

Comparing production–biomass ratios of benthos and suprabenthos in macrofaunal marine crustaceans

J.E. Cartes, T. Brey, J.C. Sorbe, and F. Maynou

Abstract: Using available data from the literature, we compared the production–biomass ratios (P/B) between the suprabenthic (= hyperbenthic) and the benthic (infauna–epifauna) species within the group of the macrofaunal marine crustaceans. This data set consists of 91 P/B estimates (26 for suprabenthos and 65 for infauna–epifauna) for 49 different species. Suprabenthic crustacean P/B was significantly higher than P/B of benthic crustacean (post-hoc Scheffé test; one-way analysis of covariance, ANCOVA; $p < 10^{-3}$) and also of other (noncrustacean) benthic invertebrate ($p < 10^{-4}$). Predictive multilinear regression (MLR) analysis for macrofaunal marine crustaceans showed P/B to depend significantly on mean annual temperature (T) and mean individual weight (W) ($R^2 = 0.367$). Adding the variable swimming capacity increased goodness-of-fit to $R^2 = 0.528$. The higher P/B of suprabenthic (= swimming) macrofauna in comparison with that of the benthic compartment seems to be related to the most apparent feature of the suprabenthos, its swimming capacity. The high P/B s reported for suprabenthic species indicate how a nontrivial part of benthic production can be ignored if suprabenthos is not well sampled, therefore biasing the models of energy flow generated for trophic webs.

Résumé : Les données de la littérature nous ont permis de comparer les rapports production–biomasse (P/B) chez les espèces suprabenthiques (= hyperbenthiques) et endobenthiques–épibenthiques de la macrofaune carcinologique marine. Ces données comprennent 91 estimations du P/B de 49 espèces (26 pour le suprabenthos et 65 pour l'endofaune–épifaune). Les P/B des crustacés suprabenthiques sont plus élevés que ceux des crustacés endo- et épibenthiques (test post-hoc de Scheffé ; analyse de covariance à un critère de classification, ANCOVA; $p < 10^{-3}$) ainsi que ceux des autres invertébrés (non crustacés) benthiques ($p < 10^{-4}$). Une analyse de régression multilinéaire (MLR) prédictive révèle que le P/B des crustacés de la macrofaune marine est significativement corrélé à la température annuelle moyenne T et à la masse individuelle moyenne W ($R^2 = 0,367$). La prise en compte de la capacité natatoire des espèces dans cette analyse améliore l'ajustement du modèle régressif aux données ($R^2 = 0,528$). Les P/B élevés des espèces suprabenthiques par comparaison aux espèces endo- et épibenthiques semblent donc être liés à leurs capacités natatoires, particularité qui caractérise le compartiment suprabenthique. De ce fait, une fraction non négligeable de la production benthique globale peut être ignorée si le suprabenthos est mal échantillonné, introduisant ainsi un biais dans les modèles de flux d'énergie générés par l'analyse des réseaux trophiques.

Introduction

Secondary production of many aquatic invertebrate populations has been analyzed by studies applying methods based on either growth and mortality of identifiable cohorts (e.g., Waters 1977; Benke 1984; Crisp 1984) or on the loss of biomass by size–frequency classes (Hynes-Hamilton and Coleman 1968; Hamilton 1969; Menzies 1980). In attempts to quantify energy flow through ecosystems, both freshwater and marine ecologists have constructed predictive empirical models to calculate benthic population production and P/B

(production–biomass ratio) from more easily obtained abiotic and population parameters. Usually these models are single regression (Robertson 1979; Banse and Mosher 1980; Edgar 1990) or multiple linear regression (e.g., Plante and Downing 1989; Morin and Bourassa 1992; Brey 1999), but more recently, alternative approaches (e.g., artificial neural network) have been adopted (Brey et al. 1996).

The biotic and abiotic parameters generally used in these models are body mass, biomass, temperature, and water depth (Brey 1990; Benke 1993; Tumbiolo and Downing 1994). Parameters related to taxonomy, life history, or functional trophic

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groups have been discussed (Benke 1993), but rarely incorporated as independent variables in models. When they have been applied, only broad taxonomic groups and general life strategies (sessile–motile, infauna–epifauna; see Brey 1999) have been considered.

Until recently, suprabenthic (= hyperbenthic) species were not included in regression models because they were not well represented in benthic samples taken with traditional endobenthic–epibenthic gear (cf. Huberdeau and Brunel 1982), i.e., grabs or box corers, which correctly estimate only the density of infauna or nonswimming epifauna (Buchanan and Warwick 1974; Sainte-Marie and Brunel 1985). Suprabenthic species (consisting of mysids, isopods, or amphipods) are characterized by their swimming capacity (see Sainte-Marie and Brunel 1985; Mees and Jones 1997). There is increasing evidence that the suprabenthos (= hyperbenthos) plays a key role in energy transfer in the benthic boundary layer (e.g., Sorbe 1981; Mees and Jones 1997; Cartes and Maynou 1998). High *P/Bs* have been reported for suprabenthic peracarids (San Vicente and Sorbe 1993, 1995; Cartes and Sorbe 1999) from coastal, shelf, and bathyal communities, leading to the question of whether suprabenthic species show generally higher *P/Bs* than infaunal species (Cartes and Sorbe 1999). Failure to address these presumably high *P/Bs* of suprabenthic species would imply ignoring a non-trivial part of the benthic production if suprabenthos is not sampled, resulting in biased models of energy flow in trophic webs.

