Meeresforsch. 32 (1990), 329–343
© 1990 Verlag Paul Parey, Hamburg und Berlin
ISSN 0341-6836

Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight[1]

THOMAS BREY

Alfred Wegener Institut für Polar- und Meeresforschung, Bremerhaven

Ms. received 30. 8. 89
Ms. accepted 25. 10. 89

Communicated by W. ARNTZ

Abstract

The empirical relations between annual somatic production P, annual P/$\overline{B}$-ratio, mean annual biomass $\overline{B}$ and mean individual weight W in macrobenthic invertebrate populations from areas between 12° and 70° latitude and down to 300 m water depth were analysed by means of multiple linear regression of the log-transformed data. In total, 337 data sets, representing 138 species were included.

The dependence of P on $\overline{B}$ and W is highly significant, whereas P/$\overline{B}$ depends only on W and not on $\overline{B}$. The regression equations differ significantly (Prob. < 0.01) among the main taxonomic groups (Mollusca, Polychaeta, Crustacea).

The comparison of original data on the production of macrobenthic populations with estimates based on the empirical relations established here shows that at the community level (i.e. sum of all species) annual production can be estimated from mean annual biomass $\overline{B}$ and mean individual weight W of each population by means of the empirical regression functions of P on $\overline{B}$ and W.

Kurzfassung

Die Schätzung der Produktivität makrobenthischer Evertebraten anhand von Biomasse und mittlerem Individualgewicht

Die empirischen Beziehungen zwischen jährlicher somatischer Produktion P, jährlicher P/$\overline{B}$-Rate, mittlerer Biomasse $\overline{B}$ und mittlerem Individualgewicht W makrobenthischer Evertebraten wurden untersucht. 337 Datensätze (138 verschiedene Arten) von Populationen aus Gebieten zwischen 12° und 70° geographischer Breite und aus Wassertiefen bis 300 m wurden mittels multipler linearer Regression der log-transformierten Werte analysiert.

Die Beziehung zwischen P sowie $\overline{B}$ und W ist hoch signifikant, während die P/$\overline{B}$-Rate nur von W und nicht von $\overline{B}$ abhängt. Zwischen den taxonomischen Hauptgruppen (Mollusca, Polychaeta, Crustacea) bestehen signifikante Unterschiede (Prob. < 0.01).

Der Vergleich von Originaldaten zur Produktion makrobenthischer Populationen mit Schätzungen auf der Basis der hier erstellten empirischen Beziehungen zeigt, daß die Produktion von benthischen Gemeinschaften (d. i. Summe aller Arten) anhand der mittleren Biomasse $\overline{B}$ und des mittleren Individualgewichts W jeder Art geschätzt werden kann.

Resumen

Estimación de la productividad de invertebrados macrobentónicos usando biomasa y peso individual promedio

Se analizó las relaciones empíricas entre la producción somática anual P, tasa P/$\overline{B}$ anual, biomasa media anual $\overline{B}$ y peso medio individual W en poblaciones de invertebrados macrobentónicos de áreas ubicadas entre 12° y 70° de latitud y hasta 300 m de profundidad. Se realizaron análises de regresión lineal multiple con datos log-transformados de 337 sets de datos representando a 138 especies.

P depende con una alta significancia de $\overline{B}$ y W, mientras que P/$\overline{B}$ depende solamente de W y no de

---

[1] AWI Publication No. 226

$\overline{B}$. Las ecuaciones de regresión difieren significativamente (Prob. < 0.01) entre los principales grupos taxonomicos (Mollusca, Polychaeta, Crustacea).

La comparación de los datos originales de producción de las poblaciones macrobentónicas con las estimaciones basadas en las relaciones empíricas establecidas aqui, muestra que a nivel comunitario (i.e. suma de todas las especies) la producción anual puede ser estimada a partir de la biomasa media anual $\overline{B}$ y del peso medio individual W de cada población por medio de funciones empíricas de regresión de P sobre $\overline{B}$ y W.

Introduction

The somatic production of macrozoobenthic populations is an important component of energy flow and organic matter cycling in aquatic ecosystems, especially in shallow water areas. With respect to the exploitation of demersal fish and shellfish stocks, benthic secondary production is also of economic importance.

The assessment of production, however, is a time-consuming and expensive work, even at the level of a single population, and therefore many colleagues searched for an easier way to get a reliable estimate of production. Mann (1969) suggested that there may be a general relationship between the annual production/biomass-ratio (P/$\overline{B}$-ratio) and life history for most organisms. Since that time, several publications have dealt with the dependence of the P/$\overline{B}$-ratio on a certain aspect of the life history of an organism. Waters (1977) showed that the annual P/$\overline{B}$-ratio of a population increases with an increasing number of generations per year. Zaika (1970), Robertson (1979) and Warwick (1980) demonstrated that the P/$\overline{B}$-ratio decreases with the life span of the organisms. The P/$\overline{B}$-ratio was found to be inversely related also to weight at sexual maturity (Banse and Mosher 1980; Heip et al. 1982) and to individual body mass per size class (Schwinghamer et al. 1986). All of these empirical findings depend on the negative exponential relation of metabolic rate to body weight in animals.

Unfortunately, these relations between P/$\overline{B}$-ratio and one independent variable may not be valid for an accurate estimation of the productivity of a single population, because the confidence intervals of the log-log regression lines may cover a range of more than a hundred percent on the linear scale (see e.g. Banse and Mosher 1980).

The first aim of this paper is to establish improved empirical relations, which may allow a more accurate estimate of productivity from parameters which are easy to obtain. The most promising approach seems to be the use of more than one independent variable, as proposed first by Humphreys (1980), who used biomass and maximum individual weight to predict assimilation and production.

The second aim of this paper is a suggestion of Warwick (1980), who assumed that it may be possible not to estimate the production of a single population, but the production of the whole community in question by empirical relationships of this kind.

This publication is part of the work of the Benthos Ecology Working Group of the International Council for the Exploration of the Sea (ICES).

Methods

I investigated the relations between annual somatic production (P), annual P/$\overline{B}$-ratio (P/$\overline{B}$), mean annual biomass ($\overline{B}$) and mean individual weight (W). The latter is assumed to be less affected by sampling error than maximum individual weight, which was used by Humphreys (1980).

