrotus (= Onisimus) litoralis (Crustacea: Amphipoda) on the Inner Continental Shelf of the SW Beaufort Sea.

Research on the feeding ecology of underice amphipods and other sympagic macrofauna in polar waters is scarce. In spring, the bloom of ice microalgae and, particularly, ice pennate diatoms is an important early food source for newly released and juvenile underice amphipods. This study relates the feeding ecology of the dominant lysianassid amphipod Pseudalibrotus litoralis to its life history patterns and potential use of this spring bloom on the inner continental shelf of the SW Beaufort Sea. The functional morphology of its antennae and mouthparts show a potential for tearing and cutting soft foods, like carrion or other macrofauna, and for crushing hard food items like diatoms. Gut contents and fecal pellets consisted of a predominance of macrofaunal crustacean parts, with some harpacticoid copepod fragments and diatom frustules. Diatom frustules were the main food item of amphipods captured in dense aggregations early in spring and in samples on May 31. The dominance of diatoms as food in late May coincided with the spring maximum primary production in the ice. The scavenging behavior of this lysianassid species and the presence of diatoms in its gut support earlier observations showing that Pseudalibrotus litoralis is a temporary inhabitant of the ice undersurface in spring.

Life History and Feeding Ecology of the Dominant Arctic Lysianassid Amphipod *Pseudalibrotus* (= *Onisimus*) *litoralis* from the Inner Continental Shelf of the SW Beaufort Sea.

by

Michel Andre Boudrias

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Typed by Michel Boudrias for Michel A. Boudrias

High peaks beaten by age and scraped by merciless weather, crowned in bitter frost, sealed in pearl and emerald ice, thrust their humped backs in snaking lines against the whipping winds which, forever swirling, gather layers of fine powdery snow from the mountains' slopes, turning them into rising sheets, hurling them forward, like giants striding across the barren land.

Eric Van Lustbader
"Shallows of Night"

There is no journey's end.

Bujun saying
from
Eric Van Lustbader
"Shallows of Night"

Whatever sea you sail
Whatever land you search
For whatever our purposes
Together on this Earth...

Like the seagulls' wings
Part of me, friend
As from the beginning
Until the very end...

Marc, 23 August 1982

What matters most is the search itself. This is more important than the searchers. Consciousness must dream, it must have a dreaming ground -- and, dreaming, must invoke ever-new dreams.

Morgan Hempstead
Lectures at Moonbase
from
Frank Herbert's "Destination: Void"

Truth suffers from too much analysis.

- Ancient Fremen Saying
from
Frank Herbert's "Dune Messiah"

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Chapter I

General Introduction

Polar research in the last two decades has explored Russian waters (Golikov and Averincev 1977; Vinogradov and Mel'nikov 1980), Antarctic seas (Llano 1977; Hoshiai 1977; Bienati et al 1977; and others), the eastern Canadian Arctic (Steele 1961; Percy 1975; Grainger et al 1980; Grainger et al 1985), the Bering Sea (Hood and Calder 1981a and b), and the Beaufort Sea (Reed and Sater 1974; Barnes et al 1984). There are some excellent reviews of Arctic and Antarctic research (Dunbar 1977a; Horner in press), and much information can also be found in data reports of the Outer Continental Shelf Environmental Assessment Program.

Sampling research beneath landfast and floating pack ice in the Arctic and the Antarctic has revealed abundant microalgae, flagellates, and numerous diatoms (Apollonio 1961, 1965; Bunt and Lee 1972; Horner and Alexander 1972; Andersen 1977; Buinitsky 1977; Horner 1977; Dunbar and Acreman 1980; Hsiao 1980; Horner and Schrader 1982; Buck and Garrison 1983), meiofaunal organisms, particularly harpacticoid and cyclopoid copepods (Carey and Montagna 1982; Grainger and Hsiao 1982; Kern and Carey 1983), and a macrofaunal community dominated by gammarid and lysianassid amphipods (Barnard 1959; George and Paul 1970; Golikov and Averincev 1977; Knox and Lowry 1977; Mel'nikov and Kulikov 1980; Griffiths and Dillinger 1981; Cross 1982; Gulliksen 1984). The ice habitat is also temporarily exploited by zooplankton (Dunbar 1946; Dunbar 1954; Grainger et al 1980; Horner and Schrader 1984), fishes (Andriashev 1954; Frost et al 1978; Lowry and Frost 1981; Bradstreet and Cross 1982; Craig et al 1984), seabirds (Divoky 1978; Bradstreet 1979, 1980, 1982), and marine mammals (Dunbar 1941; McLaren 1958; Fay 1974; Thomson 1984).

On the inner continental shelf of the southwestern Beaufort Sea, the macrofaunal (adults > 0.5 mm) communities in both the ice and sediment habitats are dominated by gammarid and lysianassid amphipod crustaceans (Carey 1984). Though the distribution and abundance data of these amphipods have been investigated (Carey 1984, in press), no information is available on their life history or feeding ecology. The main objectives of this thesis address these questions with particular emphasis on the numerically dominant species *Pseudalibrotus* (= *Onisimus*) *litoralis*. [The amphipod genera *Pseudalibrotus*, *Onisimus*, and *Boeckosimus* are closely related and under revision (Barnard 1969) and can thus be considered equal.] The two main objectives of this research effort are: 1.) a study of the spatial and temporal patterns in the life history of the dominant lysianassid amphipod *Pseudalibrotus litoralis* from the inner continental shelf of the SW Beaufort Sea; and 2.) an analysis of the feeding ecology of this amphipod species. The following paragraphs review these objectives in more detail.

1.) Spatial and Temporal Patterns in the Life History of Pseudalibrotus litoralis. (Chapter II)

Though the data for a detailed study of the population dynamics of this amphipod species cover only one season of their life cycle, spring is a crucial period for underice fauna. The algal blooms that occur at the ice surface in late May (Horner and Schrader 1982, 1984) provide an important food source for underice organisms. The life history and population dynamics of amphipods that can use the ice habitat to advantage should reflect some of the temporal and spatial differences associated with temporary utilization of the ice. The emphasis of this chapter is to investigate the temporal variability in population structure in the ice habitat, the spatial variability between dense aggregations and standard transect samples, and the spatial variation in population structure between the ice, water column, and sediment habitats. The research focusses on Pseudalibrotus litoralis because of its clear numerical dominance of the amphipod assemblages.

2.) Feeding ecology of Pseudalibrotus litoralis. (Chapter III)

The aim of this study was to determine the feeding ecology and diet of sympagic, or "within ice" (Whitaker 1977), P. litoralis. These data strengthen the hypothesis of temporary utilization of the ice habitat. Detailed studies on the functional morphology of the antennae and mouthparts of this lysianassid species provide data on its potential diet. Photographic and microscopic analyses of the gastrointestinal tract and fecal pellet contents reveal its actual diet throughout the spring. The combined results from the morphological and dietary analyses are used to evaluate the importance of the spring algal bloom in the life cycle of *P. litoralis*.

The thesis is organized in the following manner: (1) a compendium of two abstracts that review the two main research chapters of the thesis; (2) the general introduction providing some background data on polar and underice biology; (3) two manuscripts, Chapters II and III that discuss the research per se; these will be submitted to scientific journals upon completion of the thesis; (4) a general discussion that summarizes the results from the whole thesis; (5) a complete bibliography that represents the individual reference sections from the end of each chapter.

Chapter II

Spatial and Temporal Variability in Life History Patterns of *Pseudalibrotus* (= *Onisimus*) *litoralis* (Crustacea: Amphipoda) in Three Habitats of the Inner Continental Shelf of the SW Beaufort Sea.

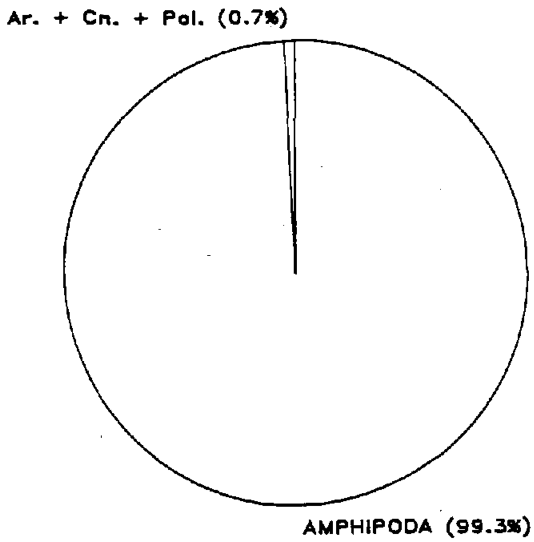
INTRODUCTION

Macrofaunal organisms living on the undersurface of sea ice are important links in planktonic and benthic food webs in Arctic waters (Barnard 1959; Griffiths and Dillinger 1981; Bradstreet and Cross 1982; Cross 1982). In spring, sea ice food web bases are composed of microflagellate and diatom blooms (Apollonio 1961, 1965; Tsurikov 1980; Sancetta 1981; Horner and Schrader 1982) and meiofaunal crustaceans (Montagna & Carey 1979; Carey and Montagna 1982; Kern and Carey 1983) while the top predators are fish (Arctic cod) and seals (Bradstreet and Cross 1982). Sympagic, or "within ice" (Whitaker 1977), macrofaunal communities are usually dominated by gammarid amphipods (Steele 1961; Dunbar 1968; Kulikov 1980; Mel'nikov and Kulikov 1980; Carey in press). These amphipod communities are characteristic of the continental shelf benthos and sea ice in the Eastern Canadian Arctic (Steele 1961; Dunbar 1968), over the deeper waters of the Central Arctic Basin (Kulikov 1980; Mel'nikov and Kulikov 1980) and in Chirikoff Basin in the Bering Sea (Thomson 1984). On the inner shelf of the SW Beaufort Sea, gammarid amphipods also dominate the sympagic and sediment habitats (Figure II.1).

Figure II.1: Relative abundance of sympagic and sediment macrofauna from the SW Beaufort Sea OCS Project during the spring of 1980.

Ar.= Arthropoda; Cn.= Cnidaria;
Pol.= Polychaeta; Ne.= Nemertina;
An.= Annelida; Mol.= Mollusca;
Cu.= Cumacea; M.= Mysidacea; O.= Ostracoda.

Sympagic Macrofauna



Sediment Macrofauna

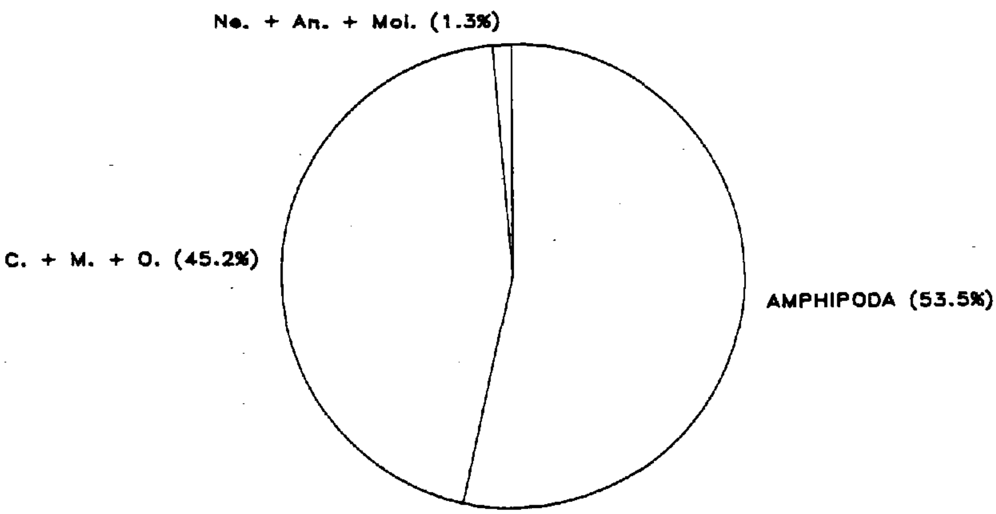


Figure II.1

The most abundant amphipod species in all habitats on the shallow shelf of the SW Beaufort Sea is Pseudalibrotus (=Onisimus) litoralis (Kroyer). This epibenthic lysianassid is characteristically most abundant in shallow waters (5 - 25 m) and sandy sediments on continental shelves of the Arctic region (Steele 1961; Griffiths and Dillinger 1981) though its distribution can extend down to 125 m in the Western Arctic and even deeper in Central Arctic waters (Mel'nikov and Kulikov 1980). On the inner shelf of the SW Beaufort Sea, near Narwhal Island, P. litoralis is the only amphipod that is abundant in the sediments, the water column, and the ice (Table II.1). This unique lifestyle demonstrates the high adaptability of P. litoralis. Its dominance of the amphipod assemblage may indicate that it is capable of trading off the high physiological costs (large salinity fluctuations during ice melt, swimming between the habitats) and higher predatory costs (exposure to benthic, pelagic and sympagic predators) associated with the ice habitat for the added energetic and survival benefits of the ice algal bloom and associated meiofauna.

