Ecology, 87(2), 2006, pp. 444–457

FEEDING BY LARVAE OF INTERTIDAL INVERTEBRATES: ASSESSING THEIR POSITION IN PELAGIC FOOD WEBS

CRISTIAN A. VARGAS,[1] PATRICIO H. MANRÍQUEZ,[2] AND SERGIO A. NAVARRETE[3]

Estación Costera de Investigaciones Marinas, Las Cruces and Center for Advanced Studies in Ecology and Biodiversity, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Abstract. One of the leading determinants of the structure and dynamics of marine populations is the rate of arrival of new individuals to local sites. While physical transport processes play major roles in delivering larvae to the shore, these processes become most important after larvae have survived the perils of life in the plankton, where they usually suffer great mortality. The lack of information regarding larval feeding makes it difficult to assess the effects of food supply on larval survival, or the role larvae may play in nearshore food webs. Here, we examine the spectrum of food sizes and food types consumed by the larvae of two intertidal barnacle species and of the predatory gastropod *Concholepas concholepas*. We conducted replicated experiments in which larvae were exposed to the food size spectrum (phytoplankton, microprotozoan and autotrophic picoplankton) found in nearshore waters in central Chile. Results show that barnacle nauplii and gastropod veligers are omnivorous grazers, incorporating significant fractions of heterotrophs in their diets. In accordance with their feeding mechanisms and body size, barnacle nauplii were able to feed on autotrophic picoplankton (<5 μm) and did not consume the largest phytoplankton cells, which made the bulk of phytoplankton biomass in spring–summer blooms. Balanoid nauplii exhibited higher ingestion rates than the smaller-bodied chthamaloid larvae. Newly hatched *C. concholepas* larvae also consumed picoplankton cells, while competent larvae of this species ingested mostly the largest phytoplankton cells and heterotrophic protozoans. Results suggest that persistent changes in the structure of pelagic food webs can have important effects on the species-specific food availability for invertebrate larvae, which can result in large-scale differences in recruitment rates of a given species, and in the relative recruitment success of the different species that make up benthic communities.

Key words: chlorophyll; diet selectivity; invertebrate larval ecology; microbial food web; omnivory; settlement.

INTRODUCTION

Most marine invertebrates have complex life cycles that include a free-swimming larval phase, which resides from few hours to months in the plankton before returning to settle in the adult habitat (Thorson 1950). In these species, settlement and subsequent recruitment can be the leading determinants of population dynamics and strongly modulate the importance and intensity of species interactions (Menge and Sutherland 1987, Connolly et al. 2001). The rate at which larvae arrive and settle on the shore depends on a complex set of biological and physical processes, including physical transport mechanisms (e.g., Pineda 1991, Shanks et al. 2000), availability of settling substratum (Strathmann et al. 1981), parent fertility and egg quality (Berntsson et al. 1997), larval mortality due to predation and, in the case of planktotrophic larvae, food availability during larval development (Baldwin and Newell 1995, Sullivan et al. 1997). Since planktotrophic larvae rely on food to grow and develop, food supply and food quality could represent an important source of presettlement mortality. In addition to the well-documented effects of temperature (Huntley and López 1992), food quality and quantity may influence early survival and growth of metamorphosed individuals (Phillips and Gaines 2002). The scarce published data available on feeding of larval stages of benthic invertebrates makes it difficult to evaluate the potential for larval starvation and its effects on pre-settlement mortality, let alone on observed patterns of recruitment. Here, we examine the spectrum of food size and food types consumed by larvae of two of the most abundant intertidal barnacle species along the coast of central Chile and of the muricid predatory gastropod *Concholepas concholepas*.

Under some conditions, food quality and concentration can drastically influence different aspects of the larval life of small suspension feeding larvae. Nutri-

Manuscript received 15 February 2005; revised 31 May 2005; accepted 18 July 2005; final version received 15 August 2005. Corresponding Editor: E. Sala.

[1] Present address: Aquatic System Unit, Environmental Sciences Center, EULA-Chile, Universidad de Concepción, Casilla160-C, Concepción, Chile.

[2] Present address: Instituto de Biología Marina ''Dr. Jürgen Winter'' and Laboratorio Costero Calfuco, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.

[3] Corresponding author. E-mail: snavarre@bio.puc.cl

tional differences among food particles may be responsible for differences in larval growth and survival (e.g., Huntley and Boyd 1984, Olson and Olson 1989) and some larvae may be very specific in their nutritional requirements (e.g., Pilkington and Fretter 1970 for prosobranch and bivalve larvae). Indeed, several studies have shown that both food quality and quantity influences larval characteristics, such as the size of larval and post larval structures (Strathmann et al. 1992, 1993, Thompson et al. 1994, Jonsson et al. 1999), duration of larval development, metamorphosis success (Boidron-Métairon 1995), and performance of postsettlers (Phillips and Gaines 2002). Planktotrophic larvae also have mechanical restrictions related to the maximum and minimum size of prey they can capture (see Hart and Strathmann 1995 and Boidron-Metairon 1995 for reviews). Therefore, the concentration and composition of suspended food particles can strongly modify larval feeding behavior and performance (e.g., Strathmann 1987, Baldwin and Newell 1995). A major impediment to understanding how these factors influence larval ecology under natural conditions is that virtually all information comes from rearing studies in which larvae are offered a laboratory-cultured monospecific or controlled mix phytoplankton diet. Under natural conditions, most larvae will encounter a rapidly changing and complex mix of potential food particles (Baldwin and Newell 1991), including not only autotrophic (i.e., small flagellates, diatoms, and dinoflagellates), but also heterotrophic prey (i.e., nanoflagellates, ciliates, and dinoflagellates). The scarce information regarding feeding preferences and rates under natural conditions (e.g., Rivkin et al. 1986, Baldwin and Newell 1990, 1991, Raby et al. 1997), makes it difficult to evaluate the trophic position of these larvae in pelagic food webs, as well as the role that food availability can have on benthic population and community dynamics. Here, we selected a characteristic predator–prey system of rocky intertidal habitats and asked four simple questions: (1) Do pelagic larvae of intertidal predator and prey species feed on similar food items and at similar rates? (2) Is there evidence of food selectivity when facing a naturally changing food supply? (3) Is the range of food sizes consumed related to mechanical restrictions? And (4) can these larvae be classified into uniform trophic levels? Though simple, these questions have at least three major implications for the general ecology of benthic communities.

First, whether larvae can fulfill their nutritional requirements for development will be determined, in part, by their ability to feed on more than one trophic level and on different particle sizes. Indeed, there is evidence that differences in metabolism between autotrophism and heterotrophism result in different biochemical composition of protists (Klein Breteler et al. 2004). Although recent studies have shown high nutritional benefits from autotrophic cells (diatoms) with high polyunsaturated fatty acids (PUFA; e.g., Brett and Müller-Navarra 1997), conventional stoichiometric theory based on carbon and nitrogen limitation suggests a higher nutritional value of diets based on heterotrophic ciliates than on phytoplankton (Stoecker and Capuzzo 1990).

Second, quantitative information on larval diet is critical for establishing a mechanistic relationship between food supply and settlement success and for determining whether patterns of total surface phytoplankton biomass, now easily measured from satellite images (e.g., Thomas et al. 2001), can be used to infer patterns of larval conditioning and recruitment over large spatial scales.

The third implication relates to the flow of energy in the nearshore pelagic food web and the nature of the links between pelagic and benthic ecosystems. The significance of the bacteria and microprotozoans, as components of the biomass and suitable prey for plankton consumers, has been widely recognized (Painting et al. 1992, Ducklow et al. 2001). Connections between larvae and components of the ''microbial food web'' have been scarcely examined (e.g., Rivkin et al. 1986, Baldwin and Newell 1990, 1991).

Through replicated rearing experiments, we determined that barnacle and *C. concholepas* larvae consume autotrophic as well as heterotrophic prey. However, the relative contribution to the diet, the food size spectrum captured, and the ingestion rates differed markedly among larval predators and their prey and between balanoid and chthamaloid barnacles.

Material and Methods

Intertidal species

Concholepas concholepas is a carnivorous gastropod that plays a key role in the ecology of intertidal and shallow subtidal communities along the Chilean coast (Castilla 1999). In the intertidal zone of central Chile, this species feeds mostly on mussels and barnacles (Navarrete and Castilla 2003). The veliger larvae hatch from clumps of benthic egg capsules at about 240–260 μm protoconch length (DiSalvo 1988). Under laboratory conditions, newly hatched larvae feed on vitelline material and on microalgal cells such as *Isochrysis galbana* or *Tetraselmis suecica*, offered as monocultures (DiSalvo 1988). The competent larval stage (i.e., larvae ready to settle) is reached after about three months at a protoconch size between 1600 and 1900 μm (DiSalvo 1988), which corresponds to the time lapse between maximal abundance of egg capsules and peak abundance of competent larvae in the water (Manríquez and Castilla 2001, Poulin et al. 2002*a*). The barnacles *Jehlius cirratus* and *Balanus flosculus* are abundant in the high and low intertidal zones, respectively (Broitman et al. 2001). They have a pelagic larval stage of between 13 and 40 days, depending on water temperature (Venegas et al. 2000). There is no information about

TABLE 1. Feeding experiments conducted with barnacle nauplii and veliger larvae during austral winter, spring, and summer situations.

