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DIET COMPONENTS OF NORTHERN SHRIMP *PANDALUS BOREALIS* FIRST STAGE LARVAE IN THE NORTHWEST GULF OF ST. LAWRENCE

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A B S T R A C T

The objective of this study was to clarify the diet composition of the first stage larvae of northern shrimp *Pandalus borealis* during the spring period of high biological production in the Northwestern Gulf of St. Lawrence (NWGSL). Data collected in spring 2006 revealed that hatching of *P. borealis* larvae took place in late April and early May during a period characterized by a phytoplankton bloom (mainly species of the genus *Chaetoceros*) and by an abundance of early stages of mesozooplankton, which demonstrated the onset of secondary production at the sampling site. Gut content examination of stage I larvae sampled at the site and feeding experiments conducted at sea revealed that omnivorous feeding starts at hatching, but a first approximation based on the quantity of pigments present in the larvae suggest that zooplankton is more important than phytoplankton to meet the larvae's energy needs. In addition, field observations of the degree of gut fullness and the low percentage (10%) of larvae with empty guts indicate a high feeding success. Hatching at the time of production of adequate prey could represent a major factor for larval northern shrimp survival in the NWGSL.

KEY WORDS: diet composition, Gulf of St. Lawrence, *Pandalus borealis*, plankton community, stage I larvae

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INTRODUCTION

For larval stages depending on exogenous feeding, it is assumed that survival of an individual will be proportionally related to the quantity and quality of food available (see Leggett and Frank, 2008). It is well documented that the seasonal cycle of pelagic production in high latitude marine ecosystems is marked by a short and intense spring phytoplankton bloom that generates a large proportion of the biological material channelled through the food web (bottom-up) via grazing by zooplankton (Edwards and Richardson, 2004; Skogen et al., 2007). Environmental conditions may regulate the timing and intensity of the seasonal cycle of plankton production and consequently the availability and abundance of prey of suitable size for the larval stages. In the St. Lawrence ecosystem (the Lower Estuary and the Gulf of St. Lawrence, GSL), the period of larval hatching of the northern shrimp, *Pandalus borealis* Krøyer, 1838, begins in late April and early May (Ouellet et al., 2007). The exact time of hatching is likely determined by spawning time and bottom water temperature, with warmer water resulting in earlier hatching (Shumway et al., 1985).

Ouellet et al. (2007) analyzed spring oceanographic conditions at the time of larval appearance and determined indices of *P. borealis* recruitment in the northwest GSL for the period between 1994 and 2003. They found that survival was best when larvae hatched during periods of weak density stratification and a deep (thermally) mixed layer followed by relatively high warming rates of the upper layer of the water column. Their interpretation of these observations was that oceanographic conditions affecting the initiation of the spring bloom and high levels of primary and secondary production at the time of larval hatching and development are favourable to northern shrimp recruitment success.

However, linking fluctuations (temporal or in intensity) in plankton production to population recruitment requires some knowledge of the specific prey that contribute to the diet of the larval stages (Castonguay et al., 2008). To date, few data concerning the food preferences of the first larval stages of *P. borealis* in nature are available. Diatoms (*Coscinodiscus* spp.) and fragments of various crustaceans and other invertebrates have been reported in the midgut of the first two larval stages of *P. borealis* in the Gulf of Maine (Stickney and Perkins, 1981). In addition, an analysis of lipid contents and fatty acid compositions of larvae caught off West Greenland suggested that larval stages I and II were feeding on phytoplankton (Pedersen and Storm, 2002).

The objective of the present study was to clarify the diet composition of first stage *P. borealis* larvae in the spring planktonic community in the northwest GSL. We present a description of the plankton community (phytoplankton and mesozooplankton) found in association with stage I northern shrimp larvae along with an analysis of the stomach contents and gut fluorescence of larvae caught in the field and from predation experiments in an attempt to identify the different prey ingested by the young larvae in this planktonic ecosystem.

MATERIALS AND METHODS

Field Sampling

Sampling was conducted between 29 April and 2 May 2006 on board the research vessel CCGS Calanus II. The sampling site was chosen based on the documented abundance of northern shrimp larvae in early spring in that region of the GSL (Ouellet and Allard, 2006). Two stations were sampled:

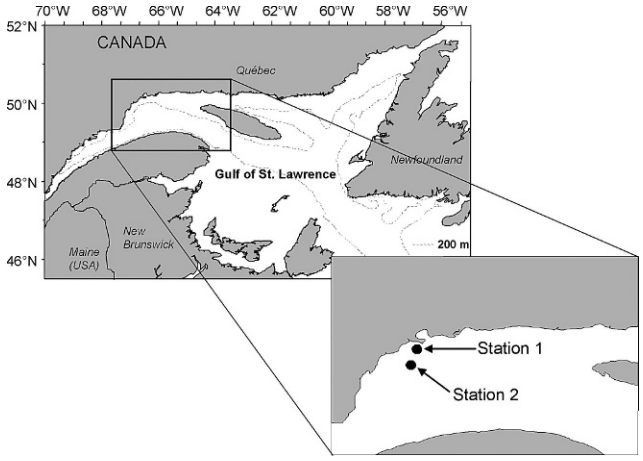

Fig. 1. Map of the Estuary and Gulf of St. Lawrence system showing the location of the sampling stations during spring 2006 in the northwest Gulf.

Station 1 was ~110 m deep and Station 2 was ~220 m deep (Fig. 1). At each station, hydrographic data (temperature, salinity and in situ fluorescence) were obtained with a Sea-Bird SBE 19 CTD. Mesozooplankton and shrimp larvae were collected in the upper 50 m with oblique net hauls using a bongo sampler (61 cm in diameter) equipped with 333 μm mesh nets and with a vertically towed ring net (75 cm in diameter, 202 μm mesh). At the deeper station, two additional bongo hauls were carried out from near-bottom to the surface to verify the presence of late copepodite stages and adult *Calanus finmarchicus* Gunnerus, 1765, and *C. hyperboreus* Krøyer, 1838, that could account for the production of young stages of these two species at the sampling site. Flow meters placed in the mouth of each net were used to estimate the volumes of water filtered. Overall, one vertical and three oblique tows were made at Station 1, and seven oblique (including two tows from the bottom to the surface) and four vertical tows were made at Station 2.

Upon retrieval of the net, *P. borealis* larvae were immediately sorted from the bongo samples. From each tow, when possible, a maximum of 30 individuals were stored in cryovials and frozen in liquid nitrogen before being transferred to a freezer (−80°C) until gut fluorescence analyses were carried out. The remainder of the larvae and zooplankton samples were preserved in a formaldehyde-seawater solution (4%).

In addition to the zooplankton samples, water samples for the determination of chlorophyll *a* (chl *a*) were collected at each station with 5 L Niskin bottles at different depths, e.g., 0, 5, 10, 15 and 25 m; we always sampled the depth of the in situ fluorescence maximum, as determined from the CTD fluorescence profiles. From each depth, a 200 mL subsample for chl *a* determination was filtered through Whatman GF/C filters, which were frozen in liquid nitrogen and stored in the dark. Subsamples were also preserved in an acid Lugol's solution for determination of alga concentrations and species identification using the Utermöhl method.

Complementary Onboard Feeding Experiments

The identification of predators' diets from direct observations of field samples can sometimes be difficult (Symondson, 2002), especially for crustacean zoeae that most likely feed on small particles or do not swallow whole organisms. Therefore, three feeding experiments (30 April, 1 May, and 2 May) were carried out at sea. In preparation for the experiments, gravid *P. borealis* females from the standing stock held at Maurice Lamontagne Institute were brought onboard and maintained in 250 L insulated containers (Xactics™ [2001] International, Inc.) to ensure that live, newly hatched (with empty guts), healthy larvae would be available for the experiments.

The experiments were conducted in 1 L plastic bottles filled with planktonic assemblages prepared at the station. These assemblages were obtained by concentrating plankton collected by vertical tows in the top 50 m of the water column with a conical (50 cm diameter) 73 μm plankton net. Each sample was passed through a 200 μm sieve to eliminate as much as possible the large mesozooplankton predators. A 100 mL subsample of this plankton concentrate was added to each bottle along with 900 mL of filtered (1 μm) seawater. It was not possible to calculate estimates of the initial plankton concentrations introduced to the bottles at sea, so the precise size-specific concentrations of plankton particles in the bottles were estimated subsequently in the laboratory (see below). Given the working conditions on board, the intention was not to conduct a quantitative experiment to precisely determine feeding rates of shrimp larvae on specific prey, but rather to help clarify the larval diet and prey selection estimations from larvae from the net samples.

