

Estimating macrobenthic secondary production from body weight and biomass: a field test in a non-boreal intertidal habitat

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ABSTRACT: Production (P) and biomass (B) data of different species from 3 stations in the intertidal zone of the Ria Formosa (southern Portugal, 37° N) were analysed. They were compared with equations from the literature to estimate P/\bar{B} ratios from body weight. A clear distinction must be made between (1) an intraspecific and (2) an interspecific comparison. (1) Results from 3 species supported a body weight exponent of -0.25 for the P/\bar{B} ratio, as is to be expected from a linear relationship between growth and respiration. (2) In an interspecific comparison, the weight exponent depends on the contribution of age or growth rate to the presence of large specimens in a sample. It is concluded that production in the specific habitat examined cannot be calculated properly from body weight and biomass by 1 simple equation which mixes interspecific and intraspecific effects, rather that both aspects should be separated into 2 different calculation steps.

INTRODUCTION

Since the first attempts to estimate secondary production by Boysen Jensen (1919), techniques have improved continuously (Winberg 1971, Waters 1977, Crisp 1984). At present, the most common methods are the increment summation method, the removal summation method, the instantaneous growth method and a production estimate by the Allen curve. All these methods are based on analysis of body weight and abundance of cohorts sampled at regular time intervals. Abundance and weight data are subsequently handled according to more or less rigid assumptions concerning their deployment over time. Gillespie & Benke (1979) demonstrated that all 4 methods basically lead to the same result.

In many ecological studies, secondary production is required not only of single abundant species, but also of whole communities. In these samples there will always be a certain number of individuals which either cannot be associated to a cohort, or which belong to species which are only represented by a few animals. In addition to this, collecting and analysing field data

by the methods described above is extremely labour intensive. In this context, an estimate of production by body size is of great interest either to fill in the missing values or to obtain a preliminary estimate of benthic production processes, when detailed data are missing.

Banse & Mosher (1980) related the quotient of annual production to mean annual biomass (P/\bar{B} ; units: kcal, m², yr) to the body weight of animals at their first sexual maturity (M_g , kcal m⁻²) and found the following relation:

$$P/\bar{B} = 0.65 M_g^{-0.37} \quad (1)$$

M_g may be a good denominator for body size in a comparison of species-specific attributes. The application of this equation to field studies, however, encounters difficulties, because M_g will not be easily obtained for rare species whose life history is poorly known. That is why for field use the empirical equation provided by Schwinghamer et al. (1986) for macrobenthos is more appropriate, relating the P/\bar{B} ratio and mean annual body weight \bar{w} :

$$P/\bar{B} = 0.525 \bar{w}^{-0.304} \quad (2)$$

An even extended analysis of 337 data sets of production, mean annual biomass and mean individual weight figures has been published by Brey (1990).

Both equations imply that the P/\bar{B} ratio depends on body size in a characteristic way. This is due to 2 effects: (1) an intraspecific or physiological effect – the P/B ratio represents a time-integrated estimate of the weight-specific growth rate (modified by mortality effects). The growth rate should depend on body size in a similar way as other physiological rates (e.g. the metabolic rate by a weight exponent of -0.25). (2) an interspecific or ecological effect, due to the fact that at a given body size and in identical environmental conditions some species of a community grow faster than others. This effect can only be monitored empirically because there is no fixed relationship between growth and mortality. In other words, specimens can be large, because they grow fast and/or because they are particularly old. For example, for a simplified hypothetical community of species with different growth rates but the same life expectation, the P/\bar{B} ratio should increase linearly with mean annual body weight.

Eqs. (1) & (2) are based mainly on data from boreal latitudes with a typical annual temperature and nutrition pattern characterized by adverse conditions during winter and favourable conditions during spring/summer. During a study in the intertidal zone of the Ria Formosa (southern Portugal, 37° N), annual macrobenthic secondary production of different systematic groups and feeding types was estimated (Sprung in press, Sprung & Cardoso in press). Temperature conditions are favourable all year round. Water temperature shows a winter minimum of about 12°C and a summer maximum of 28°C. Most of the fauna profits from detritus (probably of macrophytes and macroalgae) which is potentially present all year round. Are the empirical equations by Banse & Mosher (1980) and Schwinghamer et al. (1986) also valid under these conditions?