TABLE II.1: Species abundances (#/100 m^3) of the benthic amphipods collected at the Narwhal Island study site in spring, 1980.

Species Name	Ice	Water Column	Sediment	TOTAL
Pseudalibrotus litoralis	7719	18	500	8237
Monoculodes borealis	0	0	1227	1227
Onisimus affinis	0	0	477	477
Halirages mixtus	414	3	11	428
Lagunogammarus setosus	349	1	11	361
Apherusa glacialis	268	1	34	303
Onisimus plautus	0	0	239	239
Acanthostepheia malmgreni	0	0	91	91
Weyprechtia pinguis	73	0	0	73
Onisimus derjugini	0	0	68	68
Oediceros borealis	0	1	45	46
Monoculopsis longicornis	0	0	45	45
Acanthostepheia incarinata	0	0	11	11

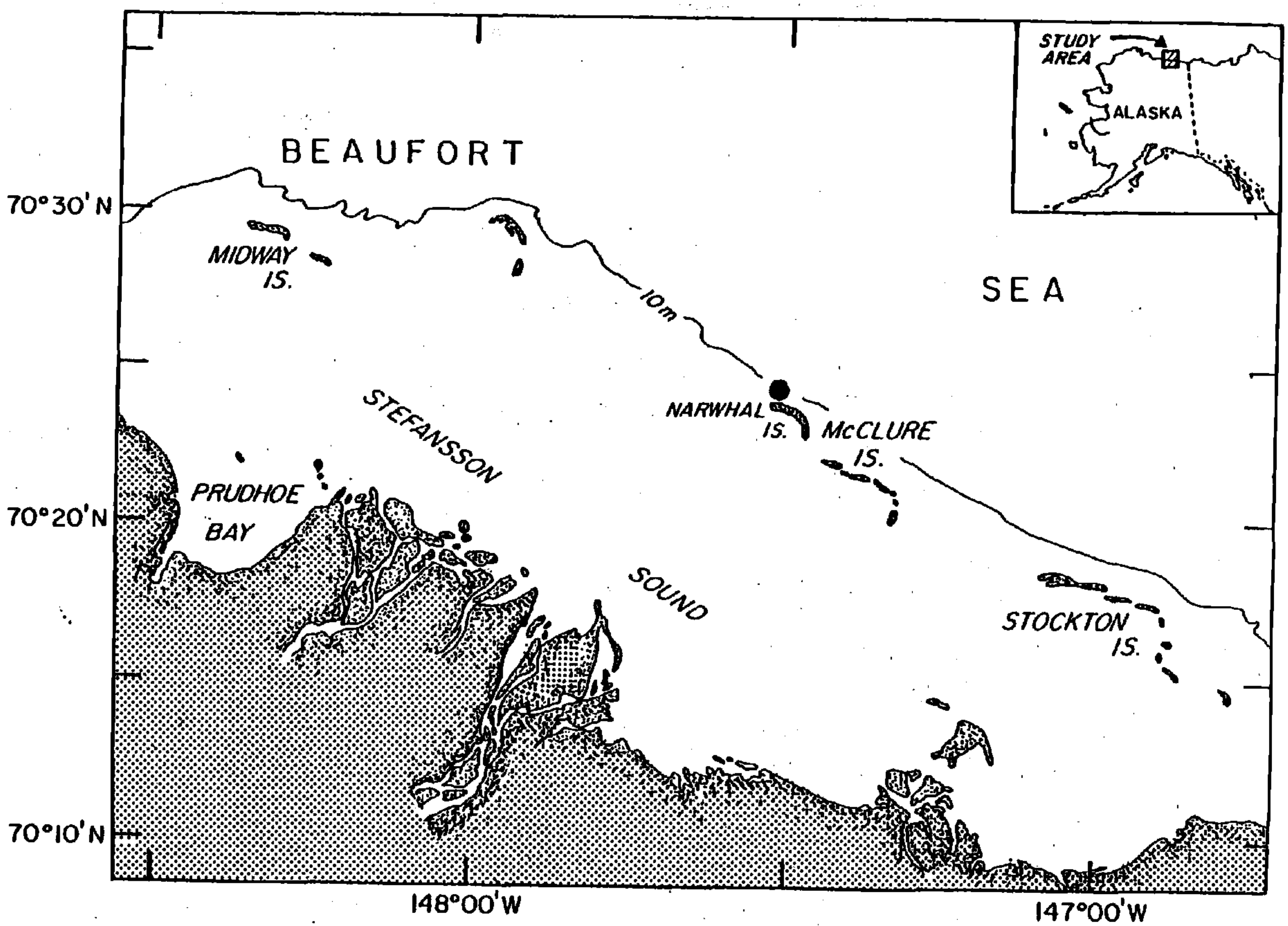
The main objective of this study was to investigate the life history patterns of Pseudalibrotus litoralis populations in the ice, water column, and sediment habitats on the continental shelf near Narwhal Island. We focussed on the spatial variability in population structure among the three habitats and on a microscale, between amphipod patches and standard transect samples, within the ice habitat. We also determined the temporal trends in population structure within the ice habitat and the diel trends in the pelagic zone. Life history patterns were analyzed from changes of length-frequency, maturity of adults, sex ratios and the number of young produced during the spring spawning season.

MATERIALS and METHODS

Macrofaunal amphipods were collected from April 13 to June 9, 1980 on the inner continental shelf of the SW Beaufort Sea close to Narwhal Island (Fig. II.2). Divers using SCUBA captured amphipods with a ˜push-net˜ along 10-m transects adjacent to the ice surface and at the sediment-water interface. A rectangular net, 32 cm by 11 cm, with a 333 um mesh was pushed along the transect and collected epibenthic amphipods. The rectangular net sampled a volume of water just below the ice surface and just above the sediments so the abundance estimates were volumetric. On the first sampling date in the ice habitat (April 13), divers inadvertently sampled dense patches of amphipods for the first two samples and the transect for the other three. This sampling artifact was useful, however, in an evaluation of microspatial variability in the population structure of sympagic P. litoralis.

Standardized midwater collections were made with a line and pulley system that pulled a 0.75 m ring net with 500 um mesh along a 10 m distance. Divers periodically checked the midwater position of the net. There was a total of 22 sampling dates for the water column habitat. On four dates, stations were sampled for 24 hour to examine diel differences in the population size structure of P. litoralis swimming between the ice and the sediments. All amphipods were fixed in 10 % buffered formalin and later transferred to 70 % ethanol for long term preservation.

Figure II.2: General location map of the southwestern Beaufort Sea. The black dot indicates the location of the Narwhal Island Sea Ice 1980 study site (Redrawn from Kern and Carey 1983).



STUDY AREA
ALASKA
BEAUFORT
SEA
10m
MIDWAY IS.
STEFANSSON
SOUND
NARWHAL IS.
McCLURE IS.
STOCKTON IS.
PRUDHOE BAY
70°30'N
70°20'N
70°10'N
148°00'W
147°00'W

Figure II.2

Identifications, counts and length measurements were assessed in the laboratory. Lengths of adults and immatures were measured using a projection microscope (Rayoscope) with fiber optics illumination to enhance contrast and reduce heat damage to the specimens (R.E. Ruff pers. comm.). With a flexible rule that conformed to the curvature of the body, the total projected length of the amphipods was measured to the nearest mm from the tip of the rostrum to the distal end of the telson.

We used a Wild dissecting microscope at 25 and 50 X magnification to determine the sex of the amphipods. Two main criteria were used: (1) the number and length of the proximal joints in the flagella of the antennae (Sars 1895; Holmquist 1965); and (2) the presence of genital papillae in males and of oostegites (brood plates) in females . Males were recognized by their numerous and short flagellar joints while females had fewer and more elongated flagellar joints. When neither of these criteria were observable, individuals were classified as immatures.

Once sex was determined the maturity of P. litoralis was estimated according to the criteria in Table II.2 (modified from Hannan et al 1979). In many cases specimens could not be precisely categorized at one maturity stage so intermediate values

TABLE II.2: Morphological characteristics used in distinguishing sexes and maturity in *Pseudalibrotus litoralis* from the inner continental shelf of the SW Beaufort Sea, spring 1980 (Adapted from Hannan et al 1979).

MALES	FEMALES
1. Mature:	
a) very large pair of genital papillae (>125 um) located ventrally on the 8^{th} thoracic segemnt.	a) fully developed oostegites with setae forming a brood pouch; may or may not be ovigerous.
b) antennal flagellae long with many short proximal joints.	b) shorter antennal flagellae with fewer and longer proximal joints.
2. Old Juvenile:	
a) intermediate genital papillae (125 um > x < 75 um)	a) moderately developed oostegites with either no or very short setae.
b) Shorter antennae and flagellae with many short articulations.	b) antennal flagellae with few and longer articulations.
3. Young Juvenile:	
a) very small genital papillae (> 75 um) or small round indentions.	a) very small or no oostegites.
b) antennal flagellae with many short articulations.	b) antennal flagellae with few, long articulations.

4. Immature

Sex was indistinguishable because of small size. Even the use of antennal flagellae articulations was impossible.

were assigned based on the condition of each animal. For example, a male with genital papillae between 75 and 125 um was scored as a maturity of 2.5, [i.e. between the youngest juvenile (maturity = 3) and older juveniles (maturity = 2)]. Sex ratios, the number of females divided by the number of males, were computed for each date in the ice habitat only. The percentage of ovigerous females and the percentage of mature females in relation to the total sympagic population were also calculated. The brood size, or number of eggs per female, could not be measured because none of the females captured were carrying eggs or young in their pouch.

Size-frequency data were plotted to depict the important spatial and temporal trends in the P. litoralis population structure. The total population structure from mid-April to early June was plotted for each habitat and compared with a Kolmogorov-Smirnov (K-S) two sample test (Sokal & Rohlf 1981) to determine the spatial variability between the ice, the water column, and the sediment habitats. Diel differences in population structure were also tested with K-S tests for the four 24-hour zooplankton samples.

The high abundance of amphipods in the ice habitat permitted better analysis of spring trends and microspatial variability. The change in size-frequency structure through time from April 13 to June 9 was tested with the K-S statistic. Mean and standard deviations for all major life history traits measured were calculated for males, females and immatures for all samples taken in the ice transects, and used in a qualitative analysis of spring temporal trends in population structure. Microspatial variability was only tested on April 13 with K-S tests to compare the population structure in dense amphipod aggregations versus that in the ice transect.

RESULTS

Based on abundance data from Table II.1, there is evidence for strong preference for the ice or sediment habitat. Five amphipod species, P. litoralis, H. mixtus, L. setosus, A. glacialis, and W. pinguis, move to the ice in the spring and use it as their principal habitat. Weyprechtia pinguis is the only underice species that does not have a residual population in the sediments during the spring of 1980. The other eight amphipod species, with the exception of a few Oediceros borealis in the water column, are exclusively confined to the sediments. Thus, only a subset of gammarid amphipods from the inner continental shelf use the ice habitat during spring.

Size-frequency analysis of sympagic P. litoralis showed two temporal trends: (1) an increase in abundance of animals through time, particularly for immatures; (2) a bimodal distribution with only 2.2 % of all specimens between 7.0 and 10.0 mm long (Fig. II.3). Counts of females decreased only slightly but the number of mature females increased with time during the spring. The number of males increased four-fold from April 13 to June 9, while the number of immatures increased 20-fold (Table II.3).

