Spring 2008

Distribution and feeding behavior of early life stages of the northern shrimp, Pandalus borealis, in relation to the spring phytoplankton bloom in the western Gulf of Maine

Erin B. Hobbs
University of New Hampshire, Durham

DISTRIBUTION AND FEEDING BEHAVIOR OF EARLY LIFE STAGES OF THE NORTHERN SHRIMP, *PANDALUS BOREALIS,* IN RELATION TO THE SPRING PHYTOPLANKTON BLOOM IN THE WESTERN GULF OF MAINE

BY

ERIN B. HOBBS
Baccalaureate Degree, University of New Hampshire, 2001

THESIS

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Master of Science
in
Zoology

May, 2008

Thesis has been examined and approved.

Thesis Co-Director, Jeffrey Runge
Research Scientist - Oceanography
University of Southern Maine
Gulf of Maine Research Institute

Thesis Co-Director, William Howell
Professor of Zoology

James Haney
Professor and Chair of Zoology

April 14, 2008
Date

ACKNOWLEDGMENTS

I would like to start by thanking New Hampshire Sea Grant for funding this research project. This research could not have been completed without their support. In addition, I would like to thank several individuals for supporting me throughout my graduate experience. To my advisor Jeffrey Runge, thank you for believing in me and taking me on as a student. I am forever thankful for your patients, the countless hours encouraging me through this process and all your knowledge. To Hunt Howell and James Haney, thank you for your continuous support and sitting on my committee. To Rebecca Jones, thank you for being a great mentor both in the field and laboratory. Your experiences, knowledge and advice were always useful and appreciated. To Timothy Moore, thank you for all your time spent running shrimp samples through the HPLC machine. I am indebted to you for all your efforts. To Debbie Goodwin and Jessica Bolker's writing seminar, thank you for reading every ounce of my thesis from start to finish and providing constructive feedback. I am now a better writer because of you. To the countless others in OPAL and the zoology department, thank you for all that you have done to support me and my research. I will forever be grateful for your friendships, knowledge and support. Finally, to my husband Dave, thank you for keeping me grounded when I wanted to fly away and standing tall when I wanted to hide. You are my rock and I love you.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

DISTRIBUTION AND FEEDING BEHAVIOR OF EARLY LIFE STAGES OF THE NORTHERN SHRIMP, *PADALUS BOREALIS,* IN RELATION TO THE SPRING PHYTOPLANKTON BLOOM IN THE WESTERN GULF OF MAINE

by

Erin B. Hobbs

University of New Hampshire, May, 2008

The northern shrimp *Pandalus borealis* is a commercially important crustacean found in the deep waters of western Gulf of Maine. In order to develop better fisheries management practices, it is essential to understand variability in *P. borealis* recruitment. Analysis of samples collected along a coastal transect (during 2005 and 2006), indicate cross-shore distribution of early planktonic larval stages is consistent with observed benthic distribution of ovigerous females. Timing of larval occurrence in relation to the spring phytoplankton bloom suggests that a match/mismatch with abundance of phytoplankton and zooplankton prey may be a primary determinant of recruitment success. Among the potential zooplankton prey, *Balanus sp.* larvae are predominant during the residence time of *P.borealis* larvae. Laboratory feeding experiments revealed stage III larvae have higher feeding rates on the diatom *Thalassiosira nordenskioeldii* than stage I. These results support efforts for coupled physical biological models that will allow testing of recruitment hypotheses.

INTRODUCTION

The Gulf of Maine is the southern limit of distribution for the northern shrimp, *Pandalus borealis,* in coastal waters of the northwest Atlantic Ocean. The fishery for *P. borealis* in the western Gulf of Maine began in 1938 and has since contributed to the local economy in Maine, Massachusetts and New Hampshire. The fishery, targeting females while they are inshore, has experienced drastic fluctuations in catch size. In 1954 landings decreased to zero and fishing ceased (Figure 1). Fishing resumed in 1958 and increased steadily until it peaked from 1969 to 1972. Landings then declined drastically into the late 1970s, and the fishery closed again. Biomass stock assessments and regulation began in 1974 but fluctuations in landings continue. In the late 1980s, management initiated use of analytical models for stock analysis, but without incorporation of biotic or abiotic influences. The importance of spatial dynamics of a stock structure and fishing processes has been well acknowledged, but in the past often ignored (Clark et al. 2000). In May 2004, the Interstate Fisheries Management Program approved an amendment to the Fisheries Management Plan requiring those involved "to manage the northern shrimp fishery in a manner that is biologically, economically, and socially sound, while protecting the resource, its users, and opportunities for participation by all stakeholders (Idoine 2006)."

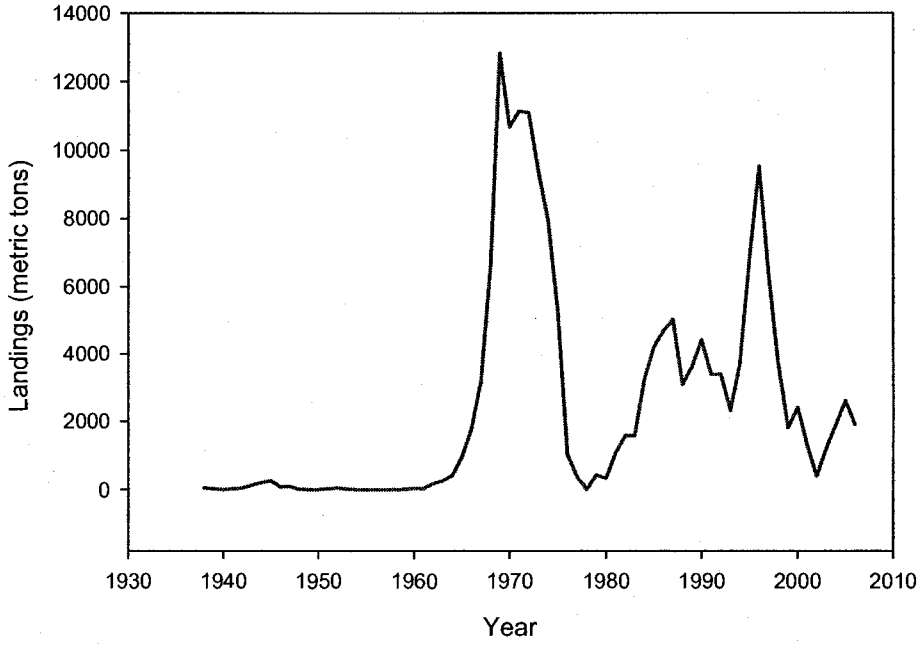

Figure 1. Commercial and recreation landings of the Northern Pink Shrimp, *Pandalus borealis*, (metric tons) from 1938 to 2006 (Idoine 2006).

Understanding the processes that influence the abundance and structure of the *P. borealis* stock, is of utmost importance to the management and success of the fishery. In the Gulf of Maine, the species can be found year-round offshore in water depths ranging from tens of meters to several hundred meters depending on the life stage. Adults prefer soft mud bottom offshore and cooler waters ranging in temperatures from 1-5°C. During winter, ovigerous females migrate from their offshore habitat to the nearshore in order to release their young. In addition, adults demonstrate negative phototaxis in their diel vertical migration, although, ovigerous females do not rise in the water (Shumway et al. 1985).

The reproductive cycle of northern shrimp in the western Gulf of Maine commences with extrusion and fertilization of eggs in late summer. Females remain offshore carrying their fertilized eggs on pleopods, where they develop at a rate that depends on ambient bottom water temperature. After the release of their larvae in the shallow waters inshore, females return immediately offshore. The planktonic larvae go through six zoeal stages in approximately 90 days (Shumway et al. 1985). Larvae remain in the water column (Ouellet and Allard 2006) until they settle to the bottom as juveniles. Larvae are born males and remain males for approximately three years. During year three, males transition into females, after which they have one or two spawning seasons (Ouellet and Allard 2006; Shumway et al. 1985).

A major factor controlling stock abundance is the annual recruitment into the adult population. Recruitment is determined by processes in the larval and juvenile life stages, although evidence from larval fish studies suggest that first order control generally occurs in the larval phase (Myers and Cadigan 1993). Since the larval phase is of prime importance in determining variability and regulation of fisheries; recruitment research needs to include the study of planktonic stages (Horwood et al. 2000). Primary determinants of success in the planktonic larval phase of fish and invertebrate stocks are thought to be physical processes (e.g., wind and circulation) leading to successful transport to juvenile nursery areas (Sinclair 1988) and physical and biological processes leading to

rapid growth and survival during the planktonic larval phase (Leggett and Deblois 1994).

A key hypothesis for successful growth and survival of the early life stages is the concept of the match of food availability during the high mortality planktonic phase. The Cushing match/mismatch hypothesis states that a first order determinant of the strength and success of a fish year-class is the availability of food during the critical period of larval development, controlled by the timing of the spring phytoplankton bloom in relationship to the timing of spawning (Cushing 1990). A recent study of haddock recruitment is consistent with a link between spring bloom timing and larval survival on the Scotian Shelf (Platt et al. 2003). In addition, freshly hatched *P. borealis* larvae have been observed surviving only six days without feeding (Wienberg 1982) and if larvae do not ingest at least some food within the first 30 hours death is inevitable even if food is obtained thereafter (Shumway 1985). I propose here that a similar relationship exists between the timing of *P. borealis* larval release, the timing of the spring phytoplankton bloom and the magnitude and type of plankton available in the western Gulf of Maine.

Stickney and Perkins (Stickney and Perkins 1981) suggested temperature and food availability may affect the survival and recruitment of *P. borealis*. However, recent observations indicate that larvae are well adapted to survive at low temperatures and food type and availability may have a stronger influence on

larval success (Ouellet and Chabot 2005). The spring phytoplankton bloom conditions and spatial distribution of larval release may therefore be very important for high recruitment. Stickney (1983) observed synchrony between peak *P. borealis* larval abundance and the late winter phytoplankton bloom. The extent and importance of this relationship is unclear due to a lack of observational data. In general, the relationship between the spring bloom and higher trophic levels such as larval fish and *P. borealis* requires further investigation (Biktashev et al. 2003).

The feeding behaviors on phytoplankton and its role in the diet of *P. borealis* larvae are not completely understood. Digestive tract examination of field-caught larvae done by Stickney and Perkins (1981) supports that early stage *P. borealis* larvae consume diatoms. Recent research on early larval stages of Penaeids suggests that some substances in phytoplankton trigger digestive enzyme production and increases growth and survival (Kumlu et al. 1992).

However, phytoplankton as a sole food is not sufficient for successful development and growth (Harms et al. 1991). Rasmussen (2000) reported stage I and II larvae had high clearance rates for algae over other foods items offered, while stage III "loses interest" in planktonic algae. Several feeding experiments with *Pandalus borealis* larvae have included *Artemia sp.* nauplii as a main food source (Harvey and Morrier 2003; Haynes 1979; Stickney and Perkins 1981; Wienberg 1982). *Artemia sp.* is not a natural food source for *P. borealis* larvae,

although it is used in laboratory studies. Stickney and Perkins (1981) observed sustainable survival of stage II larvae when the combination of zooplankton and phytoplankton reached their maximum levels. They also concluded the concentration of both zooplankton and phytoplankton at the timing of larval release is important to larval survival.

Detailed information on the feeding characteristics (ingestion rate and food selectivity in relation to changes in environmental conditions, food availability, developmental stage) is needed for predictions of survival probability of larvae during the first year (Harvey and Morrier 2003). It has been suggested by Ouellet (2005) that a combination of diet and temperature influence larval survival and therefore that food type and availability during the time of larval development is a major contributing factor to larval survival. I provide evidence here that interannual variation in the timing of larval release (controlled primarily by bottom temperature in the female habitat) and the timing and composition of the spring bloom (controlled primarily by the wind) will have an impact on survivability of larvae and their recruitment to the adult population.

Ultimately, the successful application of the match/mismatch concept to the management of the northern shrimp fishery will involve the integration with other determinants of recruitment success, such as larval transport. This integration is now feasible with the development of coupled physical biological models (Bates 2007; Cushing 1996; De Younge et al. 2004; Runge et al. 2004). By merging

simulation of physical forcing (circulation and mixing) with biological simulation (processes controlling food availability, feeding and growth of the planktonic larval stages) in computer models, the potential exists for mechanistic forecasting of environmental conditions for recruitment success at time scales useful for management decisions.

In this research, I investigated processes that contribute to the successful survival of *P. borealis* larvae in the Gulf of Maine. I observed the spatial distribution of larvae in western Gulf of Maine to provide data needed by physical transport models. I investigated the connection between spatial and temporal distribution of larval stages and the availability of phytoplankton and zooplankton in the water column. I conducted laboratory experiments to understand feeding behavior of the early planktonic stages. This research contributes to the overall effort of formulating and parameterizing feeding and growth of larval shrimp for incorporation into coupled models. These models can be used to quantify the match/mismatch hypothesis, leading to predictions that can be tested against field data.

CHAPTER I

FIELD TRANSECT

Introduction

Variability in survival of the early planktonic life stages of marine fish and invertebrates may be of first order importance in setting recruitment into the shrimp fisheries (Horwood et al. 2000). In populations of the northern shrimp, *Pandalus borealis*, primary determinants of success in the planktonic larval phase are thought to be physical processes (e.g., wind and circulation) leading to successful transport to juvenile nursery areas (Sinclair 1988) and biological processes influencing larval survival and growth (Ouellet et. al. 2007). Bates (2007) assumed a cross shelf distribution of northern shrimp larvae based on published and unpublished data on the distribution ovigerous females on the inner shelf of the western Gulf of Maine in winter. He concluded that variation in larval transport success due to interannual variability in winds affecting circulation could not explain the observed recruitment fluctuations in Gulf of Maine northern shrimp, implying that biological processes were the controlling factors. Ouellet et. al. (2007) hypothesized that food type and food availability have a greater influence on larval survival through the match and mismatch of larval feeding and growth with their prey (Cushing 1990). The spring phytoplankton and zooplankton concentrations in relation to the spatial and temporal distribution of larvae may therefore be of primary importance for recruitment success.

In order to test the hypotheses about control of recruitment variability in the *P. borealis* population in the western Gulf of Maine, there is a need for fundamental observations about the spatial and temporal distribution of planktonic larval stages, as well as the timing and composition of potential phytoplankton and zooplankton prey. I conducted a series of cross shore transects over two years in the western Gulf of Maine to investigate processes that contribute to the successful survival of *P. borealis* larvae. Here I report on observations of the timing, duration and spatial distribution of larvae and the salinity and temperature characteristics of the water in which the planktonic stages reside. I examine the assumption that the distribution of first stage larvae (30 – 100 m: Bates 2007) is similar to the distribution of ovigerous females (Lewis Incze, personal communication). I investigate the connection between spatial and temporal distribution of larval stages and the availability of phytoplankton and zooplankton in the water column. This research contributes to the overall effort needed to formulate and parameterize the early life history of northern shrimp for incorporation into coupled physical-biological models. These models can be used to quantify the match/mismatch hypothesis, leading to predictions that can be tested against field data.

Methods

A transect of 7 to 8 stations was established in the western Gulf of Maine. The transect started with an inshore station near Portsmouth and extended past the

Isles of Shoals, spanning a distance of over 30 km (Figure 2). Station depths ranged from 30 m to 115 m (Table 1). The transect was sampled semimonthly between February and May in 2005 and 2006. In 2006, difficult weather conditions prevented a complete sampling of all stations along transects from February to March, and only one transect was completed in April, due to limited ship availability.

Larval *P. borealis* abundance was estimated at each transect station from samples taken with a 65 cm bongo net with a mesh size of 333 μm or 500 μm (to reduce clogging and subsequent larval avoidance in high phytoplankton concentrations). The bongo net was towed obliquely at two knots from 5m off the bottom to the surface. Volume samples were determined with a General Oceanics flowmeter centered in each net. Larval shrimp were sorted immediately from one of the two bongo samples, frozen in liquid nitrogen and later stored at -80°C. The remaining samples were preserved in 4% formaldehyde. In the laboratory, all *P. borealis* larvae were sorted from the bongo samples and identified to developmental stages using criteria established by Haynes (1979). Carapace lengths (measured from the base of the rostrum to the back of the carapace) of 20 larvae were measured for each stage within every bongo sample during 2005. Carbon content of larvae was determined using a Perkin Elmer 2400 Series II CHNS/O analyzer. Prior to analysis, frozen larvae were staged and their carapace lengths measured. Twenty-five larvae were available for

carbon analysis (seven stage I, eight stage II, five stage III, two stage IV and three stage V).

