An empirical model for the prediction of secondary production in marine benthic invertebrate populations

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ABSTRACT: An existing marine benthos production model, based on population characteristics, and a freshwater invertebrate production model, based on population characteristics and temperature, were tested for applicability to marine benthos populations from around the world. The freshwater model makes poor predictions of marine secondary production while the marine model makes better predictions but errors are correlated with both water temperature and water depth. A new marine benthos production model is therefore constructed that accounts for world-wide variation in benthos biomass, individual body mass, water temperature and depth. This multivariate analysis shows that secondary production rises with biomass (B) as $\propto B^1$ as others have found and production varies with population maximum body mass (W_m) as $W_m^{-0.25}$ as suggested by allometric theory. The strong effect of temperature indicates that the Q_{10} of secondary production is between 2 and 2.5. The effect of depth is strongly negative, suggesting that food quality may be lower at greater depth but the effect of depth is lessened in cold seas. Residual analyses accounting for the influences of biomass, body mass, temperature and depth suggest that anthropogenically enriched regions of the sea are more productive than oligotrophic waters. Our results suggest that rare, large animals living in the depths of cold seas support the lowest rates of exploitation and are thus at greatest risk of extinction from overexploitation.

KEY WORDS: Allometry · Biomass · Depth · Marine resources · Model · Invertebrates · Production · Renewal · Temperature

INTRODUCTION

The measurement of secondary production has assumed a fundamental role in the quantification of ecosystem dynamics, since production is one of the major pathways of energy flow (Edmondson 1974, Waters 1977). The animal and plant biomass produced per unit time is the most important parameter for estimating the sea's total productivity (Greze 1978). The estimation of secondary production is of basic importance to the rational management of natural resources (Waters 1977, Downing 1984), because it is the primary instrument for the evaluation of the trophic potential of the components of each ecosystem. For example, marine benthic invertebrates represent an important link in the energy flow from primary producers to fish and in the recycling of sedimented organic matter (Crisp 1984). Therefore, an understanding of the factors influencing the production of marine benthic invertebrates is of central importance to the comprehension of the functioning of marine ecosystems.

In spite of the fact that marine invertebrates provide over 3.5 billion kg of food annually worth $10 billion (FAO 1993), previous production research has concentrated primarily on the production of freshwater organisms. Many authors (Allen 1951, Hynes & Coleman 1968, Hamilton 1969) have developed methods for the

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estimation of secondary production that can be applied in marine or freshwater environments. Unfortunately, these methods are expensive and time consuming to apply. A model elucidating global patterns in secondary production that would allow it to be estimated without long and costly study would be of obvious importance to the theory and practice of marine ecology.

Marine researchers have been estimating secondary production of marine environments since the early 1970s (e.g. Buchanan & Warwick 1974, Chambers & Milne 1975, Warwick & Price 1975, Carrasco & Arcos 1980, Josefson 1982, Andersin et al. 1984, Kristensen 1984, Collie 1985, George & Warwick 1985). Unfortunately, few attempts have been made to discern patterns or regularities in these individual estimates of marine invertebrate production. Robertson (1979) first related the production to biomass ratio (P/B) to the lifespan of populations, providing estimates of marine macrobenthos production for populations of known biomass and life-span. This model is difficult to apply, in practice, because field longevity can depend more on mortality due to predation than on absolute maximum life-span. Further, life-span is highly variable in temperate multivoltine species that overwinter as larvae or adults (Banse & Mosher 1980). Therefore, Banse & Mosher (1980) advanced a simpler model relating P/B to adult body mass, which is easier to determine and less variable than longevity. The only other attempt to find patterns in the production of marine invertebrates is that of Brey (1990), who considered 2 fundamental population parameters: mean annual biomass (B) and mean individual body mass (W). Brey found that production varies as: $\log P = -0.4 + 1.007 \log B - 0.27 \log W$.