Experiment	Date	Species	Stage	Size (μm)†	Density (no./mL)†	*n*‡	Duration (h)	Temperature (°C)
I	17–18 Jul.	*Jhelius cirratus*	nauplii V	480 ± 10	0.02 ± 0.002	3	10	17
II	10–12 Aug.	*Jhelius cirratus*	nauplii V	420 ± 25	0.02 ± 0.002	3	10	16.5
III	17–18 Oct.	*Concholepas concholepas*	newly hatched	248 ± 5	0.08 ± 0	3	5	13.7
IV	17–18 Oct.	*Concholepas concholepas*	newly hatched	245 ± 5	0.08 ± 0	3	5	12.8
V	10–12 Dec.	*Concholepas concholepas*	competent	1697 ± 26	0.004 ± 0	3	12	16
VI	10–12 Dec.	*Concholepas concholepas*	competent	1702 ± 12	0.004 ± 0	3	12	16
VII	12–14 Dec.	*Balanus flosculus*	nauplii V	880 ± 25	0.011 ± 0.002	3	12	16.5
VIII	12–14 Dec.	*Balanus flosculus*	nauplii V	820 ± 15	0.013 ± 0.002	3	12	16.5

† Mean ± SD.
‡ Number of replicate grazing bottles.

feeding preferences or particle sizes consumed by these barnacle or gastropod larvae.

Collection of nauplii and veliger larvae

Jehlius cirratus *and* Balanus flosculus *larvae*.—Experiments with barnacle nauplii were conducted on three separate occasions during 2003, determined mostly by their availability in the plankton and weather conditions: (a) 17–18 July (Exp I), (b) 10–12 August (Exp II), and (c) 12–14 December (Exp VII and VIII; Table 1). All nauplii used in the experiments were collected at a coastal station within the Management and Exploitation Area (MEA) of Caleta El Quisco, central Chile (33°23′ S, 71°42′ W). Slow vertical hauls with a WP-2 net (mesh size 200 μm; Hydro-Bios, Kiel-Holtenau, Germany) and a large cod end (~40–60 L) was used to obtain larvae from the upper 25 m of the water column. After collection, samples were immediately transferred to a thermobox and taken to the laboratory of the Estación Costera de Investigaciones Marinas (ECIM) at Las Cruces. Within 1 h of collection, undamaged nauplii were sorted under the stereomicroscope.

Concholepas concholepas *larvae*.—Experiments with newly hatched and competent *C. concholepas* larvae were conducted on two separate occasions during 2003: (a) 17–18 October (Exp III and IV) and (b) 10–12 December (Exp V and VI; Table 1). Newly hatched veligers were obtained from egg capsules laid by female individuals reared in the laboratory. Clumps of mature egg capsules were removed from the rearing aquarium and maintained in a glass bottle filled with 1 L of 0.45-μm filtered seawater (FSW). To allow larvae to consume the vitelline material retained in the larval gut (DiSalvo 1998), after hatching and before beginning the experiments, larvae were maintained for 24 h in a 500 mL glass beaker filled with FSW. Competent larvae were collected from the plankton using an epineustonic net at MEA-El Quisco during the peak of larval abundances (August to December [Poulin et al. 2002*a*]) and transported to the laboratory.

Feeding experiments

Seawater used in the experiments was collected from the first 10 m of the water column with clean, 5-L, Teflon-coated, Niskin bottles GO-FLO (General Oceanic, Miami, Florida, USA). Seawater was then screened through a 200-μm net to remove the majority of grazers and large debris. Larvae selected for the experiments were pipetted into 250-mL (barnacle nauplii and small veliger larvae) or 500-mL (competent veliger) acid-washed polycarbonate bottles filled with the screened seawater. Care was taken to avoid air bubbles in the bottles. Three control bottles without larvae and three bottles with three to 20 larvae each, depending on larval stage and species (Table 1), were incubated for 5 to 12 h, and periodically rotated by hand. Bottles were immersed in a container with flow-through seawater at ambient temperature, which kept temperature fluctuation during a given experiment within one degree. Ambient temperature ranged between 13° and 17°C (Table 1). The resultant concentration of nauplii in experimental bottles ranged between 0.012 and 0.02 individuals/mL for different experiments (Table 1), whereas veliger concentrations were 0.08 and 0.004 individuals/mL for newly hatched and competent larvae, respectively. Since there is some evidence of diel patterns of activity in *C. concholepas* larvae (Poulin et al. 2002*b*), we evaluated the effect of hour of the day on feeding behavior of the newly hatched veligers. To this end, we conducted 5-h incubations during day (Exp III) and night (Exp IV) hours. In all experiments, 60 mL subsamples from the control bottles were immediately preserved with 2% acid Lugol's solution for cell counts. At the end of the incubation, 60-mL subsamples from all bottles were taken and preserved in acid Lugol's solution to determine cell concentration. Subsamples of 100 mL were also taken from each bottle to quantify size-fractioned chl *a* using dark extraction of the fractions in 95% acetone (Strickland and Parsons 1972). Measurements were conducted in a TD 700 Turner fluorometer (Sunnyvale, California, USA). To recover the larvae used in the experiments, the re-

maining volume was gently poured through a 20-μm sieve.

Cell counts and calculation of clearance and ingestion rates

Large cells (> ~10 μm) were counted from subsamples of 50 mL that were allowed to settle for 24 h in sedimentation chambers (Utermöhl 1958) and then examined under an inverted microscope Leica LEITZ DMIL (Leica Microsystems, Wetzlar, Germany). All diatoms, dinoflagellates, silicoflagellates, and ciliated microprotozoans were identified, counted, and measured. Plasma volumes (Edler 1979) were calculated and averaged from a minimum of 50 cells/species. Biovolumes of ciliates were calculated assuming conical shapes with a length to diameter ratios of 1.25 and 2 for ciliates <50 μm and >50 μm, respectively (Tiselius 1989). Carbon to plasma volume ratios of 0.11 pg C/μm^3 for diatoms (Edler 1979), 0.3 for heavily thecate and 0.19 pgC/μm^3 for athecate dinoflagellates, (E. J. Lessard, *unpublished data*; Gifford and Caron 2000), and 0.148 pgC/μm^3 for ciliates (Ohman and Snyder 1991) were used in calculations.

Clearance and ingestion rates, measured as chl *a* depletion, were calculated according to Frost (1972), modified by Marín et al. (1986), from size-fractioned chl *a* concentrations. During experiments I and II (*J. cirratus*), we fractioned the chl *a* in three size classes: <5 μm (picophytoplankton [P] and small nanophytoplankton [SN]); 5–20 μm (nanophytoplankton [N]); and >20 μm (microphytoplankton [M]). In all later experiments (Exp III–VI), chl *a* was fractioned in four size classes: <5 μm (P), 5–10 μm (SN), 10–23 μm (N); and >23 μm (M). To estimate carbon ingestion, ingested chl *a* was multiplied by the mean carbon concentration of cells obtained from 10–20 m Niskin bottle samples, using the biovolume to carbon ratios indicated above. Since we estimated cell carbon based on counts under a microscope only for sizes >10 μm, we had to assume similar C:chl *a* ratio for smaller fractions (<5 and 5–10 μm).

Clearance and ingestion rates, based on direct counts of large cells, were estimated for the following groups: autotrophic and heterotrophic dinoflagellates (ADINO and HDINO, respectively), silicoflagellates, ciliates, pennate and centric diatoms, and chain forming diatoms. Because recent studies have shown that most dinoflagellates are mixotrophs (Bockstahler and Coats 1993, Li et al. 1996), we classified as autotrophic only those species predominantly photosynthetic (e.g., *Ceratium tripos*; Hansen and Nielsen 1997). Due to their small size, the clearance rates on autotrophic and heterotrophic nanoflagellates could not be determined by direct counts. It was therefore assumed that they were cleared at the same rates as chl *a* fraction between 2 and 20 μm. As a general criterion, clearance was only calculated when the difference in prey concentration between control and experimental bottles was significantly different (*t* tests, $P < 0.05$).

A potentially important bias when estimating ingestion rates from incubation experiments with ''natural'' communities is the propagation of effects through the trophic web present in the bottles. For instance, if the trophic web includes a top omnivorous grazer that feeds on both phytoplankton and dinoflagellates, and given that dinoflagellates also consume phytoplankton, comparing bottles with and without the omnivorous grazer could lead to an underestimation of the actual grazing on phytoplankton (''trophic effect''; Roman and Rublee 1980). Solutions to this problem are not simple, as they generally require estimates of ingestion and interactions among all trophic levels (Tang et al. 2001). In our experiments, the only grazers that could alter our estimates were ciliates and dinoflagellates. However, both of these groups, especially dinoflagellates, were scarce and their ingestion rates generally are an order of magnitude lower (Vargas and González 2004*b*) than the rates we measured for competent larvae (see *Results*). Moreover, the short incubation times (<12 h) did not allow significant population growth of these grazers (Strom and Morello 1998). We therefore considered that the ''trophic effect'' did not significantly alter our estimates and discuss the potential bias introduced by this decision.

To characterize the food supply, field cell concentration and biomass for autotrophic picoplankton (measured as chlorophyll <5 μm), as well as auto- and heterotrophic dinoflagellates, silicoflagellates, ciliates, and diatoms were estimated through water samples collected at the surface and at 10 m depth with a clean bucket and 5-L, Teflon-coated, Niskin bottles GO-FLO, respectively. Cells retained by nauplii and veliger larvae were expressed as equivalent spherical diameter (ESD) to represent particle size of different taxa, and compared with anatomical measurements reported in the literature as relevant structures used in the feeding process by these larvae (e.g., Gallager 1988, Stone 1989). Therefore, we measured the space between setules on setae of the first and second antennae and mandibles in barnacle nauplii and mouth size in veliger larvae.