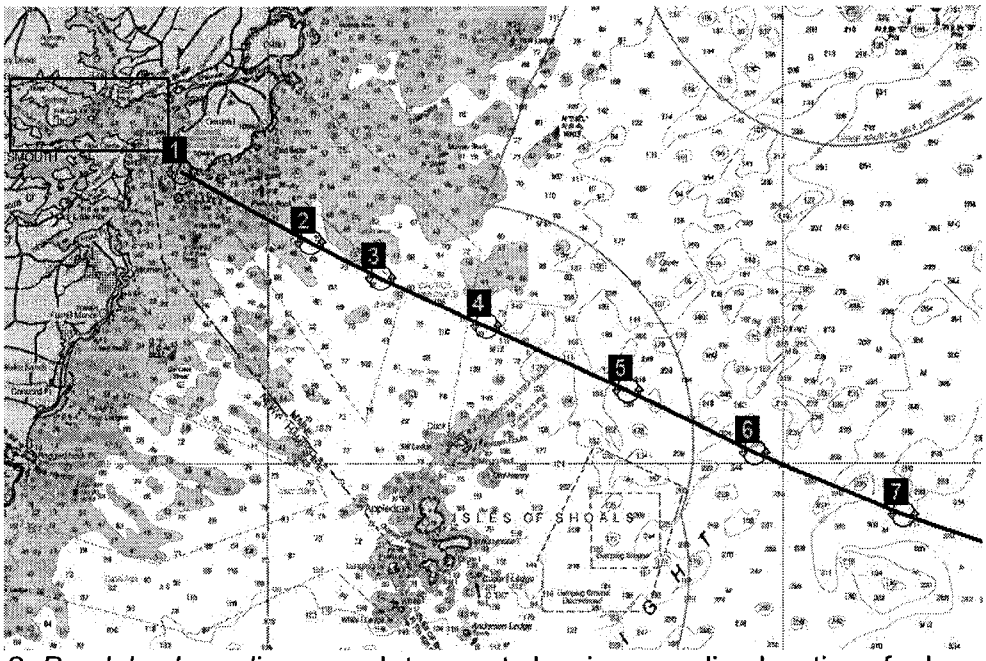

Figure 2. *Pandalus borealis* research transect showing sampling locations for larval abundance, zooplankton abundance and hydrographic data.

Table 1. *Pandalus borealis* research station location, station depth, distance offshore and sampling methods completed.

Station	Latitude and Longitude	Station Depth (m)	Distance off-shore (km)	Bongo Net	Ring Net	Nisken Bottles	CTD
1	4302.945,N 7039.174,W	30	3.84	X	X	X	X
2	4302.463,N 7037.823,W	35	5.82	X			
3	4301.825,N 7035.779,W	45	8.87	X			
4	4300.971,N 7033.019,W	70	12.9	X	X	X	X
5	4300.144,N 7030.552,W	85	16.6	X			
6	4259.316,N 7027.662,W	100	20.8	X			
7	4358.488,N 7024.184,W	115	25.8	X	X	X	X
8*	4357.621,N 7020.724,W	115	30.2	X	X	X	X

Note*: Station eight was eliminated in April of 2005

Samples for zooplankton abundance and composition were collected at Stations 1, 4 and 7 (Table 1). Duplicate vertical tows with a 65 cm 200 μm mesh ring net were made from 5 m off the sea floor to the surface. Volume sampled was estimated with a General Oceanics flow meter centered in the mouth of the ring. The catch was preserved in 4% formaldehyde. In the laboratory, the samples were split in half using a Folsom plankton splitter. One split was passed through a 200 μm mesh screen and placed in a drying oven at 64°C for 24 hours for estimation of zooplankton dry weight. A 5 ml subsample was removed from the other split with a Stemple pipette and counted using a dissecting microscope for estimation of species composition and abundance.

Additional plankton and hydrographic sampling was conducted at stations 1, 4 and 7 (Table 1). A SEA BIRD 19+ CTD was deployed from 5 m off the bottom to the surface, providing a vertical profile of conductivity, temperature and density. Phytoplankton samples were collected with 5 l Nisken bottles at depths of 0, 10, 20, 30, 40 and 50 m. From each bottle, a 100 ml subsample was collected and then filtered onto a 1 μm glass microfiber filter (GF/F). The filters were frozen immediately in liquid nitrogen and stored at -80°C until processing. In the laboratory, the GF/F filters were vigorously stirred with a vortex and then cold extracted in 10 ml of 90% acetone in the dark for 24hrs. Chlorophyll *a* and pheopigment concentrations were estimated using a Turner Designs (Model 10-AU) fluorometer and calculations described below (Trees et al. 2003).

The concentration of chlorophyll (Chl: $\mu g\ L^{-1}$):

$$Chl = (F_b - F_a - Blk_b + Blk_a) \frac{\tau}{\tau - 1} F_R \frac{V_{EXT}}{V_{FILT}}$$

The concentration of pheopigments (Pheo: $\mu g\ L^{-1}$):

$$Pheo = ((F_a - Blk_a)\ \tau - (F_b - Blk_b)) \frac{\tau}{\tau - 1} F_R \frac{V_{EXT}}{V_{FILT}}$$

Where: F_a: Acidified fluorescence signal

F_b: Standard fluorescence signal

Blk_a: Acidified acetone blank

Blk_b: Non-acidified blank

τ: Fluorometer's sensitivity to pheopigments

F_R: Fluorometer's response factor ($\mu g\ L^{-1}$ per fluorescence signal)

V_{EXT}: Volume extracted

V_{FILT}: Volume filtered

Frozen larvae were processed for gut pigment analysis using high performance liquid chromatography (HPLC). Larvae were staged and separated under semidark conditions and placed into groups of 5 – 15 for analysis. Pigments were extracted by homogenizing the larvae in 90% acetone. The samples were then analyzed with a Perkin Elmer Series 200 HPLC system using methods described by Van Heukelem (2001) to determine concentrations of pigments and their

associated phytoplankton functional groups (Jeffrey Runge personal communication, (Moore and Campbell 2008).

Results

Larval *P. borealis* abundance and distribution – Stage I *P. borealis* larvae were observed in temperatures ranging from 1.1 to 4.2 °C and salinities ranging from 30.8 to 32.5 psu (Figure 3a). All stages of *P. borealis* larvae were observed in temperatures ranging from 1.1 to 7.2 °C and salinities ranging from 23.8 to 32.5 psu (Figure 3b).

In 2005, stage I larval abundance appeared to have peaked by year day 66 (March 7, Figure 4a). The average temperature and salinity of the mixed layer (Station 1, 4, 7 and 8) during this time varied between 2 to 3 °C and approximately 32 psu, respectively (Figure 5). The later larval stages appeared successively after the stage I peak. The highest stage II and stage III abundance was observed on year day 82 (March 23) and year day 104 (April 14), respectively.

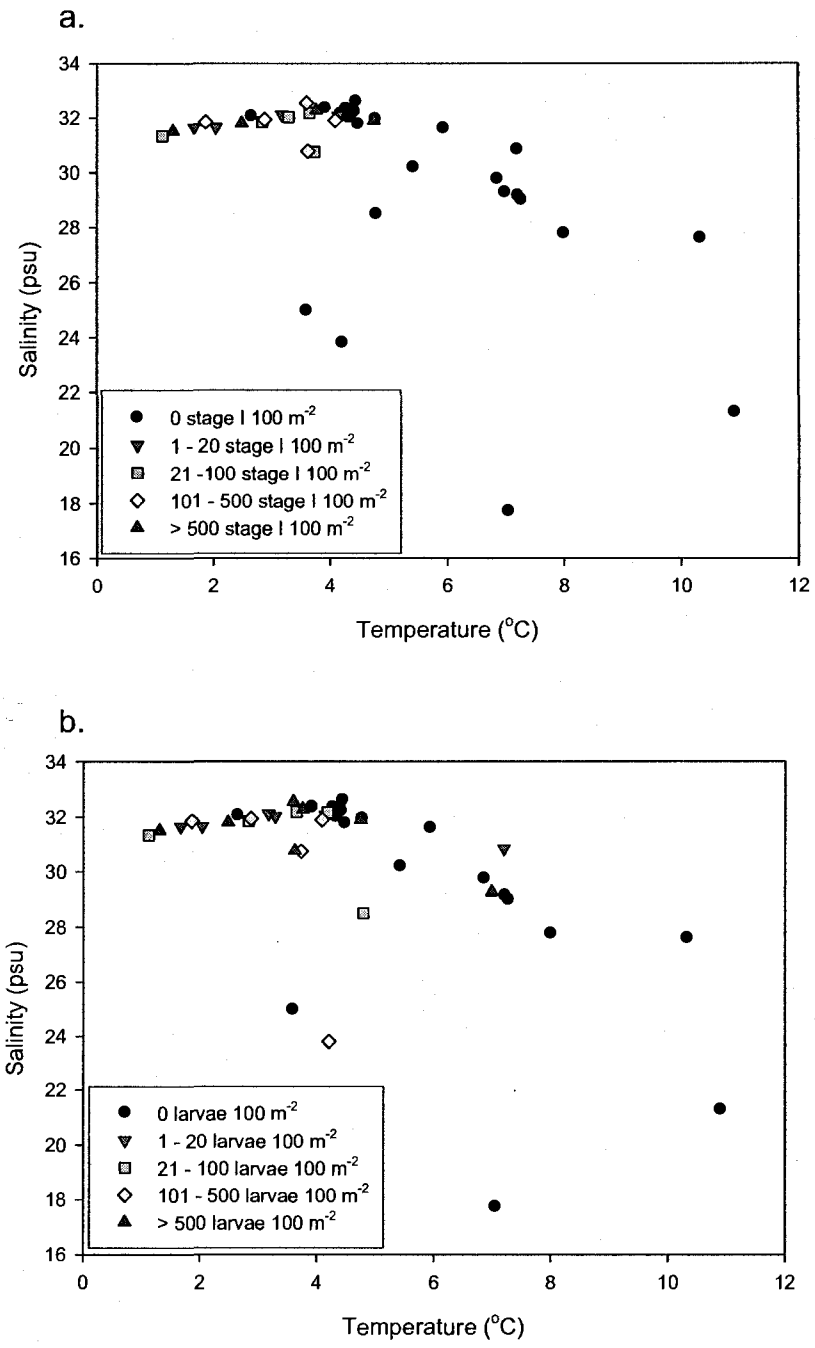

Figure 3. Relationship between temperature and salinity sampled at Stations 1, 4, 7 and 8 during 2005 and 2006. Plots show (a) stage I larval abundance and (b) total larval abundance.

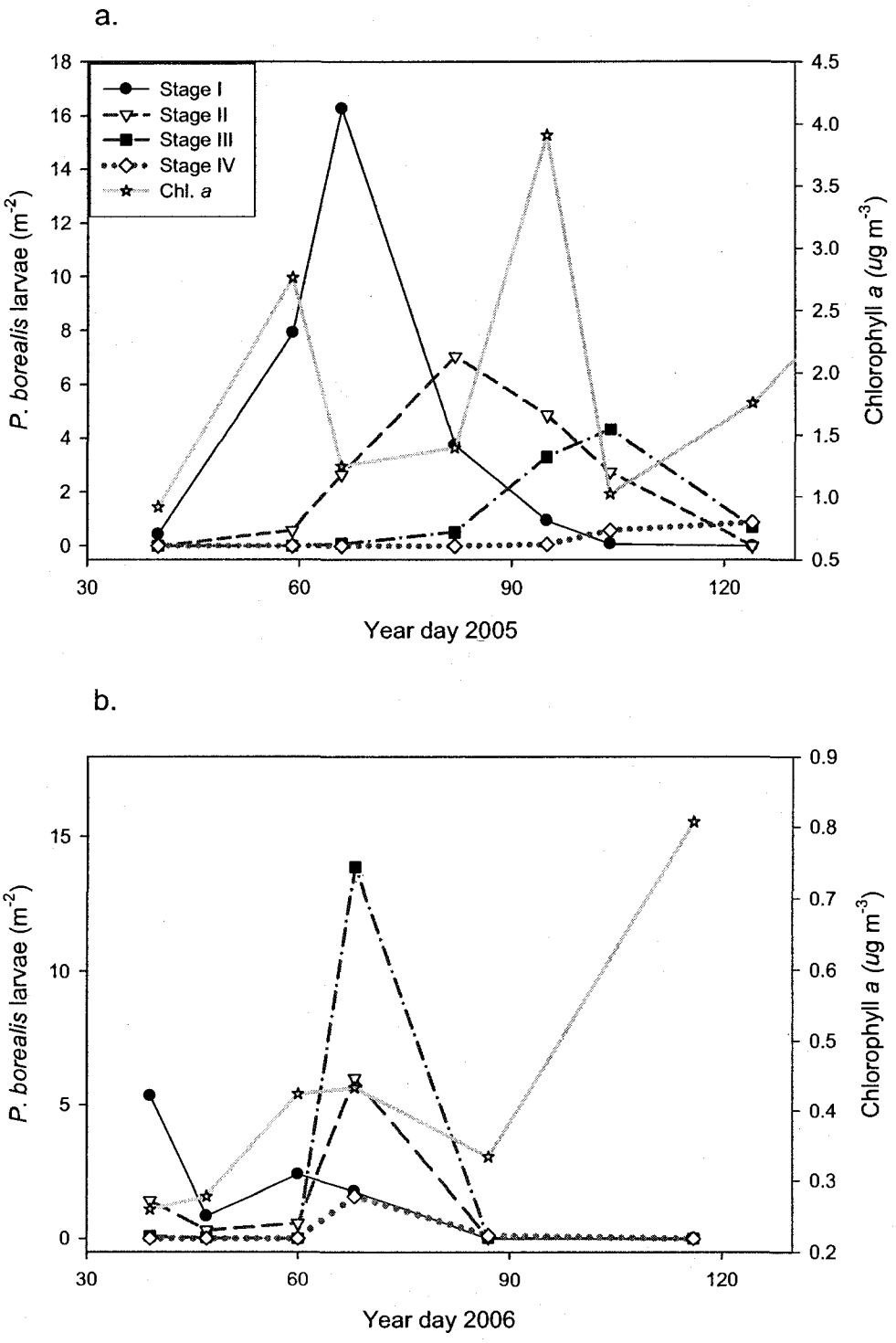

Figure 4. Relationship between *Pandalus borealis* larval stages I, II, III, IV (m^{-2}) and mean chlorophyll *a* (μg m^{-3}) for the surface layer (30 m) over all stations at each sampling date during (a) 2005 and (b) 2006. Note: difference in chlorophyll *a* scale between years.

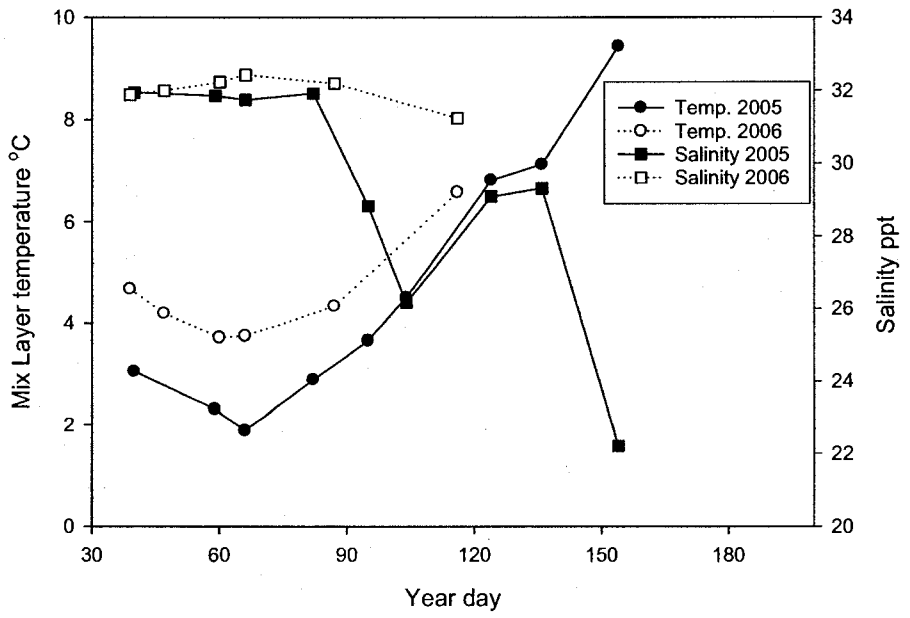

Figure 5. Relationship between Salinity and Temperature of the mixed layer during 2005 and 2006.

In 2006, the highest stage I larval abundance peak was found on year day 39 (February 8, Figure 4b), although it was lower (5 larvae m^{-2}) than the maximum in the previous year. The mixed layer temperature was 5°C (Figure 5) and stage I, II (1.4 larvae m^{-2}) and III (< 1 larvae m^{-2}) were also present (Figure 4b). The stage II larval abundance peak (6 larvae m^{-2}) and stage III abundance peak (14 larvae m^{-2}) both occurred on year day 68 (March 8). The highest chlorophyll *a* concentration was observed on year day 116 (April 27). During April 2006, the *R.V. Gulf Challenger* was unavailable. As a consequence, there was no sampling during a three week period and it is possible the peak phytoplankton bloom arose earlier and may have reached a higher peak than was evident from Figure 4b.