MATERIAL AND METHODS

The analysis refers to the same data as in Sprung (in press) and Sprung & Cardoso (in press) from 3 stations in the intertidal zone (mud flat, sand flat, seagrass *Zostera noltii* bed) sampled every second month during 1990–91, i.e. 7 times during the course of the year, duplicating the first and the last month.

No statistics were necessary to separate cohorts, either because they were obvious or – in the case of *Scrobicularia plana* – because shell characteristics (shell colour or growth rings) gave better information. Secondary production (P) was estimated by the increment summation method in most cases with the original data:

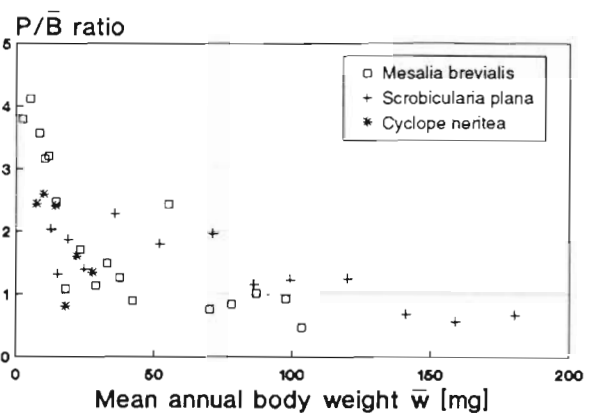


Fig. 1. Intraspecific comparison of ratios of annual production to mean annual biomass with animals of different body weight exemplified for 3 species; regressions are presented in Table 1

$$P_{1,2} = [(n_1 + n_2)/2] (\bar{w}_2 - \bar{w}_1)$$

where $P_{1,2}$ = production between 2 sampling dates; n_1 , n_2 = abundances at 2 sampling dates; and \bar{w}_1 , \bar{w}_2 = ash free dry body weight (AFDW) at sampling dates.

In cases where numbers of adult individuals did increase or intermittently no individuals of this cohort were recorded at a sampling date, figures with neighbouring sampling dates were averaged.

For *Carcinus maenas* an instantaneous growth rate has been calculated for individuals of 2 year classes present in the intertidal zone:

$$\text{1st year class: } w = 0.264 e^{0.0207d}, n = 91, r = 0.55$$

$$\text{2nd year class: } w = 73.27 e^{0.0133d}, n = 8, r = 0.62$$

where w = body weight (mg AFDW); d = day of the year; n = number of data points; and r = correlation coefficient.

In some cases some individuals could not be associated with cohorts. This missing production was supplemented as follows: a P/\bar{B} ratio was calculated from the identified cohorts. This was regarded as an estimate of a typical P/\bar{B} of the species ($P/\bar{B}_{\text{spec.}}$) at mean body weight \bar{w} . From this $P/\bar{B}_{\text{spec.}}$, the P/B at the specific individual body weight $w_{\text{ind.}}$ (the $P/\bar{B}_{\text{ind.}}$) was extrapolated using a weight exponent of -0.25 :

$$P/B_{\text{ind.}} = (P/\bar{B}_{\text{spec.}}/\bar{w}^{-0.25}) w_{\text{ind.}}^{-0.25} \quad (3)$$

The justification of this procedure is given later in the text. For analysis, only data from those species whose supplemented proportion did not exceed 50% of the production estimate were considered.

Mean annual body weight \bar{w} was calculated from the AFDW (loss of weight after 3 h at 450°C) of whole animals (including shells of the molluscs) at the 7 sampling dates. As the first and the last sampling referred

to the same season, their average was treated as 1 estimate. The body weight M_g was approximated by the average weight of the animals of a cohort at the moment when the first specimens of the following cohort appeared in the sample.