Environmental parameters such as oxygen concentration, food availability and quality, and temperature may influence growth rates. The first model to consider the possible effects of environment on invertebrate productivity was developed by Plante & Downing (1989) (hereafter referred to as the Plante-Downing model) for lentic freshwater invertebrates. This analysis showed that secondary production is correlated with mean annual biomass, maximum individual body mass (W_m) and annual mean surface water temperature (T_s) as: $\log P = 0.06 + 0.79 \log B - 0.16 \log W_m + 0.05\,T_s$. Morin & Bourassa (1992) and Benke (1993) have developed similar models for stream invertebrates. Freshwater production models thus account for the influence of some environmental variables on secondary production, but marine production models still only account for simple population parameters. It is unknown whether Brey's model can adequately describe the production of organisms from diverse environments, or whether there is a difference between secondary production in marine environments and that predicted by the more complex freshwater models.

There is ample reason to believe that marine benthos production is strongly influenced by environmental factors such as temperature and depth. In general, production should be greatest where temperature is highest, because physiological rates are greater in warm ectotherms (Robinson et al. 1983). Because organic matter decomposes as it sinks (Ferrante & Parker 1977, Urrère & Knauer 1981, Mann 1988), food quality may decrease with increasing depth (Honjo 1980, Pommeroy et al. 1984, Roman & Tenore 1984). Wolff (1977) suggested that differences in food availability to benthic communities may give rise to positive relationships between benthic biomass and surface productivity, and negative relationships between benthic biomass and depth (Spärck 1935, Rowe 1971). Alternatively, species that live at great depth may be well adapted to low food quality (Lopez & Levinton 1987). Depth may influence production beyond the simple physiological effect of temperature, however. Food quality may also change with depth at different rates in warm and cold climates (Honjo & Roman 1978, Hobbie & Cole 1984, Amon & Herndl 1991), therefore depth may have less effect on production in cold seas than in warm ones. Depth may have more impact on secondary production in marine than freshwaters (cf. Plante & Downing 1989) and the effect of depth may vary with water temperature.

The objective of this study was to test the efficacy of the Brey and Plante-Downing models for the prediction of marine invertebrate production. Because these 2 models inaccurately account for variation in the production of marine invertebrates, a new model was sought to account for world-wide variations in the production of this important faunal group.

MATERIALS AND METHODS

Patterns in production of marine benthos populations were investigated using estimates of population secondary production collected from the world literature. We wished to consider the widest possible range of populations, but concerns about data reliability and measurement consistency led us to consider only estimates derived using classical methods such as the increment summation, the removal summation, the Allen curve, the instantaneous growth rate and size-frequency methods (Allen 1951, Hynes & Coleman 1968, Hamilton 1969). Production rates estimated indirectly as the product of general P/B ratios and B, and as functions of respiration, were rejected a priori.

The annual production, the average annual biomass and the maximum individual body mass were deter-

mined for each population. For those populations for which several years of sampling were available, annual means were extracted for each year. Estimates calculated on a period less than 12 mo or for which some cohorts were excluded from consideration were not included in our analyses. All the estimates were converted to common units of g dry mass m^{-2} for annual mean biomass and mg dry mass for individual body mass in order to test the Plante-Downing model. Particular care was taken with molluscan masses in order that they be comparable with other organisms' masses. We therefore retained only molluscan biomass, production and individual body mass values which were obtained by dissolving shells with HCl prior to weighing. A conversion factor (Brey et al. 1988) was sometimes used to convert ash-free dry masses (AFDM) to dry masses without shells. The Brey model was created using AFDM, not simple dry masses, so dry mass data were converted to g AFDM m^{-2} using published conversion factors (Waters 1977, Brey et al. 1988), where necessary, to test this model.

The maximum individual body mass (W_m, mg dry mass) was read from size-frequency histograms, from mean length of the largest size class, or from age:body mass relationship using length:weight relationships provided by authors. In 1 case, body mass was determined from data on a close congener.

The annual mean bottom (T_b) and surface (T_s) water temperatures (°C) were either obtained from the authors of specific production studies or were calculated from published, site-specific temporal trends in water temperature. In 27% of the cases, T_s was taken from an Atlas of World Temperature (U.S. Navy 1955). Although these data were collected several years ago, average annual ocean temperatures are time-stable (Tait 1981) and have changed little over this century (Bethoux et al. 1990). Daily and annual variations in temperature are known to influence the physiological demands on benthic organisms (Kinne 1970, Aarset & Aunas 1990), but temperature variation could not be considered because of the rarity of such detailed, site-specific information. Depth (Z) was expressed in meters, assigning a value of 0 m to all intertidal sampling stations.