To determine the cross-shore distribution of *P. borealis* stage I larvae, the larval abundance at each transect station and date was converted to a percent, where the total stage I larvae observed on that sampling date equaled 100% (Table 1 and Figure 6). Locations along the transect are represented by station depths. A Kruskal-Wallis One-Way ANOVA based on ranks revealed a statistically significant difference between average larval abundance at sampling stations (Table 2: $p < 0.001$). The highest stage I abundance occurred at Station 4 (70 m), followed by Station 3 (45 m), which together accounted for about 60% of all larvae captured. More than 90% of the larvae were found inshore of the 90m isobaths.

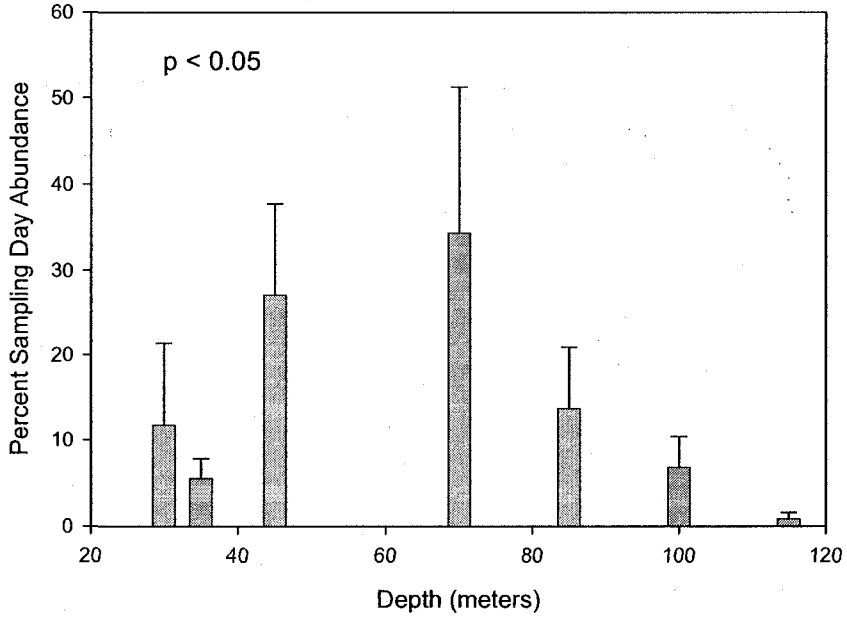

Figure 6. Relative stage I *Pandalus borealis* abundance arranged by cross-shelf station depths. Mean percent and standard errors of total larval abundance occurring at each station during each transect for all transects during 2005 and 2006

Table 2. An all pairwise multiple comparison procedures (Tukey Test) was used to determine significant differences ($p < 0.05$ and $n = 10$ for each depth) in stage I *P. borealis* larval abundance between stations with varying depths.

	Station 2 35 m	Station 3 45 m	Station 4 70 m	Station 5 85 m	Station 6 100 m	Station 7 115 m
Station 1 30 m	No	**Yes**	No	No	No	No
Station 2 35 m		No	No	No	No	No
Station 3 45 m			No	No	**Yes**	**Yes**
Station 4 70 m				No	No	**Yes**
Station 5 85 m					No	No
Station 6 100 m						No

The mean carapace lengths (CL) for *P. borealis* larval stages ranged from 1.36 mm (± 0.0037) for stage I to 2.58 mm (± 0.027) for stage IV (Figure 7). A One-Way ANOVA revealed the mean CL differed statistically between stages ($p = <0.001$). The carbon mass (μg C individual^{-1}) of *P. borealis* larval stages (Figure 8) ranged from 123.2 μg C (±10.33) for stage I to 817.4 μg C (±180.0) for stage V. The relationship between stage carbon content was fit with a logarithmic linear regression (adjusted $r^2 = 0.982$ and $p < 0.001$). The relationship between *P. borealis* larval stage mean carbon content and their mean carapace length was graphed and fitted with a nonlinear regression (Figure 9: adjusted $r^2 = 0.988$ and $p = 0.006$).

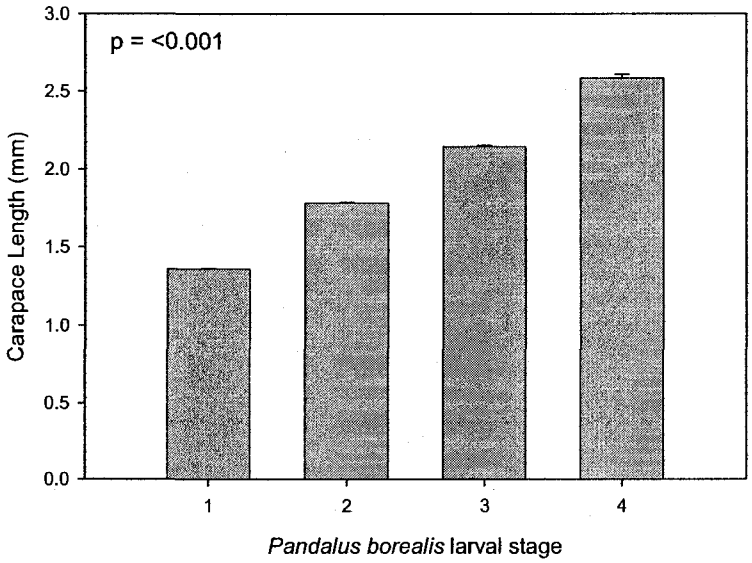

Figure 7. *Pandalus borealis* larval stage (n = 240 stage I individuals, 241 stage II individuals, 147 stage III individuals, and 34 stage IV individuals) mean carapace length. Mean carapace length between stages are statistically different (p = <0.001).

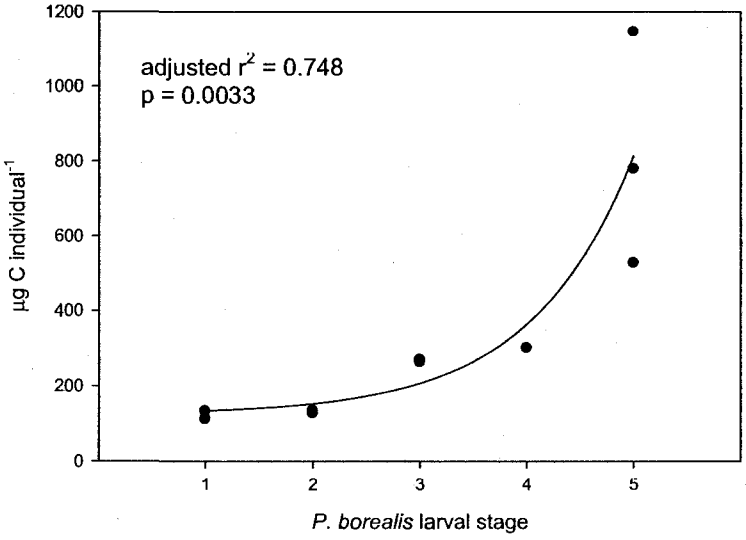

Figure 8. Carbon content (µg C inidvidual^{-1}) for *Pandalus borealis* larval stages was measured. This relationship was fit with a nonlinear regression ($y = 124.5 + 3.42e^{1.06x}$).

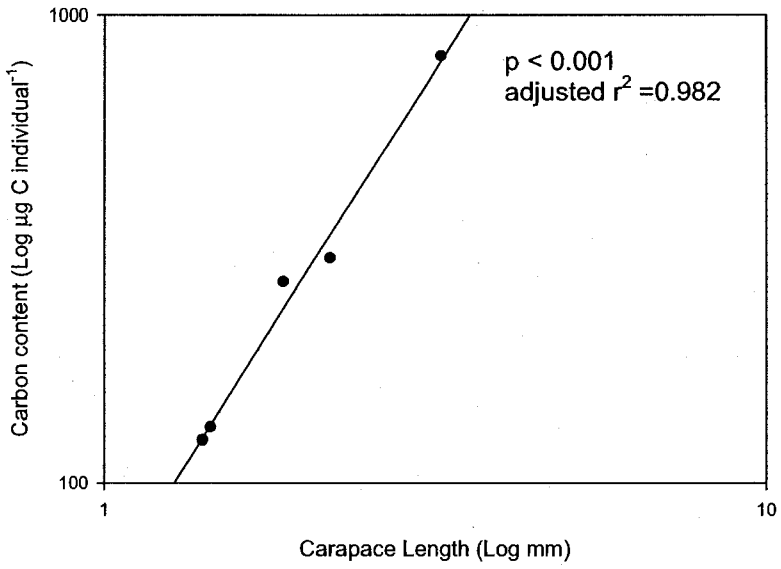

Figure 9. Logarithmic relationship between *Pandalus borealis* larval stage mean carapace length (CL: mm) and mean carbon content (C: µg C individual^{-1}).The linear relationship was significant with a p value <0.001 (Log C = 1.763 + (2.239 x Log CL).

Phytoplankton and Zooplankton Prey Fields – The phytoplankton resource available for zooplankton and *P. borealis* larvae was estimated from the integrated chlorophyll *a* concentration, shown in Figure 4 as the average across Station 1, 4, 7 and 8 of the surface layer (30m). Chlorophyll standing stocks were >1.5 µg Chl *a* m^{-3}, suggesting bloom conditions, on three dates in 2005 (Figure 4a). Ring nets were consistently filled with an unidentified chain-forming diatom. In contrast, in 2006 chlorophyll *a* standing stocks never exceeded 1 µg Chl *a* m^{-3} (Figure 4b), indicating much lower phytoplankton availability and the absence of a substantial phytoplankton bloom in February to March of that year.

In order to examine *P. borealis* larval feeding on phytoplankton, high performance liquid chromatography (HPLC) gut pigment analysis was performed on 172 individuals at stage I, 157 individuals at stage II, 162 individuals at stage III and 32 individuals at stage IV from all stations in 2006. The major pigments observed in larval guts were fucoxanthin and chlorophyll *a* and equivalents (pheophorbide and pheophytin). The presence of fucoxanthin suggests preferential grazing on diatoms. Concentrations of chlorophyll *a* and equivalents found in stages II, III and IV were significantly greater than stage I ($p < 0.001$) (Figure 10). No significant differences of fucoxanthin concentrations were observed between larval stages ($p = 0.350$).

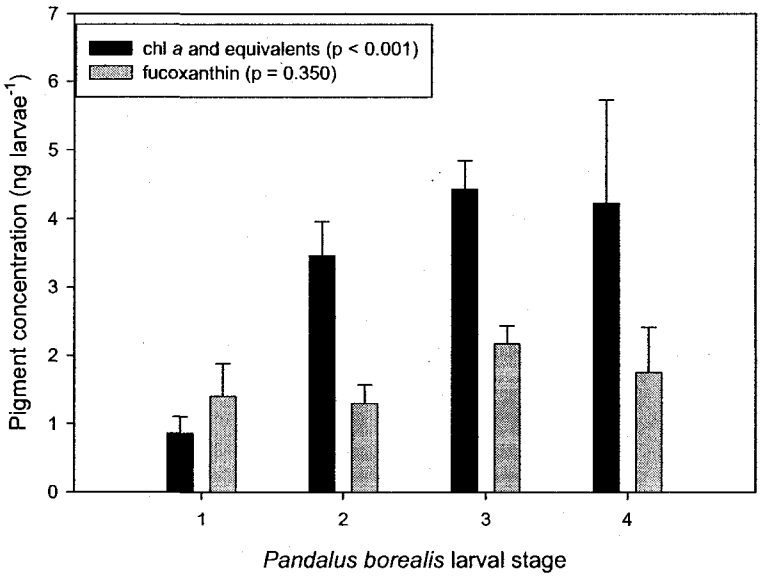

Figure 10. From HPLC analysis, concentration of fucoxanthin and chlorophyll *a* and equivalents (ng larvae^{-1}) in the gut of *Pandalus borealis* larval stages I through IV (Chlorophyll n = 18 stage I, 16 stage II, 16 stage III, 4 stage IV and fucoxanthin n = 18 stage I, 16 stage II, 16 stage III, 4 stage IV).

The availability of zooplankton prey for *P. borealis* larvae in the water column was evaluated from the ring net samples. The following Phyla were represented in the ring net samples: Cnidaria, Chaetognatha, Mollusca, Annelida, Arthropoda (*Balanus* sp. Copepoda, Euphausiid, *P. borealis*), Echinodermata, and Chordata (*Oikopleura sp.* and Icthyoplankton). Dominant potential zooplankton prey included *Acartia sp., Balanus sp., Calanus finmarchicus,* invertebrates (eggs and nauplii), *Metridia sp., Microcalanus pusillus,, Oithona similis, Pseudocalanus sp.* and *Temora longicornus* (Figure 11). During the period of larval shrimp presence (February - April) in both years, the plankton larval stages of *Balanus sp.* (barnacles) dominated the plankton community at Stations 1 and 4 during 2005 (Figure 11a and 11c) and 2006 (Figure 11b and 11d). It is not known whether *Balanus* larvae can be captured by larval shrimp, but, given the magnitude of their dominance, I will consider *Balanus* larvae as potential zooplankton prey for the northern shrimp early life stages.

Although similar possible prey species were observed in both years, there was a marked difference in zooplankton abundance. Total abundances in 2005 were typically an order of magnitude higher than in 2006 (Figure 11). A tenfold difference in zooplankton dry weight between 2005 and 2006 was also measured (Figure 12).

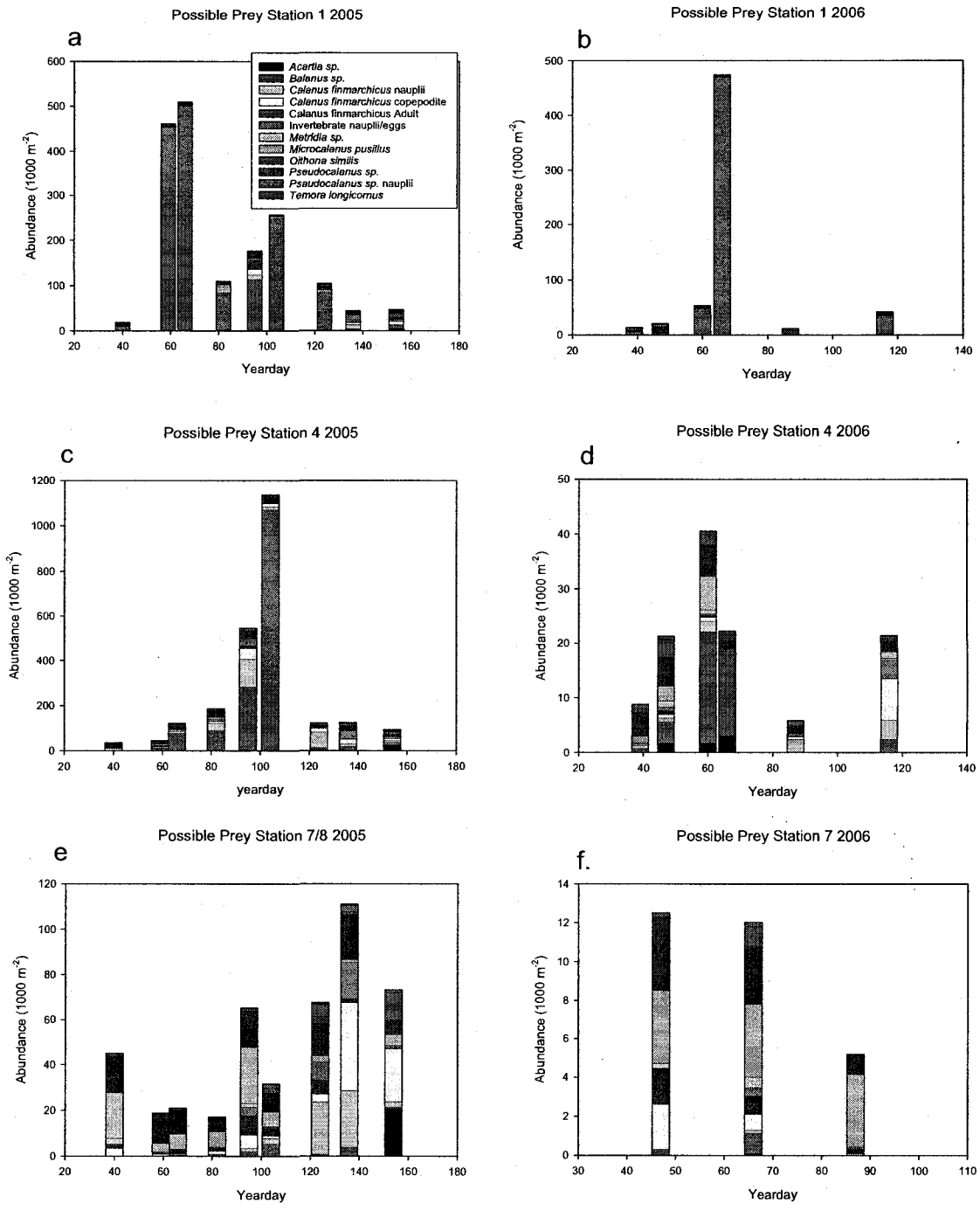

Figure 11. Zooplankton abundance m^{-2} of possible *Pandalus borealis* larval prey collected during 2005 at Stations 1 (a), 4 (c), 7 and 8 (e) and during 2006 at Stations 1 (b), 4 (d) and 7 (f). A 65 cm ring net with a 200µm mesh was used to collect the vertical profile of zooplankton. Note: abundance scaling differs between panels.