In the present study, we review the available data on suprabenthic macrofaunal secondary production and *P/B* and compare suprabenthic with benthic (infaunal and epifaunal) species productivity. New models to predict production and *P/B* for marine macrobenthic crustaceans are generated including suprabenthic species. Our aim is not only to summarize the available data on suprabenthos production, but also to stimulate more interest for the study of this fauna as a key compartment in the functioning of trophic webs.

Material and methods

The species were classified as belonging to either the suprabenthic or the infaunal–epifaunal groups according to the gear with which they were collected: grabs or corers to sample benthos and sledges to sample suprabenthos. Both types of gear capture quite dissimilar fauna and they are complementary methods, as indicated by the different dominance of peracarid crustacean species captured with box corers and sledges (Sainte Marie and Brunel 1985; Elizalde 1994; J. Cartes, unpublished data). Suprabenthos is only correctly sampled using sledges because of its swimming capacity, which is the main distinctive feature of suprabenthos compared with benthos. Presently, because of the incomplete knowledge of the biology and ecology of most species, no biological criteria are available to separate benthic and suprabenthic species. The aim of this study was to test possible differences between benthic and suprabenthic species as a function of the biological variable *P/B*.

P/B data of sublittoral suprabenthic and infaunal–epifaunal (benthic) crustaceans were taken from our unpublished results and from the literature (Table 1). The selected species are included in the macrofaunal component and were

captured or sieved (benthos) through mesh sizes of 0.5 mm (range: 0.3–1.0 mm). Twelve of the 65 *P/Bs* of benthos and four of the 26 *P/Bs* of suprabenthos were obtained using mesh sizes >0.5 mm. Additional data on other benthic (non-crustacean) invertebrates were taken from the data compiled by Brey (1990). All *P/B* data used in this study were computed by cohort-based (Waters 1977; Crisp 1984), growth rate based (Crisp 1984), or size–frequency methods (Hynes-Hamilton and Coleman 1968; Hamilton 1969; Menzies 1980). The latter requires neither separation of cohorts nor knowledge of the exact growth function. Indirect estimations obtained either by multiplying *P/B* and mean annual biomass estimations or as function of respiration (no field data) were not considered. For suprabenthic crustaceans, secondary production (*P*) and *P/B* have been estimated in previous studies (Cartes and Sorbe 1999; Cartes et al. 2000, 2001) using the size–frequency or Hynes-Hamilton method (Menzies 1980), where

$$P = \left[\sum (d_j - d_{j+1})(w_j w_{j+1})^{0.5} \right] \cdot 12/\text{CPI}$$

and d_j and w_j are the density and biomass of each size class, respectively. The cohort production interval (CPI, months) requires a basic knowledge of the life history of species. Other studies in suprabenthic (hyperbenthic, neritic) species also used methods based on the lost (or gained) biomass of cohorts (see Waters 1977; Crisp 1984; Gage 1992) distinguishable in size–frequency histograms. The *P/B* and *P* for *Natantolana borealis* was estimated using the weight-specific growth rate method (see Crisp 1984; Brey et al. 1990). The growth parameters were adopted from the study by Kaïm-Malka (1997) off Marseille, and the mean annual biomass was taken from our own unpublished data obtained from a seasonal sampling at bathyal depths off Barcelona (Cartes and Sorbe 1999).

Suprabenthic and benthic crustacean *P/Bs* were compared by analysis of covariance (ANCOVA) (*P/B* vs. suprabenthic crustaceans – benthic crustaceans – other benthic species with mean body weight as covariate) and post-hoc Scheffé test. A multiple linear regression model (model MLR₁) relating *P/B* to mean body weight (W , mg dry weight (DW)), mean annual temperature (T , °C), and water depth (Z , m) was established by forward stepwise multiple regression using the complete data set (91 cases). Additionally, a model MLR₂ was constructed using the qualitative variable swimming capacity S_{cap} (0, 1) to check for significant differences between benthic and suprabenthic species. Species captured with grabs or corers are considered to have no swimming capacity (0) vs. species captured with sledges (1). All MLR models were generated using the software Statistica 4.5. All mass units were converted to mg DW using conversion factors from the original data source or from the literature (references in Brey 1990, 1999). All quantitative variables except temperature (Plante and Downing 1989) were log-transformed to linearize the relations and reduce heteroscedasticity.

Various previously published empirical models were tested for suitability in estimating *P/B* of suprabenthic crustaceans. Seven MLR models were tested, two for marine benthic invertebrates (Brey 1990; Tumbiolo and Downing 1994), four for freshwater species (Plante and Downing 1989; Morin and Bourassa 1992; Benke 1993), and the aquatic inverte-

Table 1. Database considered to generate the multilinear regression (MLR) model (from sources cited in the reference list).

