

Food consumption by bathyal decapod crustacean assemblages in the western Mediterranean: predatory impact of megafauna and the food consumption-food supply balance in a deep-water food web

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ABSTRACT: Estimates of the daily ration consumed by decapod assemblages were obtained from 2 continuous sampling cycles conducted over the middle and lower slope (610–710 m and 1178–1240 m depth respectively) of the Catalan Sea (NW Mediterranean). Annual food consumption by decapods decreased from 82.2 mg dry weight (DW) m⁻² yr⁻¹ on the middle slope to 20.4 mg DW m⁻² yr⁻¹ on the lower slope. Additionally, from literature sources, the food consumption by fishes and the secondary production of macrobenthos and macroplankton were assessed for our deep-sea area. Combining the food consumption of megafauna (decapod crustaceans plus fishes), a model of the food supply-food consumption balance was proposed for the middle slope, the only depth stratum for which adequate information exists. On the middle slope, annual food consumption by megafauna amounted to 160 mg DW m⁻² yr⁻¹ while secondary production by the dominant macrobenthic taxa (suprabenthos, epibenthos and infauna) was estimated at 150 mg DW m⁻² yr⁻¹. Benthos was the main contributor to the food supply in our megafaunal mid-slope communities. The mean annual contribution of macroplankton was secondary, although it can be seasonally important. Euphausiids were the dominant macroplankton taxon over the middle slope, and only 10.6% of their secondary production (7.3 mg DW m⁻² yr⁻¹) was estimated to be consumed by decapods, whereas the total estimated euphausiid production consumed by our mid-bathyal community hardly attained 20%. Our results showed a tight equilibrium between food consumption and food supply on the middle slope. Estimated food consumption by mid-slope megafauna (0.059 g C m⁻² yr⁻¹) is equivalent to calculated values for production by benthic and suprabenthic macrofauna. This value is also consistent with estimates of mid-slope organic carbon through sedimentation (1.8 g C m⁻² yr⁻¹), after correcting for metabolism by benthos (from macrofauna to sediment bacteria). These results are consistent with the commonly accepted idea that food is the main limiting factor in deep-sea trophic webs.

KEY WORDS: Daily ration · Food consumption · Food supply · Secondary production · Deep-sea ecology

INTRODUCTION

The growing interest in quantifying trophic relationships in marine communities has led to the adoption of daily-ration methods to determine the amount of food consumed by marine organisms in natural conditions (Durbin et al. 1983, Worobec 1984, Macpherson 1985, Pakhomov et al. 1996, Maynou & Cartes 1997). Other

authors have followed this approach to estimate the food consumed by dominant characteristic species, usually target species in mono-specific fisheries (Yang & Livingston 1988, Bulman & Koslow 1992), or even to estimate the food required by a whole taxocenosis (Clarke 1978, Naumov 1985, Pakhomov et al. 1996, Pakhomov 1997). Fish are the main target group in these studies, as they are the dominant megabenthic taxon in most marine communities, particularly in deep-water communities (May & Blaber 1989, Berg-

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stad 1990, Gordon & Mauchline 1990). The results derived from these studies are of interest in trophic ecology and in the study of energy flow through trophic webs, including topics such as the contribution of the benthic and planktonic compartments to maintaining demersal trophic chains, or the predation pressure on key prey species in particular ecosystems (e.g. *Euphausia superba* in Antarctic waters; Pakhomov et al. 1996, Pakhomov 1997).

The quantitative relationship between the food consumed by marine fishes, the major consumers at the top level of trophic chains, and the availability of food produced by the benthos has been established in shallow-water systems for the Atlantic Ocean (Steele 1974, Jones 1978). To this end, several authors have proposed integrated studies of biological production by macrofauna, the basis of the megafaunal diet in shelf communities (Buchanan & Warwick 1974). The aim of such studies consists basically in establishing the relationship between primary production and secondary production, and ultimately in linking the latter to fish stock (Mills 1975, Rosenberg et al. 1977, Petersen & Curtis 1980). Most of these studies have focused on the continental shelf, where the interest in commercially exploited species justifies the study of energy flow dynamics. On the other hand, there is a notable lack of studies addressing the highest levels of trophic webs and linking food consumption to food supply, i.e. secondary production derived from prey exploited by fish (Pakhomov 1997). These kinds of studies are non-existent for deep-water bathyal or abyssal depths, despite the general consideration that food availability is the main limiting factor in deep-sea environments (Gage & Tyler 1991). While there are practically no quantitative studies on production at bathyal and abyssal depths, food-consumption studies are limited to some upper-slope environments (Macpherson 1985, Bulman & Koslow 1992), as well as some mid-water communities (Pakhomov et al. 1996).

Although the density of deep-sea organisms tends to decrease with depth (Rowe 1983, Haedrich & Merret 1992), the fact that deep-sea areas cover most of the globe suggests that an important part of energy flow and carbon biomass moves through deep-sea food webs (Haedrich & Merret 1992). Estimates of the food required by deep-water organisms can be a source of information on the carrying capacity of deep environments for sustaining given levels of abundance, biomass and diversity.

Recently we applied daily ration models to the deep-water shrimp *Aristeus antennatus* (Maynou & Cartes 1997), a widely dominant decapod crustacean in the middle- and lower-slope megabenthic communities in the Catalan Sea (NW Mediterranean; Cartes & Sardà 1992, Cartes et al. 1994a). This is now a relatively well

documented area, where both studies on the depth distribution of megabenthic biomass (Cartes & Sardà 1992, Stefanescu et al. 1993) and detailed studies on dietary preferences of the dominant decapod species (Cartes 1998) have been undertaken. Fish and decapod crustaceans represent most of the biomass in bathyal Mediterranean communities, while other groups such as cephalopods or echinoderms are present at very low levels. Several decapod crustaceans are target species of commercial fisheries in the deep western Mediterranean, especially the deep-sea shrimps *A. antennatus* and *Aristaeomorpha foliacea* (Bas et al. 1985). For the study of the dynamics of food resources exploited by the megafauna, data on the biology and ecology of vagile macrofauna (suprabenthos) have recently been published (Cartes & Sorbe 1996) and some initial data on the secondary production of characteristic species have already been obtained (Cartes & Sorbe unpubl.). In this context, the objectives of the present work are: (1) to estimate the food consumed by, and the predatory impact of, the entire megafaunal community, particularly the decapod crustacean assemblages, and (2) using data on macrofaunal production, to establish a first estimate of the balance between food consumption and food supply over the middle-slope level, the depth stratum for which the most complete information exists.