The analysis is based on 107 publications on macrobenthic productivity which were selected from the available literature until 1989. The majority of the authors used the increment or removal summation method according to Crisp (1984). Some authors calculated somatic production from growth and mortality rates or by means of the size-frequency method (Hynes and Coleman 1968; Menzie 1980). In a few cases somatic production was obtained from an energy flow analysis. If necessary, weight data were converted to ash free dry weight (AFDW) using conversion factors taken from Rumohr et al. (1987), Brey et al. (1988) or the original authors. Generally, mean individual weight W had to be calculated from biomass and abundance data, i.e. they are not statistically independent. In some cases abundance had to be estimated from figures showing annual variations in numbers. In order to exclude data which may be biased due to sampling and measurement errors (very low figures of biomass, weight, production), all data sets included comply with the following biological conditions:

- Mean annual biomass $\overline{B}$: $\overline{B} > 0.01$ gAFDW m^{-2}
- Mean individual weight W: $W >= 0.00001$ gAFDW
- Annual production P: $P >= 0.01$ gAFDW m^{-2} y^{-1}

Aquatic larvae of insects (e.g. Chironomidae, Ephemeroptera) have been excluded completely because their life history is unique among macrobenthic animals.
The general form of the relations we are interested in is:

$$P = f(\overline{B}, W) \quad (1)$$
$$P/\overline{B} = f(\overline{B}, W) \quad (2)$$

The aim of this paper is to find equations, which are not too complex and which describe these multiple relations best. In most cases the empirical relations between different parameters of population energetics are nonlinear and a linearization by log-transformation allows the application of a linear regression model (see e.g. Banse and Mosher 1980; Humphreys 1979; McNeill and Lawton 1970; Robertson 1979). In contrast to Humphreys (1980), who integrated biomass and weight in one variable ($\overline{B}/W^{0.75}$), a multiple regression model is used here:

$$\log(P) = a + b_1 \cdot \log(\overline{B}) + b_2 \cdot \log(W) \quad (3)$$
$$\log(P/\overline{B}) = a' + b_1' \cdot \log(\overline{B}) + b_2' \cdot \log(W) \quad (4)$$

However, a few transformations of equ. (3) show that equ. (3) and equ. (4) are nearly equivalent:

$$\log(P) = a + (b_1 - 1) \cdot \log(\overline{B}) + b_2 \cdot \log(W) + \log(\overline{B})$$
$$\log(P) - \log(\overline{B}) = a + (b_1 - 1) \cdot \log(\overline{B}) + b_2 \cdot \log(W)$$
$$\log(P/\overline{B}) = a + (b_1 - 1) \cdot \log(\overline{B}) + b_2 \cdot \log(W) \quad (4')$$

At the right side, equ. (3) and (4') only differ in the coefficient of $\log(\overline{B})$, b_1 and $(b_1 - 1)$, respectively.

The data were ${}_{10}$log-transformed and first examined for significant correlations by means of the calculation of the partial correlation coefficients, which express the degree of correlation between two variables after the effect of an additional variable has been removed.

Subsequently, multiple linear regressions were calculated at the level of all data sets and at the level of main taxonomic groups. Those equations which showed significant dependences were applied to data on macrobenthic community production published by several authors; the estimates of P were compared with the original production figures.

Results

The data base

A total of 337 data sets of P, P/$\overline{B}$, $\overline{B}$ and W, referring to 138 species (Table 1), was selected. Most of these were of marine or brackish water origin (111 species, 281 data sets), only a minority represents animals inhabiting freshwater sites (27 species, 56 data sets). The data

Table 1. List of macrobenthic species included in the analysis

Mollusca
Abra nitida
Abra prismatica
Ancylus fluviatilis
Anodonta anatina
Anodonta piscinalis
Arctica islandica
Bellamya unicolor
Cardium edule
Chione cancellata
Chlamys islandica
Chlamys varia
Cleopatra bulimoides
Corbicula africana
Donax incarnatus
Donax vittatus
Dreissena polymorpha
Ensis directus
Ensis siliqua
Gyraulus acronicus
Gyraulus deflectus
Hiatella byssifera
Hydrobia neglecta
Hydrobia sp.
Hydrobia ulvae
Hydrobia ventrosa
Lissarca miliaris
Littorina saxatilis
Lymnaea peregra
Macoma balthica
Macoma calcarea
Melania tuberculata
Mercenaria mercen.
Mesodesma donacium
Modiolus demissus
Mya arenaria
Mya truncata
Mytilus edulis
Nacella concinna
Nucula annulata
Nucula nitidosa
Nucula paulula
Nucula turgida
Pandora gouldiana
Pharus legumen
Physa gyrina
Pillucina neglecta
Pisidium compressum
Pisidium sp.
Placopecten magellan.
Scapharca inaequi.
Scrobicularia plana
Serripes groenlandicus
Spisula eliptica
Spisula solidissima
Syndosmya alba
Tegula funebralis
Tellina agilis
Tellina fabula
Tellina martinicensis
Tellina tenuis
Theora lubrica
Thyasira flexuosa
Turbo sarmaticus
Unio pictorum
Unio tumidus
Valvata piscinalis
Venerupis aurea
Venus ovata
Venus striatula
Veremolpa micra

Polychaeta
Ammotrypane aulog.
Ampharete acutifrons
Ampharete finmarch.
Arenicola marina
Capitella capitata
Cauleriella caput.
Chaetozone setosa
Euzonus mucronata
Glycera alba
Harmothoe lunulata
Harmothoe sarsi
Heteromastus filiformis
Lumbrinereis fragilis
Magelona mirabilis
Magelona papillicornis
Melinna palmata
Nephtys hombergi
Nephtys incisa
Nereis diversicolor
Nereis virens
Paraprinospio pinn.
Paraprionospio sp.
Pectinaria californ.
Pectinaria gouldii
Pectinaria hyperborea
Pectinaria koreni
Sabellaria spinulosa
Sigalion mathildae
Spiophanes bombyx
Spiophanes kroyeri
Terebellides stroemi
Tharys marioni

Crustacea
Ampelisca agassizi
Ampelisca auracana
Ampelisca brevicornis
Ampelisca tenuicornis
Ampelisca typica
Asellus aquaticus
Calocaris macandreae
Cirolana imposita
Corophium insiduosum
Corophium volutator
Crangonyx richmon.
Diastylis rathkei
Emerita analoga
Ericthonius fasciatus
Gammarus aequicauda
Gammarus pseudolimn.
Gammarus pulex
Hyalella azteca
Mesidothea entomon
Pontoporeia affinis
Pontoporeia femorata
Proasellus coxalis
Unicola inermis

Echinodermata
Amphiura filiformis
Moira atropes
Ophiotrix fragilis
Ophiura texturata
Strongylocentr. dr.
Strongylocentr. int.

Miscellaneous
Branchiura sower.
Glossiphonia heter.
Helobdella stagnalis
Herpobdella octocu.
Herpobdella test.
Limnodrilus spp.
Tubifex castatus

sources are listed in the appendix, the complete data set is available on request from the author. In Table 2, the median is given as an average value, together with the range of values for the main taxonomic groups and the total data, because the distributions of $\overline{B}$, W and P are strongly righttailed.

Fig. 1 and Fig. 2 show the distribution of the total data with respect to geographical latitude and water depth. The bulk of the data represents populations from northern boreal intertidal and shallow subtidal sites.