Figure II.3: Length-frequency histograms for the sympagic population of *Pseudalibrotus litoralis* in the SW Beaufort Sea, spring 1980. Note the bimodal population structure on the six sampling dates.

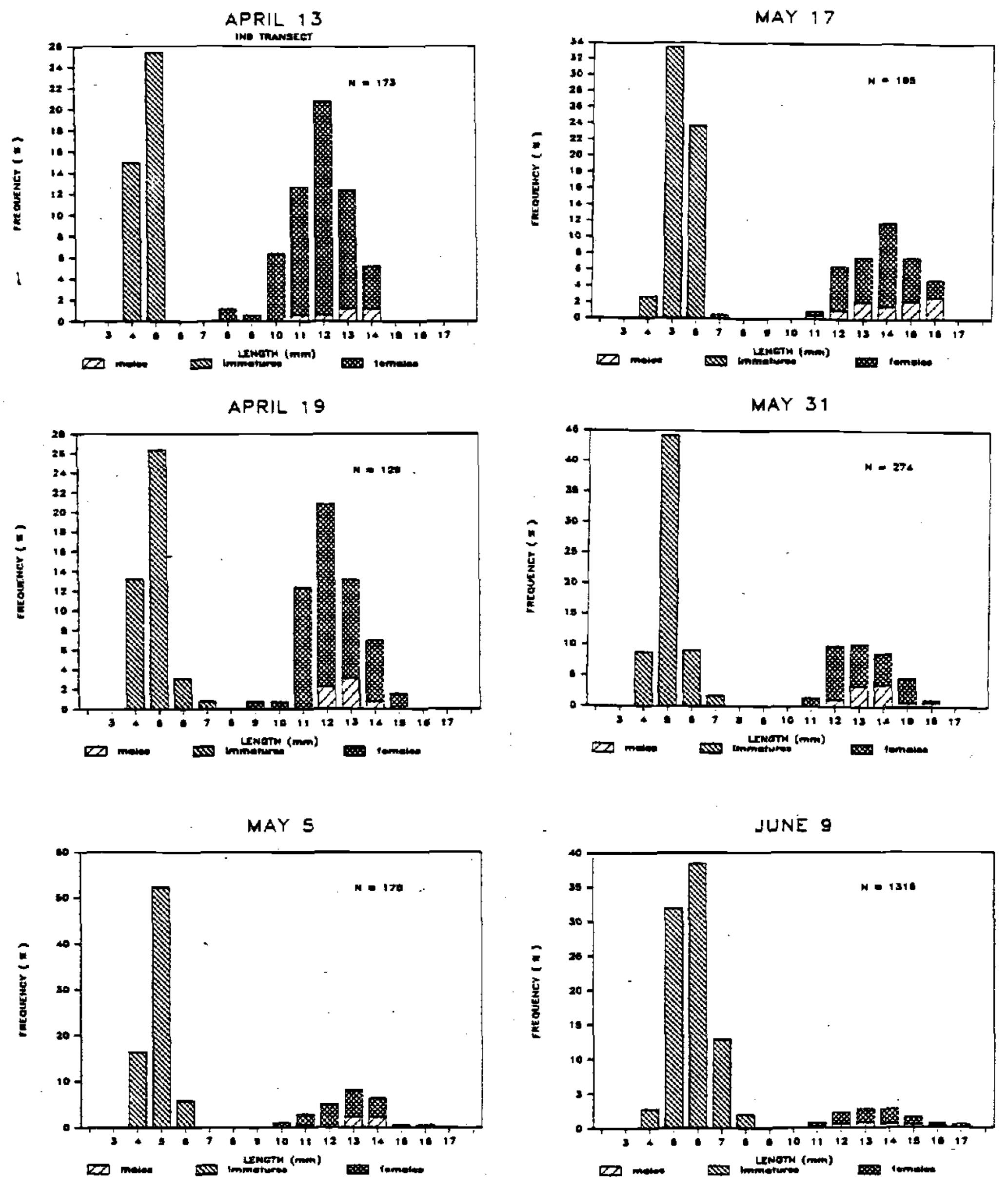


Figure II.3

Table II.3. Number, mean and standard deviation of the life history traits of *Pseudalibrotus litoralis* in the ice habitat at Narwhal Island, Spring 1980.

	April 13	April 19	May 5	May 17	May 31	June 9
	x ± std	x ± std	x ± std	x ± std	x ± std	x ± std
NUMBER						
immatures	56	55	62	112	175	1165
males	6	8	11	19	26	23
females	97	65	32	54	73	73
mature female	1	6	10	19	16	27
sex ratio*	16.17	8.13	2.91	2.84	2.81	3.17
LENTGH (mm)						
immatures	4.19 ± 0.45	4.36 ± 0.61	4.38 ± 0.41	4.83 ± 0.50	4.59 ± 0.52	5.35 ± 1.11
males	12.05 ± 1.11	12.21 ± 0.62	13.30 ± 1.18	13.81 ± 1.80	13.16 ± 1.02	13.19 ± 1.98
females	11.34 ± 1.17	11.81 ± 1.15	11.98 ± 1.03	13.27 ± 1.35	12.59 ± 1.17	12.81 ± 2.27
MATURITY						
males	2.58 ± 0.59	2.31 ± 0.70	1.55 ± 0.50	1.71 ± 0.71	2.14 ± 0.74	2.28 ± 0.81
females	2.71 ± 0.38	2.45 ± 0.54	2.24 ± 0.79	2.04 ± 0.68	2.33 ± 0.69	2.36 ± 0.84

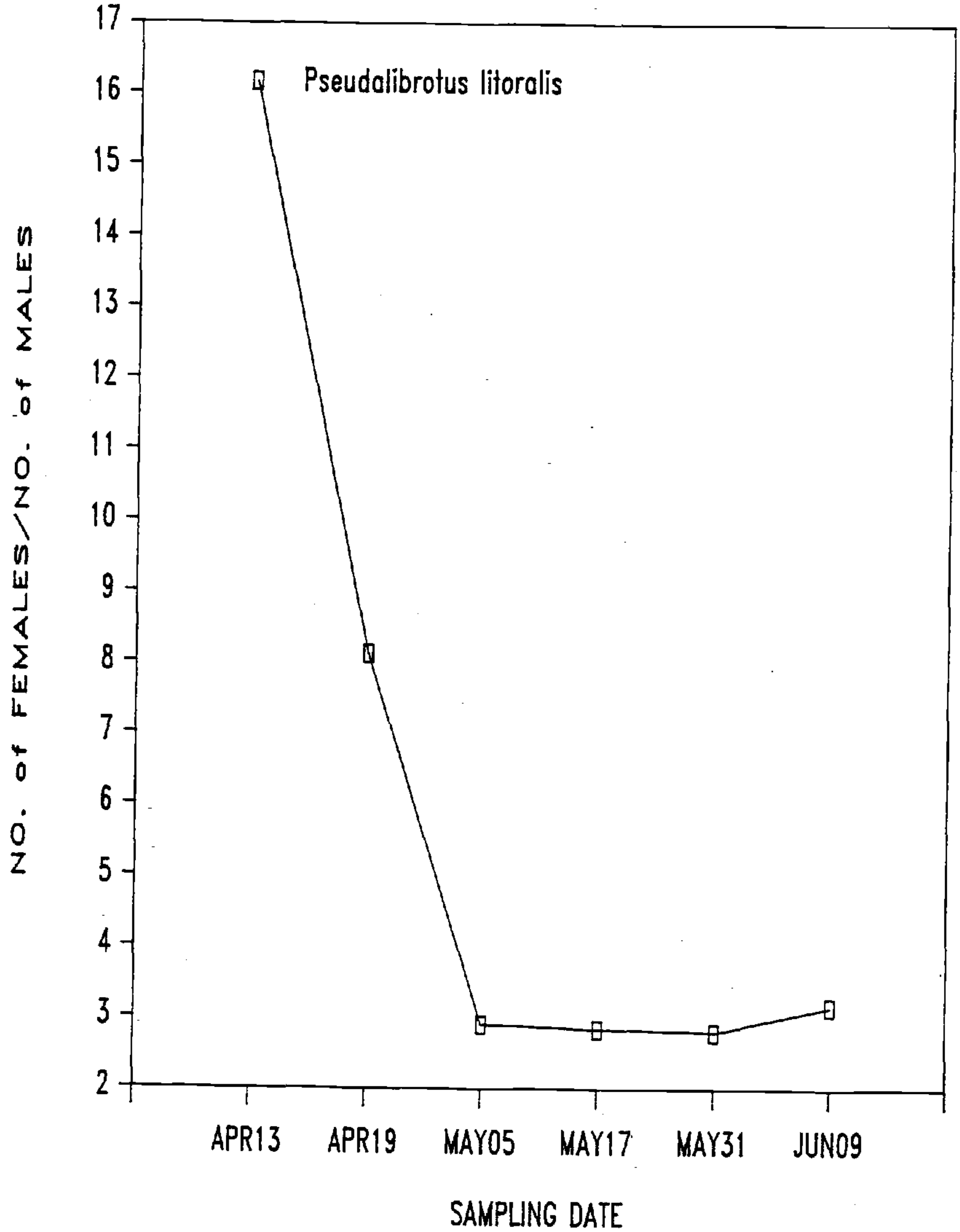
* = the sex ratio is calculated as the number of females / the number of males.

Two-sample K-S tests showed that the ice transect samples of April 13 and April 19 were statistically identical but all other comparisons through time were significantly different (Table II.4). Though all the length-frequency histograms were bimodal, the results revealed a change at the 0.05 and 0.01 probability level in the population structure from April 19 to June 9, especially in the length of immatures and adults and in the number of immatures.

There was a dramatic change in the sex ratio of the ice population of <u>P.litoralis</u> during the spring, with a five-fold decrease from 16.17 on April 13 to 3.17 on June 9 (Fig. II.4 and Table II.3). This change resulted from the combined effect of an overall decrease in the number of females and a corresponding increase in the number of males.

Finally, three other life history parameters varied during the sampling period. Though regression analysis only showed significant correlation ($R^2 = 0.66$) for females, the general trends for males, females, and immatures indicated an increase in length through time with a peak between May 17 - May 31 (Fig. II.5). The change in mature females as a percentage of the total amphipods and of ovigerous females as a percentage other females resulted in similar plots with a peak on May 17 and a plateau on later dates (Fig. II.6). Thus, these three life history parameters showed the same temporal trend in the ice habitat during the spring.

Figure II.4: The change in sex ratio through time for sympagic *Pseudalibrotus litoralis* at the 1980 Narwhal Island ice station.



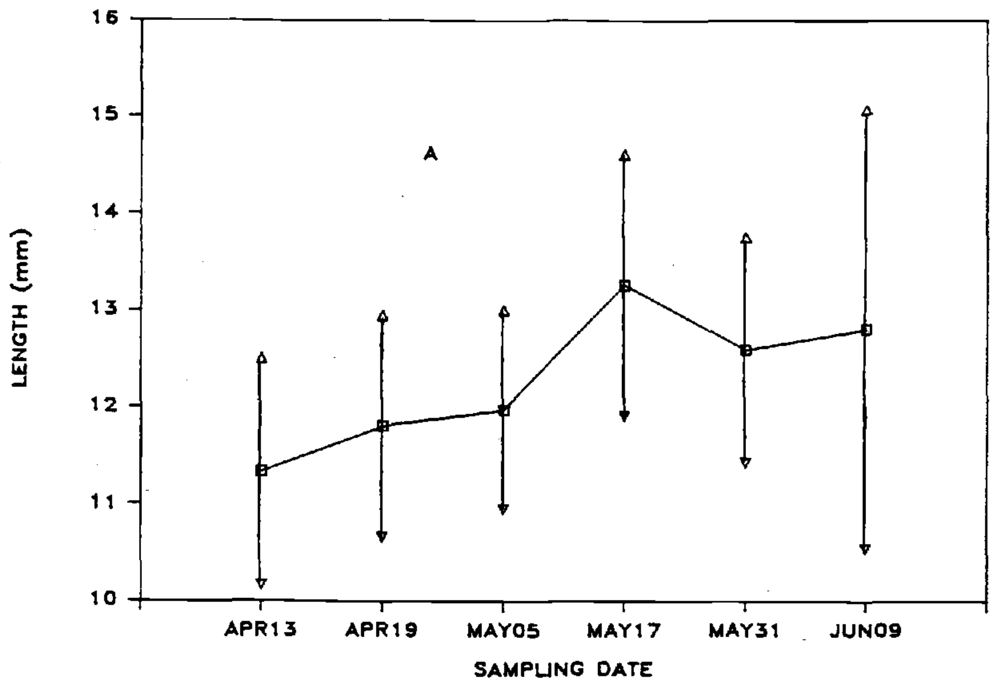
Pseudalibrotus litoralis
NO. of FEMALES/NO. of MALES
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
APR13
APR19
MAY05
MAY17
MAY31
JUN09
SAMPLING DATE

Figure II.4

Figure II.5: Spring trend of increase in length through time for sympagic *Pseudalibrotus litoralis* from the inner continental shelf of the SW Beaufort Sea (mean and one standard deviation).