MATERIAL AND METHODS

Decapod crustaceans: data source and estimation of daily ration. Two continuous samplings were performed in the Catalan Sea (NW Mediterranean) over the middle slope (cruise DN-1) and the lower slope (cruise BT-1). During DN-1, 5 trawls were carried out in the vicinity of 41° 07' N, 02° 03' E, at depths between 610 and 710 m, on red shrimp *Aristeus antennatus* commercial fishing grounds. Trawling comprised an 18 h period between 17:30 h on 13 July and 11:05 h on 14 July 1989. Daily rations were calculated for 6 species of decapods in addition to *A. antennatus* (Table 1): the shrimps *Pasiphaea multidentata*, *Acantheephyra eximia*, *Plesionika martia* and *Plesionika acanthonotus*, the polychelid lobster *Polycheloides typhlops* and the crab *Geryon longipes*. The daily ration for the dominant species *A. antennatus* has been published recently (Maynou & Cartes 1997). All these species represented 97.7% (in biomass) of the total decapod assemblage at those depths, based on the catch data of the 5 trawls (see Table 2). A red shrimp commercial trawl was used in this sampling (trawled area: 116 080 m² h⁻¹; opening between wings: 25 m; values estimated with the aid of the acoustic monitoring system SCANMAR at a towing speed of 2.6 knots). A detailed description of station

data is available in Maynou & Cartes (1997). Table 1 summarizes the basic sampling data for each species studied.

The BT-1 sampling cycle was performed at 41° 00' N, 02° 15' E, from 1178 to 1240 m depth. Nine trawls were carried out between 08:50 h on 17 March and 02:37 h on 19 March 1994 (41 h period). The duration of hauls was always 1 h, while time between effective hauls varied between 2 h 10 min and 4 h 40 min. The sampling was carried out with a MTS bottom trawl (Cartes et al. 1994a) and a 1-bridle bottom trawl (trawled area: 65 005 m² h⁻¹; opening between wings: 14 m) specially designed for deep-sea sampling, at a towing speed of 2.6 knots. Diet composition (%F, frequency of occurrence) and daily ration were computed for the 3 dominant species of decapods on the lower slope (Table 1), the shrimps *Acantheephyra eximia* and *Pontophilus norvegicus* and the anomuran crab *Munida tenuimana*. These species, together with *Aristeus antennatus* and *Geryon longipes*, represented 97.0% of the total decapod assemblage (in biomass) at those depths (Table 2). To estimate the food consumed by decapod assemblages in the 1178 to 1240 m depth range, the daily ration calculated for *A. antennatus* and *G. longipes* from cruise DN-1 was also considered in this case.

In summary, a total of 885 and 531 individuals were studied and dissected during the DN-1 and BT-1 cruises respectively. Carapace length (CL) and wet weight of individuals were measured on board. The size spectra for the major portion of decapods collected varied between 16.0 and 47.0 mm CL (Table 1). In the laboratory, stomachs were removed and the stomach content dry weight obtained after drying in the oven at 100°C for 24 h. The stomach fullness index is

expressed as g dry weight food per 100 g predator wet weight (% DW/WW).

Before drying, the diet composition was analyzed in detail for each species. Complete results for DN-1 species have already been published in Cartes (1993), while data for the lower-slope stratum are also included in the present paper. Seventy individuals of *Acantheephyra eximia*, 37 of *Pontophilus norvegicus*, and 139 of *Munida tenuimana* were examined for dietary studies, and %F calculated for the main prey taxa. We classified stomach contents in the following 5 categories, based on their predominance in the foreguts of food of different origin: pelagic (macroplankton), benthic and suprabenthic (i.e. non-mobile and vagile macrofauna, respectively, retained in a mesh size of 500 µm), megafaunal remains and unidentified items. Usually one of these categories dominated by weight in the foregut and it was relatively easy to directly assign the weight of the stomach contents to one of the 5 groups established. The only exception was *Aristeus antennatus*, a species with a very high trophic diversity and a high number of prey of different origin in each stomach. The prey often appear broken and mixed (Cartes 1994). To allocate the weight of the stomach contents in this species, the estimated volume (in fresh stomachs) occupied by each prey was distributed according to the subjective points method (Swynerton & Worthington 1940). This method assigns a number of points (100, 75, etc.) according to the relative volume occupied by each prey item in a foregut. The volume occupied by each prey item in the contents is visually estimated under a stereomicroscope (10× to 40×), and according to their dominance a number of points is assigned to each prey category. Thus, we obtained a sum of points and a percentage of estimated

Table 1. Sampling data on dominant decapods in bathyal assemblages on the middle and lower slope of the Catalan Sea (NW Mediterranean) for food consumption estimates. n (max–min) is the number of individuals analysed for each species, specifying the maximum and minimum number in each sample. CL: carapace length; N: number of samples in which the species were present

| Species | n (max–min) | Size range (CL, mm) | Mean size (min–max) (CL, mm) | Sampled time interval (h) | N |
|---|-------------|------------------------|---------------------------------|------------------------------|---|
| DN-1 (July 1989) | | | | | |
| <i>Aristeus antennatus</i> ^a | 165 (36–30) | 17.2–59.9 | | 18 | 5 |
| <i>Pasiphaea multidentata</i> | 189 (71–19) | 23.0–45.1 | 29.2–33.9 | 18 | 5 |
| <i>Acantheephyra eximia</i> | 48 (19–5) | 26.3–39.9 | 30.2–31.9 | 18 | 4 |
| <i>Plesionika martia</i> | 163 (54–11) | 16.2–26.7 | 20.9–21.7 | 18 | 5 |
| <i>Plesionika acanthonotus</i> | 75 (31–14) | 12.0–18.7 | 14.0–14.4 | 13 | 3 |
| <i>Polychaetes typhlops</i> | 150 (56–10) | 16.0–44.3 | 30.1–32.7 | 18 | 5 |
| <i>Geryon longipes</i> | 95 (37–7) | 22.9–68.0 | 54.7–59.8 | 18 | 5 |
| BT-1 (March 1994) | | | | | |
| <i>Acantheephyra eximia</i> | 85 (23–8) | 17.0–47.0 | 23.9–26.2 | 41 | 8 |
| <i>Pontophilus norvegicus</i> | 198 (38–13) | 4.8–12.0 | 8.6–9.7 | 27 | 7 |
| <i>Munida tenuimana</i> | 248 (57–31) | 5.3–22.3 | 15.2–16.4 | 27 | 6 |

^aFrom Maynou & Cartes (1997)

volume for the 5 food categories established. This percentage was later applied to the total weight of the stomach contents.