For each experiment, the bottles were incubated for 2 or 4 h, and for each incubation time there were 5 bottles with 10 newly hatched (< 24 h) stage I *P. borealis* larva and 5 controls (bottles without larvae). For incubations, the bottles were placed in the insulated containers and water temperature (~ 6°C) was maintained by constant pumping of cold subsurface water from the station. Nevertheless, during the experiment of 30 April, water temperature in the containers reached 10.3°C and 12.8°C after 2 and 4 h, respectively. Since the high water temperature could have affected the larvae, we did not consider data from that experiment; only the results from the 1 and 2 May experiments are presented. At the end of each incubation time, the 10 shrimp larvae were removed; 5 were preserved in a formaldehyde-seawater solution (4%) and 5 were preserved in liquid nitrogen. The remaining bottle contents (without the shrimp larvae) were preserved in the formaldehyde-seawater solution (4%).

Laboratory Analyses

Zooplankton net samples were rinsed for a few minutes under tap water and poured into a sorting tray. Organisms larger than 20 mm, e.g., Euphausiacea and Chaetognatha, were separated out. The sample was then diluted ~1/30 to 1/50, and a 10 mL Stempel pipet was used to take subsamples with about 200 specimens of the most abundant taxa. Copepods were identified to the species level when possible and naupliar and copepodite stages were identified and recorded. The abundances of *Calanus finmarchicus* and *C. glacialis* Jaschnov, 1955, were pooled. Individuals of the genera *Acartia*, *Metridia*, *Pseudocalanus*, *Oithona*, and *Oncaea* were not identified to the species level. Organisms that we were not able to positively identify were grouped into major categories, generally class, order, or phylum, e.g., unidentified harpacticoid copepods, three categories of copepod eggs (135-160, 160-195, and 200-250 μm), invertebrate eggs, Gastropoda, Bryozoa, and Cirripedia.

The plankton size spectrum (between 75 and 200 μm) and particle concentrations from the feeding experiment samples were estimated using a Coulter Counter® (Ariza, 2008). Half of the content of each bottle was concentrated and then separated into three subsamples of 10 mL each. Fifteen mL of filtered (0.2 μm) seawater were added to each subsample (final volume = 25 mL) to dilute the concentrate and to allow three 2 mL subsamples to be estimated with the Coulter Counter. The mean size-spectrum and particle concentrations were estimated from the replicates. The other half of the bottle sample was used for species identification and abundance estimation of mesozooplankton by examination of three 5 mL subsamples from each bottle. In contrast to the field samples, all naupliar stages (NI-NVI) of calanoid copepods were pooled for the incubation experiments. For others copepods, copepodite stages (CI-CVI) and naupliar stages (NI-NVI) were pooled after identification to the species or genus level. One difference from the zooplankton groups identified from the field samples (see above) was the creation of a 75-100 μm egg group, a consequence of sampling with the 73 μm mesh net. Nauplii/larvae from other taxa were grouped into major categories, e.g., Appendicularia, Polychaeta, Echinodermata, Hemichordata, Euphausiacea, and Ascidiacea.

All *P. borealis* stage I larvae preserved in the formaldehyde-seawater solution (4%) were used to evaluate diet composition. Cephalothorax lengths were determined before dissection. Larva guts were dissected out with micro needles under a Leica M 10 (20 to 40×) binocular microscope. The degree of gut fullness was assessed visually and coded as empty (0%), half full (50%), or full (100%). In addition, two gut content states (loose or compacted) were defined. Midgut contents were examined after dissection: extracted contents were mounted on a glass slide in glycerine and crushed slightly under a cover glass. The composition of food items was determined using a microscope at 400× equipped with a digital camera. Food items were identified as precisely as possible and the following categories were defined: phytoplankton, diatoms, zooplankton (including heterotrophic plankton), and not identified (others).

Concentrations of chl *a* and phaeopigments were measured in all frozen larvae (Table 1). For each tow, at least three replicates of approximately 10 larvae were used (there were four exceptions). All frozen larvae were

Table 1. Number of larvae (stage I and II) sorted from the bongo tows and preserved for gut fluorescence analyses.

Station	Date	Stage I	Stage II
1	1 May	2	0
2	29 April	30	2
2	30 April	59	5
2	1 May	46	0
2	2 May	66	0

sorted under dim light in a cold room, washed in 1 µm filtered seawater to avoid contamination by external phytoplankton particles, and extracted in 7 mL of 90% acetone for 4 h at 4°C (Tirelli and Mayzaud, 1999). Larvae were not homogenized (Morales et al., 1991). Samples were then centrifuged at 3000 rpm for 10 min. Extracts were analyzed on a Turner Designs Model 10 fluorometer before and after acidification. Gut pigment contents were calculated as the sum of the chl *a* and phaeopigment concentrations per larva.

We also determined chl *a* and phaeopigments in seawater samples by fluorometric analysis after extraction in 10 mL of 90% acetone for 18 h (Parsons et al., 1984). However, the linear regression between in situ fluorescence and estimated chl *a* concentrations at specific depths was poor ($R^2 = 0.346$), therefore we present the data as the raw fluorescence unit and the corresponding converted chl *a* values when appropriate.

Data Analyses

A two-sample Student *t*-test was carried out on transformed [$\log_{10}$ (x + 1)] chl *a* plus phaeopigment concentrations to test for differences in pigment concentrations between the first and second larval stages from the net samples. The importance of phytoplankton ingestion by stage I shrimp larvae during the feeding experiments was assessed by comparing gut fluorescence (chl *a* + phaeopigments) in larvae incubated for 2 and 4 h with control larvae (newly hatched larvae). Non-parametric Kruskal-Wallis tests were used to test for differences in larva gut pigment contents between controls and incubation times due to extreme values (outliers) in the dataset. For each zooplankton species or category, ANOVAs followed by *a posteriori* mean comparisons (Dunn-Sidak procedure), or Kruskal-Wallis tests when variances were not homogenous among groups (i.e., incubation times), were used to detect significant changes in abundance among control (C) bottles (C0h, C2h, C4h) and among controls and bottles incubated (I) with shrimp larvae (I2h, I4h).

Results

Hydrographic Structure

The water column was stratified at the time of the sampling. The mean surface temperature was similar at both stations (Station 1: 3.10°C; Station 2: 3.28°C), with the mean thermocline depth at about 15 m at Station 1 and 18 m at Station 2 (Fig. 2). At Station 1, the relative values of fluorescence for the upper 50 m of the water column showed a maximum at 14 m and a second peak at 23 m (Fig. 2). At Station 2, peaks were found between 9 and 12 m (Fig. 2). The Chl *a* concentrations could not be determined from the in situ fluorescence from these profiles because there was a problem with calibration of the fluorometer, but the chl *a* concentrations in the water samples collected during the mission suggest that the maximum was around 3 µg L^{-1}.

Even though the two stations had similar hydrographic conditions, a higher concentration of northern shrimp *P. borealis* larvae was found at Station 2. The larvae were also more abundant in the bongo samples than in the ring net. Overall, 8.2 larvae m^{-3} were captured on average at Station 2 whereas only 2.4 larvae m^{-3} were captured at Station 1. The great majority (96.5%) of the larvae were at stage I with a few stages II larvae.

