

- cesses of the alga *Ulva lactuca* L. *Hydrobiologia*. **260/261**: 457–462.
- . 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thalassia testudinum* and *Cymodocea nodosa*. *Mar. Biol.* **118**: 767–776.
- KOOP, K., AND OTHERS. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar. Pollut. Bull.* **42**: 91–120.
- KUO, J., AND A. J. MCCOMB. 1989. Seagrass taxonomy, structure and development, p. 6–73. In A. W. D. Larkum [eds.], *Biology of seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier.
- LARNED, S. T., AND M. J. ATKINSON. 1997. Effects of water velocity on NH_4 and PO_4 uptake and nutrient-limited growth in the macroalga *Dictyosphaeria cavernosa*. *Mar. Ecol. Prog. Ser.* **157**: 295–302.
- LAWS, E. 1984. Isotope dilution models and the mystery of the vanishing ^{15}N . *Limnol. Oceanogr.* **29**: 379–386.
- LEE, K. S., AND K. H. DUNTON. 1999. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: Development of a whole-plant budget. *Limnol. Oceanogr.* **44**: 1204–1215.
- MCRROY, C. P., AND J. J. GOERING. 1974. Nutrient transfer between the seagrass *Zostera marina* and its epiphytes. *Nature* **248**: 173–174.
- MONCREIFF, C. A., M. J. SULLIVAN, AND A. E. DAEHNICK. 1992. Primary production dynamics in seagrass beds of Mississippi Sound: The contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Mar. Ecol. Prog. Ser.* **87**: 161–171.
- PATTERSON, M. R. 1992. A chemical engineering view of cnidarian symbioses. *Am. Zool.* **32**: 566–582.
- , K. P. SEBENS, AND R. R. OLSON. 1991. In situ measurements of flow effects on primary production and dark respiration in reef corals. *Limnol. Oceanogr.* **36**: 936–948.
- PELTON, D. K., S. N. LEVINE, AND M. BRANER. 1998. Measurements of phosphorus uptake by macrophytes and epiphytes from the LaPlatte River (VT) using ^{32}P in stream microcosms. *Freshw. Biol.* **39**: 285–299.
- SAND-JENSEN, K., N. P. REVSACH, AND B. B. JORGENSEN. 1985. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. *Mar. Biol.* **89**: 55–62.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman.
- SOLORZANO, L. 1969. Determination of ammonium in natural waters by the phenolhypochlorite method. *Limnol. Oceanogr.* **14**: 799–801.
- STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. *A practical handbook of seawater analysis*. Fish. Res. Board Can.
- THOMAS, F. I. M., AND M. J. ATKINSON. 1997. Ammonium uptake by coral reefs: Effects of water velocity and surface roughness on mass transfer. *Limnol. Oceanogr.* **42**: 81–88.
- , C. D. CORNELISEN, AND J. M. ZANDE. 2000. Effects of water velocity and canopy morphology on ammonium uptake by seagrass communities. *Ecology* **81**: 2704–2713.
- WHEELER, W. N. 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* **56**: 103–110.
- WINNING, M. A., R. M. CONNOLLY, N. R. LONERAGAN, AND S. E. BUNN. 1999. ^{15}N enrichment as a method of separating the isotopic signatures of seagrass and its epiphytes for food web analysis. *Mar. Ecol. Prog. Ser.* **189**: 289–294.