For the data presented in Fig. 1 and Table 1 (intraspecific comparison), production and biomass were related to the age of the individuals. The P/\bar{B} ratios were calculated from production and biomass values of the cohort during 1 yr, as outlined above. The time span was moved stepwise to advanced ages in 2 mo intervals. With *Scrobicularia plana* this met the difficulty that the first year class was poorly represented when compared to the following ones. Abundance figures of this cohort had to be corrected by average mortality rates and abundance figures of the advanced cohorts.

All statistical tests are based on methods described in Sachs (1978).

RESULTS

Data from this study revealed different relationships between the P/\bar{B} ratio and body weight in (1) an intraspecific comparison and (2) an interspecific comparison.

Intraspecific comparison

The fauna of the intertidal zone was dominated by species with a typical life expectation of about 1 yr (only a few individuals may live longer). *Carcinus maenas* preferably migrates to the subtidal area after its first year. In only 3 species of this sample set was the life span regularly longer: the gastropods *Mesalia brevia* and *Cyclope neritea* and the bivalve *Scrobicularia plana*. On the whole, the exponents which relate the body weight of animals of different size of the same species to the P/\bar{B} quotient did support a value of -0.25 (Table 1) as was expected for theoretical reasons outlined in the 'Discussion'.

Interspecific comparison

The calculated P/\bar{B} ratios, mean annual body weights (\bar{w}) and body weights at first sexual maturity (M_g) are compiled in Table 2. The data are displayed graphically in Fig. 2. P/\bar{B} ratios showed a high degree of variation between the species. Note also that for the same species at different sample sites quite different

Table 1 Regressions relating P/\bar{B} ratios to mean annual body weight (\bar{w} ; mg) as obtained from cohorts of different age (see text). Data are presented in Fig. 1 and are fitted by a power curve: $P/\bar{B} = a\bar{w}^b$; constants a and b are indicated together with their standard deviations (\pm SD); r : correlation coefficient; n : number of data pairs

Species	a	b	r	n
<i>Mesalia brevia</i>	6.95 ± 0.15	-0.309 ± 0.043	-0.87	18
<i>Cyclope neritea</i>	5.07 ± 0.41	-0.307 ± 0.152	-0.71	6
<i>Scrobicularia plana</i>	3.84 ± 0.19	-0.159 ± 0.047	-0.71	13

P/\bar{B} ratios were obtained (*Bittium reticulatum*, *Nereis diversicolor*, *Cyathura carinata*).

The P/\bar{B} ratios were fitted by a power curve to M_g (analogous to Banse & Mosher 1980), to \bar{w} (analogous to Schwinghamer et al. 1986) or by linear regression to \bar{w} (Table 3). The latter would be the most straightforward interpretation without transforming the data. However, frequency distribution of the P/\bar{B} ratios and of body weight data show a tailing at high values, which is why the logarithmic presentation of both the dependent and the independent variables is more appropriate for statistical analysis. With M_g as independent variable, a t -test implied that the weight exponent was significantly different from zero (and consequently also from -0.37 , indicated by Banse & Mosher 1980). Also the correlation coefficient was significantly positive ($\alpha < 0.05$). With \bar{w} as independent variable, this was not true for the weight exponent and correlation coefficient. However, even in this case, the exponent was significantly different from -0.304 indicated by Schwinghamer et al. (1986) and also from -0.25 , as to be expected from the intraspecific comparison ($\alpha < 0.0001$).

DISCUSSION

A comparison between the P/\bar{B} ratio of species studied in the Ria Formosa and estimates from the literature indicates a high degree of variation (Table 4). This is due to the following facts:

(1) The P/\bar{B} ratio depends on the age structure of a population. This is a consequence of a decline of the weight-specific growth rate with age (e.g. according to the von Bertalanffy equation; von Bertalanffy 1938).