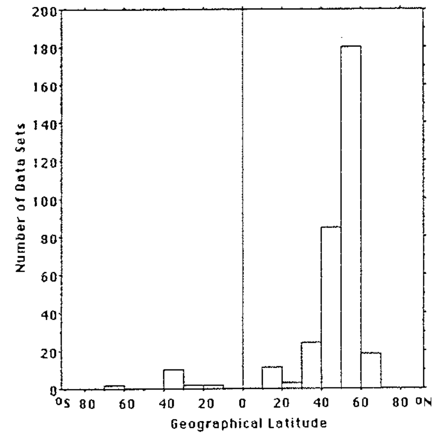

Fig. 1. Distribution of the total data with respect to geographical latitude (°N and °S).

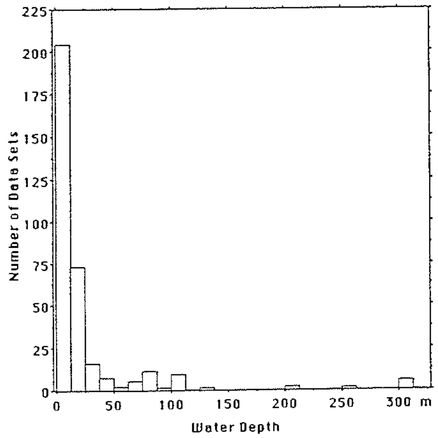

Fig. 2. Distribution of the total data with respect to water depth (m).

Empirical relations between P, P/$\overline{B}$, $\overline{B}$ and W

The partial correlation coefficients based on the total data (Table 3) indicate a strong positive correlation between P and $\overline{B}$ ($r = 0.909$) and a somewhat weaker negative correlation between P and W ($r = 0.589$). P/$\overline{B}$ is not correlated with $\overline{B}$, but there is a negative correlation between P/$\overline{B}$ and W, which is as strong as the one between P and W.

The corresponding multiple linear regression equations are shown in Table 3. As expected (see methods), the two equations differ only in the slope b_1. Therefore equ. (4) was not used further in the analysis.

The data were tested on significant differences among the main taxonomic groups (see

Table 2. **Distribution of data**

$\bar{B}$: mean annual biomass [gAFDW m^{-2}]
W: mean individual weight [gAFDW]
P: annual production [gAFDW m^{-2} y^{-1}]
P/$\bar{B}$: annual P/$\bar{B}$-ratio [y^{-1}]
N_{Sp}, N_{Dat}: Number of species, number of data sets

	N_{Sp}	N_{Dat}		median	range
Mollusca	70	182	$\bar{B}$	2.14	0.02 – 1208.00
			W	0.00600	0.00004 – 22.071
			P	1.76	0.02 – 1545.00
			P/$\bar{B}$	1.13	0.05 – 15.11
Polychaeta	32	72	$\bar{B}$	0.85	0.02 – 20.12
			W	0.00200	0.00003 – 0.973
			P	2.44	0.02 – 50.76
			P/$\bar{B}$	1.83	0.17 – 12.67
Crustacea	23	65	$\bar{B}$	0.43	0.02 – 522.00
			W	0.00100	0.00008 – 0.346
			P	1.02	0.08 – 217.50
			P/$\bar{B}$	4.00	0.12 – 11.29
Echinodermata	6	7	$\bar{B}$	7.34	0.20 – 21.00
			W	0.06600	0.02000 – 0.990
			P	6.47	0.10 – 31.50
			P/$\bar{B}$	0.87	0.48 – 1.82
Miscellaneous	7	11	$\bar{B}$	0.33	0.01 – 0.88
			W	0.00200	0.00010 – 0.007
			P	1.27	0.03 – 4.07
			P/$\bar{B}$	3.50	2.38 – 12.50
Total	138	337	$\bar{B}$	1.09	0.01 – 1208.00
			W	0.00200	0.00003 – 22.071
			P	1.77	0.02 – 1545.00
			P/$\bar{B}$	1.82	0.05 – 15.11

Table 3. **Partial correlation coefficients and multiple linear regression of P and P/$\bar{B}$ on $\bar{B}$ and W, total data (N = 337)**

$\bar{B}$: mean annual biomass [gAFDW m^{-2}]
W: mean individual weight [gAFDW]
P: annual production [gAFDW m^{-2} y^{-1}]
P/$\bar{B}$: annual P/$\bar{B}$-ratio [y^{-1}]

Partial correlation coefficients:

	W removed	$\bar{B}$ removed
P	$r_{P\bar{B}.W} = 0.909$	$r_{PW.\bar{B}} = -0.589$
P/$\bar{B}$	$r_{P/\bar{B}\bar{B}.W} = 0.015$	$r_{P/\bar{B}W.\bar{B}} = -0.587$

Multiple linear regression

Model: $_{10}\log(Y) = a + b_1 * {}_{10}\log(\bar{B}) + b_2 * {}_{10}\log(W)$

Y	Coefficients		95 % interval	Probability of error	R^2
P	a	−0.473			0.851
	b_1	1.007	± 0.050	< 0.0001	
	b_2	−0.274	± 0.041	< 0.0001	
P/$\bar{B}$	a	−0.473			0.478
	b_1	0.007	± 0.050	< 0.7798	
	b_2	−0.274	± 0.041	< 0.0001	

Table 4. **Multiple linear regression of P on $\bar{B}$ and W, main taxonomic groups**

$\bar{B}$: mean annual biomass [gAFDW m^{-2}]
W: mean individual weight [gAFDW]
P: annual production [gAFDW m^{-2} y^{-1}]
P/$\bar{B}$: annual P/$\bar{B}$-ratio [y^{-1}]
Model: $_{10}\log(P) = a + b_1 * {}_{10}\log(\bar{B}) + b_2 * {}_{10}\log(W)$

	Coefficients		95 % interval	Probability of error	R^2
Mollusca	a	−0.591			0.869
	b_1	1.030	± 0.065	< 0.0001	
	b_2	−0.283	± 0.057	< 0.0001	
Polychaeta	a	−0.018			0.861
	b_1	−1.022	± 0.116	< 0.0001	
	b_2	−0.116	± 0.081	< 0.0057	
Crustacea	a	−0.614			0.913
	b_1	1.022	± 0.081	< 0.0001	
	b_2	−0.360	± 0.098	< 0.0001	
Total	a	−0.473			0.851
	b_1	1.007	± 0.050	< 0.0001	
	b_2	−0.274	± 0.041	< 0.0001	

Table 2) by means of the inclusion of these groups as additional dummy variables in the regression model. Mollusca, Polychaeta and Crustacea have significantly different (Prob. < 0.01) regression equations, which are shown in Table 4.

Estimation of production by empirical relations

Table 5 gives the results of the comparison of production values calculated by the original authors for four different communities with values estimated by means of the regression of P on $\bar{B}$ & W. At the population level, the deviations between calculated and estimated production reach several hundred per cent in some cases (mean = 74 %), whereas at the community level (i.e. sum of all species) the largest deviation is 66 % only (mean = 21 %).

