Journal of Plankton Research Vol.20 no.5 pp.957–972, 1998

Ingestion rates of phytoplankton by copepod size fractions on a bloom associated with an off-shelf front off NW Spain

Susana Barquero, Jesús A.Cabal[1], Ricardo Anadón[1], Emilio Fernández[2], Manuel Varela and Antonio Bode

Instituto Español de Oceanografía, Centro Costero de La Coruña, Apdo. 130, E 15080 La Coruña, [1]Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, E 33006 Oviedo and [2]Departamento de Ecología y Biología Animal, Universidad de Vigo, Campus Lagoas-Marcosende, E 36200 Vigo, Spain

Abstract. Herbivory by copepods was studied from the coast towards the ocean, during a bloom in May 1994 off NW Spain. Ingestion rates were estimated by the gut chlorophyll content method in three size fractions. The chlorophyll content displayed significant daily cycles. Three different water bodies were described: coastal, shelf break and oceanic; the latter two zones separated by a thermohaline frontal structure. Marked differences in plankton species composition, vertical distribution and biological rates were found between zones. The highest phytoplankton biomass, dominated by chain-forming diatoms, occurred in the oceanic zone associated with low primary production rates. Copepod feeding had a low effect on oceanic phytoplankton; up to 0.2% of carbon stock and <3% of carbon production was consumed daily. In contrast, medium-sized and large copepods removed 3% of carbon stock and 12% of primary production daily near the coast, where phytoplankton were dominated by small flagellates in active growth. The highest variability in both plankton composition and ingestion rates was found in the shelf-break zone, probably due to displacements of the front. Copepods exerted a moderate predation pressure on phytoplankton in coastal waters. Meanwhile, the impact of copepods on the offshore bloom was negligible and the fate of the accumulated particulate carbon would be mostly determined by sedimentation and water dynamics.

Introduction

Copepod feeding generally has a relatively low impact on phytoplankton spring blooms (Bautista and Harris, 1992; Dagg, 1993; Dam *et al.*, 1993). This could be mainly attributed to the time lag in the growth of overwintering copepod populations, when compared to the faster growth of phytoplankton. However, copepods may sometimes consume high absolute amounts of carbon in shelf areas (e.g. Landry *et al.*, 1994a). The effect of foraging strongly depends on the size structure of copepod populations, as feeding rates are related to body mass (Head *et al.*, 1996).

In this paper, we study ingestion rates of three size fractions of planktonic copepods during a phytoplankton spring bloom near the continental slope off Galicia (NW Spain), which extended from coastal to oceanic waters across a thermohaline front, during May 1994 (Bode *et al.*, 1994b). Fronts or transition structures between different water masses are common during winter and early spring over the NW Spanish shelf. Their causative mechanisms have been related to the poleward currents that flow parallel to the shelf break along the NW European shelf (Frouin *et al.*, 1990; Haynes and Barton, 1990). Chemical and physical characteristics of the water zones related to fronts, along with the associated water dynamics, are known to affect the distribution and composition of planktonic organisms

strongly. These interactions are particularly important in early spring, when the highest concentrations of phytoplankton and primary production rates occur in this region (Bode *et al.*, 1990, 1997; Fernández *et al.*, 1991, 1993; Casas *et al.*, 1997). However, the effect of consumers on those front-associated phytoplankton blooms has not yet been investigated. Previous studies off the Galician coast estimated that zooplankton grazing would be able to remove a considerable fraction of the phytoplankton stock and production (Braun *et al.*, 1990; Tenore *et al.*, 1995). In contrast, other studies indicate that the bulk of phytoplankton biomass after blooms either sinks, with the help of local hydrographic phenomena (Varela *et al.*, 1991; Bode *et al.*, 1994b, 1998), or is consumed '*in situ*' by entering into microbial food webs (Bode and Varela, 1994).

Method

Water column observations and plankton samples were taken during the AMBAR-594 cruise carried out on board RV 'Cornide de Saavedra' off the Galician coast (NW Spain) in May 1994. In six stations out of a transect of 15 (Figure 1), plankton variables were sampled intensively through cycles of 24 h, and two swift runs were made for environmental measurements along the whole transect [a description of the chemical, physical and biological conditions during the cruise is available in Bode *et al.* (1994b)]. Vertical profiles of temperature and salinity were recorded along the transect using a CTD SBE-25. Samples for the determination of chlorophyll *a* concentration, phytoplankton species composition, carbon concentration of seston and ^{14}C incubations to estimate primary production were obtained by vertical casts with Niskin and Go-Flo bottles. At least six sampling depths were chosen within the euphotic layer. Water samples were filtered onto Whatman GF/F filters to analyse chlorophyll *a* concentration by the fluorimetric method described by Yentsch and Menzel (1963). Chlorophyll *a* measurements were made before each zooplankton sampling. Particulate carbon of seston was determined in material collected by Whatman GF/F filters using a Perkin Elmer 2400 CNH elemental analyser. Phytoplankton composition and protozoan (ciliates) abundance were determined on samples preserved with Lugol's solution using an inverted microscope. Only species or groups of diatoms, dinoflagellates and phytoflagellates >10 μm in diameter were counted. Primary production was measured in samples from five depths between the surface and 50 m (photic layer) using the ^{14}C method, during onboard short-term (2–3 h) incubations simulating '*in situ*' light conditions. Daily production was computed assuming a daylight period of 14.5 h.