RESULTS

Composition of the food assemblage

Phytoplankton and protozoan assemblages varied in abundance and composition among the experiments according to natural variation in the field (Fig. 1). As it is typical in nearshore waters (e.g., Wieters et al. 2003), large changes in total chl *a* (~0.8 and 3 mg chl *a*/m^3) were recorded during the study (Fig. 1a). In winter (Exp I and II, Table 1), chl *a* levels were low (<1 mg chl *a*/m^3), with an important contribution of pico- and small nanophytoplankton (~45% of chl *a* < 5 μm) to the total phytoplankton standing stock. In spring (Exp III

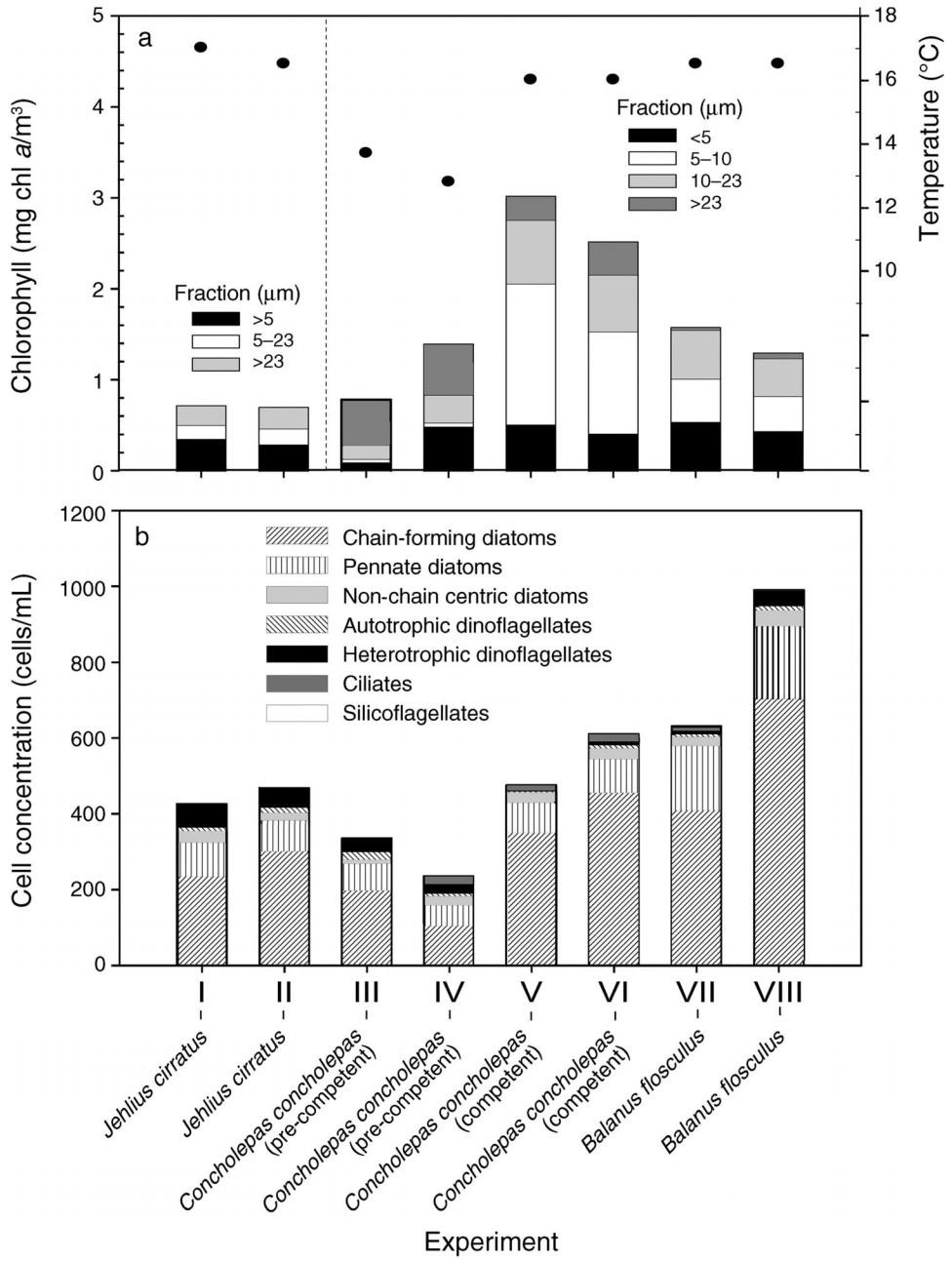

FIG. 1. (a) Contribution of different fractions to total chlorophyll *a* during the feeding experiments. Size fractions are: <5 μm, picophytoplankton and small nanophytoplankton; 5–20 μm, nanophytoplankton; >23 μm, microphytoplankton. During Experiments II–VIII, the nanophytoplankton size fraction was divided into two subfractions: 5–10 μm and 10–23 μm. Temperature during experiments is also indicated. (b) Contribution of major taxonomic groups to cell concentration of autotrophic and heterotrophic prey >10 μm in the incubation water used in feeding experiments.

and IV, Table 1), chl *a* concentration was slightly higher, with increased contribution of the microphytoplankton size fraction (~30%, measured as chl $a > 23$ μm). Toward the end of spring (Exp V–VIII, Table 1), chl *a* concentration was higher (1.2–3.1 mg chl a/m^3) and corresponded mostly to cells larger than 5 μm (>80% of chl *a* between 5 and 23 μm). Throughout the experiments, small pennate diatoms (8–23 μm), such as *Cylindroteca* sp. and *Navicula* sp., also contributed to the nanophytoplankton pool (Fig. 1b). Although there were important differences in cell concentrations of microphytoplankton and protozoans among the experiments, in general the composition was dominated (200–700 cells/L) by chain-forming diatoms, mostly *Schröderella delicatula*, *Stephanopyxis turris*, and *Skeletonema* sp. (Fig. 1b). In all experiments, ADINO,

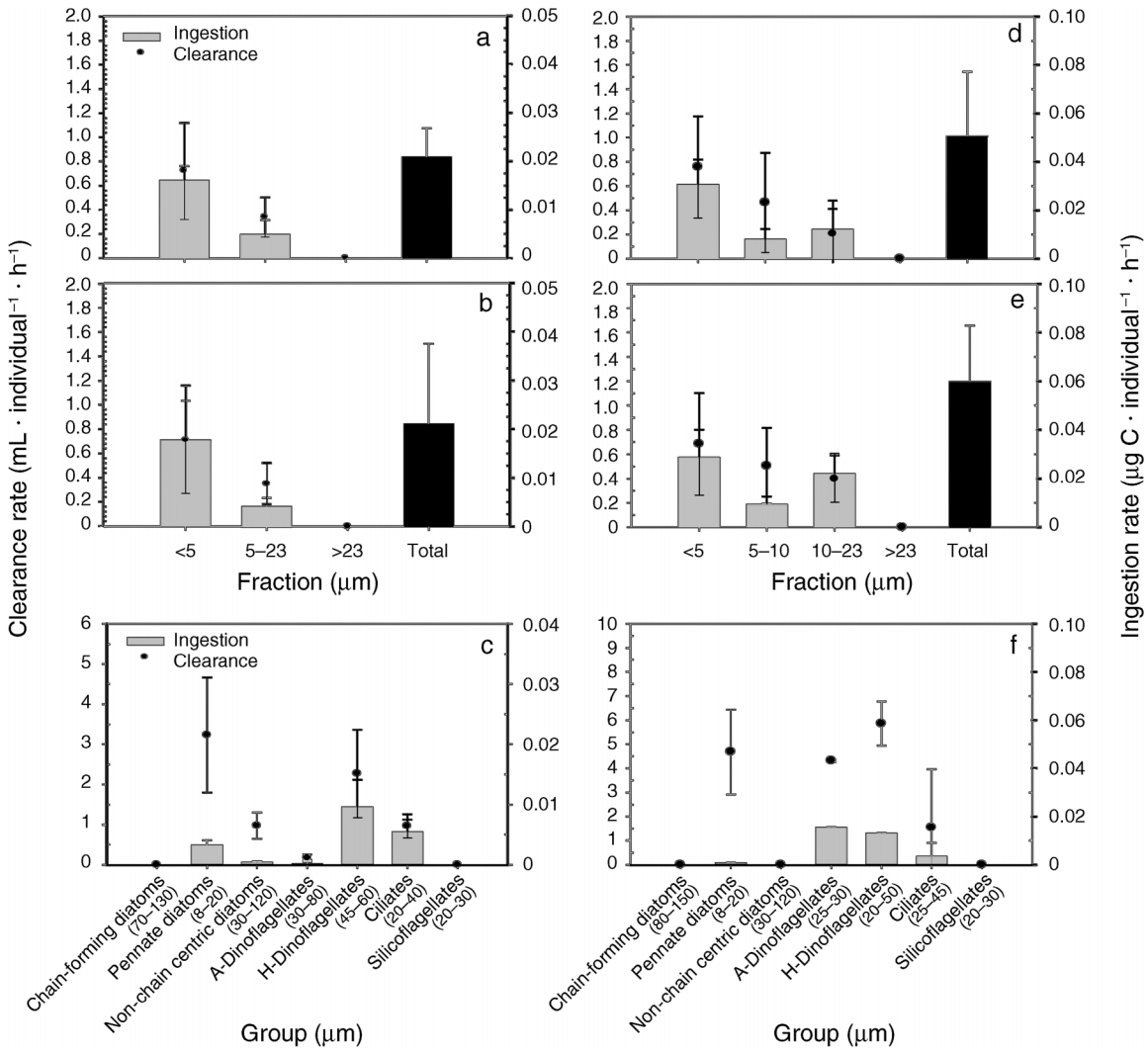

FIG. 2. (a, b, d, e) Clearance and ingestion rates of size-fractioned chlorophyll *a* by nauplii of *Jhelius cirratus* during (a) Experiment I and (b) Experiment II, and by *Balanus flosculus* during (d) Experiment VII, and (e) Experiment VIII. (c, f) Mean clearance and ingestion rates on autotroph and heterotroph prey counted under an inverted microscope for (c) *J. cirratus* and (f) *B. flosculus*. The size range of each group is indicated. The bars labeled ''Total'' represent ingestion on total chl *a*. Error bars show SD from replicate bottles ($n = 3$).