Received: 11 May 2001
 Amended: 15 March 2002
 Accepted: 1 April 2002

Life history bottlenecks in *Diaptomus clavipes* induced by phosphorus-limited algae

Abstract—Considerable information has accumulated on food quality effects on certain cladocerans; meanwhile, other zooplankton have received comparatively little nutritional study. In particular, little is still known about nutrition of copepods with more complex ontogenetic changes. Recent studies have identified strong ontogenetic differences in phosphorus content of copepods, which have been found to be highest for late naupliar stages. Laboratory experiments were set up to examine the life cycle of a calanoid copepod relative to mineral P limitation on a pure algae diet. We hypothesized that P imbalance would cause nauplii particularly to be affected by algal nutrient status. Developmental rates, growth rates, and fecundity of *Diaptomus clavipes* under excess (1.0 mg C L^{-1}) P-deficient and P-sufficient *Scenedesmus obliquus* were determined. We found strong differences between diets in survival to maturity: nauplii developed into copepodites and adults that successfully reproduced when fed the P-sufficient algae but invariably died after molting into copepodite CII when reared on the P-deficient algae. Differences in developmental rates were small for most life stages of nauplii for both food types but were substantial both for copepodite CI and particularly for CII that lived without molting up to 22 d on P-deficient food before dying. Surprisingly, copepodites that fed on P-

deficient algae had similar or higher specific somatic growth rates than animals on P-sufficient algae. Although these experiments demonstrate a strong ontogenetic component to copepod nutrition, and a heretofore undocumented dependence of copepod success on algal P content, the life history bottleneck occurs at a later stage than we hypothesized.

Probably among the most important and at the same time the most difficult task of the zooplankton ecologist is to assess nutritional status. To date, we are still far from a unified view of zooplankton nutrition, especially for copepods. Experiments of food limitation on copepods are scarce, perhaps because of the complex life history of copepods and their relatively long development times. However, studying the ontogeny of an organism, with focus on nutrition, raises the intriguing question of stage-dependent performance. Population bottlenecks may mean that success of one stage is a poor predictor of the success of other stages.

When food levels allow for maximum population per capita growth, food quality becomes particularly relevant for

zooplankton development. Food quality has been defined as a complex function of size, morphology, motility, and biochemical composition (McKinnon 1996). Although the importance of these factors has long been recognized to have effects on the life history traits of crustaceans (e.g., Twombly et al. 1998), the appreciation of mineral limitation, and in particular the relevance of algal P content is more recent (Sterner 1993). Organisms with low body C:P ratios (high P contents) will have high P demands for growth, and should be most constrained by a low algal P content (Sterner and Hessen 1994). Therefore, body C:P ratio influences the degree of zooplankton sensitivity to limitation by food P (Sterner and Elser in press). Because of low P content in adults (high N:P and C:P ratios; Andersen and Hessen 1991) and the lack of information on the elemental composition of copepod naupliar stages, many studies have assumed that copepods may be C or N limited in nature and have failed to examine the role of P in growth and demographic performance. Although studies have tested the nutritional adequacy of unialgal diets for the growth of calanoid copepods (e.g., Hart and Santer 1994), studies to directly test the influence of varying elemental composition of specific algae for the ontogenetic development of copepods are lacking.

Recent studies have indicated marked variation in P composition related to ontogeny in copepods (Villar-Argaiz et al. 2000). Because of their high P content (maximum values of ~1.4% P as dry weight), it has been suggested that the growth of naupliar stages (Carrillo et al. 2001) like certain cladocerans (Elser et al. 1996) may be constrained by low-P food environments. Indeed, published work has supported this hypothesis for cladocerans (Urabe et al. 1997; Sterner and Elser in press), although no study to our knowledge has tested P limitation in copepods. Thus, and in spite of the long recognition of nauplii as a potential "bottleneck" stage of copepods (e.g., Feller 1980), the potential mechanistic role of P constraining metamorphosis at this stage has only recently been proposed (Villar-Argaiz et al. 2002) but until now had not been tested.

In this study, we examined the hypothesis that the growth of copepods is constrained by the phosphorus content of their food. Nauplii were raised individually on two diets: P-deficient or P-sufficient *Scenedesmus obliquus* (formerly referred to as *S. acutus*). We measured the effects of food quality on a suite of life history traits, including survivorship, developmental rates, growth rates, and fecundity over the life cycle of the calanoid copepod *Diatomus clavipes*. On the basis of work elsewhere on copepod stoichiometry, we predicted that nauplii should be more susceptible than copepodite and adult copepods to growth limitation by mineral P.