A = Females

B = Males


16
15
14
13
12
11
10
A
LENGTH (mm)
APR13
APR19
MAY05
MAY17
MAY31
JUN09
SAMPLING DATE

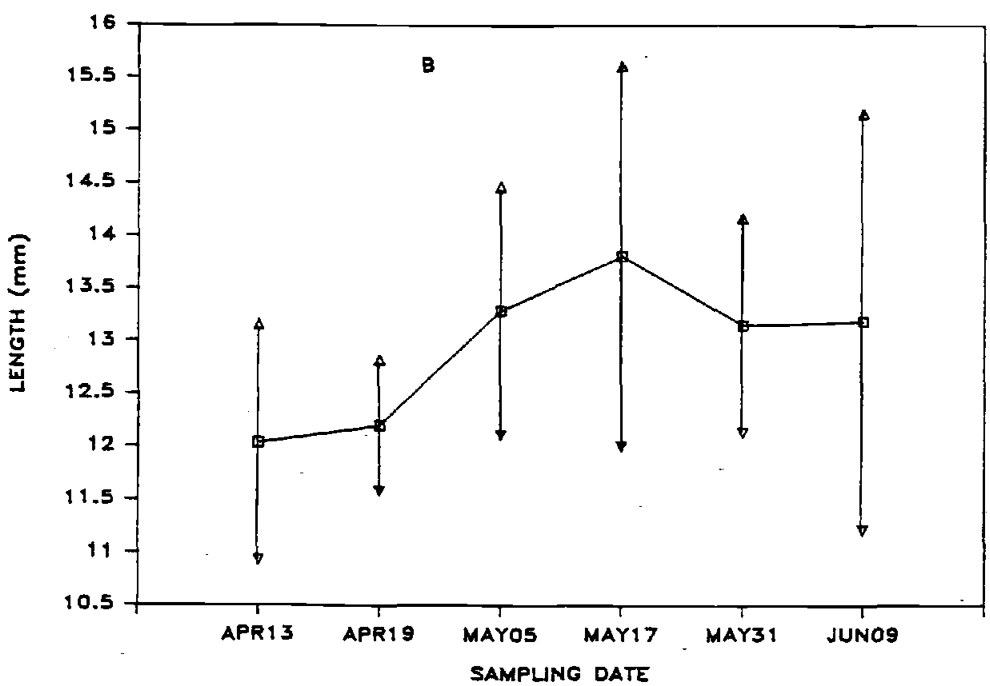

16
15.5
15
14.5
14
13.5
13
12.5
12
11.5
11
10.5
B
LENGTH (mm)
APR13
APR19
MAY05
MAY17
MAY31
JUN09
SAMPLING DATE

Figure II.5

Figure II.6: Temporal trend in (A) the percentage of mature females and (B) the percentage of ovigerous females for the sympagic population of *Pseudalibrotus litoralis* at the 1980 Narwhal Island ice station.

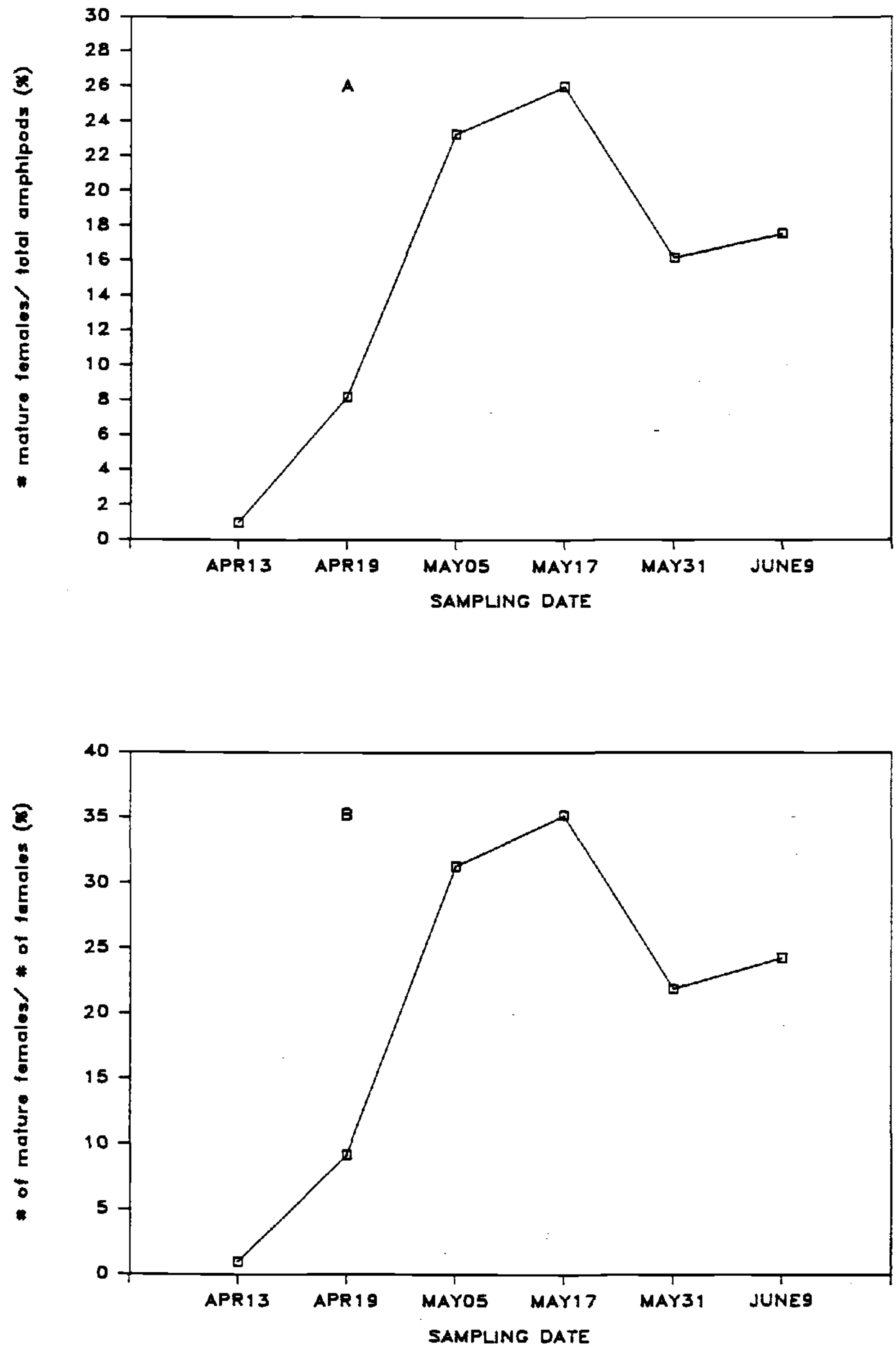

A
mature females/ total amphipods (%)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
APR13
APR19
MAY05
MAY17
MAY31
JUNE9
SAMPLING DATE
B
# of mature females/ # of females (%)
0
5
10
15
20
25
30
35
40
APR13
APR19
MAY05
MAY17
MAY31
JUNE9
SAMPLING DATE

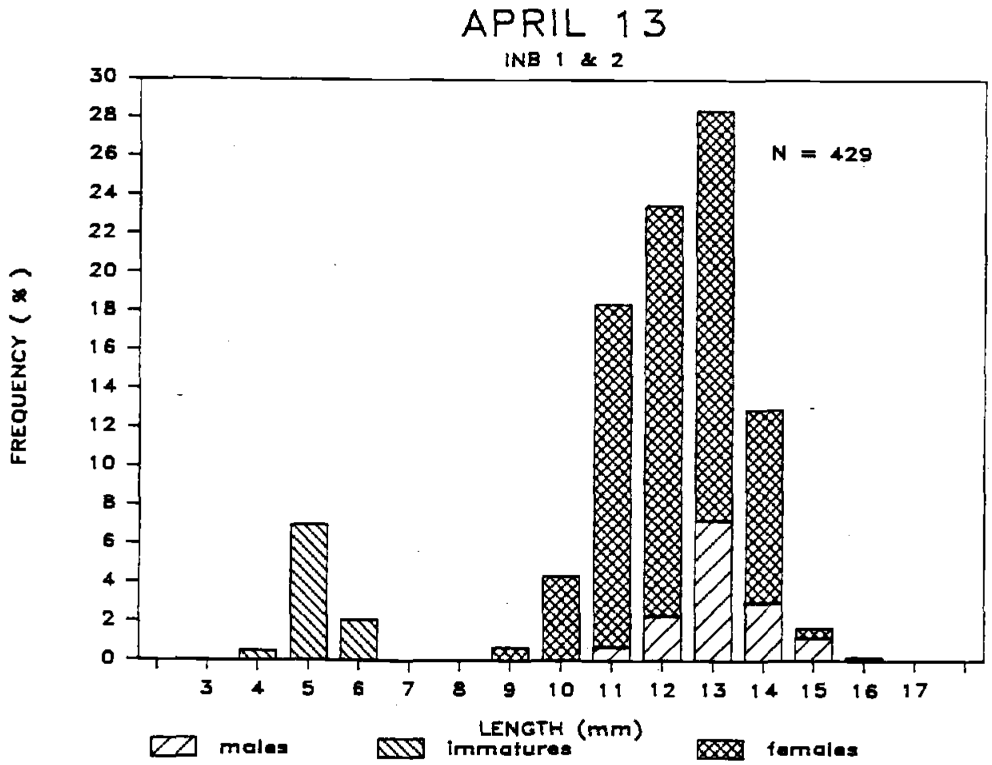
Figure II.6

Microspatial variability was analyzed between two dense underice amphipod aggregations and three standard ice transect samples taken on April 13, 1980. Though this sampling scheme was not repeated on other dates, the results demonstrated some notable differences in population structure (Fig. II.7). A K-S test between the size-frequency structure of the amphipod patch versus the structure of the transect indicated a significant difference ($P = 0.01$) (Table II.4). Furthermore, a chi-square analysis comparing the number of mature females in the patch (n=43) to that in the transect (n=1) was significant for the two sub-habitats sampled on the same date (chi-square = 144; d.f.= 1; $P = 0.005$). Finally, the ratio of females to males was 5.16 compared to 16.17 for the transect on April 13. Thus, dense aggregations of amphipods in the ice were characterized by more males, more mature females and in general, a different size-frequency structure than transects sampled on the same date at the same fixed ice station.

Because the number of P. litoralis in the sediments and in the water column was low, detailed temporal trends could not be analyzed for these two habitats. However, total abundance for the sampling period was large enough to permit a statistical comparison among the three habitats. Using standardized abundance data from the size-frequency histograms (Fig. II.8) for the ice, water column, and sediment habitats, K-S two-sample tests indicated no statistical difference ($P= 0.01$) in the bimodal population structure of Pseudalibrotus litoralis among the three habitats of the continental shelf of Narwhal Island (Table II.4).

