Feeding selectivity and egg production of *Calanus helgolandicus* in the English Channel

X. Irigoien, R. N. Head, R. P. Harris, D. Cummings, and D. Harbour

Plymouth Marine Laboratory, Centre for Coastal and Marine Science, Prospect Place, Plymouth PL1 3DH, United Kingdom

B. Meyer-Harms

Alfred-Wegener Institute, Columbusstr., 27568 Bremerhaven, Germany

Abstract

Copepods are able to discriminate between different foods on the basis of particle size and nutritional quality. However, the extent of selective feeding behavior and the mechanisms controlling it in the field are still poorly understood. In this study, we investigated selective feeding behavior and egg production for *Calanus helgolandicus* feeding on natural phytoplankton (using high-performance liquid chromatography techniques), and egg production, at a coastal station off Plymouth with the annual phytoplankton cycle from July 1996 to June 1997. The phytoplankton succession included biomass peaks of dinoflagellates, prymnesiophytes, and diatoms. *C. helgolandicus* showed little selective feeding behavior throughout the study with a slight preference for diatoms. The influence of the diet composition on egg production was analyzed using forward stepwise regression methods. Prymnesiophytes and diatoms were shown to have positive effects whereas the effect of dinoflagellates was negative. The effect of the different phytoplankton peaks is analyzed and discussed in relation to the phytoplankton taxonomic composition and dietary diversity.

Since the initial controversies (*see* Harvey 1937) the ability of calanoid copepods to discriminate between different particles, either as a function of size (Frost 1972) or of food quality (Huntley et al. 1983; Cowles et al. 1988) has been clearly demonstrated in laboratory experiments using phytoplankton cultures. Video techniques have also helped us to understand the mechanisms used by copepods to detect, capture, and manipulate different particles as a function of their characteristics, their concentration, or the physical environment (Paffenhöfer 1988; Price 1988; Kiørboe and Saiz 1995).

However, field studies are less conclusive (Poulet 1978; Huntley 1981) and the factors, other than the size (Cowles 1979), governing selective feeding from natural particulate assemblages are still doubtful. Optimal foraging theory has been advanced as an explanation of selectivity in the field (DeMott and Moxter 1991; DeMott 1993, 1995*a,b*), hypothesizing that the intensity of selection should depend on the concentration of high-quality food. This has been demonstrated in the laboratory with pairs of particles (DeMott 1993) and in the field with the same food (DeMott 1995*a,b*). However, other studies provide evidence for nonselective feeding by copepods on natural particle mixtures (Huntley 1981; Turner and Tester 1989).

On the other hand, the fact that different phytoplankton species have a different nutritional value is generally acknowledged (Koski et al. 1998) and it has been shown that models based on carbon or Chl *a* ingestion are often not adequate to explain variations in copepod secondary production (Ohman and Runge 1994; Pond et al. 1996). Furthermore, the traditionally dominant role of diatoms in copepod nutrition has been challenged in favor of dinoflagellates and heterotrophic microzooplankton (Kleppel et al. 1991; Ohman and Runge 1994) though it is likely that results have to be considered in the context of both area and season (Kiørboe and Nielsen 1994).

In the present work, we addressed these problems by studying the composition of the diet in the field, together with selectivity and egg production, in relation to annual phytoplankton succession for one of the dominant copepods in the North Atlantic, *C. helgolandicus*.

Material and methods

Weekly samples were collected between July 1997 and June 1998 from a coastal station (Sta. L4: 50°15′N, 4°13′W) about 10 km off Plymouth in the English Channel.

Seawater for the experiments was collected from 10 m with a water bottle. Animals for feeding and egg production experiments were collected by slow and short duration oblique tows using a 500-μm WP2 net. All samples were transported back to the laboratory within 2 h of collection.

Water samples for microplankton species identification and carbon estimation were preserved with 1% final concentration Lugol's iodine solution and a separate sample was fixed with neutral formalin for determination of coccolithophorids (Holligan and Harbour 1977). One hundred milliliter subsamples were settled (Utermöhl) and counted with an inverted microscope. Phytoplankton carbon biomass was es-

timated from cell volume according to Strathman (1967) and using a factor of 0.21 pg C μm^{-3} (Ohman and Runge 1994) for ciliates. Heterotrophic dinoflagellates were separated from autotrophic forms according to taxonomical considerations (Lessard and Swift 1986).

Samples of 500 ml were filtered through a 25 mm Whatman GF/F filter, and stored frozen at $-30°$C for POC analysis. Before analysis the filters were fumed with sulfurous acid to eliminate carbonates, then dried at $50°$C to remove excess acid, and analyzed with a Carlo-Erba Elemental Analyser, Model NA1500.

Feeding rates on the different phytoplankton taxa were estimated by incubating 5 to 10 healthy female *C. helgolandicus* in 1-liter bottles filled with the natural particulate assemblage collected at 10 m. Four replicates and three control bottles were incubated for 24 h at sea surface temperature, 12 h dark/light cycle, and rotating on a plankton wheel at 0.2 rpm. At the end of the experiments, individuals were checked for mortality though no mortality was found in any of the experiments. A 1-liter sample was taken at the start of the experiment and 900-ml samples from each of the replicates and controls were collected at the end of the experiment. All the samples were filtered through Whatman GF/F filters and frozen at $-80°$C until further high-performance liquid chromatography (HPLC) analysis.

Marker pigments were analyzed by HPLC following Barlow et al. (1997). The marker pigments identified and employed to determine taxon specific contribution to Chl *a* were: chlorophyll c3, chlorophyll c1 + c2, peridinin, 19′-butanoyloxyfucoxanthin, fucoxanthin, 19′-hexanoyloxyfucoxanthin, diadinoxanthin, alloxanthin, zeaxanthin, lutein, Chl *b*, and Chl *a*.

The contribution of each major phytoplanktonic taxon to Chl *a* was calculated by using the CHEMTAX program developed by Mackey et al. (1996). The calculated concentration of each algal group to Chl *a* was used to calculate the taxon specific grazing rates according to Frost (1972).

