

Seasonal variation of mesozooplankton biomass, abundance and copepod grazing in the central Cantabrian Sea (southern Bay of Biscay)

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SUMMARY: Size fractionated mesozooplankton biomass, abundance and copepod grazing were investigated over an annual cycle (1998) at two stations off Cudillero (central Cantabrian Sea). Mesozooplankton biomass was higher in summer/early autumn, reaching ~3000 mg dw m⁻² in September. Copepods were the most abundant taxonomic group, representing 91 and 81% of the total mesozooplankton abundance in the coastal and shelf-break station respectively. Copepod gut contents were higher in summer at the coastal station, while the shelf-break station showed maximum gut contents in April. Gut contents were linearly related to integrated chlorophyll, except in the case of large animals at the shelf break station. Copepod community carbon ingestion was higher from June to September at both stations, reaching a maximum value of ~165 mg C m⁻² day⁻¹. Calculated grazing rates translates into an average daily consumption values of 8.7% (coast) and 5.25% (shelf-break) of total chlorophyll stock, or 20% (shelf-break) of total primary production.

Keywords: mesozooplankton, copepod, grazing, gut contents, Cantabrian Sea.

RESUMEN: VARIACIÓN ESTACIONAL DE LA BIOMASA Y ABUNDANCIA DEL MESOZOOPLANCTON Y HERBIVORÍA DE COPÉPODOS EN EL CANTÁBRICO CENTRAL (SUR DEL GOLFO DE VIZCAYA). – A lo largo del año 1998, se estudió la biomasa y abundancia del mesozooplancton (en distintas fracciones de tamaño) así como la ingestión de la comunidad de copépodos en dos estaciones cercanas a Cudillero (Mar Cantábrico). La biomasa del mesozooplancton presentó sus valores más elevados en verano y a principios del otoño, alcanzando máximos de ~3000 mg Peso Seco m⁻² en Septiembre. Los copépodos fueron el grupo taxonómico más abundante, representando el 91% y el 81% de la abundancia total del mesozooplancton en las estaciones de costa y talud respectivamente. El contenido estomacal de los copépodos en la estación costera fue más elevado durante el verano, mientras que en la estación situada sobre el talud, el contenido estomacal más elevado se encontró en el mes de Abril. Se encontró una relación lineal entre el contenido estomacal de los copépodos y el valor de clorofila integrado en la columna de agua, excepto en el caso de los copépodos grandes en la estación de talud. La ingestión de carbono de la comunidad de copépodos fue más elevada entre Junio y Septiembre en ambas estaciones, alcanzando valores máximos de ~165 mg C m⁻² día⁻¹. La ingestión de la comunidad de copépodos representa un consumo diario del 8.7% (costa) y 5.25% (talud) de la clorofila total, y un 20% (talud) de la producción primaria total.

Palabras clave: mesozooplancton, copépodos, ingestión herbívora, contenido estomacal, Mar Cantábrico.

INTRODUCTION

One of the main challenges of oceanography is to improve the knowledge of the relationships between physical/biological characteristics of marine ecosystems and global change processes. In

view of this, it is necessary to perform temporal studies that are extensive enough for a better understanding of the oceanic processes at a global scale. Seasonal studies in oceanography are especially important in regions where environmental conditions present a high degree of variation throughout

the year. Most of the studies carried out in these areas deal with productive phases of the annual cycle, like spring blooms (Bautista and Harris, 1992), or hydrographic features related to productive events, like upwellings (Bode *et al.*, 1998) or fronts (Barquero *et al.*, 1998). In addition, environmental factors of coastal areas are variable and complex due to interactions between land and ocean influences (Siokou-Fangou, 1996). The study of seasonal variation, covering the wide range of changing conditions in temperate regions, is a key factor for a better understanding of the functioning of coastal ecosystems.

The central Cantabrian Sea can be defined as a typical temperate region. As in most temperate areas, the main factor controlling plankton dynamics on a seasonal scale is the alternation between winter mixing of the water column and further thermal stratification (Fernández and Bode, 1991). However, within this general pattern, several studies performed in this area have pointed to the importance of different hydrographic features, such as intrusions of high-salinity waters during mixing periods (Bode *et al.*, 1990; Fernández *et al.*, 1993) and coastal small-scale upwellings in summer (Botas *et al.*, 1990), which are important sources of variability in regional plankton communities.

In the last decade, many authors have investigated the physical (Botas *et al.*, 1989; Botas *et al.*, 1990) and biological (Fernández and Bode, 1991; Bode and Fernández, 1992; Marañón *et al.*, 1998; Serret *et al.*, 1999) features of this region. However, not so many studies deal with the zooplankton community, although it plays a key role in marine ecosystems by transferring energy from phytoplankton to higher trophic levels, including fisheries. Most of the zooplankton studies carried out in the region describe the biomass distribution and taxonomic composition of mesozooplankton (Cabal, 1993), paying special attention to the group of appendicularians (Acuña and Anadón, 1992; Acuña, 1994) and to the influence of shelf-break fronts (Fernández *et al.*, 1993). In particular, little attention has been paid in this region to zooplankton grazing, whose mediation in vertical carbon flux (Dam *et al.*, 1995) and in the control of phytoplankton populations (Banse, 1995) has been widely suggested. The only study concerning this subject is that of López-Urrutia *et al.* (2003), which was restricted to the appendicularian community. The main objective of this paper is to describe the seasonal variation in

mesozooplankton abundance and copepod grazing through an annual cycle in a temperate coastal area: the central Cantabrian Sea.

METHODS

Sampling was carried out monthly at two stations off Cudillero (central Cantabrian Sea, Fig. 1) between January 1998 and January 1999 (except August 1998) onboard B/O José Rioja. At every station, vertical profiles of temperature and salinity were obtained with an SBE25-03 CTD. Sampling depth was 50 and 100 m at stations E1 (coast) and E2 (shelf-break) respectively.