The diel changes in population structure of P. litoralis swimming between the ice and sediment habitats were also investigated. The 24-hour samples were taken on April 30 - May 2, May 7-8, May 19-20, and June 2-3. Results of two-sample K-S tests for all sampling dates indicated no significant difference between day and night size-frequency structure. We found the same result when a total day-night test was performed for all four 24 hour samples combined. However, the abundance of immatures and adults was higher at night in samples taken on April 30 - May 1 and on May 7-8 (Carey 1984).

Figure II.7: Length-frequency histograms comparing the population structure in dense amphipod aggregations (April 13, INB 1 & 2) to the structure of a standard ice transect (April 13, INB transect) at the Narwhal Island ice station, spring 1980.


APRIL 13
INB 1 & 2
N = 429
FREQUENCY (%)
LENGTH (mm)
males
immatures
females

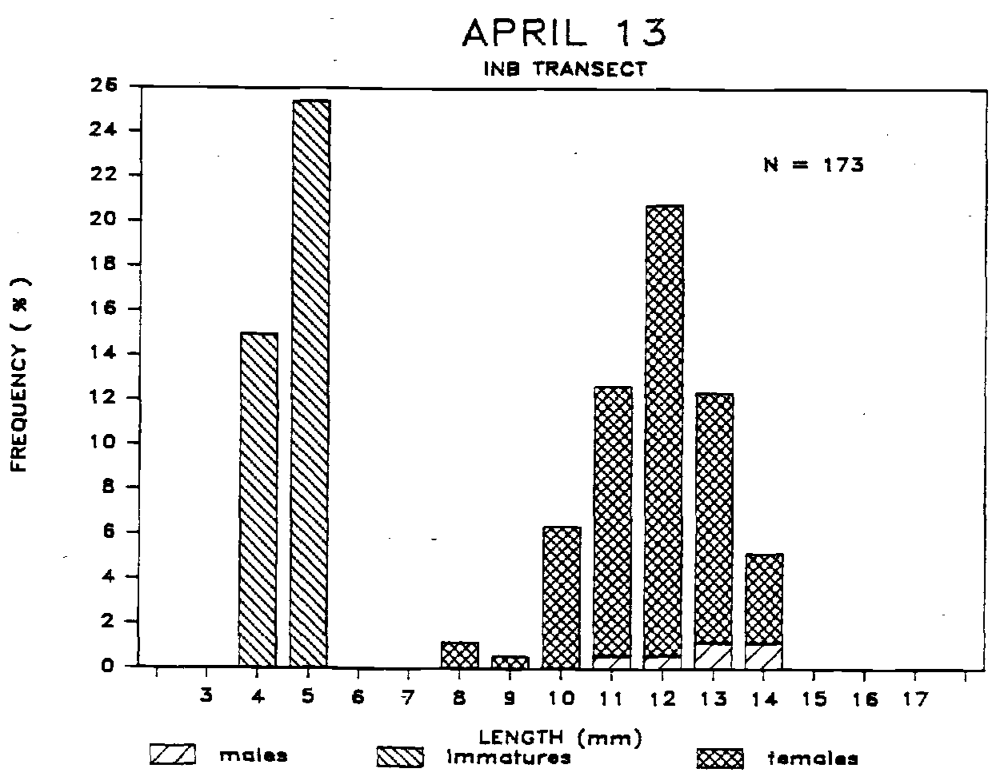

APRIL 13
INB TRANSECT
N = 173
FREQUENCY (%)
LENGTH (mm)
males
immatures
females

Figure II.7

Figure II.8: Length-frequency histograms comparing the total population structure of the ice, water column, and sediment habitats at the 1980 Narwhal Island ice station, SW Beaufort Sea.

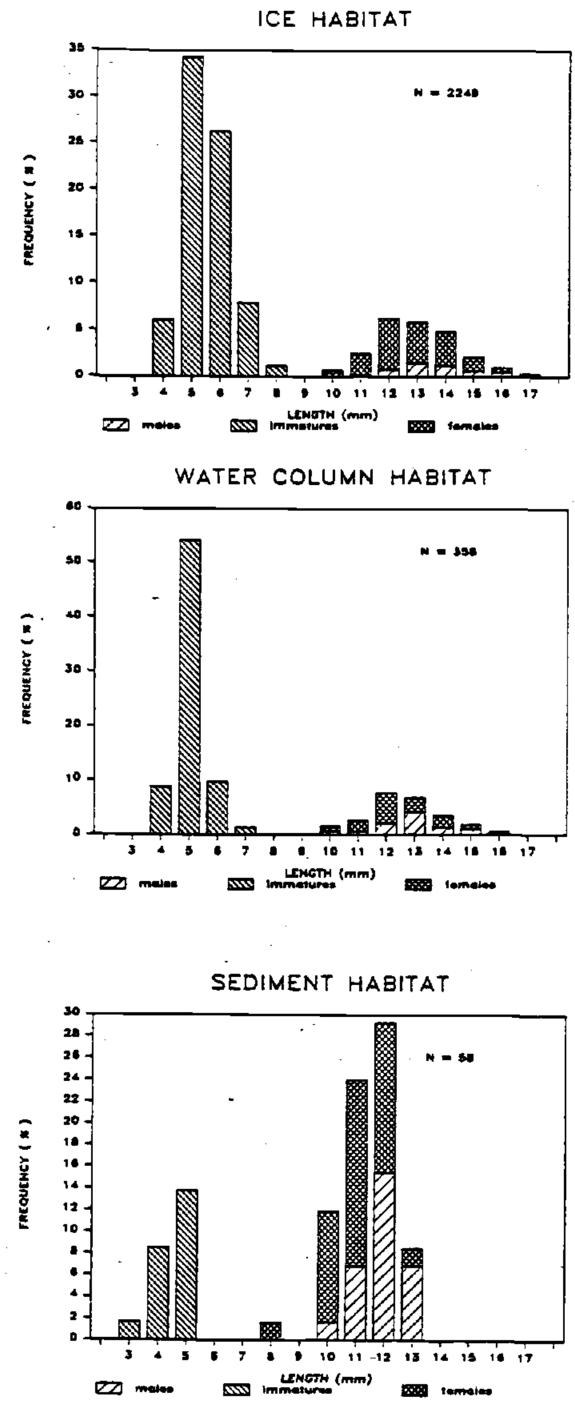

ICE HABITAT
FREQUENCY (%)
LENGTH (mm)
males
immatures
females
WATER COLUMN HABITAT
FREQUENCY (%)
LENGTH (mm)
males
immatures
females
SEDIMENT HABITAT
FREQUENCY (%)
LENGTH (mm)
males
immatures
females

Figure II.8

TABLE II.4: Results of the Kolmogorov - Smirnov two sample tests on *Pseudalibrotus litoralis* from the ice, water column, and sediment habitats of the Narwhal Island study site, spring 1980.

	Dcalc.	D@=0.05	D@=0.01	Comments
ICE				
April 13 vs April 19	0.04	0.19	0.23	Accept Ho[$] ; NS
April 19 vs May 5	0.32	0.21	0.25	Reject Ho[!] ; **
May 5 vs May 17	0.33	0.19	0.23	Reject Ho; **
May 17 vs May 31	0.17	0.17	0.21	Reject Ho; *
May 31 vs June 9	0.25	0.13	0.16	Reject Ho; **
PATCH vs TRANSECT				
April 13 (1 & 2) vs April 13 (transect)	0.34	0.20	0.24	Reject Ho; **
TOTAL HABITAT TESTS				
Ice vs Sediment	0.52	2.43	2.92	Accept Ho; NS
Ice vs Water Column	0.23	1.47	1.76	Accept Ho; NS
Sediment vs Water Column	0.50	2.72	3.26	Accept Ho; NS

$ = the two samples are statistically identical and the null hypothesis of K-S tests is accepted (Sokal and Rohlf 1981).

! = the two samples are statistically different at the probability level chosen and the null hypothesis is rejected.

NS = Non - Significant
* = Significant at P = 0.05
** = Significant at P = 0.01

DISCUSSION

Three major caveats affect the interpretation of our data: (1) it is logistically difficult to sample year-round in the Arctic, so our sampling was limited to part of the amphipod life cycle; (2) we had no indication of the brood size of P. litoralis in the SW Beaufort Sea because none of the females captured was carrying eggs or young; and (3) the results of the microspatial analysis implied large differences in the population structure of a transect compared to a dense aggregation; therefore, using transect data may have biased our results. The lack of young in the brood pouch may have occurred because amphipod females in the Eastern Canadian Arctic usually carry their eggs in the summer and their young in the fall and winter (Steele 1961) or because they released their young upon capture or preservation (J. Percy pers. comm.). Also research in the Eastern Canadian Arctic has shown that P. litoralis females are rarely captured with embryos, eggs or young in the brood pouch (Cota & Watson per. comm.).

Nonetheless, our data provide a reasonable insight into the life cycle of Pseudalibrotus litoralis in the shallow SW Beaufort Sea. The bimodal population structure with one large peak of animals between 4.0 - 6.0 mm and another in the size range of 11.0 - 14.0 mm, has been used as evidence for two year life cycles (Schneider 1891; Steele 1961; Kanneworff 1965; Kulikov 1980; Cross 1982). The small-sized immatures were either newly released (3.0 - <5.0 mm) or at most two or three months old

(5.0 - <7.0 mm). They could not have been spawned by the older and larger (10.0 - 14.0 mm) juveniles found simultaneously. Fully mature females of 13.5 mm or more and males of 14.0 - 17.0 mm, were rare in our samples and probably died after spawning (females) or mating (males). Our data suggest the following life cycle: (1) release of young (3.0 - 6.0 mm), death of fully mature adults, and growth of older juveniles in the spring (year 1); (2) growth of immatures and maturation of older juveniles in the summer (year 1); (3) breeding in the fall with continued growth of immatures to young juveniles (year 1); (4) overwintering of new adults and juveniles (year 1); (5) adults release new immatures, die after spawning, and the young of the previous year become the older juveniles of the spring season (year 2).

Regression of length adult females with time and the degree of maturity of males and females also support the two year life cycle hypothesis. Females were the only group to show a significant increase in length through time (0.03 mm / day) but the qualitative analysis for all sexes implied a slow growth rate during the spring. Slow growth was consistent with other research in the Arctic which has shown the prevalence of multiyear life cycles (Steele 1961; Kanneworff; Dunbar 1968; Kulikov 1980; Griffiths and Dillinger 1981; Cross 1982). Males and females attained an average maturity close to 2.0 implying the presence of older juveniles (Table II.3). Males and females with a maturity of 2.0 were not in the ice to spawn but rather to feed on the early production of diatoms.

The lack of difference in the bimodal length-frequency among the three habitats, and the low abundance in the sediments (1/15 that of the ice habitat) suggest that there was only one population of P. litoralis. This population moved from the sediments to the ice in the spring to feed on the early carbon source of ice microalgae, diatoms and associated meiofauna. Ice and sediment samples were collected the same way and at the same time during the spring, so the large difference in abundance data (Table II.1) could well have resulted from a mass movement of amphipods from the sediments to the ice. These results are concordant with data from the Central Arctic Basin where P.litoralis temporarily inhabited the ice in the spring to spawn and gain energy for the upcoming breeding season (Mel'nikov and Kulikov 1980). Movement to the ice in early and mid-spring in the SW Beaufort Sea and a return to the sediments in June after ice break-up, as well as continuous swimming between these two benthic habitats, confounded the diel and temporal trends in population structure in the water column habitat. This may have resulted in the lack of statistical difference between day and night population structure.

The increase in the number of young with time, the peak in length of males and females, and the peaks in the percentage of mature and ovigerous females all occurred between May 17 and May 31. This period coincided with the maximum primary production in the ice habitat during the spring of 1980 (Horner and

Schrader 1982, 1984). Similarly the dramatic change in the sex ratio of the sympagic population happened between May 5 and May 17, suggesting that more males were moving up to the ice habitat to feed on its early carbon source. Pseudalibrotus litoralis temporarily inhabit the ice during spring and profit from the early carbon source of microalgae, diatoms, and harpacticoid and cyclopoid copepods (Carey and Boudrias in prep). This life history strategy may permit a higher survival of recruits due to the concentrated food sources available, and additional nutrition for the maturing juveniles preparing for the fall breeding season. The fast-ice habitat in the southwestern Beaufort Sea can be categorized as a temporary but highly efficient spawning and nursery ground for Pseudalibrotus litoralis.