Discussion

Many authors who analyzed the empirical relations between productivity and other parameters of animal populations made quite rigorous demands on the quality of the data to be included in their calculations. In contrast, I tried to maximize the number of data, although there is a considerable spread in the quality of the publications which are included here. This seems to be a more advantageous approach, if we assume that statistical error (i.e. the difference between the true values of $\bar{B}$, W, P and P/$\bar{B}$ and the published values) is randomly distributed among these data.

Up to now, the most common approach to establish empirical relations between productivity and other population parameters for macrobenthic invertebrates was the correlation of the P/$\bar{B}$-ratio to various parameters (see introduction), which are more or less equivalent to average body weight. All of these depend on the negative exponential relation of metabolic rate to body weight. This relation has been found here again, but it is not the main topic of this paper.

The results presented here show that P/$\bar{B}$ does not depend on $\bar{B}$ at an empirical basis. This is in contrast to several single species studies, which demonstrated density-depending reductions in productivity or related parameters, see e.g. MORRISEY (1987) or ZAJAK (1986). In an ecological context, the independence of P/$\bar{B}$ from $\bar{B}$ indicates that intraspecific density-dependent mechanisms, e.g. intraspecific competition for food, do not cause the observed variability in the $P/\overline{B}$-ratio of various species and populations. The remaining variance of the $P/\overline{B}$ data, which is not explained by W, must be due to other factors like interspecific competition, predation or environmental parameters which were not taken into account for this investigation.

Table 5. Comparison of calculated production values with values estimated from multiple regression equations

P_{calc}: Production calculated by the original authors
P_{est}: Computed with multiple regression of P on $\overline{B}$ & W.
Original authors: Community No. 1: Buchanan & Warwick 1974
No. 2: Warwick & Price 1975
No. 3: Warwick et al. 1978
No. 4: Warwick & George 1980

Species	$\overline{B}$ gAFDW m^{-2}	W gAFDW	P_{calc} gAFDW m^{-2} y^{-1}	P_{est}	Deviation %
Community No. 1					
Abra nitida	0.11	0.00688	0.12	0.11	−8
Ammotryphane aulogaster	0.17	0.00181	0.36	0.33	−8
Chaetozone setosa	0.04	0.00048	0.05	0.09	60
Heteromastus filiformis	0.29	0.00129	0.30	0.59	97
Lumbrinereis fragilis	0.06	0.00200	0.08	0.11	38
Spiophanes kroyeri	0.12	0.00347	0.20	0.21	5
Calocaris macandreae	1.21	0.12100	0.14	0.64	286
Sum	2.00	–	1.25	2.08	66
Community No. 2					
Macoma balthica	0.34	0.00692	0.31	0.34	10
Mya arenaria	5.54	0.02828	2.66	4.10	54
Scrobicularia plana	2.15	0.03746	0.48	1.43	198
Ampharete acutifrons	0.43	0.00113	2.32	0.89	−62
Nepthys hombergii	3.95	0.01407	7.34	6.41	−13
Sum	12.41	–	13.11	13.17	<1
Community No. 3					
Donax vittatus	0.34	0.00449	0.72	0.39	−46
Ensis siliqua	5.10	0.82524	1.37	1.45	6
Pharus legumen	28.82	0.16707	16.12	13.56	−16
Tellina fabula	0.33	0.00162	0.29	0.50	72
Venus striatula	1.50	0.06608	0.62	0.84	35
Glycera alba	0.29	0.00380	0.28	0.52	86
Magelona papillicornis	0.63	0.00032	0.69	1.52	120
Sigalion mathildae	0.38	0.01667	0.17	0.57	235
Spiophanes bombyx	0.69	0.00061	3.35	1.55	−54
Tharys marioni	0.02	0.00011	0.02	0.05	150
Ophiura texturata	0.67	0.06569	0.46	0.47	2
Sum	38.77	–	24.09	21.42	−11
Community No. 4					
Abra alba	0.30	0.00572	0.41	0.32	−22
Nucula turgida	2.62	0.00345	1.35	3.44	155
Spisula elliptica	6.23	0.00770	10.29	6.69	−35
Ampharete finmarchica	0.02	0.00159	0.03	0.04	33
Nephtys hombergii	0.46	0.00106	0.37	0.96	159
Diastylis rathkei	0.33	0.00223	0.40	0.71	78
Ophiura texturata	0.20	0.02048	0.10	0.19	90
Sum	10.16	–	12.95	12.35	−5

From the user's point of view the absent relation between $P/\overline{B}$ and $\overline{B}$ may be the main disadvantage of any empirical regression which uses $P/\overline{B}$ as the dependent variable, because $\overline{B}$ is required to estimate P from $P/\overline{B}$ also, but $\overline{B}$ is not used in this way to increase the precision of the estimate of P.

The multiple regression equations between P and $\overline{B}$ & W are proposed here as as a tool for estimating the annual production of macrobenthic communities. Table 5 shows that – as suggested by WARWICK (1980) – the empirical relations between P and $\overline{B}$ & W result in reasonable estimates of community production, although there are large differences between calculated and estimated production at the species level. In three of the four examples presented, the deviations in the estimates of community production are below 20 %. With respect to the first example (BUCHANAN and WARWICK 1974), the deviation is much higher (66 %). This may be due to the extraordinary low standing stock and production of this community, which is a strong outlier with respect to the data base of the equations. A disadvantage of this comparison is the fact that the production data of these four communities are part of the data basis of the empirical regressions which are to be tested here. Only independent data on community production allow a real test on the validity of the regression equations. Those data, however, are not available up to now.

One important question is the establishment of confidence limits for an estimate of community production derived from these regression equations. If we estimate the production of a single population only, the 95 % confidence limits of the predicted production value are the appropriate parameter, which can be calculated according to DRAPER and SMITH (1981). The community production estimate consists of a sum of population production estimates, this makes the calculation of a statistically valid estimate of variability somewhat difficult.

To overcome this problem, I propose the application of "worst case" 95 % limits to the estimate of community production. They simply consist of the sum of the lower and upper 95 % confidence limits of the predicted production values of all populations. These "worst case" limits may be interpreted as the two opposite situations of systematic deviation, i.e. the P-$\overline{B}$-W coordinates of all populations of the community in question show a deviation from the regression plane in the same direction. They are not real confidence limits, but they may be a useful measure of variation of the calculated community production, especially when different communities are to be compared. Table 6 contents all data required to calculate the 95 % confidence limits of values estimated from the regression equations of P on $\overline{B}$ and W.

In Table 7, the "worst case" 95 % limits of the production estimates of the four communities of Table 5 are shown. In three of the four cases, these limits include the calculated production value; the calculated production of community 1, however, is below the lower 95 % limit.