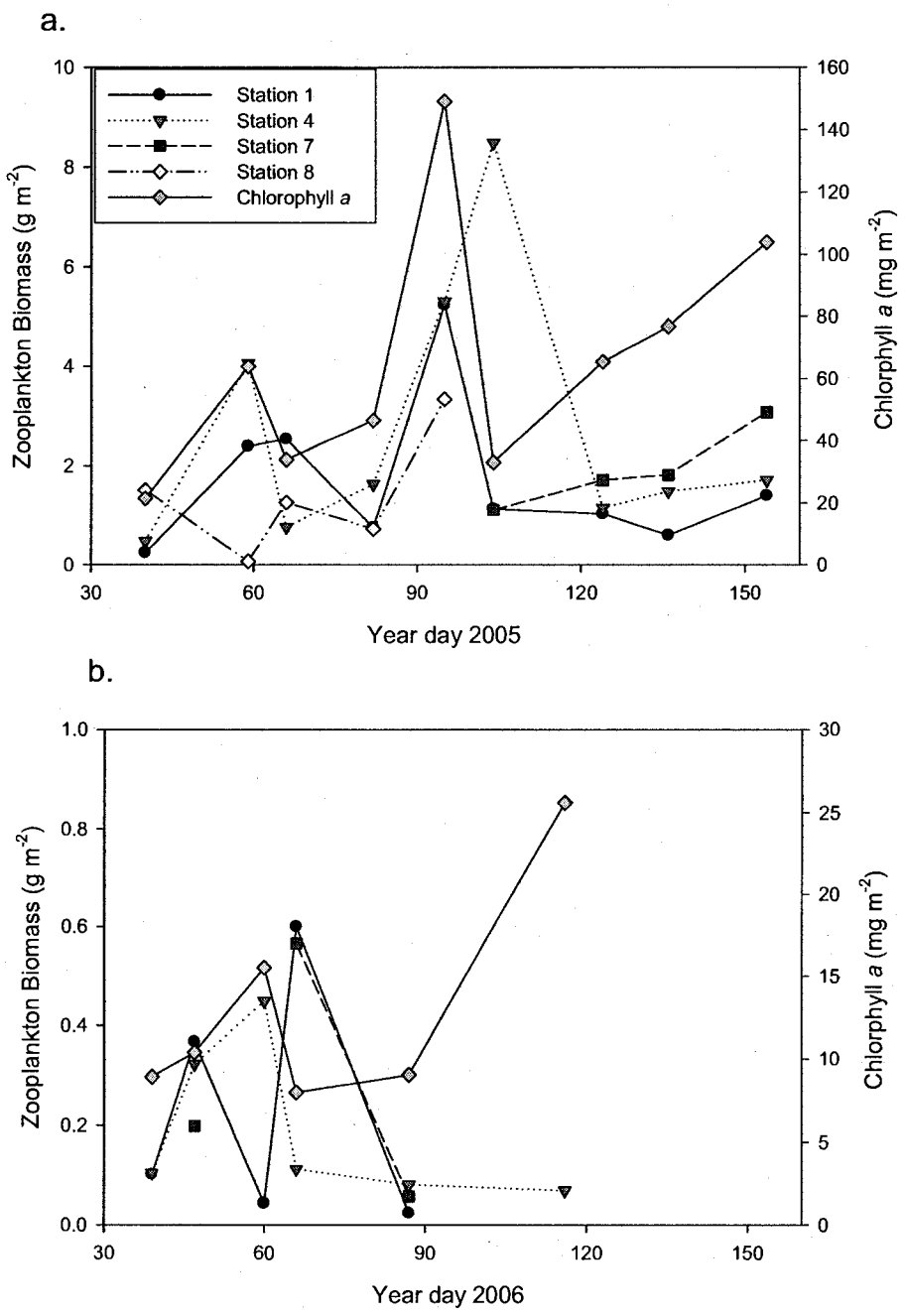

Figure 12. Zooplankton biomass (gm^{-2}) and water column Chlorophyll *a* ($mg\ m^{-2}$) standing stock sampled at Stations 1, 4, 7 and 8 during (a) 2005 and (b) 2006. Chlorophyll standing stock integrated from bottle samples over 20m at station 1 and over 50m at all other stations. Note: differences in zooplankton biomass and Chlorophyll *a* scales between years

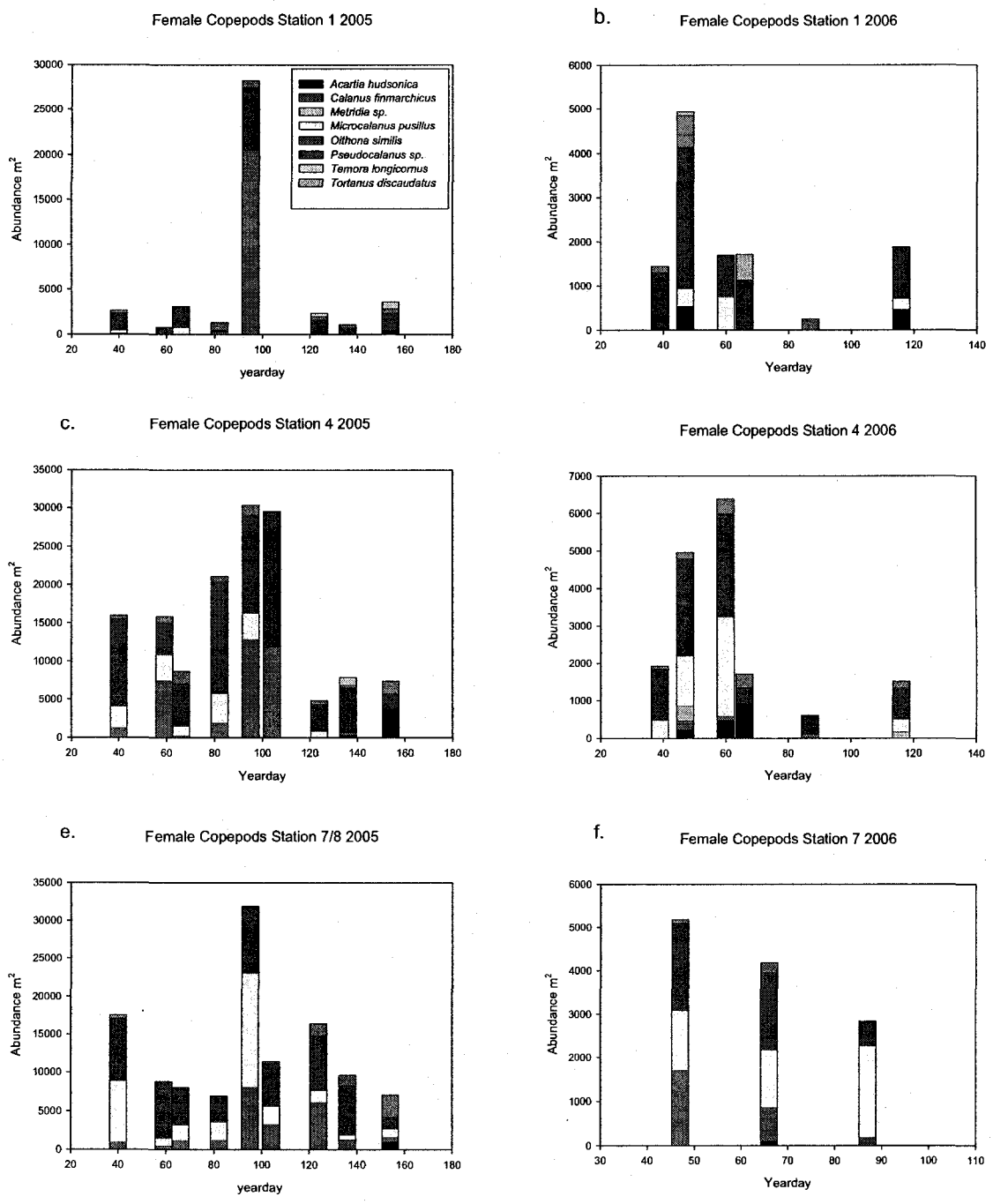

Figure 13. Female copepod abundance (m^{-2}) collected during 2005 at Stations 1 (a), 4 (c), 7 and 8 (e) and during 2006 at Stations 1 (b), 4 (d) and 7 (f). A 65 cm ring net with a 200µm mesh was used to collect the vertical profile of zooplankton. Note: abundance scaling differs among panels.

At all stations during 2005 and 2006, *Calanus finmarchicus, M. pusillus, O. similus and Pseudocalanus sp.* dominated the copepod community (Figure 13). Females of these species were likely producing eggs hatching into nauplii, potential prey for shrimp larvae. These components of the *P. borealis* larval prey field would have been ineffectively captured by the 200 μm mesh of the ring nets. In order to estimate availability of copepod eggs and nauplii, I calculated egg production rates from the abundance of females and estimates of the female-specific egg production rate. The greatest abundance of female copepods in 2005 (Figure 13a, 13c and 13e), exceeded 30,000 copepods m^{-2} during peak abundance. In 2006, the female copepod abundance (Figure 13b, 13d and 13f) never exceeded 7,000 copepods m^{-2}. During both 2005 and 2006, female *M. pusillus* and *O. similis* were both dominant and *Pseudocalanus sp.* was consistently present. Female *C. finmarchicus* were more abundant in 2005 than in 2006. The daily production of carbon mass of copepod eggs (Figure 14) was calculated assuming a female specific egg production rate and egg carbon content for *C. finmarchicus* (25 eggs $female^{-1}$ day^{-1} and 0.23 μg C egg^{-1}), *M. pusillus* (30 eggs $female^{-1}$ day^{-1} and 0.04 μg C egg^{-1}), *O. similis* (2 eggs $female^{-1}$ day^{-1} and 0.045 μg C egg^{-1})and *Pseudocalanus sp.* (5 eggs $female^{-1}$ day^{-1} and 0.14 μg C egg^{-1}) (Ohman 1994; Ringuette et al. 2002)(Jeffrey Runge personal communication). The total carbon production from copepod eggs is shown along with chlorophyll *a* concentration (μg C L^{-1}) and *Balanus sp.* abundance for both 2005 (Figure 15a) and 2006 (Figure 15b). Mean chlorophyll *a* concentrations

(Figure 4) were converted to μg C L^{-1} using a Carbon:Chlorophyll *a* ratio of 50:1 (Runge personal communication). In 2005, chlorophyll *a* concentration peaks coincided with peak copepod eggs, but this correlation was not observed in 2006. Both chlorophyll *a* concentration and egg production were ten times greater in 2005 than 2006.

The relationship between the timing of the spring phytoplankton bloom, potential zooplankton prey abundance and the northern shrimp planktonic phase was examined by comparing *P. borealis* larval abundance to chlorophyll *a* concentration, the abundance of *Balanus* larvae and the egg production rate of dominant copepods over time (Figure 15). During 2005, the chlorophyll *a* standing stock was at approximately the half saturation chlorophyll concentration for copepod growth and reproduction (Runge et al. 2006) except for two occasions (year day 95 and year day 154) when it was >100 mg m^{-2} (Figure 12a). The peak stage I larval abundance, on year day 66 (March 7) proceeded this peak in chlorophyll standing stock and corresponding copepod egg production rate (Figures 12a and 15a). Apart from this peak in chlorophyll and copepod egg production, *Balanus* larvae were abundant throughout March and April and, if consumed by shrimp larvae, would have been their dominant zooplankton prey. Stage II and stage III larvae appeared just before and during the maximum in phytoplankton abundance as well as high copepod egg production and *Balanus* larval abundance at Stations 1 and 4.

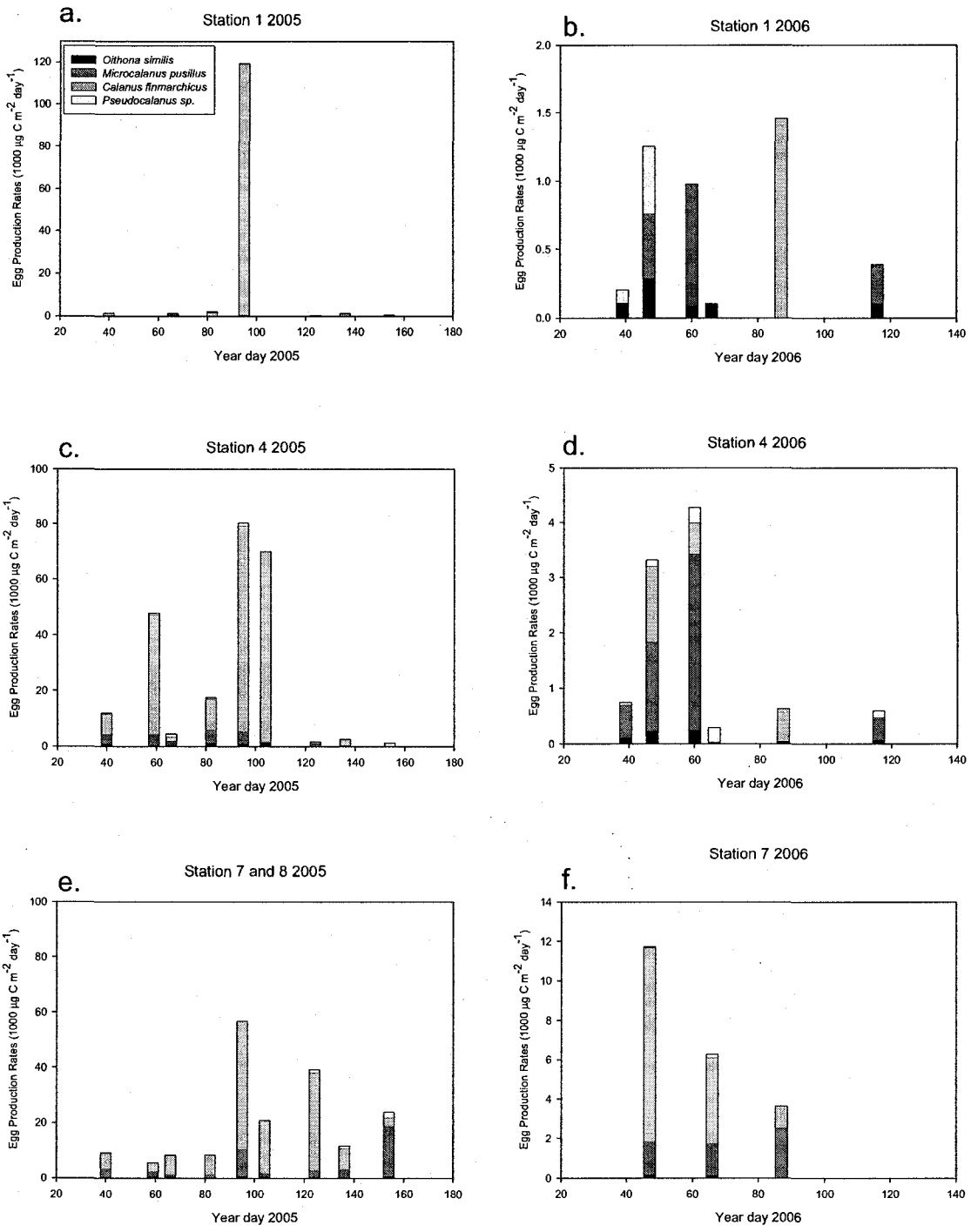

Figure 14. Copepod egg production rate in terms of carbon mass (1000 µg C m^{-2} day^{-1}) for *Calanus finmarchicus, Microcalanus pusillus, Oithona similis* and *Psuedocalanus sp.* during 2005 at Stations 1 (a), 4 (c), 7 and 8 (e) and during 2006 at Stations 1 (b), 4 (d) and 7 (f). Note: abundance scaling differs between panels.