Chlorophyll *a* (Chl *a*) concentration was determined fluorimetrically. Water samples were collected with 5 l Teflon Niskin bottles from 6-8 depths at each station, introduced in dark bottles and transported to the land laboratory in a cold box. Samples were filtered onto GF-F filters, extracted in 10 ml of 90% acetone overnight at 4°C and measured on a Turner Designs 10 fluorometer before and after acidification with HCL 0.1 N.

Primary production was determined by ¹⁴C incubations of water collected at three depths (surface,

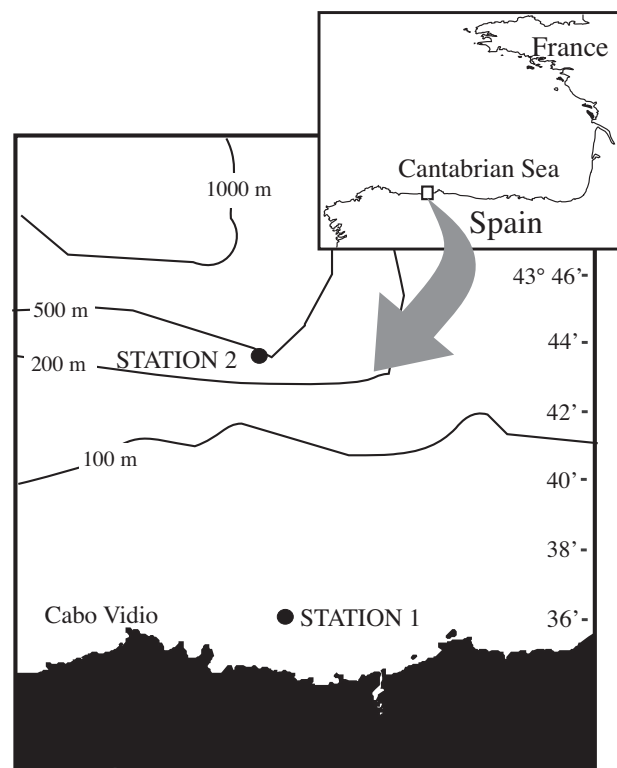


FIG. 1. – Location of stations E1 and E2.

chlorophyll maximum and limit of the photic layer) from station E2. Back in the laboratory, water samples were inoculated with 370 kBq ($10 \mu\text{Ci NaH}^{14}\text{CO}_3$) and incubated for 24 h. Three light bottles (100 mL) and one dark bottle (control) were incubated for each depth. Temperature and light profiles were simulated following preliminary test CTD casts. After incubation, samples were filtered onto polycarbonate filters, exposed for 12 hours to concentrated HCl fumes to remove inorganic ^{14}C , and counted in a Wallac 1409 scintillation counter. Quenching was corrected by the internal standard method. Primary production and chlorophyll concentration were expressed as integrated values in the water column.

At every station, two treble-ring (37 cm \varnothing , 200 μm mesh) net casts were deployed at 50 (station E1) or 100 m (station E2). Sampling was always carried out between 12.00 and 13.00 h. The contents of the first net (recovered at 1 m s^{-1}) were devoted determining the mesozooplankton biomass and taxonomic composition, while the second net (recovered at 0.5 m s^{-1}) was used for grazing experiments. In both cases, cod end (filtrating) contents were immediately screened through 200, 500 and 1000 μm meshes to create three different size fractions: 200-500 μm (small), 500-1000 μm (medium) and >1000 μm (large). For biomass measurements, subsamples were filtered onto 47 mm \varnothing GF-A precombusted filters, maintained for 48 h at 60°C and weighed. Biomass was expressed as mg Dry Weight m^{-2} . Biomass data from March are not available. For taxonomic composition, samples were fixed with 4% buffered formaldehyde and subsamples were determined in an Olympus SZ-40 stereomicroscope to the level of main taxonomic groups.

Copepod grazing was estimated using the gut fluorescence technique (Mackas and Bohrer, 1976). Subsamples from each size fraction were filtered onto sharkskin filters, stored in Petri dishes and immediately frozen at -70°C in the dark for further gut content analysis.

For gut evacuation experiments, animals from each size fraction were placed in a cool box containing filtered (0.2 μm) surface seawater, and kept in darkness at surface water temperature. The copepods were subsampled every 5 minutes for half an hour, filtered onto sharkskin filters and frozen as above.

Twenty five copepods for the large, 50 for the medium and 75 for the small fraction were picked

from the filters using jeweller's forceps under a microscope with dim light. No attention was paid to copepod species or development stage. The copepods were placed in 20 ml glass vials with 5 ml of acetone (90%) and extracted for 24 h at 4°C in the dark. The fluorescence of the sample was measured using a Turner Fluorometer before and after acidification and expressed as ng chlorophyll *a* equivalents (chlorophyll *a* + phaeopigments). Due to the wide range of pigment destruction reported in the literature (0-100%, Tirelli and Mayzaud, 1998), we chose not to apply any conversion factor and consider our estimates to be conservative values.

Gut evacuation data were fitted to an exponential decay model (Dagg and Wyman, 1983):

$$G_t = G_0 \cdot e^{-kt}$$

where G_0 is the initial gut content, G_t is the gut content at time t and k is the instantaneous gut evacuation constant rate. Gut evacuation rates were also calculated using the empirical relationship with temperature proposed by Dam and Peterson (1988):

$$k = 0.0117 + 0.001794 T$$

Individual grazing rates for each size-fraction were obtained by multiplying the initial gut content by the gut evacuation rate. Community grazing rates were calculated by multiplying individual rates by copepod abundance, and were compared with integrated Chl *a* standing stock and primary production to estimate grazing impact. A C:Chl index of 50 was used (Quevedo and Anadón, 2000).