Development and reproduction—Ovigerous females of *D. clavipes* were collected during September 2000 from Lake Nokomis, ~5 km south of Minneapolis, MN, and were isolated in 100 ml of 0.45 μm -filtered lake water, and then kept at 20°C on a 12:12 light:dark photocycle until eggs hatched. At these same conditions, 40 newborn nauplii (<12 h old) were reared individually in high- and low-P diets of *S. obliquus* at a concentration of 1.0 mg C L⁻¹ in culture

vials that contained 15 ml of 0.45- μm filtered lake water. Food dilutions were based on measured light extinctions at 800 nm of algal cultures in relation to calibration curves of carbon content and optical density. Copepods were transferred to 50-ml vials on reaching the first copepodite instar (CI). All vials were shaken to reduce food depletion caused by algae sedimentation. Also every day, animals were removed from vials with a pipette, measured (total length for nauplii or from the anterior end of the cephalothorax to the end of the furcal rami for copepodites and adults) under a compound microscope by use of a calibrated ocular micrometer (at 100 \times from NI to CI and at 40 \times from CII to adults), and transferred to fresh medium until maturity or death to yield estimates of developmental time and size for each stage. At maturity (final copepodite molt), adult males and females of a single treatment were randomly paired and transferred to 100-ml jars (six replicates) to measure fecundity as clutch size and clutch frequency for 20 d. Every day, medium and food were replenished, and females were examined visually for eggs. To measure clutch size, females carrying eggs were narcotized in carbonated water, isolated, and eggs within egg sacs quantified. Microscopic observations and measurements of algal abundance by use of a cell counter (CASY 1, Schärfe system) before food replenishment showed that adults of *D. clavipes* ingested P-deficient and P-sufficient *S. obliquus* at a rate of ~10,200 cell d⁻¹ copepod⁻¹ (~2.3 ml d⁻¹ copepod⁻¹ at experimental concentration), assuring that they were never limited by food quantity.

S. obliquus from the culture collection at the Max-Planck Institute of Limnology at Plön was grown in chemostats on COMBO medium (Kilham et al. 1998) under different nitrogen and phosphorus loading ratios to produce food of different molar C:P ratios, as described elsewhere (Sterner 1993): a high P content food (a diet referred to here as MON) with a C:P of 122 \pm 12 and a severely P limited food (a diet referred to here as LOP) with a C:P of 1094 \pm 104. To stabilize food quality, continuous cultures were run at a constant dilution rate throughout the experimental period. The carbon, nitrogen, and phosphorus content of the food were measured by filtering chemostat outflow onto pre-combusted (550°C), acid-washed GF/F filters. The carbon and nitrogen samples were analyzed on a CNH analyzer (Perkin Elmer), and P was measured spectrophotometrically as soluble reactive P after a potassium persulfate digestion (Langer and Hendrix 1982).

Survivorship of copepods as a function of time was calculated as the percentage of original cohort alive at a certain stage. The stage-specific developmental times were calculated from observed changes in stage molting with time and cumulative developmental time was the result of adding up stage-specific developmental times.

Food quality, as measured by the P content of a pure algal diet, had significant effects on the individual growth, development rates, survival, and hence reproduction of *D. clavipes*. *D. clavipes* raised on a P-sufficient diet matured successfully (survivorship of 93.3%) but on a P-deficient food failed to complete development, invariably dying after copepodite stage CII (Fig. 1).