Structure of Phytoplankton Community

The structure of the phytoplankton community was examined for one water sample at Station 2 as part of the

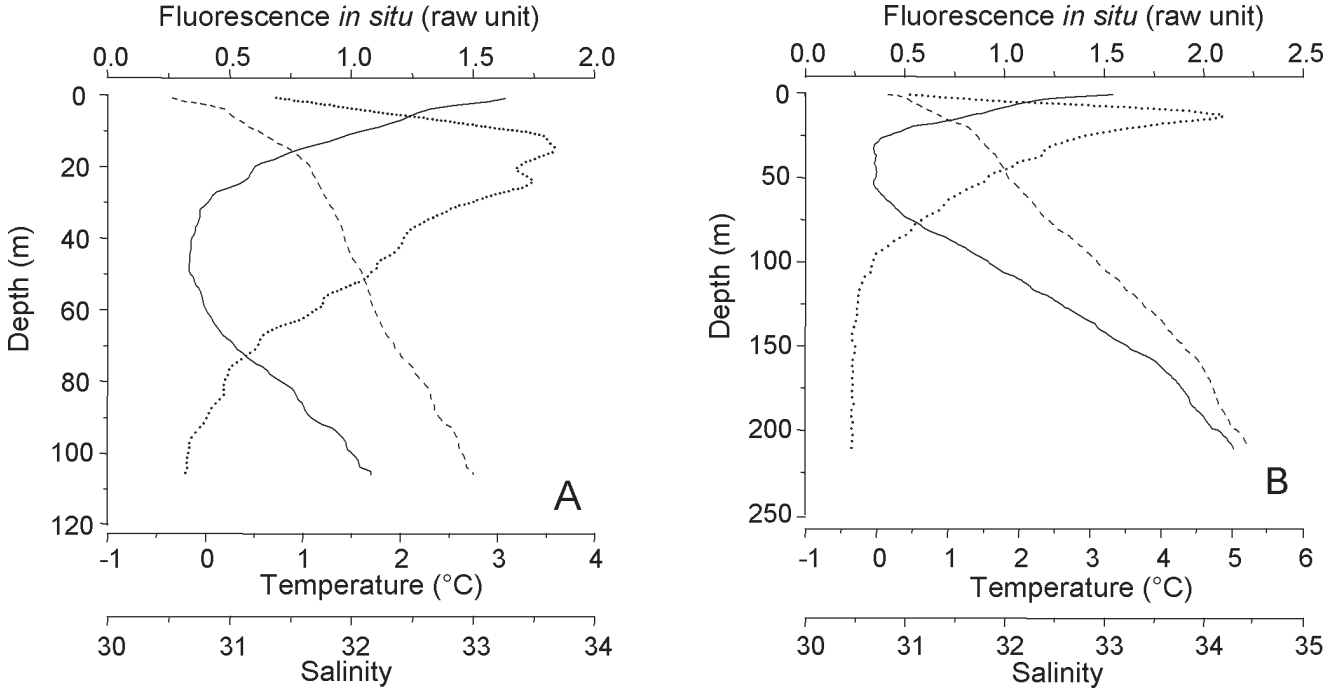

Fig. 2. Vertical profiles of averaged temperature (solid line), salinity (dashed line) and relative in situ fluorescence (dotted line) at Station 1 (A) and Station 2 (B) in the northwest Gulf of St. Lawrence.

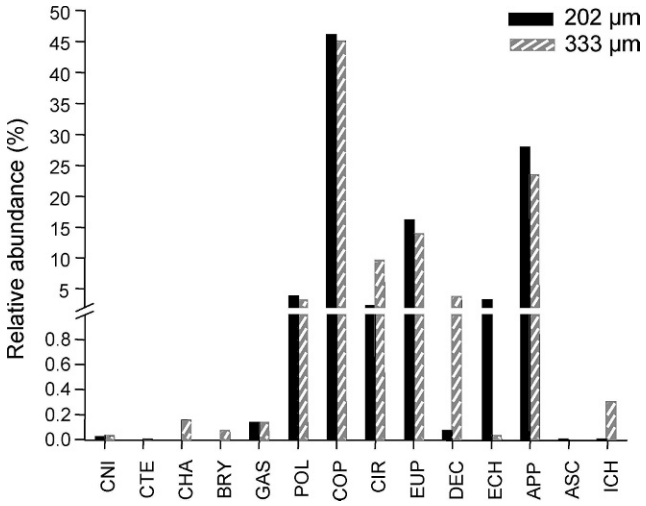

Fig. 3. Relative abundance (mean of Station 1 and 2) of the 14 taxonomic categories found (0-50 m). CNI: Cnidaria; CTE: Ctenophora; CHA: Chaetognatha; BRY: Bryozoa; GAS: Gastropoda; POL: Polychaeta; COP: Copepoda; CIR: Cirripedia; EUP: Euphausiacea; DEC: Decapoda; ECH: Echinodermata; APP: Appendicularia; ASC: Ascidiacea; ICH: ichthyoplankton.

Department of Fisheries and Oceans (Canada) oceanographic monitoring program for the GSL (Mitchell et al., 2002) [for a complete list of the biota, see supplemental data file for DOI 10.1651/0803113.1]. Diatoms dominated the phytoplankton community at the depth of the fluorescence/chl *a* maximum (9 to 14 m), with a concentration of 1194.07 $\times 10^3$ cells L^{-1} (54.4% of the total cell abundance). A total of 56 diatom species were identified, most of these represented by very few individuals. *Chaetoceros*, represented by 23 species, accounted for 52.8% of the total cells. Dinoflagellates, Cryptophyceae, Prymnesiophyceae, and flagellates were also abundant, representing 4.6%, 2.9%, 3.9%, and 23.9% of the total phytoplankton concentration, respectively. For the dinoflagellates, the more numerically abundant genera were *Amphidinium*, *Gymnodinium*, *Gyrodinium*, *Heterocapsa*, and *Prorocentrum*. For Cryptophyceae, the most represented genera were *Hemiselmis*, *Plagioselmis*, and *Teleaulax*. Prymnesiophyceae were represented by the genus *Chrysochromulina*, with individual cells between 2 and 10 µm. Cells between 2 and 5 µm were the most numerous among the flagellates.

Zooplankton Community Structure

On average, the 202 µm net captured 1807.54 ind. m^{-3} at Station 1 and 1888.80 ind. m^{-3} at Station 2; the 333 µm net captured only 230.65 (Station 1) and 152.42 (Station 2) ind. m^{-3} (including *P. borealis* larvae). Among the higher taxonomic categories enumerated from the zooplankton samples, Copepoda (all species and stages) dominated (14 species) in both nets, making up 45.1% and 46.1% of the relative total abundance from the 333 µm and 202 µm nets, respectively (Fig. 3). *Calanus finmarchicus* accounted for 11.3% and 17.5% of all the copepods caught in the 202 µm and 333 µm nets, respectively (Fig. 4). *C. finmarchicus* was the second most abundance species among all copepods after *Oithona* spp. in the 202 µm net. The *C. finmarchicus* population was represented by a new generation (nauplii and all copepodite stages), with NIV-NVI and CI-CIII being the most abundant stages (Fig. 5). The older copepodite stages IV-VI (females and males) were mostly found in the deep tows at Station 2. *C. hyperboreus* was also very abundant in the bongo samples, making up 19.1%