CHEMTAX requires the use of input matrices with approximate marker pigment Chl *a* ratios to calculate the final marker pigment Chl *a* ratio and the group-specific Chl *a* concentration. During the study the dominance of some species with particular marker pigments required the use of different input matrices for particular periods:

a) From 21 July 1997 to 18 August 1997: The dinoflagellate bloom was strongly dominated by *Gyrodinium aureolum* (>90% of the carbon) and required special initial marker pigments : Chl *a* ratio matrix for this period because its pigment composition differs from the normal pigment composition of dinoflagellates which have peridinin as the marker carotenoid (Wright and Jeffrey 1997). This species has 19′-hexanoyloxyfucoxanthin and fucoxanthin instead of peridinin (Johnsen and Sakshaug 1993).

b) From 18 August 1997 to 1 September 1997: The haptophytes were solely represented by *Emiliania huxleyi*. Hence the pigment to Chl *a* ratios of this group was used in the input matrix (*see* Jeffrey and Wright 1994).

c) From 7 May 1998 to 11 May 1998: The haptophyte bloom was dominated by *Phaeocystis pouchetii* and required special initial marker pigments : Chl *a* ratio matrix because its pigment composition with fucoxanthin as marker pigment

differs from the general pigment composition of haptophytes with 19′-hexanoyloxyfucoxanthin as marker carotenoid (Jeffrey and Wright 1994).

d) The input matrix focused on the residual sampling period. The pigment to Chl *a* ratios used correspond to the common ratios used for each group according to Mackey et al. (1996).

The input and output matrices of marker pigments Chl *a* ratio used and obtained with CHEMTAX can be found as a Web table in the Limnology and Oceanography website ⟨http://www.aslo.org/lo/pdf/vol_45/issue_1/0044al.pdf⟩ or upon request to the authors.

Selective feeding behavior was characterized in two ways:

- Using the chi-square (χ^2) test to compare the frequency distribution of food types in the diet and the frequency distribution in the environment in each experiment (Cowles 1979; Kleppel et al. 1996); and
- By comparing the slopes (ANCOVA analysis of covariance) of the taxon specific ingestion versus taxon abundance regressions to integrate all the information.

Food selection on specific phytoplankton groups was quantified using the selectivity index (SI) α (Chesson 1978):

$$\alpha_i = r_i/p_I\{(r_i/p_i)/[(r_i/p_i) + (r_j/p_j)]\}$$

where r_i is the frequency of prey i in the diet, p_i is the frequency of prey i in the environment, r_j is the frequency of other prey in the diet and p_j is the frequency of other prey in the environment. This index, α, varies between 0 and 1 with $\alpha_i = 0.5$ indicating nonselective feeding towards the prey i, $\alpha_i > 0.5$ indicates a preference for the prey i and $\alpha_i < 0.5$ indicates discrimination against the prey i.

Egg production was measured by placing 5 females in 2-liter glass beakers filled with GF/A filtered seawater. Each beaker contained a Plexiglas egg production tube (500-μm mesh) to avoid egg cannibalism. Five replicates were incubated for 24 h in filtered seawater at environmental temperature.

Results

Phytoplankton succession—During summer and autumn of 1997, the phytoplankton was dominated by two successive blooms of dinoflagellates each of which was practically monospecific (more than 90% of the carbon due to a single species). The first one, reaching a maximum Chl *a* concentration of 6 mg m^{-3} was composed of the dinoflagellate *Gyrodinium aureolum* (~25 μm ϕ), known to be ichthyotoxic, whereas the second was composed of *Prorocentrum balticum* (~9–15 μm ϕ), and only reached a Chl *a* concentration of 2 mg m^{-3}. The winter period was dominated by diatoms and small flagellates (haptophytes and cryptophytes) with Chl *a* concentrations usually under 0.5 mg m^{-3}. From the end of January to the beginning of March 1998 Chl *a* showed an initial peak around 1 mg m^{-3} due to an increase in diatoms, mainly *Nitzschia closterium* (~2 × 25 μm), *Skeletonema costatum* (~3 μm cells, 8 or 16 cells per chain), *Podosira stelliger* (~40 μm ϕ), and small *Thalassiosira* sp. (~5–10 μm ϕ). By the middle of April 1998 a bloom of the haptophyte *Phaeocystis pouchetii* (~6 μm ϕ each cell, mm
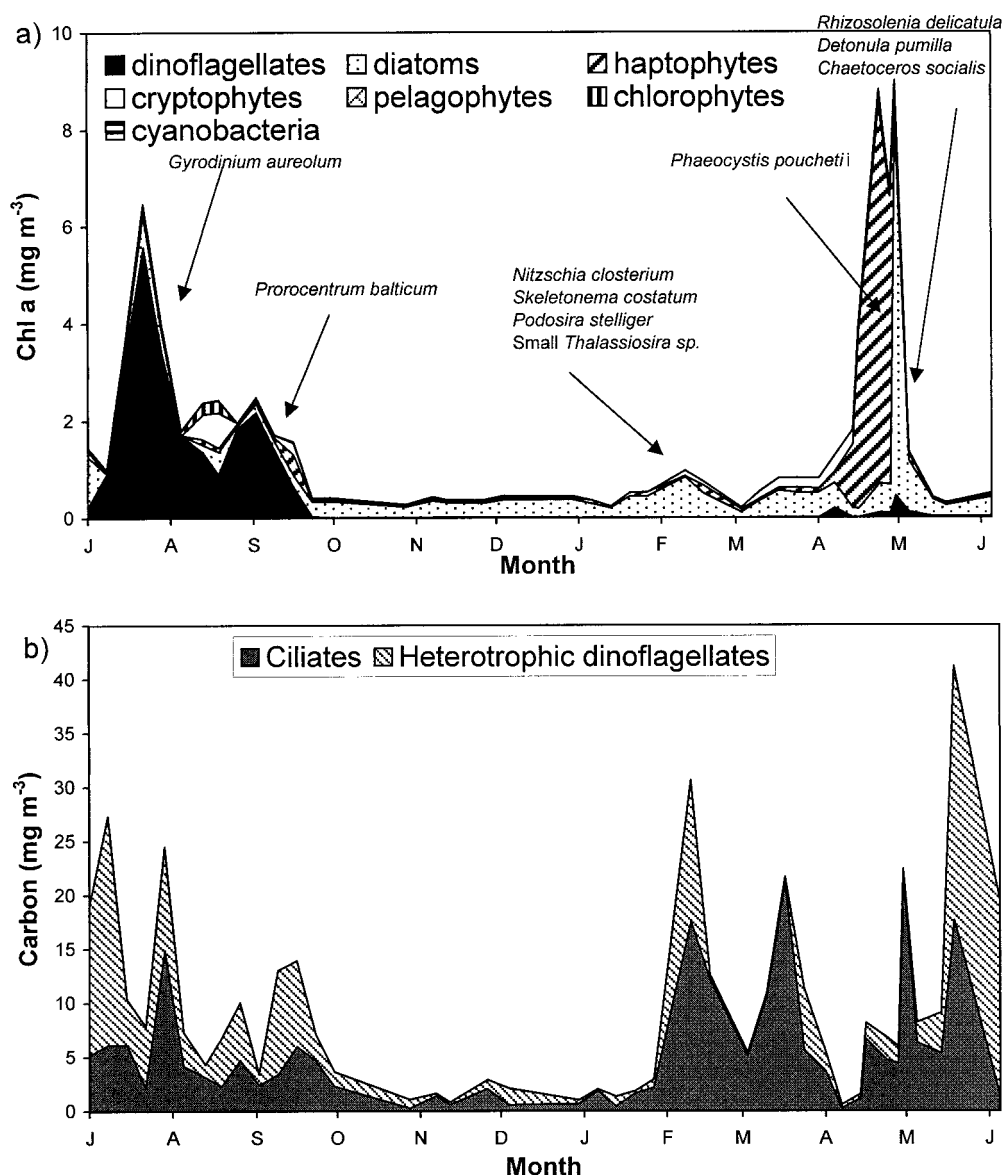
Fig. 1. Seasonal evolution of the contribution of the different groups to the microplankton biomass. (a) Contribution of the different phytoplanktonic groups to total Chl *a*. The most abundant species are indicated. (b) Seasonal evolution of the heterotrophic microplankton biomass.