Zooplankton sampling

Zooplankton were sampled with a triple WP_2 net (40 cm mouth diameter, 200 μm mesh size). Each of the six zooplankton stations was visited at least twice: in daylight and in the dark. In addition, two diel cycles were performed at stations C and T, at intervals of 4 h. Zooplankton nets were hauled at 1 m s^{-1} from 100 m depth to the surface. The three replicates from each haul were used to determine

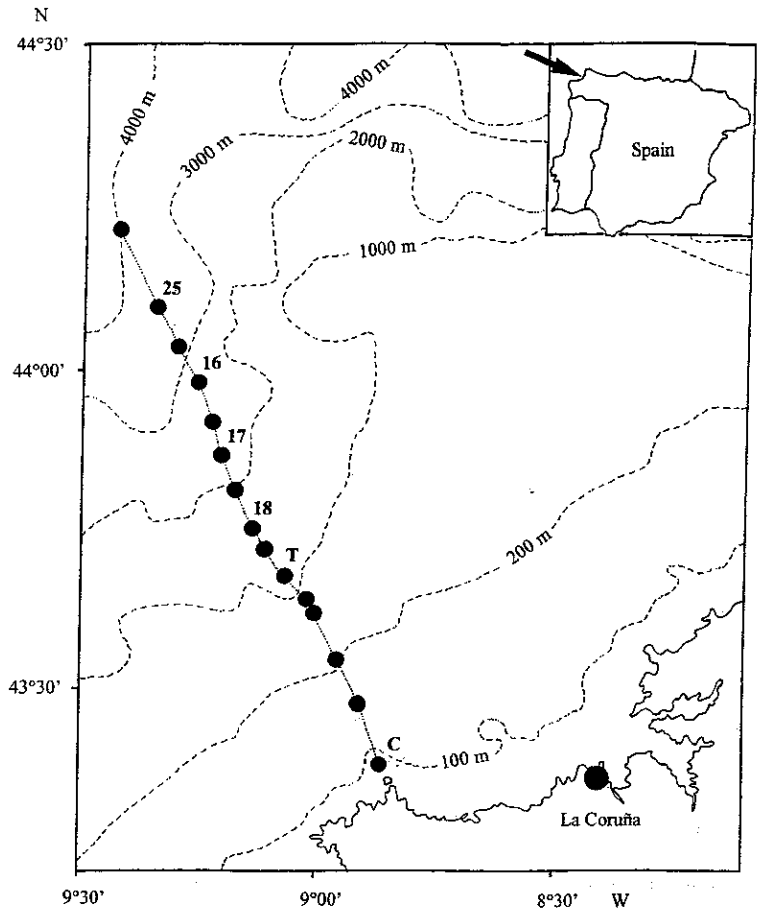

Fig. 1. Map of the transect of stations sampled during the cruise AMBAR-594, only the stations where zooplankton samples were collected have been labelled.

zooplankton biomass, species composition and gut chlorophyll *a* content of copepods (GC), respectively. All zooplankton samples were previously sieved into four size classes: 0.2–0.5 mm (small mesozooplankton), 0.5–1 mm (medium mesozooplankton), 1–2 mm (large mesozooplankton) and >2 mm (macrozooplankton).

Biomass samples were filtered on pre-weighed Whatman GF/F filters and kept frozen. Samples for zooplankton composition were preserved in buffered formaldehyde (4% final concentration). Finally, samples for GC were taken from the three mesozooplankton fractions (small, medium and large), gently filtered on paper filters, rinsed and kept frozen. At the laboratory, zooplankton biomass was measured as dry weight (55°C for 24 h). The specific compositions of copepods and other general groups were determined using a stereoscopic microscope. As far as possible, omnivorous, herbivorous and carnivorous copepods were

distinguished. We used the sum of abundances of herbivores plus omnivores for calculations of copepod ingestion rates, so, from now on, the term 'herbivores' will includes both groups of potential foragers.

Copepod gut chlorophyll content

GC values were determined for small, medium and large copepods using the gut fluorescence method of Mackas and Bohrer (1976), as modified by Morales *et al.* (1990) and Morales and Harris (1990). At the laboratory, copepods were counted under a binocular dissecting microscope and gently picked up with forceps, rejecting damaged individuals and carnivorous species. The whole handling was quickly carried out in dim light and low temperatures. Pigment extraction was at 4°C in the dark for 12–17 h. After centrifugation, fluorescence was measured in a Turner Designs 10-005R fluorimeter. Calculations were made as in Dagg and Wyman (1983), and the resultant GC reported in chlorophyll *a* equivalents per copepod, and corrected for background fluorescence.

Copepod gut evacuation experiments

A series of experiments was performed at stations C and T in order to estimate the evacuation rate of the gut content when copepods are deprived of food (k). Living animals were collected from hauls (50 m depth to the surface) carried out in daylight (between 8:30 a.m. and 17:00 p.m. local time). They were immediately gently rinsed with filtered sea water to wash away coarse phytoplankton cells, placed in an isothermal incubator filled with 20 l of filtered (Whatman GF/F) surface water collected '*in situ*', and kept dark. The temperature of the incubation bath was kept within ±2.4°C of the surface seawater temperature. Five experiments were performed with the small fraction, and four with each of the medium and large fractions. Subsamples were taken sequentially between 0 and 90 min to measure the decrease of individual GC with time (GC_t). The procedure of measuring GC_t was the same as for copepod gut content. The evacuation rate (k) was calculated by adjusting the exponential equation (Dagg and Wyman, 1983):

$$GC_t = GC_0 \cdot e^{-kt}$$

where GC_0 is the initial gut content per copepod, GC_t is the gut content at time t and k is the instantaneous gut evacuation constant rate (expressed in units of time^{-1}). Finally, the ingestion rate (I) for each size fraction was estimated as in the expression:

$$I = GC \cdot k \cdot A$$

using the herbivorous copepod abundances (A) averaged from dark and daylight samples, but considering the mean GC values obtained separately during the dark (9.5 h) and daylight (14.5 h).