Copepod body length at the stage level did not differ sig-

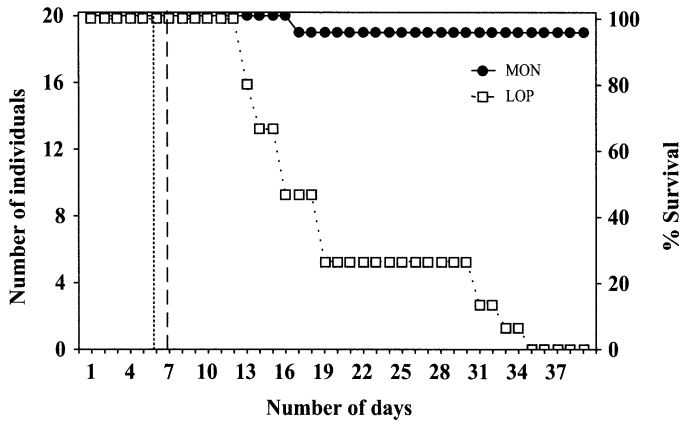


Fig. 1. Survivorship as a function of time of *D. clavipes* reared under P-sufficient and P-deficient algal diets. Vertical lines indicate time at metamorphosis in P-deficient (dotted line) and P-sufficient (dashed line) diets.

nificantly between the LOP and MON treatments (t test, $P > 0.05$), although a tendency to lower body lengths in late naupliar and early copepodite stages in the LOP treatment was apparent (Fig. 2). Developmental time of *D. clavipes* also was dependant on P content of the algae, particularly for early copepodite stages (Fig. 3). Thus, age at metamorphosis was slightly different between diets: individuals consistently developed into copepodites CI 1 d ahead on P-sufficient food than on P-deficient food (Fig. 1). However, developmental rate trajectories of animals diverged strongly after metamorphosis, and stage durations considerably increased in LOP treatment for copepodite stages CI and especially for CII (Fig. 3). As a consequence, and although all copepods in the LOP treatment died as copepodites CII, age at death varied extensively among individuals (cumulative development time 12–35 d), and some CII individuals lasted up to 22 d before dying.

Females raised on MON produced four clutches in 20 d. Average egg production per female was rather constant at 2 eggs d^{-1} , and clutch size varied from 10 to 11 eggs $clutch^{-1}$ (average 10.3 eggs $clutch^{-1}$).

Growth rate—To test the effect of P content of the diet on copepod growth rate, we measured *D. clavipes* somatic growth rates at three distinct life cycle transitions by rearing nauplii up to nauplii stage VI, copepodite stage II (stage at which copepods died in LOP treatments), and maturity (copepodite CV molt into adult) in 0.45- μm screened natural water that was supplemented with P-sufficient and P-deficient *S. obliquus*. Cohorts (a total of 60 nauplii) were commenced and raised by use of the same methods described above, except that nauplii stocks were obtained from the offspring of the above experimental mating. One third of the replicates were terminated when animals reached naupliar stage VI for both treatments. A second third of the replicates was terminated when animals had completed the molt into copepodite CII and the rest when animals reached maturity (solely for the MON treatment). Growth periods lasted 6–7 d for nauplii, 8–11 d for copepodite CII, and 34–36 d for

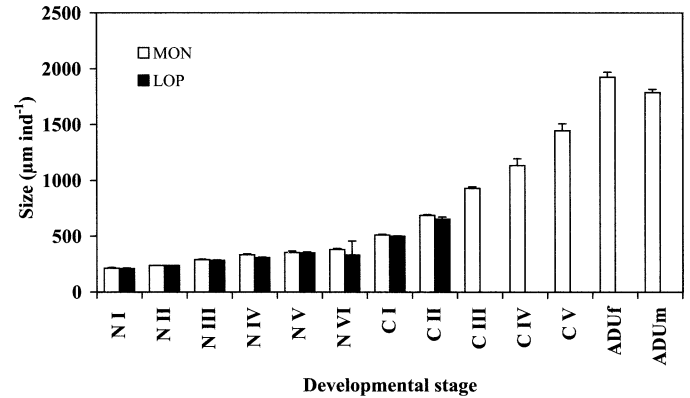


Fig. 2. Body length at each developmental stage of copepods raised in P-deficient and P-sufficient *S. obliquus* (LOP and MON treatments, respectively). ADUf, adult female; ADUm, adult male; CI–CV, copepodites; and NI–NVI, nauplii.

adults. The zooplankton to be weighed, including newborn nauplii, were placed in preweighed aluminum boat capsules, dried at 60°C overnight and reweighed on a Mettler UMT2 ultramicrobalance ($\pm 0.1 \mu g$). Dry masses were converted into growth rates (g) with the formula

$$g = [\ln(M_t) - \ln(M_0)]/t \quad (1)$$

where M_t is the final body mass, M_0 is the initial body mass of nauplii, and t is the time (in days) at which animals were collected for their weight.