Growth and metabolic rate are closely related. Engelmann (1966) postulated a linear relationship, which is hence called the 'Engelmann line'. In subsequent years this relationship was confirmed in many studies which are reviewed and compiled by Humphreys (1979). In a monograph, Hemmingsen (1960) concluded on an ample basis of data that the weight exponent of the weight-specific metabolic rate is generally -0.25 for a given species, corresponding to

Table 2. Quotients of annual production to mean annual biomass (P/\bar{B}), mean annual body weight (\bar{w}) and body weight at first sexual maturity (M_g) (both mg ash free dry weight) from species examined at 3 different localities in the Ria Formosa – a sand flat, a mud flat, and a seagrass bed; % = percentage of the production supplemented by the method outlined under 'Material and methods'

Species	Locality	P/\bar{B}	\bar{w}	M_g	%
Bivalvia					
<i>Abra ovata</i>	Mud	2.3	1.2	1.5	0.01
<i>Cerastoderma edule</i>	Sand	4.8	32.8	10.0	1.4
<i>Loripes lacteus</i>	Seagrass	1.1	11.2	14.0	0
<i>Scrobicularia plana</i>	Mud	1.8	90.8	40.0	0
<i>Tellina tenuis</i>	Sand	1.9	13.4	15.0	1.3
Gastropoda					
<i>Bittium reticulatum</i>	Sand	2.1	1.2	1.6	0.3
<i>Bittium reticulatum</i>	Seagrass	1.3	1.8	1.6	0
<i>Cyclope neritea</i>	Sand	2.0	13.7	13.0	0
<i>Haminea hydatis</i>	Seagrass	1.7	7.5	12.0	0.7
<i>Hydrobia ulvae</i>	Mud	1.8	0.6	1.5	49.7
<i>Mesalia brevisalis</i>	Sand	1.8	7.0	10.0	0
Polychaeta					
<i>Audoinia filigera</i>	Seagrass	3.0	9.1	10.0	2.2
<i>Glycera convoluta</i>	Seagrass	3.4	7.3	25.0	0
<i>Melinna palmata</i>	Seagrass	2.3	3.9	6.0	0
<i>Nereis diversicolor</i>	Seagrass	5.3	4.0	60.0	0
<i>Nereis diversicolor</i>	Mud	3.3	5.3	60.0	0
Crustacea					
<i>Carcinus maenas</i>	Mud	6.4	141.7	700.0	0
<i>Cyathura carinata</i>	Seagrass	3.0	1.0	2.3	0
<i>Cyathura carinata</i>	Mud	1.8	1.7	2.3	0
<i>Idotea chelipes</i>	Seagrass	3.8	0.8	3.0	0
<i>Upogebia pusilla</i>	Seagrass	3.1	73.8	70.0	31.7

a weight exponent of 0.75 for the absolute metabolic rate. Hence, a weight exponent of -0.25 also for an intraspecific comparison between the P/\bar{B} ratio and body weight is plausible.

Reviewing literature data concerning this point, Banse (1979), however, found on average a quotient of

production to respiration in the range of 0.1 to 1.0. It should be related to body weight by a power curve. This is a contradiction of the straight Engelmann line.

(2) The P/B ratio depends on the environmental conditions. This involves temporal and spatial aspects. Depending on the conditions, production figures can