Results

Hydrographic conditions

There were important changes in temperature and salinity distribution progressing from the coast towards the ocean along the transect of stations. Firstly, thermal stratification intensified towards the outer stations (Figure 2A). Secondly, relatively high-saline waters were detected near the shelf break which seemingly contributed to intensify stratification and vertical stability (Figure 2B). Three hydrographic zones could be differentiated: an oceanic zone with a well-developed vertical stratification, represented by stations 25 and 16; a shelf-break zone affected by highly saline waters, involving stations 17, 18 and T; and a coastal zone, represented by station C, where a relative vertical stability was possible due to the influence of surface, low-salinity waters of continental origin. In addition, a thermal front formed between the oceanic and the shelf-break waters. This

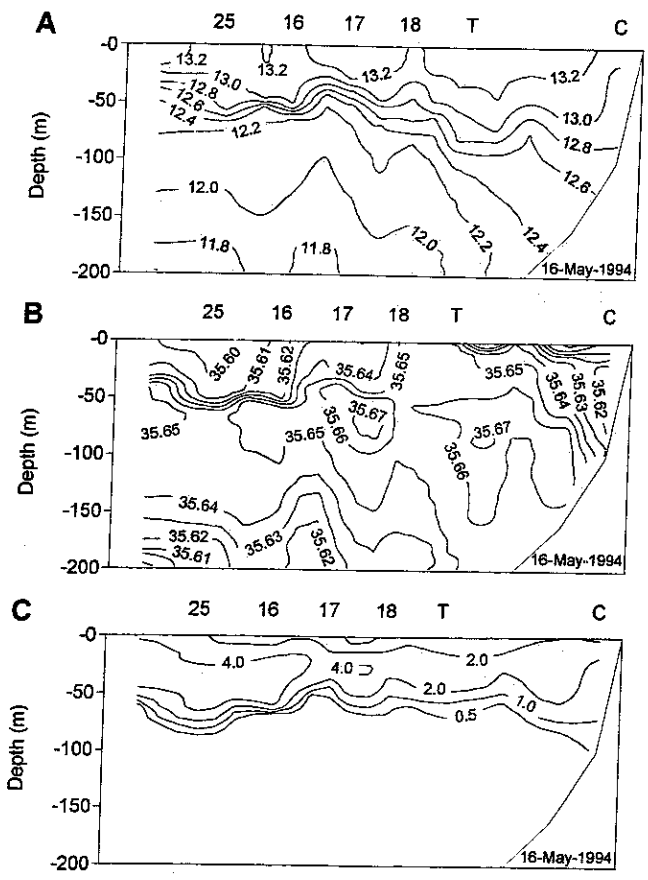

Fig. 2. Contour plots of temperature (°C) (**A**), salinity (‰) (**B**) and chlorophyll *a* (mg chlorophyll *a* m^{-3}) (**C**) along the transect. The location of zooplankton stations is noted.

pattern of relatively confined water bodies was proved appropriate to explain plankton distribution and production rates in the studied region (Bode *et al.*, 1994b).

Phytoplankton

Phytoplankton biomass, here estimated as chlorophyll *a* concentration, had maximal values offshore (Figure 2C). In the stratified oceanic waters, chlorophyll *a* concentration almost reached 7 mg m^{-3} in the subsurface maximum, while near the coast values remained below 3 mg m^{-3}. As a result, the highest integrated chlorophyll biomass appeared in the oceanic zone, and the lowest in the shelf-break waters (Table I). In the shelf-break zone, the depth of the subsurface chlorophyll maximum shifted with the displacement of the thermohaline front on consecutive sampling dates (Bode *et al.*, 1994b). Carbon to chlorophyll ratios reached very high values at stations T, 17 and 16, suggesting relatively large amounts of suspended detritus. However, ratios close to 50 were found at both ends of the transect (stations C and 25), indicating that living phytoplankton was a substantial part of seston at these stations. Primary production rates were maximal near the coast (up to 2600 mg C m^{-2} day^{-1}) (Table I).

Phytoplankton specific composition differed markedly between the three water zones. Near the coast, phytoplankton communities were basically formed by relatively small, mostly motile species (Table II). In shelf-break waters, high amounts of chain-forming diatoms appeared (e.g. *Nitzschia* cf. *pungens*, *Leptocylindrus danicus*, *Rhizosolenia* sp.), along with a noticeable abundance of dinoflagellates and Cryptophyceae. Finally, chain-forming diatoms were causing the oceanic bloom, basically composed of the same species as in the shelf-break zone.

Ciliates

Abundances of large (>30 μm) ciliates varied from 6 to 13 cells ml^{-1} between stations C and 17, but they increased abruptly in oceanic waters up to 36 cells ml^{-1} (Table II). Small (<30 μm) ciliates varied within 19–37 cells ml^{-1} with no clear pattern.

Table I. Stock and primary production rates of phytoplankton. Phytoplankton stock (integrated 0–100 m depth) is expressed as chlorophyll *a* (mg chlorophyll *a* m^{-2}) and as carbon (mg C m^{-2}) using the measured C:Chl (carbon to chlorophyll *a*) ratios. Primary production (mg C m^{-2} day^{-1}) was integrated from 0 to 50 m depth (photic layer). Values were pooled from several measurements made at each station

		Chlorophyll *a*	C:Chl	Primary production
Oceanic zone	Stn 25	301	45.55	1722
	Stn 16	282	98.37	996
Shelf-break zone	Stn 17	197	70.16	1924
	Stn 18	120	66.15	1836
	Stn T	125	78.43	1442
Coastal zone	Stn C	182	55.02	2599

Table II. Average abundances (cells ml^{-1}) of some cell size groups of phytoplankton. Ciliate abundances divided into two size categories are also reported. Values were pooled from samples taken at each station