Animals gained mass in both food regimes, which indicates that they were above the individual threshold for food limitation. Still, food regimes demonstrated different rates of biomass accumulation, evidencing food quality limitation. No statistical difference was observed for naupliar stage VI;

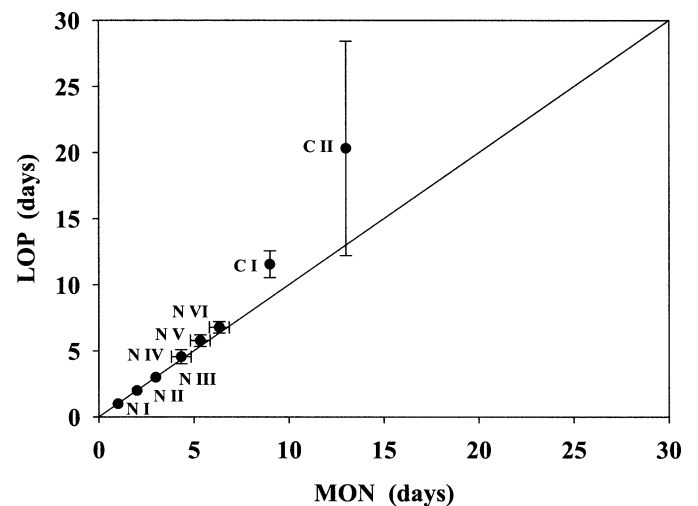


Fig. 3. Relationship between cumulative stage durations (in days) in MON versus LOP cultures. The solid line (slope of 1) denotes equal development time for both treatments. Error bars represent SDs. Error bars are too small to be seen for some stages and food treatments.

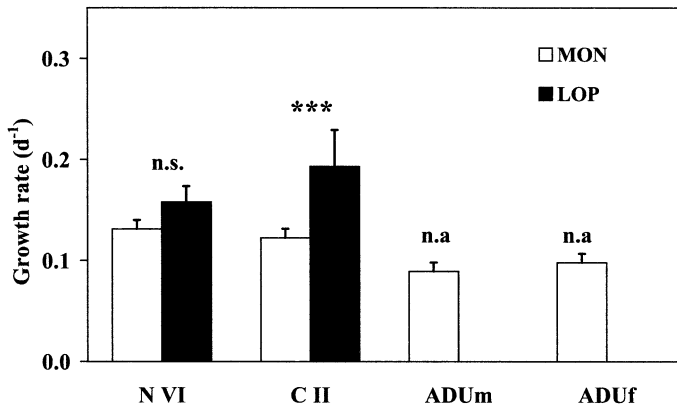


Fig. 4. Growth rate comparisons of *D. clavipes* for nauplii NVI, copepodite CII, and adult stages raised on MON and LOP treatments. Results of Student's *t* test are included to test for differences in the growth rate between treatments for each stage; n.a., not applicable; n.s., not significant; and ***, significant at the 0.1% level.

however, the growth rate of copepodite CII was 58% higher when fed on P-deficient than on P-sufficient food (Fig. 4; *t* test; $P < 0.001$). Because the development time for nauplii and copepodites CII raised on both diets was similar, the effect of food treatment on growth rates was primarily caused by differences in the specific weight of animals. Thus, the mean body weight of nauplii NVI for both treatments was not statistically different ($1.25 \pm 0.12 \mu\text{g}$ dry weight [DW] ind⁻¹ in MON versus $1.52 \pm 0.15 \mu\text{g}$ DW ind⁻¹ in LOP; *t* test; $P > 0.05$), whereas the mean weight of copepodites CII in LOP nearly doubled that of the copepodites in MON ($2.67 \pm 0.53 \mu\text{g}$ DW ind⁻¹ vs. $4.21 \pm 0.06 \mu\text{g}$ DW ind⁻¹). In spite of the higher growth rates in the LOP treatment, copepodites CII died before molting into next stage and showed large lipid droplets filling most of their body, as well as a noticeable red color in the last segments of the first antenna.