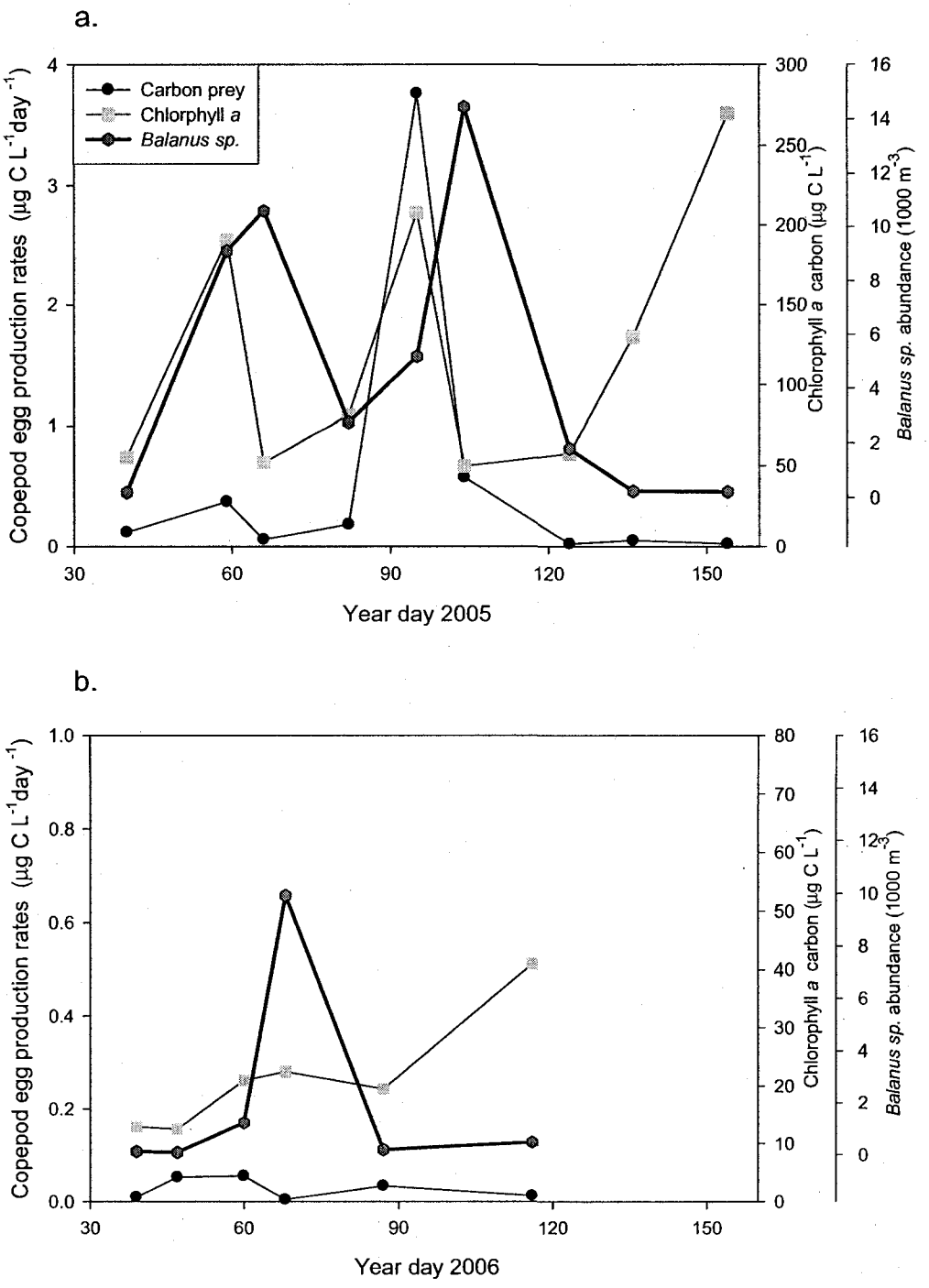

Figure 15. Total mean prey availability estimated at Stations 1 and 4, from daily copepod egg production (µg C L^{-1} day^{-1}: *Calanus finmarchicus, Microcalanus pusillus, Oithona similis* and *Psuedocalanus sp.*), *Balanus sp.* abundance (1000 m^{-3}) and integrated phytoplankton concentration (µg C L^{-1}) estimated from mean chlorophyll *a* concentrations (integrated over 20 m for station 1 and 50 m for station 4) for 2005 (a) and 2006 (b). Note: scales are different between years.

During 2006, chlorophyll *a* standing stock was considerably lower than values observed in the previous year. The peak stage I larval abundance was observed on year day 39 (February 8, Figure 4b). At this time, chlorophyll standing stocks (<25 mg chl *a* m^{-2}) and copepod egg production rates were extremely limited (Figure 15b). Stage II and stage III larval abundance peaks were both observed on year day 68 (March 8) when *Balanus* larvae were present but phytoplankton concentrations and copepod egg production were very low. Increased chlorophyll standing stocks were not observed until year day 116 (April 27).

Discussion

Phytoplankton and Zooplankton Prey Fields – The importance of algae in the diet of *P. borealis* larvae has long been a subject of interest. Despite synchronistic occurrence between the peak *P. borealis* larval abundance and late winter phytoplankton bloom (Stickney 1983), the extent and importance of this relationship is not completely understood. HPLC gut content analysis is a possible method for identifying the functional groups of algae consumed by larvae. The presence of fucoxanthin (a pigment found in diatoms) suggests larval stages I, II, III and IV consume algae, and more specifically, diatoms (Figure 10). These results support earlier examination on digestive tracks of field-caught larvae (Stickney and Perkins 1981). In addition, it was believed later stage larvae "loses interest" in planktonic algae (Rasmussen et al. 2000)..The concentrations of chlorophyll *a* equivalent pigments and fucoxanthin are significantly greater in stages II, III and IV than in stage I larvae. In addition,

concentrations of fucoxanthin, were not significantly different among stages. Therefore, these results suggest the guts of later stage larvae found in the field contain similar concentrations of diatoms as earlier stages.

While use of HPLC as a means of analyzing larval feeding preference is promising, it needs further analysis and refinement. HPLC chromatograms for zooplankton are known to alter pigment marker results, making it difficult to determine accessory pigment concentrations (Quiblierlloberas et al. 1996). It is very possible larvae consumed other species of phytoplankton, but pigment signals were missed due to either breakdown of pigments in the digestive tract or low pigment concentrations. In future investigation, increased numbers of larvae in sample groups is suggested. This would allow pigments to concentrate for a stronger HPLC chromatogram signal.

Past gut content analysis of *P. borealis* has revealed that larvae eat a variety of zooplankton prey in addition to diatoms, including Polychaetes, Copepod (adults, copepodites, nauplii, and eggs), other invertebrate larvae (Harvey and Morrier 2003; Stickney and Perkins 1981). Laboratory experiments (Harvey and Morrier 2003) indicate that the majority of earlier stage larval prey is small (copepod nauplii, invertebrate eggs and nauplii), whereas prey eaten by later stages includes both small and large prey (*Calanus finmarchicus* copepodid stages). In the western Gulf of Maine, many of these prey types were available during 2005 and 2006 (Figure 11). In addition, during both 2005 and 2006, larval *Balanus sp.*

were very abundant in the water column when shrimp larvae were present. *Balanus sp.* dominates the zooplankton community at Stations 1 and 4 during a time of high *P. borealis* larval abundance (Figure 4). The coincidence of larval *P. borealis* emergence and abundance of *Balanus sp.* needs to be investigated further as a major prey source for larvae in the western Gulf of Maine.

Larval *P. borealis* abundance and distribution – The spatial distribution of stage I larvae in the western Gulf of Maine compares well with the location of adult ovigerous female *P. borealis*. High catch rates of adult female *P. borealis* have been observed between 60 and 90 m (Lewis Incze, personal communication). Correspondingly, the majority of Stage I larvae were found at depths between 30 and 85 m. Very few larvae were in depths greater than 100 m and most larvae were found within 26 km of shore. Shore proximity may be important for successful transport to nursery areas (Bates 2007).

Pandalus borealis larvae are not present south of Cape Cod. Larvae need to remain inshore to avoid advection into southern warmer waters by physical forces (currents and wind). A computer model for *P. borealis* larval transport done by Bates (2007) suggests favorable conditions (mild wind conditions or a southwesterly wind direction) influence an onshore advection keeping larvae close to shore. Unfavorable conditions (northeasterly wind direction) push water masses offshore, forcing larvae into southbound currents moving around Cape Cod. The observations made during this study provide evidence in support of the

model assumption that stage I larval shrimp distribution coincides with adult female distribution.

Weather conditions in 2005 were mild in comparison to the severe weather patterns observed in 2006. In 2005, larvae were present throughout the sampling season (Figure 4a). At the beginning of February in 2006, larvae were present. Two weeks later, larval abundance decreased and few larvae were observed (Figure 4b). Following a severe storm, March 1 sampling found a high abundance of stage III larvae. By the end of March, larval abundance was very low. This suggests unfavorable weather patterns transported stage III larval from northern waters into the sampling transect and eventually further south.

Previous laboratory research suggested optimal salinity conditions for *P. borealis* larvae are between 31.0 to 32.6 psu and mortality greatly increases with salinity lower than 28.0 psu (Wienberg 1982). The results from this field research indicate that stage I larvae occur within a salinity range (30.8 to 32.5 psu) found in previous laboratory experiments (Figure 3a). Later stage larvae (II, III and IV) were found in salinity conditions as low as 23.8 psu (Figure 3b) in 2005. Salinity flux in the later half of the 2005 season likely had a limited impact on successful survival because later stages have a higher tolerance for lower salinity levels (Wienberg 1982).

Several studies have shown temperature changes within the water column greatly influence larval growth and ultimately survival to recruitment. The exact time of *P. borealis* hatching can be directly related to temperature, with warmer water resulting in earlier larval hatching. A 1 or 2°C difference in mean winter water temperature could accelerate or slow down eggs hatching by 2 to 3 weeks (Shumway et al. 1985). The near 2°C temperature difference between seasons may have resulted in an earlier egg hatching time in 2006 (Figures 4 and 5). In addition to timing, increased temperatures increase molting frequency and growth. As a result, larvae have higher metabolic requirements; therefore more food is required for survival (Shumway et al. 1985).

In order to formulate and parameterize feeding and growth of larval shrimp, it was necessary to determine carapace length and the carbon content of *P. borealis* larvae. To my knowledge, measurements of carbon content of northern shrimp larvae are not available in the literature. Knowledge of the carbon content of prey and the carbon content of larvae was needed for comparison of larval feeding between developmental stages. This eliminated variations of energy requirements and usage between stages. These results revealed a difference in carapace lengths between stages (Figure 7) and exponential relationship in carbon content of larval stages I through V (Figure 8). In addition, a power relationship between carapace length and carbon content was observed (Figure 9).

Timing of larval shrimp appearance with the spring bloom – This study demonstrates the potential for interannual variation in the timing of larval release and the spring plankton bloom on larval survival and their availability of zooplankton. The correlation between hatching time due to temperature and the type and abundance of food is critical for larval growth and development, which may exert primary control on the strength and success of a year-class. Early larval hatching, as apparently occurred in 2006, may have resulted in larvae with inadequate food to achieve high growth rate or even facing starvation. Stage I larvae need to ingest at least some food within 30hrs after hatching or death even with food available is inevitable (Shumway et al. 1985). Suboptimal growth rates lead to longer duration in the high mortality planktonic phase and perhaps higher susceptibility to predation, resulting in lower survival (Cushing and Horwood 1994; Houde 1987). Both algae and zooplankton are components of the larvae's prey field. Though similar prey types were present between 2005 and 2006, the differences in timing and abundance of phytoplankton and zooplankton prey were dramatic. The zooplankton biomass prey in 2005 was ten times greater (Figure 12a) than 2006 (Figure 12b).

The timing of larval appearance in 2005 coincided with a greater abundance of both phytoplankton and zooplankton prey, much more of a successful "match" than 2006. Stage I larval abundance peaked in 2005 on March 7 immediately following an increase in phytoplankton standing stock (Figure 4a). While zooplankton biomass was lower at this time in comparison to the rest of the

season (Figure 12a), the maximum zooplankton biomass prey and chlorophyll *a* in mid April occurred in early to mid April when larval stages II and III dominated the water column.

It is possible that warmer winter waters in 2006 resulted in an earlier larval release (Figure 5), as initial sampling in the first week of February revealed the presence of stages I, II and III. Both zooplankton and phytoplankton prey availability was limited throughout February and March compared to 2005 (Figure 7 and 12). By the end of March zooplankton biomass was extremely low and *P. borealis* larvae were almost completely absent from the water column (Figure 4b). Reduced plankton prey and severe weather conditions at the time of larval emergence would likely drastically hinder survival, and I hypothesize that 2006 was a "mismatch" year.

CHAPTER II

LABORATORY OBSERVATIONS

Introduction

Understanding feeding behavior of the early planktonic stages of the northern shrimp, *Pandalus borealis*, is necessary for the overall effort of formulating and parameterizing its feeding and growth rates. This chapter discusses laboratory feeding experiments conducted to determine feeding rates and prey selectivity of young (stage I) and older (stage III) planktonic larvae. Knowledge of larval shrimp feeding behavior is limited. Larvae have been observed consuming diatoms in the laboratory and in the field (Stickney and Perkins 1981). While it is presumed that stage I larvae have a higher clearance rate of algal prey than other prey items offered (*Artemia sp* : (Rasmussen et al. 2000), algae alone is believed to be insufficient for successful development and growth (Harms et al. 1991). It has also assumed that later stage (older than stage III) become carnivorous and "lose interest" in phytoplankton prey (Rasmussen et al. 2000). Several feeding experiments with *Pandalus borealis* larvae have included *Artemia sp.* nauplii as a main food source (Harvey and Morrier 2003; Haynes 1979; Stickney and Perkins 1981; Wienberg 1982). No study of larval shrimp feeding behavior so far has established the critical concentrations of food (either algae or zooplankton prey) at which ingestion rate (hence growth rate) becomes food limited.

Here I conduct a series of experiments to observe feeding on phytoplankton and *Artemia sp.* I tested the hypothesis that early life stages feed more on phytoplankton than later stages and that larvae ingest greater quantities of diatoms than other algae in mixtures. I determine the critical concentration of food at which ingestion rate becomes food limited. Finally, I observe feeding on *Artemia sp.* nauplii and investigate differences between younger and older stages in their feeding rates and selectivity for phytoplankton and zooplankton prey.

Laboratory Methods

Larval Collection and Maintenance – Approximately 75 adult, egg bearing female *P. borealis* were collected by fishermen off Boothbay Harbor, Maine using both trawl and trap methods. Adults and hatched larvae were maintained at UNH's Coastal Marine Laboratory in New Castle, New Hampshire. During larval release, adult shrimp were held in two hatching tanks (Figure 15). Larvae were removed daily from the collection containers and held in three-foot flow through tanks. Seawater in tanks underwent UV and particle filtration (0.5 µm), temperatures ranged from 1.2 to 5.3 °C and salinity ranged from 25 to 33 psu. Larvae were fed a diet of algae (a common diatom, *Thalassiosira nordenskioeldii* and a common flagellate used in culture, *Isochrysis galbana*) and INVE ^{tm} *Artemia sp.* nauplii enriched with INVE^{tm} DC DHA SELCO. Larvae were later transferred to a cold room located at University of New Hampshire, Durham campus for experiments.

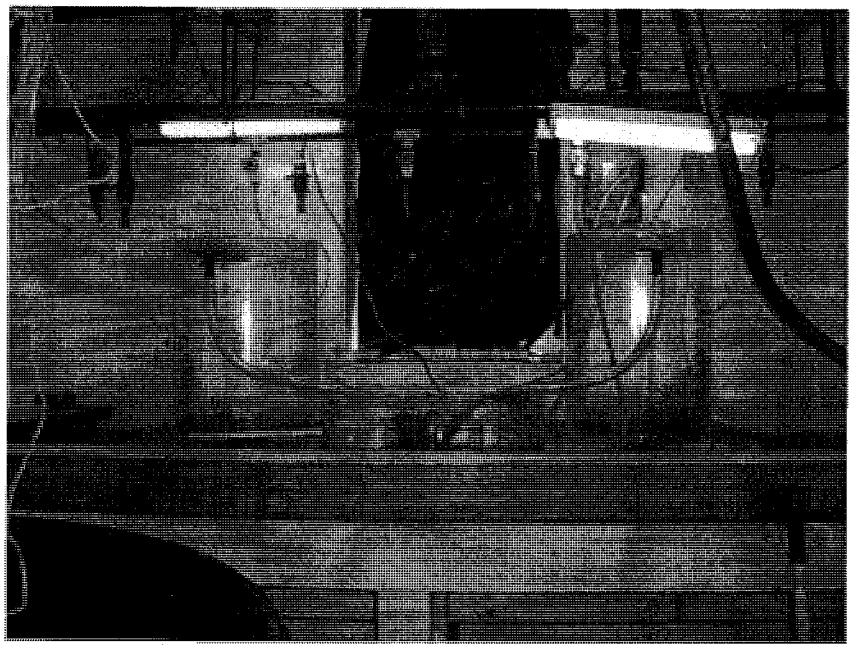

Figure 16. *Pandalus borealis* larval hatching tanks maintained at the University of New Hampshire's Marine Coastal Laboratory in New Castle, NH.