for colonies), with maximum Chl *a* concentrations around 9 mg m^{-3} developed. This bloom was succeeded by a bloom of diatoms with comparable Chl *a* concentrations (9 mg m^{-3}) mainly composed of *Rhizosolenia delicatula* (~12 × 35 μm), *Detonula pumila* (~25 × 25 μm), and *Chaetoceros socialis* (~5 μm cells, 5 or 10 cells per chain) (Fig. 1a).

Heterotrophic microplankton (ciliates and colorless dinoflagellates) showed three periods of higher abundance; summer 1997, February–March 1998 coinciding with the small diatom bloom, and June 1998 (Fig. 1b). During summer 1997, the ciliate population shifted from a *Mesodinium* (~15–20 μm φ) dominance to a *Strombidium* (~10–20 μm φ) dominance, whereas the dominant colorless dinoflagellates were *Polykrikos schwartzii* (~10 × 25 μm) and *Noctiluca scintillans* (~500 μm φ). During the winter the dom-

inant ciliate type was *Strombidium* and the colorless dinoflagellate *Gyrodinium* sp. (~25 × 10 μm).

During the ciliate peak in February–March the composition shifted from *Mesodinium* to *Strombidium* dominance, which then persisted for the rest of the study period. During spring 1998, the dominant colorless dinoflagellates were *Gyrodinium* sp. and *Protoperidinium* sp. (~30 μm φ).

Except for some easily identifiable species, carbon to chlorophyll ratios could not be estimated for each of the phytoplankton groups because haptophytes, cryptophytes, and pelagophytes were not distinguished in the microscopic counting. Considering the phytoplankton carbon estimated from all cells together and the Chl *a* value measured, we obtained an average C:Chl *a* ratio of 51.1 (SE = 8.1).

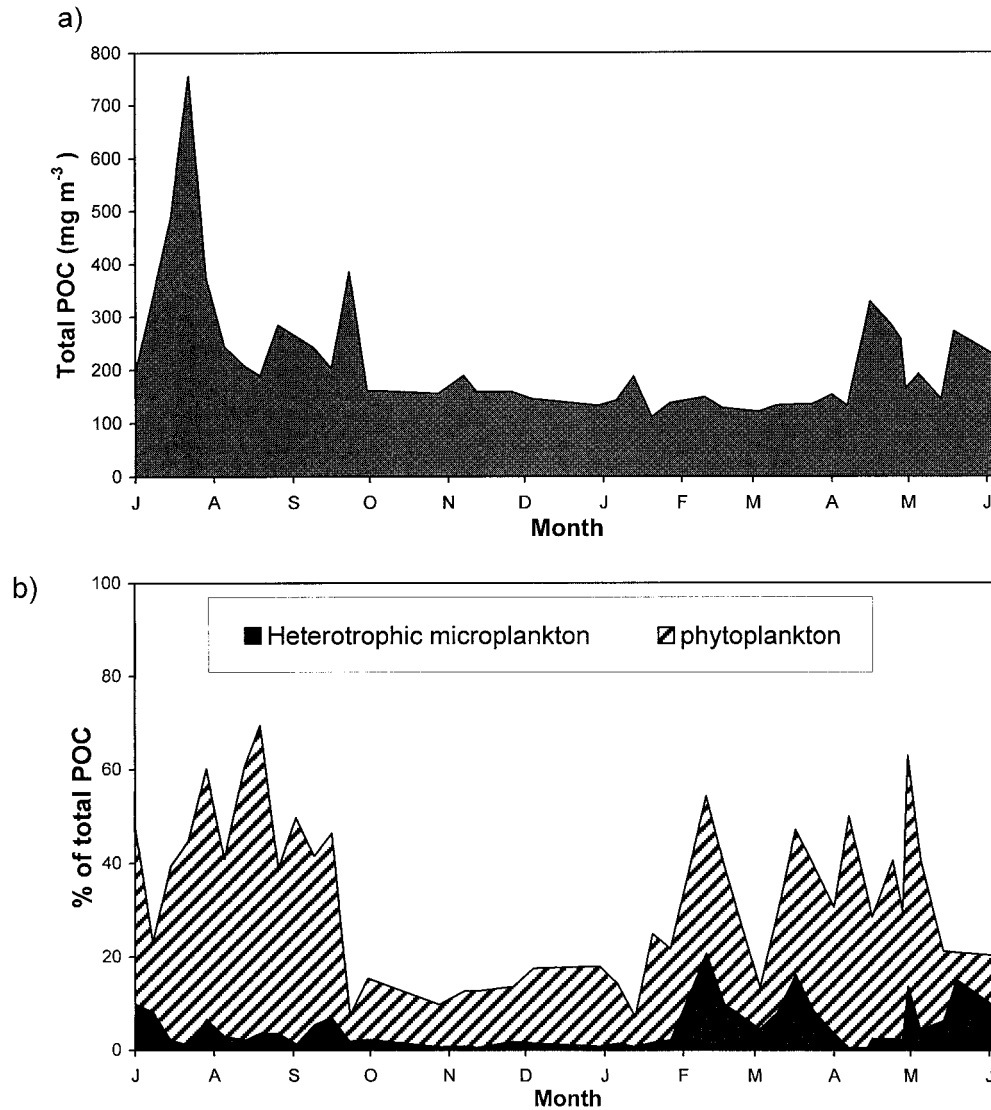Total POC and the percentage of the total POC repre-