HDINO, and ciliates were scarce (<50 cells/mL). Ciliates were mostly represented by small organisms, such as *Strombidium* sp., and occasionally by large tintinid species (*Helicostomella* spp. and *Euntintinnus* spp.). Most dinoflagellates were heterotrophs, principally represented by small species of *Protoperidinium* and *Gyrodinium*.

Nauplii and veliger clearance and ingestion rates

Results of size-fractioned chl *a* depletion showed that in both experiments with *J. cirratus* and *B. flosculus* nauplii (Exp I–II and VII–VIII), they were mainly clearing and ingesting picophytoplankton and small nanophytoplankton (Fig. 2a, b, d, e), which represented more than 40% and 90% of the total chl *a* in ambient seawater respectively (Fig. 1a). Nevertheless, nauplii could have been feeding on nonpigmented heterotrophic pico- and nanoplankton cells, which are not detected by chl *a* depletion measurements. Larvae of these species did not select the chl *a* fraction >23 μm. Total carbon ingestion rate of autotrophs by *B. flosculus*, estimated from chl *a* depletion, was about three times higher than the ingestion rate of the smaller *J. cirratus* larvae (~0.06 vs. ~0.02 μg C·individual^{-1}·h^{-1}, respectively; Figs. 3a, b and 3d, e), a result that was consistent across experiments (two-way ANOVA, factor ''species,'' $F_{1,8} = 12.0$, df = 1, 8, $P = 0.0085$; with no significant ''species × exp'' interaction, $F_{1,8} = 0.59$, $P = 0.4635$). Direct cell counts under a microscope showed an important contribution of large cells to total carbon ingestion by *J. cirratus*, but of heterotrophic organisms, such as dinoflagellates (45–60 μm) and cil-

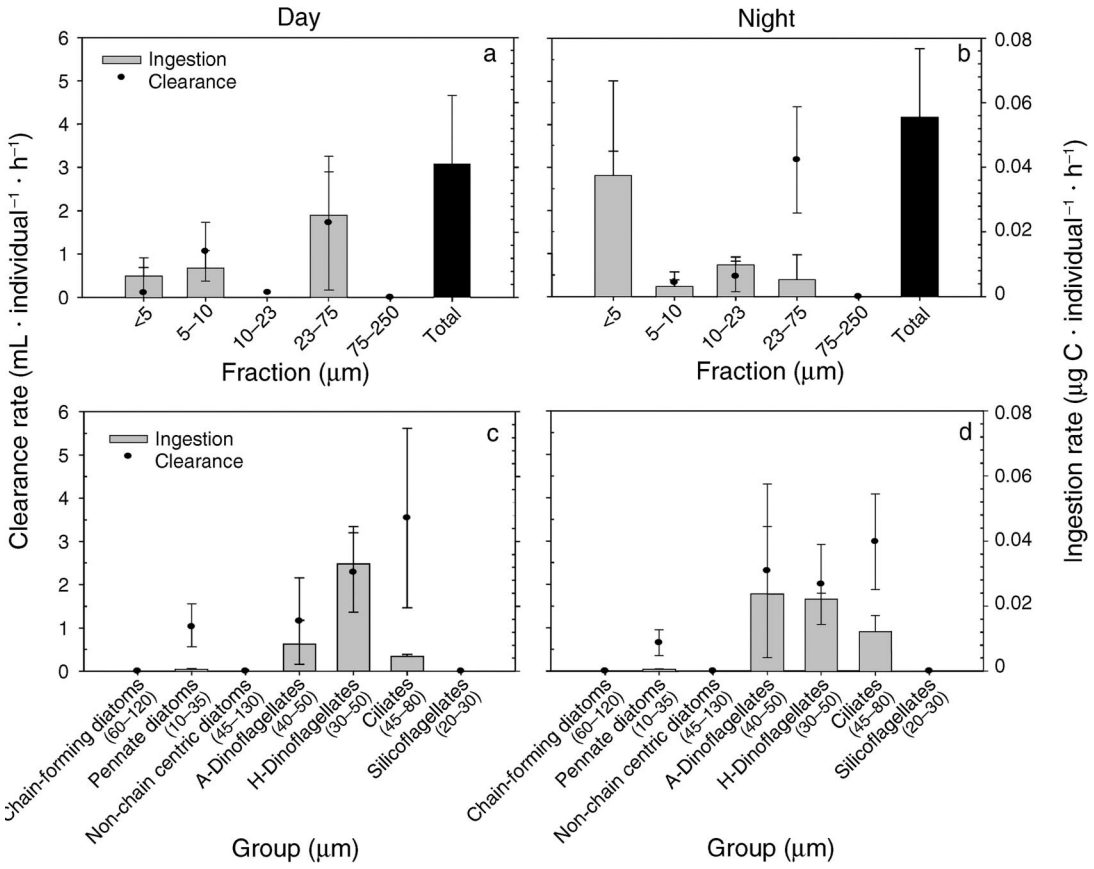

FIG. 3. (a, b) Clearance and ingestion rates of size-fractioned chlorophyll by newly hatched larvae of *Concholepas concholepas* during (a) Experiment III (day) and (b) Experiment IV (night). (c, d) Mean clearance and ingestion rates of autotroph and heterotroph prey counted under an inverted microscope during (c) day and (d) night experiments. The size range of each group is indicated. The bars labeled ''Total'' represent ingestion on total chl *a*. Error bars show SD from replicate bottles ($n = 3$).

iates (20–40 µm), which are not detected in chlorophyll depletion analyses (Fig. 2c). In fact, HDINO were cleared faster than ADINO of relatively similar size. Predation on heterotrophic prey by *B. flosculus* was also revealed from the high clearance of HDINO (i.e., *Protoperidinium* spp. of ~50 µm), and ciliates (Fig. 2f). It is interesting to note that the clearance rate by *B. flosculus* on large ADINO was over an order of magnitude higher than that exhibited by *J. cirratus* (Fig. 2c, f). Since the availability of this food item was slightly different between experiments, we made no statistical comparisons between species for specific food items. Clearance and carbon ingestion estimated from direct cell counts showed that the 10–23 µm chl *a* fraction corresponded mostly to small *Cilindroteca* spp., pennate diatoms, and some small autotrophic dinoflagellates (*Prorocentrum* ~23 µm). Heterotrophic picoplankton and nanoflagellates could have been ingested, but because of their small size they were not detected under the inverted microscope (Fig. 2).

Total carbon ingestion by newly hatched *C. concholepas* larvae was not significantly different between daytime (Exp IV) and nighttime hours (Exp III) (mean ± SD = 0.042 ± 0.02 and 0.06 ± 0.02 µg C · individual^{-1}·h^{-1}, respectively; Fig. 3a, b; one-way ANOVA, $F_{1,4} = 1.52$, $P = 0.2854$). The fraction of phytoplankton removed by larvae was different between day and night experiments, but ambient seawater composition also changed slightly between experiments (Fig. 1a). During the day, *C. concholepas* larvae fed mainly on the 23–75 µm microphytoplankton fraction and secondarily on picophytoplankton and small nanoflagellates. These fractions represented 34% and 11% of the total chl *a*, respectively. At night, larvae fed mostly on picophytoplankton, which represented about 35% of the total chl *a*. Direct cell counts showed that the removed microphytoplankton fraction corresponded mostly to ADINO. In both experiments, newly hatched larvae actively preyed on large heterotrophic cells like ciliates and HDINO (Fig. 3c, d).

Competent larvae of *C. concholepas* fed on different chl *a* fractions than newly hatched larvae. Despite the dominance (>60%) of chl *a* <10 µm in ambient seawater (Fig. 1a), competent larvae exhibited high clear-

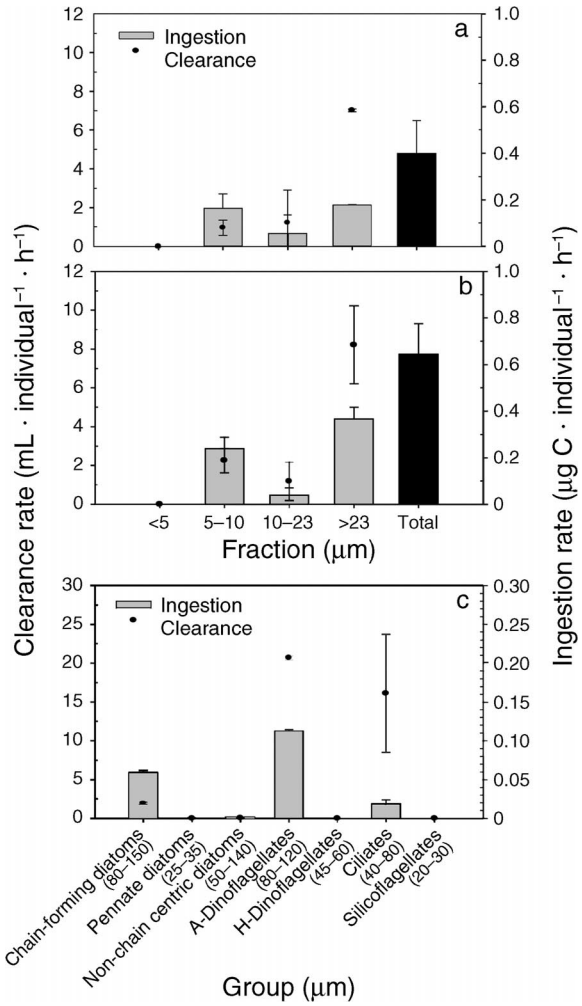

FIG. 4. Clearance and ingestion rates of size-fractioned chlorophyll by competent veliger of *Concholepas concholepas* during (a) Experiment V and (b) Experiment VI. (c) Mean clearance and ingestion rates of autotroph and heterotroph prey counted under an inverted microscope. The size range of each group is indicated. The bars labeled ''Total'' represent ingestion on total chl *a*. Error bars show SD from replicate bottles ($n = 3$).

ance of microphytoplankton >23 μm, and did not feed on picophytoplankton (Fig. 4a, b). Nevertheless, they were able to remove nanoflagellates between 5 and 10 μm. Mean ingestion rate was maximum (~0.11μg C·individual^{-1}·h^{-1}) on ADINO consisting mostly of large thecate cells between 80 and 120 μm in size, despite their naturally low abundance (7–12 individuals/mL; Fig. 1b). Low clearance (due to high cell concentration in the field), but high carbon ingestion, was observed on large (80–150 μm) chain-forming diatoms.