		Diatoms			Dinoflagellates	Cryptophyceae	Ciliates	
		Chain forming	>100 µm	<100 µm	<30 µm	<30 µm	>30 µm	<30 µm
Oceanic zone	Stn 25	231	19	19	64	17	36	21
	Stn 16	344	9	14	115	53	18	37
Shelf-break zone	Stn 17	91	5	0	149	222	8	23
	Stn 18	160	12	0	81	116	11	19
	Stn T	230	6	4	57	86	13	25
Coastal zone	Stn C	1	0	43	96	183	6	34

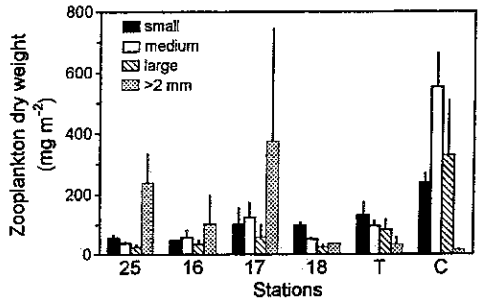

Fig. 3. Mean values of size-fractionated zooplankton dry weight (mg m^{-2}). The vertical bars represent the SEM (station 25, $n = 3$; stations 16, 17 and 18, $n = 2$; station T, $n = 6$; station C, $n = 8$)

Zooplankton

At station C, the medium size fraction accounted for almost 50% of total zooplankton dry weight, followed in importance by the large fraction (Figure 3). This coastal station exhibited the highest biomass of mesozooplankton fractions. In shelf-break and oceanic waters, large mesozooplankton had the lowest mean values. Macro filterers like salps and other gelatinous organisms accounted for most of the biomass in outer waters.

The most abundant groups of macrozooplankton were Cnidaria, appendicularians and large crustaceans (e.g. euphausiids), whereas copepods ranged from 2 to 6 individuals m^{-2} and never exceeded 58% of total macrozooplankton abundance. However, copepods were the most important taxon in mesozooplankton, globally accounting for up to 99% of abundance. At station C, medium-sized copepods were the most abundant (>660 $\times$ 10^3 individuals m^{-2}), closely followed by the small copepods. Offshore, small copepods dominated abundance values at all stations (range 72–268 $\times$ 10^3 individuals m^{-2}), followed by medium and large copepods. Most species of herbivorous copepods were widespread, sharing dominance throughout all the stations: *Oithona* spp. (mainly *Oithona helgolandica*), *Paracalanus parvus* and *Clausocalanus* sp. (Table III). In general, herbivorous species peaked at station C, except for two calanoids (*Calocalanus styliremis* and *Calanus tenuicornis*, small and medium sized, respectively) which had their maxima in the shelf-break zone.

Gut content and evacuation rates of copepods

The three copepod fractions displayed nycthemeral feeding patterns (Figure 4). Mean GC values measured in the dark were significantly higher than during the daylight period (Mann–Whitney *U*-test: $P < 0.005$ for small, $P < 0.0005$ for both medium and large fractions). Ranges of the mean GC (ng chlorophyll *a* copepod^{-1}) during the dark phase were 0.07–0.15 in small, 0.33–0.86 in medium and 1.62–5.02 in large copepods; and during the daylight were 0.04–0.10 in small, 0.08–0.19 in medium and 0.22–0.76 in large copepods. Medium- and large-sized

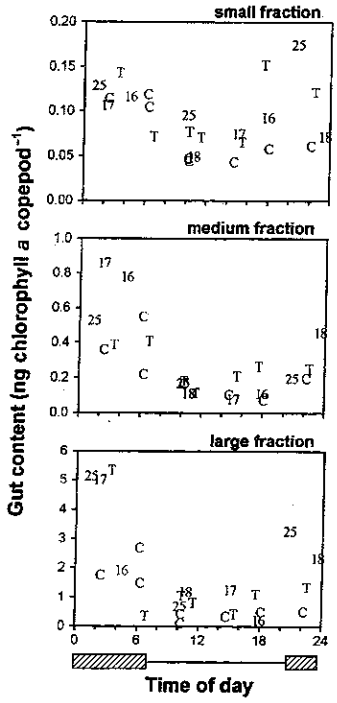

Fig. 4. Values of GC (ng chlorophyll *a* copepod^{-1}) at each station at different times for the three size fractions of copepods. The horizontal bar at the bottom shows the duration of dark and daylight periods.

copepods had the highest GC within 2–5 h before dawn, whereas GC of the small fraction peaked, in general, at dusk. In all cases, the lowest GC were found around noon.

Exponential regression estimated gut clearance curves from the gut evacuation experiments performed with each size fraction of copepods (Figure 5). The resulting k rates were 0.012 (small copepods), 0.023 (medium copepods) and 0.320 min^{-1} (large copepods).

Ingestion rates

The variability of herbivorous ingestion by the copepod community in the studied area roughly resembled that of the abundance pattern (Figure 6, see also Table III). The total ingestion rate was maximal at station C, principally due to feeding activity of the very abundant medium and large copepods (131 and 163 mg C m^{-2} day^{-1}, respectively). Offshore, no clear differences between total rates were found, still it seemed that small and medium-sized copepods were more important at stations 17 and 16 (frontal waters), whereas large copepods dominated herbivory at the other stations. Otherwise, considering per copepod ingestion