a)

b)

Fig. 2. Seasonal evolution of: (a) The total POC concentration, and (b) the percentage of the total POC represented by phytoplanktonic and heterotrophic microplanktonic carbon.

sented by phytoplankton and heterotrophic carbon is presented in Fig. 2a,b. Phytoplankton and heterotrophic carbon represented from 40 to 60% of the total POC during the bloom periods and less than 20% during the winter period.

Ingestion and selectivity—Ingestion by *C. helgolandicus* was never detected for three of the seven phytoplankton groups determined with CHEMTAX, pelagophytes, green algae, and cyanobacteria. On the contrary, their abundance increased in the incubation bottles compared to the controls suggesting a cascade effect on the food chain, *C. helgolandicus* relaxing the predation pressure on those groups by feeding on ciliates and heterotrophic dinoflagellates. However, pelagophytes, green algae, and cyanobacteria were of minor importance in terms of overall abundance.

The seasonal variation in the total and relative taxonomic specific contribution to the diet is presented in Fig. 3a,b. The ingestion of the most abundant phytoplankton groups, di-

noflagellates, diatoms, haptophytes, and cryptophytes was linearly related to the concentration of those groups (Fig. 4a–d). Table 1 summarizes the regressions established for each group, both with all the data, and also excluding the bloom values in the case of diatoms (one point), and haptophytes (four points). In order to determine if there was a general preference for any of those groups the slopes of the regressions were compared using an Analysis of Covariance (ANCOVA). When all the data were included the slope of the ingestion versus concentration regression for diatoms appeared to be significantly higher than the slopes for haptophytes, cryptophytes, and dinoflagellates. The slope for haptophytes was significantly higher than that of dinoflagellates but not so when compared to that of cryptophytes. If the highest point of the diatom regression is excluded, the slope for diatoms was no longer significantly greater than the ones for haptophytes and cryptophytes but remained significantly higher than that for dinoflagellates. When the bloom of *P.*
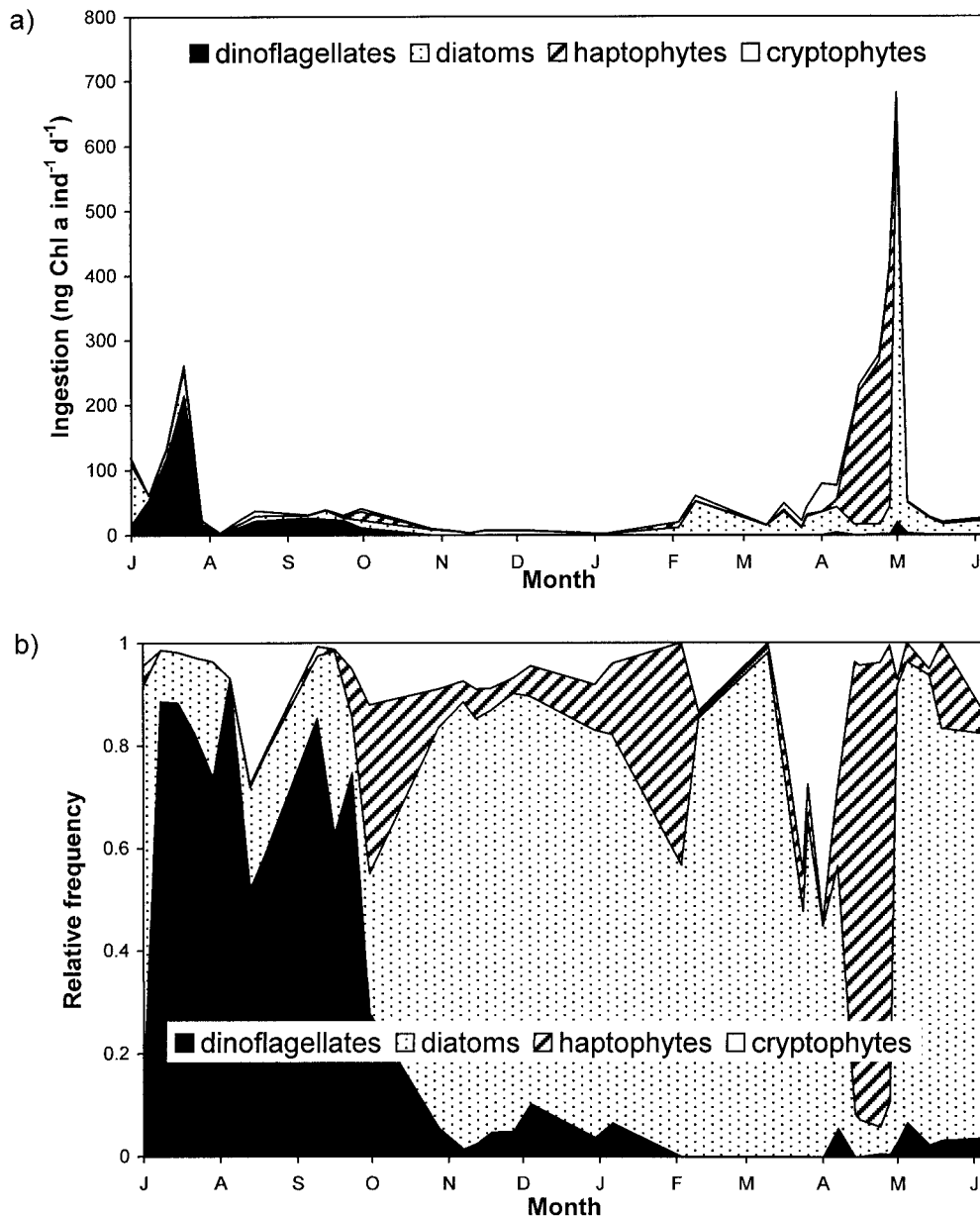
Fig. 3. Evolution of the phytoplanktonic taxon specific ingestion. (a) Total contribution of each phytoplankton group. (b) Relative contribution of each phytoplankton group.

pouchetii was excluded from the analysis the slope for haptophytes was not significantly different from that of dinoflagellates (Table 2).

