Calanoid copepods and nutrient enrichment determine population dynamics of the appendicularian *Oikopleura dioica*: a mesocosm experiment

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ABSTRACT: Appendicularians, an important group of marine gelatinous zooplankton, are highly efficient filter feeders of small phyto- and bacterioplankton. It is not known which factors regulate their abundance and biomass in the field. In a mesocosm experiment, we manipulated nutrient loading and initial densities of calanoid copepods (almost exclusively the genera *Temora* sp., *Centropages* and *Pseudocalanus*) and followed plankton dynamics over 2 wk. Peak appendicularian densities were inversely related to initial copepod densities. We observed more than 100-fold variation in *Oikopleura dioica* density among treatments, even though our experimental variables were kept within ecologically relevant magnitudes. The differences between copepod-reduced and copepod-enhanced treatments were much larger at high and moderate nutrient loadings than in treatments without nutrient enrichment. Thus, appendicularians are under strong pressure from calanoid copepods. Calanoid copepods appear to structure the plankton community via direct negative effects on large algae, ciliates and appendicularians and indirect positive effects on small algae resulting from the release of these from predation by ciliates and appendicularians.

KEY WORDS: *Oikopleura* · Appendicularia · Calanoid copepods · Top-down regulation · Mesocosms · Omnivory

INTRODUCTION

In general, 3 main functional groups may be present in the so called 'herbivorous' zooplankton of marine pelagic systems. The first group is small unicellular predators such as ciliates or flagellates which have high maximum growth rates, short generation times in the range of days, and feed on small (<20 µm) nano- and picoplankton (Gismervik et al. 1996, Hansen et al. 1997, Perez et al. 1997). The second group is calanoid copepods, which have a preference for larger particles (>20 µm) such as microphytoplankton and ciliates (Paffenhöfer & Knowles 1980, Kleppel 1993, Fessenden & Cowles 1994, Sommer et al. 2000). The third group is gelatinous filter-feeders such as appendicularians,

salps and doliolids, which have a potentially large food size spectrum but show a clear preference for small particles <20 µm (Flood et al. 1992, Sommer et al. 2000). Compared to calanoid copepods, which have generation times of several weeks or more in temperate waters, appendicularians have much shorter generation times, on the order of several days (Uye & Ichino 1995). Ciliates and appendicularians may therefore show much quicker population responses to sudden increases in algal production. Thus, while the population dynamics of algae and ciliates and of algae and appendicularians may exhibit a tight predator–prey coupling, algae may temporarily outgrow copepods.

Appendicularians are ubiquitous in the marine zooplankton. They filter their food with highly effective fil-

tration structures (Deibel & Powell 1987, Acuna 2001). In recent years, appendicularians have gained the deserved attention of marine biologists for several reasons. First, because of their efficient grazing of small particles (Flood et al. 1992) they constitute an important link between bacterial and picoalgal production and higher trophic levels (Cushing 1989). This pathway of energy transfer up the food chain is more direct than that through heterotrophic flagellates and ciliates. Second, their highly specialized morphology and life-history allow appendicularians to live in environments with low abundance of food not accessible to other large metazoan herbivores (Acuna 2001). Third, their production of mucoid 'filter houses' can be responsible for a large part of particulate carbon sedimentation during appendicularian blooms (Alldredge 1976).

Suggestions about factors regulating appendicularian abundances include phytoplankton blooms (Valentin et al. 1987, Nakamura 1998), water temperature (Acuna & Anadon 1992) and predation by fish larvae (Shelbourne 1962, Ryland 1964, Nakamura 1998), yet only limited data exist to evaluate these suggestions. Appendicularian abundances often fluctuate (Landry et al. 1994). However, in some regions they can sometimes represent the most abundant metazoan zooplankton group (Deibel 1998), a position normally held by calanoid copepods. Food size could be an important factor determining the success of copepods and appendicularians. Their preferences for differently sized food particles result in low food size overlap between copepods and appendicularians (Sommer et al. 2000). Therefore, the size distribution of the phytoplankton community could be an important factor influencing their relative abundances (Sommer & Stibor 2002). In addition to these bottom-up-related hypotheses, top-down processes are only rarely considered to be important in structuring marine pelagic food webs (Verity & Smetacek 1996). Recently, however, it became evident that copepods can have strong predatory effects on ciliate populations (Stoecker & Capuzzo 1990, Kleppel 1993, Pierce & Turner 1995) which, in turn, may indirectly influence algal community structure since small algae would thus be released from grazing pressure by ciliates.