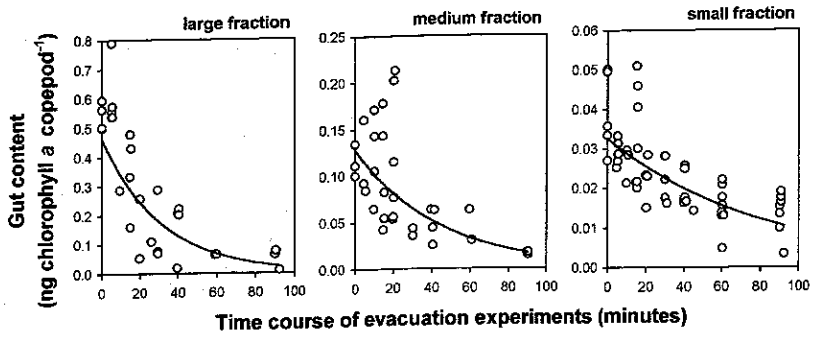

Fig. 5. Time course (minutes) of the decrease of GC (ng chlorophyll *a* copepod^{-1}) in the three copepod size fractions during the gut evacuation experiments. The exponents in the negative exponential equation from each curve represented the respective evacuation rates (large copepods: 0.032, $r^2 = 0.61$; medium copepods: 0.023, $r^2 = 0.67$; small copepods: 0.012 min^{-1}, $r^2 = 0.50$)

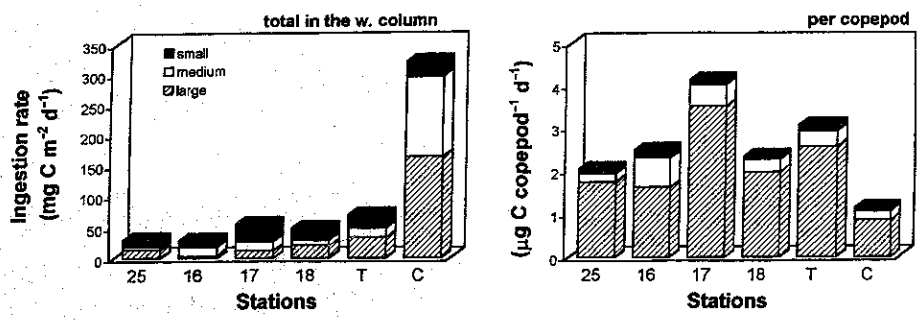

Fig. 6. Individual ingestion rates (µg C copepod^{-1} day^{-1}) and total community ingestion rates integrated for the water column (mg C m^{-2} day^{-1}), along the transect of stations.

rates (Figure 6), maximal rates of the three size fractions were associated with frontal stations (0.2 and 0.7 µg C copepod^{-1} day^{-1} at station 16 for small and medium copepods; 3.5 µg C copepod^{-1} day^{-1} at station 17 for large copepods).

In coastal waters, daily ingestion by the copepod community relative to phytoplankton biomass stock was <3%, and almost 12% in terms of primary production (Table IV). Offshore, the ingestion pressure on phytoplankton stock and production was less important and decreased progressively towards the oceanic, phytoplankton-rich zone (<1% of carbon stock and <5% of carbon production).

Relationships with ciliates

The possible relationships between copepod abundance and ciliate abundance, and between individual copepod ingestion and ciliate abundance, were explored to find indications of a possible complement of copepod diets with ciliates. During

Table III. Abundances ($\times 10^3$ individuals m^{-2}) of the main herbivorous species of copepods, and totals by size classes, integrated from 0 to 100 m depth. Values were pooled from several samples from each transect station. (Σ sum of the three size classes)

	Oceanic zone		Shelf-break zone			Coastal zone
	Stn 25	Stn 16	Stn 17	Stn 18	Stn T	Stn C
Paracalanus parvus	35.5	14.1	68.9	90.5	25.5	447.0
Oithona spp.	49.6	29.0	94.7	93.9	83.1	253.9
Clausocalanus sp.	40.1	13.0	65.8	64.9	43.8	152.6
Acartia clausi	8.9	8.1	25.8	28.2	11.3	195.8
Calanus helgolandicus	9.3	12.0	6.5	7.2	18.2	158.1
Pseudocalanus elongatus	1.1	3.9	11.0	11.7	7.5	143.0
Centropages typicus	1.3	1.2	2.8	2.1	0.3	37.1
Calanoides carinatus	0.7	1.0	0.5	0.5	0.2	35.1
Calocalanus styliremis	2.7	1.3	5.7	2.1	2.2	1.4
Calanus tenuicornis	2.1	2.5	2.6	1.5	1.3	0.0
Temora longicornis	0.0	0.1	0.0	0.0	0.0	3.1
Oncaea media	0.0	0.0	0.2	0.2	0.2	2.1
By size classes						
Small	123.8	63.6	252.9	265.6	139.9	591.3
Medium	20.2	20.9	29.0	26.8	41.6	648.8
Large	8.2	2.1	3.5	10.6	13.0	190.8
Σ	152.2	86.6	285.3	303.0	194.5	1430.8

our study, no definite relationships were found between ciliates and copepods. At first sight, the abundance of some size classes (e.g. small copepods) seemed to be inversely related to ciliate abundance, whereas no tendency at all was observed when considering all sizes and the relationships between individual herbivorous activity of copepods and ciliate abundance (Figure 7). Overall, there was no significant correlation to validate those relationships

Discussion

During this study, copepods exhibited a consistent diel rhythm in their GC values in daylight and dark phases, with mean values within the published ranges (Dagg *et al.*, 1989; Bautista and Harris, 1992; Checkley *et al.*, 1992; Landry *et al.*, 1994b; Irigoien and Castel, 1995; Satour *et al.*, 1996). Nevertheless, it was noticeable that GC of small copepods was quite low throughout the study. In the coastal zone, the total feeding rate by small copepods was even lower, despite their peak of abundance (>500 $\times$ 10^3 individuals m^{-2}), than it was in the shelf-break zone (maximal rate at station 17). As we will discuss later, it could be that those small copepods were actually behaving as omnivores, so as to meet their nutritional requirements.