Retention efficiency and food size restrictions

Cell size had a major effect on clearance rates of barnacle and gastropod larvae. To obtain retention efficiency estimates for cells < 10 μm, we used size-fractioned chl *a* values, considering the average cell size for these fractions (i.e., 2.5 and 7.5 μm for <5 and 5–10 μm chl *a* fractions). Retention efficiency (%) as a function of the equivalent spherical diameter (ESD) showed that maximum retention efficiency by nauplii of *J. cirratus* and *B. flosculus* occurred on small cells <40 μm (Fig. 5). These results agree well with anatomical features of the main feeding structures used by nauplii when handling food particles (Stone 1989). Measurements of spacing between the first and the second setae of the antennae indicated that the individuals could catch particles <20 μm (Fig. 6c–e).

Newly hatched larvae of *C. concholepas* grazed on small cells <40 μm ESD and not on the largest dinoflagellates (~130 μm ESD). Moreover, retention was generally higher on ciliates compared to similarly sized dinoflagellates and centric diatoms. In contrast, competent larvae were able to feed on a wider range of prey sizes, from ~10 to 120 μm ESD. Maximum retention efficiency was observed on large prey (>60 μm) and they did not feed on picophytoplankton and nanoflagellates <5 μm, suggesting that the 10-μm ESD size is close to the lower limit for particle capture of this large veliger larva (Fig. 6d). Since dinoflagellates and ciliates were very scarce in all experiments (Fig. 1b), the observed high clearances suggest a high selectivity for these groups. Differences in retention efficiency between newly hatched and competent veligers corresponded well with mean mouth sizes of about 40 μm and 130 μm, respectively (Fig. 6).

DISCUSSION

Availability of food particles and feeding performance of larval stages

We observed large differences between barnacle and competent *C. concholepas* larvae in terms of ingestion rates as well as their ability to consume small and large food particles. Nauplii and veligers exhibited high consumption of heterotrophs. Food availability in our experiments differed in concentration and specific composition, which makes it difficult to compare feeding selectivity across the different experiments. Nevertheless, the experiments represented the natural spectrum of particle sizes and variable composition to which larvae are exposed in the water column, and our results are a good indication of actual larval feeding selection for a given condition.

We observed high selective clearance of dinoflagellates and ciliates by nauplii and veliger larvae in all experiments, despite the low concentration of these preys. Larvae may have been actively seeking, attacking, and ingesting these preys because of their large size and mobility. But the possibility of simple mechanical selection determined by morphological characteristics of the filtering structures cannot be ruled out at this point. More direct observations of larval feeding

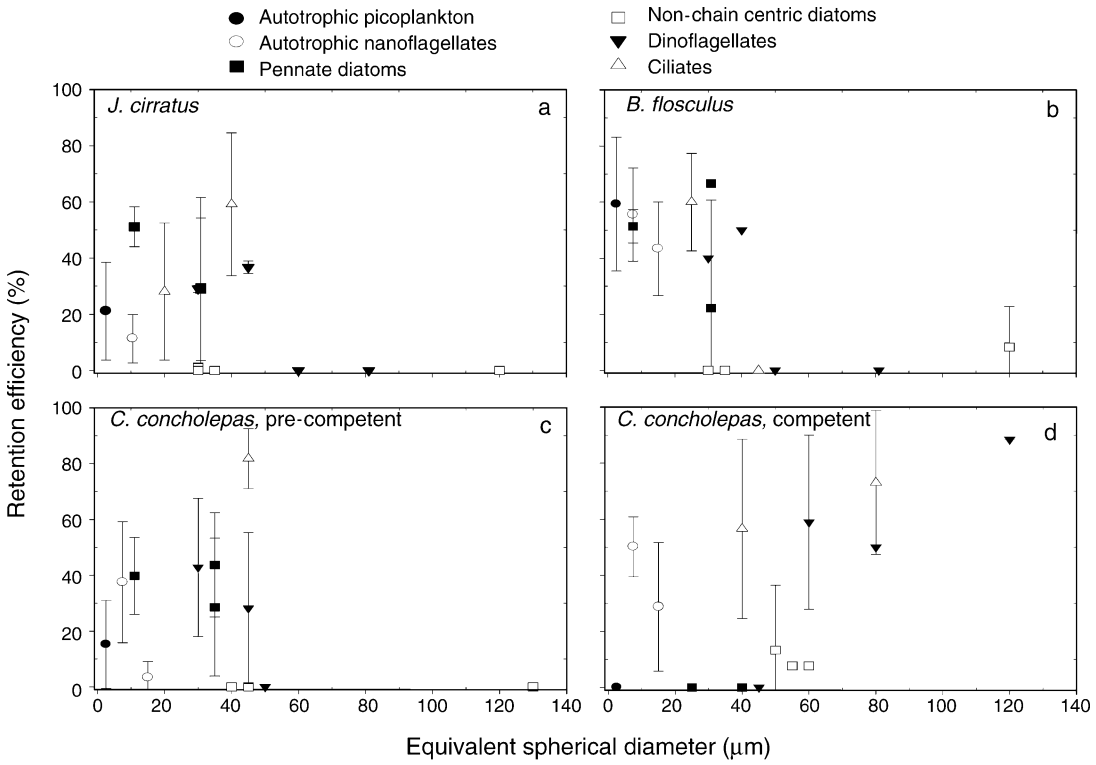

FIG. 5. Particle retention efficiency for (a) nauplii of *J. cirratus*, (b) nauplii of *B. flosculus*, (c) newly hatched veliger of *C. concholepas*, and (d) competent veliger of *C. concholepas* on different taxon-specific cell sizes (ESD). Error bars indicate ±SD.

behavior are needed to determine the importance of active selection (Gallager 1988). In any case, an omnivorous diet should reduce the risk of starvation (Baldwin and Newell 1991) and might explain why larvae maintain positive growth in environments where the concentration of phytoplankton is thought to be growth limiting (e.g., Crisp et al. 1985). Studies on oyster veliger larvae have also highlighted the importance of omnivorous feeding in nutritionally enhancing the diet, especially in the absence of phytoplankton (Crisp et al. 1985, Baldwin and Newell 1990, 1991, 1995). Unfortunately, there is little information about natural diet of other invertebrate larvae to draw conclusions regarding the generality of omnivorous feeding.

Considering the great attention that barnacles have received in studies of settlement and recruitment on most shores of the world, the scarce information available on the natural larval diet is particularly surprising. In one of the few studies on this group, Turner et al. (2001) found that nauplii of *Balanus* cf. *crenatus* fed primarily on phytoplankton, with low clearance rates around 0.8–1.7 mL·individual^{-1}·h^{-1} for ciliates and 0.3–0.8 mL·individual^{-1}·h^{-1} for dinoflagellates. We estimated higher clearance rates on dinoflagellates and ciliates, ranging from 1 to 6 mL·individual^{-1}·h^{-1}. Differences between the studies do not seem to be due to differences in ambient concentration of prey between Turner et al.'s (2001) study and our study (2–11 cells/mL and 3–35 cells/mL, respectively). Thus, these results might reflect interspecific differences in selectivity for heterotrophic prey.

Clearance estimates for *C. concholepas* larvae are higher than published values for any other mollusk species, both on autotrophic and heterotrophic prey. For instance, Baldwin and Newell (1991) found that veligers of the eastern oyster *Crassostrea virginica* cleared autotrophic C^{14}-labeled cells between 0.2 and 30 μm at 0.082 mL·individual^{-1}·h^{-1}, and heterotrophic H^3-labeled prey (bacteria and phagotrophic protozoans) at ~0.002 mL·individual^{-1}·h^{-1} (see also Baldwin and Newell 1995). Newly hatched *C. concholepas* veligers cleared dinoflagellates and ciliates at rates around 2–3 and 1–2 mL·individual^{-1}·h^{-1}, respectively—over an order of magnitude higher than *C. virginica*. Differences in clearance rates may be due to several factors, including field food concentration, incubation temperature and, more importantly, differences in larval body size. Indeed, all feeding structures, such as length of the prototrochal ciliary band, prototrochal cilia, and the angular velocity of the cilia scale with larval body size (Strathman and Liese 1979).