Effect of food quality on copepod life history—There is potentially a conspicuous ontogenetic dimension in nutrition in copepods caused by the different food requirements owing to varying body composition throughout development (Hansen and Santer 1995). Differences in nutritional requirements between stages may for example reflect a change from structural growth in juveniles that requires high protein translation rates, and hence ribosomal RNA rich in P, to lipid requirement in adults for egg production and for survival (Elser et al. 2000). On the basis of the reported ontogenetic differences in the P content of calanoid copepods, being highest for late naupliar stages (Carrillo et al. 1996, 2001; Villar-Argaiz et al. 2002), we predicted that there could be a bottleneck in *D. clavipes* population fed P-deficient food before metamorphosis to copepodite stages. However, diet quality affected the life cycle in unexpected ways, and although we did observe a pronounced nutritional bottleneck as a function of P status of the algae, it was later during development at copepodite stage CII that failed to molt to CIII.

Knowing which factor determines copepod failure to grow offers the promise of predictive mechanistic models where

zooplankton nutrition and community structure can be linked in nature. We hypothesize that the failure of copepodites to develop into adults when reared on P-deficient food could be attributable to several limiting substances. First, to P per se. Recent literature has suggested a widespread occurrence of P limitation of some zooplankton, and particularly for those with highest P needs (e.g., Urabe et al. 1997). If the ontogenetic differences in the specific P content of the calanoid copepod *Mixodiaptomus laciniatus* were found to be a general feature of calanoid copepods, the high specific P content of copepodites CII (~1.2% P as DW; Villar-Argaiz et al. 2000) should make them as sensitive to P limitation as late naupliar stages. Second, to individual fatty acids. It is known that nutrient-limited algae produce lesser amounts of essential highly unsaturated fatty acids (Brett and Müller-Navarra 1997). Among them, eicosapentaenoic acid (EPA, 20:5 ω 3) and docosahexaenoic acid (DHA, 22:6 ω 3) are major constituents of polar lipids rich in cell membranes. It is possible that a lack of EPA and DHA or other essential substances (Harrison 1990) could block the development of the molting processes of crustaceans at a stage where demands for these biochemicals are particularly high. Because other food quality effects cannot be disregarded, these hypothesis raise the intriguing challenge to test the exact mechanisms by which deficiency of P becomes evident at a precise stage, and not before.

As is known for daphnids (Sterner 1993), a chemical imbalance between autotrophs and consumers fed a P-deficient algae may generate an excess of C relative to P that can be responsible for the storage of lipids in discrete droplets. Energy accumulated in the lipids might enable copepods not only to survive in an environment with scarce or deficient food for a long time (Vanderploeg et al. 1992) but also to attain a metabolic status similar to an "active diapause" (sensu Santer et al. 2000) that enables copepods to enter diapause at different phases of their life cycle. Also the intensive accumulation of lipid droplets may help to explain the observed higher gain of animal DW and therefore somatic growth rates in P-deficient in comparison to P-sufficient food (Fig. 4). In contrast to *Daphnia*, this result questions the appropriateness of using body mass growth rate as a summary measure of copepod fitness and recommends the study of the whole life cycle, including the production of living eggs.