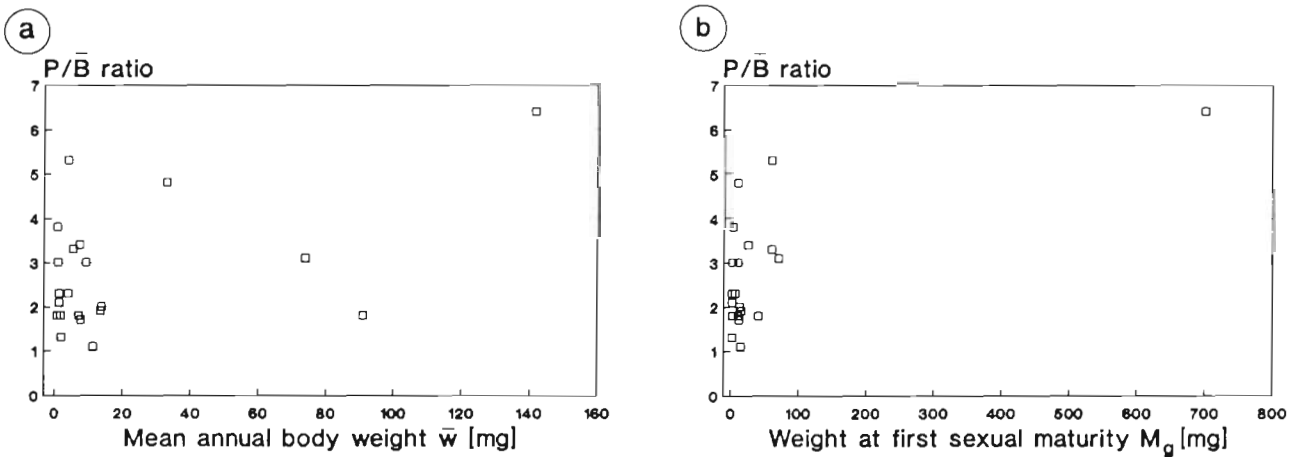


Fig. 2. Interspecific comparison of ratios of annual production to mean annual biomass (original data in Table 2); data are plotted against (a) mean annual body weight \bar{w} and (b) body weight at first sexual maturity M_g (both ash free dry weight including mollusc shells)

vary between zero and a maximum, which characterizes the potential production (i.e. the productivity of a species). Especially in temperate regions many animals regularly undergo starvation periods caused by shortage of food (Epp et al. 1988), and/or inappropriate physiological conditions (e.g. moulting of crabs). Body weight can also decline rapidly because of the release of gametes. In ecological studies like the present one, total

Table 3. Regressions of the data presented in Table 2 and Fig. 2: a power curve of the form $y = ax^p$ is fitted to the data (log-log plot) or a linear regression of the form $y = a + bx$; the constants a and b are presented together with their standard deviations (\pm SD); r : correlation coefficient; n : number of data points

	a	b	r	n
Log-log P/\bar{B} vs M_g	1.76 ± 0.16	0.148 ± 0.056	0.52	21
Log-log P/\bar{B} vs \bar{w}	2.18 ± 0.15	0.075 ± 0.064	0.26	21
Linear P/\bar{B} vs \bar{w}	2.40 ± 0.31	0.018 ± 0.008	0.47	21

Table 4. Comparison between the P/\bar{B} ratios estimated in this study and data reported in the literature for different localities

Species	P/\bar{B}	Locality	Source
<i>Cerastoderma edule</i>	4.8	Ria Formosa, Portugal	This study
	0.2	Tamar Estuary, England	Warwick & Price (1975)
	1.1–2.6	Mud flat, England	Hibbert (1976)
	0.7–8.9	Grevelingen Estuary, Netherlands	Wolff & de Wolf (1977)
	2.2–21.0	Swedish west coast	Möller & Rosenberg (1983)
1.6 ^a	Ria de Aveiro, Portugal	Moreira (1988)	
<i>Cerastoderma glaucum</i>	2.5–4.8	Prevost Lagoon, France	Guelorget & Mazoyer-Mayere (1985)
<i>Scrobicularia plana</i>	1.8	Ria Formosa, Portugal	This study
	0.2	Tamar Estuary, England	Warwick & Price (1975)
	0.6–0.9	Mud flat, N. Wales	Hughes (1970) (quoted by Ansell et al. 1978)
	0.8–5.7	Gironde Estuary, France	Bachelet (1982)
3.7	Prevost Lagoon, France	Guelorget & Mazoyer-Mayere (1983)	
<i>Tellina tenuis</i>	1.9	Ria Formosa, Portugal	This study
	0.3–0.9	Sand flat, Scotland	Trevallion (1971) (quoted by Ansell et al. 1978)
<i>Bittium reticulatum</i>	1.3; 2.1	Ria Formosa, Portugal	This study
	2.9–3.5	Spanish north coast	Borja (1988)
<i>Hydrobia ulvae</i>	1.8	Ria Formosa, Portugal	This study
	1.2–1.8	Grevelingen Estuary, Netherlands	Wolff & de Wolf (1977)
	1.9–4.1	Firth of Forth, Scotland	McLusky et al. (1978)
	1.25	German Wadden Sea	Asmus (1982)
4.5–6.1	Gironde Estuary, France	Bachelet & Yacine-Kassab (1987)	
<i>Melinna palmata</i>	2.3	Ria Formosa, Portugal	This study
	2.2	English Channel	Oyeneken (1988)
<i>Nereis diversicolor</i>	3.3; 5.3	Ria Formosa, Portugal	This study
	3.1	Ythan Estuary, Scotland	Chambers & Milne (1975)
	2.5	Brackish-water ponds, Belgium	Heip & Herman (1979)
	2.6	Norsminde Fjord, Denmark	Kristensen (1984)
	3.5–5.9	Swedish west coast	Möller (1985)
2.2	Loire Estuary, France	Gillet (1990)	
<i>Carcinus maenas</i>	6.4	Ria Formosa, Portugal	This study
	4.5	Swedish west coast	Pihl & Rosenberg (1982)
	0.3–0.7	Swedish west coast	Baden & Pihl (1984)
	6.7	Swedish west coast	Möller et al. (1985)
2.8; 3.4	Swedish west coast	Pihl (1986)	