In previous field mesocosm experiments we have observed an inverse relationship between copepod and appendicularian abundances (H. Stibor unpubl. data). We therefore hypothesized that copepods may not only influence ciliate numbers but also appendicularian abundances. To investigate this question in detail we conducted a mesocosm experiment in a sheltered bay on the coast of Norway. The experiment was designed to test the influence of copepod abundance on the structure and dynamics of lower trophic levels in the pelagic food web. To broaden the generality of our results, both copepod and nutrient loads were manipulated within natural ranges.

MATERIALS AND METHODS

The experiment was arranged as a 3×3 factorial experiment, with mesozooplankton (calanoid copepod) density as one factor and nutrient loading as the second factor. The experiment was carried out during August– September 2000 in the landlocked coastal bay Hopavågen (63° 36′ N, 9° 33′ E), west of Trondheim, central Norway (for details about the bay of Hopavågen see van Marion 1996). We moored 9 mesocosms made from transparent polyethylene tubes to floating stands. The volume of each bag was approximatelx 5 m³, with a diameter of 0.9 m and a total depth of 6.5 m, consisting of a 6 m straight tube and a sealed, conical bottom. We filled the mesocosms on the evening before the start of the experiment (Day 0) by lifting them from ca. 7 m depth to the surface. The water columns in the bags did not stratify and were well mixed by wave action. We assigned 3 mesocosms to each of 3 copepod treatments: reduced density (removal of calanoid copepods by means of vertical hauls with a 200 µm plankton net), ambient density, and enhanced density (addition of calanoid copepods carefully collected by net hauls in Hopavågen). The calanoid copepod community consisted of *Temora longicornis*, *Centropages* sp., *Pseudocalanus elongatus* and *Acartia longiremis*. More than two-thirds of the biomass was copepods of the genera *Temora* and *Pseudocalanus*, which were fairly equal in biomass. In addition, the cyclopoid copepod *Oithona similis* was present in all mesocosms. Its density was approximately the same in all treatments and was always below 5 individuals (ind.) l^{-1}. Non-crustacean zooplankton consisted mainly of bivalve veliger larvae and polychaetes (*Tomopteris* sp.); it never exceeded 4 ind. l^{-1} and did not show major changes in abundance or composition during the experiment (Lippert 2001).

We added nutrients to the mesocosms on the evening of Day 1 and each of the 11 evenings thereafter. Each mesozooplankton treatment was cross-classified with 3 different nutrient regimes: no addition, normal, and high addition. The normal regime was comparable to the natural load of the system (Vadstein et al. 2004, this volume). We added nutrients in an atomic ratio of 16:16:1 for Si:N:P. Si was in the form of silicate, P of phosphate, and N of nitrate and ammonia (1:1). The daily P additions were 0, 0.5 and 2.5 µg P l^{-1} d^{-1}. Background levels of dissolved inorganic nutrients were close to detection limit for Si and N and between 3 and 5 µg l^{-1} for P.

We sampled the entire water column of each enclosure every 3 d between 07:00 and 08:00 h with an opaque tube sampler covered with black plastic to protect the plankton from light exposure (length 2 m, diameter 0.12 m; Ramberg 1976). Zero to 6 m depth-integrated water samples (25 l) were transferred to low-transparency bottles. We used 21 l from each sample to collect the mesozooplankton, which we concentrated on a 35 µm net, transferred to a 250 ml plastic vial, and fixed with acid Lugol's iodine to a final concentration of 1%. Subsamples for analysis of chlorophyll *a* were taken from the remaining water. We filtered these through a 200 µm net and collected the samples on Whatman GF/F glass-fiber filters. The filters were extracted in methanol, and chlorophyll *a* was quantified by fluorometry using a Turner Designs fluorometer; 2 replicates were analyzed per sample.