RESULTS

Figure 2 shows the vertical profiles of temperature and salinity at both stations. The hydrographic features of the study area are those of a typical temperate sea, with a period of mixing in the water column during winter, and thermal stratification between May and September. Surface temperature increased from 13.6°C (March) to 18.3°C (July) at station E1, and from 13.6°C (February) to 19.6°C (September) at station E2. Summer stratification translates into the development of a thermocline which progressively deepens to reach a maximum depth of 50 m. Upwelling of cold water was detected at station E2 in May, July, September and

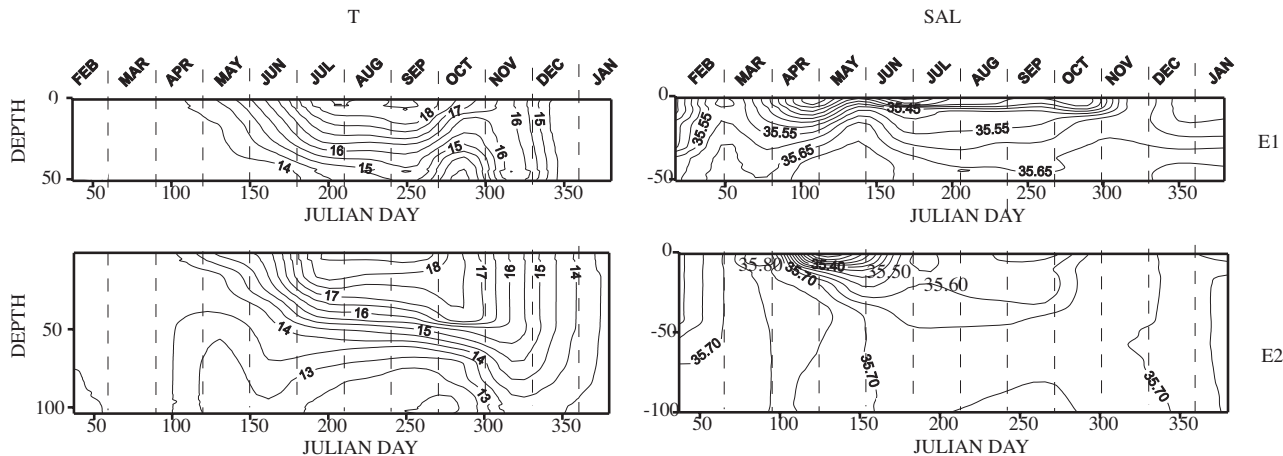


FIG. 2. – Vertical profiles of temperature and salinity at stations E1 and E2 from January 1998 to January 1999.

October, as reflected by the upward displacement of the 13°C isotherm. Uplifting of isotherms was also observed in October at station E1. Summer upwelling was confirmed by the positive Ekman transport values obtained from June to August (López, unpublished data). These values were calculated by averaging data from the four days previous to the sampling.

The coastal station showed a strong saline stratification from March to November. Low surface

salinity suggests mixing with waters of continental origin. An intrusion of relatively high salinity water (>35.70) was detected at the shelf-break station in winter and spring, reaching surface values above 35.80 in March.

Integrated chlorophyll concentration (Fig. 3) ranged between 0.8 mg m⁻² (March) and 43 mg m⁻² (April and July) at station E1, while station E2 showed a maximum value of 65 mg m⁻² (April) and a minimum value of 1.3 mg m⁻² (March). Primary

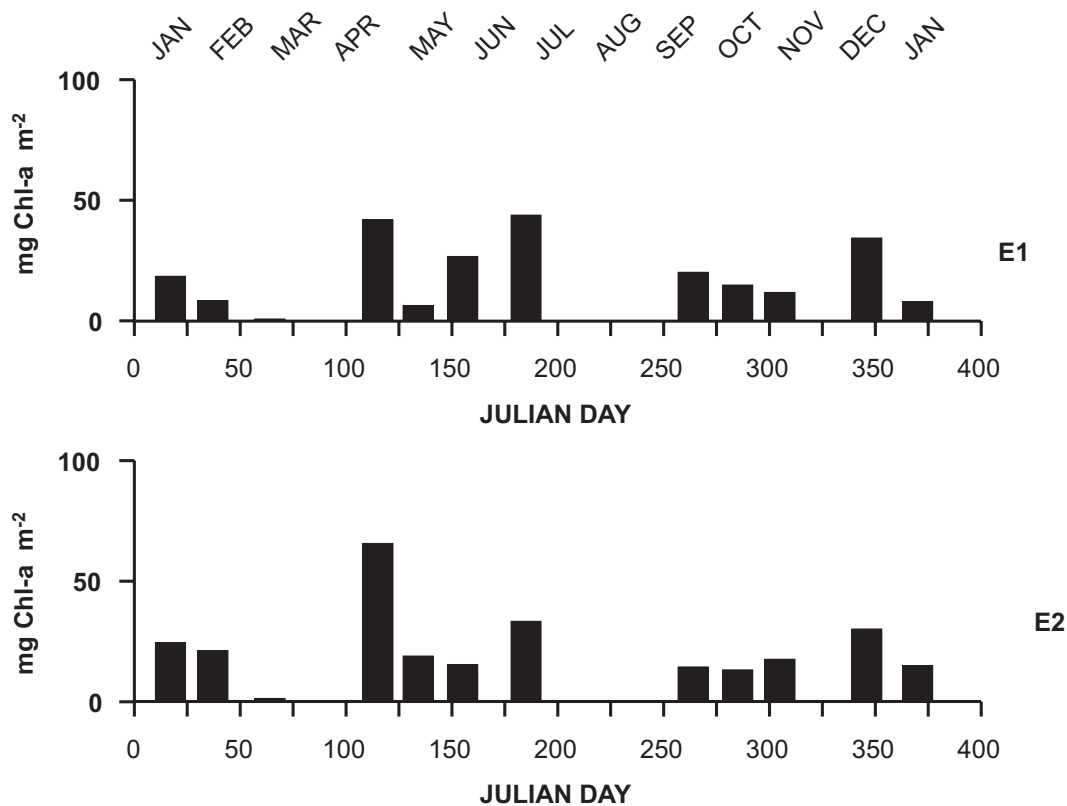


FIG. 3. – Seasonal variation of integrated Chlorophyll *a* concentration at stations E1 and E2.