^aRecalculated not subtracting weight losses

production and not only somatic production is relevant. That is why these losses must not be subtracted from production figures. Rather, production encompasses all substances once built up during a time interval, independently of whether they persist until the end of the observation period or not (Clarke 1946, Banse & Mosher 1980). This also includes products which are extremely difficult to quantify under field conditions, such as e.g. mucus, exuviae or byssus threads. Consequently, the time scale for production is conveniently 1 yr. During this interval the species had passed through all possible physiological situations.

The actual nutritional condition of a species in a particular environment depends on the feeding type. Some modes of feeding can be more profitable than others under specific conditions. Boudreau et al. (1991) discuss in this context 'trophic positions' which influence P/\bar{B} levels.

Extremely high production figures can be attained by carnivorous species in culture systems (e.g. Brett & Groves 1979). It is not by chance that also in this study the predator *Carcinus maenas* holds a very special position (Fig. 2).

The other group are filter feeders. Levinton (1972) postulated that they pursue a feeding strategy which is adapted to a food source which is highly variable in space and time. When fed properly, production rates can be enormous; this makes them a profitable target in aquaculture systems (Mason 1976).

What is the best way under these conditions to obtain production figures from body weight and biomass? Extrapolations by the regressions presented by Banse & Mosher (1980), Schwinghamer et al. (1986) and Brey (1990) imply a degree of exactness which is not matched by reality. As outlined above, production figures depend strongly on the specific conditions under which a population exists. This fact is not taken into account by these extrapolations. That is why they should only be applied when the 'good old way' for estimating secondary production is not feasible (Brey 1990).

Especially in nonboreal habitats these regressions should be treated with utmost care. Banse & Mosher (1980) deduced their equation from species living between 5 and 20°C (annual average temperature). They speculate that the regression may be translocated parallel to higher values for species living in warmer climates. In fact, in the habitat studied here, the consequence is not a translocation but rather a rotation of the regression line. It may result in weight exponents even greater than zero. This in turn is an effect of the emphasis of the main factor which actually causes a large body size in the specific environment, whether it is the longevity of a species or its high specific growth rate. Under these conditions, the intra-

specific trend and the interspecific trend, which are mixed in these equations, may show a different orientation. Consequently, a 2-step approach is preferable as applied in the 'Methods' section: (1) obtain the best P/\bar{B} possible for this species ($P/\bar{B}_{\text{spec.}}$) at an average body weight (\bar{w}) in this particular environment. This estimate can be extrapolated from other populations or species of similar feeding mode, from literature data, or from regression analysis as in Fig. 2. (2) Calculate the actual P/B ($P/B_{\text{ind.}}$) for the body weight encountered ($w_{\text{ind.}}$), assuming a weight exponent of -0.25 for the intraspecific comparison (Eq. 3).