Earlier studies have questioned the N limitation of marine copepods (Anderson and Hessen 1995). Also, the classical view that copepods should not be severely affected by the P content of its food, owing to their higher N:P and C:P ratios (Andersen and Hessen 1991), is not confirmed in this study. Therefore, the consideration of the role of P-limiting copepod development at early copepodite stages would represent an important step identifying the selective pressure behind crustacean competition and copepod success. What determines zooplankton populations and succession in nature is still a hotly contested topic in zooplankton ecology. Although to date poorly understood, food quality bottlenecks might be extremely important in explaining zooplankton population dynamics in natural ecosystems.

Manuel Villar-Argaiz¹ and Robert W. Sterner

Department of Ecology, Evolution and Behavior
University of Minnesota
1987 Upper Buford Circle
St. Paul, Minnesota 55108

References

- ANDERSEN, T., AND D. O. HESSEN. 1991. Carbon, nitrogen and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.* **36**: 807–814.
- , AND ———. 1995. Carbon or nitrogen limitation in marine copepods? *J. Plankton Res.* **17**: 317–331.
- BRETT, M. T., AND D. MÜLLER-NAVARRA. 1997. The role of highly unsaturated fatty acids in aquatic food web processes. *Freshw. Biol.* **38**: 483–499.
- CARRILLO, P., I. RECHE, AND L. CRUZ-PIZARRO. 1996. Intraspecific stoichiometric variability and the ratio of nitrogen to phosphorus resupplied by zooplankton. *Freshw. Biol.* **36**: 363–374.
- , M. VILLAR-ARGAIZ, AND J. M. MEDINA-SÁNCHEZ. 2001. Relationship between N:P ratio and growth rate during the life cycle of calanoid copepod: An *in situ* measurement. *J. Plankton Res.* **23**: 537–547.
- ELSER, J. J., D. DOBBERFUHL, N. A. MACKAY, AND J. H. SCHAMPEL. 1996. Organisms size, life history, and N:P stoichiometry: Towards unified view of cellular and ecosystem processes. *BioScience* **46**: 674–684.
- , AND OTHERS. 2000. Biological stoichiometry from genes to ecosystem. *Ecol. Lett.* **3**: 540–550.
- FELLER, R. J. 1980. Development of the sand-dwelling meiobenthic harpacticoid copepod *Huntemannia jadensis* Poppe in the laboratory. *J. Exp. Mar. Bio. Ecol.* **46**: 1–15.
- HANSEN, A. M., AND B. SANTER. 1995. The influence of food resources on the development, survival and reproduction of the two cyclopoids copepods: *Cyclops vicinus* and *Mesocyclops leuckarti*. *J. Plankton Res.* **17**: 631–646.
- , AND ———. 1995. Carbon or nitrogen limitation in marine copepods? *J. Plankton Res.* **17**: 317–331.
- BRETT, M. T., AND D. MÜLLER-NAVARRA. 1997. The role of highly unsaturated fatty acids in aquatic food web processes. *Freshw. Biol.* **38**: 483–499.
- CARRILLO, P., I. RECHE, AND L. CRUZ-PIZARRO. 1996. Intraspecific stoichiometric variability and the ratio of nitrogen to phosphorus resupplied by zooplankton. *Freshw. Biol.* **36**: 363–374.
- , M. VILLAR-ARGAIZ, AND J. M. MEDINA-SÁNCHEZ. 2001. Relationship between N:P ratio and growth rate during the life cycle of calanoid copepod: An *in situ* measurement. *J. Plankton Res.* **23**: 537–547.
- ELSER, J. J., D. DOBBERFUHL, N. A. MACKAY, AND J. H. SCHAMPEL. 1996. Organisms size, life history, and N:P stoichiometry: Towards unified view of cellular and ecosystem processes. *BioScience* **46**: 674–684.
- , AND OTHERS. 2000. Biological stoichiometry from genes to ecosystem. *Ecol. Lett.* **3**: 540–550.