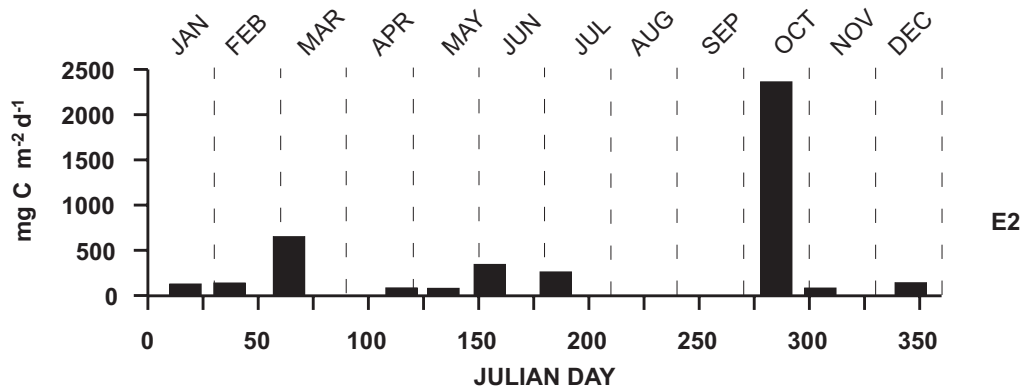


FIG. 4. – Seasonal variation of integrated primary production at station E2.

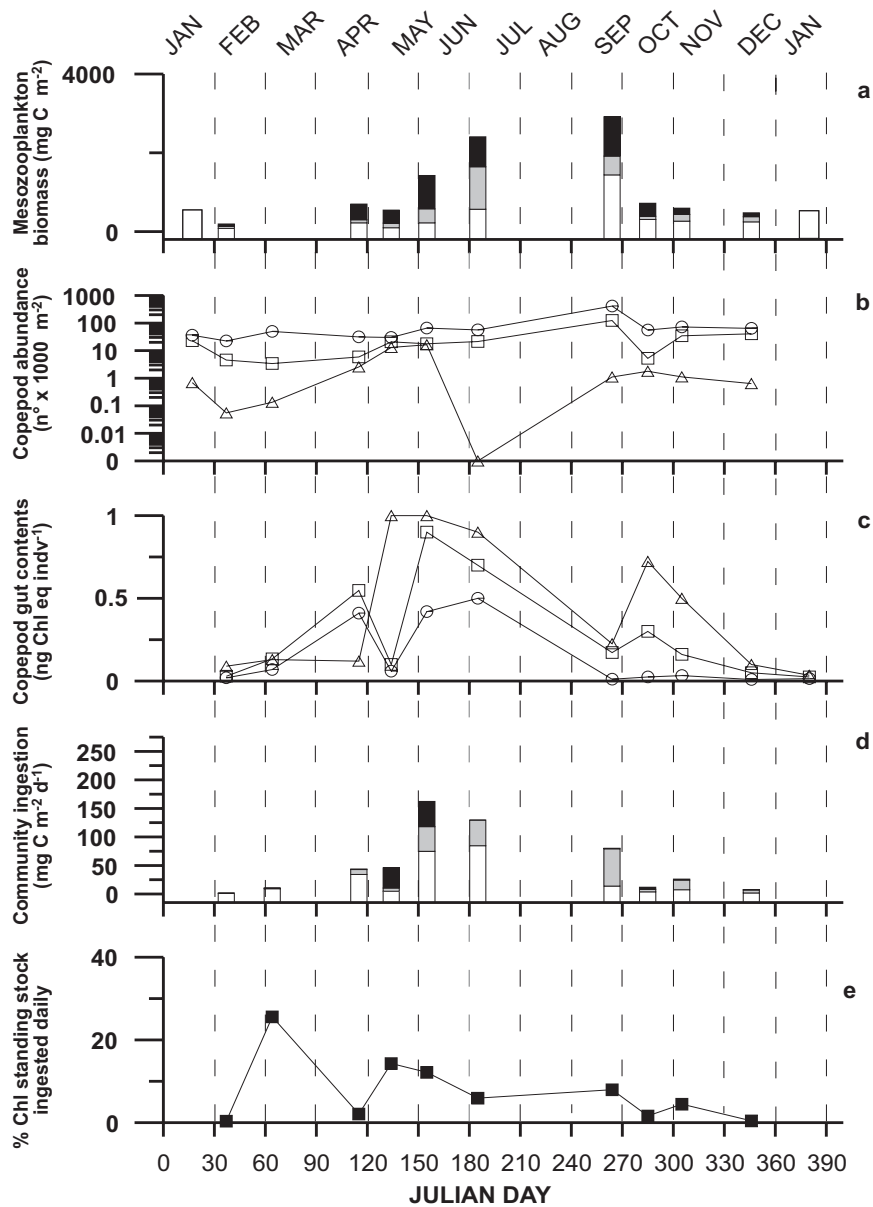


FIG. 5. – Seasonal variation in mesozooplankton biomass (a), copepod abundance (b), copepod gut contents (c), total community grazing rate (d), and grazing impact on phytoplankton biomass (e) at station E1. Legend - a and d: White 200-500 μm , Grey 500-1000 μm , Black 1000-2000 μm . b and c: circle 200-500 μm , square 500-1000 μm , triangle 1000-2000 μm .

TABLE 1. – Abundance (individuals m⁻²) of the different taxonomic groups sampled at stations E1 and E2. AMP-Amphipods, APP-Appendicularians, CLA-Cladocerans, COP-Copepods, DOL-Doliolids, JELL-Jellyfish, NAUP-Copepod nauplii, OST-Ostracods, POL-Polychaeta, PTER-Pteropods, CHA-Chaetognata, SALP-Salps, SIPHO-Siphonophors, F EGG-Fish eggs, DECL-Decapod larvae, EUFL-Euphausiids larvae, FISHL-Fish larvae