Evacuation rates (k) clearly increased with copepod size, meaning higher ingestion rates per copepod for the largest size class. This direct, body size dependence of k is coincident with the findings of Bautista and Harris (1992) and Head *et al.* (1996), among others. In this study, the k rates derived empirically for each size

Table IV. Ratios of the phytoplanktonic carbon ingested by copepods and phytoplankton carbon stock (daily%) and phytoplankton carbon production (daily%), by each copepod size fraction and by the total copepod community (Σ)

		Ingestion/carbon stock				Ingestion/primary production			
		Small	Medium	Large	Σ	Small	Medium	Large	Σ
Oceanic zone	Stn 25	0.1	<0.1	0.1	0.2	0.7	0.2	0.8	1.7
	Stn 16	<0.1	0.1	<0.1	0.1	1.1	1.4	0.3	2.9
Shelf-break	Stn 17	0.2	0.1	0.1	0.4	1.5	0.8	0.6	2.9
zone	Stn 18	0.2	0.1	0.3	0.6	1.0	0.4	1.1	2.6
	Stn T	0.2	0.2	0.3	0.7	1.4	1.0	2.3	4.8
Coastal zone	Stn C	0.3	1.3	1.6	3.2	1.0	5.0	6.3	12.3

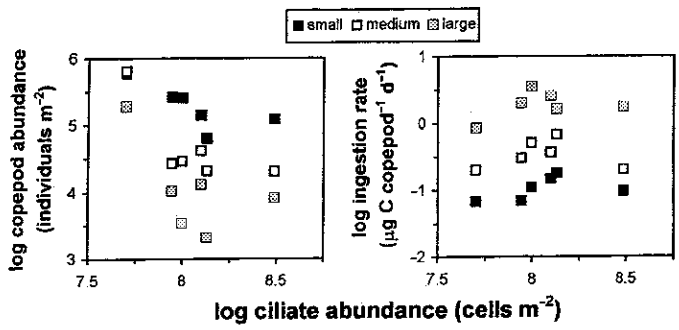

Fig. 7. Relationships between copepod abundance (log individuals m^{-2}) and per copepod feeding rates (log µg C $copepod^{-1}$ day^{-1}), and ciliate abundance (log cells m^{-2}) along the transect of stations.

fraction were used in ingestion calculations as the best approach to the field situation. Because copepods for evacuation experiments were collected during daylight (low-GC period), the evacuation curves might be somewhat biased in their initial slopes and it might be that the *k* rates were underestimated. However, the evacuation rate is considered a conservative property of copepod feeding in the sea [see Small and Ellis (1992) and references therein].

The characterization of the three water zones (oceanic, shelf break and coastal) was based on the seasonal hydrography of NW Spanish waters (Frouin *et al.*, 1990; Haynes and Barton, 1990), and the description of the distribution of plankton communities related to hydrographic features during the cruise (Bode *et al.*, 1994b). In the coastal zone, the phytoplankton bloom was dominated by small-sized cells growing actively. In this zone, copepod populations displayed characteristics of a spring peak, with predominating species of small and medium size. Specific diversity agreed with the published data for this region (Braun *et al.*, 1990; Valdés *et al.*, 1990; Fernández de Puelles *et al.*, 1996), although abundances ranked notably high in our case. During spring, coastal waters in this Atlantic region are steady enough to allow copepod populations to achieve very high densities (Colebrook, 1979; Tenore *et al.*, 1995). Herbivorous copepods, essentially those of large and medium sizes, were daily removing >10% of

phytoplankton carbon production near the coast. Our estimations of ingestion rates onshore (319 mg C m^{-2} day^{-1}) are almost twice the maximal rate of 169 mg C m^{-2} day^{-1} for mesozooplankton feeding estimated by Braun *et al.* (1990) using ^{14}C labelling techniques. In general, the impact of copepod predation on phytoplankton in similar shelf areas during spring has been found to be relatively low in terms of carbon stock, although the relative impact on primary production may be important (Bautista and Harris, 1992; Landry *et al.*, 1994a). On a seasonal scale, although the ingested amounts relative to carbon standing stock would remain low, the observed copepod feeding might restrain further phytoplankton growth onshore, with rate values close to primary production, as copepods achieve their spring peak and phytoplankton growth rates decay due to nutrient depletion. Furthermore, herbivorous zooplankton could even consume most of the primary production during given periods, as summarized by Walsh (1988) from various studies in the NE American shelf.

The shelf-break waters showed high physical variability. In particular, shifts were observed either in the location or intensity of the deep chlorophyll maximum, along with horizontal displacements of the thermohaline front, suggesting important movements of water (Bode *et al.*, 1994b). The cell-size structure of phytoplankton in this area showed two major categories of particles: chain-forming diatoms and small flagellated cells. Inner shelf-break waters (station T) were dominated by flocs of diatoms, while frontal waters (station 17) were dominated by flagellates. Large-sized copepods, often considered as potential predators of large phytoplankton particles, displayed maximal per copepod feeding rates in the latter. In contrast, the highest per copepod feeding rates of the medium- and small-sized classes occurred at the oceanic side of the front (station 16), where diatom aggregates dominated. In this case, those copepods could actually be eating other phytoplanktonic cells (i.e. dinoflagellates) or detritus instead of diatoms, while large copepods, which showed their minimal abundance and herbivorous activity at station 16, would be outcompeted in these conditions. Therefore, it appears that the formation of dense aggregations and chains of diatoms makes difficult the ingestion of these planktonic particles by herbivorous copepods, which may capture smaller particles like individual cells more efficiently. Our results agree with several studies in the nearby Bay of Biscay that find a close relationship between the structure of the pelagic food webs and different water bodies during similar hydrographic events (Fernández *et al.*, 1991, 1993). Finally, copepods are known to be omnivorous, as their diet may include heterotrophic organisms like ciliates or flagellates and detritus, in a proportion which depends on the food environment and the physiological state of copepods (Kleppel *et al.*, 1991, 1996). As we mentioned earlier, we indirectly inferred that mainly small copepods, but also the larger species, could be preying on ciliates and detritus, but there is no clear evidence of an effect on the prey populations. Direct grazing of microheterotrophs by copepods was not measured during our study, and therefore we cannot discard copepod feeding on other food particles in addition to phytoplankton.