To sum up, the following procedure is proposed for the estimation of community production by means of the empirical relations presented here:

1. Calculate mean annual biomass $\overline{B}$ (gAFDW) and mean individual weight W (gAFDW) of all populations which belong to the community in question.
2. Compute the estimate of annual production of each population by means of the regression equations of P on $\overline{B}$ and W (Tables 3 and 4). Use the equations for taxonomic groups (Mollusca, Polychaeta, Crustacea) wherever possible.
3. Add up the population production values to get an estimate of community production.
4. Compute the "worst case" 95 % limits of community production by adding up the 95 % confidence limits of the predicted production values of the populations. Calculate these limits by means of the data given in Table 6 (e.g. according to DRAPER and SMITH 1981).

In order to decrease the probability of extremely misleading estimates of annual production, the empirical relations presented here should not be applied to

Table 6. Computation of the 95 % confidence limits of a production value which was predicted from the empirical regression equations Notation according to Draper and Smith (1981)

$t = t_{n-3,\ 0.975}$ (onetailed)

s^2 = Residual mean square of multiple regression

$$X_0 = \begin{bmatrix} 1 \\ \log(\overline{B}_i) \\ \log(W_i) \end{bmatrix} \qquad X = \begin{bmatrix} 1 & \log(\overline{B}_1) & \log(W_1) \\ \vdots & \vdots & \vdots \\ 1 & \log(\overline{B}_n) & \log(W_n) \end{bmatrix}$$

$$C = (X'X)^{-1}$$

Calculation: lower 95 % limit $= \log(P_i) - t * \sqrt{s^2 * X_0'CX_0}$

upper 95 % limit $= \log(P_i) + t * \sqrt{s^2 * X_0'CX_0}$

Taxon	S^2	C
Mollusca	0.127	$\begin{bmatrix} 0.037222 & -0.012411 & 0.014153 \\ -0.012411 & 0.008481 & -0.004876 \\ 0.014153 & -0.004876 & 0.006434 \end{bmatrix}$
Polychaeta	0.091	$\begin{bmatrix} 0.122647 & -0.038806 & 0.044492 \\ -0.038806 & 0.036950 & -0.016493 \\ 0.044492 & -0.016493 & 0.018218 \end{bmatrix}$
Crustacea	0.046	$\begin{bmatrix} 0.515868 & -0.042474 & 0.160610 \\ -0.042474 & 0.035476 & -0.017372 \\ 0.160610 & -0.017372 & 0.051981 \end{bmatrix}$
Total Data	0.118	$\begin{bmatrix} -0.003395 & 0.001047 & -0.001241 \\ 0.001047 & 0.002847 & 0.000114 \\ -0.001241 & 0.000114 & 0.000004 \end{bmatrix}$

Table 7. The effect of the 95 % confidence intervals of the multiple regression functions on the estimate of community production

P_{calc}: Production calculated by the original authors.

P_{est}: Computed with multiple regression of P on $\overline{B}$ & W.

"worst case" 95 % limits: Sum of the lower and upper 95 % confidence limits of the predicted production values

Community No.	P_{calc}	P_{est}	"worst case" 95 % limits lower	upper
1	1.25	2.08	1.51	2.87
2	13.11	13.17	11.08	15.70
3	24.09	21.42	17.82	25.84
4	12.95	12.35	10.63	14.35

1. communities dominated by one species with extraordinary high biomass like mussel beds,
2. communities with only a few (< 5) species,
3. communities exposed to very stressing environmental conditions.

If situations of this kind are excluded, the empirical relations between P and $\overline{B}$ & W presented here seem to be useful for a first rough estimate of production of shallow water (down to 300 m water depth) macrobenthic communities. However, the existence of empirical relations of this kind should not keep students and scientists from carrying out production studies in the „good old way". The results presented here show very clearly that production estimates based on empirical relations are close to reality *up to the average*, but they may be quite misleading in certain cases.

Geographical latitude and water depth may be two abiotic parameters which influence benthic secondary production and P/$\overline{B}$-ratio via primary production, water temperature and amount of available food. However, with respect to these parameters the data do not cover a sufficient range for a valid analysis (Fig. 1 and Fig. 2). Further work on macrobenthic secondary production in the neglected areas may provide additional data to overcome this problem.

References

Banse, K.; Mosher, S., 1980: Adult body mass and annual production/biomass relationships of field populations. Ecol. Monographs 50, 355–379.

Brey, T.; Rumohr, H.; Ankar, S., 1988: Energy content of macrobenthic invertebrates: General conversion factors from weight to energy. J. Exp. Mar. Biol. Ecol. 117, 271–278.

Crisp, D. J., 1984: Energy flow measurements. In: Holme, N. A.; McIntyre, A. D. (Eds): Methods for the study of marine benthos. Oxford: Blackwell Scientific. 284–372.

Draper, N. R.; Smith, H., 1981: Applied regression analysis. New York: Wiley. 709 pp.

Heip, C.; Herman, P. M. J.; Coomans, A., 1982: The productivity of marine meiobenthos. Academiae Analecta 44, 1–20.

Humphreys, W. F., 1979: Production and respiration in animal populations. J. Anim. Ecol. 48, 427–453.

Humphreys, W. F., 1980: Towards a simple index based on live-weight and biomass to predict assimilation in animal populations. J. Anim. Ecol. 50, 543–561.

Hynes, H. B. N.; Coleman, M. J., 1968: A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13, 569–573.

Mann, K. H., 1969: The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6, 1–81.

McNeill, S.; Lawton, J. H., 1970: Annual production and respiration in animal populations. Nature 225, 472–474.

Morrisey, D. J., 1987: Effect of population density and presence of a potential competitor on the growth rate of the mud snail *Hydrobia ulvae* (Pennant). J. Exp. Mar. Biol. Ecol. 108, 275–295.

Robertson, A. L., 1979: The relationship between annual production: biomass ratios and lifespans for marine macrobenthos. Oecologia 38, 193–202.

Rumohr, H.; Brey, T.; Ankar, S., 1987: A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. Balt. Mar. Biol. Publ. No. 9, 56 p.

Schwinghammer, 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.

Warwick, R. M., 1980: Population dynamics and secondary production of benthos. In: Tenore, K. R.; Coull, B. C. (Eds): Mar. Benthic Dyn. Univ. South Carolina Press, 1–24.

Waters, T. F., 1977: Secondary production in inland waters. Adv. Ecol. Res. 10, 91–164.

Zaika, V. Y., 1970: Relationship between the productivity of marine mollusks and their life-span. Oceanology (USSR) 10, 547–552.

Zajac, R. N., 1986: The effects of intra-specific density and food supply on growth and reproduction in an infaunal polychaete, *Polydora ligni* Webster. J. Mar. Res. 44, 339–359.

Appendix – Data sources

Andersin, A.-B.; Lassig, J.; Sandler, H. 1984: On the biology and production of Pontoporeia affinis Lindstr. in the Gulf of Bothnia. Limnologica 15, 395–401.