In a previous work, we applied 3 models for the determination of daily ration food consumption by *Aristeus antennatus* (Maynou & Cartes 1997): the models of Eggers (1977, 1979) and Elliott & Persson (1978). The daily ration estimates derived from these 3 models were not significantly different. In a recent work (Maynou & Cartes 1998, this issue) we extended the analysis to 8 other species of decapod crustaceans. The daily rations estimated by the 3 models did not differ significantly in this case either, and for our multispecific approach in this study, we chose the results obtained using the Eggers (1977) model. We considered this model to be the best suited for our study because: (1) most species did not show significant feeding peaks (Maynou & Cartes 1998, this issue), which is the basic assumption in this model; (2) according to Bosclair & Leggett (1988), this model is recommended when using field data and when R (the evacuation rate) cannot be determined experimentally, as in our case. Additionally, the application of a single model to all species eases comparison among them by standardizing the results, because the differences among models could mask the variability among species. Thus, the consumption of each species over a 24 h cycle is:

$$C = F_{24} R 24 \quad (1)$$

where F_{24} is the mean stomach fullness index over 24 h, in % DW/WW. This model assumes that the weight of the stomach contents does not change significantly between the beginning and the end of the

study period. R , the gastric evacuation rate, is required for the estimation of daily ration. We adopted the experimental value of R recalculated from data in Sardà & Valladares (1990) in their study of *Nephrops norvegicus* performed in the laboratory at 13°C, the same temperature as in deep-water Mediterranean environments (justified in Maynou & Cartes 1997). Three R values were computed, one for each of the different feeding guilds of the species studied (see Cartes 1998 and Maynou & Cartes 1998 for details), basically depending on the type of food consumed by the predator species: soft, hard or mixed prey. As shown by Elliott & Persson (1978) and Bromley (1994), the evacuation rate depends mainly on temperature and type of prey. *Pasiphaea multidentata*, a mesopelagic shrimp characterized by regular vertical migrations between the water column and the slope bottom (Franqueville 1971), is a problematic species due to its particular feeding behaviour and was subjected to a different analysis (Maynou & Cartes 1998).

Determination of annual food consumption in decapod crustacean assemblages. The present study comprised 2 specific sampling cycles performed at 650–710 and 1178–1240 m depth. These depths are representative of 2 different bathyal communities regarding decapod crustaceans and megafaunal composition (Cartes & Sardà 1993, Cartes et al. 1994a, Sardà et al. 1994). Oceanographic conditions were also different in the 2 periods sampled. While in summer (DN-1 cruise) the most important oceanographic feature is the stratification of the water column, March (BT-1 cruise) coincides with a mixing period when a peak in primary production is regularly reported in the study area.

We extrapolated the results of DN-1 to an annual scale, bearing in mind that both daily ration and biomass can vary seasonally. Unfortunately, daily rations for different seasons are not available, although changes in mean percentage of stomach fullness can be indicative of changes in food consumption. *Aristeus antennatus*, the species responsible for the largest share of the food consumed on the middle slope, due to its dominance in biomass, did not show significant changes in mean % of fullness between DN-1 and the rest of the monthly samples in the period 1988–89 (Fig. 1). Mean fullness during DN-1 (July 1989) was 45.1%, slightly higher than the yearly mean of 41.7% (deduced from data in Fig. 1). Megafaunal crustacean densities were higher in July 1992 (66.9 ind. per 10 000 m²) than the annual average (49.3 ind. per 10 000 m²) for the period 1991–1992 (Fig. 2). These data may suggest that our annual

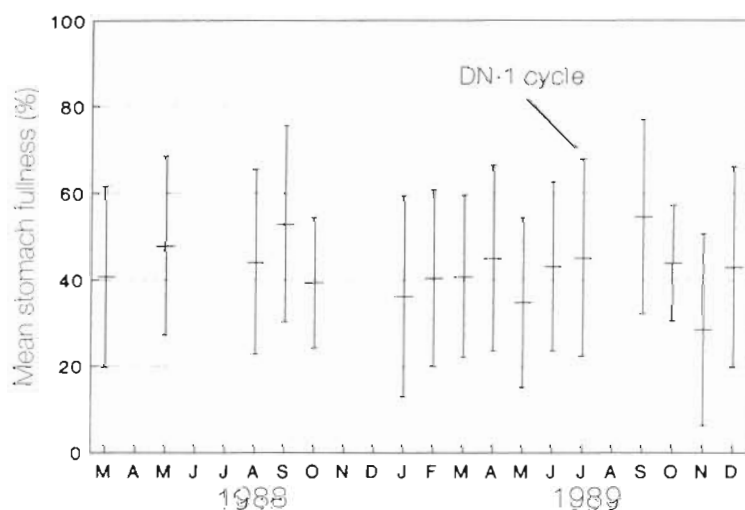


Fig. 1. *Aristeus antennatus*. Seasonal variations of mean stomach fullness of shrimp on the middle slope (570–728 m depth) in the studied area during March 1988 to December 1989 (2371 individuals analyzed; between 72 and 414 ind. mo⁻¹)

extrapolation from the July 1989 results slightly overestimate the annual food consumed by decapod assemblages on the middle slope.

For the lower slope, we adopted the values of daily ration obtained for *Aristeus antenatus* and *Geryon longipes* on the middle slope. We can assume this extrapolation for *A. antenatus* is adequate, considering that the temperature in Mediterranean deep waters is constant and relatively high throughout the year, $13 \pm 0.5^\circ\text{C}$ below 200 m depth (Hopkins 1985). However, stomach fullness, as a primary indicator of food consumption, decreased with depth and thus was higher on the middle slope (~1.2 times) than on the lower slope (see Cartes 1994), producing a slight overestimation when extrapolating daily ration values from the middle slope to the lower slope. On the other hand, the density values obtained in winter (March 1992) were lower than the values obtained in spring and autumn 1991 and in summer 1992 (Fig. 2), hence our data in the BT-1 cycle probably underestimate the annual predatory intensity on the lower slope. *G. longipes* is a secondary species in the lower-slope assemblage, and furthermore no appreciable changes in % of fullness or biomass were detected between 610 and 1322 m in a previous work (Cartes 1993).

Daily ration and annual food consumption in bathyal fish. No data on daily ration for bathyal Mediterranean fishes are available. However, studies exist on bathyal fishes for other geographical areas, such as the southeastern Atlantic off Namibia (Macpherson 1985) and the southwestern Pacific off South Australia (Bulman & Koslow 1992, Koslow 1996), while the daily ration in mesopelagic *Lampanyctus* spp. has been deduced from metabolic rates (Childress et al. 1980). These studies sometimes included the same species (or similar species in the same family) as those species dominating middle-slope fish assemblages in the western Mediterranean (i.e. Macrouridae, *Helicolenus dactylopterus*, *Lophius* spp., Myctophidae). Also, some basic biological characteristics of these bathyal species, such as morphology and diet, are close to those of dominant fish in our slope area (see data sources cited in Table 4). Furthermore, other species such as *Hoplostethus atlanticus* seem to have a food niche similar to that of our benthopelagic species, such as the blue whiting gadid *Micromesistius poutassou*. We obtained a rough estimate of daily ration for our fish assemblages by multiplying a mean value of daily ration deduced from 7 bathyal species from other areas (see Table 4) by estimates of mean annual biomass for fish assemblages in our study area (Cartes et al. 1994a, Sardà et al. 1994). We obtained values of fish biomass from 2 different samplings (RETRO and GEOS cruises) during both 1991 and 1992. In the RETRO cruise a fixed station was sampled in each season of the year