In the oceanic zone, some biological features like high biomass levels, low primary production rates and downward progress of the deep chlorophyll

maximum were pointing to the collapse of the bloom (Bode *et al.*, 1994b). Phytoplankton assemblages resembled those typical of a spring bloom in this area, characterized by very high biomass levels and dominance of large-sized and chain-forming cells (Bode *et al.*, 1994a; Casas *et al.*, 1997). Although our study was limited to an area somewhat restricted and not far indeed from the continental shelf, our estimations of copepod ingestion in outer waters agreed with other studies on spring blooms in open-ocean regions (e.g. Dagg, 1993; Dam *et al.*, 1993; Tsuda and Sugisaki, 1994). The impact of copepods on phytoplankton stock or production was too low to be thought of as a chief pathway for the carbon biomass generated in the bloom.

There are several studies suggesting that copepods eventually do not restrict phytoplankton blooms (Walsh, 1988; Morales *et al.*, 1991; Dagg, 1993; Dam *et al.*, 1993). One reason would be the practical omnivory of copepods, their diet including diverse hetero-organisms and detritus, and the growing evidence that diatoms are often rejected in favour of more palatable or nutritive food particles (Kleppel *et al.*, 1991; Kleppel, 1993). During our study, the spring bloom appeared to be out of the control of the mesozooplankton. However, the hydrographic conditions that led to the thermohaline differentiation of water zones originated different pelagic habitats in which there were different impacts of copepods on phytoplankton. On the one hand, the onset of spring maximum of copepods would make them capable of a significant effect on the growth of phytoplankton populations in the coastal zone. On the other hand, phytoplankton reached high concentrations, but copepod abundance was low in deeper waters, and losses of carbon due to copepod feeding were negligible. We suggest that the bulk of particulate carbon in the oceanic bloom would bypass the classical planktonic herbivores, and its fate would eventually depend on the physical forces acting in the area, like displacements of water masses or direct sinking of phytoplanktonic particles.

Acknowledgements

We are grateful to the captain and crew of the RV 'Cornide de Saavedra', and also to all the participants in the cruise for their kind assistance. We are especially indebted to J.Lorenzo, F.Arenas and J.Sostres for technical support. R.González-Quirós helped with zooplankton collection and analysis, and J.L.Acuña gave expert directions for the experimental design and lent valuable comments to a previous draft of this manuscript. We acknowledge the comments from two anonymous referees to an earlier version of this paper. This work was supported by funds of CICYT Projects AMB92/0834 and AMB93/0014, and of the Instituto Español de Oceanografía. S.B. was granted a FPI fellowship by the Ministerio de Educación y Ciencia (Spain).

References

Bautista,H. and Harris,R.P. (1992) Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Mar. Ecol. Prog. Ser.*, **82**, 41–50.

Bode,A. and Varela,M. (1994) Plankton carbon and nitrogen budgets for the N-NW Spanish shelf: The role of pelagic nutrient regeneration during upwelling events. *Sci. Mar.*, **58**, 221–231.

Bode,A., Fernández,E., Botas,A. and Anadón,R. (1990) Distribution and composition of suspended particulate matter related to a shelf-break saline intrusion in the Cantabrian Sea (Bay of Biscay). *Oceanol. Acta*, **13**, 2, 219–228.

Bode,A., Casas,B. and Varela,M. (1994a) Size-fractionated primary productivity and biomass in the Galician shelf (NW Spain): Netplankton versus nanoplankton dominance. *Sci. Mar.*, **58**, 131–141.

Bode,A., Varela,M., Fernández,E., Arbones,B., González,N., Carballo,R., Alvarez-Ossorio,M.T., Anadón,R. and Barquero,S. (1994b) Biological characteristics of the plankton associated to a shelf-break front off the Galician Coast. *Gaia*, **8**, 9–18.

Bode,A., Varela,M., Barquero,S., Alvarez-Ossorio,M.T. and González,N. (1998) Preliminary studies on the export of organic matter during phytoplankton blooms off La Coruña (NW Spain). *J. Mar. Biol. Assoc. UK*, **78**, 1–15.

Bode,A., Casas,B., Fernández,E., Marañón,E., Serret,P. and Varela,M. (1997) Phytoplankton biomass and production in the shelf waters of NW Spain: spatial and seasonal variability in relation to the upwelling, *Hydrobiologia*, **341**, 225–234.

Braun,J.G., Alvarez-Ossorio,M.T., Fernández-Puelles,M.L. and Camiñas,J.A. (1990) Estudio sobre la estructura, biomasa y producción del meso y microzooplancton en la plataforma de Galicia en abril de 1982. *Bol. Inst. Esp. Oceanogr.*, **6**, 81–96.

Casas,B., Varela,M., Canle,M., González,N. and Bode,A. (1997) Seasonal variations of nutrients, seston and phytoplankton, and upwelling intensity off La Coruña (NW Spain). *Estuarine Coastal Shelf Sci.*, **44**, 767–778.

Checkley,D.M.,Jr, Dagg,M.J. and Uye,S. (1992) Feeding, excretion and egg production by individuals and populations of the marine, planktonic copepods, *Acartia* spp. and *Centropages furcatus*. *J. Plankton Res.*, **14**, 71–96.

Colebrook,J.M. (1979) Continuous plankton records. seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *Mar. Biol.*, **51**, 23–32.

Dagg,M. (1993) Grazing by the copepod community does not control phytoplankton production in the subarctic Pacific Ocean. *Prog. Oceanogr.*, **32**, 163–183.

Dagg,M.J. and Wyman,K.D. (1983) Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N.cristatus* calculated from gut contents. *Mar. Ecol. Prog. Ser.*, **13**, 37–46.