Mesozooplankton was identified and counted in a Wild MZ3 dissecting microscope. When copepod/appendicularian abundances in a sample exceeded 400 individuals we split the sample and analyzed a 50% sub-sample. Aliquots of copepods and appendicularians were burned in a C-Mat 500 carbon analyzer to determine mesozooplankton biomass.

RESULTS

Our manipulations of copepod numbers in the different experimental treatments were effective (Fig. 1A). Differences in the means of the initial copepod densities between treatments with reduced, ambient and enhanced copepod densities were significant (Kruskal-Wallis test, $H = 6.5$ with 2 df, p = 0.011. A pairwise multiple comparison procedure (Student-Newman-Keuls) resulted in significant differences between ambient and enhanced copepod treatments and reduced and enhanced copepod treatments.

Copepod numbers and the composition of the copepod community did not change in a significant way during the experiment (Fig. 2 and Lippert 2001).

Nutrient additions also had distinct effects. Chlorophyll *a* levels at the start of the experiment were about 3 µg chlorophyll *a* l^{-1}. At the end of the experiment levels ranged between 2.3 and 14.6 µg chlorophyll *a* l^{-1} (Fig. 1B). The differences in mean chlorophyll *a* levels between different nutrient addition regimes were significant (ANOVA, $F_{(2,6)} = 82.7$; p < 0.001). A pairwise multiple comparison procedure (Tukey's) resulted in significant differences between normal and high nutrient loading and zero and high nutrient loading. Chlorophyll dynamics were similar in bags with the same nutrient regime (Fig. 2).

In all mesocosms, appendicularian abundances were near or below the detection limit on Day 1
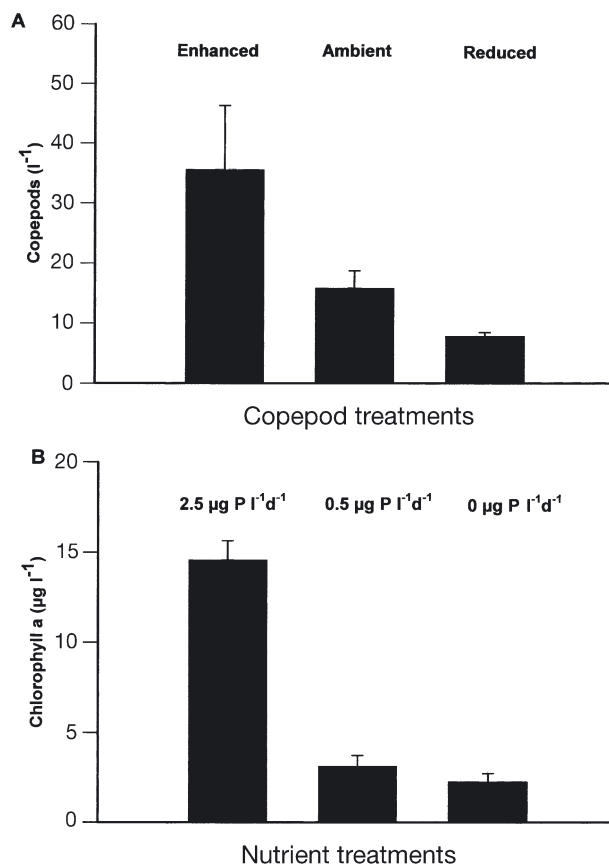

Fig. 1. (A) Copepod numbers as a function of initial abundance; (B) chlorophyll levels as a function of nutrient load; chlorophyll *a* levels in each mesocosm on Days 10 and 12 were averaged and treated as single mean. Error bars = SE