Species	Type ^a	Data source	Habitat (depth, m)	Area
Decapoda				
<i>Caloparis macandreae</i>	2	Buchanan and Warwick 1974	Shelf (80)	Southern England
<i>Philocheirus bispinosus</i>	1	Sorbe 1984	Shelf (91)	Bay of Biscay
Mysidacea				
<i>Anchialina agilis</i>	1	Sorbe 1984	Shelf (91)	Bay of Biscay
<i>Anisomysis mixta australis</i>	1	Fenton 1996	Estuarine	Tasmania
<i>Boreomysis megalops</i> *	1	Elizalde 1994	Upper slope (320)	Bay of Biscay
<i>Boreomysis arctica</i> *	1	Cartes et al. 2001	Mid-slope (550)	Bay of Biscay
<i>Boreomysis arctica</i> *	1	Cartes et al. 2001	Mid-slope (500–1200)	Catalan Sea
<i>Neomysis integer</i>	1	Mees et al. 1994	Estuarine (10)	North Sea
<i>Paramesopodopsis rufa</i>	1	Fenton 1996	Estuarine	Tasmania
<i>Parapseudomma calloplura</i> *	1	Cartes et al. 2001	Upper slope (400)	Bay of Biscay
<i>Parapseudomma calloplura</i> *	1	Cartes et al. 2001	Upper slope (400–500)	Catalan Sea
<i>Ropalophthalmus terratenalis</i>	1	Wooldridge 1986	Estuarine	South Africa
<i>Schistomysis parkeri</i>	1	San Vicente and Sorbe 1993	Brackish-estuarine	Bay of Biscay
<i>Schistomysis spiritus</i>	1	San Vicente and Sorbe 1995	Shelf (31)	Bay of Biscay
<i>Schistomysis kervillei</i>	1	San Vicente and Sorbe 1995	Shelf (31)	Bay of Biscay
<i>Schistomysis ornata</i>	1	San Vicente and Sorbe 1995	Shelf (91)	Bay of Biscay
<i>Tenagomysis tasmaniae</i>	1	Fenton 1996	Estuarine	Tasmania
Isopoda				
<i>Cyathura carinata</i>	2	Olafsson and Persson 1986	Subtidal	Baltic Sea
<i>Cyathura carinata</i>	2	Olafsson and Persson 1986	Subtidal	Baltic Sea
<i>Munnopsurus atlanticus</i> *	1	Cartes et al. 2000	Upper slope (400)	Bay of Biscay
<i>Munnopsurus atlanticus</i> *	1	Cartes et al. 2000	Mid-slope (500–1200)	Catalan Sea
<i>Ilyarachna longicornis</i> *	1	Cartes et al. 2001	Upper slope (400)	Bay of Biscay
<i>Ilyarachna longicornis</i> *	1	Cartes et al. 2001	Mid-slope (500–1200)	Catalan Sea
Amphipoda				
<i>Ampelisca abdita</i>	2	Franz and Tancredi 1992	Estuarine (1–10)	Jamaica Bay (northeastern U.S.A.)
<i>Ampelisca agassizi</i>	2	Collie 1985	Shelf (69–84)	Georges Bank (northeastern U.S.A.)
<i>Ampelisca araucana</i>	2	Carrasco and Arcos 1984	Sublittoral (65)	Bay of Concepción (Chile)
<i>Ampelisca armoricana</i>	2	Dauvin 1988d	Sublittoral (17)	English Channel
<i>Ampelisca sarsi</i>	2	Dauvin 1984	Sublittoral (17)	English Channel
<i>Ampelisca birulai</i>	2	Highsmith and Coyle 1990	Shelf (35–50)	Bering Sea
<i>Ampelisca brevicornis</i>	2	Dauvin 1988b	Sublittoral (4–17)	English Channel
<i>Ampelisca brevicornis</i>	2	Klein et al. 1975	Shelf (28)	North Sea
<i>Ampelisca macrocephala</i>	2	Highsmith and Coyle 1990	Shelf (35–50)	Bering Sea
<i>Ampelisca tenuicornis</i>	2	Dauvin 1988a	Sublittoral (4–17)	English Channel
<i>Ampelisca tenuicornis</i>	2	Shearer 1977	Sublittoral (7)	Northeastern England
<i>Ampelisca typica</i>	2	Dauvin 1988c	Sublittoral (17)	English Channel
<i>Biblyx japonicus</i>	2	Sudo and Azeta 1996	Sublittoral (10)	Japan
<i>Casco bigelowi</i>	2	Wildish 1983	Sublittoral (80)	Bay of Fundy (eastern Canada)
<i>Corophium sextoni</i>	2	Hughes 1978	Sublittoral (15)	Torbay (England)
<i>Corophium volutator</i>	2	Möller and Rosenberg 1982	Subtidal	Baltic Sea
<i>Erichthonius brasiliensis</i>	2	Hughes 1978	Sublittoral (15)	Torbay (England)
<i>Erichthonius fasciatus</i>	2	Collie 1985	Shelf (69–84)	Georges Bank (northeastern U.S.A.)