The adequacy of existing production models (Plante & Downing 1989, Brey 1990) was examined by testing the hypothesis that the relationship between observed and predicted points is 1:1 (t-test). Statistical lack of fit attributable to environmental conditions was determined by examining the relationship between the residuals of the predicted

values using the Brey (1990) and Plante & Downing (1989) models and the ambient T_s, T_b and Z. The LOWESS procedure, an unbiased estimator of non-linear trends (Cleveland 1979), was used to assess the form of these relationships.

Stepwise, least-squares multiple regression was used to explore the relationship between P and B, W_m, T_b, T_s and depth [$\log(Z+1)$]. All variables except temperature (Plante & Downing 1989) were transformed to their logarithms to linearize responses and reduce heteroscedasticity. Depth was transformed to $\log(Z+1)$ because many intertidal populations ($Z = 0$ m) were included in the data set. The interaction term ($T_b Z$) was used to assess whether temperature effects were constant with depth. Only variables with partial effects significant at the $p < 0.001$ level were retained, and insignificant variables were eliminated using forward selection (Hocking 1976). Tukey's Studentized range test was used to compare the estimated production for different taxonomic groups, zones and environments.

RESULTS

The data collected include 125 populations of marine benthic invertebrates, drawn from 34 different sites, covering 16 amphipod species, 17 bivalves, 1 harpacticoid copepod, 3 decapods, 3 echinoderms, 3 gastropods, 3 isopods, 1 leptostrac and 13 polychaetes. Data were collected from a broad range of geographical regions (Fig. 1). Body mass varied from as little as 10 g dry mass in *Canuella perplexa* in the Scadovari lagoon, Italy (Ceccherelli & Mistri 1991) to 62 g in *Leptogorgia hebes* in the soft bottom out of Mobile Bay, Alabama, USA (Mitchell et al. 1992).
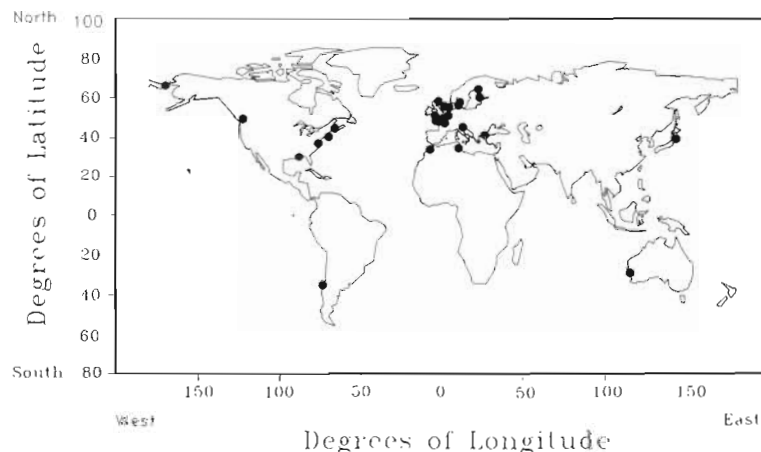