We observed larvae swimming more actively at night and resting at intervals of time on the bottom of the incubation bottles during day hours. Moreover, in a field study, Poulin et al. (2002*b*) observed diel differ-

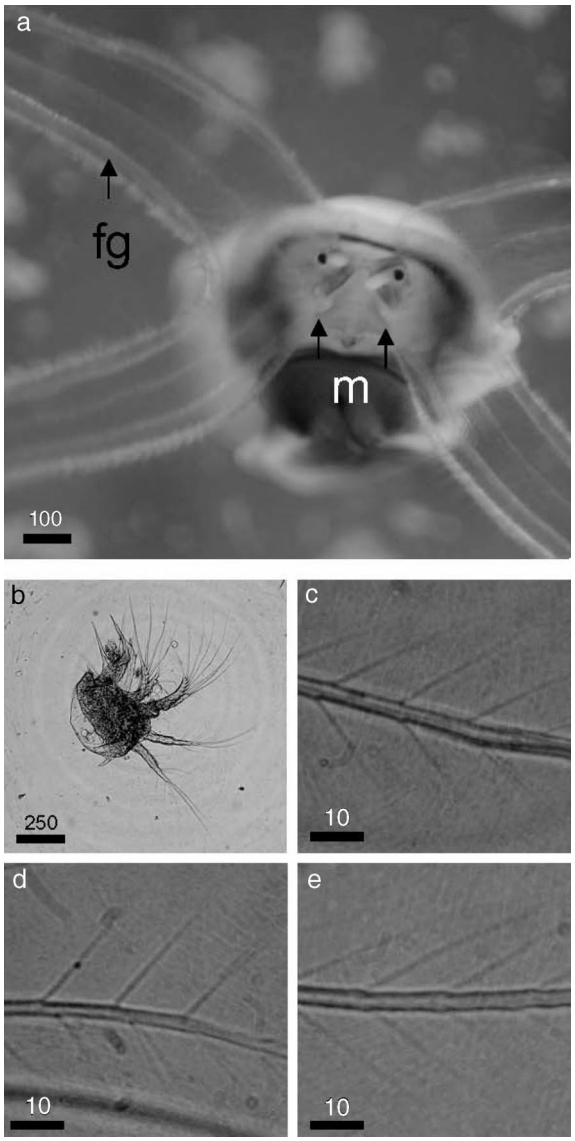

FIG. 6. Photographs of veliger larvae and barnacle nauplii, showing the structures involved in larval feeding: (a) detail of the mouth of *C. concholepas* competent veliger (fg, food groove; m, mouth), (b) chthamaloid barnacle nauplii, (c–e) setae in antenulles of *Jhelius cirratus*. Scale bars are in μm.

ences in competent larval abundance. Therefore, it was somewhat surprising that clearance of newly hatched larvae did not differ between day and night time. This suggests that larvae are able to feed when swimming or ''resting'' and probably use different feeding mechanisms. Direct observations of newly hatched larvae revealed that they are capable of removing particles from the surrounding seawater, even when the velum is retracted inside the larval shell (P. Manríquez, *unpublished data*). Differences in feeding modes between swimming and ''resting,'' or between day and night, could explain the observed differences in clearance of different chl *a* fractions. Further experiments are needed to examine diel differences in more detail.

One potential bias in our study is the existence of what has been termed ''food-chain effects,'' which occurs during incubations (Vargas and González 2004*a*). That is, as incubation progresses, diatom growth in experimental bottles with barnacle nauplii and veliger larvae could be higher than in control bottles because larvae feed on HDINO, which in turn feeds on diatoms. This cascading effect could have led to underestimates of grazing rates on diatoms. Such effects are difficult to quantify without detailed knowledge of dinoflagellate grazing rates and food selectivity. The short incubation time in our experiments, ranging from 5 to 12 h, should have reduced any food chain effects, especially by the much smaller and comparatively scarce HDINO. Therefore, we consider that this effect did not significantly alter our estimates of ingestion.

Biomechanical considerations suggest that barnacle nauplii could efficiently feed on small cells, such as pico-phytoplankton and small nanoflagellates (Stone 1989, Turner et al. 2001). Their ability to feed on small prey hinges on the small spaces between setules, which in our study ranged from 10 to 18 μm for *J. cirratus* and *B. flosculus*. Fringes of closely spaced setae along the preaxial edge of the antennal expodite may also assist in collecting even smaller food particles, around 3–5 μm (Stone 1989). In agreement with these morphological measurements, we found that nauplii based their diet mostly on small pico- and nanoplankton (Fig. 2). However, in other suspension feeders, such as copepods, the small setose appendages are not only used as passive filters, but they can use them to actively select their preys (e.g., Paffenhöfer and Lewis 1990). It is unknown whether this behavioral mechanism occurs in barnacle nauplii. Morphological differences between the antennal setules are probably correlated with behavioral differences associated with the mechanics of limb motion that is required to actively respond to and trap individual prey particles, which could explain some of the variation in feeding selectivity observed between barnacle species.

Prey size restrictions in veliger larvae have also been the subject of several studies (e.g., Crisp et al. 1985, Strathmann 1987, Gallager 1988). Before ingestion, particles come within reach of the prototroch, are transported into the food groove between the prototroch and metatroch, and moved to the mouth via the food groove, presumably by cilia (Hart and Strathmann 1995). Our results showed that the size of preferred prey items depended on the age and/or size of *C. concholepas*. Ontogenetic differences in food-size restrictions have been noted in other mollusk species (e.g., Riisgård et al. 1980, Hansen 1991). For instance, studies by Riisgård et al. (1980) with 5–13-d-old larvae of the mussel *Mytilus edulis* showed that they cannot consume particles smaller than 1 μm or larger than 9 μm (see also Sprung 1984), while before settlement, when larvae

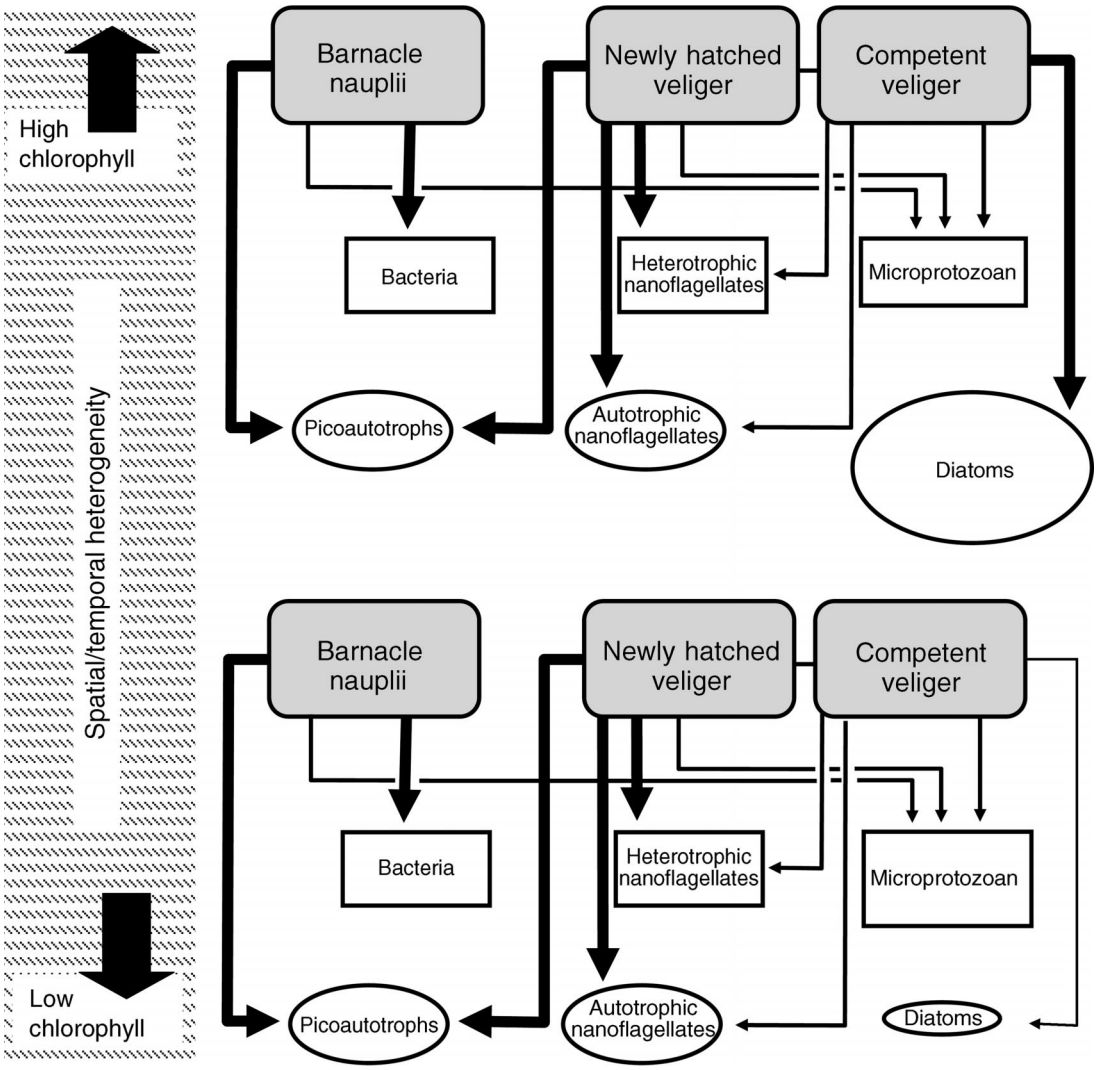

FIG. 7. Conceptual scheme of main pathways of interaction in coastal food webs involving barnacle and gastropod larvae of the species considered in this study (*Jehlius*, *Balanus*, and *Concholepas*), under varying spatial/temporal chlorophyll levels. We included ontogenetic changes in veliger larvae. The thickness of the arrows represents main predator–prey interactions. The sizes of the boxes or circles represent the dominance in terms of biomass of a specific food item under each condition. Trophic interactions between larvae and bacteria and/or heterotrophic nanoflagellates are assumed to be similar to those on picoautotrophs and autotrophic nanoflagellates, respectively.

reach up to 400 μm, larger cells become part of their diet. The largest cells (~120 μm) caught by competent larvae of *C. concholepas* seem too large to be transported by the larval food groove (~30 μm width). It is possible that mouth size directly determines the maximum size of food particles that can be ingested (see also Gallager 1988). It is also possible, however, that the food grove width changes behaviorally with food particle size (R. Strathmann, *personal communication*).