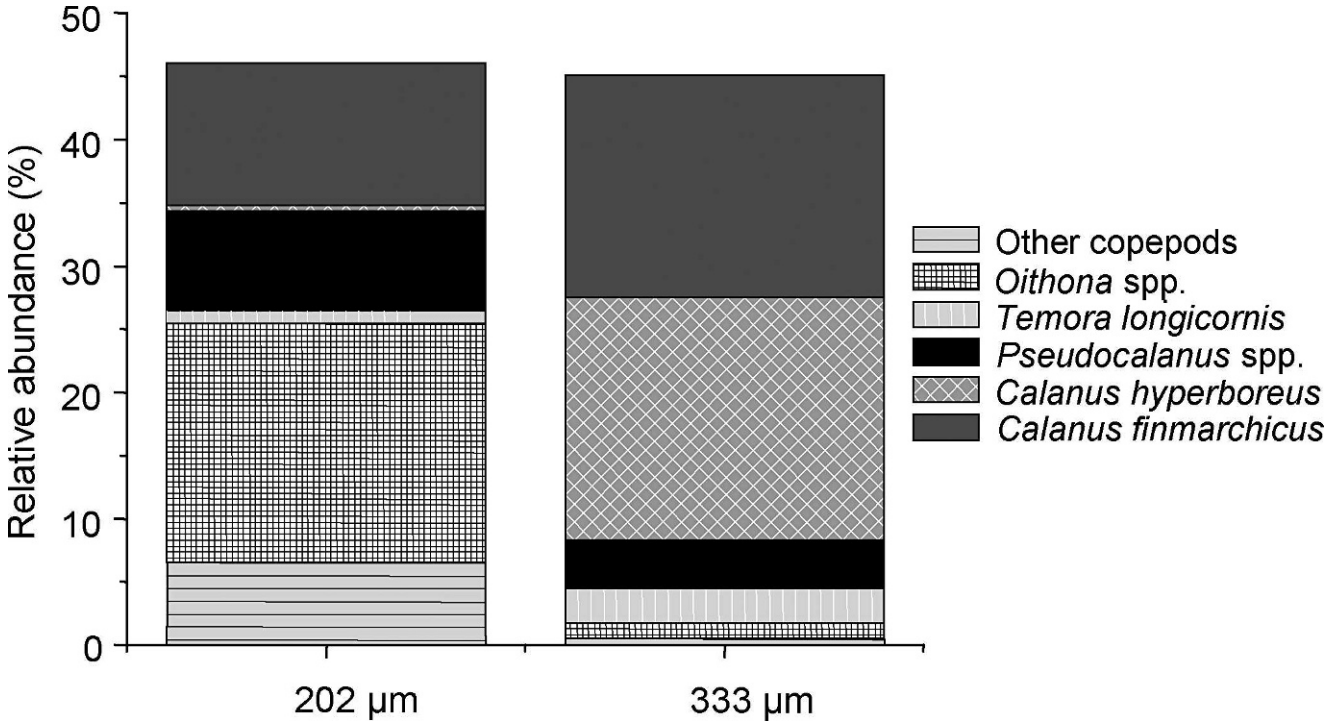

Fig. 4. Relative abundance of the principal species within the Copepoda at the sampling site (mean of Station 1 and 2).

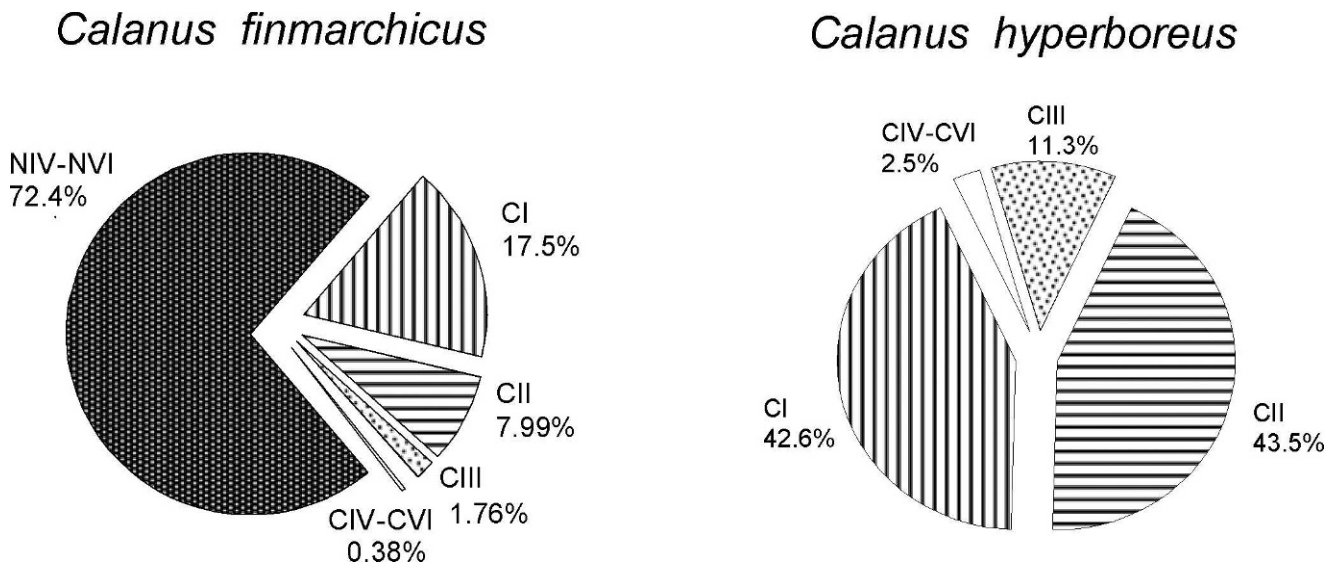

Fig. 5. Stage structure of the two most abundant species from the Copepoda: *Calanus finmarchicus* and *C. hyperboreus* (bongo plus ring net; mean of Stations 1 and 2).

of the relative abundance of all copepods (Fig. 4). This species was also represented by a new generation consisting of copepodites I, II and III (Fig. 5). The late-stage copepodites (CIV-CV) and adults were better represented in the deeper hauls, although they accounted for less than 10% of the relative abundance. The three categories of copepod eggs (diameters of 135-160, 160-195, and 200-250 μm) were only caught in the 202 μm net and represented less than 2% of the copepod community.

The small copepods *Oithona* spp., *Pseudocalanus* spp., and *Temora longicornis* O. F. Müller, 1785, were also abundant at the sampling sites (Fig. 4). *Oithona* spp. was the most abundant small copepod on average in the 202 μm net. The population structure of this species was characterized by older copepodite stages (CIV-CV) and females, a number of which were carrying egg sacs; males were relatively rare. *Pseudocalanus* spp. was the second most abundant species, making up 7.9% of all copepods caught with the 202 μm net. All stages of *Pseudocalanus* spp. were recorded, with stages CI-CIII being the most numerous followed by NIII and NIV. Bongo net samples showed a better representation of the older stages CIV-CV, whereas females and especially males were less abundant. *T. longicornis* was better represented in bongo net samples (2.8%), with males being particularly dominant and only a few females, copepodite stages CI-CV, and nauplii being found. Finally, the copepod species *Acartia* sp., *Paraeuchaeta norvegica* Boeck, 1872, *Metridia* sp., *Microsetella norvegica* Boeck, 1865, *Oncaea* sp., *Scolecithricella minor* Brady, 1883 and calanoid nauplii (NI-NII) were recorded in low numbers (mostly in the 202 μm net); these, along with copepod eggs, were grouped as ''other copepods'' (Fig. 4).

Appendicularia (*Fritillaria* sp. and *Oikopleura* sp.) were the second most abundant taxonomic category, constituting 23.1% and 28.0% of the total abundance from the 333 μm and 202 μm nets, respectively (Fig. 3). *Fritillaria* sp., especially the juvenile stage (mean trunk length 400-500 μm) clearly dominated this category. Euphausiacea (juvenile stages) were also numerous, and their relative abundance was similar between the two nets. However, the subcategories eggs, nauplii, and metanauplii were found in higher numbers in the 202 μm net. Cirripedia larvae, Polychaeta larvae, and Echinodermata larvae were three other categories noticeably abundant in the zooplankton samples.

Size Spectrum and Species Composition of the Bottle Assemblages

The initial total phytoplankton and zooplankton density (75 to 200 μm) was estimated at 5284 and 5344 particles L^{-1} ($= 5.3 \times 10^6$ particles m^{-3}) for the 1 May and 2 May experiments, respectively. The higher abundances were observed between 75 and 120 μm (Fig. 6). Closer examination revealed that the zooplankton accounted for 54.6% of all the particles in the initial assemblages, with phytoplankton cells accounting for the rest (45.4%). However, compared to the water sample analysis at Station 2, only ca. 11% of the phytoplankton community fell within that size range, with most of the phytoplankton at the sampling sites made up of cells smaller than 75 μm.