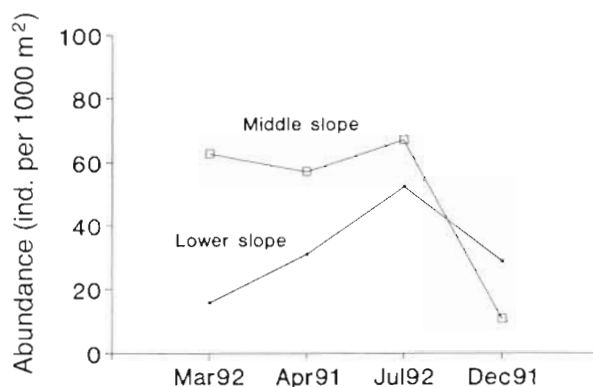


Fig. 2. Seasonal changes in decapod crustacean abundance at the middle slope and the lower slope in the studied area during the period April 1991 to July 1992

(12 trawls carried out between 545 and 692 m; see details in Sardà et al. 1994). In the GEOS cruise 13 trawls were performed in an area between $41^\circ 07' \text{N}$, $1^\circ 36' \text{E}$ and $41^\circ 14' \text{N}$, $2^\circ 33' \text{E}$, at depths between 514 and 730 m (Maynou et al. 1996) off Barcelona. We followed this approach only for the middle-slope depth stratum, as our lower-slope fish assemblages have special characteristics, with species such as *Alepocephalus rostratus* and *Bathypterois mediterraneus*, whose diets are based on gelatinous plankton and copepods (Carrasson 1994), and show a biomass peak at 1000 to 1200 m (Stefanescu et al. 1993, 1994). These characteristics, together with the lack of information on food consumed by comparable species, preclude a sensible extrapolation like that undertaken for our middle-slope fish assemblages.

Estimating food supply: secondary production and biomass of macrofauna and macroplankton. We obtained estimates of production of the different species or taxa which dominate the benthic compartment (macrofauna) and macroplankton in the study area. We considered 3 compartments in macrofaunal communities, based on the habitat of the species and the different methods existing to sample each compartment. Thus, macroplankton was traditionally sampled with IKMT or RMT pelagic gears, epibenthic and endobenthic fauna was sampled with grabs or quantitatively with box-corers, while suprabenthos (hyperbenthos or vagile macrofauna) was sampled with sledges (Cartes et al. 1994b). Euphasiids, mainly *Meganyctiphanes norvegica*, were selected as the most representative taxa in macroplankton communities (Franqueville 1971, Sardou et al. 1996), peracarid crustaceans as the dominant group in suprabenthic communities (authors' unpubl. data), and polychaetes as the dominant taxa among the infauna (Reyss 1971). We used wet weights (authors' unpubl. data) to calculate production for macrofauna. Although biomass val-

ues for macrofauna are often expressed as DW or AFDW (ash-free dry weight), these methods are destructive of the samples, and in deep-sea studies the non-destructive measurement of wet weight is alternatively recommended (Gage 1992). We obtained wet weight after drying samples on blotting paper for 15 min. Both in this case and also for megafauna (fish and decapods) we applied conversion factors for converting wet weight to dry weight based on our own data. When data was not available, a standard conversion factor of 0.25 (DW/WW ratio) was applied. DW was converted to carbon equivalents using a mean conversion factor of 0.369 from results summarized in Jorgensen et al. (1991) using different benthic and plankton taxa.

Meganyctiphanes norvegica represents between 19 and 23% of the total abundance of macroplankton (Franqueville 1971, Sardou et al. 1996). This species, together with 2 smaller species, *Euphausia krohni* and *Nematoscelis megalops*, which make up 13% of the total macroplankton abundance (Sardou et al. 1996), forms the largest share of the euphausiid bathyal assemblages in our study area. Thus the contribution of euphausiids to macroplankton communities in terms of biomass must be even greater, due to their high mean individual weight (0.09 to 0.15 g WW for *M. norvegica*; Franqueville 1971). P/B (production/biomass) ratios for these 3 euphausiids have been obtained by different authors in Atlantic and Mediterranean waters (Lindley 1982, Mauchline 1985, Labat & Cuzin-Roudy 1996). P/B was 3.4 and 6.1 for *N. megalops* and *E. krohni* respectively in North Atlantic waters (Lindley 1982, Mauchline 1985). P/B for *M. norvegica* was 1.24 in the northwestern Mediterranean (Labat & Cuzin-Roudy 1996), and 1.6 in the Rockall Trough, northeastern Atlantic (Mauchline 1985).

An estimate of secondary production and P/B for the 4 dominant peracarid species in our bathyal assemblages was obtained by applying both the Morin & Bourassa (1992) empirical model and the Hynes-Hamilton frequency method (Cartes & Sorbe unpubl.). The equation of the Morin & Bourassa (1992) model to estimate P is:

$$\log P = -0.75 + 1.01 \log B - 0.34 \log W + 0.037 T$$

Where P is annual production; B is the mean annual biomass (g DW m⁻²); W is the mean individual weight (g DW), computed as the quotient B/D , where D is the mean annual density (ind. m⁻²); and T is the temperature (°C). Compared to other production models, Morin & Bourassa's has the advantage of incorporating temperature. In the NW Mediterranean the temperature of the water masses below 200 m is nearly constant year-round (13.0 ± 0.5°C, Hopkins 1985). Based on our own unpublished data, we used a value of 13.1°C in this equation.

The most abundant peracarids in our study were the mysid *Boreomysis arctica*, strongly dominant in our bathyal communities (Cartes & Sorbe 1995), the amphipods *Rhachotropis caeca* and *Rhachotropis gabra*, and the cumacean *Leucon longirostris*. The mean P/B computed for those species was 8.05 and was extrapolated to the entire peracarid community. The mean P/B value obtained with this empirical model was close to the value obtained with the Hynes-Hamilton method (Cartes & Sorbe unpubl.). An estimate of peracarid mean biomass (non-destructive wet weight) was obtained from 4 sampling cruises conducted between April 1991 and July 1992 (see details in Cartes et al. 1994b). This sampling covered a depth range between 389 and 1355 m at 4 fixed stations (upper slope, between 389 and 402 m; canyon, between 389 and 506 m; middle slope, between 549 and 601 m; lower slope, between 1250 and 1355 m) and 4 annual seasons (R1: April 1991; R2: December 1991; R3: March 1992; R4: July 1992). Samples were obtained with a Macer-GIROQ sledge (Cartes et al. 1994b).

Finally, no quantitative data for infaunal density and biomass is available in our study area. In studies of the biocenosis of the neighbouring Lacaze-Duthier and Cap de Creus canyons, polychaetes were largely the dominant group in this category (58% of the total macrofauna collected). Studies quantifying polychaete biomass are restricted to the continental shelf in our area (e.g. Guille 1971, to depths of 91 m). We adopted values for deep-sea polychaete biomass (0.027 g DW m⁻²) from the study of Tselepidis & Eleftheriou (1992) in the south Aegean Sea (eastern Mediterranean). Given the lack of P/B ratios for deep-water polychaetes, we used a value of 1.83, based on a study of Brey (1990) summarizing the P/B ratios for 32 shallow-water polychaetes from subarctic to temperate areas. Although it is known that production is clearly lower in deep-water suprabenthic peracarids (Cartes & Sorbe unpubl.) and bivalves (Gage 1992) than in shallow-water species, the P/B ratio falls in the same range for shallow and bathyal species (Cartes & Sorbe unpubl.). Based on this finding we feel that we can reasonably extrapolate P/B ratios from shallow-water to deep-water polychaetes, within the framework of our approach.