CONCLUSIONS

(1) Sympagic *Pseudalibrotus litoralis* from the shallow continental shelf of the SW Beaufort Sea probably have a two year life cycle. This result is based primarily on the bimodal population structure of this amphipod during the spring.

(2) The maturity of males and females, the increase in length of adults and immatures, and the increase in number of immatures through time also support the two year life cyle hypothesis.

(3) *Pseudalibrotus litoralis* temporarily inhabit the ice in the spring and use the early production of microalgae, diatoms, and copepods, as an important food source for newly spawned young and for juveniles preparing for fall mating.

(4) The lack of spatial variability in the bimodal population structure between the three habitats of the continental shelf and the low abundance of *P. litoralis* in the sediments suggest the presence of only one population of this lysianassid species. This benthic amphipod moves from the sediments to the ice habitat in the spring to take advantage of the early carbon source in the ice (Horner and Schrader 1982, 1984).

(5) The increase in length of adults, the peak in the percentage of mature and ovigerous females, and the decrease in sex ratio, coincide with the maximum spring primary production in the ice habitat. These results also support the early carbon hypothesis.

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Chapter III

Feeding Ecology of *Pseudalibrotus* (= *Onisimus*) *litoralis* (Crustacea: Amphipoda) on the Inner Continental Shelf of the SW Beaufort Sea.

INTRODUCTION

Though researchers have been studying the ecology of high arctic ice edge communities for many decades (see Grainger et al 1985 and Carey in press for good reviews), few studies have concentrated on the food web dynamics and feeding ecology of underice fauna. Griffiths and Dillinger (1981) studied the life histories and feeding ecology of mysids and amphipods in Simpson Lagoon from 1977 - 1979. Their research showed that the mysids *Mysis relicta* and *M. litoralis* were omnivorous and the lysianassid *Onisimus glacialis* fed primarily on ice-associated pennate diatoms and underice crustaceans. Bradstreet and Cross (1982) provided the best quantitative data on trophic relationships at high arctic ice edges. Their results indicated that: (1) seabirds and marine mammals eat arctic cod, and to a lesser extent, zooplankton and underice amphipods; (2) arctic cod (*Boreogadus saida*) fed on ice amphipods, underice meiofauna, and zooplankton; (3) calanoid copepods, the planktonic amphipod *Parathemisto spp.*, and the ice-associated amphipods, *Onisimus glacialis*, *Apherusa glacialis*, and *Gammarus wilkitzii*, fed primarily on epontic pennate diatoms. Grainger et al (1985) summarize the available data on trophic dynamics in Arctic sea ice ecosystems. Their results show that the trophic links are from bacteria, microflagellates, and diatoms, to calanoid, cyclopoid and harpacticoid copepods, and planktonic and benthic amphipods, to ctenophores and chaetognaths,and finally to fishes, birds and mammals.

Research on the inner continental shelf of the southwestern Beaufort Sea, near Narwhal Island (141 degrees 30' W, 70 degrees 24' N), has shown that lysianassid amphipods, particularly Pseudalibrotus (=Onisimus) litoralis, dominate the macrofaunal underice community (Carey 1984; Boudrias and Carey in prep). Both littoral and deep-sea lysianassids are described as scavengers that rapidly consume bait, and presumably food falls, in a few hours (Bousfield 1973; Dahl 1979; Ingram and Hessler 1983; Sainte - Marie 1984; Smith and Baldwin 1984). Abyssal scavenging amphipods are adapted in three ways for carrion feeding: (1) they have chemosensory receptors to detect and locate their food; (2) their mouthparts are designed to tear, cut, and crush both soft and hard food items; and (3) their expandable gut permits storage of large quantities of food (Dahl 1979). Sainte - Marie (1984) found that four subarctic circalittoral lysianassids, including Onisimus litoralis, had the same morphological adaptations for scavenging and necrophagy than the deep-sea lysianassid genera Hirondellea, Eurythenes, and Orchomene. Experimental evidence from Arctic waters showed that the lysianassid Onisimus affinis used chemoreception to locate meat or fish bait (Busdosh et al 1982). Animals moved to the trap only from a downcurrent direction from distances of up to 30 m and approximately 20,000 individuals were trapped in one day (Busdosh et al 1982). Thus, shallow-water lysianassids from the Arctic, using chemoreception, may be adapted to feed on dead and dying crustaceans and possibly other food sources such as diatoms.

The main objective of this study is to describe the feeding ecology of the dominant underice lysianassid *Pseudalibrotus litoralis*. Three aspects are investigated: (1) the functional morphology of the mouthparts and antennae; (2) gut contents; and (3) trap-collected fecal pellets. The use of underice algae as an added source of food for ice-associated macrofauna is discussed in conjunction with these data, and with a previous study on the life history of *P. litoralis* (Boudrias and Carey in prep.).

MATERIALS and METHODS

Underice amphipods were captured with a rectangular net, 32 cm X 11 cm, with a 0.33 mm mesh pushed along 10 m transects by SCUBA divers. The study was conducted from April 13 to June 9, 1980 at a fixed ice station (141 degrees 30' W, 70 degrees 24' N) near Narwhal Island on the inner continental shelf of the SW Beaufort Sea. The amphipods were preserved in 10% buffered formalin at the ice station and later transferred to 70% ethanol.

After detailed life history research was completed (Boudrias and Carey in prep. for details), antennae, mouthparts, and gastrointestinal tracts of adult Pseudalibrotus litoralis with full or partially full guts were carefully dissected in the lab. Using a Wild binocular dissecting microscope at 25 and 50 X magnification, we sheared off the head, dissected each mouthpart, and removed food items from the stomodeum (anterior gut section). Mouthparts and gnathopods were individually drawn with the aid of a camera lucida. Antennae, the oral cone and the mandibles of an adult female P. litoralis were air dried, mounted on aluminum stubs, coated under vacuum with gold, and viewed with an International Scientific Instruments Mini-SEM, Model MSM-2, scanning electron microscope. Gut contents were placed on glass slides, spread out under a coverslip, and viewed with a Zeiss compound microscope at 200 and 500 X magnification. We described gut contents viewed under the compound microscope and some of the contents from the stomodeum were air dried, mounted on aluminum stubs and viewed with the scanning electron microscope.

Fecal pellets were collected on glass-fiber filter beds in PVC particle collectors with a 3:1 height to width ratio deployed for five days every two weeks during the spring sampling period. Four collectors were mounted on each of the two frames deployed on the bottom. The particle collectors were lowered to the bottom in 9 m of water below the ice, and falling organic matter and fecal pellets were preserved in situ with rock salt tablets and sodium azide. Divers retrieved the collectors and the bases simultaneously, and the water above the filter was drained through the filters which were frozen. Fecal pellets collected from the filters were photographed, identified to species or genus, and some were viewed with the scanning electron microscope for more detailed analyses.

RESULTS

Functional Morphology

We focussed on two aspects of the functional morphology of Pseudalibrotus litoralis feeding appendages: (1) antennal structure, particularly the presence of chemosensory hairs/setae; and (2) the shape and design of individual mouthparts within the oral cone and of the gnathopods. Using a scanning electron microscope, we observed dense tufts of setae on the ventral side of the antennula of adult female P. litoralis (Fig. III.1). These resemble the chemosensory type setae found in other scavenging lysianassids (Dahl 1979). Without experimentation it was impossible to detect if the setae were used in food location (Dahl 1979) or for pheromone reception (Dahl et al 1970). However, our field observations indicated that P. litoralis and other lysianassids were attracted to baited traps. The research by Busdosh et al (1982) on Onisimus affinis also support the chemosensory potential of Arctic lysianassids.

The individual mouthparts forming the oral cone are designed for tearing, shearing, and crushing different food items (Fig. III.2). The labrum and labium have sharp cutting edges, the maxilulla (Mx 1) bears stout and robust spines with sparse setulation, the maxillae (Mx 2) have short setae for tearing, and the mandible is especially well suited for cutting soft food items with its incisor and crushing hard foods with its triturative

Figure III.1: Scanning electron microscope photographs showing

(A) antenna 1 and accessory flagellum of an adult female with concentrated tufts of chemosensory (?) setae. (X150); size bar = 100 um.

(B) antenna 2 with concentrated tufts of chemosensory setae on the peduncle. (X150); size bar = 100 um.

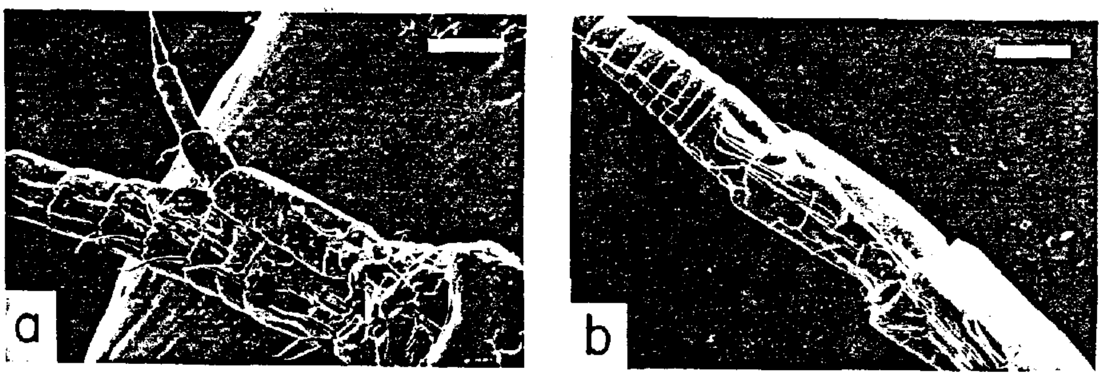

Figure III.1

Figure III.2: Camera lucida drawings of Pseudalibrotus litoralis mouthparts; Mx1 = Maxilla 1 with many spines; Mx2 = Maxilla 2 with short setae; Md = mandible with a sharp incisor, a bowl-shaped corpus mandibulae, and a spinulose palp; Mxp = maxilliped with sharp cutting edges on its inner plate (ip), and a robust dactyl on its palp (p).