(Fig. 2). In bags with reduced initial copepod abundances, appendicularians (exclusively the species *Oikopleura dioica*) started to increase about 7 d into the experiment. This fits well with reported generation times of approximately 1 wk for *O. dioica* (Uye & Ichino 1995). In the bags with reduced initial copepod abundances, *O. dioica* abundance peaked on Days 10 to 12, when *O. dioica* accounted for 20 to 70% of total zooplankton abundance, depending on the nutrient load. The bags receiving normal and high nutrient additions reached peak *O. dioica* densities of about 65 ind. l^{-1} on Day 12, whereas in the bag without nutrient addition *O. dioica* peaked at only about 20 ind. l^{-1} on Day 10 (Fig. 2)

In enclosures with ambient initial densities of calanoid copepods, *Oikopleura dioica* densities remained low (mostly <5 ind. l^{-1} throughout the experiment (Fig. 2) After 12 d the proportion of *O. dioica* was between 10 and 30% of total zooplanton abundance (Fig. 2). In enclosures with high initial densities of calanoid copepods and high nutrient addition, *O. dioica* never accounted for more than 10% of total
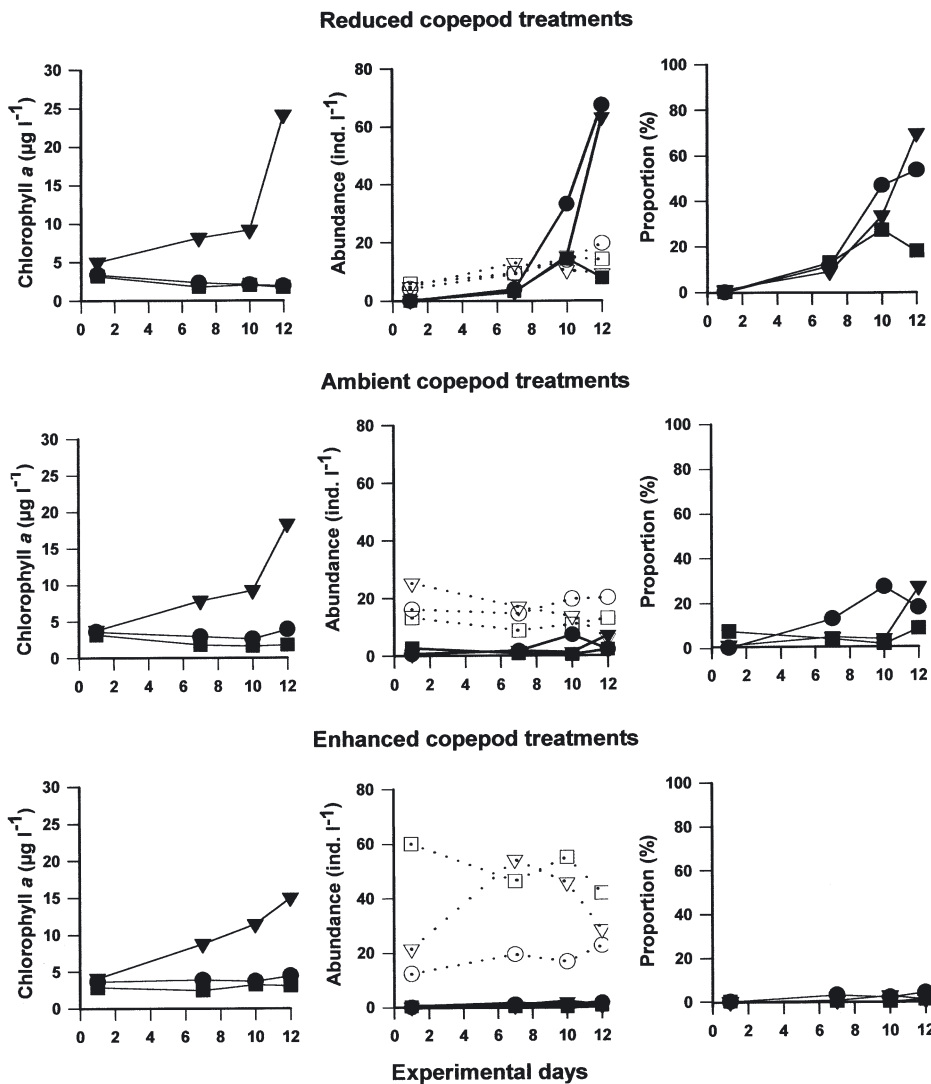
Reduced copepod treatments