RESULTS

Daily rations of decapods and annual food consumption

The estimates of daily ration (% DW/WW) for the dominant species in each depth stratum are shown in Table 2. The daily rations ranged from 1.205%

Table 2. Daily ration (DR; % DW/WW) and mean biomass (g WW per 10 000 m²) of dominant decapods in bathyal assemblages on the middle and lower slope of the Catalan Sea. N: number of samples in which the species were present for mean biomass estimates. p: pelagic; b: benthic

| Species | DR | Mean biomass | N |
|--|----------------------|--------------|----|
| DN-1, middle slope | | | |
| <i>Aristeus antennatus</i> | 0.223 | 771.9 | 5 |
| <i>Pasiphaea multidentata</i> ^a | 0.729 (b); 1.205 (p) | 23.6 | 5 |
| <i>Acantheephyra eximia</i> | 0.435 | 10.6 | 5 |
| <i>Plesionika martia</i> | 0.442 | 20.4 | 5 |
| <i>Plesionika acanthonotus</i> | 0.323 | 9.5 | 5 |
| <i>Polychaetes typhlops</i> | 0.096 | 30.8 | 5 |
| <i>Geryon longipes</i> | 0.061 | 172.1 | 5 |
| Total | | 1062.8 | |
| BT-1 lower slope | | | |
| <i>Aristeus antennatus</i> ^b | 0.223 | 81.2 | 10 |
| <i>Acantheephyra eximia</i> | 0.750 | 11.3 | 10 |
| <i>Pontophilus norvegicus</i> | 0.680 | 2.6 | 10 |
| <i>Munida tenuimana</i> | 0.904 | 28.4 | 10 |
| <i>Geryon longipes</i> ^b | 0.061 | 24.7 | 10 |
| Total | | 148.8 | |

^aFrom Maynou & Cartes (1997)

^bDR data adopted from the middle-slope level

DW/WW for the mesopelagic shrimp *Pasiphaea multidentata* to 0.061% DW/WW for the crab *Geryon longipes*, with mean values of 0.364% DW/WW on the middle slope and 0.524% DW/WW on the lower slope. Shrimps and prawns had higher daily rations than lobsters and crabs (see Maynou & Cartes 1998, for a detailed discussion). The biomass contribution was different for each species: *Aristeus antennatus* dominated both over the middle slope (DN-1, July 1989; 771.9 g WW per 10 000 m²) and the lower slope (BT-1, March 1994; 81.2 g WW per 10 000 m²), while the contribution of other species was lower (Table 2). From these results, the food consumed by our decapod assemblages was estimated at 2.251 and 0.556 g DW per 10 000 m² d⁻¹ on the middle and lower slope, respectively. These values represent an annual food consumption of 82.2 mg DW m⁻² yr⁻¹ on the middle slope, and 20.4 mg DW m⁻² yr⁻¹ on the lower slope.

Dietary composition

The diet composition of the dominant decapod megafauna has been reported on in detail for DN-1 species (Cartes 1994). Here we describe the dietary composition of the lower-slope species *Acantheephyra eximia*, *Pontophilus norvegicus*, and *Munida tenuimana*. The main food items occurring in stomachs of *A. eximia* were natantian decapods (*Acantheephyra pelagica*, *Pasiphaea multidentata*), gelatinous remains, hyperiid amphipods

(*Phrosina semilunata*), and fish remains. Gelatinous remains were often associated with hyperiid remains, and perhaps are attributable to salp or gelatinous plankton. *Pontophilus norvegicus* based its diet mainly on polychaetes (Table 3). The preferred food of *Munida tenuimana* was euphausiids (*Meganyctiphanes norvegica*), fish remains and, secondarily, siphonophores (Table 3). While the major part of the diet in *A. eximia* and *M. tenuimana* was of pelagic origin, *P. norvegicus* based its diet on benthic macrofauna.

The quantitative food composition of decapods in terms of biomass is shown in Fig. 3. Benthic resources were dominant on the middle slope (43.7% of total weight), and were constituted by (in decreasing order of importance) *Calocaris macandreae*,

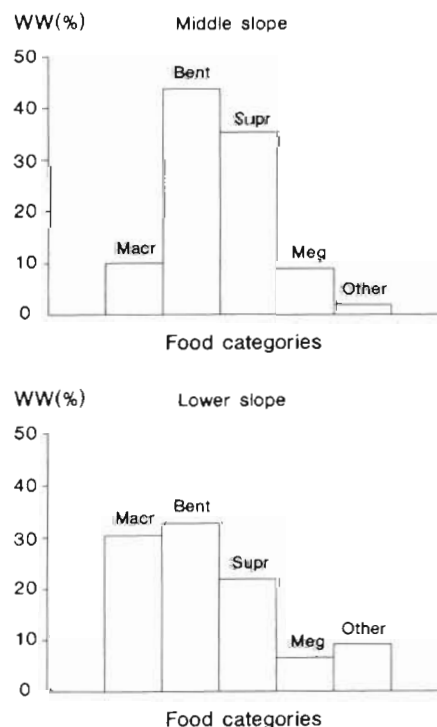


Fig. 3. Percentage contribution of the main compartments or food categories to the diet of decapod assemblages at the 2 bathymetric levels studied. Macr: macroplankton prey items; Bent: benthic macrofauna (epifauna + infauna) prey items; Supr: suprabenthos (vagile epifauna; macrofauna) prey items; Meg: megafaunal (fish + large decapods) remains; Other: mainly unidentified items

Table 3. *Acantheephyra eximia*, *Pontophilus norvegicus* and *Munida tenuimana*. Composition of the diet of 3 dominant decapods on the lower slope. Values are %F (frequency of occurrence). n: number of stomach contents analyzed

| Prey taxon | <i>A. eximia</i> n = 70 | <i>P. norvegicus</i> n = 37 | <i>M. tenuimana</i> n = 139 |
|---|----------------------------|--------------------------------|--------------------------------|
| Siphonophora (<i>Chelophyes appendiculata</i>) | 2.9 | – | 8.6 |
| Glyceridae | – | 5.4 | – |
| Unidentified polychaeta | 1.4 | 75.7 | 5.0 |
| <i>Acantheephyra pelagica</i> | 24.3 | – | – |
| <i>Pasiphaea multidentata</i> | 7.1 | – | 5.0 |
| <i>Gennadas elegans</i> | 1.4 | – | – |
| <i>Sergia robusta</i> | 1.4 | – | – |
| Decapoda Natantia | 2.9 | – | 2.9 |
| Other Decapoda (<i>Munida tenuimana</i>) | – | – | 2.2 |
| Euphausiacea (<i>Meganyctiphanes norvegica</i>) | 2.9 | – | 46.0 |
| Hyperideia | 18.6 | – | 4.3 |
| Gammaridea | – | 2.7 | – |
| Tanaidacea (<i>Apseudes</i> sp.) | – | 5.4 | – |
| Unidentified crustacea | 12.9 | – | 3.6 |
| Fish remains | 22.9 | – | 19.4 |
| Gelatinous remains | 30.0 | – | 6.5 |
| Unidentified debris (detritus, mud, etc.) | 11.4 | 8.1 | 5.0 |