Dagg,M.J., Frost,B.W. and Walser,W.E.,Jr (1989) Copepod diel migration, feeding, and the vertical flux of pigments. *Limnol. Oceanogr.*, **34**, 1062–1071.

Dam,H.G., Miller,C.A. and Jonasdottir,S.H. (1993) The trophic role of mesozooplakton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Res.*, **40**, 197–212.

Fernández,E., Bode,A., Botas,A. and Anadón,R. (1991) Microplankton assemblages associated with saline fronts during a spring bloom in the central Cantabrian Sea: differences in trophic structure between water bodies. *J. Plankton Res.*, **13**, 1239–1256.

Fernández,E., Cabal,J., Acuña,J.L., Bode,A., Botas,J.A. and García-Soto,C. (1993) Plankton distribution across a slope current-induced front in the southern Bay of Biscay. *J. Plankton Res.*, **15**, 619–614.

Fernández de Puelles,M.L., Valdés,L., Varela,M., Alvarez-Ossorio,M.T. and Halliday,N. (1996) Diel variation in the vertical distribution of copepods off the north coast of Spain. *ICES J. Mar. Sci.*, **53**, 97–106.

Frouin,R., Fiúza,A.F.G., Ambar,I. and Boyd,T.J. (1990) Observations of a poleward surface current off the coasts of Portugal and Spain during winter. *J. Geophys. Res.*, **95**, 679–691.

Haynes,R. and Barton,E.D. (1990) A poleward flow along the Atlantic coast of the Iberian Peninsula. *J. Geophys. Res.*, **95**, 11425–11441.

Head,E.J.H., Harrison,W.G., Irwin,B.I., Horne,E.P.W. and Li,W.K.W. (1996) Plankton dynamics and carbon flux in an area of upwelling off the coast of Morocco. *Deep-Sea Res.*, **43**, 1713–1748.

Irigoien,X. and Castel,J. (1995) Feeding rates and productivity of the copepod *Acartia bifilosa* in a highly turbid estuary: the Gironde (SW France). *Hydrobiologia*, **311**, 115–125.

Kleppel,G.S. (1993) On the diets of calanoid copepods. *Mar. Ecol. Prog. Ser.*, **99**, 183–195.

Kleppel,G.S., Holliday,D.V. and Pieper,R.E. (1991) Trophic interactions between copepods and microplankton: A question about the role of diatoms. *Limnol.Oceanogr.*, **36**, 172–178.

Kleppel,G.S., Burkart,C.A., Carter,K. and Tomas,C. (1996) Diets of calanoid copepods on the West Florida continental shelf: relationships between food concentration, food composition and feeding activity. *Mar. Biol.*, **127**, 209–217.

Landry,M.R., Lorenzen,C.J. and Peterson,W.K. (1994a) Mesozooplankton grazing in the southern California Bight. II. Grazing impact and particulate flux. *Mar. Ecol. Prog. Ser.*, **115**, 73–85.

Landry,M.R., Peterson,W.K. and Fagerness,V.L. (1994b) Mesozooplankton grazing in the southern

California Bight. I. Population abundances and gut pigment contents. *Mar. Ecol. Prog. Ser.*, **115**, 55–71

Mackas,D. and Bohrer,R. (1976) Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. Exp. Mar. Biol. Ecol.*, **25**, 77–85

Morales,C.E. and Harris,R.P. (1990) A review of the gut fluorescence method for estimating ingestion rates of planktonic herbivores. ICES (International Council for the Exploration of the Sea) C.M. 1990/L:26, Biological Oceanographic Committee.

Morales,C.E., Bautista,B. and Harris,R.P. (1990) Estimates of ingestion in copepod assemblages: gut fluorescence in relation to body size. In Barnes,M. and Gibson,R.N. (eds), *Trophic Relationships in the Marine Environment, Proceedings from the 24th European Marine Biology Symposium*. Aberdeen University Press, Aberdeen, pp. 565–577

Morales,C.E., Bedo,A., Harris,R.P. and Tranter,P.R.G. (1991) Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction. *J. Plankton Res.*, **13**, 455–472.

Satour,B., Artigas,F., Harbland,A. and Laborde,P. (1996) Zooplankton grazing impact in the plume of dilution of the Gironde estuary (France) prior to the spring bloom. *J. Plankton Res.*, **18**, 835–853.

Small,L.F. and Ellis,S.G. (1992) Fecal carbon production by zooplankton in Santa Monica Basin: the effects of body size and carnivorous feeding. *Prog. Oceanogr.*, **30**, 197–221

Tenore,K.R. *et al.* (1995) Fisheries and oceanography off Galicia, NW Spain. mesoscale spatial and temporal changes in physical processes and resultant patterns of biological productivity *J. Geophys. Res.*, **100**, 10943–10966.

Tsuda,A. and Sugisaki,H. (1994) In situ grazing rate of the copepod population in the western subarctic North Pacific during spring. *Mar. Biol.*, **120**, 203–210.

Valdés,J.L., Roman,M.R., Alvarez-Ossorio,M.T., Gauzens,A.L. and Miranda,A. (1990) Zooplankton composition and distribution off the coast of Galicia, Spain. *J. Plankton Res.*, **12**, 629–643.

Varela,M., Díaz del Río,G., Alvarez-Ossorio,M.T. and Casas,B. (1991) Factors controlling phytoplankton size-class distribution in the upwelling area of the Galician Continental shelf (NW Spain). *Sci. Mar.*, **55**, 505–518.

Walsh,J.J. (ed.) (1988) *On the Nature of Continental Shelves* Academic Press, New York, 520 pp.

Yentsch,C.S. and Menzel,D.W. (1963) A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence *Deep-Sea Res.*, **10**, 221–231.

Received on June 3, 1997; accepted on December 17, 1997