The zooplankton community in the bottles for the 1 May and 2 May experiments consisted mostly of early and juvenile stages of Appendicularia (*Fritillaria* sp.), Polychaeta, Copepoda, Echinodermata, Hemichordata, Euphausiacea, and Ascidiciacea. These taxonomic groups were also identified as the most abundant from the net samples. The initial zooplankton mean (± SD) density in the bottles was estimated at 3280.5 ± 448.9 (1 May) and 2611.9 ± 853.1 (2 May) individuals L^{-1} ($t = 1.698$, $d.f. = 10$, $P = 0.12$). Copepoda was the dominant taxon (ca. 77.5% of total abundance), and the group was represented mostly by calanoid (*Calanus*, *Pseudocalanus* and *Metridia*) nauplii (NI-NVI). Nauplius stages (NI-NVI) of *T. longicornis* and

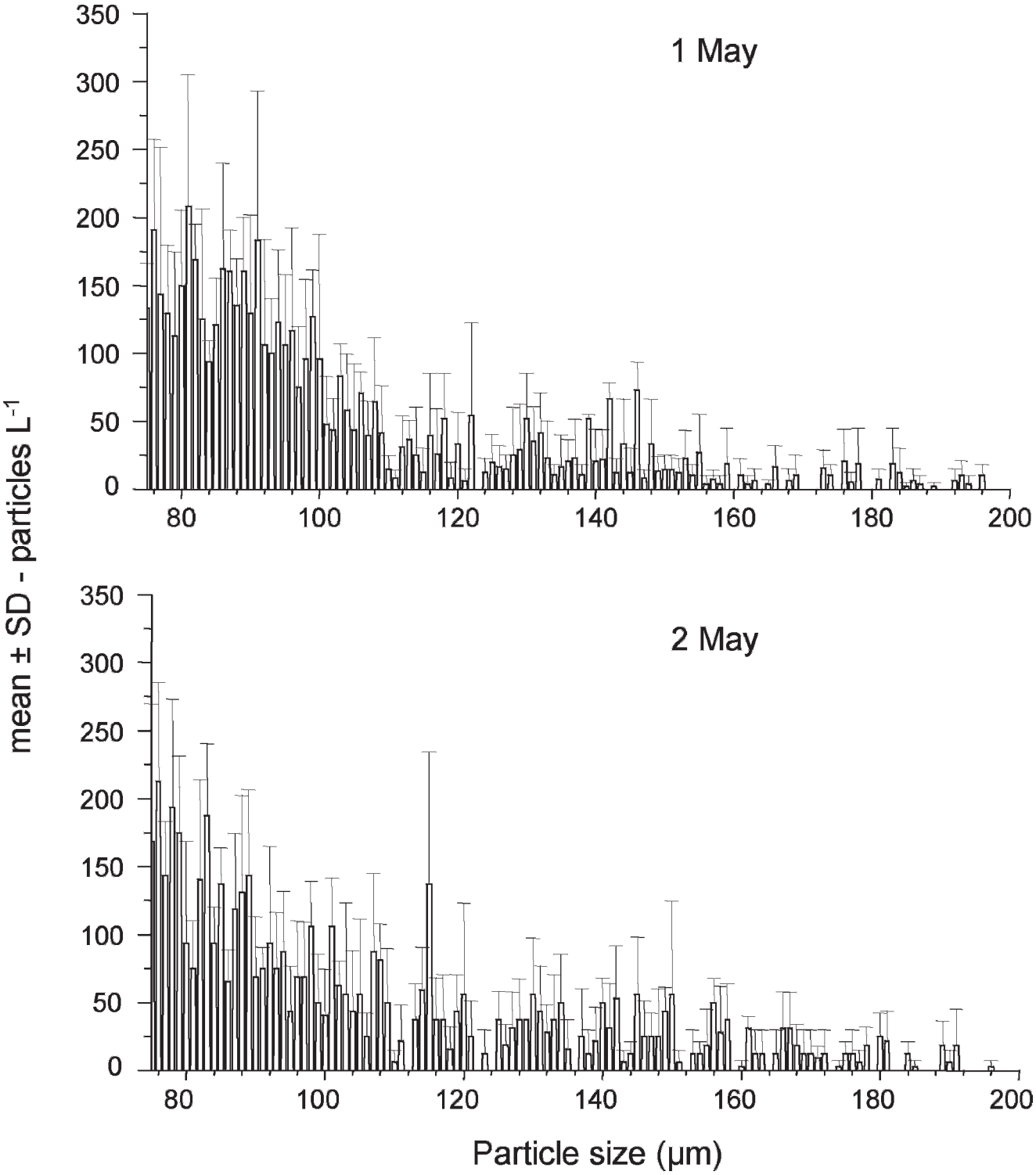

Fig. 6. Size spectrum (75 to 200 µm) of the plankton assemblages used for the 1 May and 2 May 2006 onboard feeding experiments. Mean concentrations with standard deviations are shown.

Oithona spp. were also abundant in the bottles, in addition to copepodite stages of other Copepoda species including *Pseudocalanus* spp., *Oncaea* spp., *Microsetella norvegica*, *Oithona* spp., and five size classes of copepod eggs (75-100, 100-135, 135-160, 160-195, 200-250 µm). Individuals from the Appendicularia (*Fritillaria* sp.), Echinodermata, Hemichordata, Euphausiacea, and Ascidiaciacea groups were less abundant and completed the bottle assemblages.

Table 2. Food items found in guts of stage I larvae from field samples. CL = carapace length (mm). The "unidentified" diet item refers to fragments of zooplankton for which it was not possible to provide taxonomic identification. nd = no data.

CL (mm)	Gut fullness (%)	Gut content state	Diet composition
1.38	50	compacted	mineral crystals, unidentified
1.34	50	compacted, clear	unidentified
1.40	0	nd	nd
1.35	100	compacted	diatoms
1.59	50	loose, clear	diatoms, fragments
1.41	50	loose, clear	diatoms, zooplankton fragments
1.38	50	compacted	unidentified
1.38	100	compacted, clear	diatoms, unidentified
1.40	50	loose, clear	unidentified
1.39	100	compacted	diatoms, zooplankton fragments
1.39	100	compacted	unidentified
1.37	100	compacted	diatoms, zooplankton fragments
1.40	100	compacted	unidentified
1.38	100	compacted	nd
1.41	0	nd	nd
1.37	100	compacted	*Thalassiosira* spp. - unidentified
1.53	100	loose, clear	diatoms
1.40	100	compacted	diatoms
1.43	0	nd	nd
1.39	100	compacted	diatoms, zooplankton fragments
1.42	50	compacted	unidentified
1.32	100	compacted	*Thalassiosira* spp. - unidentified
1.39	100	compacted	diatoms, fragments
1.30	100	compacted	diatoms, mineral crystals
1.37	100	compacted	dark fragments, unidentified
1.32	100	compacted	diatoms, zooplankton fragments
1.38	50	loose	small fragments, unidentified
1.35	100	compacted	dark fragments, unidentified
1.39	100	compacted	diatoms, mineral crystals
1.35	100	compacted	diatoms, zooplankton fragments

Larva Diet Composition

From the net samples, the gut contents of 210 shrimp larvae (stages I and II) were assayed fluorometrically. Chl *a* plus phaeopigment concentrations ranged from 0.60 to 3.25 ng larva^{-1} (mean = 1.08, SD = 0.65). It was possible to examine only 7 stage II larvae; the mean gut pigment concentration was 0.84 ng larva^{-1} (SD = 0.39). Results from the Student's *t*-test indicated that there was no significant difference in pigment content between the two larval stages ($t = 0.697$, $d.f. = 23$, $P = 0.493$). Only 30 larvae (all stage I) were examined microscopically. The microscopic examination of the gut contents revealed that material was present in the gut of most larvae, with only 10% having an empty gut. In general, the food remains were clear and easy to separate once removed from the gut cavity. When it was densely packed, the mass remained compacted once removed and it was more difficult to differentiate the fragments and prey items. In general, the mass was obscure, with small dark granules and some translucent brown matter. Material was rarely present throughout the entire alimentary canal. It was easier to recuperate the material present in the anterior part of the tube and it was also less digested; as a consequence, only the material observed in the midgut was used to determine the larva diet composition. Only a few larvae had identifiable food items in their guts, and all revealed the same general diet composition: individual cells of *Thalassiosira* spp. and *Navicula* spp. along with other materials like diatom fragments, mineral particles, and (generally non-identifiable) zooplankton fragments (Table 2). A visual assessment of prey remains found in the gut suggested that, by volume, about half of the particles were phytoplanktonic (diatoms) and most of the other half appeared to be zooplankton fragments with some mineral particles.

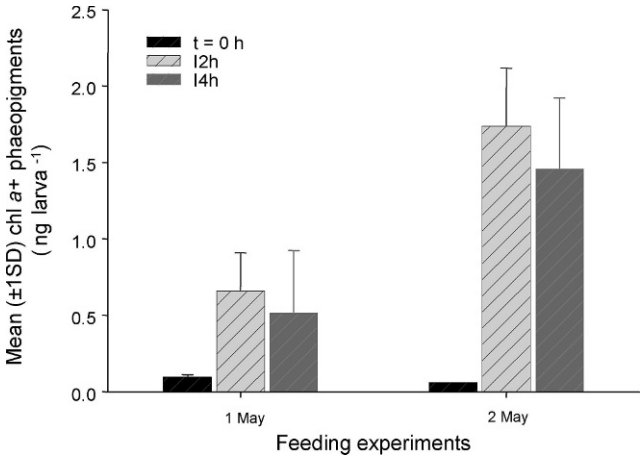

Fig. 7. Comparison of mean (± standard error) gut pigment concentrations between control (newly hatched) larvae and larvae after 2 or 4 h of incubation for the 1 May and 2 May 2006 onboard feeding experiments.