Ankar, S., 1980: Growth and production of *Macoma balthica* (L.) in a Northern Baltic soft bottom. Ophelia Suppl. 1, 31–48.

Ansell, A. D.; Sivadas, P.; Narayanan, B.; Trevallion, A., 1972: The ecology of two sandy beaches in South West India. II. Observations on the population of *Donax incarnatus* and *D. spiculum*. Mar. Biol. 17, 318–332.

Asmus, H., 1987: Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Mar. Ecol. Prog. Ser. 39, 251–266.

Bergh, G., 1974: Production of *Macoma balthica* (L.) (Lamellibranchiata) and notes on other ecologically important animals in Tvären Bay in the Baltic. Zoon 2, 143–152.

Beukema, J. J., 1980: Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: I. The Tellinid bivalve *Macoma balthica*. Neth. J. Sea Res. 14, 323–338.

Beukema, J. J., 1982: Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: I. The edible cockle, Cerastoderma edule. Neth. J. Sea Res. 15, 391–405.

Beukema, J. J.; de Vlas, J., 1979: Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 13, 331–353.

Birklund, J., 1977: Biomass, growth and production of the amphipod *Corophium insiduosum* Crawford, and preliminary notes on *Corophium voluntator* (Pallas). Ophelia 16, 187–203.
Brey, T., 1986: Estimation of annual P/B-ratio and production of marine benthic invertebrates from length-frequency data. Ophelia Suppl. 4, 45–54.
Buchanan, J. B.; Warwick, R. M., 1974: An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. J. Mar. Biol. Ass. U. K. 54, 197–222.
Burke, M. V.; Mann, K. H., 1974: Productivity and production:biomass ratios of bivalve and gastropod populations in a Eastern Canadian estuary. J. Fish. Res. Bd. Canada *31*, 167–177.
Carrasco, F. D.; Arcos, D. F., 1984: Life history and production of the sublittoral amphipod *Amphelisca araucana*. Mar. Ecol. Prog. Ser. 14, 245–252.
Cederwall, H., 1977: Annual macrofauna production of a soft bottom in the northern Baltic proper. In: Keegang, B. F.,; Ceidigh, P. O. (Eds): Biology of benthic organisms. Oxford: Pergamon, 155–164.
Chambers, M. R.; Milne, H., 1975: The production of *Macoma balthica* (L.) in the Ythan estuary. Estuar. Coast. Mar. Sci. 3, 443–455.
Collie, J. S., 1985: Life history and production of three amphipod species on Georges Bank. Mar. Ecol. Prog. Ser. 22, 229–238.
Cranford, P. J.; Peer, D. L.; Gordon, D. C., 1985: Population dynamics and production of *Macoma balthica* in Cumberland Basin and Shepody Bay, Bay of Fundy. Neth. J. Sea Res. 19, 135–146.
Craeymeersch, J. A.; Herman, P. M. J.; Meire, P. M., 1986: Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S. W. Netherlands). Hydrobiologia 133, 107–115.
Curtis, M. A., 1977: Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. Ophelia 16, 9–58.
Dall, P. C., 1979: Ecology and production of the leeches *Erprob-della octoculata* L. and *Erpobdella testacea* Sav. in lake Esrom, Denmark. Arch. Hydrobiol. Suppl. 57, 188–220.
Dauvin, J.-C., 1985: Dynamique et production d'une population de *Venus ovata* Pennant (Mollusque-Bivalve) de la Baie de Morlaix (Manche Occidentale). J. Exp. Mar. Biol. Ecol. 91, 109–123.
Dauvin, J.-C., 1986a: Biologie, dynamique et production d'une population d' *Abra alba* (Wood) (Mollusque-Bivalve) de la Baie de Morlaix (Manche Occidentale). J. Exp. Mar. Biol. Ecol. 97, 151–180.
Dauvin, J.-C., 1986b: Dynamique de la population d' *Abra prismatica* (Mollusque, Bivalve) de la Baie de Morlaix (Manche Occidientale). Ann. Inst. Oceanogr. (Paris) 62, 1–12.
Dauvin, J.-C., 1988a: Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentiale. 1. *Ampelisca tenuicornis* (Liljeborg). J. Exp. Mar. Biol. Ecol. 118, 55–84.
Dauvin, J.-C., 1988b: Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentiale. 2. *Ampelisca brevicornis* (Costa). J. Exp. Mar. Biol. Ecol. 119, 213–233.
Dauvin, J.-C., 1988c: Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentiale. 3. *Ampelisca typica* (Bate). J. Exp. Mar. Biol. Ecol. 121, 1–22.
Flössner, D., 1982: Untersuchungen zur Biomasse und Produktion des Makrozoobenthos der Ilm und mittleren Saale. Limnologica 14, 297–327.
Flössner, D., 1987: Populationsdynamik und Produktion von *Asellus aquaticus* (L.) and *Proasellus coxalis* (Dollfus) in der mittleren Saale. Limnologica 18, 279–295.
Foberg, M., 1976: Productionsberäkningar för nagra makroevertebrater i Lulea skärgard sommaren 1976. Zoll Inst. Univ. Stockholm, internal report.
Fuji, A.; Kawamura, K., 1970: Studies on the biology of the sea urchin – VII. Bio-economics of the population of Strongylocentrotus intermedius on a rocky shore of southern Hokkaido. Bull. Jap. Soc. Sci. Fish. 36, 763–775.
George, C L.; Warwick, R. M., 1985: Annual macrofauna production in a hard-bottom reef community. J. Mar. Biol. Ass. U. K. 65, 713–735.
Gillespie, D. M., 1969: Population studies of four species of molluscs in the Madison river, Yellowstone National Park. Limnol. Oceanogr. 14, 101–114.
Golikov, A. N.; Scarlato, O. A., 1970: Abundance, dynamics and production properties of populations of edible bivalves *Mizuhopecten yessoensis* and *Spisula sachalinensis* related to the problem of controllable submarine farms at the Western shores of the Sea of Japan. Helgol. Wiss. Meeresunters. 20, 498–513.
Gratto, G. W.; Thomas, M. L. H., 1983: Growth and production of the intertidal amphipod *Corophium volutator* (Pallas) in the inner Bay of Fundy. Proc. N. S. Inst. Sci. 33, 47–55.
Hastings, M. H., 1981: The life cycle and productivity of an intertidal population of the amphipod *Ampelisca brevicornis*. Est. Coast. Shelf Sci. 12, 665–677.
Heip, C.; Hrman, R., 1979: Production of *Nereis diversicolor* O. F. Müller (Polychaeta) in a shallow brackish water pond. Estuar. Coast. Mar. Sci. 8, 297–305.
Hibbert, C. J., 1976: Biomass and production of a bivalve community on an intertidal mudflat. J. Exp. Mar. Biol. Ecol. 25, 249–261.