Ambient copepod treatments

Enhanced copepod treatments

Experimental days

Fig. 2. Dynamics of chlorophyll *a*, calanoid copepods and *Oikopleura dioica* as a function of nutrient load. (▼) High nutrient load (2.5 µmol P l^{-1} d^{-1}); (●) medium nutrient load (0.5 µmol P l^{-1} d^{-1}); (■) zero nutrient load. Left-hand graphs: chlorophyll *a* levels; centre graphs: copepod and *O. dioica* abundances (filled symbols and continuous lines = *O. dioica* abundances, open symbols and dotted lines = copepod abundances); right-hand graphs: proportion of *O. dioica* in total zooplankton (%)

zooplankton numbers (Fig. 2). Its contribution to total zooplankton abundance was even lower (<5%) in the bags with moderate and zero nutrient addition. *O. dioica* numbers were always below 2 ind. l^{-1} (Fig. 2).

The strong negative effect of copepods on *Oikopleura dioica* toward the end of the experiment was supported by a Kruskal-Wallis analysis of the 3 copepod treatments (Fig. 3; H = 7.2 with 2 df, p = 0.004). A pairwise multiple comparison procedure (Student-Newman-Keuls) resulted in significant differences between all treatments.

A multiple regression revealed a strong, negative effect of copepod biomass and a positive effect of nutrient load on *O. dioica* biomass (r^2 = 0.978, p < 0.001; Table 1). The tight negative relationship between appendicularian and calanoid copepod biomass is also evident from a simple regression excluding nutrient load (Fig. 4; r^2 = 0.863, p < 0.001).

DISCUSSION

In marine systems, research on the factors structuring planktonic food webs has often focussed on the investigation of bottom–up forces such as nutrient supply and food abundance (Verity & Smetacek 1996). Zooplankton has often only been considered as a passive link between primary production and fish yield. Recently, however, it has become clear that omnivory is a common feature among many zooplankton groups such as protozoans, soft-bodied tunicates (e.g. appendicularians and salps) and calanoid copepods, which were originally thought to be strict herbivores. Numerous evidences of calanoid copepods feeding on ciliates clearly show that predation within the zooplankton should not be neglected (Stoecker & Capuzzo 1990, Gifford & Dagg 1991, Kleppel 1993, Pierce & Turner 1995, Nejstgaard et al. 1997). We have presented strong evidence
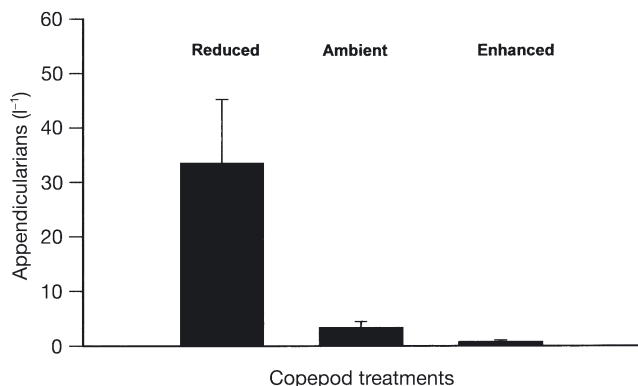
Fig. 3. *Oikopleura dioica* mean numbers in different copepod treatments. Numbers in each mesocosm from Days 10 and 12 were averaged and treated as a single mean. Error bars = SE