The analyses of the larvae from the bottle experiments revealed that chl *a* and phaeopigments in the gut of newly hatched larvae (t = 0 h) varied between 0.10 ± 0.02 (1 May, $N = 29$) and 0.15 ± 0.0 (2 May, $N = 10$) ng larva^{-1}. After incubation, mean gut pigment concentrations increased to 0.66 ± 0.28 and 0.52 ± 0.46 ng larva^{-1} after 2 and 4 h, respectively, on 1 May and to 1.74 ± 0.42 and 1.46 ± 0.52 ng larva^{-1} on 2 May (Fig. 7). For each experiment, a comparison of mean pigment (chl *a* + phaeopigments) concentrations revealed significant differences (Kruskal-Wallis $P < 0.01$) between the control larvae and larvae after 2 and 4 h of incubation.

The gut contents of 145 larvae were examined microscopically. As we found for larvae from the net samples, visual inspection of the gut content of the incubated larvae clearly revealed small cells, e.g., diatoms (*Thalassiosira* spp., *Navicula* spp.), a silicoflagellate (*Dictyocha speculum* Ehrenb.), ciliates (*Parafavella* spp.), and fragments most likely of zooplankton origin. Again, like larvae from the net samples, centric (such as *Thalassiosira*) and pennate (*Navicula* spp.) diatoms, with cell sizes between 20 and 50 μm, were easily indentified whereas they represented less than 1% of the natural phytoplankton community. Flagellates (ca. 20 μm) and cilates (> 50 μm) were also observed in larva guts, even though these groups were rare (less than 1%) in the natural phytoplankton community.

Comparison of the Bottle Assemblages Before and After Incubation

In control bottles (C0h, C2h and C4h; no shrimp larvae), there were very few significant differences in the abundance of the zooplankton species or categories between time zero and after 2 or 4 h of incubation, the exceptions were Polychaeta larvae and *Oithona* spp. CI-CVI after 2 h and 135-160 μm eggs after 4 h (Fig. 8). After

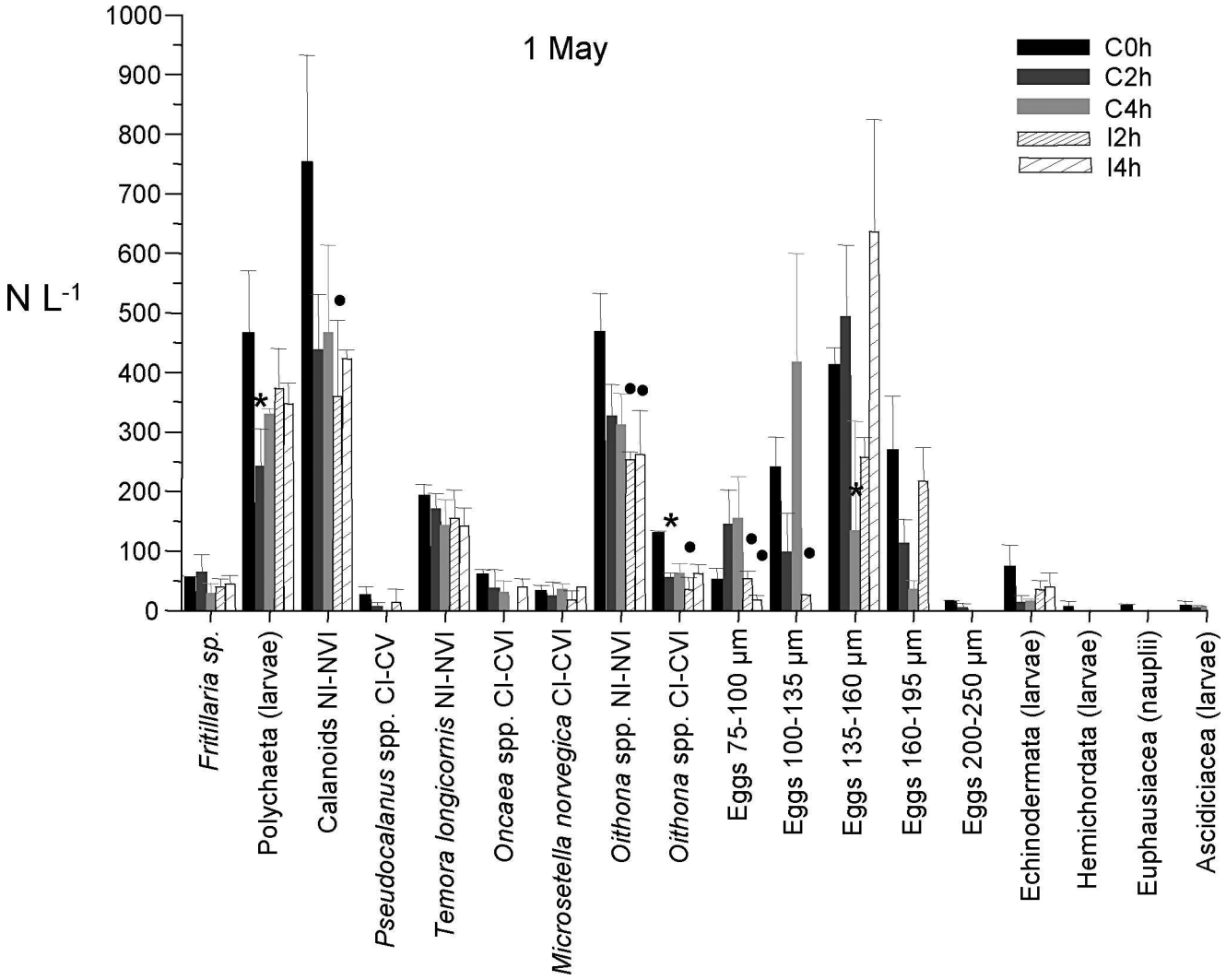

Fig. 8. Comparison of zooplankton taxa abundances (mean ± 1SD) before (C0h) and after 2 and 4 h of incubation (control: C2h, C4h; with larvae: I2h, I4h) for the 1 May 2006 onboard feeding experiment. The asterisks indicate significant differences between the controls whereas the black dots indicate significant differences between incubation and control ($P < 0.05$; ANOVA, *a posteriori* Dunn-Sidak mean comparisons).

incubation in the presence of stage I shrimp larvae for the 1 May experiment, the abundance of calanoid nauplii ($P = 0.058$), *Oithona* spp. nauplii and copepodites, and 100-135 µm eggs were significantly lower ($P < 0.05$) after I2 hours compared to their abundance at C0h (Fig. 8). However, even though abundances were generally lower for all groups, the differences between the I2h bottles and the C2h bottles were significant for only two cases, 100-135 µm and 135-160 µm eggs (Fig. 8). The differences were less marked after 4 h but were still significant for *Oithona* spp. nauplii and 75-100 µm eggs between C4h and I4h (Fig. 8). Although the abundance of calanoid nauplii NI-NVI decreased after 2 and 4 h of incubation, no significant differences (at $P > 0.05$) were observed for the 2 May experiment except for 135-160 µm eggs between C2h and I2h (Fig. 9). Overall, the results from the 1 May and 2 May experiments suggest that the taxonomic groups calanoid nauplii, *Oithona* spp. (nauplii and calanoids), and small copepod eggs were selected as prey by stage I shrimp larvae during the incubations.