Fig. 1. Map showing sampling sites for which reliable data were found on the secondary production of marine benthic invertebrates
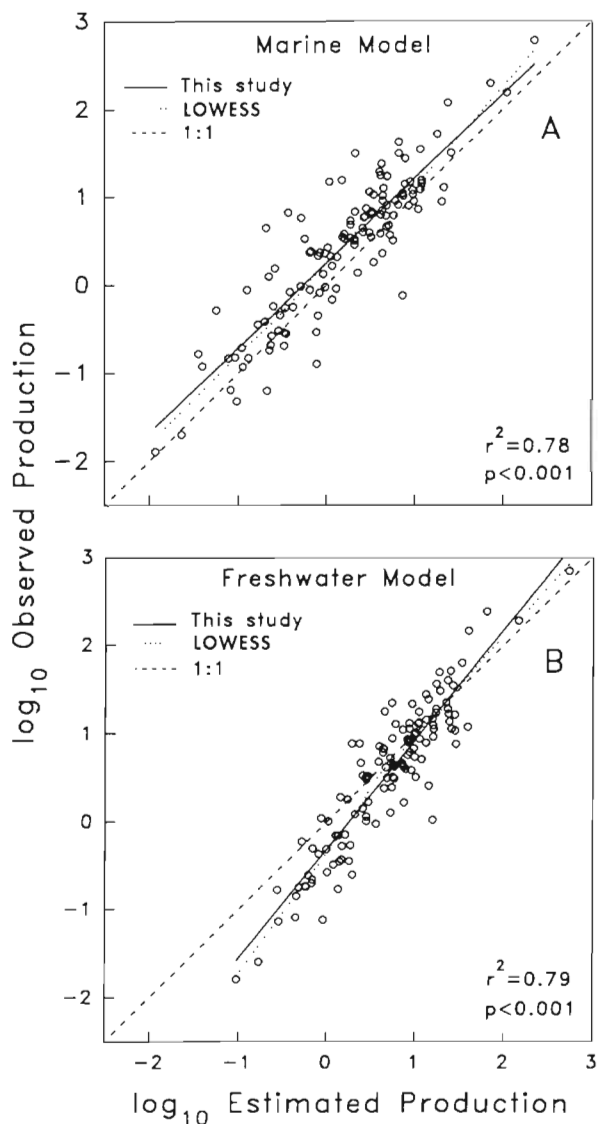
Fig. 2. Relationship between the observed production in 125 populations of benthic invertebrates and the production predicted using (A) the Brey (1990) marine model based on estimates of biomass and individual body mass, and (B) the Plante & Downing (1989) freshwater invertebrate model, based on estimates of biomass, individual body mass, and water surface temperature. LOWESS trends are an unbiased, model-free method of finding the trend in bivariate data (Cleveland 1979)

Standing biomass varied from 3.8 mg dry mass m^{-2} in *Ampelisca sarsi* in the Bay of Morlaix, France (Dauvin 1989) to >800 g m^{-2} for *Perna picta* in the lower intertidal zone of the Moroccan Atlantic coast (Shafee 1992). Depth was near 0 m in very shallow intertidal populations to 300 m for a population of *Abra nitida* in the Skagerrak of Sweden (Josefson 1982). Average temperature was very low for several populations

studied at the bottom of the Baltic Sea (T_b = −0.5 °C, T_s = 6.1 °C; Highsmith & Coyle 1991), and very high in a coastal sampling station off the coast of Florida, USA (T_b = T_s = 22.6 °C; Mitchell et al. 1991). The biomass turnover rate or P/B varied from as little as 0.17 to as much as 23. The full data set and list of sources is available on request from the authors.

The marine production model of Brey (1990) fits the data well while the freshwater model of Plante & Downing (1989) underestimates marine production. The Brey model fits the data with no systematic lack of fit (Fig. 2A) The slope of the relationship between $\log_{10}P$ predicted using Brey's model and the $\log_{10}P$ observed in the field was not significantly different from 1 (p < 0.05). The LOWESS curve shows that the slope is closest to 1 for highest production values. The freshwater model of Plante & Downing (1989) fits the marine data less well. The slope of the relationship between predicted $\log_{10}P$ and observed production in marine ecosystems is significantly different from 1 (Fig. 2B), indicating that the production of low productivity marine populations is overestimated by the freshwater model, while the productivity of highly productive populations is underestimated. The LOWESS analysis shows that the error is proportionally greatest for populations with low production.

Although Brey's marine production model correctly estimates the influence of biomass and body mass, the errors are large and are systematically correlated with environmental conditions. Analysis of the residuals of this model shows clear covariation with both temperature and depth (Fig. 3). The Brey model makes errors of >10-fold for extremely warm or cold seas or for very shallow or deep sites (Fig. 3). This residual analysis demonstrates that accurate models of secondary production must account for variations in environmental conditions.