Table 1. *Oikopleura dioica*. Results of a multiple linear regression of appendicularian biomass on copepod biomass and nutrient load. A: appendicularian biomass ($\mu g\,C\ l^{-1}\ d^{-1}$); C: copepod biomass ($\mu g\,C\ l^{-1}\ d^{-1}$); N: nutrient loading ($\mu mol\,P\ l^{-1}\ d^{-1}$). Appendicularia biomass was log-transformed to ensure homogenity of variances: $\log A = 2.770 - (0.0542 \times C) + (0.241 \times N)$; $r^2 = 0.978$; ANOVA: $F_{(2,6)} = 135.02$; $p < 0.001$

	Coefficient	SD	t	p
Constant	2.77	0.123	22.43	<0.001
C	−0.0542	0.003	−16.20	<0.001
N	0.241	0.042	5.634	<0.01

that copepods may control appendicularian abundance. This should result in even stronger indirect effects of copepods on small algae, since the latter are the preferred food of both ciliates and appendicularians (Flood et al. 1992, Sommer et al. 2000). Copepods may therefore not only have direct negative effects on large algae, ciliates and appendicularians, but also indirect effects on algal community composition through the suppression of consumers of small algae.

Appendicularians have the potential to attain very fast growth rates (Uye & Ichino 1995). It is therefore not surprising that their success in the different mesocosms was also determined by nutrient load which stimulated the production of algal food. At zero nutrient loading the increase in appendicularian numbers was not high enough for them to reach dominance in the zooplankton community, even in the reduced copepod treatment, in which appendicularians increased only slightly after the reduction of calanoid copepods, but the increase was not very strong. In the mesocosms receiving moderate and high nutrient enrichment, the increase in appendicularian abundances after copepod removal was several-fold stronger.

Our results indicate that negative effects of calanoid copepods can override the discussed positive effects of nutrients on appendicularian abundance. For example, high-nutrient-addition bags with ambient and enhanced initial calanoid copepod densities had higher chlorophyll concentrations (both total chlorophyll and chlorophyll <20 µm) during the first days of the experiment (Lippert 2001, Vadstein et al. 2004) than the bag with reduced initial copepod densities. Nevertheless, appendicularian abundances were about 100 times higher in the latter bag at that time.

What are the mechanisms behind the suppression of appendicularians by copepods? One possibility is competition for food. This would mean that food overlap between copepods and appendicularians is larger than previously thought (Sommer et al. 2000). If this possibility is real we would, however, expect some differences among treatments with enhanced copepod numbers but different nutrient loadings. Increasing food levels at constant copepod numbers should alleviate competition, in which case appendicularians should increase. However, appendicularians in the enhanced copepod treatments always stayed below 2 ind. l^{-1}, regardless of the food situation. Clogging of the appendicularian filters at high chlorophyll levels seemed to be of minor importance as appendicularians increased dramatically in high food treatments after the removal of copepods. A second possibility could be predation. As it becomes increasingly clear that calanoid copepods do feed on ciliates, nauplii and other types of animal food, it seems possible that they also feed on appendicularian eggs and larval stages. These stages are in a size range ingestible by calanoid
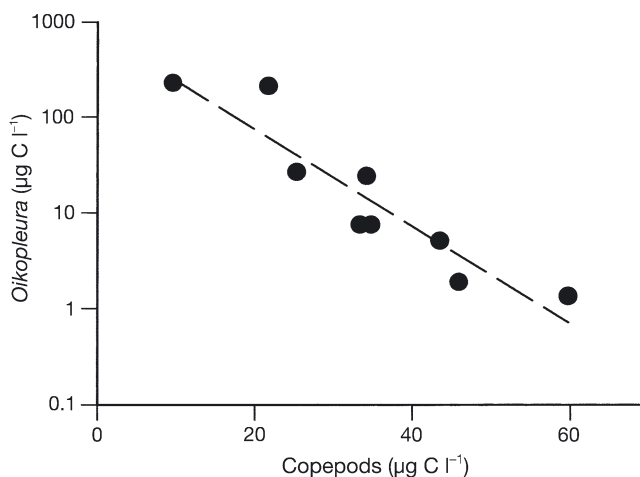