Discussion

Shrimp larvae and other plankton sampled over a small time window in early spring 2006 provide unique data on the Northwestern Gulf of St. Lawrence (NWGSL) plankton community at an important time for the productivity of this ecosystem. The conditions observed also represent an ''average'' spring as estimated by the stratification index (differences in water density [sigma-t] between 5 and 30 m divided by the depth interval) of 0.03, which is close to the long-term mean obtained from an 11-year (1994 to 2004) time series for that region of the NWGSL (Ouellet et al., 2007). At the time of our study, the spring warming of the water had begun, as revealed by the thermal stratification observed in the upper layer of the water column. The level of chl *a* concentrations (the highest values were estimated at 3.1 µg L^{-1}) indicates that high primary production was occurring at the time of the sampling. The phytoplankton community was dominated by centric diatoms, mainly by species of the genus *Chaetoceros*. As for the mesozooplankton community structure, spawning and development

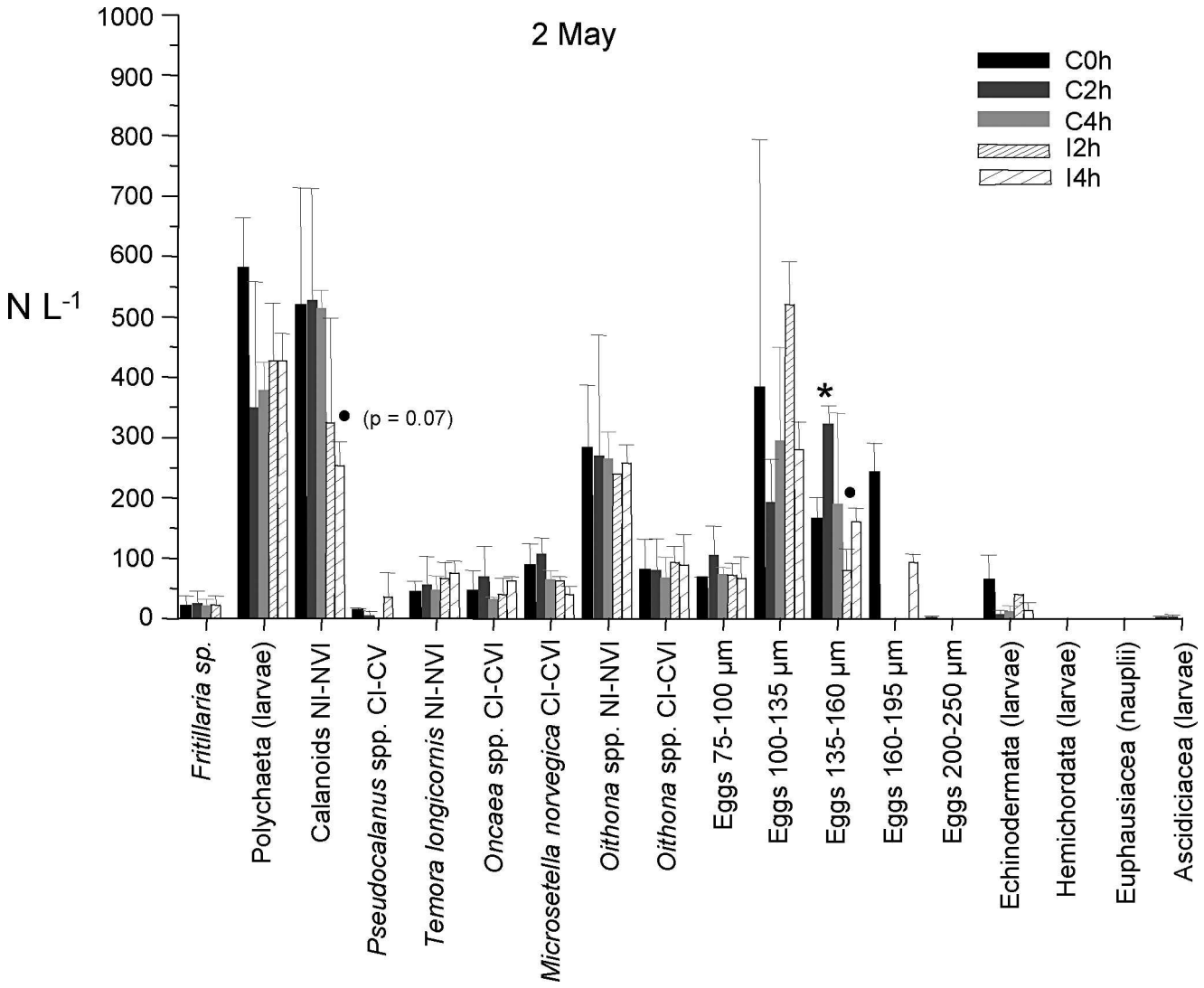

Fig. 9. Comparison of mesozooplankton taxa abundances (mean ± 1SD) before (C0h) and after 2 and 4 h of incubation (control: C2h, C4h; with larvae: I2h, I4h) for the 2 May 2006 onboard feeding experiment. The asterisks indicate significant differences between the controls whereas the black dots indicate significant differences between incubation and control ($P < 0.05$; ANOVA, *a posteriori* Dunn-Sidak mean comparisons).

of many species/groups had clearly started in the area, as indicated by the abundance of early and juvenile stages of calanoid copepods, e.g., *C. finmarchicus*, *C. hyperboreus*, and *Pseudocalanus* spp., as well as Appendicularia and Euphausiacea, and the relatively high abundance of Cirripedia, Polychaeta, and Echinodermata larvae.

Earlier studies (Rivkin et al., 1996; Doyon et al., 2000) have documented that average chl *a* values over the euphotic zone of around 2.1 µg L^{-1} (cells < 200 µm) correspond to spring bloom concentrations in the NWGSL. Therefore, the estimated maximum chl *a* value of 3.1 µg L^{-1} in our study would suggest that the sampling was carried out when high phytoplankton production was still occurring. Furthermore, our late April/early May chl *a* values correspond well with spring bloom values observed in the Anticosti Gyre (a quasi-permanent cyclonic gyre that characterizes the NWGSL) in 2001 (Starr et al., 2002). It has long been considered that the spring phytoplankton bloom occurs in the Gulf of St. Lawrence during April-May (Sévigny et al., 1979). The analyses revealed that *Chaetoceros* spp. accounted for more than half of all the diatom cells counted, with *C. socialis* (Lauder) being the most common species. This genus along with other diatoms, e.g., *Thalassiosira nordenskioeldii* Cleve, 1873, typically dominates the phytoplankton biomass during the spring bloom in the Lower St. Lawrence Estuary and in the Gaspé Current (Therriault and Levasseur, 1985; Levasseur et al., 1992). A recent study carried out in similar ecosystems (northern Norway fjords) reported the high production rates of *C. finmarchicus* during a diatom-dominated (*Chaetoceros* spp., *Thalassiosira* spp.) spring bloom (Koski, 2007).

Of the 14 most common higher taxonomic levels of zooplankton recorded in the study area (Decapoda, Ascidiacea, Bryozoa, Chaetognatha, Cirripedia, Cnidaria, Copepoda, Ctenophora, Echinodermata, Euphausiacea, Gastropoda, ichthyoplankton, Polychaeta, and Appendicularia), the Copepoda dominated the metazoan zooplankton

community. However, using 333 μm and 202 μm mesh nets may have underestimated the abundance of smaller species, e.g., *Oithona* spp., and the juvenile stages of other groups such as Echinodermata, Euphausiacea, Appendicularia, and Polychaeta. Many female *Oithona* spp. with egg sacs were recorded, but nauplii of this species were rare in the water column samples. It has been argued that sampling with a 202 μm mesh net compared to a 62 or 73 μm mesh net greatly underestimates the contribution of the smaller species to the total abundance and biomass of copepod communities due to the loss of the nauplius and copepodite (below CV in *Oithona* spp.) stages (Hopcroft et al., 2005). Indeed, nauplii (NI-NVI) of *T. longicornis* and *Oithona* spp. were abundant in the incubation bottles, a fact that can be explained by the use of the 73 μm net to sample the upper water column for preparation of the plankton assemblages. Overall, the abundance of juvenile stages of *C. finmarchicus*, *C. hyperboreus*, *Pseudocalanus* spp., *T. longicornis*, and *Oithona* spp. (nauplii and copepodite stages CI-CIII), Appendicularia, Euphausiacea (eggs, nauplii, and metanauplii), and the presence of larval Cirripedia, Polychaeta and Echinodermata during the sampling clearly indicate that spawning of these species/groups and high secondary production was occuring in the area, likely in response to the high primary production.