	Station	AMP	APP	CLA	COP	DOL	JELL	NAUP	OST	POL	PTER	CHA	SALP	SIPHO	F EGG	DECL	EUFL	FISHL
JAN	E1	16	676	-	60495	-	-	-	-	8	-	-	-	32	72	637	-	8
FEB	E1	-	111	-	27398	-	-	8944	16	95	-	32	-	-	501	1894	-	-
MAR	E1	-	16	-	53516	-	-	5698	56786	64	-	8	-	-	716	1448	-	-
APR	E1	-	7846	-	40242	111	-	64	573	-	223	-	-	80	1735	525	-	-
MAY	E1	-	10345	557	64824	2196	1241	302	-	414	1194	48	-	13242	207	541	-	32
JUN	E1	-	10189	22623	101116	890	32	1866	-	159	32	934	-	2269	498	997	-	329
JUL	E1	-	424	689	78820	2015	64	1495	-	-	1590	32	414	95	64	-	64	-
SEP	E1	-	-	191	542566	-	8	191	-	24	-	263	2204	223	8	127	390	16
OCT	E1	40	271	32	63885	-	-	32	-	16	-	334	88	-	-	72	199	-
NOV	E1	40	7125	665	108949	223	754	242	-	267	76	159	2157	600	318	24	48	111
DEC	E1	8	11361	-	107086	159	1557	1368	-	135	350	332	629	844	151	8	199	-
JAN	E2	-	16	-	36351	-	8	-	-	-	-	32	-	32	294	1210	-	-
FEB	E2	-	159	-	33781	-	-	700	159	16	-	16	-	-	1225	1981	-	-
MAR	E2	-	-	-	86588	-	-	2578	4902	-	-	24	-	-	135	1488	-	-
APR	E2	16	1456	-	18637	-	390	-	159	-	-	-	-	-	64	358	-	8
MAY	E2	-	589	318	62023	80	16	286	95	16	127	-	-	16	32	286	-	-
JUN	E2	-	7289	2165	58999	159	446	16	-	32	398	875	-	971	637	2300	-	95
JUL	E2	8	1503	795	60417	2362	970	297	32	8	350	175	-	642	85	371	175	53
SEP	E2	103	1411	53	159857	-	24	159	-	360	-	1210	5674	422	-	48	3080	8
OCT	E2	16	2737	16	51041	-	56	127	80	48	111	56	255	24	-	-	64	-
NOV	E2	21	2063	5	46149	153	-	217	74	124	48	39	-	13	23	34	18	10
DEC	E2	15	261	103	41237	1176	-	91	-	8	29	63	-	3	4	22	154	7

production (only estimated at station E2, Fig. 4) was maximum in October (2363 mg C m⁻² d⁻¹) and minimum in May (78 mg C m⁻² d⁻¹).

Zooplankton

Station E1

Mesozooplankton biomass (Fig. 5 a) was higher in summer, reaching 2900 mg dw m⁻² in September, while it remained lower than 700 mg dw m⁻² for the rest of the year. The contribution of the different size fractions to total biomass averaged 35, 24 and 41% for the small, medium and large size fractions respectively. Medium and large animals dominated mesozooplankton biomass from April to July (>60% of total biomass). Copepods were the most abundant group throughout the year (Table 1), averaging 81% of total mesozooplankton. Copepod abundance (Fig. 5b) was higher than 10⁵ individuals m⁻² in June,

November and December, reaching 55 10⁴ individuals m⁻² in September.

Copepod gut contents (Fig. 5 c) ranged between 0.01 and 0.5, 0.025 and 0.9, 0.03 and 1 ng Chl *a* eq indv⁻¹ for the small, medium and large size fractions respectively, with all the fractions showing higher contents in summer (June and July). Gut contents in the small and medium size fractions, but not in the large one, were linearly related to integrated chlorophyll concentration (Table 2 and Fig. 6). We only obtained four successful (statistically significant fit to an exponential decay model) gut evacuation curves (Fig. 7), so we used rates obtained from Dam and Peterson (1988) to calculate grazing at both stations (Table 3)

Copepod community carbon ingestion (Fig. 5d) showed maximum values in summer/early autumn (>80 mg C m⁻²), reaching 162 mg C m⁻² in June and remaining lower than 50 mg C m⁻² the rest of the year. Most of this carbon (>95%) was ingested by

TABLE 2. – Linear equations relating copepod gut contents (GC) and integrated chlorophyll *a* concentration (Chl) in the three copepod size fractions considered; *p<0.05, ***p<0.001; n=11 in all the cases.

	Equation	Small	r ²	Equation	Medium	r ²	Equation	Large	r ²
E1	GC = 0.0095 Chl - 0.045		0.53*	GC = 0.0129 Chl + 0.028		0.41*	-	-	-
E2	GC = 0.0061 Chl + 0.021		0.52*	GC = 0.016 Chl + 0.03		0.54*	GC = 0.079 Chl - 0.59		0.81***

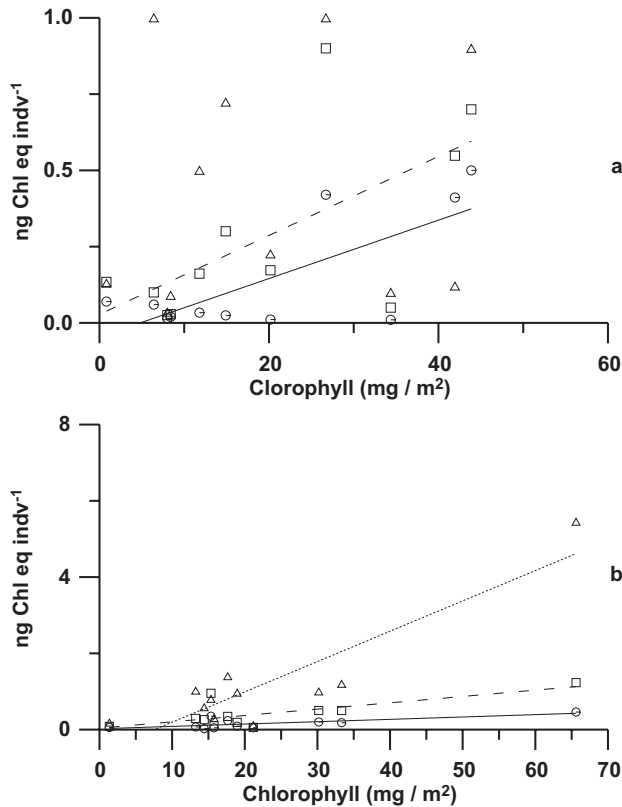


FIG. 6. – Copepod gut contents versus integrated chlorophyll concentration at stations E1 (a) and E2 (b). Legend: circle 200-500 μm , square 500-1000 μm , triangle 1000-2000 μm . Linear regressions: continuous line 200-500 μm , dashed line 500-1000 μm , dotted line 1000-2000 μm .

small and medium copepods, except in May, June and October, when grazing of large animals represents 77, 27 and 30% of the total. On average, copepods ingested daily 8.72% of chlorophyll standing stock (Fig. 5 e), ranging between 0.36% in February and 25.5% in March.