Howe, S.; Leathem, W., 1984: Secondary production of benthic macrofauna at three stations of Delaware Bay and coastal Delaware. NOAA Tech. Mem. NMFS-F/NEC-32, 62 pp.
Howe, S.; Maurer, D.; Leathem, W., 1988: Secondary production of benthic molluscs from the Delaware Bay and coastal area. Estuar. Coast. Shelf Sci. 26, 81–94.
Hughes, R. N., 1970: An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (da Costa). J. Anim. Ecol. 39, 357–381.
Hummel, H., 1985: An energy budget for a *Macoma balthica* (Mollusca) population living on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res., 19, 84–92.
Hylleberg, J.; Brock, V.; Jørgensen, F., 1978: Production of sublittoral cockles, *Cardium edule* L. with emphasis on predation by flounders and sea stars. Nat. Jutl. 20, 183–191.
Jackson, D.; Mason, C. F.; Long, S. P.; 1985: Macro-invertebrate populations and production on a salt-marsh in east England dominated by *Spartina anglica*. Oecologia 65, 406–411.
Josefson, A. B., 1982: Regulation of population size, growth, and production of a deposit-feeding bivalve: A long-term field study of three deep-water populations off the Swedish west coast. J. Exp. Mar. Biol. Ecol. 59, 125–150.
Kafanov, A. I., 1985: Growth an production of the bivalve mollusc *Macoma balthica* in Nabil' lagoon (Northeastern Sakhalin). Sov. J. Mar. Biol. 11, 313–320.
Kay, D. G.; Brafield, A. E., 1973: The energy relations of the polychaete *Neanthes* (= *Nereis*) *virens* (Sars). J. Anim. Ecol. 42, 673–692.
Kemp, P. F., 1988: Production and life history of a deposit-feeding polychaete in an atypical enviroment. Estuar. Coast. Shelf Sci. 26, 437–446.
Kevrekidis, T.; Lazaridou-Dimitriadou, M., 1988: Relative growth and secondary production of the amphipod *Gammarus aequicauda* (Martynov, 1931) in the Evros Delta (N. Aegean Sea). Cah. Biol. Mar. 29, 483–495.
Kirkegaard, J. B., 1978: Production by polychaetes on the Dogger Bank in the North Sea. Medd. Danm. Fisk. Havunders. 7, 497–509.
Klein, G.; Rachor, E.; Gerlach, S. A., 1975: Dynamics and productivity of two populations of the benthic tube-dwelling Amphipod *Amphelisca brevicornis* (Costa) in Helgoland Bight. Ophelia 14, 139–159.
Kristensen, E., 1984: Life cycle, growth and production in estuarine populations of the polychaetes *Nereis virens* and *N. diversicolor*. Holarct. Ecol. 7, 249–256.
Kuenzler, E. J., 1961: Structure and energy flow of a mussle population in a Georgia salt marsh. Limnol. Oceanogr. 6, 191–204.
Lappalainen, A., 1980: Reproduction, growth and production of *Hydrobia ulvae* (Pennant) in the Northern Baltic Proper. Askö Laboratory, Univ. of Stockholm, unpublished manuscript.
Leveque, C., 1973: Dynamique des peuplements biologie, et estimation de la production des mollusques benthiques du Lac Thead. Cah. O.R.S.T.O.M., Ser. Hydrobiol. 7, 117–147.
Lewandowski, K.; Stanzcykowska, A., 1975: The occurence and role of bivalves of the family Unionidae in Mikolajskie lake. Ecol. Pol. 23, 317–334.
López-Jamar, E.; González, G.; Mejuto, J., 1987: Ecology, growth and production of *Thyasira flexuosa* (Bivalvia, Lucinacea) from Ría de la Coruña, North-west Spain. Ophelia 27, 111–126.
MacDonald, B. A.; Thompson, R. J., 1986: Production, dynamics and energy partitioning in two populations of the giant scallop *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 101, 285–299.
Madsen, P. B.; Jensen, K., 1987: Population dynamics of *Macoma balthica* in the Danish Wadden Sea in an organically enriched area. Ophelia 27, 197–208.
Mathias, J. A., 1971: Energy flow and secondary production of the amphipods *Hyalella azteca* and *Crangonyx richmondensis occidentia lis* in Marion Lake, British Columbia. J. Res. Bd. Canada 28, 711–726.
Melo, C.; Yang, G., 1976: Evaluation de la production d' une population littorale du crabe Hippidae *Emerita analoga* (Stimpson) par integration des parametres de croissance et de mortalité. In: Proc. 10th Eur. Symp. Mar. Biol. Ostend. Wetteren, Belgium: Universa Press, 2, 129–150.
Menzie, C. A., 1980: A note on the Hynes method of estimating secondary production. Limnol. Oceanogr. 25, 700–773.
Miller, R. J.; Mann, K. H., 1973: Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. Mar. Biol. 18, 99–114.
Möller, P.; Rosenberg, R., 1982: Production and abundance of the amphipod *Corophium volutator* on the west coast of Sweden. Neth. J. Sea Res. 16, 127–140.
Moore, H. B.; Lopez, N. N., 1966: The ecology and productivity of *Moira atropes* (Lamarck). Bull. Mar. Sci. 16, 648–667.
Moore, H. B.; Lopez, N. N., 1969: The ecology of *Chione cancellata*. Bull. Mar. Sci., 19, 131–148.
Mukai, H., 1974: Ecological studies on distribution and production of some benthic animals in the coastal waters of Central Inland Sea of Japan. J. Sci. Hiroshima Univ. Ser.B, Div. 1 (Zool), 25, 1–82.

Munch-Petersen, S., 1973: An investigation of a population of the soft clam (*Mya arenaria* L.) in a Danish estuary. Medd. Danm. Fisk. Havunders. N.S. 7 (3), 47–73.

Negus, C. L., 1966: A quantitative study of growth and production of Unionid mussles in the River Thames at Reading. J. Anim. Ecol. 35, 513–532.

Nichols, F. H., 1975: Dynamics and energetics of three deposit-feeding benthic invertebrate populations in Puget Scound, Washington. Ecol. Monogr. 45, 57–82.

Nicolaidou, A., 1983: Life history and productivity of *Pectinaria koreni* Malmgren (Polychaeta). Estuar. Coast. Shelf Sci. 17, 31–43.

O'Connor, B.; Bowmer, G.; McGrath, D.; Raine, R., 1986: Energy flow through an *Amphiura filiformis* (Ophiuroidea: Echinodermata) population in Galway Bay, west coast of Ireland: A preliminary investigation. Ophelia 26, 351–357.

Oyenekan, J. A., 1983: Production and population dynamics of *Capitella capitata*. Arch. Hydrobiol. 98, 115–126.

Oyenekan, J. A., 1987: Population dynamics and secondary production in an estuarine population of *Caulleriella caputesocis* (Polychaeta, Cirratulidae). Mar. Biol. 95, 267–273.