<i>Gammarus mucronatus</i>	2	Fredette et al. 1990	Subtidal	Chesapeake Bay (Virginia, U.S.A.)
<i>Harpinia propinqua</i>	2	Wildish 1983	Sublittoral (80)	Bay of Fundy (eastern Canada)
<i>Haploops fundiensis</i>	2	Wildish 1983	Sublittoral (80)	Bay of Fundy (eastern Canada)
<i>Pontoporeia affinis</i>	2	Andersin et al. 1984	Shelf (105–125)	Gulf of Bothnia (Baltic Sea)
<i>Pontoporeia affinis</i>	2	Sarvala and Uitto 1991	Sublittoral (21–46)	Baltic Sea
<i>Pontoporeia femorata</i>	2	Sarvala and Uitto 1991	Sublittoral (46)	Baltic Sea
<i>Pontoporeia femorata</i>	2	Wildish and Peer 1981	Sublittoral (10)	St. Margaret's Bay (eastern Canada)
<i>Photis reinhardi</i>	2	Wildish 1983	Sublittoral (80)	Bay of Fundy (eastern Canada)
<i>Rhachotropis caeca*</i>	1	Cartes et al. 2001	Upper slope (400)	Bay of Biscay
<i>Rhachotropis caeca*</i>	1	Cartes and Sorbe 1999	Mid-slope (500–1200)	Catalan Sea
<i>Rhachotropis glabra*</i>	1	Cartes and Sorbe 1999	Mid-slope (550)	Catalan Sea
<i>Rhepoxynius abronius</i>	2	Kemp et al. 1985	Sublittoral (5)	Yaquina Bay (Oregon)
<i>Unciola inermis</i>	2	Collie 1985	Shelf (69–84)	Georges Bank (northeastern U.S.A.)
Cumacea				
<i>Diastrylis rathkei</i>	2	Rachor et al. 1982	Sublittoral (17–24)	North Sea
<i>Leucon longirostris*</i>	1	Cartes and Sorbe 1999	Mid-slope (550)	Catalan Sea
<i>Cumopsis goodsir</i>	1	Corbera et al. 2000	Sublittoral (1.5–10)	Catalan Sea
Leptostracea				
<i>Nebalia</i> sp.	2	Rainer and Unsworth 1991	Subtidal (1)	Australia
<i>Nebalia daytoni</i>	2	Vetter 1996	Sublittoral (20)	Southern California

Note: Data includes 49 different Crustacea species (2 decapods, 13 mysids, 3 isopods, 26 amphipods, 3 cumaceans, and 2 leptostracans). Freshwater, beach, and intertidal species were not included. Asterisk (*) denotes species used to compare the *P/B* values obtained with the size-frequency method and the MLR-ANN models in Fig. 2, and Table 5. ANN, artificial neural network.

[†]1, suprabenthic species; 2, benthic species.

brate model of Brey (1999) (Table 2). The latter model also considers habitat, living mode, and taxon as qualitative (0,1) variables. From freshwater studies, we adopted the models developed by Benke (1993); both the general and the crustacean models) and Morin and Bourassa (1992) for stream (running-water) organisms and the model by Plante and Downing (1989) for lake (lentic-water) organisms. Additionally, the artificial neural network (ANN) model published by Brey et al. (1996) was tested. The main advantage of this method is that a priori assumptions about the relationships between independent and dependent variables, as required for the MLR models, are not necessary, although these relationships cannot be expressed in traditional mathematical terms by using ANN (see Brey et al. (1996) for more detailed explanation of ANN methods applied to production studies). The accuracy and the precision of the models compared with the observed (field) data were determined by calculating the average residuals of each model and their respective variances. For this comparison, we considered the data of the 13 bathyal suprabenthic peracarid populations for the southeast Bay of Biscay (off Arcachon) and the Catalan Sea (off Barcelona) (see Table 1).

Besides the parameters included in these MLRs, other variables may affect *P/B*. However, the available data were insufficient to allow their entry as independent (quantitative) variables into MLRs. A preliminary analysis of the effect of these variables on *P/B* can be carried out by examining the correlation between these and the MLR residuals (see Plante and Downing 1989). For this purpose, we examined the correlation between *P/B* residuals of the MLR₁ model (constructed based on quantitative variables only) and the following variables: (i) the swimming coefficient K_t , which is deduced from the distribution of fauna at different distances above the sediment–water interface and is related to the swimming capacity S_{cap} of species (cf. Sainte-Marie and Brunel 1985; Cartes 1998); (ii) the trophic diversity (H' ; Shannon–Wiener index) calculated on the diet of each species (see Cartes et al. 2001); and (iii) the organic matter content (%OM) of the species. In the same way, we calculated the correlation between *P/B* values and the cited functional (or trophic) variables, not included in the models, using the nonparametric Spearman correlation coefficient. The number of observations for the variables considered here ranged from 20 (H') to 78 (K_t).

Results

The database

Our data set consists of 91 cases, including 49 different crustacean macrobenthic species (2 decapods, 13 mysids, 4 isopods, 26 amphipods, 3 cumaceans, and 2 leptostracans). Twenty-six populations (21 species) are suprabenthic, whereas 65 populations (28 species) belong to the infauna–epifauna. The data set contains marine species inhabiting shallow subtidal (0–0.5 m) to deep bathyal (to 1852 m) environments in subpolar–temperate regions (40°–60°N latitude), covering a temperature range from 0.4 to 21.6°C, although most data were from subpolar–temperate regions with mean annual *T* ranging from 6 to 13°C. Freshwater beach and intertidal species were not considered. Mean annual biomass ranged from

Table 2. Multiple linear regression (MLR) models adopted to estimate P/B (production–biomass ratio) for our suprabenthic species.