Fig. 4. *Oikopleura dioica* regression of appendicularian biomass on copepod biomass. Linear regression analysis gave: $\log A = 2.895 - 0.0508 \times C$; $F_{(1,7)} = 44.207$; $p < 0.001$, where $A =$ *O. dioica* biomass (mean for Days 10 and 12), and $C =$ copepod biomass (mean biomass during experiment)

copepods (between 40 and 80 µm). Predation on eggs and larval stages could effectively suppress the recruitment of appendicularians. However, until now, copepod predation on appendicularians has only been reported for the carnivorous *Candacia bipinnata* (Ohtsuka & Onbe 1989). Predation by copepods could be influenced by food availability. It depends on the selectivity of copepods for appendicularian eggs/larvae and algae or other microplankton food whether high chlorophyll levels (acting as an alternative food source) can form a refuge from predation for appendicularians. Our results show that copepods also suppressed *Oikopleura dioica* at very high chlorophyll levels. If predation on appendicularian eggs or larvae is the reason for their suppression, high alternative food levels did not offer a refuge from predation.

Inverse relations between the abundances of copepods and appendicularians have also been observed in other studies. King et al. (1980) observed a bloom of *Oikopleura dioica* (13 and 6 ind. l^{-1}) in 2 mesocosms after calanoid copepods declined. A rapid development of *Oikopleura* sp., reaching densities of about 8 ind. l^{-1}, was also observed in mesocosm experiments with low copepod densities (<10 ind. l^{-1}; Koshikawa et al. 1999). Finally, a recent mesocosm study also reported a negative correlation between copepod and appendicularian numbers (Sommer et al. 2003). In addition, field data suggest an inverse relationship between copepod and appendicularian numbers. In a time series of Baltic Sea zooplankton, appendicularians reached high numbers (>20 ind. l^{-1}) only when copepod numbers dropped below 10 ind. l^{-1} (Behrends 1996). We were able to confirm a negative relationship between appendicularian and calanoid copepods through direct experimental manipulation of copepod numbers in controlled conditions under different nutrient conditions. These experimental manipulations resulted in more than 100-fold differences in appendicularian numbers as a function of high and low copepod abundances in the same nutrient regime.

The observed suppression of appendicularians and ciliates by calanoid copepods confirms a role for copepods as a keystone group in the marine plankton (Stibor et al. 2004). Calanoid copepods can have strong top-down effects on both of the other 2 important functional zooplankton groups (unicellular predators and gelatinous filter-feeders). Hence, calanoid copepods may not only structure the zooplankton community but also the phytoplankton community. Copepods simultaneously promote small pico- and nanoplankton by suppressing their main grazers and decimate larger algae such as diatoms and dinoflagellates by direct grazing.

The increasing evidence for calanoid copepods acting as important structuring components of pelagic food webs should be of some relevance to marine aquaculture. Techniques of harvesting copepods as a natural food resource for fish farming have recently gained attention. Such techniques should take into consideration that — at least on a timescale of 2 wk — zooplankton community composition could shift towards gelatinous forms and ciliates if copepods are reduced below a critical density. The initial copepod numbers in the mesocosms (ca. 8 to 50 ind. l^{-1}) was within the normal range observed in Hopavågen during summer for the period 1996–2000 (I. Gismervik unpubl. data). Our data are consistent across the 3×3 experimental treatment matrix; also, on a short timescale, it has been well documented that the transient responses observed in mesocosms of the size we used are both reproducible and ecologically relevant (Castberg et al. 2001). We therefore claim that in addition to the qualitative conclusions regarding mechanisms, our observations should be directly applicable to natural pelagic communities. From our data, we would consider a density of about 10 copepods l^{-1} (copepods of the size of *Acartia* spp. or *Temora* spp.) a critical level below which appendicularians may bloom. Whether this limit is relevant also for long-term field situations requires additional studies of the copepod–appendicularian interaction on a timescale longer than those normally used in mesocosm experiments.

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