Selectivity in each experiment was analyzed by comparing the frequency distribution of the four main phytoplankton groups in the diet to the frequency distribution of the same groups in the environment by means of a χ^2 test. Additionally, selectivity for each group was tested using the Chesson (1978) α selectivity index. In none of the experiments was the frequency distribution in the diet significantly different from that in the environment ($P > 0.05$) (Fig. 5a). Some higher χ^2 values were related to high values of the selectivity index for cryptophytes and diatoms (Fig. 5a,b), but the χ^2 value did not show any relation to the abundance of any

particular group or to the total Chl a (Fig. 6). The inclusion of the three remaining groups, pelagophytes, cyanobacteria, and green algae, in the χ^2 calculation does not result in significant differences from the previous results because their contribution to the diet is considered to be zero and their contribution to the total Chl a is also very low (*see* Fig. 1).

The highest selectivity indices corresponded to cryptophytes at the end of the first dinoflagellate bloom, to diatoms during the second dinoflagellate bloom, and to dinoflagellates during the winter period (Fig. 5b). In general terms selectivity indices were positive for diatoms and cryptophytes, and negative for dinoflagellates and haptophytes (Fig. 7). Selectivity indices distributions for diatoms were significantly different from those of dinoflagellates, hapto-
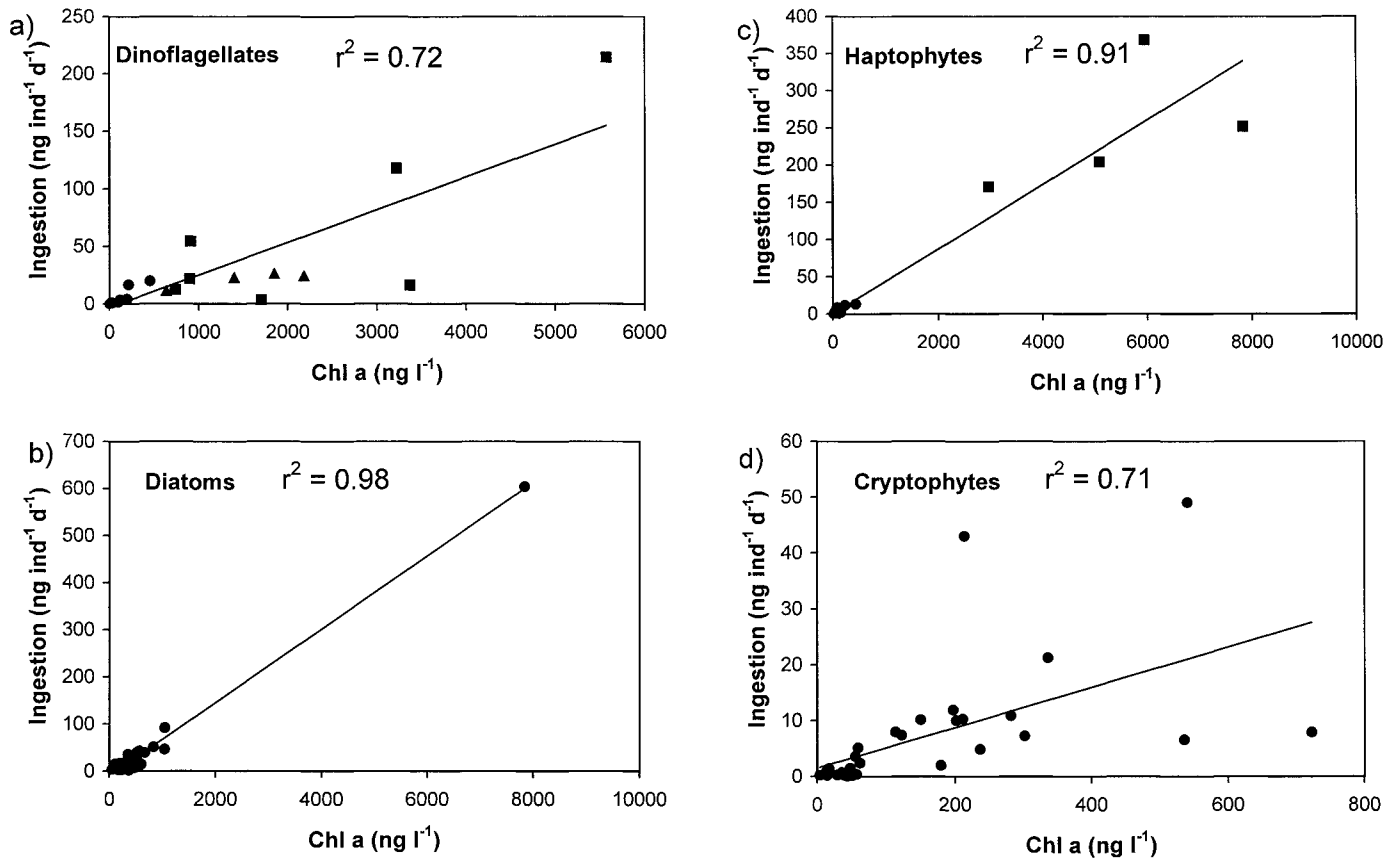
Fig. 4. Relationship between taxon specific ingestion and taxon specific abundance for the different phytoplankton groups. Squares for *G. aureolum* and triangles for *P. balticum* in the figure for dinoflagellates and squares for *P. pouchetii* in the figure for haptophytes.

phytes, and cryptophytes (Kolmogorov–Smirnov, $P < 0.05$). There were no significant differences between the dinoflagellates, haptophytes, and cryptophytes (Kolmogorov–Smirnov nonparametric, $P > 0.05$). The selectivity indices were not related either to the concentration of the specific group or to the concentration of total Chl *a*.