polychaetes and bivalves. Suprabenthos was the second food group in terms of biomass (35.2%), with isopods such as *Natanolana borealis* and *Munnopsurus atlanticus*, large amphipods (basically Lysianassidae, Eusiridae, and Oedicerotidae), the mysid *Boreomysis arctica* and cumaceans as the most representative prey items. Macroplankton food resources were clearly secondary (only 10.0%) and were mainly represented by the euphausiid *Meganyctiphanes norvegica* and mesopelagic fishes (Myctophidae, *Cyclothone* spp.). Megafaunal remains (pieces of large decapods, fishes or cephalopods) contributed 8.9% of the prey items of middle-slope dominant decapods and unidentified material (1.9%) completed the diet at this depth level.

On the lower slope, benthic resources were also dominant (32.7% of total weight), together with macroplankton prey (30.4%) and suprabenthos (21.8%). Benthic prey were represented here by polychaetes, bivalves and large foraminiferans, macroplankton were represented by *Meganyctiphanes norvegica* and, secondarily, by the shrimp *Acantheephyra pelagica*, while the suprabenthos was represented by the same groups cited for the middle slope, except the large isopod *Natanolana borealis*. Both megafaunal remains (6.5%) and unidentified material (9.1%) were secondary food sources.

Daily rations of fish and annual food consumption

For fish we adopted a mean daily ration of 0.611% WW/WW, deduced from values in Table 4. The mean biomass values for the middle-slope assemblages were

1221.6 g WW per 10 000 m² (RETRO cruises), and 1562.7 g WW per 10 000 m² (GEOS cruises). Combining the daily ration estimates and the biomass estimates, we calculated the annual food consumption during the 2 cruises as 7.463 and 9.548 g WW per 10 000 m² d⁻¹ respectively. Annual food consumption in dry weight (using a DW/WW ratio of 0.25) was between 68.2 and 87.1 mg DW m⁻² yr⁻¹. Obviously, these estimates are less precise than the estimates for decapods and are employed here solely for comparative purposes.

Production data and biomass of prey taxa

We obtained direct and indirect data on macroplankton-macrofauna production. The taxa that we considered here are those well represented in the diet of megabenthic fish and decapods, as deduced from studies of stomach contents (Macpherson 1977, 1981, Carrasson et al. 1992). We do not include here taxa which are merely dominant in abundance, such as copepods, because of their small size and their small contribution to the diet of benthopelagic megafauna on the middle slope.

Sardou et al. (1996), for the northwestern Mediterranean area, gave a mean annual density value for *Meganyctiphanes norvegica* of 130 ind. per 100 m², integrating the water column between 800 m depth and the surface. We deduced a mean annual biomass of 156 mg WW m⁻², considering the specimens captured to have a wet weight of 0.12 g (based on the annual mean given in Franqueville 1971). Applying a

Table 4. Daily ration (DR) of bathyal-benthopelagic and mesopelagic fishes considered to estimate a mean daily ration for fish assemblages on the middle-slope zone of the Catalan Sea. T: temperature. Data source: (1) Macpherson (1985); (2) Childress et al. (1980), combining data deduced from metabolic rates of 2 species, *Lampanyctus ritteri* (DR 0.87) and *Lampanyctus regalis* (DR 0.68); (3) Bulman & Koslow (1992); (4) Koslow (1996). –: no temperature data in the original source

| Species | DR (% WW/WW) | T (°C) | Location (depth) | Source |
|---|--------------------|--------|------------------------------|--------|
| <i>Helicolenus dactylopterus</i> | 0.360 ^a | 8–10 | Off Namibia (300–350 m) | 1 |
| <i>Coelorhynchus fasciatus</i> | 0.875 | 8–10 | Off Namibia (300–350 m) | 1 |
| <i>Lophius upsicephalus</i> | 1.072 ^a | 8–10 | Off Namibia (300–350 m) | 1 |
| <i>Lampanyctus</i> spp. | 0.78 | – | Off S. California (50–500 m) | 2 |
| <i>Hoplostethus atlanticus</i> | 1.03 | – | Off S. Australia (650 m) | 3 |
| <i>Coryphaenoides rupestris</i> | 0.05 | – | Off S. Australia (550 m) | 4 |
| <i>Coryphaenoides acrolepis</i> | 0.11 | – | Off S. Australia (490 m) | 4 |
| ^a Diana method (cf. Macpherson 1985) | | | | |

P/B of 1.24 (Labat et al. 1996) and a DW/WW ratio of 0.20 (authors' unpubl. data) we obtained a production of 38.7 mg DW m⁻² yr⁻¹. If we apply a P/B ratio of 1.6, as proposed by Mauchline (1985), production reached 49.9 mg DW m⁻² yr⁻¹ for this species. For the other smaller euphausiids dominant in our area we obtained a P of 24.3 mg DW m⁻² yr⁻¹ (mean annual density = 75.2 ind. per 100 m², Sardou et al. 1996; mean wet weight = 0.034 g, authors' unpubl. data; mean P/B = 4.75, Lindley 1982, Mauchline 1985). Euphausiids, which represent ~1/3 of total macroplankton abundance in the study area, have a total production of 63.0 to 74.2 mg DW m⁻² yr⁻¹ on the middle slope.

For peracarid communities we obtained a mean annual biomass of 0.013 g WW m⁻² between 389 and 1255 m which increased on the middle slope to 0.023 g WW m⁻². This value, obtained by direct weighing after blotting, is probably an underestimate due to the fragility of most of these organisms, especially mysids, which appear broken in the samples. Despite this, considering the mean deduced P/B of 8.05, we estimated peracarid annual production at 26.2 mg DW m⁻² yr⁻¹ along the whole slope (46.3 mg DW m⁻² yr⁻¹ on the middle slope, 549 to 601 m). Other suprabenthic groups in bathyal communities of the Catalan Sea comprised essentially small decapods (Processidae, Pandalidae and Crangonidae) which represented around 25% of the total biomass for these communities on the middle slope (from Macer-GIROQ samplings).