Model	
Plante and Downing (1989)	
$\log P = 0.060 + 0.790 \log B + 0.050T - 0.160 \log W_{\max}$	$(r^2 = 0.79)$
Morin and Bourassa (1992)	
$\log P = -0.750 + 1.010 \log B - 0.340W + 0.037T$	$(r^2 = 0.97)$
Benke (1993)	
$\log P/B = 0.546 + 0.035T - 0.247 \log W_{\max}$	$(r^2 = 0.47; \text{general})$
$\log P/B = 1.023 - 0.011T - 0.234 \log W_{\max}$	$(r^2 = 0.48; \text{Crustacea})$
Brey (1990)	
$\log P/B = -0.473 - 0.274 \log W$	$(r^2 = 0.48)$
Tumbiolo and Downing (1994)	
$\log P = 0.240 + 0.960 \log B + 0.030T - 0.160 \log (Z + 1)$	$(r^2 = 0.86)$
Brey (1999)	
$\log P/B = 8.256 - 2.226 \log W - 2432.055(1/T + 273) + 0.239(1/Z) + 0.241(\text{DE-Subt}) + 0.203(\text{DL In-Epi}) + 0.242(\text{DL ME}) - 0.287(\text{DT M}) - 0.203(\text{DT P}) - 0.128(\text{DT C}) - 0.457(\text{DT E}) - 0.116(\text{DH L})$	$(r^2 = 0.77)$

Note: B , mean annual biomass; W , mean individual weight; W_{\max} , maximum individual weight; T , mean annual temperature ($^{\circ}\text{C}$); Z , depth (m). The following variables from Brey's (1999) model are qualitative (0,1) variables: DE-Subt, subtidal species; DL In-Epi, infaunal–epifaunal species; DL ME, motile fauna; DT M, Mollusca; DT P, Polychaeta; DT C, Crustacea; DT E, Echinodermata; DH L, lake habitat.

0.024 to 42 600 mg DW·m⁻², whereas mean individual weight ranged from 0.032 to 180.6 mg DW·individual⁻¹.

A previous (one-tailed) t test showed no significant differences between the $\log P/B$ of species sampled using different mesh sizes (mesh size >0.5 mm and ≤ 0.5 mm), both for benthos ($t = -0.404$; $p = 0.34$) and suprabenthos ($t = 0.106$; $p = 0.46$). Furthermore, the mesh size was not an explanatory variable of P/B when it was incorporated as an independent variable into the multilinear regression models (see below).

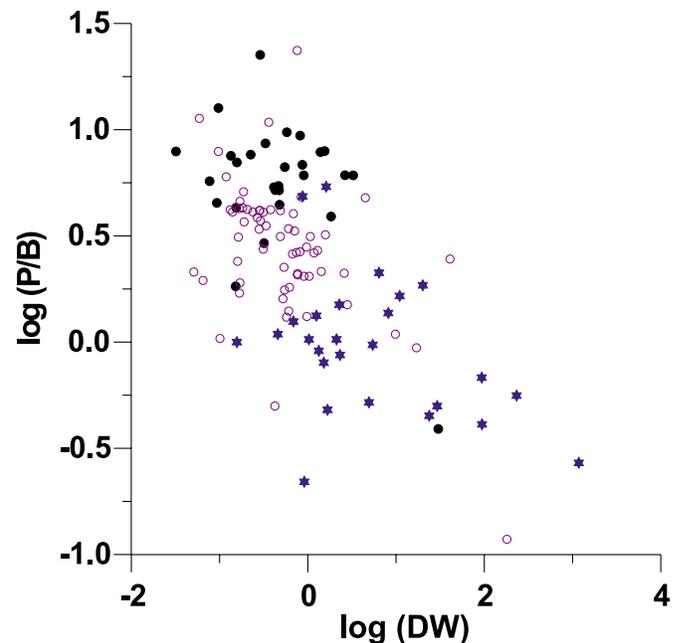
Production–biomass ratios (P/B s)

P/B s of suprabenthic and benthic (infaunal–epifaunal) crustaceans, as well as other benthic invertebrates, are shown as a function of mean weight (W) (Fig. 1). An analysis of covariance (one-way ANCOVA, with post-hoc Scheffé test) using suprabenthic and benthic crustaceans, and other invertebrates as factors and $\log W$ as covariate, showed that mean $\log P/B$ of suprabenthic crustaceans (0.744 ± 0.285 ; $n = 26$) was significantly higher than P/B of benthic crustaceans (0.466 ± 0.329 ; $n = 65$; $p < 10^{-3}$) and other invertebrates (-0.034 ± 0.326 ; $n = 28$; $p < 10^{-4}$). $\log P/B$ of benthic crustaceans was also significantly higher ($p < 10^{-4}$) than $\log P/B$ of other invertebrates. Slopes of the relation between P/B and mean weight did not differ significantly among the three groups ($F = 0.092$; $p = 0.912$). One-way analysis of variance (ANOVA) and post-hoc Scheffé test detected significant differences in $\log W$ between suprabenthic crustaceans and other invertebrates ($p < 10^{-8}$), as well as between benthic crustaceans and other invertebrates ($p < 10^{-11}$), whereas no significant differences in $\log W$ between suprabenthic and infaunal crustaceans ($p = 0.99$) were found. Hence, P/B comparisons are particularly reliable between suprabenthic and benthic crustaceans, whereas species of the category other invertebrates had higher mean body mass, which implies lower P/B .