Station E2

Mesozooplankton biomass (Fig. 8 a) was higher than 1000 mg dw m^{-2} from May to July, reaching 2610 mg dw m^{-2} in September. Small animals contributed 38% of the total biomass, while medium and large fractions represented 24 and 38% of biomass respectively. As at station E1, copepods were the most abundant group (Table 1), averaging 91% of total mesozooplankton abundance. More than 55 10^3 copepods m^{-2} were found from May to July, reaching $16 \cdot 10^4$ individuals m^{-2} in September (Fig. 8 b). Copepods were also abundant in March, reaching $86 \cdot 10^3$ individuals m^{-2} (biomass not available that month).

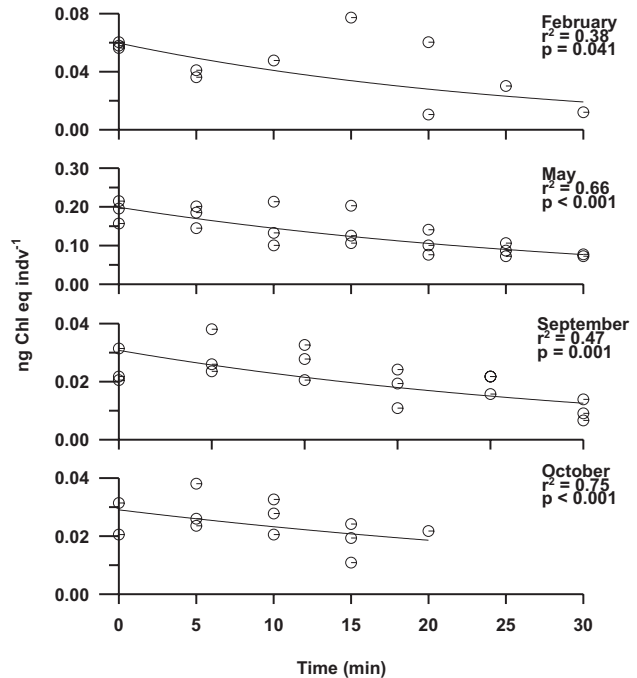


FIG. 7. – Successful curves obtained in the gut evacuation experiments; r^2 and p value for the adjust to an exponential decay model.

Copepod gut contents (Fig. 8 c) ranged between 0.02 and 0.46, 0.05 and 1.23, 0.11 and 5.45 ng Chl a eq indiv^{-1} for the small, medium and large size fractions respectively, with maximum values for all the fractions in April. Gut contents in all the size fractions were linearly related to integrated chlorophyll concentration (Table 2 and Fig. 6), but not to integrated primary production.

Copepod carbon ingestion (Fig. 8 d) showed the same seasonal pattern observed at station E1, being higher from June to September, and reaching maximum values (84 mg C m^{-2}) in June. On average,

TABLE 3. – Gut evacuation rates (k) used to calculate copepod ingestion. Evacuation rates were estimated using the Dam and Peterson (1988) relationship with temperature (T). Field calculated evacuation rates are also presented (k^*).

MONTH	E1		k	E2 k^*	T
	k	T			
Feb 98	0.036	13.5	0.036	0.037	13.2
Mar 98	0.036	13.6	0.036		13.5
Apr 98	0.036	13.8	0.036		13.7
May 98	0.036	14	0.035	0.031	13.5
Jun 98	0.037	14.1	0.036		13.3
Jul 98	0.041	16.4	0.038		13.8
Sep 98	0.042	16.9	0.038	0.035	14.9
Oct 98	0.038	14.7	0.039	0.035	14.9
Nov 98	0.041	16.8	0.039		15.2
Dec 98	0.037	14.2	0.037		15.7
Jan 99	0.037	14.1	0.035		14.2