Egg production and its relation to taxon specific ingestion—Variations in *C. helgolandicus* egg production are shown in Fig. 8. Egg production rates ranged from 1 egg fem^{-1} d^{-1} during the winter to a maximum of 33 egg fem^{-1} d^{-1} during the 1998 spring bloom. Interesting features are

Table 1. Regressions between the taxon specific ingestion and taxon specific abundance.

Regression	r^2	n	P
IR Chl a = 0.049 Chl a − 15	0.76	40	<0.01
IR Dino = 0.028 Dino − 3.53	0.72	28	<0.01
IR Diat = 0.078 Diat − 10.23	0.98	36	<0.01
IR Hapto = 0.043 Hapto + 0.74	0.91	32	<0.01
IR Crypto = 0.036 Crypto + 1.5	0.71	33	<0.01
IR Diat* = 0.06 Diat − 3.6	0.57	35	<0.01
IR Hapto† = 0.037 Hapto − 0.42	0.71	28	<0.01

* Excluding the highest Chl *a* value.
† Excluding the *P. pouchetii* bloom.

the significant increase in egg production during February 1998 which coincides with a small peak of Chl *a*, and the high egg production level maintained after the 1998 spring bloom. However, these periods also correspond with periods of high concentrations of heterotrophic dinoflagellates and ciliates (Fig. 1b).

The influence of the composition of the diet on egg production was investigated using forward stepwise regressions between egg production and the ingestion rates of the different groups. The ingestion rates were transformed as $\ln(x + 1)$ to linearize the relation between egg production and ingestion. Results for different data combinations are shown in Table 3. In general terms, egg production was explained by haptophyte and diatom ingestion whereas the effect of dinoflagellates appeared to be negative. The relative influence of the different blooms was investigated by repeating the analysis without the data corresponding to a specific peak. Excluding the *G. aureolum* bloom, a species known to be potentially toxic, from the analysis, the negative effect of dinoflagellates remained with an even increased significance. Excluding the two dinoflagellate bloom periods, only haptophytes and diatoms were significant. Excluding the haptophyte bloom (*P. pouchetii*, four points), diatoms were the main factor explaining egg production ($r^2 = 0.36$) with a small but significant negative influence of dinoflagellates (Table 3).

Table 2. Results from the ANCOVA comparison of the slope of the regressions presented in Table 1. The probability of the slopes to be significantly different is in parentheses.

	Chl a	Dino	Diat	Hapto	Crypto	Diat*
Chl a						
Dino	5.88 ($P < 0.05$)					
Diat	16.88 ($P < 0.01$)	178.9 ($P < 0.01$)				
Hapto	0.75 (n.s.)	11.24 ($P < 0.05$)	102.1 ($P < 0.01$)			
Crypto	0.06 (n.s.)	0.17 (n.s.)	12.2 ($P < 0.01$)	0.12 (n.s.)		
Diat*	0.12 (n.s.)	5.49 ($P < 0.05$)	3.47 (n.s.)	1.28 (n.s.)	2.99 (n.s.)	
Hapto†	0.01 (n.s.)	0.04 (n.s.)	3.16 (n.s.)	0.023 (n.s.)	0.001 (n.s.)	1.1 (n.s.)

* Excluding the highest Chl a value.
† Excluding the *P. pouchetii* bloom.

Egg production was not related to temperature, either taking temperature as a single factor or including it in the forward multiple regression model with the components of the diet. Surprisingly, neither was there a relation between the heterotrophic microplankton concentration and egg production (Fig. 9).

Discussion

Except for the complete lack of feeding on pelagophytes, cyanobacteria, and green algae, *C. helgolandicus* showed little selectivity between the four main phytoplankton groups during the seasonal cycle off Plymouth. In general, there appears to be a preference for diatoms (higher slope of the diatom ingestion–diatom abundance relationship and higher selectivity indexes in general), but when the experiments were considered individually no significant differences between the diet and environmental abundance were found. Overall, these results agree with the findings of Huntley (1981) for related species of the same genus (*C. finmarchicus, C. glacialis*, and *C. hyperboreus*) who found a nonselective and nonsaturated feeding behavior. In our case, we found a nonsaturated feeding behavior for a range of Chl a concentrations ranging from 0.5 to 9 mg m^{-3} and with weak selectivity. In contrast, Meyer-Harms et al. (1999), for *C. finmarchicus* in the Norwegian Sea, found nonsaturated but clearly selective feeding behavior. However, this difference may be explained because during this study, green algae, which were not ingested as in our case, were much more abundant in the Norwegian Sea, ranging from 10 to 40% of the total Chl a. This indicates that the statistical results have to be considered carefully because the same behavior can be interpreted as selective or nonselective as a function of the composition of phytoplankton population.

The lack of feeding on pelagophytes and cyanobacteria (*Synechococcus* sp.) could be explained by size selection, both groups being represented by small cells which are generally believed not to be efficiently captured (Paffenhöfer 1988; Kleppel et al. 1998). Feeding on green algae seems to be species specific, with some works reporting avoidance (Johnson et al. 1982; Meyer-Harms et al. 1999) or poor reproductive success (Støttrup and Jensen 1990; Koski et al. 1998), whereas other results with other species suggest a higher nutritive value (Koski et al. 1998; DeMott 1995a; DeMott and Müller-Navarra 1997). Nevertheless, in our
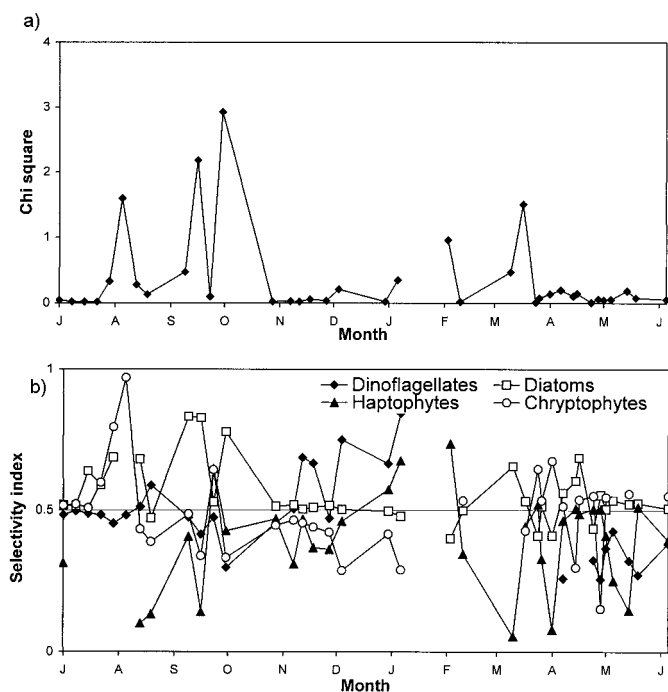