Standard for all experiments – Phytoplankton species were obtained from the Bigelow Laboratory for Ocean Sciences (CCMP 993, 762, and 1323) and cultured in the laboratory. Large volumes of algae were cultured in both 20 l glass carboys (UNH laboratory) and 100 l fiberglass cylinders (UNH Coastal Marine Laboratory). Prior to an experiment, phytoplankton cell concentrations in stock cultures were determined and then diluted to experimental concentrations with filtered (0.2 μm) sea water. Phytoplankton cell concentrations were measured with a ZBI Coulter Counter or by counting under a Leica compound microscope with a 1 ml gridded Sedwick Rafter. Samples for the ZBI Coulter Counter were collected before and after experiments from all bottles containing phytoplankton, kept on ice and counted immediately. Microscope counts were made on two 20 ml sub-samples preserved in acid Lugol's solution.

All experiments were conducted with stage I and stage III larvae. Larvae were staged under a dissecting microscope using developmental descriptions by Haynes (1979). Experimental bottles were placed on a plankton wheel rotating at a speed of 1 rpm for 24 hours (Figure 16) at temperatures between 3-5 °C. At the end of an experiment, larvae were removed from experimental container. For experiments 1 and 2, described below, the experimental larvae were immediately frozen in liquid nitrogen, stored at -80°C and analyzed for pigment composition. The pigment extractions methods used for HPLC analysis were established by Moore and Campbell (2008). Analysis involved homogenizing larvae and then cold extracting pigments in 10 ml of 90% acetone in the dark for 24hrs. Samples were processed with a PerkinElmer HPLC system.

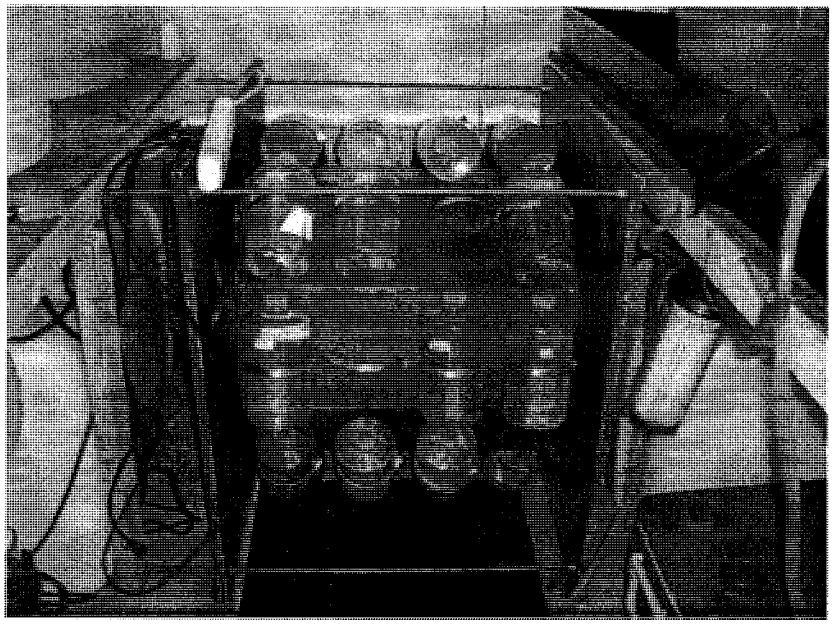

Figure 17. Experimental plankton wheel, rotating at a speed of 1 rpm with 2.2 l experimental bottles attached.

Experiment 1: Functional Response to Algal Prey Concentration – The functional response of *P. borealis* stage I and III larvae to algal prey was investigated using various cell concentrations of *T. nordenskioeldii*. The initial stage I experiment included two duplicate 2.2 L bottles containing control concentrations (1 000, 3 000, and 6 000 cell ml^{-1}) and 10 experimental concentrations (500, 1 000, 1 500, 2 000, 3 000, 4 000, 5 500, 7 000, 8 500, 10 000 cell ml^{-1}). Five larvae were selected from stock and added to each experimental bottle. The first trial of the experiment did not reach a critical concentration, therefore experimental cell concentrations were increased in the control concentrations (3 000, 6 000, and 10 000 cell ml^{-1}) and experimental concentrations (2 000, 3 000, 4 000, 6 000, 8 000, 10 000, 13 000, 16 000, 20 000, 25 000 cell ml^{-1}).

Experiment 2: Selection of Algal Prey in Mixtures – Selectivity of shrimp larvae in mixtures of algal prey was investigated using three algal species, *T. nordenskioeldii, Rhodomonas sp.,* and *I. galbana* (Table 3). Using 2.2 L bottles, the experiment included two control and four experimental bottles, all containing 500 µg C l^{-1} of each algal species. Cellular carbon content of each algal species was determined using the Carbon:Volume regression equation established by (Menden-Deuer and Lessard 2000). Five larvae were added to each experimental bottle. Algal concentration were counted using methods previously described.

Table 3. The cell volume (mm3) and carbon content (in pgC cell-1 and mgC cell-1) for *T. nordenskioeldii, Rhodomonas sp.* and *I. galbana.*

Algae	Cell Volume (μm3)	pgC cell^{-1}	μgC cell^{-1}
Rhodomonas sp.	525.5	57.10	0.00005710
I. galbana	50.32	7.724	0.00000772
T. nordenskioeldii	2066	140.5	0.0001405

Experiment 3: Functional Response to Zooplankton Prey – The ingestion rates of *P. borealis* stage I and later stage III larvae on *Artemia sp.* nauplii was measured. The experiment used *Artemia* hatched for 24 hrs. Using 1.1 L bottles, each experimental concentration (6, 12, 24, 48, 96, 150, 300 and 500 *Artemia* prey L^{-1}) had two replicates. In addition, two control bottles contained 50 prey L^{-1}. Three larvae were added to each experimental bottle. Upon completion, larvae and remaining nauplii were removed and preserved in a 4% formaldehyde solution and later counted using a dissecting microscope.

Experiment Four: Selection of Algal and Zooplankton Prey in Mixtures– Feeding behaviors of *P. borealis* stage I and III larvae were examined by providing larvae with a selection of algal prey (*T. nordenskioeldii, Rhodomonas sp., I. galbana),* and newly hatched *Artemia sp.* nauplii. Using 1.1 l bottles, the experiment included four controls and four experimental bottles all containing 500 μg C L^{-1} of each algal species. Two of the controls contained just algae. The remaining two controls and four experimental bottles, contained algae and 500 μg C L^{-1} of *Artemia sp.* nauplii. Mean *Artemia* dry weight is 2.3 μg individual^{-1} and carbon

mass of newly hatched *Artemia* varies between 40.1 to 45.5% (Evjemo and Olsen 1999). Three shrimp larvae were added to each experimental bottle. Upon completion, the larvae and nauplii were removed and preserved in 4% formaldehyde and later counted using a dissecting microscope.

Statistical Analyses – Ingestion and clearance rates were calculated using equations established by Frost (1972). Clearance rate (F) is defined as $F = Vg/N$ (ml individual^{-1} hr^{-1}) where V is the volume (ml) of the bottle, N is the number of shrimp larvae and *g* is the grazing coefficient. Ingestion rate (I) is defined as $I = C \times F$ (cells eaten individual^{-1} hr^{-1}) where C is the average cell concentration and F is the clearance rate.

Ingestion rates for Experiments One and Four were fitted with a nonlinear regression using the Ivlev equation ($y = a(1 - e^{-bx})$) (Ivlev 1961) and tested using an Analysis of Variance (ANOVA) using Sigma Plot 9.0 and Sigma Stat 3.1. Clearance rates and carbon ingestion rates for Experiments 1 and 3 were fitted with a rectilinear regression. Clearance rates measured in Experiments 2 were compared with a One-Way ANOVA using the Holm-Sidak method. Clearance rates for Experiment 4 were compared with a One-Way ANOVA based on ranks using the Tukey method and students t-test.

Laboratory Results

Functional Response to Algal Prey Concentration –The ingestion rates of stage I *P. borealis* on *T. nordenskioeldii* increased as cell concentrations increased, reaching a maximum and then remaining relatively constant (Figure 18a). An Ivlev nonlinear regression analysis produced an adjusted r^2 value of 0.657 and a p value <0.0001 (Table 4). The maximum ingestion rate observed for stage I larvae was 21 227 cells individual^{-1} hr^{-1}.

Table 4. Equations for Experiments (Exp.) 1 and 3 for Figures 18 and 21, respectfully.

Exp.	Equation	Exp.	Equation
18a	NL: **I** cells indivual^{-1} hr^{-1}= 17977 $(1 - e^{-0.00013\ P})$ RL: **I** cells indivual^{-1} hr^{-1} = -343.6 + (1.6 x P) Max **I** mean = 16023	21a	NL: **I** *Artemia* nauplii individual^{-1} hr^{-1} = 0.8261 $(1 - e^{-0.0129\ P})$ RL: **I** *Artemia* nauplii individual^{-1} hr^{-1} = 0.0752 + (0.00491 x P) Max **I** mean = 0.796
18b	NL: **I** cells indivual^{-1} hr^{-1} = 64166 $(1 - e^{-0.000096\ P})$ L: **I** cells indivual^{-1} hr^{-1} = 14378 + (1.8 x P)	21b	NL: **I** *Artemia* nauplii individual^{-1} hr^{-1} = 2.187$(1 - e^{-0.0026\ P})$ L: **I** *Artemia* nauplii individual^{-1} hr^{-1} = 0.106 + (0.00317 x P)
18c	**F** ml individual^{-1} hr^{-1} = 2.48 $e^{-0.000054\ P}$ Max F mean = 1.603	21c	**F** ml individual^{-1} hr^{-1}= 21.2 $e^{-0.0062\ P}$
18d	**F** ml individual^{-1} hr^{-1} = 6.34$e^{-0.000046\ P}$ Max F mean = 5.950	21d	**F** ml individual^{-1} hr^{-1}= 9.15 $e^{-0.0015\ P}$
18e	NL: **IC** µgC Ingested µgC individual^{-1} day^{-1} = 0.492 + (0.0009 x PC) RL: **IC** µgC Ingested µgC individual^{-1} day^{-1} = -0.0094 + (0.00031x PC) Max IC mean = 0.438	21e	NL: **IC** µgC Ingested µgC individual^{-1} day^{-1} = 0.1572 + (0.0150 x PC) RL: **IC** µgC Ingested µgC individual^{-1} day^{-1} = 0.0740 + (0.00555 x PC) Max IC mean = 0.153
18f	NL: **IC** µgC Ingested µgC individual^{-1} day^{-1} = 48.5 + (0.043 x PC) L: **IC** µgC Ingested µgC individual^{-1} day^{-1} =0.8111 $(1 - e^{-0.0007\ PC})$	21f	NL: **IC** µgC Ingested µgC individual^{-1} day^{-1} = 0.105 + (0.0031 PC) L: **IC** µgC Ingested µgC individual^{-1} day^{-1} = 0.1939 $(1 - e^{-0.0029\ PC})$

Results of two separate experiments with stage III larvae showed high variability with zero values (Figure 19). HPLC analysis of stomach contents of the shrimp larvae revealed the presence of pigments (19' butanoyloxyfucoxanthin) produced by cryptophytes. This suggests certain batches of *T. nordenskioeldii* did not contain a monoculture and may have been contaminated with another alga (such as *I. galbana).* The first run of this experiment used algal cultures from both laboratory carboys and UNH Coastal Marine Laboratory cultures. Therefore, all experimental containers having this pigment within the larval gut were removed from the remaining results for stage III larvae. The adjusted ingestion rates were fitted with an Ivlev nonlinear regression for stage III larvae had an adjusted r^2 value of 0.695 and $p < 0.0001$ (Figure 18b). The maximum ingestion rate observed for stage III larvae was 77 245 cells individual^{-1} hr^{-1}.

Clearance rates are used to asses the maximal rate at which larvae can process a particle of food such as the diatom *T. nordenskioeldii.* The mean maximum clearance rate for stage I *P. borealis* was 1.6 ml individual^{-1} hr^{-1} (Figure 18c). Stage III maximum mean clearance rates was 6.0 ml individual^{-1} hr^{-1}, about three times greater than stage I clearance rate (Figure 18d).

For comparison among stages and between zooplankton taxa, the rate of ingestion is more clearly expressed in carbon mass equivalents (Frost 1972). The carbon content of stage I larvae is 123 $\pm$ 10.3 µg C. Using a rectilinear regression, stage I larvae ingestion increased and reached a mean maximum of

54 µgC prey µgC individual^{-1} day^{-1} (Figure 18e) implying that stage I larvae were consuming a maximum of 44% of their body carbon a day when feeding on *T. nordenskioeldii*. Stage III larvae do not appear to reach a maximum ingestion rate, but their maximum ingestion observed is 234 µgC prey µgC individual^{-1}day^{-1} (Figure 18). With a carbon mass of 267 µg ± 2.9, stage III larvae are consuming 88% of their body carbon per day.

Selection of Algal Prey in Mixture – Clearance rates of stage I and III *P. borealis* feeding in a mixture of three algal species (*T. nordenskioeldii, Rhodomonas sp., I. galbana*) were compared. Stage I larvae removed *I. galbana* and *T. nordenskioeldii* from the experimental container. Little or no clearance was observed of the more mobile flagellate *Rhodomonas sp* (Figure 20). Stage III larvae cleared a significantly greater ($p = 0.000116$ with a critical level of 0.004) concentration of *Rhodomonas sp.* than stage I (Table 5). Stage III larvae mean clearance rate of *T. nordenskioeldii* (mean = 2.5 ± 0.8 ml individual $^{-1}$ hr^{-1}) was greater than that of stage I (mean = 1.1 ± 0.69 ml individual $^{-1}$ hr^{-1}), although not significant ($p = 0.125$ with a critical level of 0.006). No additional significant differences in clearance rate among algal prey within stage was observed for either stage I or stage III larvae.

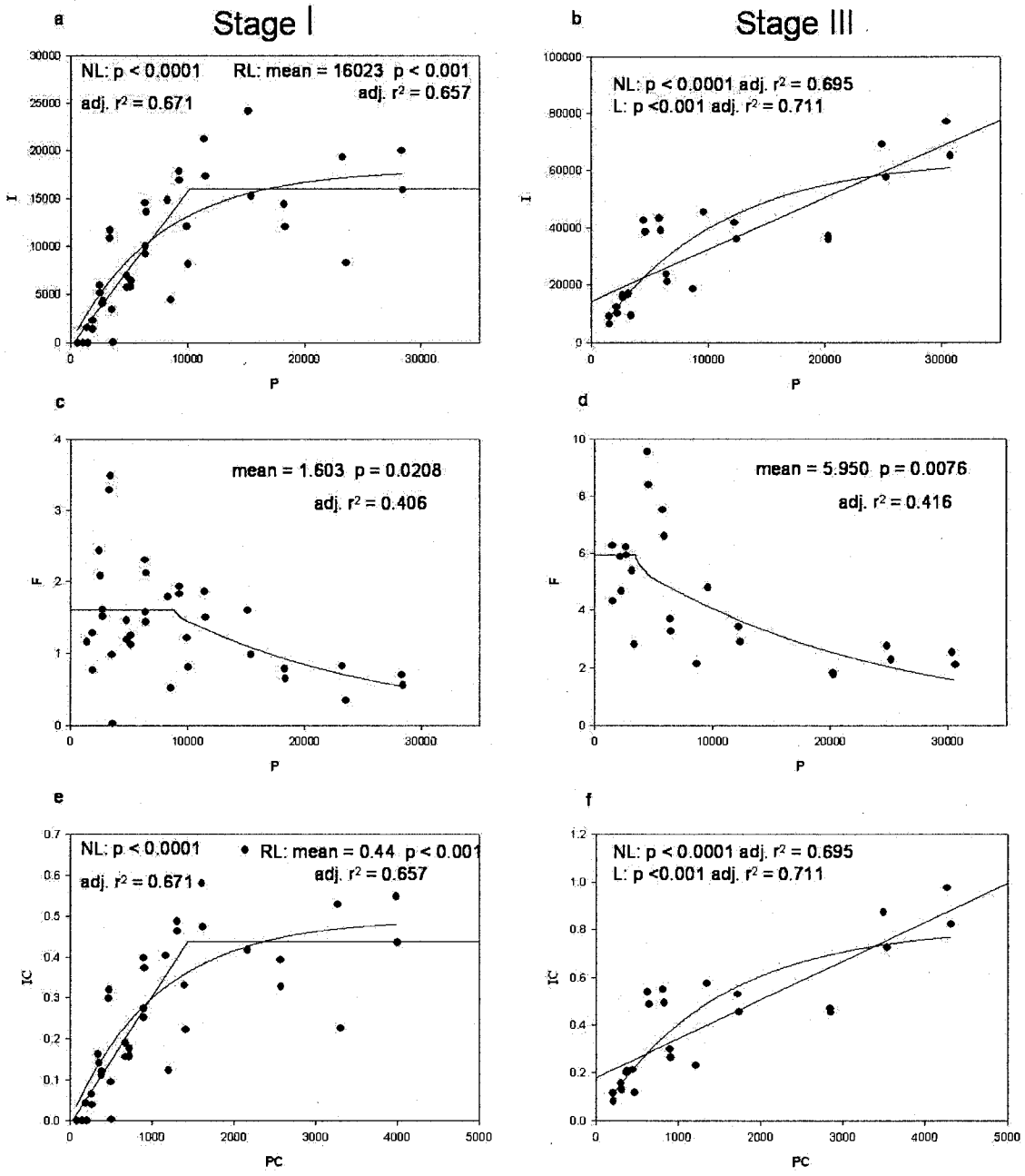

Figure 18. Ingestion rates (I: cells indivual^{-1} hr^{-1}) of *P. borealis* stage I larvae (a) and stage III larvae (b) on *T. nordenskioeldii* (P: cells ml^{-1}), fit with a nonlinear regression (NL), rectilinear regression (RL) and or linear (L). Clearance rates (F: ml individual^{-1} hr^{-1}) of *P. borealis* stage I larvae (c) and stage III larvae (d) at various cell concentration, fit with rectilinear regression. Ingestion rates (IC: µg C Ingested µg C individual^{-1} day^{-1}) of *P. borealis* stage I larvae (e) and stage III larvae (f) in relation to prey carbon concentrations available (PC: µg C L^{-1}), fit with a nonlinear regression (NL), rectilinear regression (RL) and or linear (L). Note: scales vary between figures