Multiple linear regression models

Two MLR P/B models were obtained for macrobenthic crustaceans (Table 3). In model MLR₁ (1), P/B is signifi-

Fig. 1. $\log P/B$ (production–biomass ratio) vs. \log mean body mass (dry weight, DW): suprabenthic crustaceans (●); infaunal–epifaunal crustaceans (○); other marine invertebrates (★) (derived from Brey 1990).



cantly correlated with environmental temperature (T) and mean individual body mass (W). The fitted equations (Table 3) showed that this model explains 36.7% of the variability in $\log P/B$. Model MLR₂ (2) included the qualitative variable S_{cap} as an additional independent variable. P/B was significantly correlated with T , W , S_{cap} , and Z , and the goodness-of-fit increased to $R^2 = 0.528$. In this second model, S_{cap} accounted for 10.4% of the variability (19.7% of the variance explained by MLR₂), and Z accounted for 5.7% of the total variability. The tolerance, which indicates the existing correlation between pairs of independent variables, was between 0.954 and 0.962 in MLR₁ and between 0.657 and 0.927 in MLR₂.

Table 3. Characteristics of the multiple linear regression (MLR) models constructed to predict P/B .

Model	n	r^2	p
(1) $\log P/B = 0.103 + 0.036T - 0.186 \log W$	91	0.367	$<10^{-6}$
(2) $\log P/B = 0.349 - 0.203 \log W + 0.020T + 0.362S_{\text{cap}} - 0.119 \log Z$	91	0.528	$<10^{-6}$
$\log P = 0.155 + 0.985 \log B - 0.269 \log W + 0.028T$	91	0.965	$<10^{-6}$

Note: Mean individual weight (W), depth (Z , pressure), and mean annual temperature (T) were the considered independent variables. S_{cap} , swimming capacity, is a qualitative (0,1) variable; $p = <0.05$ for all the independent variables. A model to predict production (P) based on the same data set also included.

Table 4. Correlations between the residuals of P/B model MLR_1 (see Table 3) obtained for macrobenthic crustaceans and some trophic or functional variables.

Variables	Pearson r (residuals)	Spearman's	n
K_i	0.258 *	0.493 *	78
%OM	0.287 ns	0.231 ns	30
H_T	0.404 ns	0.367 ns	20

Note: K_i , swimming coefficients; %OM, organic matter content (%); H_T , trophic diversity. Correlations using the nonparametric Spearman's coefficients between P/B from the original field data and the same variables have been also included. *, $p < 0.05$; ns, nonsignificant.

Therefore, dependence (redundancy) between pairs of independent variables was generally low.

A P model was also constructed on the same database ($n = 91$). In this model, P for macrobenthic crustaceans was significantly correlated with the mean annual biomass (B ; $\text{mg DW}\cdot\text{m}^{-2}$), W , and T (Table 3). The goodness-of-fit was $R^2 = 0.965$.

Analysis of residuals of MLR_1 (excluding S_{cap} as a variable) gave a positive correlation between P/B residuals and K_i of the species. Spearman coefficients gave parallel significant results (Table 4), with K_i being positively correlated with P/B .

The empirical models tested here fall into three categories (Fig. 2): (i) three models, those of Brey (1990) and Tumbiolo and Downing (1994) and the ANN model of Brey et al. (1996), overestimated size–frequency method (SFM) results, with log mean residuals around +0.4; (ii) the freshwater models of Plante and Downing (1989), Morin and Bourassa (1992), and Benke (1993; both the general and the crustacean models) underestimated SFM results with log mean residuals distributed between -0.2 and -0.7 ; and (iii) the aquatic model of Brey (1999). Finally, MLR_2 gave residuals very close to zero in comparison with the SFM field data. Residuals of all models of group i and those of the freshwater models of Plante and Downing (1989) and Benke (1993; both models) were significantly (a posteriori t tests; $p < 0.05$) different from zero. Models of group i overestimated suprabenthic P/B , whereas the freshwater models of Plante and Downing (1989) and Benke (1993; both models) underestimated suprabenthic P/B . In contrast, the model by Morin and Bourassa (1992), the aquatic model of Brey (1999), and MLR_2 did not differ significantly from field P/B calculations (Table 5). One-tailed F tests were used to compare the pairwise variances between models. The results of these comparisons were not significant for most cases (Table 5), but they were significant for some of the comparisons involving the Plante–Downing model. Among the published models, the best overall fit to suprabenthos

P/B was obtained by the model of Brey (1999; which is not significantly different from 0, $p = 0.96$; t test), which incorporates the motility of benthos (sessile or nonsessile organisms) as an independent variable.