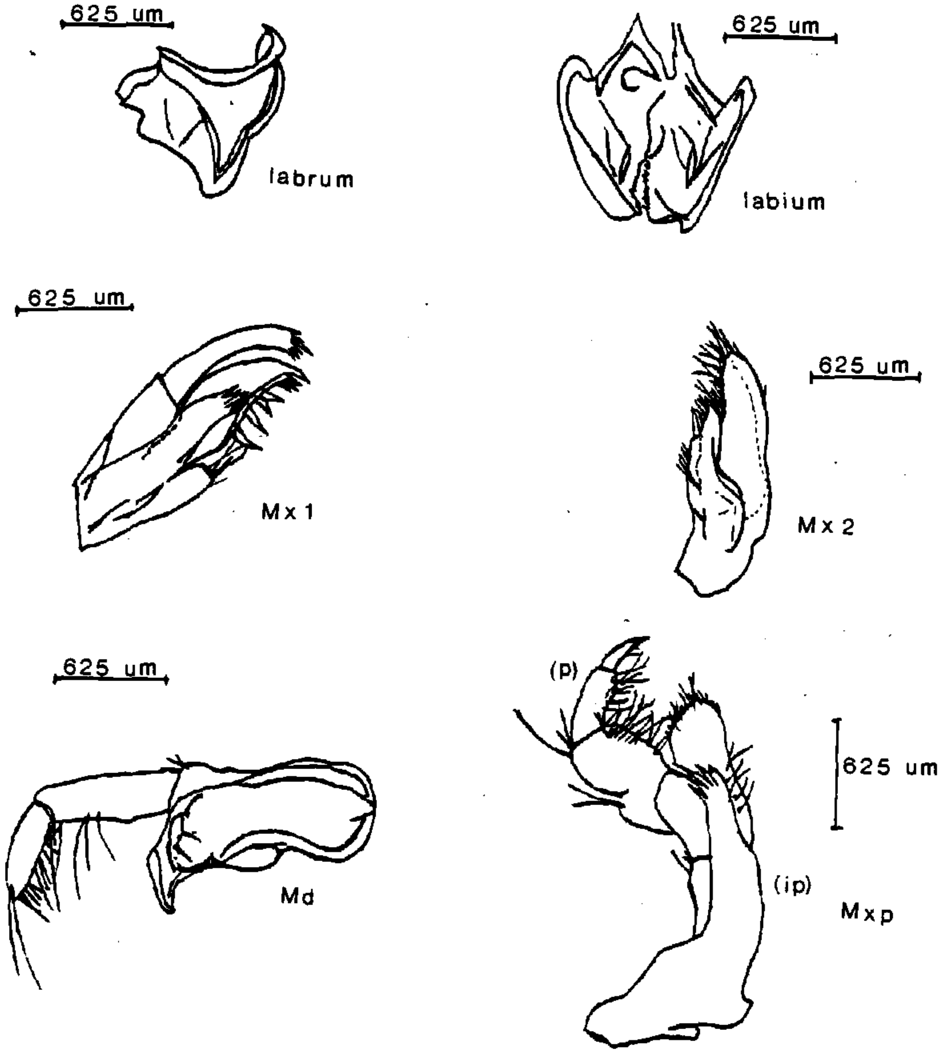
625 um
labrum
625 um
labium
625 um
Mx1
625 um
Mx2
625 um
Md
(p)
625 um
(ip)
Mxp

Figure III.2

molar (Sainte - Marie 1984). The corpus mandibulae is bowl-shaped to permit larger bites (Fig. III.3A). The maxillipeds (Mxp) which close the oral cone have a sharp cutting edge on the inner plate (ip) and a robust dactyl on the palp (p) to tear into soft foods (Fig. III.2 and Fig. III.3B). The two gnathopods are also well adapted for tearing carrion or other soft foods and for holding large food items (Fig. III.4).

Gut Content Analysis

The small percentage (5%) of adult *P. litoralis* with full or partially full gastrointestinal tracts precluded statistical analysis of temporal trends in feeding ecology. However, our qualitative data were consistent with other studies depicting lysianassids as efficient and voracious scavengers (Bousfield 1973; Dahl 1979; Thurston 1979; Ingram and Hessler 1983; Sainte - Marie 1984; Smith and Baldwin 1984). We found numerous macrofaunal and meiofaunal crustacean parts and some diatom frustules mainly in the stomodeum or foregut of the amphipods (Fig. III.5). Crustacean parts, including antennal segments, compound eyes, mouthparts, thoracopods, pleopods, setae, nauplii, muscle fibers, and other body tissues, were present in close to 90 % of all gastrointestinal tracts examined. The majority of these crustacean fragments (90 % or more) were from immature and adult amphipods.

Diatom frustules were present in the foreguts and hindgut (one animal) of amphipods captured in dense aggregations on April 13 (see Boudrias and Carey in prep. for details) and especially in adult females captured on May 31. In these late May samples, diatom frustules comprised between 50 and 70 % of the total gut contents. Diatom frustules were absent from animals captured at other times during the spring.

Fecal Pellet Analysis

Fecal pellets collected throughout the spring were identified, based on their light color, encapsulating membrane, and their length and diameter, as those of *Onisimus* (= *Pseudalibrotus*) *litoralis* (D. Schneider pers. comm.). Using scanning electron microscopy to study the details of well-preserved pellets, the photographs revealed the presence of diatoms and diatom frustules. No crustacean parts were observed in these fecal pellets. The mean number of *P. litoralis* fecal pellets increased from mid-April to late May with a maximum in production between May 31 and June 2, 1980 (Fig. III.6). Detailed data on the organic carbon, organic nitrogen, and overall particle flux from the ice to the sediments is discussed elsewhere (Carey in prep.).

Figure III.3: Scanning electron microscope photographs of

(A) the mandible of an adult *Pseudalibrotus litoralis* showing the cutting edge of the incisor, the lacinia mobilis, and the bowl-shaped corpus mandibulae.
(X300); size bar = 100 um.

(B) ventral view of the oral cone showing the cutting edge of the inner plate of the maxillipeds, and the setualtion of the maxilliped palp.
(X100); size bar = 100 um.

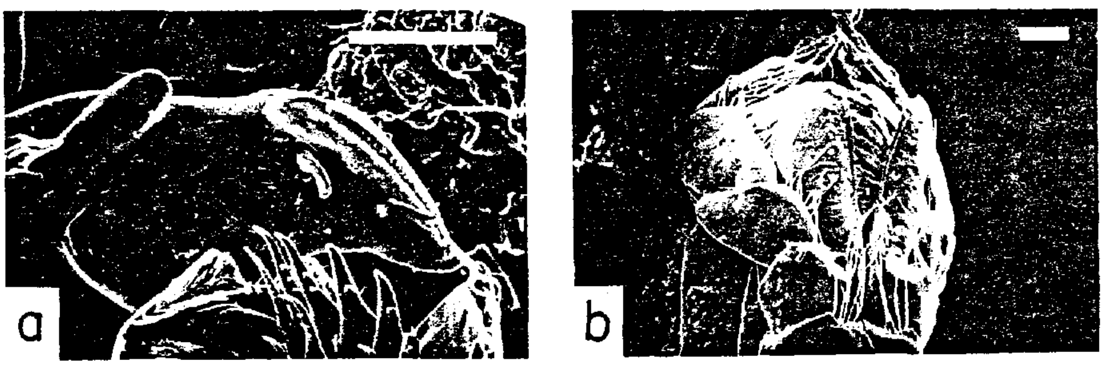

Figure III.3

Figure III.4: Camera lucida drawings of gnathopods 1 and 2 of an adult *Pseudalibrotus litoralis* showing the subchelate dactyls, and robust spines and setae.

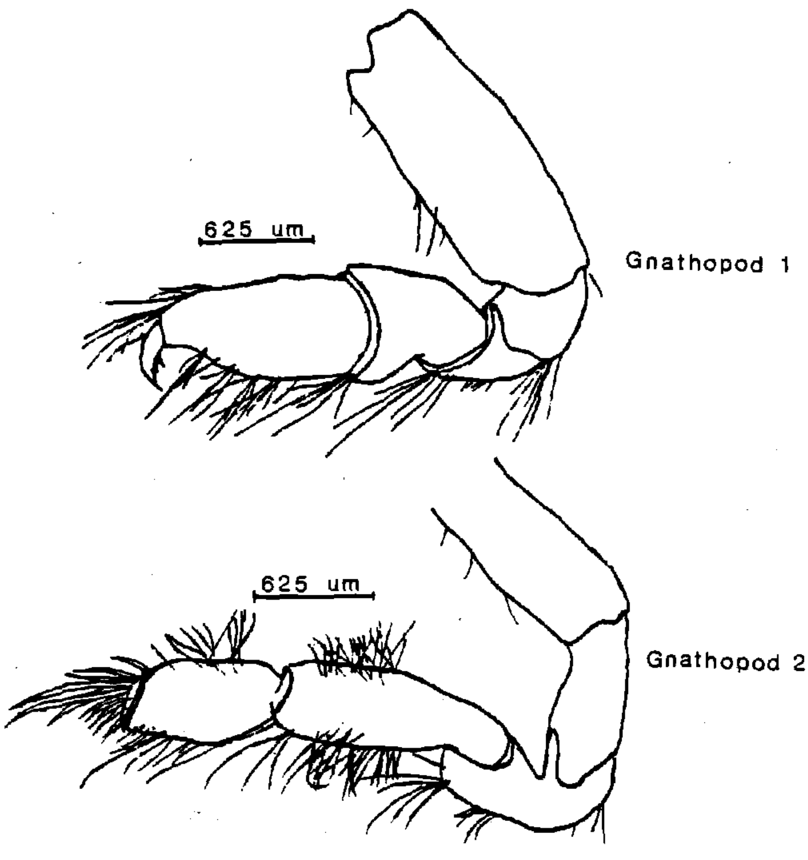

Figure III.4

Figure III.5: Scanning electron microscope photographs of underice adult *Pseudalibrotus litoralis* gut contents.

(A) general view revealing the presence of macrofaunal crustacean parts and diatoms. (X600); size bar = 100 um.

(B) macrofaunal crustacean part, probably a segment of a female oostegite with long setae. (X350); size bar = 100 um.

(C) broken pennate diatom fragments. (X4000); size bar = 10 um.

(D) propodus and dactylus of another amphipod showing the crushing strength of *P. litoralis* mouthparts. (X500); size bar = 100 um.

(E) close-up of broken and crushed diatom frustules. (X4000); size bar = 10 um.

(F) pennate diatom frustule among unidentifiable gut contents. (X1500); size bar = 10 um.

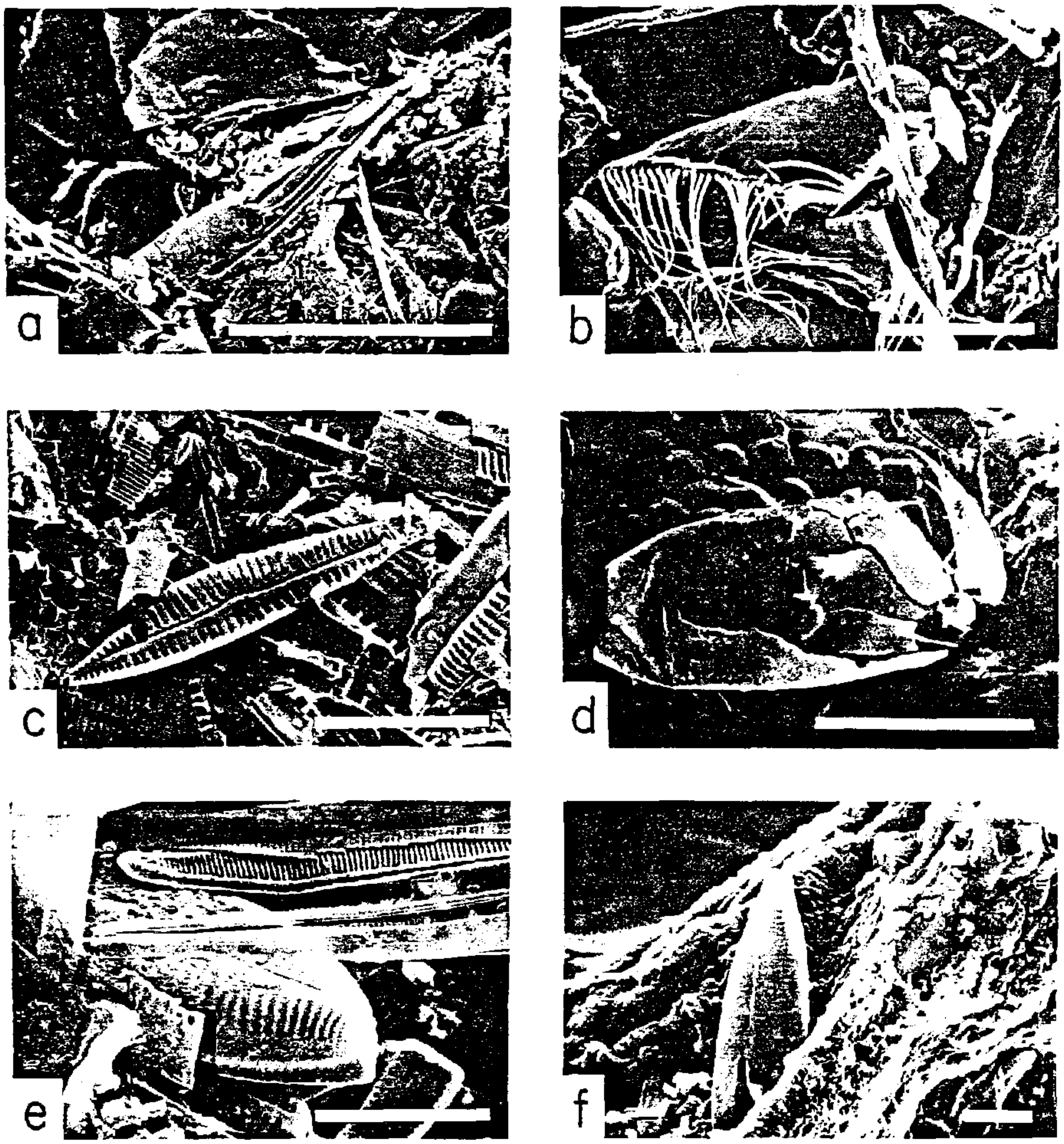

Figure III.5

Figure III.6: Flux of *Pseudalibrotus litoralis* fecal pellets to the sediments during the spring, 1980 at the Narwhal Island Ice station.