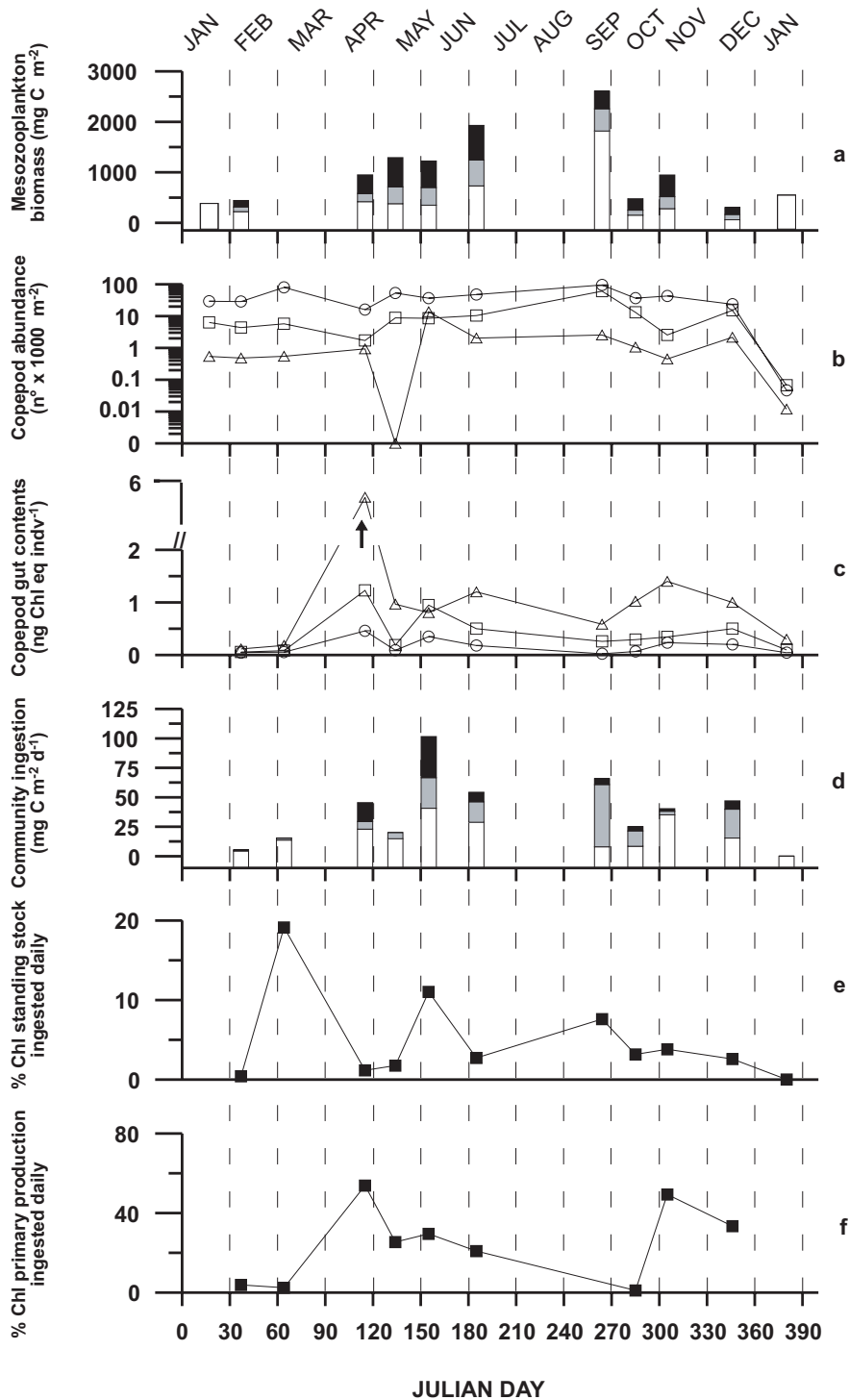


FIG. 8. – Seasonal variation in mesozooplankton biomass (a), copepod abundance (b), copepod gut contents (c), total community grazing rate (d), grazing impact on phytoplankton biomass (e) and production (f) at station E2. Legend - a and d: White 200-500 μ , Grey 500-1000 μ , Black 1000-2000 μ . b and c: circle 200-500 μ , square 500-1000 μ , triangle 1000-2000 μ .

small and medium animals accounted for 86% of total grazing, although in April and June the contribution of larger copepods increased up to 30%. Grazing impact on phytoplankton standing stock (Fig. 8 e) ranged between <0.5% ingested daily in

January and 19% in March, averaging 5.24% for the whole year. On average, copepod community ingested 20% of primary production (Fig. 8 f), with maximum impact in April (44 %) and minimum in October (0.8%).

DISCUSSION

Gut fluorescence measurements, combined with gut evacuation experiments, have been the most popular and widely used procedure for estimating in situ zooplankton grazing rates in the last few decades (see review in Calbet, 2001). It is easy to perform in the field, not time-consuming, and the experimental manipulation of animals is minimal (Head and Harris, 1996). However, its accuracy is open to discussion, mainly due to a possible degradation of chlorophyll to non-fluorescent compounds during digestion in the animals' gut (Penry and Frost, 1991; Head and Harris, 1996; McLeroy-Etheridge and McManus, 1999). Dam and Peterson (1988) proposed an average destruction value of 33%, which has usually been applied when direct estimates are not available (Morales *et al.*, 1991; Dam *et al.*, 1993; Peterson and Dam, 1996), and would lead to an underestimation by a moderate factor of only 1.5, which is not a substantial change. However, other authors have found pigment destruction to be much higher, ranging from 0 to 95% (see review in Harris *et al.*, 2001). We are also aware of the uncertainties arising from the use of gut evacuation rate values obtained from the literature, but this is a common procedure when direct estimates of k are not available. In fact, observed and estimated rates are very similar at the four stations when both of them are available (see Table 3). Finally, we must consider that all zooplankton samples in our study were obtained during daytime, so mesozooplankton abundance and grazing could be biased if vertical migration or diel feeding rhythms were present.

Although seasonal studies in oceanography provide a useful means of describing general patterns in the functioning of marine ecosystems, they also involve several limitations, mainly due to the sampling scale. Usually, description of variation over an annual cycle is based on monthly sampling (Villate, 1991; Gislason and Astthorsson, 1995; Siokou-Frangou, 1996; Razouls *et al.*, 1998). Although this sampling periodicity could be enough to summarise general trends, it is inadequate to detect small-scale hydrographic events. The central Cantabrian Sea is usually influenced by hydrodynamic singularities such as intrusions of saline water (Bode *et al.*, 1990) and summer upwellings (Botas *et al.*, 1990) that could affect our results. As suggested by Botas *et al.* (1990), regional phenomena in this area could be more important than general circulation in regulating biological production.

Since the early studies carried out by Harvey *et al.* (1935) and Clarke (1939), mesozooplankton grazing has widely been suggested to be a key factor in controlling phytoplankton production in the ocean (e.g. Banse, 1995). The grazing impact of copepods has been widely reported in the literature (see refs. in Head *et al.*, 1999; Huskin *et al.*, 2001a), and appears to be highly variable depending on season or location. Calbet (2001) suggests a decline in the relative importance of mesozooplankton grazing with increasing primary production. Despite the time-lag between samples, we observed a progressive decrease in phytoplankton biomass from January to March, related to a slight increase in the copepod community grazing rate caused by increases in both copepod abundance and individual gut contents. In fact, the minimum phytoplankton biomass over the annual cycle was found in March, coinciding with the higher grazing impact of copepods on phytoplankton stocks ($\approx 20\%$). Primary production showed a different pattern (at least at station E2), increasing from January to March, when copepod grazing controls only 2% of primary production. In spite of the observed increases in individuals gut contents, the lag in the response of zooplankton to the faster growth of phytoplankton means that copepod feeding has a relatively low impact on phytoplankton stocks. Morales *et al.* (1991) suggest that, in general, grazing pressure of copepods in the NE Atlantic is very low during the spring blooms, and this is what makes the bloom initiate. As the bloom develops, zooplankton cannot respond to increases in phytoplankton, and consequently the bloom is underexploited by copepods (Morales *et al.*, 1991; Bautista and Harris, 1992). High production and low grazing during March translates into the observed accumulation of phytoplankton in April, when copepods ingest less than 2% of the phytoplankton biomass. Several studies carried out in the area (Fernández and Bode, 1991 and Bode and Fernández, 1992) have also reported high phytoplankton biomass coinciding with the spring transition between mixing and stratification. Low production values and a high grazing impact on primary production (reaching 44%) suggests that in April the bloom was in a late stage of development.