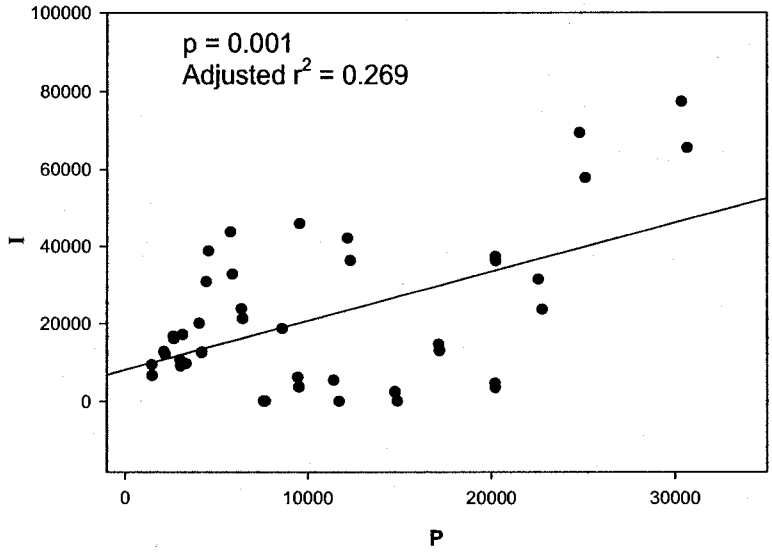

Figure 19. Ingestion rate (I: cells individual^{-1} hr^{-1}) of stage III *P. borealis* on Algal prey concentration (P: cells ml^{-1}) prior to the removal of data points believed to be errors based on results from HPLC analysis (I = 8093 + (1.266 x P)).

Table 5. Experiment 2: Unadjusted P values from an ANOVA Comparing Stage I (St1) and stage III (St III) *P. borealis* clearance rates of algal prey (*T. nordenskioeldii, Rhodomonas sp., I. galbana*). Significant values (*) and significant critical levels (CI) are represented. Stage I n values = 8 and stage III values = 8.

	***Rhodomonas sp.* St I**	***I. galbana* St I**	***T. nordenskioeldii* St III**	***Rhodomonas sp.* St III**	***I. galbana* St III**
***T. nordenskioeldii* St I**	0.00822 CI 0.004	0.976 CI 0.05	0.125 CI 0.006	0.147 CI 0.009	0.961 CI 0.025
***Rhodomonas sp.* St I**		0.00934 CI 0.005	0.0000874* CI 0.003	0.000116* CI 0.004	0.0076 CI 0.004
***I. galbana* St I**			0.113 CI 0.005	0.135 CI 0.007	0.937 CI 0.017
***T. nordenskioeldii* St III**				0.928 CI 0.013	0.132 CI 0.006
***Rhodomonas sp.* St III**					0.156 CI 0.01

Effects of Nauplii Prey Concentration – Ingestion rates of *P. borealis* larvae feeding at various concentrations of *Artemia* nauplii were measured. Similar to its feeding rates on algae, the ingestion rates of stage I *P. borealis* also increase asymptotically as nauplii prey concentrations increases (Figure 21a). An Ivlev nonlinear regression analysis (Table 4) yielded an adjusted r^2 value of 0.590 ($p < 0.0001$). The maximum ingestion rate observed for stage I larvae was 1.2 *Artemia* nauplii individual^{-1} hr^{-1}. Stage III ingestion rates did not reach a constant maximum (Figure 21b). The maximum ingestion observed was 2.6 *Artemia*. nauplii individual^{-1} hr^{-1}. An Ivlev nonlinear regression (Table 4) yielded an adjusted r^2 of 0.606 ($p < 0.0001$).

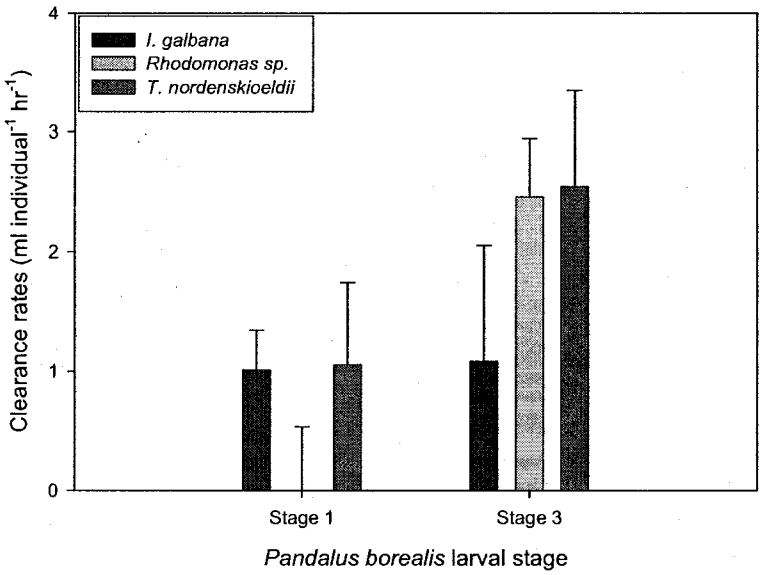

Figure 20. *P. borealis* stage I and stage III larvae prey selection experiment Clearance rates (ml individual^{-1} hr^{-1}) for prey species including *T. nordenskioeldii, Rhodomonas sp.,* and *I. galbana.* Significant differences exist between stage I and stage III larvae preying on *Rhodomonas sp.*($p = 0.000116$ with a critical level of 0.004).

Clearance rates of larvae on *Artemia* were fitted with a nonlinear regression. Maximum clearance rates observed for stage I larvae were 50.0 ml individuals^{-1} hr^{-1} and the regression (Table 4) yielded an adjusted r^2 of 0.346 ($p < 0.0002$) (Figure 21c). Maximum clearance rates observed for stage III larvae were 28.0 ml individual^{-1} hr^{-1} and the regression (Table 4) yielded an adjusted r^2 of 0.025 ($p < 0.1890$) (Figure 21d).

Stage I larvae ingestion increased and reached a mean maximum of 0.15 µg C prey µg C individual^{-1} day^{-1}. The rectilinear regression (Table 3) had an adjusted r^2 of 0.731 ($p = 0.001$) (Figure 21e). Stage I larvae consumed a mean maximum of 15% of their body carbon a day when feeding on *Artemia*. The mean maximum observed ingestion rate of stage III shrimp larvae was 0.15 µg C prey µg C individual^{-1} day^{-1} (Figure 21f) corresponding to 23% of their body carbon per day. The linear regression (Table 4) yielded an adjusted r^2 of 0.594 ($p = 0.001$).

Selection of Algal and Zooplankton Prey in Mixture– Stage I and III *P. borealis* clearance rates on algal species (*T. nordenskioeldii, Rhodomonas sp., I. galbana*) were compared to clearance rates of *Artemia* nauplii during a selection experiment (Figure 22). A student's t-test revealed stage I larvae had a significantly greater ($p = 0.007$) clearance rate on *T. nordenskioeldii* than stage III and stage III larvae had a significantly greater ($p = 0.013$)

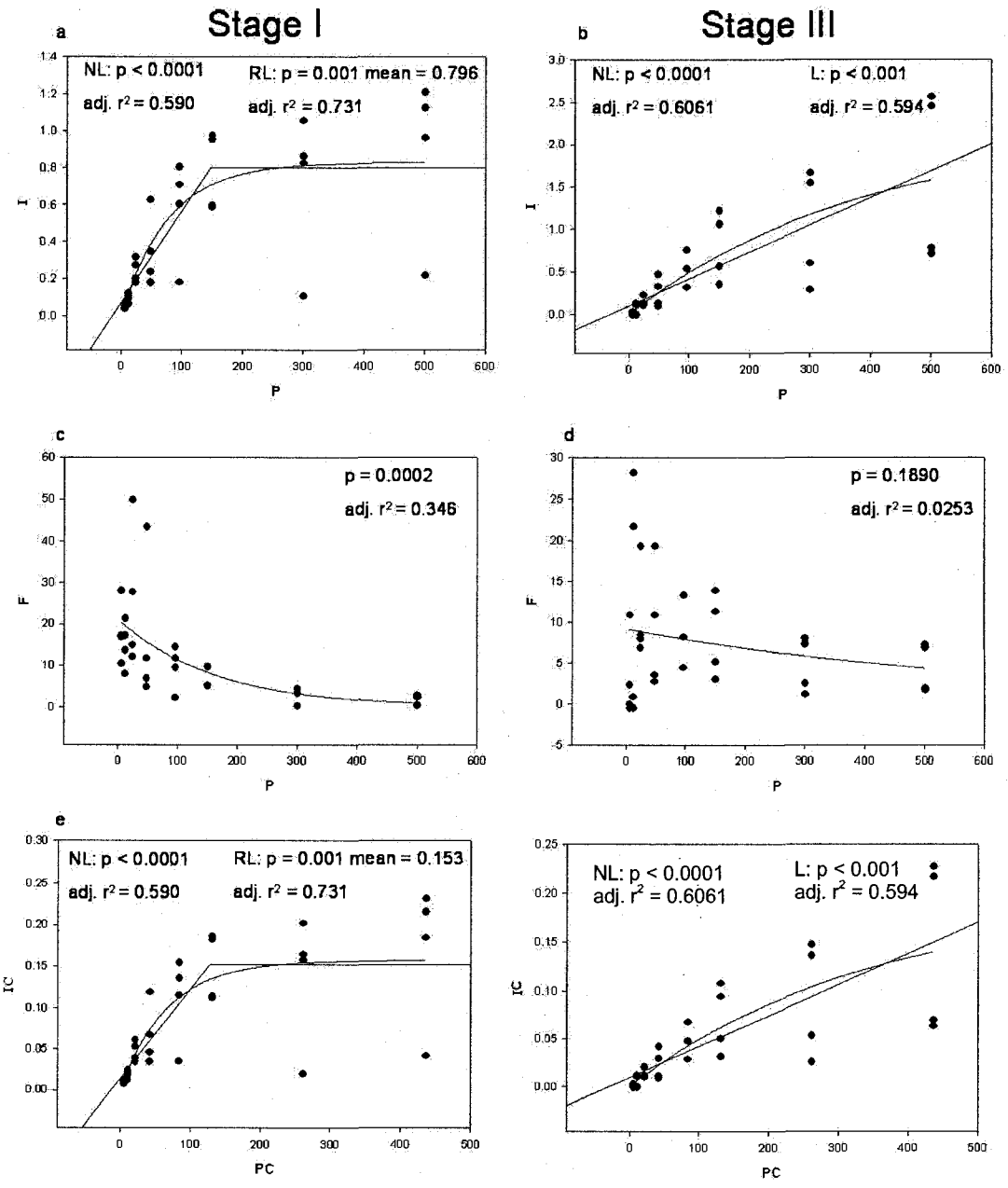

Figure 21. Ingestion rates (I: *Artemia* nauplii individual^{-1} hr^{-1}) of *P. borealis* stage I larvae (a) and stage III larvae (b) on *Artemia* nauplii (P: nauplii l^{-1}), fit fit with a nonlinear regression (NL), rectilinear regression (RL) and or linear (L). Clearance rates (F: ml individual^{-1} hr^{-1}) of *P. borealis* stage I larvae (c) and stage III larvae (d). Ingestion rates (IC: *Artemia* nauplii µg C individual^{-1} day^{-1}) of *P. borealis* stage I larvae (e) and stage III larvae (f) in relation to prey carbon available (PC: µg C L^{-1}), fit with a nonlinear regression (NL), rectilinear regression (RL) and or linear (L). Note: scales are different between figures.

clearance rate on *Artemia sp.* nauplii. Little or no feeding on *Rhodomonas sp.* and *I. galbana* was observed by either stage I or III larvae (Figure 22).

A One-Way ANOVA based on ranks showed that stage I clearance rates on *Artemia* and *I. galbana* were significantly different. Stage III clearance rates on *Artemia.* and *I. galbana* and also *Artemia.* and *T. nordenskioedii* were significantly different.

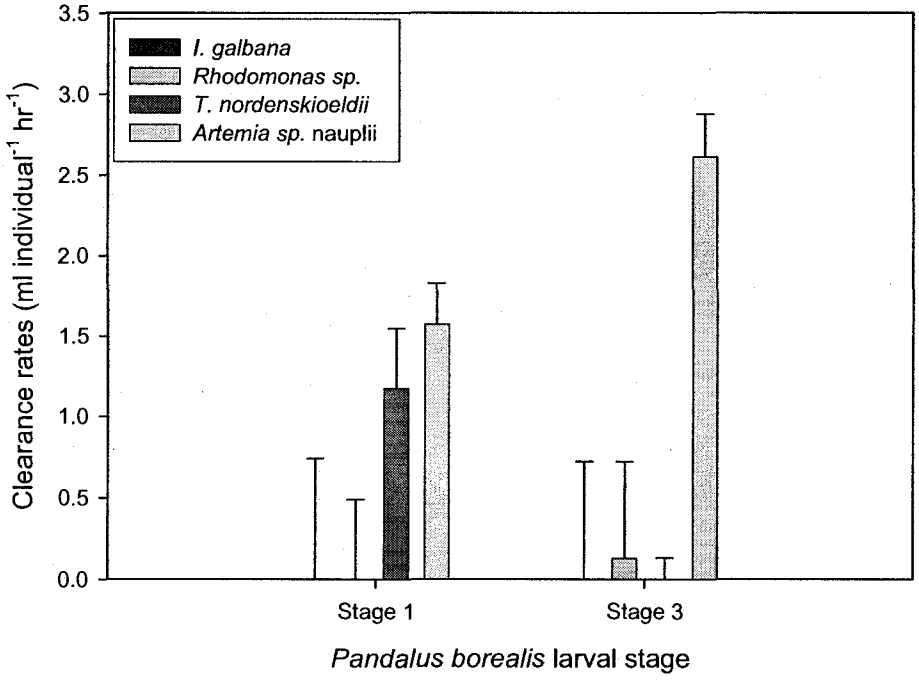

Figure 22. *P. borealis* stage I and stage III larvae prey selection experiment Clearance rates (ml individual^{-1} hr^{-1}) for prey species including *T. nordenskioeldii, Rhodomonas sp., I. galbana* and *Artemia* nauplii. Significant differences exist between stage I and stage III larvae preying on *T. nordenskioeldii* ($p = 0.007$) and *Artemia* ($p = 0.013$). Stage I n value = 8 and stage III n values = 8.

Discussion

The critical concentration of *T. nordenskioeldii* at which ingestion rate of stage I *P. borealis* larvae is approximately 15 000 cells individual^{-1} hr^{-1}. The maximum ingestion rate of *T. nordenskioeldii* for stage III larvae (slight plateau at 65 000 cells individual^{-1} hr^{-1}) was three times greater than stage I larvae (Figure 18a and 18b). In addition, the clearance rate of stage III on the diatom *T. nordenskioeldii* was much higher than stage I (Figure 18c and 18d).