Discussion

P/B is a standardized measure allowing comparisons between species having different individual biomass (Plante and Downing 1989). Our P/B values obtained for suprabenthos (= swimming) macrofauna are generally higher than those obtained for infauna–epifauna within the group of the macrobenthic crustaceans. The method used to estimate P/B for suprabenthos was mainly the size–frequency method (SFM), because it is not possible in multivoltine species to follow the growth of cohorts. Generally, cohort-based methods, as well as growth rate based methods, of production calculation are more accurate than the size–frequency method, because the latter makes quite simple assumptions about individual growth (linear) and age (cohort production interval, i.e., maximum lifespan only) (see Morin et al. 1987; Benke 1993; Mees et al. 1994). The bias involved in the SFM depends mainly on the shape of the growth curve: the more linear the curve, the better the SFM estimate of P/B . The P/B of most suprabenthic species used in this study was computed by SFM, whereas all three approaches were used to compute P/B of benthic species. Hence, a possible systematic bias could be introduced. Simultaneous use of SFM and cohort-based methods in stream benthos production studies, however, showed that (i) differences between P/B estimated by these methods were generally less than 10–30% and (ii) SFM estimates were not consistently higher than cohort-based estimates (Benke 1993). Similar results were also reported in estuarine mysids (Mees et al. 1994). In the case of *Neomysis integer*, SFM resulted in values very similar to those obtained with cohort methods when it is possible to apply to cohorts separately (Mees et al. 1994), a consequence of strong differences in the life history of each cohort. Our suprabenthic data contain a number of bathyal species with generations having a similar life span (Cartes and Sorbe 1999; Cartes et al. 2000). Therefore, deep species probably better match the assumptions of the size–frequency method evidenced by Mees et al. (1994). Likewise, using the data that form the basis of the Brey (1999) model, no significant effects of the method on P/B estimations could be detected (T. Brey, unpublished data).

Our MLR_1 to estimate P/B for small macrobenthic crustaceans had $R^2 = 0.367$, at the lower end of the range of variance explained by previous P/B models, both for marine and freshwater organisms. Noting this low R^2 for P/B models, it has been postulated that other factors besides temperature

Fig. 2. Residuals (field data – models data) of log P/B (production–biomass ratio, \pm standard error) between the observed (field) data and a collection of empirical models for 13 bathyal suprabenthic peracarids for the southeast Bay of Biscay (off Arcachon) and the Catalan Sea (off Barcelona). Field values were obtained applying the size–frequency method (SFM). A total of seven empiric multiregression models and the artificial neural network (ANN) model by Brey et al. (1996) were used to estimate P/B for the 13 selected species. MLR, multiple linear regression.

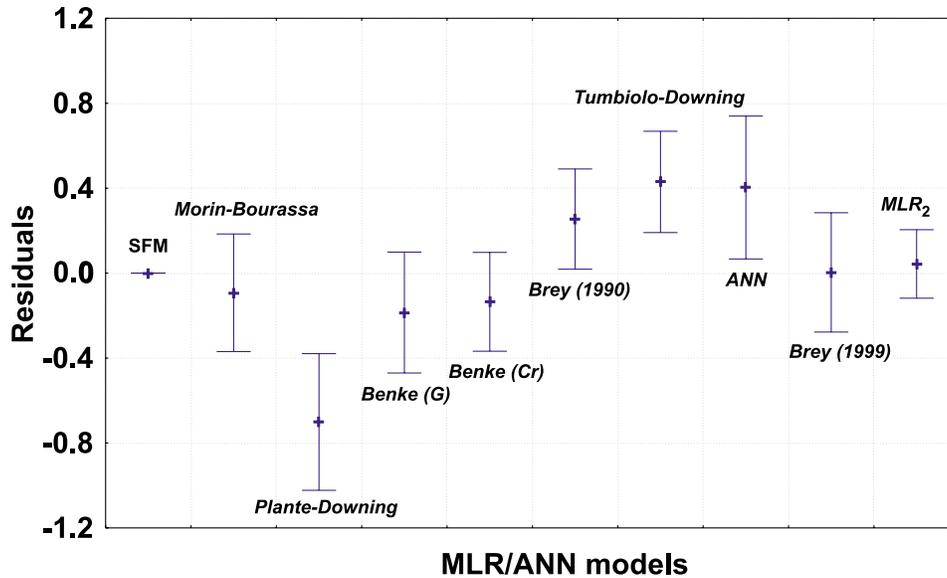


Table 5. Results of t tests between the residuals of P/B (production–biomass ratio) obtained from field data (SFM, size–frequency method) and those obtained after applying multiple linear regression (MLR) and artificial neural network (ANN) models.