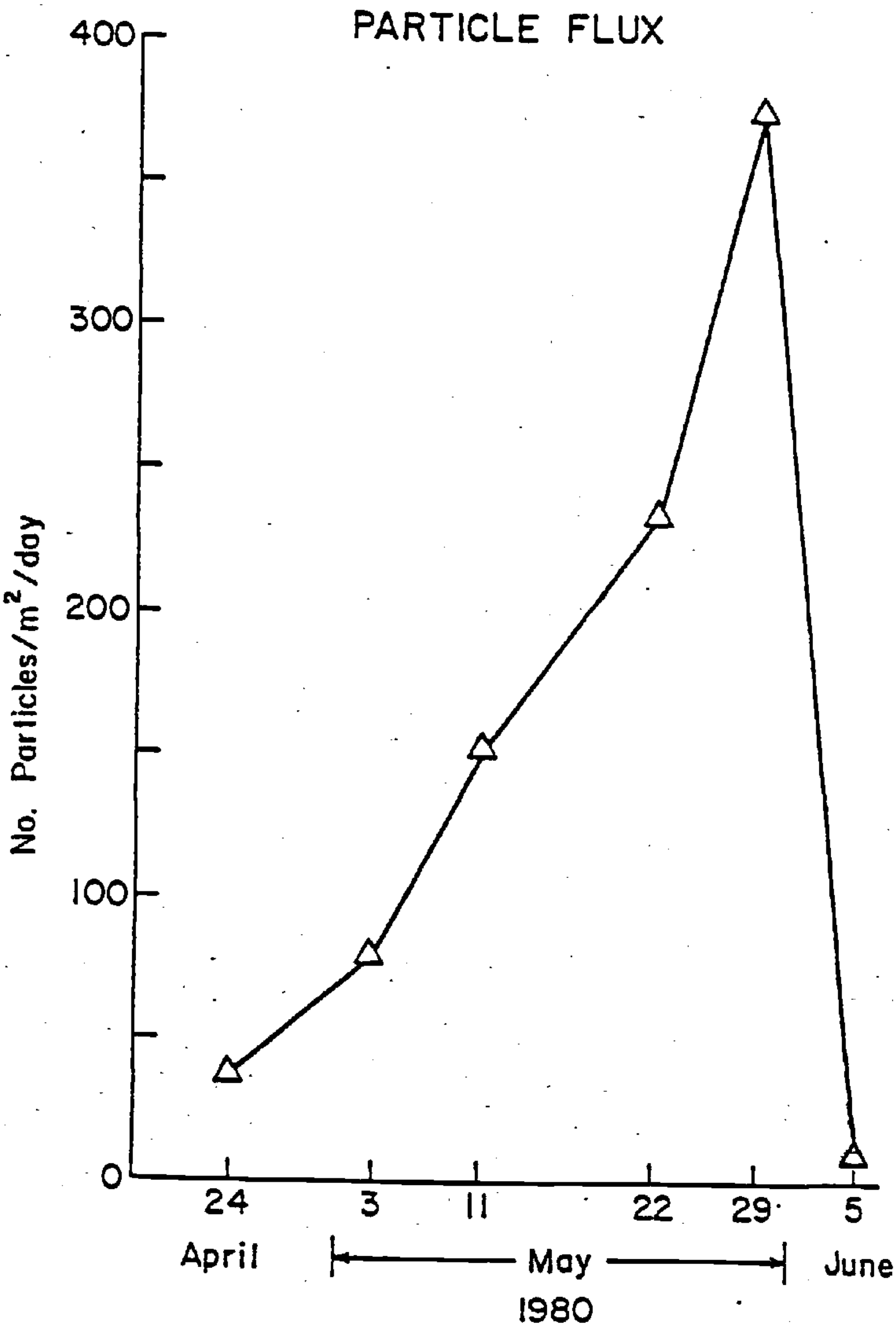
PARTICLE FLUX
400
300
200
100
0
No. Particles/m²/day
24
3
11
22
29
5
April
May
June
1980

Figure III.6

DISCUSSION

Based on the functional morphology of their antennae and mouthparts, and on the food in their guts and fecal pellets, underice *Pseudalibrotus litoralis* are omnivorous. The chemosensory-type setae on their antennae may permit localization and recognition of potential food. Their mouthparts, particularly the mandible and the gnathopods, are well adapted for tearing and cutting large, soft prey or carrion, while the bowl-shaped corpus mandibulae and the triturative mandibular molar can be used for crushing harder food items like diatoms. Their gut contents revealed an abundance of crustacean parts, mainly from other amphipods, and, especially for late May samples, many diatom frustules. Complementary data from fecal pellet analysis also indicated the importance of diatoms as food. These data from a shallow-water littoral habitat in the Arctic, reinforce Sainte - Marie's (1984) contention that subarctic circalittoral *Onisimus litoralis*, (= *P. litoralis*) is a member of the "demersal guild" of scavenging lysianassid amphipods defined by Ingram and Hessler (1983).

More importantly, the presence of pennate diatoms and meiofaunal harpacticoid parts in the gut of this dominant underice lysianassid support the "early carbon hypothesis" [Dunbar 1977b; Boudrias and Carey (in prep.)]. Some benthic amphipods temporarily inhabit the undersurface of the ice to take advantage of the early primary production and associated meiofaunal production occurring during spring (Mel'nikov and Kulikov 1980). Diatoms and microflagellates are present in the lower reaches of the ice throughout the spring with the maximum in primary production occurring in late May (Horner and Schrader 1982, 1984). Diatom frustules were found in low proportions (<10 %) in some amphipods captured in April, in fecal pellets collected throughout spring (100 % diatoms), and in high proportion (50 - 70 %) in gut contents of adult female P. litoralis caught on May 31. Harpacticoid copepod limbs occured in low proportion (<5 %) in the gut contents throughout the spring. These results, along with the life history data from a previous study (Boudrias and Carey in prep.), indicate that Pseudalibrotus litoralis temporarily use the ice habitat as a nursery for recruits and a feeding ground for juvenile and adult amphipods preparing for fall breeding.

However, the predominance of macrofaunal crustacean parts, such as compound eyes, large antennal fragments, and malacostracan limbs and mouthparts, creates some ambiguity in our interpretation. These amphipod fragments may originate from: (1) a sampling artifact of intra-sample predation where amphipods left in the same container feed on each other; (2) actual predation on immatures and adults of other ice-associated amphipods; (3) the smaller amphipod parts, from immature animals, could be due to cannibalism of adult P. litoralis on young of the same species; and (4) as efficient scavengers, P. litoralis juveniles and pre-adults could be feeding on dead or dying underice amphipods that have already spawned their young. Data on other lysianassids depict them as necrophages and scavengers (Dahl 1979; Thurston 1979; Ingram and Hessler 1983), but Eurythenes gryllus, an abundant abyssal amphipod, exhibits some predatory behavior when it swims many meters above the bottom (Smith and Baldwin 1984). With the available data, we can not distinguish which feeding behavior is most prevalent.

CONCLUSIONS

(1) *Pseudalibrotus litoralis* is a scavenging lysianassid amphipod, omnivorous in diet. It has chemosensory type setae on its antennae that can be used in location and identification of food. Its oral cone and gnathopods are designed for tearing and cutting large and soft foods, like carrion, while the corpus mandibulae and triturative molar of its mandibles can be used to crush hard food items like diatoms.

(2) Results from gut content and fecal pellet analyses also indicate an omnivorous diet with macrofaunal crustacean parts (about 90%), meiofaunal, especially harpacticoid copepod parts (< 5%), and diatoms (usually < 10%) comprising the totality of the contents.

(3) Amphipods captured on May 31 and in dense aggregations earlier in spring (April 13) had their foreguts filled with diatom frustules. The abundance of diatoms in their diets in late May coincided with the maximum primary production of underice microalgae and diatoms.

(4) Our results support the contention that *P. litoralis* is a temporary inhabitant of the ice in spring. This lysianassid amphipod uses this habitat as a spawning and nursery ground for recruits and a feeding ground for juveniles preparing for fall breeding.

(5) The dominance of large, macrofaunal crustacean parts in the guts may originate from intrasample feeding of captured amphipods, predation on other amphipods, cannibalism on young of the same species, and/or scavenging on dead or dying amphipods.

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Chapter IV

General Discussion

The spring bloom of pennate diatoms, and to a lesser extent microalgae, on the shallow continental shelf of the southwestern Beaufort Sea is an important early source of primary production (Horner and Schrader 1982, 1984). Dunbar (1977b) describes the importance of ice biota to the evolution of polar ecosystems as:

> " Its [ice biota] chief relevance in the evolutionary context of the present paper is, first, that it spreads the production and food supply over a longer period of the year than would be possible without it, and, second, that it provides an example of a tight, almost two-dimensional concentration of production in an otherwise very unproductive region. In this respect the ice biota might be compared with coral reefs and turtle grass beds in the tropics, which constitute regions of very high production in surroundings of low productivity."

Mel'nikov and Kulikov (1980) relate the presence of underice primary productivity to the population dynamics of year-round sympagic fauna (autochtonous species) and temporary inhabitants of the ice undersurface (allochtonous species). In my study area, it may also be an important structuring force in underice and sediment amphipod assemblages.

The numerically dominant lysianassid in both the ice and sediment habitats, Pseudalibrotus litoralis, has been described as a temporary inhabitant of the ice in the Central Arctic Basin (Mel'nikov and Kulikov 1980). With its bimodal population structure throughout the spring, and primarily a scavenging feeding behavior, P. litoralis resembles other dominant arctic lysianassids (Griffiths and Dillinger 1981; Bradstreet and Cross 1982; Busdosh et al 1982; Cross 1982).

Although _P. litoralis_ is abundant in the sandy sediments of the shallow continental shelf near Narwhal Island in spring, it completely dominates the sympagic habitat. The lower abundance in the sediments and the lack of variability in the total population structure between the three habitats studied suggest the presence of only one population of _P. litoralis_ that temporarily uses the ice undersurface in the spring.

Important life history traits, (the number of males and of mature females, the maximum growth rate of adults, the percentage of ovigerous and of mature females, the number of young released, and the decline in sex ratio) reach their maxima or minima at the time of maximum underice primary production. Also, the dietary composition of the gastrointestinal tracts of these amphipods changes from an almost complete dominance of macrofaunal crustacean parts to a dominance of diatoms in samples taken late in May. Thus, the main population trends and the diet of _P. litoralis_ in late May strongly correlate with the largest peak in primary production in the ice (Horner and Schrader 1982, 1984). Though the limited study period of this research project precludes any year-round description of its behavior, its life history patterns in the ice, water column, and sediment habitats, and its feeding ecology support the "early carbon hypothesis" (Dunbar 1977b).

Future research on this amphipod and other arctic amphipods should focus on year-round life history patterns and more detailed visual assessment of feeding behavior and general ecology. Improved sampling procedures should include preservation of individual females to permit estimations of brood size, photographic and cinematic assessment of locomotion, migration between the habitats, and feeding behavior, and immediate preservation of animals to prevent intrasample feeding. Experimental research might include attempts at demonstrating chemosensory adaptations of these lysianassids, exclusion of predators, and removal and transplantation experiments to test for the importance of competition and predation as structuring forces in the amphipod assemblages. More detailed natural history observations, and particularly, more physiological studies would also provide much valuable information.

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