Considering that stage III larvae have a higher metabolic requirement than stage I, the carbon content of *T. nordenskioeldii* consumed was compared to the larval carbon content (µg C individual^{-1}). Stage III consumed a maximum 88% of their body carbon in algae a day and stage I larvae consumed a maximum of 44% of their body carbon (Figure 18e and 18f). These results indicate that later stage larvae do consume algal prey. However, the concentrations used in this experiment were thought to far exceed concentrations observed in the natural environment; therefore it would be likely that phytoplankton alone are not adequate food to support larval survival in the field (Stickney and Perkins 1981). This proved true when examining phytoplankton availability in the field. Chlorophyll concentrations during 2005 field sampling showed maximum concentrations of 175 µg C L^{-1} day^{-1} and during 2006 concentrations never exceeded 50 µg C L^{-1} day^{-1} (Figure 15).

The results suggest that algal size was not a factor for selection of algal prey by stage I or stage III larvae, as no significant difference in clearance rates was observed between the largest algal prey (*T. nordenskioeldii)* and the smallest (*I. galbana*) (Figure 21). Stage I larvae did not consume the medium size algal prey (*Rhodomonas sp.*) while stage III did. Laboratory observation revealed *Rhodomonas sp.* to be a very mobile alga in comparison to *I. galbana* and the non-flagellated *T. nordenskioeldii.* It is very possible *Rhodomonas sp.* was able to avoid the feeding current created by stage I larvae but not that of stage III. However, it is possible that since larvae were reared on *T. nordenskioeldii* and *I. galbana*, they may not have been adapted to feeding on *Rhodomonas sp.* In this experiment, this is the only difference in prey selectivity observed between younger and older stages when offered an alga mixture.

Several *P. borealis* larvae feeding experiments have included *Artemia sp.* nauplii as a main food source (Harvey and Morrier 2003; Haynes 1979; Stickney and Perkins 1981; Wienberg 1982). Results from this experiment showed later stage larvae consume more zooplankton prey than earlier stages. The maximum ingestion rates observed for stage I and stage III larvae in prey concentrations of 500 L^{-1} was 1.21 *Artemia* nauplii individual^{-1} hr^{-1} and 2.57 *Artemia* individual^{-1} hr^{-1}, respectively (Figure 21a and 21b). However, the carbon weight specific ingestion rates were similar between the two stages. Both stage I and stage III larvae consumed a mean maximum of

15% of their body carbon a day (Figure 21e and 21f). These results also suggest stage I larvae begin to reach a critical prey concentration at 150 *Artemia* L^{-1}(150 μg C L^{-1}). An ingestion rate plateau was not found for stage III larvae.

The presence of *Artemia* nauplii prey in the algal mixture experiment changed the selectivity of algae compared to the experiment using algal mixtures alone. Little or no clearance of *Rhodomonas sp.* and *I. galbana* was observed by either stage I or III larvae (Figure 22). More importantly, stage I larvae had a significantly greater clearance rate of the diatom, *T. nordenskioeldii,* than stage III and stage III larvae had a significantly greater clearance rate of *Artemia sp.* nauplii.

The results from this selection experiment suggest younger and older stages differ in their selectivity for phytoplankton and zooplankton prey. When presented with both algal and nauplius prey, stage I larvae selectively preyed on both the larger algal prey (diatoms) and *Artemia* nauplii. Stage III, on the other hand, selectively preyed upon only *Artemia sp.* and not the algal prey.

CHAPTER III

SUMMARY AND CONCLUSIONS

This research investigated processes that contribute to the growth and survival of *P. borealis* larvae. A combination of physical variables (winds and temperature) and food availability led to a dramatically different set of conditions for *P. borealis* larvae during two successive years. In 2005, calm weather likely favored retention of larvae close to shore. Both phytoplankton and zooplankton prey were substantially more abundant in 2005 than in 2006 during the northern shrimp planktonic phase. Severe storms in 2006 likely affected larval transport and the limited prey availability during the larval period may have resulted in starvation or low growth rates contributing to high larval mortality. I predict very different levels in recruits per spawning female between the two years.

In the future, larval distribution in relation to winds needs to be examined using a series of parallel transects. The North to South larval transport can then be tracked over space and time and variations in cross-shelf larval distribution can be examined. Ideally, the result that stage I larvae occur in similar depth as adult females observed by Inze et. al. (2007), should be confirmed by comparing contemporaneous measurements of distribution of ovigerous females and stage I larvae.

Results from both the laboratory feeding experiments and HPLC gut content analysis of wild-caught larvae identify diatoms and possibly other algae important components of the larval prey field, especially to stage I larvae. The transect survey results also implicate *Balanus sp.* larvae as a potentially important prey source for *P. borealis* larval growth and survival. The overwhelming abundance of *Balanus sp.* during the planktonic phase of northern shrimp and the confirmation with laboratory experiments of the ability of *P. borealis* larvae to consume a variety of prey types suggests that *Balanus sp.* may be an unidentified key contributor to larval success in the western Gulf of Maine. There is a need for future investigation on the importance of *Balanus sp.* nauplii as a prey item for *P. borealis* larvae.

This research also provided detailed information about the feeding characteristics of *P. borealis* stage I and III larvae. This information can be applied in integrative models predicting survival probability of larvae during their first year. In laboratory experiments, earlier stage larvae preyed upon both diatoms and zooplankton, while later stages selectively preyed upon zooplankton. However, in the absence of available zooplankton prey, both larval stages consumed a variety of algal prey in order to survive. In future investigation, identifying and using natural zooplankton prey in larval feeding experiments would strengthen the relationship between field and laboratory studies. A detailed description of feeding mechanics for various larval stages is also necessary.

The ability to monitor variability of phytoplankton and zooplankton prey in the coastal zone and to quantify the match/mismatch hypothesis using models is necessary for prediction of climate forced environmental change on recruitment into the Gulf of Maine northern shrimp fisheries. This research is only one contribution to the overall effort needed for formulating and parameterizing feeding and growth of larval shrimp for incorporation into coupled models. Further fine-scale analysis of the spatial distribution and physical factors influencing larval transport is necessary.

REFERENCES

Bates, M. J. 2007. Modeling physical controls on northern shrimp (*Pandalus borealis*) dispersal, retention and settlement success in the Gulf of Maine. University of New Hampshire.

Biktashev, V. N., J. Brindley, and J. W. Horwood. 2003. Phytoplankton blooms and fish recruitment rate. J. Plankton Res. **25:** 21-33.

Clark, S. H., S. X. Cadin, D. F. Schick, P. J. Diodati, M. P. Armstrong, and D. Mccarron. 2000. The Gulf of Maine northern shrimp (*Pandalus borealis*) Fishery: a review of the records. Northwest Atlantic Fisheries Science **27:** 193 - 226

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations - an update of the match mismatch hypothesis. Adv. Mar. Biol. **26:** 249-293.

Cushing, D. H. 1996. Towards a science of recruitment in fish populations. Ecology Institute, Oldendorf/Luhe.

Cushing, D. H., and J. W. Horwood. 1994. The growth and death of fish larvae. J. Plankton Res. **16:** 291-300.

De Younge, B., F. Heath, F. E. Werner, B. Chai, B. A. Megrey, and P. Monfray. 2004. Challenges of modeling decadal variability in ocean basin ecosystems. Science **304:** 1463 - 1466.

Evjemo, J. O., and Y. Olsen. 1999. Effect of food concentration on the growth and production rate of *Artemia franciscana* feeding on algae (T-iso). J. Exp. Mar. Biol. Ecol. **242:** 273-296.

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus Pacificus*. Limnology and Oceanography **17:** 805 - 815.

Harms, J., K. Anger, S. Klaus, and B. Seeger. 1991. Nutritional effects on ingestion rate, digestive enzyme-activity, growth, and biochemical-composition of *Hyas-araneus* (Decapoda, Majidae) Larvae. J. Exp. Mar. Biol. Ecol. **145:** 233-265.

Harvey, M., and G. Morrier. 2003. Laboratory feeding experiments on zoea of northern shrimp *Pandalus borealis* fed with natural zooplankton. Mar. Ecol.-Prog. Ser. **265:** 165-174.

Haynes, E. 1979. Description of larvae of the northern shrimp, *Pandalus-Borealis*, reared insitu in Kachemak Bay, Alaska. Fish. Bull. **77:** 157-173.

Horwood, J. W., D. H. Cushing, and T. Wyatt. 2000. Plankton determination of variability and sustainability of fisheries. J. Plankton Res. **22:** 1419-1422.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability American Fisheries Society Symposium **2:** 17 - 29.

Idoine, J. S. 2006. Assesment report for Gulf of Maine northern shrimp. *In* N. F. S. Center [ed.], Status of Fishery Resources off the Northeastern US.

Ivlev, V. S. 1961. Experimental Ecology of the feeding of fishes. Yale Univ. Press.

Kumlu, M., E. Sarihan, and N. Tekelioglu. 1992. Trypsin activity in larvae of *Penaeus-Monodon fabricius*, 1789 (Crustacea, Decapoda, Penaeidae) in relation to their diet. Isr. J. Aquac.-Bamidgeh **44:** 103-110.

Leggett, W. C., and E. Deblois. 1994. Recruitment in marine fishes - Is It regulated by starvation and predation in the egg and larval stages. Neth. J. Sea Res. **32:** 119-134.

Menden-Deuer, S., and E. J. Lessard. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography **45:** 569-579.

Moore, T., and J. Campbell. 2008 An evaluation of methods for estimating phytoplankton community composition in the western Gulf of Maine using HPLC pigment Analysis. submitted to Journal of Plankton Research.

Myers, R. A., and N. G. Cadigan. 1993. Is juvenile natural mortality in marine demersal fish variable. Can. J. Fish. Aquat. Sci. **50:** 1591-1598.

Ohman, M. D. 1994. Sustained fecundity when phytoplankton resources are in short supply: Omnivory by Calanus finmarchicus in the Gulf of St. Lawrence. Limnology and Oceanography **39:** 21 - 36.

Ouellet, P. 2007. Spring oceanographic conditions and northern shrimp *Pandalus borealis* recruitment success in the western Gulf of St. Lawrence. Marine Ecology Progress Series **339:** 229 - 241.

Ouellet, P., and J. P. Allard. 2006. Vertical distribution and behaviour of shrimp *Pandalus borealis* larval stages in thermally stratified water columns: laboratory experiment and field observations. Fish Oceanogr. **15:** 373-389.

Ouellet, P., and D. Chabot. 2005. Rearing *Pandalus borealis* (Kroyer) larvae in the laboratory. Mar. Biol. **147:** 869-880.

Platt, T., C. Fuentes-Yaco, and K. T. Frank. 2003. Spring algal bloom and larval fish survival. Nature **423:** 398-399.

Quiblier-Lloberas, C., G. Bourdier, C. Amblard, and D. Pepin. 1996. A qualitative study of zooplankton grazing in an oligo-mesotrophic lake using phytoplanktonic pigments as organic markers. Limnology and Oceanography **41:** 1767-1779.

Rasmussen, T., M. Aschan, and J. S. Christiansen. 2000. The implementation of laboratory studies to shrimp recruitment modelling - a brief review of experimental procedure. International Council for the Exploration of the Sea **CM2000**.

Ringuette, M., M. Castonguay, J. A. Runge, and F. Gregoire. 2002. Atlantic mackerel (*Scomber scombrus*) recruitment fluctuations in relation to copepod production and juvenile growth. Can. J. Fish. Aquat. Sci. **59:** 646-656.

Runge, J. A. et al. 2004. Diagnosis and prediction of variability in secondary production and fish recruitment processes: Developments in physical-biological modeling p. 413 - 473. *In* A. R. Robinson and K. H. Brink [eds.], The Sea. President and Fellows of Harvard College.

Runge, J. A., S. Plourde, P. Joly, B. Niehoff, and E. Durbin. 2006. Characteristics of egg production of the planktonic copepod, *Calanus finmarchicus*, on Georges Bank: 1994-1999. Deep-Sea Res., Part II, Top. Stud. Oceanogr. **53:** 2618-2631.

Shumway, S. E., H. C. Perkins, D. F. Schick, and A. P. Stickney. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Kroyer 1838. NOAA Tech report: 57.

Sinclair, M. 1988 Marine Populations: An essay on population and speciation. Washington Sea Grant Program: 252.

Stickney, A. P. 1983. Relationship between the abundance of larval shrimp (*Pandalus borealis* Kryer) and the late winter phytoplankton blooms in Sheepscot Bay, 1978 - 1983. ME Department of Marine Resources.

Stickney, A. P., and H. C. Perkins. 1981. Observations on the food of the larvae of the northern shrimp, *Pandalus borealis* Kroyer (Decapoda, Caridea). Crustaceana **40:** 36-49.

Trees, C. C., R. R. Bidigare, D. M. Karl, and L. Van Heukelem. 2003. Fluorometric Chlorophyll a: Sampling, laboratory methods, and data analysis protocols, p. 15 - 25. *In* J. L. Mueller [ed.], Ocean optics protocols for satellite ocean color sensor validation. Goddard Space Flight Space Center.

Van Heukelem, L., and C. S. Thomas. 2001. Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. Journal of Chromatography **910:** 31 - 49.

Wienberg, R. 1982. Studies on the Influence of temperature, salinity, light, and feeding rate on laboratory reared larvae of deep-sea shrimp, *Pandalus borealis* Kroyer 1838. Meeresforschung-Reports on Marine Research **29:** 136-153.

APPENDICES

APPENDIX A

CHLOROPHYLL MEASUREMENTS 2005

Chlorophyll *a* ($\mu g\ L^{-1}$) concentrations sampled from various depths (m) at field transect stations 1, 4, 7 and 8 during 2005.

Station	Depth (m)	02/09/05	02/28/05	03/07/05	03/23/05	04/05/05	04/14/05	05/04/05	05/16/05	06/03/05
1	0	2.01	5.11	--	1.10	3.06	1.14	0.62	4.07	3.75
1	10	1.21	5.34	1.62	1.48	2.99	0.56	0.58	3.32	13.86
1	20	--	--	1.61	--	2.24	--	--	2.15	3.07
4	0	1.12	2.77	1.47	1.91	1.67	1.41	0.86	5.73	2.58
4	10	0.81	2.77	1.63	2.33	8.05	0.86	1.37	3.03	6.43
4	20	0.54	2.70	1.86	2.76	6.99	1.55	2.12	1.61	1.59
4	30	0.49	2.45	--	1.79	6.25	1.55	3.65	1.64	0.78
4	40	0.40	2.03	0.67	1.55	4.42	0.72	0.64	0.59	0.51
4	50	0.37	1.25	0.37	0.91	1.91	0.57	0.56	0.38	0.33
7 or 8	0	0.43	0.38	0.63	0.70	3.49	1.43	0.70	2.29	2.30
7 or 8	10	0.40	0.36	0.43	0.72	5.43	1.17	1.63	2.47	0.72
7 or 8	20	0.40	0.41	0.45	0.85	3.25	0.36	6.61	1.59	0.39
7 or 8	30	0.33	0.37	0.40	0.54	0.74	0.51	1.72	0.56	0.31
7 or 8	40	0.32	0.44	0.40	0.28	0.28	0.40	0.14	0.62	0.42
7 or 8	50	0.30	0.41	0.39	0.20	0.32	0.40	0.12	0.64	0.33

APPENDIX B

CHLOROPHYLL MEASUREMENTS 2006

Chlorophyll *a* ($\mu g\ L^{-1}$) concentrations sampled from various depths (m) at field transect stations 1, 4 and 7 during 2006.

Station	Depth	02/08/06	02/16/06	03/01/06	03/08/06	03/29/06	04/27/06
1	**0**	0.20	0.30	0.40	0.40	0.55	0.74
1	**10**	0.29	0.34	0.38	0.47	0.44	1.35
1	**20**	0.22	0.28	0.30	0.25	0.37	0.68
4	**0**	0.30	0.14	0.37	0.53	0.29	0.55
4	**10**	0.27	0.15	0.56	0.52	0.46	1.02
4	**20**	0.27	0.20	0.54	0.46	0.39	0.64
4	**30**	0.28	0.27	0.49	0.52	0.21	0.56
4	**40**	0.16	0.19	--	--	0.22	0.37
4	**50**	--	0.11	0.36	0.47	--	0.40
7	**0**	0.31	0.22	--	0.41	0.17	--
7	**10**	0.30	0.40	--	0.41	0.35	--
7	**20**	0.21	0.41	--	0.40	0.19	--
7	**30**	0.22	0.34	--	0.44	0.13	--
7	**40**	0.18	0.25	--	--	0.07	--
7	**50**	0.11	0.09	--	0.35	--	--