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LITERATURE CITED

- Ansell, A. D., McLusky, D. S., Stirling, A., Trevallion, A. (1978). Production and energy flow in the macrobenthos of two sandy beaches in South West India. Proc. R. Soc. Edin. (Sect. B) 76: 269–296
- Asmus, H. (1982). Field measurements on respiration and secondary production of a benthic community in the northern Wadden Sea. Neth. J. Sea Res. 16: 403–413
- Bachelet, G. (1982). Quelques problèmes liés à l'estimation de la production secondaire. Cas des bivalves *Macoma balthica* et *Scrobicularia plana*. Oceanol. Acta 5: 421–431
- Bachelet, G., Yacine-Kassab, M. (1987). Intégration de la phase post-recrutée dans la dynamique des populations du gastéropode intertidal *Hydrobia ulvae* (Pennant). J. exp. mar. Biol. Ecol. 111: 37–60
- Baden, S., Pihl, L. (1984). Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. Ophelia 23: 65–90
- Banse, K. (1979). On weight dependence of net growth efficiency and specific respiration rates among field populations of invertebrates. Oecologia 38: 111–126
- Banse, K., Mosher, S. (1980). Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 355–379
- Borja, A. (1988). Biología y ecología de tres especies de moluscos gasterópodos intermareales: *Rissoa parva*, *Barleeia unifasciata* y *Bittium reticulatum*. III. Producción. Cah. Biol. mar. 29: 319–330
- Boudreau, P. R., Dickie, L. M., Kerr, S. R. (1991). Body size spectra of production and biomass as system-level indicators of ecological dynamics. J. theor. Biol. 152: 329–339
- Boysen Jensen, P. (1919). Valuation of the Limfjord. I. Rep. Dan. Biol. Stn 26: 3–44
- Brett, J. R., Groves, T. D. D. (1979). Physiological energetics. In: Hoar, W. S., Randall, D. J., Brett, J. R. (eds.) Fish physiology, Vol. 8. Academic Press, New York, p. 279–352
- Brey, T. (1990). Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. Meeresforsch. 32: 329–343
- Chambers, M. R., Milne, H. (1975). Life cycle and production of *Nereis diversicolor* O. F. Müller in the Ythan estuary,