Finally, our estimate of polychaete production was based on a biomass value of 0.027 g DW m⁻² (from the 400 to 1000 m depth interval in the south Aegean Sea; Tselepidis & Eleftheriou 1992) and a P/B ratio of 1.83. The annual production of polychaetes was thus 49.4 mg DW m⁻² yr⁻¹. This approach probably underestimates the real value of polychaete production in the Catalan Sea, considering the oligotrophic characteristics of the south Aegean Sea (Tselepidis & Eleftheriou 1992). However, the polychaete biomass re-

ported on the Catalan Sea shelf (0.337 g DW m⁻² between 87 and 91 m depth; Guille 1971) was of the same order of magnitude as that reported by Tselepidis & Eleftheriou (1992) for the deeper 200 to 300 m interval (0.164 g DW m⁻²), suggesting that the 2 areas probably do not differ substantially in their infauna biomass values. Polychaete assemblages constituted 58% of total macrofauna sampled with grabs in the bathyal mud communities in the Catalan Sea (Reyss 1971).

DISCUSSION

In the Catalan Sea area, total food consumption by bathyal decapod assemblages was higher on the middle slope than on the lower slope at around 1200 m. This must be mainly due to a decrease of megafaunal decapod biomass at those depths (Cartes & Sardà 1993, Sardà et al. 1994), because, at a species level, those decapods dwelling at 1200 m did not show lower daily ration values. The decrease in food consumption by decapod assemblages with depth is also consistent with a general decrease in food availability: from suprabenthos, one of the main food sources of decapods, to infaunal species, such as *Calocaris macandreae*, or mesopelagic decapods and euphausiids, different prey taxa decrease in abundance with depth (Carpine 1970, Cartes 1998) along the northwestern Mediterranean slope. Considering this decrease in food availability, it would be expected that species inhabiting deeper levels would show lower daily rations, coinciding with results reporting a significant linear decrease in stomach fullness with depth (Cartes 1998) for Catalan Sea decapods. To explain this apparent inconsistency, the special characteristics of the 1200 to 1300 m depth stratum can be invoked. Some species (i.e. *Munida tenuimana* and *Pontophilus norvegicus*) showed maxima in mean size over this

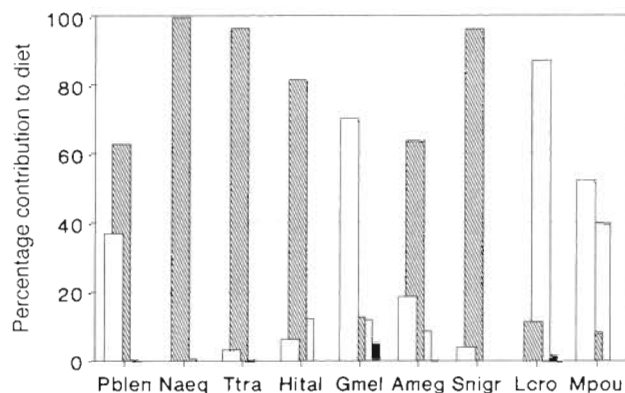


Fig. 4. Percentage contribution of the main food categories to the diet of the dominant fish in the middle-slope assemblages of the Catalan Sea. (□) Megafauna + micronekton; (▨) macrobenthos (benthos + suprabenthos); (■) macroplankton; (■) other (including unidentified items). In decreasing order of abundance: Pblen: *Phycis blennoides*; Naeq: *Nezumia aequalis*; Ttra: *Trachyrhynchus trachyrhynchus*; Hital: *Hymenocephalus italicus*; Gmel: *Galeus melastomus*; Ameg: *Antonogadus megalokynodon*; Snigr: *Symphurus nigrescens*; Lcro: *Lampanyctus crocodilus*; Mpou: *Micromesistius poutassou*. Data sources: Carrasson et al. (1992), Macpherson (1977, 1981), Stefanescu & Cartes (1992)

depth interval, while a fish-biomass peak occurred at around 1200 m (Stefanescu et al. 1993, 1994). This suggests that at this depth stratum a secondary peak of production occurs, within the general decrease of biomass with depth. The flux derived from the DCM (deep chlorophyll maximum) detected in oceanic waters (Estrada 1991) over the lower slope may contribute to this local trend affecting biomass and size structure distributions in megafauna. Estimates of daily ration for the lower slope (below 1300 m) would be of great interest in addressing this question.

Over the middle slope, fish communities are dominated by relatively small species, such as macrourids and *Phycis blennoides* (Sardà et al. 1994, Stefanescu et al. 1994). Dominant species on the middle slope base their diets on macrofauna and macroplankton, and only large specimens of *P. blennoides* and some secondary species such as sharks and *Micromesistius poutassou* also prey on megafaunal decapods, cephalopods and other fishes (Fig. 4). The small contribution of pelagic resources to fish diet (Fig. 4) applies only to the middle slope, not to deeper slope levels.

On the Catalan Sea lower slope, pelagic and bathypelagic prey increase their contribution to fish food requirements (Carrasson 1994), in accordance with the general trend described for other deep-sea fish assemblages (cf. Gordon & Mauchline 1990). On the middle slope, decapods and fishes represent practically the entire megafaunal biomass, while other macrobenthos-macroplankton consumers, such as cephalopods

or even some echinoderms, such as *Astropecten irregularis*, are comparatively scarce (Carpine 1970, Reyss 1971, Sardà et al. 1994). On the basis of the results from our study, we can conclude that total food consumption by this community should be close to the $160 \text{ mg DW m}^{-2} \text{ yr}^{-1}$ calculated for decapods and fish, and also that the major part of this food is supplied by macroplankton and macrobenthic organisms (Fig. 4). Production by benthic and suprabenthic macrofauna was estimated at $\sim 95 \text{ mg DW m}^{-2} \text{ yr}^{-1}$ considering only the 2 dominant taxa (polychaetes and peracarid crustaceans) in our area. Both groups comprise nearly $\frac{2}{3}$ of the total benthos, and total production by benthos can be roughly estimated at $150 \text{ mg DW m}^{-2} \text{ yr}^{-1}$, in close agreement with the biomass consumed by megafaunal communities.

As deduced from stomach data, the contribution of macroplankton to this scheme is secondary. Considering our data from summer (cruise DN-1), only 10% of the stomach content weight is of macroplankton origin. However, macroplankton consumption by bathyal organisms in the northwestern Mediterranean follows a seasonal pattern. Euphausiids become seasonally important in the diet of decapods in September–October and also in spring (Cartes 1991), approximately coinciding with vertical or ontogenic migrations by *Meganyctiphanes norvegica* to deep waters in the study area (Sardou et al. 1996). An annual estimated volume (Cartes 1991), covering all seasons, increases the total volume of macroplanktonic food consumed by decapods to $\sim 20\%$, of which euphausiids constitute $\sim 45\%$ (9% of total). This 9% euphausiid portion of total food consumed by decapods ($\sim 7.3 \text{ mg DW m}^{-2} \text{ yr}^{-1}$) represents 10.6% of euphausiid production. Euphausiids, as part of the macroplankton, are only preyed upon by some secondary fishes in middle-slope communities, such as *Lampanyctus crocodilus* and the blue whiting *Micromesistius poutassou* (Macpherson 1977, 1981, Stefanescu & Cartes 1992) (see Fig. 4). The contribution of euphausiids to food supply seems lower for mid-slope fish than that deduced for decapods, and thus the percentage of euphausiid production consumed by our mid-bathyal communities hardly attains 20%. This contribution, although lower than that estimated for Antarctic krill *Euphausia superba* (39% of the yearly krill production is consumed by Antarctic demersal fish; Pakhomov 1997), still can be significant for deep-water communities.