Paine, R. T., 1971: Energy flow in a natural population of the herbivorous gastropod *Teguls funebralis*. Limnol. Oceanogr. 16, 86–98.

Peer, D. C., 1970: Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperboreia*. J. Fish. Res. Bd. Canada 27, 2143–2153.

Penzias, L. P., 1969: Tellina martinicensis (Mollusca: Bivalvia): Biology and production. Bull. Mar. Sci., 19, 568–579.

Picken, G. B., 1980: The distribution, growth, and reproduction of the Antarctic limpet Nacella (Patinigera) concinna (Strebel, 1908). J Exp. Mar. Biol. Ecol. 42, 71–85.

Pollack, H., 1979: Populationsdynamik, Produktivität und Energiehaushalt des Wattwurms *Arenicola marina* (Annelida, Polychaeta). Helgol. Wiss. Meeresunters. 32, 313–358.

Potter, D. W. B.; Learner, M. A., 1974: A study of the benthic macro-invertebrates of a shallow eutrophic reservoir in South Wales with emphasis on the Chironomidae (Diptera); their lifehistories and production. Arch. Hydrobiol. 74, 189–226.

Price, R.; Warwick, R. M., 1980: Temporal variations in annual production and biomass in estuarine populations of two polychaetes, *Nephtys hombergi* and *Ampharete acutifrons*. J. Mar. Biol. Ass. U.K. 60, 481–487.

Rachor, E.; Arntz, W. E.; Rumohr, H.; Mantau, K.-H., 1982: Seasonal and long-term population fluctuations in Diastylis rathkei (Crustacea: Cumacea) of Kiel Bay and German Bight. Neth. J. Sea Res. 16, 141–150.

Rachor, E., 1976: Structure, dynamics and productivity of a population of *Nucula nitosa* (Bivalvia, Protobranchiata) in the German Bight. Ber. Dt. Wiss. Komm. Meeresforsch. 24, 296–331.

Rainer, S. F., 1985: Population dynamics and production of the bivalve *Abra alba* and implications for fisheries production. Mar. Biol. 85, 253–262.

Rees, H. L., 1983: Pollution investigations off the north-east coast of England: Community structure, growth and production of benthic macrofauna. Mar. Environ. Res. 9, 61–110.

Richards, S. W.; Riley, G. A., 1967: The benthic epifauna of Long Island Sound. Bull. Bingham Oceanogr. Coll., 19, 89–135.

Richardson, M. G., 1979: The ecology and reproduction of the brooding Antarctic bivalve *Lissarca miliaris*. Br. Antarct. Surv. Bull. 49, 91–115.

Salzwedel, H., 1979: Zur Ökologie von Tellina fabula Gmelin (Bivalvia) in der Deutschen Bucht. Ph.D. thesis, Universtiy of Kiel, F.R.Germany, 182p.

Sanders, H. L., 1956: Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. Bull. Bingham Oceanogr. Coll. 15, 345–414.

Sheader, M., 1977: Production and population dynamics of *Ampelisca tenuicornis* (Amphipoda) with notes on the biology of its parasite *Sphaeronella longipes* (Copepoda). J. Mar. Biol. Ass. U.K. 57, 955–968.

Shafee, M. S.; Conan, G., 1984: Energetic parameters of a population of *Chlamys varia* (Bivalvia: Pectinidae). Mar. Ecol. Prog. Ser. 18, 253–262.

Siegismund, H. R.; 1982: Life cycle and production of *Hydrobia ventrosa* and *H. neglecta* (Mollusca: Prosobranchia). Mar. Ecol. Prog. Ser. 7, 75–82.

Stanczykowska, A., 1976: Biomass and production of *Dreissena polymorpha* (Pall.) in some Masurian lakes. Ecol. Polska 24, 103–112.

Streit, B., 1976: Energy flow in four different populations of *Ancylus fluviatilis* (Gastropoda-Basommatophora). Oecologia 22, 261–273.

Tamai, K., 1985: Production estimation of Spionid polychaete *Paraprinospio sp.* (type B) in Suo-nada, Japan. Bull. Jap. Soc. Sci. Fish. 51, 213–218.

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.

Tudorancea, C.; Florescu, M., 1968: Cu privire la fluxul energetic al populatiei de Unio pictorum din Balta Crapina. Anal. Univ. Bucuresti Ser. Stiin. Naturii 17, 233–243.

Vahl, O., 1981: Energy transformations by the iceland scallop, *Chlamys islandica* (O. F. Müller), from 700N. II. The population energy budget. J. Exp. Mar. Biol. Ecol. 53, 297–303.

Valderhaug, V. A., 1985: Population structure and production of *Lumbrineris fragilis* (Polychaeta: Lumbrineridae) in the Oslofjord (Norway) with a note on metal content of jaws. Mar. Biol. 86, 203–211.

Vázquez, F. C.; Rojas, D. A., 1980: Estimación de la producción secundaria de *Paraprinospio pinnata* (Spionidae, Polychaeta) frente a Bahía de Concepción, Chile. Bol. Inst. Oceanogr. São Paulo 29 (2), 79–82.

Walker, R. L.; Tenore, K. R., 1984: The distribution and production of the hard clam, *Mercenaria mercenaria*, in Wassaw Sound, Georgia. Estuaries 7, 19–27.

Warwick, R. M.; George, C. L., 1980: Annual macrofauna production in an Abra community. In: Collins, M. B.; Banner, F. T.; Tyler, P. A.; Wakefield, S. J.; James, A. E. (Eds): Industrialized embayments and their environmental problems. Oxford: Pergamon, pp. 517–538.

Warwick, R. M., George, C. L.; Davies, J. R., 1978: Annual macro-fauna production in a Venus community. Estuar. Coast. Mar. Sci. 7, 215–241.

Warwick, R. M.; Price, R., 1975: Macrofauna production in an estuarine mud-flat. J. mar. Biol. Ass. U.K. 55, 1–18.

Waters, T. F.; Hokenstrom, J. C., 1980: Annual production and drift of the sream amphipod *Gammarus pseudolimnaeus* in Valley creek, Minnesota. Limnol. Oceanogr. 25, 700–710.

Wildish, D. J.; Peer, D., 1981: Methods for estimating secondary production in marine Amphipoda. Can. J. Fish. Aquat. Sci. 38, 1019–1026.

Winther, U.; Gray, J. S., 1985: The biology of *Mya arenaria* (Bivalvia) in the eutrophic inner Oslofjord. Sarsia 70, 1–9.

Yanling, L., 1984: Annual production of *Branchiura sowerbyi* (Oligochaeta: Tubificidae) in the Donghu lake, Wuhan, China. Chin. J. Oceanol. Limnol. 2, 102–108.

Author's adress: Dr. Thomas Brey, Alfred Wegener Institut für Polar- und Meeresforschung,
Columbusstraße, D-2850 Bremerhaven. FRG