- Scotland. Estuar. coast. mar. Sci. 3: 133–144
- Clarke, G. L. (1946). Dynamics of production in a marine area. Ecol. Monogr. 16: 321–335
- Crisp, D. J. (1984). Energy flow measurements. In: Holme, N. A., McIntyre, A. D. (eds.) Methods for the study of marine benthos. Blackwell, Oxford, p. 284–372
- Engelmann, M. D. (1966). Energetics, terrestrial field studies and animal productivity. Adv. ecol. Res. 3: 73–115
- Epp, J., Bricelj, V. M., Malouf, R. E. (1988). Seasonal partitioning and utilization of energy reserves in two age classes of the bay scallop *Argopecten irradians irradians* (Lamarck). J. exp. mar. Biol. Ecol. 121: 113–136
- Gillespie, D. M., Benke, A. C. (1979). Methods of calculating cohort production from field data – some relationships. Limnol. Oceanogr. 24: 171–176
- Gillet, P. (1990). Biomasse, production et dynamique des populations de *Nereis diversicolor* (annélide polychète) de l'estuaire de la Loire (France). Oceanol. Acta 13: 361–371
- Guelorget, O., Mazoyer-Mayere, C. (1983). Growth, biomass and production of *Scrobicularia plana* in a Mediterranean lagoon: the Prevost Lagoon (Palavas, Hérault, France). Vie mar. 5: 13–22
- Guelorget, O., Mazoyer-Mayere, C. (1985). Croissance, biomasse et production de *Cerastoderma glaucum* dans une lagune méditerranéenne: l'Etang du Prevost (Hérault, France). Vie mar. 7: 15–27
- Heip, C., Herman, R. (1979). Production of *Nereis diversicolor* O.F. Müller in a shallow brackish-water pond. Estuar. coast. mar. Sci. 8: 297–305
- Hemmingsen, A. M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rep. Steno Mem. Hosp. 9: 1–110
- Hibbert, C. J. (1976). Biomass and production of a bivalve community on an intertidal mud flat. J. exp. mar. Biol. Ecol. 25: 249–261
- Hughes, R. N. (1970). An energy budget for a tidal flat population of the bivalve *Scrobicularia plana* (Da Costa). J. Anim. Ecol. 39: 357–382
- Humphreys, W. F. (1979). Production and respiration in animal populations. J. Anim. Ecol. 48: 427–453
- Kristensen, E. (1984). Life cycle, growth and production in estuarine populations of the polychaetes *Nereis virens* and *N. diversicolor*. Holarct. Ecol. 7: 249–256
- Levinton, J. (1972). Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am. Nat. 106: 472–486
- Mason, J. (1976). Cultivation. In: Bayne, B. L. (ed.) Marine mussels, their ecology and physiology. Cambridge University Press, Cambridge, p. 385–410
- McLusky, D. S., Elliot, M., Warnes, J. (1978). The impact of pollution on the intertidal fauna of the estuarine Firth of Forth. In: McLusky, D. S., Berry, A. J. (eds.) Proc. 12th Eur. mar. Biol. Symp. Pergamon Press, Oxford, p. 203–210
- Möller, P. (1985). Production and abundance of juvenile *Nereis diversicolor*, and oogenic cycle of adults in shallow waters of western Sweden. J. mar. biol. Ass. U.K. 65: 603–616
- Möller, P., Pihl, L., Rosenberg, R. (1985). Benthic fauna energy flow and biological interaction in some shallow marine soft bottom habitats. Mar. Ecol. Prog. Ser. 27: 109–121
- Möller, P., Rosenberg, R. (1983). Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow water, western Sweden. Ophelia 22: 33–55
- Moreira, M. H. (1988). Estudo da comunidade benthica num banco de lodo intertidal da Ria de Aveiro, com especial incidência no crescimento, biomassa e produção do berbigão, *Cardium edule* (L.). Ciênc. biol. ecol. Syst. 8: 47–75
- Oyekan, J. A. (1988). Population dynamics and secondary production in *Melinna palmata* (Polychaeta: Ampharetidae). Mar. Biol. 98: 247–251
- Pihl, L. (1986). Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. Neth. J. Sea Res. 20: 75–83
- Pihl, L., Rosenberg, P. (1982). Production, abundance and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. J. exp. mar. Biol. Ecol. 57: 273–301
- Sachs, L. (1978). Angewandte Statistik – Planung und Auswertung, Methoden und Modelle. Springer, Berlin
- Schwinghamer, P., Hargrave, B., Peer, D., Hawkins, C. M. (1986). Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar. Ecol. Prog. Ser. 31: 131–142
- Sprung, M. (in press). Macrobenthic secondary production in the intertidal zone of the Ria Formosa – a lagoon in southern Portugal. Estuar. coast. Shelf Sci.
- Sprung, M., Cardoso, A. C. (in press). Recruitment and production of the shore crab *Carcinus maenas* in the Ria Formosa. Boletim UCA, Univ. do Algarve, Faro
- Trevallion, A. (1971). Studies on *Tellina tenuis* Da Costa. III. Aspects of general biology and energy flow. J. exp. mar. Biol. Ecol. 7: 95–122
- von Bertalanffy, L. (1938). A quantitative theory of organic growth. Inquiries on growth laws. II. Hum. Biol. 10: 181–213
- Warwick, R. M., Price, R. (1975). Macrofauna production in an estuarine mudflat. J. mar. biol. Ass. U.K. 55: 1–18
- Waters, T. F. (1977). Secondary production in inland waters. Adv. ecol. Res. 10: 91–164
- Winberg, G. G. (1971). Methods for the estimation of production of aquatic animals. Academic Press, London
- Wolff, W. J., de Wolf, L. (1977). Biomass and production of zoobenthos in the Grevelingen Estuary, The Netherlands. Estuar. coast. mar. Sci. 5: 1–24

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