Our results on food supply and food consumption suggest the existence of a delicate balance in the bathyal community studied, adding evidence to the commonly accepted idea of food supply being the main limiting factor in deep-sea trophic webs (Gage & Tyler 1991). In the NW Mediterranean, all macrobenthic and macroplanktonic production is apparently consumed

by megafauna, as is usually assumed in models of C flux in trophic webs (Huntley et al. 1991). Fish and decapods showed similar levels of food consumption, and our results point to a 50% share of each of these taxa in the consumption of macroplankton-macrobenthos production. The ~50% of production exploited by our benthopelagic fish community would be within the range of ca 40 to 76% of annual secondary production consumed by mesopelagic fish reported by Huntley et al. (1991) and Pakhomov et al. (1996) in the Southern Ocean and Antarctic waters.

Comparing the food consumption calculated for decapods and the value deduced for fishes, similar levels of annual food consumption for both dominant megafaunal groups were obtained on the middle slope, despite the fact that fish biomass was ~1.7 times higher than decapod biomass in the same samplings (Cartes et al. 1994a). At this level, decapods annually consume 3.09 times their mean biomass (in dry weight), while demersal fish consume 2.23 times theirs. These values are below the value of 600% of fish body weight estimated for mesopelagic fish (Naumov 1985, in Pakhomov et al. 1996) in the Southern Ocean, suggesting benthopelagic bathyal communities are more efficient than midwater ones, although here we are comparing different areas with different estimates of biomass (at a bathymetric level in our case and over an extensive area in the Antarctic studies). Unfortunately, *P* and *P/B* values for megafaunal bathyal species are not available, and comparisons between the efficiencies of different taxa are not possible yet. Assuming similar levels of *P* for fish and decapods in our area, one could speculate that fish are more efficient than decapod crustaceans on the middle slope.

In any case, the benthos is the main contributor to food supply in our bathyal megafaunal communities on the middle slope, coinciding with other trophic webs in shallow waters of subarctic and temperate areas (Steele 1974, Mills 1975, Petersen & Curtis 1980). Furthermore, in the NW Mediterranean, suprabenthic production (traditionally ignored in other studies) increases the importance of benthos compared to zooplankton in terms of food supply.

Advective inputs of organic matter to the seabed have been reported at 1 to 10 g C m⁻² yr⁻¹ (Buscail et al. 1990), depending on the method used, in the adjacent slope of the Lacaze-Duthier Canyon in the northern Catalan Sea. These values are probably a high estimate for our open-slope station (interfluvial) on the middle slope, due to the fact that organic C in surface sediments is lower in the open slope between canyons than in canyons (Buscail et al. 1990). Between 49 and 60% of this flux is consumed by benthic organisms while the rest is buried, i.e. not immediately consumed (Buscail et al. 1990). According to these authors, the

proportion of C would amount to 0.6 to 4.9 g C m⁻² yr⁻¹. A mean value of 2.75 g C m⁻² yr⁻¹ with a canyon/interfluvial ratio of 1.5 for organic C in sediments (cf. Buscail et al. 1990) gives an estimate of 1.83 g C m⁻² yr⁻¹ that we can adopt for our study area. Macrobenthos can consume this C either directly (e.g. *Boreomysis arctica*; authors' unpubl. data) or via meiofauna (foraminiferans, harpacticoides). Foraminiferans, for instance, which accumulate a high benthic biomass, consume mainly planktonic and other detritus (Gooday 1988), while they are preyed upon by suprabenthic isopods (Svavarsson et al. 1993) and amphipods (authors' unpubl. data). The efficiency with which this production is transferred up through food chains, called ecological efficiency, is regularly assumed to be 10% (Lindeman 1941), although, in one study of benthic marine food chains, Steele (1974) obtained efficiencies of 23 to 25% for macro- and meiobenthos. This would represent between 0.018 and 0.183 g C m⁻² yr⁻¹ (efficiency = 10%) or between 0.105 and 0.421 g C m⁻² yr⁻¹ (following Steele's estimations) being available to megafaunal communities at 600 to 710 m depth, depending on whether consumption is direct or occurs via meiofauna by infauna and suprabenthos. The role of bacteria in this food input could be particularly important in the deep Mediterranean due to the relatively high temperature (13°C) in the water column below 200 m. Their dominance in the deep-sea benthos (Pfannkuche 1992) and their degradation activity must add another step in food webs, reducing the amount of C supply available for megafauna and upper food chains. Our estimation of food consumption for middle-slope megafaunal communities is, based on DW calculations, 0.059 g C m⁻² yr⁻¹, closely matching the supply of C deduced from flux data. Assuming that this value is close to the food supply (production) by benthos, and adopting the values mentioned above for ecological efficiency (10 to 23%), macrobenthic communities would consume between 0.6 and 0.26 g C m⁻² yr⁻¹, which is less than 1% of annual primary production (mean value between 77 and 100 g C m⁻² yr⁻¹; Miquel et al. 1994) in the western Mediterranean.

In a comparative study of shallow-water communities, Petersen & Curtis (1980) linked the ratio of zooplankton/benthos (excluding suprabenthos) production to a latitudinal gradient. This ratio was 6:1 in a tropical ecosystem and 3:1 in a temperate area, and decreased to 1:1 in subarctic systems. This is also in agreement with a general decrease of deep-sea benthos biomass from high to low latitudes (Rowe 1983). In our results from the dominant taxa in the macroplankton (euphausiids) and benthos (polychaetes), this ratio is closer to 1:1. Considering the high and similar proportion of these taxa in their respective compartments, one can extrapolate this ratio to the entire macroplank-

ton-benthos (suprabenthos excluded). Thus, despite the fact that our study area is located in a temperate-subtropical zone, its bathyal trophic webs are more closely related to subarctic areas in terms of zooplankton/benthos production. This suggests that an increase in depth could have a similar influence on trophic web structure to a latitudinal increase. A common origin for both polar and deep-sea fauna has already been proposed (Lipps & Hickman 1982). There are some species common to both Mediterranean and Atlantic faunas, presenting a bathyal distribution in the Mediterranean and occupying shallow waters in North Atlantic boreal waters (Carpine 1970). At our ecological level, the macroplankton-benthos production balance seems to agree well with these faunistic and biogeographic considerations. Suprabenthos, which can constitute an important part of benthic production in our system, has traditionally been ignored in other balances. The zooplankton-benthos ratio is also related to the development of demersal or pelagic fisheries in a concrete area (Petersen & Curtis 1980). Thus, while demersal fish are important in subarctic ecosystems, they are comparatively unimportant in the tropics. Deep-water fisheries in our slope area are exclusively directed at demersal species, especially shrimps (Bas et al. 1985), adding some evidence to the scheme proposed by Petersen & Curtis.

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