- FELLER, R. J. 1980. Development of the sand-dwelling meiobenthic harpacticoid copepod *Huntemannia jadensis* Poppe in the laboratory. *J. Exp. Mar. Bio. Ecol.* **46**: 1–15.
- HANSEN, A. M., AND B. SANTER. 1995. The influence of food resources on the development, survival and reproduction of the two cyclopoids copepods: *Cyclops vicinus* and *Mesocyclops leuckarti*. *J. Plankton Res.* **17**: 631–646.
- HARRISON, K. E. 1990. The role of nutrition in maturation, reproduction and embryonic development of decapod crustaceans: A review. *J. Shellfish Res.* **9**: 1–28.
- HART, R. C., AND B. SANTER. 1994. Nutritional suitability of some uni-algal diets for freshwater calanoids: Unexpected inadequacies of commonly used edible greens and others. *Freshw. Biol.* **31**: 109–116.
- KILHAM, S. S., D. A. KREEGER, S. G. LYNN, C. E. GOULDEN, AND L. HERRERA. 1998. COMBO: A defined freshwater culture medium for algae and zooplankton. *Hydrobiologia* **377**: 147–159.
- LANGER, C. L., AND P. F. HENDRIX. 1982. Evaluation of persulfate digestion method for particulate nitrogen and phosphorus. *Water Res.* **16**: 1451–1454.
- MCKINNON, A. D. 1996. Growth and development in the subtropical copepod *Acrocalanus gibber*. *Limnol. Oceanogr.* **41**: 1438–1447.
- SANTER, B., E. BLOHM-SIEVERS, C. E. CACERES, AND N. G. HAIRSTON. 2000. Life-history variation in the coexisting freshwater copepods *Eudiaptomus gracilis* and *Eudiaptomus graciloides*. *Arch. Hydrobiol.* **149**: 441–458.
- STERNER, R. W. 1993. *Daphnia* growth on varying quality of *Scenedesmus*: Mineral limitation of zooplankton. *Ecology* **74**: 2350–2360.
- , AND J. J. ELSER. In press. Ecological stoichiometry: The biology of elements from molecules to the biosphere. Princeton Univ. Press.
- , AND D. O. HESSEN. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.* **25**: 1–29.
- TWOMBLY, S., N. CLANCY, AND C. W. BURNS. 1998. Life history consequences of food quality in the freshwater copepod *Boeckella triarticulata*. *Ecology* **79**: 1711–1724.
- URABE, J., J. CLASEN, AND R. W. STERNER. 1997. Phosphorus limitation of *Daphnia* growth: Is it real? *Limnol. Oceanogr.* **42**: 1436–1443.
- VANDERPLOEG, H. A., W. S. GARDNER, C. C. PARRISH, J. R. LIEBIG, AND J. F. CAVALETTO. 1992. Lipids and life-cycle strategy of a hypolimnetic copepod in Lake Michigan. *Limnol. Oceanogr.* **37**: 413–424.
- VILLAR-ARGAIZ, M., J. M. MEDINA-SÁNCHEZ, L. CRUZ-PIZARRO, AND P. CARRILLO. 2000. Life history implications of calanoid *Mixodiptomus laciniatus* in C:N:P stoichiometry. *Int. Verh. Verein. Limnol.* **27**: 527–531.
- , ———, AND P. CARRILLO. 2002. Linking life history strategies and ontogeny in crustacean zooplankton: Implications for homeostasis. *Ecology* **83**: 1899–1914.

Received: 26 June 2001

Accepted: 19 February 2002

Amended: 2 April 2002

¹ Corresponding author (mvillar@ugr.es). Present address: Departamento de Biología Animal y Ecología, Facultad de Ciencias, 18071 Granada, Spain.

Acknowledgments

We thank Judy Olson and Andrea Plevan for elemental analysis during the study and Dr. N.G. Hairston for assistance in the copepod species identification. We are also grateful to two anonymous reviewers who provided helpful comments on the manuscript. This study was supported by NSF grants to R.W.S. and by a postdoctoral fellowship from the University of Granada and the Ministry of Education, Culture and Sports/Fulbright to M.V.A.