Ecological implications for benthic communities

It has largely been assumed that phytoplankton is the most important food item for planktotrophic invertebrate larvae. While ciliates and other protozoan microplankton are generally major contributors to heterotrophic microplankton biomass in natural assemblages (see Stoecker and Capuzzo 1990 for review), they have generally not been included in controlled laboratory studies of larval feeding. Our estimates of protozoan concentration are consistent with published values (e.g., Vargas and González 2004*a*, *b*), and suggest that dinoflagellates and, to a lesser extent, ciliates could represent a significant source of food for larvae in coastal waters. Recent studies have shown the importance of microprotozoan prey in the diet of many planktonic organisms such as copepods (Tiselius 1989), appendicularians (Vargas and González 2004*b*), and salps (Vargas and Madin 2004), highlighting that omnivorous feeding in mero- and holoplanktonic organisms is the norm. While laboratory experiments

have shown that variation in the concentration of algal monocultures produce a wide variety of responses in larval feeding, growth, and development (e.g., Strathmann et al. 1992), it is unclear in which way these results can be used to draw conclusions about larval ecology in the complex webs found in nature.

High levels of omnivory in larval stages of benthic invertebrates suggest that estimates of standing stock of phytoplankton (e.g., measured as total chl *a* biomass) may not always be a good measure of food supply. The abundance of small heterotrophic nanoflagellates, mixotrophic nanoflagellates, and ciliates are not necessarily well correlated with total chl *a*. In fact, published information suggests that small heterotrophs, a component of the microbial food web, are more abundant at times of the year when chlorophyll concentration is low (e.g., González et al. 1989). In consequence, correlations between total phytoplankton biomass and invertebrate recruitment (e.g., Menge et al. 1999, Navarrete et al. 2002) might be more complex and less general than we originally envisioned.

Identifying trophic relationships is the first step in understanding the role species may play in natural food webs. However, predicting the dynamics of the component populations and communities requires an understanding not only of the structure of species interactions, but also their relative strengths (Berlow et al. 1999, Bascompte et al. 2005). Our results identify the major links of the pelagic food web in which these invertebrate larvae are immersed. We use estimates of feeding rates as a coarse proxy for relative strengths between prey and predatory larvae. This information is used in a preliminary model that illustrates the consequences that persistent temporal or spatial variation in food supply can have on larval performance, which in turn will influence patterns of recruitment to the benthic habitat. Despite high variability in plankton composition, there are well-documented, persistent temporal and spatial differences in plankton structure and abundance. For instance, large and geographically persistent heterogeneity in chl *a* level has been documented along the Chilean coast (Thomas et al. 2001), with lower chl *a* levels to the north of latitude 32° S. Similarly, a large percentage of the chl *a* is in the large phytoplankton fraction in permanent upwelling areas off northern Chile (Iriarte and González 2004) as well as during spring at seasonal upwelling sites (González et al. 1989). This large chl *a* fraction is not easily consumed by barnacle larvae or newly hatched veligers, but is readily consumed by competent veligers. Field observations suggest that the small pico- and nanoplankton fractions do not exhibit large seasonal fluctuations. Thus, under conditions of high chl *a* level when large diatom chains dominate the phytoplankton, feeding performance of competent *C. concholepas* larvae should be enhanced (Fig. 7a). Since barnacle nauplii and newly hatched veligers base their diets mostly on autotrophic and heterotrophic small picoplankton and pico- and nanoplankton, they should not be directly affected (Fig. 7a). However, barnacle nauplii could be negatively affected in areas of high chl *a* if blooms of large algae interfere with their feeding. In contrast, under low chl *a* condition, both barnacle nauplii and newly hatched veligers should be able to feed efficiently on small prey (piconanoplankton), but large competent veligers will perceive a reduced offer of large diatoms. Unless competent larvae are able to efficiently switch to feed on smaller prey, this scenario will result in food limitation for this larval type. Larval starvation is not the only way in which food availability can result in a different supply of larvae to adult populations. Changes in larval growth rates, larval size, and conditioning produced by changes in food can all drastically alter the rates of return to the adult habitat and the probability of successful metamorphosis (Boidron-Métairon 1995, Phillips and Gaines 2002). Thus, spatial and temporal variations in plankton composition and abundance, in combination with physical transport processes (Shanks 1995) could result in large-scale differences not only in recruitment rates of a given species, but on differences in relative recruitment success of the different species that make up benthic communities.

Although this is a preliminary evaluation of the relative importance of trophic links for these invertebrate species, it allows us to make general predictions about the effects of pelagic food web structure on benthic communities, and highlights the potential for far-reaching, coupled dynamics of these ecosystems. The challenge now is to start quantifying the strength of these trophic links and the implications of the wide spectrum of larval food items consumed by larval invertebrates on growth and survival as a determinant factor of variation in recruitment in intertidal communities.

Acknowledgments

We acknowledge the skillful help of F. Véliz during fieldwork. We are very grateful to P. E. Neill and Dick Strathmann for valuable criticism and suggestions that substantially improved this manuscript. We also want to thank two anonymous referees for their helpful suggestions that substantially improved this presentation. Financial support for this study was provided by the Andrew Mellon Foundation and FONDAP-Fondecyt Grant 1501-0001 to the Center of Advanced Studies in Ecology and Biodiversity, for which we are most grateful. FONDECYT Projects No. 3020035 to P. H. Manríquez, No. 3040034 to C. A. Vargas, and No. 1040787 to S. A. Navarrete supported this research during the final preparation of the manuscript.

Literature Cited

Baldwin, B. S., and R. I. E. Newell. 1990. The natural diet of oyster larvae: the importance of heterotrophic food organisms. American Zoologist **30**:100A.

Baldwin, B. S., and R. I. E. Newell. 1991. Omnivorous feeding by planktotrophic larvae of the eastern oyster *Crassostrea virginica*. Marine Ecology Progress Series **78**:285–301.

Baldwin, B. S., and R. I. E. Newell. 1995. Relative importance of different size food particles in the natural diet of

oyster larvae (*Crassostrea virginica*). Marine Ecology Progress Series **120**:135–145.

Bascompte, J., C. J. Melián, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceeding of the National Academy of Sciences (USA) **102**:5443–5447.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Power, and B. A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology **80**:2206–2224.

Berntsson, K., P. R. Jonsson, S. A. Ê. Wängberg, and A. S. Carlsson. 1997. Effects of broodstock diets on fatty acid composition, survival and growth rates in larvae of *Ostrea edulis*. Aquaculture, Amsterdam **154**:139–153.

Bockstahler, K. R., and D. W. Coats. 1993. Grazing of the mixotrophic dinoflagellates *Guimnodinium snaguineus* on ciliate populations of Chesapeake Bay. Marine Biology **116**:477–487.

Boidron-Métairon, I. 1995. Larval nutrition. Pages 223–248 *in* L. McEdward, editor. Ecology of marine invertebrate larvae. CRC Press, Washington, D.C., USA.

Brett, M. T., and D. C. Müller-Navarra. 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshwater Biology **38**:483–499.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of southeastern Pacific intertidal communities. Marine Ecology Progress Series **224**: 21–34.

Castilla, J. C. 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends in Ecology and Evolution **14**:280–283.

Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast pacific ocean. Ecology **82**:1799–1813.

Crisp, D. J., A. B. Yule, and K. N. White. 1985. Feeding by oyster larvae—the functional response, energy budget and a comparison with mussel larvae. Journal of the Marine Biological Association of the United Kingdom **65**:759–784.

DiSalvo, L. H. 1988. Observations on the larval and postmetamorphic life of *Concholepas concholepas* (Bruguière 1789) in laboratory culture. Veliger **30**:358–368.

Ducklow, H. W., D. C. Smith, L. Campbell, M. R. Landry, H. L. Quinby, G. F. Steward, and F. Azam. 2001. Heterotrophic bacterioplankton in the Arabian Sea: basin wide response to year-round high primary productivity. Deep-Sea Research II **42**:1303–1323.

Edler, L. 1979. Recommendations for marine biological studies in the Baltic Sea. Baltic Marine Biology Publication **5**: 1–38.

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

Gallager, S. C. 1988. Visual observations of particle manipulation during feeding in larvae of a bivalve mollusc. Bulletin Marine Science **43**:344–365.

Gifford, D. J., and D. A. Caron. 2000. Sampling, preservation, enumeration and biomass of marine protozooplankton. Pages 193–221 *in* R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley, editors. ICES zooplankton methodology manual. Academic Press, London, UK.

González, H., S. Pantoja, J. L. Iriarte, and P. Bernal. 1989. Winter–spring variability of size-fractioned autotrophic biomass in Concepción Bay, Chile. Journal of Plankton Research **11**:1157–1167.

Hansen, B. 1991. Feeding behaviour in larvae of the opisthobranch *Philine aperta*. II. Food size spectra and particle selectivity in relation to larval behaviour and morphology of the velar structures. Marine Biology **111**:263–270.

Hansen, P. J., and T. G. Nielsen. 1997. Mixotrophic feeding of *Fragilidium subglobosum* (Dynophyceae) on three species of *Ceratium*: effects of prey concentration, prey species and light intensity. Marine Ecology Progress Series **147**: 187–196.