There are no previous studies of mesozooplankton grazing in the central Cantabrian Sea, but Barquero *et al.* (1998) reported a grazing rate of <3% and <12% of phytoplankton biomass and production respectively off NW Spain, during a spring

bloom associated with an off-shelf front. Other studies have been carried out in temperate regions of the NE Atlantic in spring, reporting a similar low grazing impact on phytoplankton biomass and production: 0.1-8% of Chl standing stock off Plymouth (Bautista and Harris, 1992), 1-12% of primary production at 47-50°N (Morales *et al.*, 1993), <2% of Chl and <6% of P.P at 47°N (Dam *et al.*, 1993), and 9-14% of Chl and 17-21% of P.P in the Bay of Biscay (Sautour *et al.*, 1996). Therefore, our results are in the range reported by previous studies located in similar regions in spring, except for the high grazing impact on primary production in April, when copepods ingest 44% of P.P.

Temperate seas are expected to present low biological production during the summer (Longhurst, 1988). However, we found a relatively high chlorophyll concentration and primary production in June (station E1) and July (both stations). The explanation could be a summer upwelling event. In this region prevailing winds are north-east in summer, which translates into an Eckman transport offshore and an upwelling of cold and nutrient rich waters, probably modulated by bottom topography (Botas *et al.*, 1990). Although spatial coverage of this study does not allow us to confirm this phenomena, a slight summer upward displacement of isotherms was observed below 60 m at station E2. An increase in phytoplankton biomass translates into higher availability of food for herbivorous zooplankton, and consequently a higher zooplankton biomass was found at both stations in summer. However, we must also consider that previous studies (e.g. Harvey *et al.*, 1935) have also found high mesozooplankton biomass in temperate areas in summer, with no apparent influence of upwelling.

Higher copepod abundance in summer translates into the maximum community grazing rates over the annual cycle. In general, the zooplankton grazing impact is higher in steady state situations which allow a high degree of coupling between phyto- and zooplankton populations, like summer time in temperate latitudes. However, due to the phytoplankton size structure in oligotrophic conditions, the importance of mesozooplankton grazing is low (Huskin *et al.*, 2001a; Huskin *et al.*, 2001b) when compared with microzooplankton (Quevedo and Anadón, 2001). In agreement with this, in our study copepods ingested less than 10% of chlorophyll standing stock in summer. However, grazing impact on primary production (up to 25% ingested daily) points to a

high importance of copepods in the control of summer production in the region, particularly if we consider that vernal increases in mesozooplankton biomass are a common feature of the area (López, unpublished data). The only grazing studies carried out in the NE Atlantic in summer always found a lower grazing impact on phytoplankton biomass or production: <1% of Chl and <2% of PP (Morales *et al.*, 1991) between 47 and 60°N, 1-22% of PP (Morales *et al.*, 1993), and 2.6-8.9% of Chl at 37°N and 1.5-2.1% of Chl at 56°N (Head *et al.*, 1999).

Increases in mesozooplankton abundance (but not in copepod gut contents) reported in early autumn (September) translate into high community grazing. However, grazing impact on phytoplankton biomass remains low (7%). The decrease in copepod abundance and grazing, combined with a considerable increase in primary production in October (probably related to an autumn bloom), translates into the lowest grazing impact on phytoplankton production of the year (<1%). This suggests that most of this production could have sunk ungrazed to depth. Part of this primary production could also be ingested by microzooplankton, especially that of small phytoplankton cells. In accordance with this, Quevedo and Anadón (2000) suggest that microzooplankton could retire daily 28% of chlorophyll standing stock in the central Cantabrian Sea. Copepod carbon ingestion mediates in carbon fluxes to depth through faecal pellet sinking (Noji, 1991). We can not infer any quantitative estimation of fluxes from our data, mainly because phytoplankton is probably a minor component of total carbon ingested by copepods (Dam *et al.*, 1993; Painting *et al.*, 1993; Roman and Gauzens, 1997; Calbet, 2001). However, the results presented here point to an important copepod mediated flux in summer/early autumn. The period from June to September showed the highest grazing rates of the annual cycle, reaching 162 mg C m⁻² d⁻¹ at the coastal station, in the range reported by previous studies carried out in the NE Atlantic: 75-300 mg C m⁻² d⁻¹ (Barquero *et al.*, 1998), 482 mg C m⁻² d⁻¹ (Dam *et al.*, 1993), 234 mg C m⁻² d⁻¹ (Bautista y Harris, 1992), 5.6-70 mg C m⁻² d⁻¹ (Morales *et al.*, 1993), 5.7-91 mg C m⁻² d⁻¹ (Head *et al.*, 1999), and 231-535 mg C m⁻² d⁻¹ (Morales *et al.*, 1991).

In summer and early autumn, high grazing rates are enhanced by the high contribution of large animals (producers of large, fast-sinking faecal pellets) to total ingestion. We must also consider the role of

other taxonomic groups in carbon flux. Fortier *et al.* (1994) proposed that the contribution of copepods to carbon flux is low when compared with that of salps, appendicularians or doliolids. These groups are able to feed on small particles and produce large fast-sinking faecal pellets, and in general showed high abundance from May to September. The only study of vertical fluxes in the Cantabrian Sea was carried out in summer by Fernández *et al.* (1995), who found that zooplankton remains and faecal pellets were a principal component of the sedimented material.

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