In spring 2006, the date of 50% of *P. borealis* larval emergence occurred on day of the year 125 (5 May; L. Savard, Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, QC, personal communication). Northern shrimp larvae have a short hatching duration (mean duration for 25% to 75% larval hatching: ~12 days; Ouellet et al., 2007), which could mean that our sampling was carried out approximately in the middle of the shrimp larval appearance, an assumption supported by the high proportion of stage I larvae at the sampling sites. The microscopic examination of gut contents and the fluorometric analyses revealed that the stage I larvae fed on a variety of food items immediately after hatching. Only a small number of dissections were carried out on field larvae and it was difficult to identify the zooplankton fragments; however, the homogeneity of the observations among the larvae examined gives us some confidence in our conclusions. Moreover, the increase in gut pigment concentrations and the significant decrease of certain zooplankton taxa during incubation experiments support the conclusion of an omnivorous feeding regime for stage I northern shrimp larvae at hatching.

We present the first direct observation of the northern shrimp stage I larva feeding regime in the NWGSL ecosystem. While phytoplankton cells seem to constitute a significant proportion of the diet, our examination of gut contents (field larvae and incubation experiments) lead us to conclude that feeding is already omnivorous at hatching, as had been proposed by Rasmussen et al. (2000). The visual assessment of prey remains in larval guts revealed that about half (by volume) of the particles were phytoplankton cells (diatoms) and most of the rest appeared to be zooplankton. In almost all the larvae examined, centric diatoms were found. They also made up the highest percentage of the phytoplankton community in the surface layer. However, although small colonial diatoms belonging to *Chaetoceros* spp. were dominant in the centric diatom group, they were not easy to identify in the larval gut contents.

The large centric diatoms *Thalassiosira* spp. and pennate diatom *Navicula* spp. (20-50 μm) were easily identifiable, even though they represented less than 1% of the total phytoplankton community. These differences could be due to a mechanical inefficiency of the larvae for catching the smaller species, e.g., *Chaetoceros* spp. cell diameters are only 5-14 μm, or to differences in the time of residence in the guts between taxonomic groups. Hence, fragile phytoplankton could be underestimated due to fragmentation of cells that makes them hard to identify.

Gut pigment examination by fluorescence also provided evidence that first stage northern shrimp larvae ingested phytoplankton during the sampling period. Pigment concentrations in stage I larvae from the combined incubations match field data (mean ± SD: field = 1.08 ± 0.65 ng larva^{-1}, after 2 h = 1.20 ± 0.31 ng larva^{-1}, after 4 h = 0.99 ± 0.44 ng larva^{-1}). It has been shown for stage I larvae that, although greater variance was observed for 2 and 4 h, predation rates were quite independent of incubation times over a 24 h experiment (Harvey and Morrier, 2003). The gut fluorescence values are comparable to those found in medium-sized herbivorous copepods (Morales et al., 1991; Bautista and Harris, 1992), but they are higher when compared with the value of 0.2 ng chl *a* ind^{-1} found by Harms et al. (1994) for crab *Carcinus maenas*, Linnaeus, 1758, larvae. Dam and Petersen (1991) estimated the gut pigment content of the female calanoid copepod *T. longicornis*, an omnivorous copepod, at 1.0-1.5 ng chl *a* per female in Long Island Sound (NE USA). It thus appears that the ingestion of planktonic algae is important in the feeding of first stage northern shrimp larvae.

Interestingly, the gut pigment concentration (G) from the field and larvae incubated for two and four hours is almost constant at ≈1 ng larva^{-1}, suggesting a steady state between ingestion (I) and egestion. If as a first approximation we apply a conservative gut evacuation rate (k) of ≈0.02 min^{-1} (e.g., typical of herbivorous copepods at 5°C; Irigoien, 1998), that will give an estimated ingestion rate ($I = k \times G$; Båmstedt et al., 2000) of ≈0.02 ng chl *a* larva^{-1} min^{-1} (≈ 28.8 ng chl *a* larva^{-1}d^{-1}). The estimated daily caloric requirement for *P. borealis* stage I larvae was estimated at 0.297 cal mg^{-1} DW (0.05 cal larva^{-1}) at a temperature of 4.5°C (Paul and Nunes, 1983). Using a conversion factor of ≈10.0 kcal g^{-1} C (Salonen et al., 1976) and assuming a C:chl *a* ratio of 40 (Båmstedt et al., 2000), our chl *a* daily ingestion estimate would correspond to 0.0115 calories, or about 20% to 25% of the larva daily needs. Therefore, even though the estimate is probably very imprecise, phytoplankton alone is unlikely to provide the required minimum number of calories needed by *P. borealis* first stage larvae. Indeed, earlier laboratory experiments have demonstrated the inadequacy of phytoplankton cells alone in supporting northern shrimp larva development and survival (Nunes, 1984; Ouellet et al., 1992).

Remains resembling zooplankton fragments were frequently observed in the microscopic gut examination. However, it was not possible to resolve the precise

taxonomic identity of the zooplankton fragments, as was done by Stickney and Perkins (1981), who reported remains of cirripedes, copepod nauplii, small larval polychaetes, larval echinoderm spines, and copepods. The high degree of fragmentation and/or the advanced state of digestion made it impossible to differentiate zooplanktonic items using a light microscope. Various authors have examined larval faeces and gut contents using scanning electron microscopy (SEM), which would increase one's ability to accurately identify the items found (Meyer-Harms and Harms, 1993).

Nevertheless, significant decreases in the abundance of specific zooplankton groups during the feeding experiments strongly suggest that these were selected as prey by stage I shrimp larvae. Small particle densities as high as those present in the incubation bottles are not unusual in laboratory feeding experiments on decapod larvae (Stickney and Perkins, 1981; Schwamborn et al., 2006). Densities of larger prey, such as Artemia nauplii, of 500 to 1000 ind. L^{-1} or higher are also not unusual when estimating decapod larva feeding rates in the laboratory (e.g., Stickney and Perkins, 1981; Paul and Nunes, 1983; Minagawa and Murano, 1993; de Lima and Souza-Santos, 2007). Although the simple onboard experiments and the short incubation times do not permit accurate estimates of specific predation rates, simple calculations based on the significant differences (1 May) in abundance of calanoid plus *Oithona* spp. nauplii give an estimate of about 180 ind. $larva^{-1}$ d^{-1} (in comparison, Paul and Nunes (1983) estimated a consumption of ~50 *Artemia* nauplii $larva^{-1}$ d^{-1}). Predators other than shrimp larvae may have contributed to the diminution of certain taxa during the incubation, but the absence of significant differences after incubations in the control bottles (without shrimp larvae) suggests rather that there was an intense predation by the stage I larvae (here again, the short incubation times may be responsible for an overestimation). Interestingly, the results were different for the 2 May experiment. On that date, gut fluorescence revealed chl *a* and phaeopigment concentrations per larva that were up to three times higher than in the 1 May larvae (see Fig. 8). It seems that larvae in the 2 May experiment were more interested in the phytoplankton cells than in the zooplankton during the incubations. Total zooplankton concentration was slightly less in the 2 May preparation relative to 1 May. In addition, a possible explanation may be that the phytoplankton community on 2 May contained a higher concentration of chain-forming phytoplankton cells (diatoms, *Chaetoceros* spp.). We have no data supporting that this was the case, but one can speculate that shrimp larvae increase their selection on phytoplankton cells when these are more abundant and easier to capture than zooplankton items.

In conclusion, our analysis of the first larval stage feeding ecology of *P. borealis* in the NWGSL confirms the omnivorous nature of the diet at hatching but also indicates that zooplankton must constitute an important contribution to the stage I larva feeding/energy needs. The beginning of the secondary production at the sampling site, reflected by a high quantity of early developmental stages from various taxonomic groups, means that the larvae have access to a wide variety (in terms of size and shape) of potential food items. Laboratory experiments have also revealed that stage II and older larvae can feed efficiently on mesozooplankton (Rasmussen et al., 2000; Harvey and Morrier, 2003). Stickney and Perkins (1981) observed that zooplankton food becomes more important than phytoplankton as the larvae get bigger. Pedersen and Storm (2002) used fatty acid analyses and found that while phytoplankton is an important component of the stage I larva diet, the importance of animal food increases in the diet of larval stages III to VI. In addition to food quantity, food quality is also considered a key factor for survival and development (Ouellet et al., 1992; Anger, 2001). Zooplankton could provide the extra calories needed to fulfill the metabolic requirements of the shrimp larvae. Nevertheless, phytoplankton may provide early stages of *P. borealis* larvae with a food source that supplies specific essential nutrients, e.g., essential polyunsaturated fatty acids, which are considered key nutrients in animal nutrition (Sargent et al., 1997).

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