Fig. 5.   Seasonal evolution of selectivity. (a) Evolution of the chi-square (χ^2) value. (b) Evolution of the selectivity index (α_i) for each group (diamonds for dinoflagellates, squares for diatoms, triangles for haptophytes, and circles for cryptophytes). For differences to be significant, the chi-square value should be over 11.
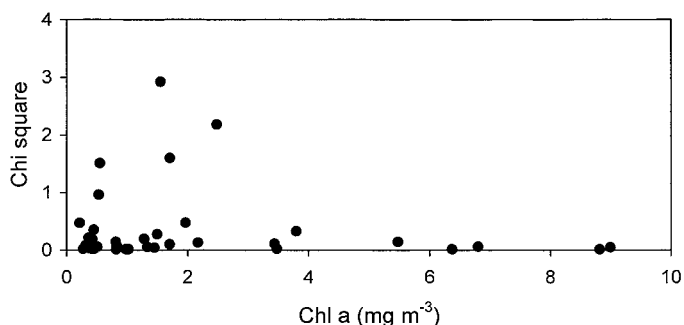

Fig. 6.   Relationship between the chi-square value and the total Chl a concentration.
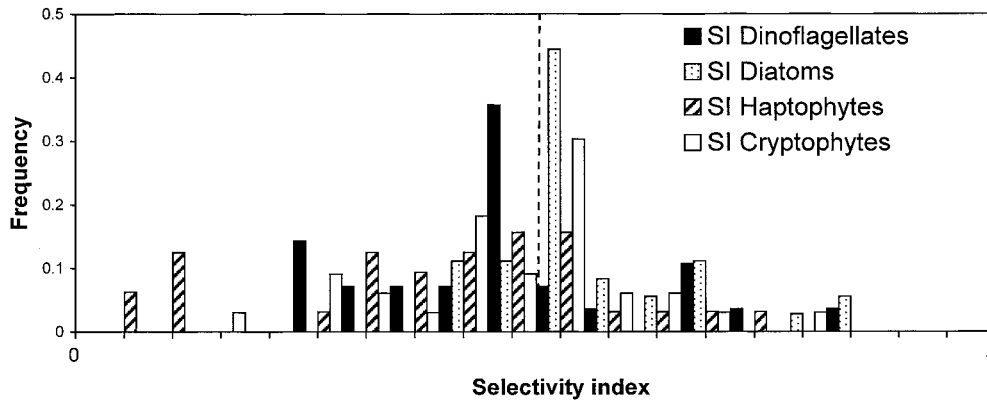
Fig. 7. Distribution of the selectivity index values (α_i) for the different groups. Each division represents a range of 0.05. The dotted line indicates the 0.5 value.

case, a size selection cannot be excluded as no green algae were identified in the fraction of cells larger than 5 μm in the microscopic counts. However, it has to be recognized that in the sea, size selection is in practice a kind of quality selection, first because the volume increases exponentially in relation to the linear dimension, so a small increase in size will represent an important increase in the volume of cytoplasm ingested and second because in the water column any large dead particle, that is without a buoyancy system or swimming activity will sink rapidly, whereas a small particle is more likely to remain in suspension even if dead.

Neither the selectivity (χ^2 value) nor the selectivity indices showed any relation with variations in Chl *a* concentration. However, this result is not necessarily in contradiction with the predictions of the optimum foraging theory because in this study we analyzed variations in selectivity between particles, which for the copepod, are, a priori, all of high quality (phytoplankton) and not between particles of very different food quality such as phytoplankton compared to detritus (DeMott 1993; DeMott 1995*a,b*).

Variations in the selectivity indices suggest a tendency to diversify the diet, with higher selectivity indices for different groups when one component of the diet is dominant, e.g., the higher selectivity towards cryptophytes and diatoms during the dinoflagellate blooms or the higher selectivity towards dinoflagellates during the winter when diatoms were dominant in the diet.

The influence of diet on egg production indicates the im-

portance of food abundance, with higher egg production rates related to the higher ingestion during spring 1998, but also emphasizes the importance of the diversity of the diet already established by Kleppel (1993). The two dinoflagellate blooms appear to have had negative effects on egg production rate. This result seems to contradict recent findings suggesting an important role of dinoflagellates in supporting copepod egg production (Kleppel et al. 1991), however, the results can also be interpreted in terms of diversity in the diet. In contrast to the diatom bloom, both dinoflagellate blooms were essentially monospecific with more than 90% of the carbon contributed by a single species. A number of studies have already shown that some phytoplankton species have low levels, or lack, essential nutritional components for growth and egg production, particularly polyunsaturated fatty acids (Jónasdóttir 1994; Jónasdóttir and Kiørboe 1996; DeMott and Müller-Navarra 1997) and some amino acids (Kleppel 1993; Kleppel et al. 1998). A wide taxonomic diversity in the nutritional quality of dinoflagellates has been reported (Gill and Harris 1987; Huntley et al. 1987; Koski et al. 1998) and in previous studies off Plymouth the *G. aureolum* bloom corresponds with low levels of polyunsaturated fatty acids in the 20–200-μm size fraction of the particulate material (Pond et al. 1996).