Models	p
MLR	
Morin–Bourassa	0.239 ns
Plante–Downing	10^{-8}
Benke (general)	0.027
Benke (Crustacea)	0.047
Brey (1990)	10^{-4}
Tumbiolo–Downing	10^{-6}
Brey (1999)	0.964 ns
MLR ₂ (present study)	0.999 ns
ANN	10^{-4}

Note: The data set consisted in 13 suprabenthic peracarids from bathyal depths of the Bay of Biscay and the Catalan Sea. ns, residuals are not significantly different from zero.

and individual mass may strongly affect P/B (Benke 1993). After incorporating some variables implying habits (i.e., motility, swimming capacity) and habitat of species (Brey 1999; present study), higher predictive precision in P/B models can be reached (77.2% of variance, Brey 1999; 52.8%, present study). Therefore, swimming capacity, or in a wider context, variables related to the motility of species are among the remaining factors significantly affecting P/B .

A variety of biological and (or) ecological variables may explain the higher P/B reported for suprabenthic crustaceans in comparison with benthic species. Thus, a higher number

and (or) smaller size of eggs have generally been reported for epifaunal amphipods than for infaunal ones (Nelson 1980; Van Dolah and Bird 1980). This trend has been related to the r and K strategies in terms of species mortality, although the influence of phylogenetic aspects has also been discussed (Fenwick 1984). Despite their interest, data on fecundity were very scarce for the species included in our P/B data set, particularly for suprabenthic crustaceans; therefore, fecundity could not be incorporated into our models. Thus, based on our database, the major difference between benthic and suprabenthic groups is related to the higher S_{cap} of suprabenthic species. The addition of S_{cap} as a new qualitative (0, 1) variable to P/B MLR models increased the goodness-of-fit from $R^2 = 0.367$ to $R^2 = 0.528$. S_{cap} also accumulated an important part (19.7%) of the explained variance. Likewise, a significant correlation between residuals of the P/B MLR₁ and K_t was also found. K_t is deduced from the distribution of fauna at different distances above the sediment–water interface (cf. Sainte-Marie and Brunel 1985; Cartes 1998) and can be considered a continuous variable related to the swimming capacity of the species. Also, as indicated by our results, among the published empirical models, the model of Brey (1999), which includes the parameter motility as an independent variable, showed the best fit, further suggesting that high P/B among suprabenthos may depend on their swimming capacity.

Swimming capacity itself may be correlated not only to different biological variables (e.g., fecundity), but also to ecological variables including the trophic level (TL) of the species. Among bathyal suprabenthos, filter feeders and scavengers–predators such as mysids (i.e., *Boreomysis arctica*) or lysianassid and eusirid amphipods show the highest K_t as well as the highest P/B . On the other hand, macrobenthic crustaceans collected with grabs are consid-

ered to be mostly deposit feeders, which probably consume more refractory food with lower nutritional value. This relation between trophic level and P/B has been discussed by Benke (1993) for stream benthos, where shredders consuming low nutritional food have lower P/B than filter feeders or (small) predators. Nevertheless, we could not detect any significant relation between P/B and the only trophic variable here considered, the trophic diversity (H'), likely because H' is not necessarily a good indicator of the trophic level of species or because of the low number of available H' data (only 20). Although it is generally possible to estimate TL with precision for macrophagous taxa such as fish (see Pauly et al. 1998), it is very difficult to obtain detailed data on the diet and TL for small (microphagous) marine macrofauna.

Published MLR models based on marine infaunal–epifaunal benthos (collected with grabs or corers) always underestimated P/B of our suprabenthic species, further suggesting different patterns in the life history of each compartment (e.g., differences in the K and r strategies) depending of the dynamics of the aquatic ecosystems that they inhabit. Besides the models incorporating the swimming capacity as independent variable, the freshwater model by Morin and Bourassa (1992) overall showed good estimations of P/B for suprabenthic marine crustaceans, as has been reported in previous studies (San Vicente and Sorbe 1993; Cartes and Sorbe 1999). However, the freshwater model by Plante and Downing (1989) highly overestimated P/B for our suprabenthic species. This bias may be attributable to the low individual mass of organisms included in this model (e.g., size magnitude of rotifers two orders below size of the species in our data base), although other variables (e.g., species habitat, food-source exploited) cannot be excluded. Freshwater MLR models refer either to stream (running-water) or to lake (lentic-water) species. Although stream models (Morin and Bourassa 1992; Benke 1993) are based on benthos, lake models are constructed combining planktonic and benthic data (Plante and Downing 1989). According to the results reported in marine environments, where zooplanktonic taxa (e.g., euphausiids or hyperiid amphipods) regularly have higher P/B (Lindley 1982; Mauchline 1985) than benthic crustaceans, Plante and Downing (1989) also recorded higher production for zooplankton than for benthos populations in lakes. These authors explained this higher production of zooplankton by the influence of colder temperatures on production in lake bottoms occupied by benthos, whereas possible influence of the dynamics of aquatic ecosystems on the life history of organisms was not discussed. The inclusion of planktonic organisms in the Plante and Downing (1989) model, presumably from warmer and more productive waters than those in our data set, could also explain the high overestimation of P/B s from our field data.

In conclusion, many factors could account for the fact that suprabenthic species generally have higher P/B values than benthos (infauna–epifauna) within the group of macrobenthic crustaceans. Although high P/B seems related to the swimming capacity of this interface fauna, this variable may correlate with other biological or ecological variables that should be further studied before they can be fully considered in numerical models. Improvements in the quality of these

models should contribute to improve both benthic production estimates and general models of energy flow in trophic webs.

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