Hart, M. W., and R. R. Strathmann. 1995. Mechanisms and rates of suspension feeding. Pages 193–222 *in* L. McEdward, editor. Ecology of marine invertebrate larvae. CRC Press, Washington, D.C., USA.

Huntley, M. E., and C. Boyd. 1984. Food-limited growth of marine zooplankton. American Naturalist **124**:455–478.

Huntley, M. E., and M. D. G. López. 1992. Temperature-dependent production of marine copepods: a global synthesis. American Naturalist **140**:201–242.

Iriarte, J. L., and H. E. González. 2004. Phytoplankton size structure during and after the 1997/98 El Niño in a coastal upwelling area of the northern Humboldt Current System. Marine Ecology Progress Series **269**:83–90.

Jonsson, P. R., K. M. Berntsson, C. André, and S. Å. Wängberg. 1999. Larval growth and settlement of the European oyster (*Ostrea edulis*) as a function of food quality measured as fatty acid composition. Marine Biology **134**:559–570.

Klein Breteler, W. C. M., M. Koski, and S. Rampen. 2004. Role of essential lipids in copepod nutrition: no evidence for trophic upgrading of food quality by a marine ciliate. Marine Ecology Progress Series **274**:199–208.

Li, A., D. K. Stoecker, D. W. Coats, and E. J. Adam. 1996. Ingestion of fluorescently labeled and phycoerythrin-containing prey by mixotrophic dinoflagellates. Aquatic Microbial Ecology **10**:139–147.

Manríquez, P. H., and J. C. Castilla. 2001. Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. Marine Ecology Progress Series **215**:201–211.

Marín, V., M. E. Huntley, and B. W. Frost. 1986. Measuring feeding rates of pelagic herbivores: analysis of experimental design and methods. Marine Biology **93**:49–58.

Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P. M. Halpin, G. Hudson, and J. L. Burnaforf. 1999. Top-down ad bottom-up regulation of New Zealand rocky intertidal communities. Ecological Monographs **69**: 297–230.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist **130**:730–757.

Navarrete, S. A., B. Broitman, G. R. Finke, A. Sotomayor, R. Venegas, and E. A. Wieters. 2002. Recruitment of barnacles and mussels in the southeast Pacific during and after the 1997–1998 El Niño. Limnology and Oceanography **47**: 791–802.

Navarrete, S. A., and J. C. Castilla. 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. Oikos **100**:251–262.

Ohman, M. D., and R. A. Snyder. 1991. Growth kinetics of the omnivorous oligotrich ciliate *Strombidium* sp. Limnology and Oceanography **36**:922–935.

Olson, R. R., and M. H. Olson. 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? Annual Reviews of Ecological and Systematics **20**:225–247.

Paffenhöfer, G.-A., and K. D. Lewis. 1990. Perceptive performance and feeding behaviour of calanoid copepods. Journal of Plankton Research **12**:933–946.

Painting, S. J., C. L. Moloney, T. A. Probyn, and B. Tibbles. 1992. Microheterotrophic pathways in the Southern Benguela Upwelling System. South African Journal of Marine Science **12**:527–543.

Phillips, N. E., and S. D. Gaines. 2002. Spatial and temporal variability in size at settlement of intertidal mytilid mussels from around Pt. Conception, California. Invertebrate Reproduction and Development **41**:171–177.

Pilkington, M. C., and V. Fretter. 1970. Some factors affecting the growth of prosobranch veligers. Helgolander Wissenschaftliche Meeresuntersuchungen **20**:576–593.

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science **253**:548–551.

Poulin, E., A. T. Palma, G. Leiva, E. Hernández, P. Martínez, S. A. Navarrete, and J. C. Castilla. 2002*a*. Temporal and spatial variations in the distribution of epineustonic competent larvae of *Concholepas concholepas* (Gastropoda: Muricidae) in the central coast of Chile. Marine Ecology Progress Series **229**:95–104.

Poulin, E., A. T. Palma, G. Leiva, D. Narváez, R. Pacheco, S. A. Navarrete, and J. C. Castilla. 2002*b*. Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in Central Chile. Limnology and Oceanography **47**:1248–1255.

Raby, D., M. Mingelbier, J. J. Dodson, B. Klein, Y. Lagadeuc, and L. Legendre. 1997. Food-particle size and selection by bivalve larvae in a temperate embayment. Marine Biology **127**:665–672.

Riisgård, H. U., A. Randlov, and P. S. Kristensen. 1980. Rates of water processing, oxygen consumption and efficiency of particle retention in veligers and young post-metamorphic *Mytilus edulis*. Ophelia **19**:37–47.

Rivkin, R. B., I. Bosch, J. S. Pearse, and E. J. Lessard. 1986. Bacterivory: a novel feeding mode of asteroid larvae. Science **233**:1311–1314.

Roman, M. R., and P. A. Rublee. 1980. Containment effects in copepod grazing experiments: a plea to end the black box approach. Limnology and Oceanography **25**:982–990.

Shanks, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates. Pages 324–367 *in* L. McEdward, editor. Ecology of marine invertebrate larvae. CRC Press, Washington, D.C., USA.

Shanks, A. L., J. Largier, L. Brink, J. Brubaker, and R. Hoff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnology and Oceanography **45**:230–236.

Sprung, M. 1984. Physiological energetics of mussel larvae (*Mytilus edulis*). I. Shell growth and biomass. Marine Ecology Progress Series **17**:282–293.

Stoecker, D. K., and J. M. Capuzzo. 1990. Predation on protozoa: its importance to zooplankton. Journal of Plankton Research **12**:891–908.

Stone, C. J. 1989. A comparison of algal diets for cirripede nauplii. Journal of Experimental Marine Biology and Ecology **132**:17–40.

Strathmann, R. R. 1987. Larval feeding. Pages 465–550 *in* A. C. Giese, J. S. Pearse, and V. B. Pearse, editors. Reproduction of marine invertebrates. Volume IX. General aspects: seeking unity in diversity. Blackwell Scientific Publications, Palo Alto, California, USA.

Strathmann, R. R., E. S. Branscomb, and K. Vedder. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. Oecologia **48**:13–18.

Strathmann, R. R., L. Fenaux, A. T. Sewell, and M. F. Strahmann. 1993. Abundance of food affects relative size of larval and postlarval structures of a molluscan veliger. Biological Bulletin **185**:232–239.

Strathmann, R., L. Fenaux, and M. F. Strathmann. 1992. Heterochronic development plasticity in larval sea urchin and its implication for evolution of nonfeeding larvae. Evolution **46**:972–986.

Strathmann, R. R., and E. Liese. 1979. On feeding mechanisms and clearance rates of molluscan veligers. Biological Bulletin. **157**:524–535.

Strickland, J. D., and T. R. Parsons. 1972. A practical handbook of seawater analysis. Second edition. Bulletin 167. Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

Strom, S., and T. Morello. 1998. Comparative growth rates and yields of ciliates and heterotrophic dinoflagellates. Journal of Plankton Research **20**:571–584.

Sullivan, B. K., C. L. Suchman, and J. H. Costello. 1997. Mechanics of prey selection by ephyrae of the scyphomedusa *Auerlia aurita*. Marine Biology **130**:213–222.

Tang, K. W., H. H. Jakobsen, and A. W. Visser. 2001. *Phaeocystis globosa* (Prymnesiophyceae) and the planktonic food web: feeding, growth, and trophic interactions among grazers. Limnology and Oceanography **46**:1860–1870.

Thomas, A. C., J. L. Blanco, M. E. Carr, P. T. Strub, and J. Osses. 2001. Satellite-measured chlorophyll and temperature variability off northern Chile during the 1996–1998 La Niña and El Niño. Journal of Geophysical Research **106**: 899–915.

Thompson, P. A., M. X. Guo, and P. J. Harrison. 1994. Influence of irradiance on the nutritional value of two phytoplankton species fed to larval Japanese scallops (*Patinopecten yessoensis*). Marine Biology **119**:89–97.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews **25**:1–45.

Tiselius, P. 1989. Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. Marine Ecology Progress Series **56**:49–56.

Turner, J. T., H. Levinsen, T. G. Nielsen, and B. W. Hansen. 2001. Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay West Greenland. Marine Ecology Progress Series **221**:209–219.

Utermöhl, H. 1958. Zur Vervollkommung der quantitativen Phytoplankton—Metodik. Mitteilungen. Internationale Vereiningung fuer Theoretische und Angewandte Limnologie **9**:1–38.

Vargas, C. A., and H. E. González. 2004*a*. Plankton community structure and carbon cycling in a coastal upwelling system. I. Diet of copepods and appendicularians. Aquatic Microbial Ecology **34**:151–164.

Vargas, C. A., and H. E. González. 2004*b*. Plankton community structure and carbon cycling in a coastal upwelling system. II. Microheterotrophic pathway. Aquatic Microbial Ecology **34**:165–180.

Vargas, C. A., and L. Madin. 2004. Zooplankton feeding ecology: clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa Cilindrica* on natural food assemblages in Mid-Atlantic Bight. Journal of Plankton Research **26**:827–833.

Venegas, R. M., V. Ortíz, A. Olguín, and S. A. Navarrete. 2000. Larval development of the intertidal barnacles *Jehlius cirratus* and *Notochthamalis scabrosus* (Cirripedia: Chthamaloidea) under laboratory conditios. Journal of Crustacean Biology **20**:495–504.

Wieters, E. A., D. M. Kaplan, A. Sotomayor, S. A. Navarrete, J. Largier, K. J. Nielsen, and F. Véliz. 2003. Alongshore and temporal variability in chlorophyll-a concentrations in Chilean nearshore waters. Marine Ecology Progress Series **249**:93–105.