Another explanation for the negative effect of the two dinoflagellate blooms may be toxicity whose effects could be confused with those of nutritional adequacy (Jónasdóttir et al. 1998). *G. aureolum* is often reported to result in im-
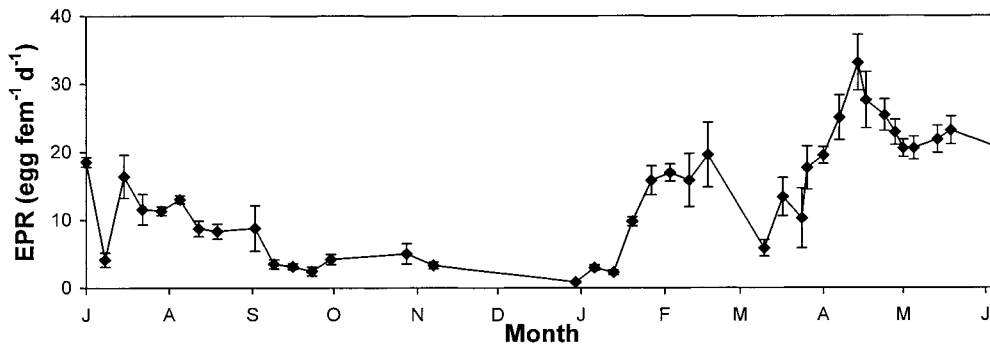

Fig. 8. Seasonal evolution of the *C. helgolandicus* egg production at L4.

Table 3. Results from the different stepwise forward multiple regression analyses between the egg production and the taxon specific ingestion. Ingestion data are transformed as Ln $(x + 1)$.

	Regression	r^2	n	Partial r^2	r^2	P
All data	EPR = 2.5 Ln (IR Hapto + 1) + 2.6 Ln (IR Diat + 1) − 0.8 Ln (IR Dino + 1) + 2.96	0.55	33	IR Hapto IR Diat IR Dino	0.43 0.1 0.02	<0.01 <0.05 0.27
Without high value diatoms	EPR = 2.7 Ln (IR Hapto + 1) + 3.1 (Ln IR Diat + 1) + 1.87	0.53	32	IR Hapto IR Diat	0.42 0.11	<0.01 <0.05
Without *G. aureolum* bloom	EPR = 2.82 Ln (IR Hapto + 1) + 4.00 Ln (IR Diat + 1) − 2.6 Ln (IR Dino + 1) + 0.33	0.68	25	IR Hapto IR Diat IR Dino	0.45 0.15 0.1	<0.01 <0.01 <0.05
Without *P. balticum* bloom	EPR = 2.83 Ln (IR Hapto + 1) + 2.23 (Ln IR Diat + 1) + 4.95	0.61	29	IR Hapto IR Diat	0.52 0.09	<0.01 <0.05
Without high dinoflagellates	EPR = 2.71 Ln (IR Hapto + 1) + 5.44 (Ln IR Diat + 1) − 9.27	0.72	18	IR Hapto IR Diat	0.52 0.2	<0.01 <0.01
Without *P. pouchetii* bloom	EPR = 3.66 Ln (IR Diat + 1) − 0.83 Ln (IR Dino + 1) + 3.37	0.39	29	IR Diat IR Dino	0.36 0.03	<0.01 <0.05

portant fish mortality (Tangen 1977) having perhaps toxic and nontoxic phases (Bullock et al. 1985). However, Partensky et al. (1989) reported that the cytotoxin content is extremely low and that the fish mortality is more likely to be due to the mucilage secreted by the algae. Gill and Harris (1987), reported low egg production by *C. helgolandicus* feeding on *G. aureolum* and also lower mortality in relation to the other diets. Other species of the genus, *C. pacificus* and *C. finmarchicus*, have been shown to have the ability to reject toxic dinoflagellates (Huntley et al. 1986) or even to select between toxic and nontoxic strains of the same dinoflagellate (Turriff et al. 1995), but in our experiments *G. aureolum* was ingested at significant rates and no mortality was detected. Furthermore, the strongest negative effect on egg production was due to *Prorocentrum balticum*, for which we have not found any report of toxicity in the literature. These considerations suggest that the negative effect on egg production was rather due to a nutritional deficiency caused by a nearly monospecific diet rather than to toxic effects of the dinoflagellates.

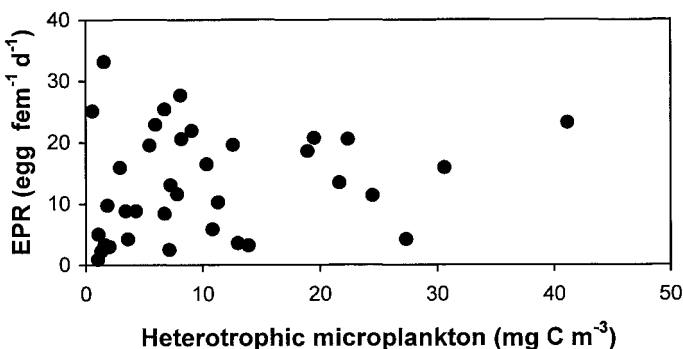Compared to the phytoplankton, heterotrophic microplankton was less abundant than in previous years (Pond et al. 1996). However, the lack of correlation between egg production and the heterotrophic microplankton biomass is still surprising because if we use egg production to calculate carbon requirements (300 ng C egg^{-1} and 30% gross growth efficiency; Pond et al. 1996; Hirche 1996) it is only during the bloom periods that >100% of the egg production requirements are covered by phytoplankton ingestion. Filtration and ingestion rates on ciliates have been reported to be higher than on phytoplankton (Gifford et al. 1995; Irigoien et al. 1998), so it is likely that the contribution of heterotrophic microplankton to the diet is disproportionate to their abundance, as is suggested by the rapid increase in the grazing bottles of some of the usual prey of the heterotrophic microplankton (pelagophytes and cyanobacteria). However, total carbon ingestion budgets extrapolated from egg production have to be considered carefully in *Calanus* because at least part of the vitellogenesis is fuelled by lipids (Gatten et al. 1980; Niehoff and Hirche 1996) that are accumulated during growth and development.

In conclusion, our results indicate little selectivity between the four main phytoplankton groups with large cells. That the selection against cyanobacteria, pelagophytes, and green algae was only due to their small size cannot be excluded.

Selectivity between the major phytoplankton groups was not related to the Chl *a* concentration, the results suggesting a tendency to diversify the diet.

In addition to the quantitative aspect, the analysis of the effect of the diet on egg production indicates the importance of the nutritional quality of the total capturable food supply, whether this is a mixed diet or a monospecific bloom.

Fig. 9. Relationship between heterotrophic microplankton biomass and the egg production rate.

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