Stepwise multiple regression analysis quantifies this strong dependence of P on B, W_m, T_s, and Z for marine benthic invertebrates:

$$\log P = 0.24 + 0.96 \log B - 0.21 \log W_m + 0.03\, T_s - 0.16 \log (Z+1) \qquad (1)$$

The variables are listed in decreasing order of their partial significance and the fitted equation (n = 125; R^2 = 0.86; F = 196; p < 0.0001) explains 86% of observed variability (Fig. 4). For simplicity of application, this and the Plante-Downing model use surface temperature as an index of the temperature experienced by the invertebrates. The use of annual mean temperature does not account for variance in production associated with seasonal or daily variations, but allows the exploration of an important relationship between biological processes and environmental conditions (Benke 1993). The bottom temperature is a more realistic mea-
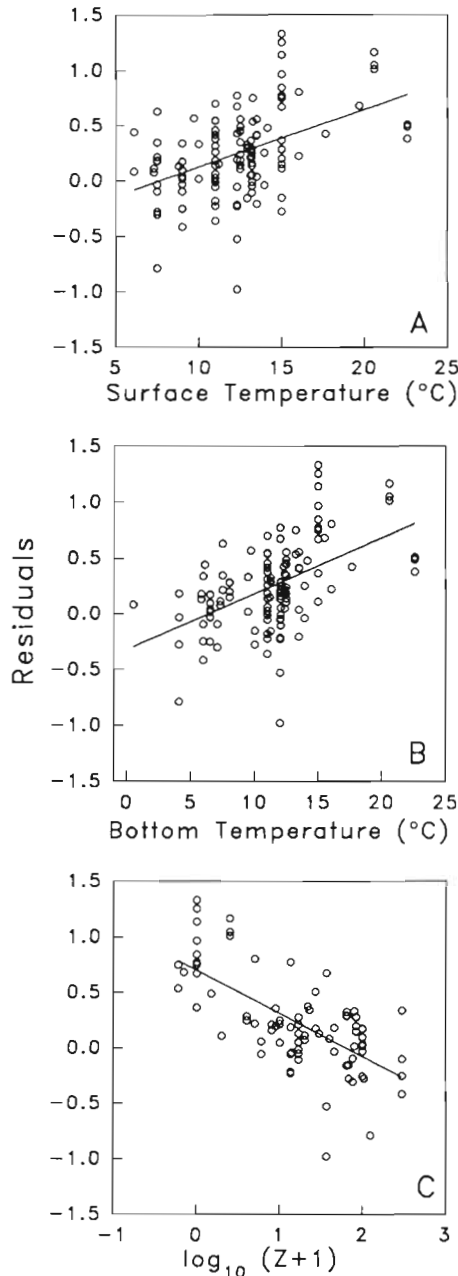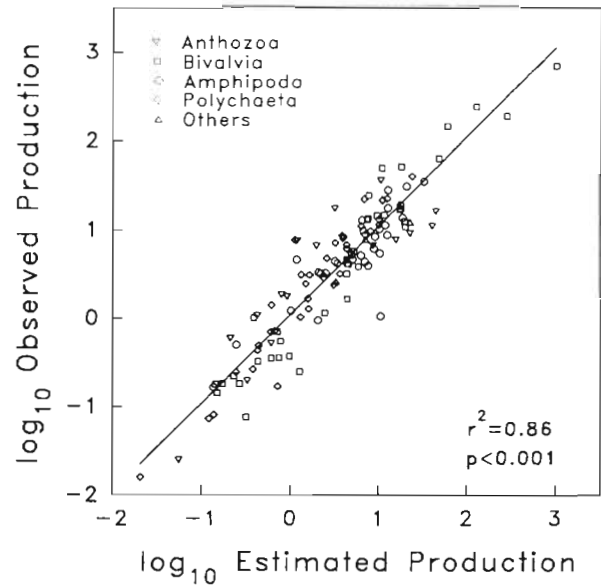
Fig. 4. Relationship between the observed production in 125 populations of benthic invertebrates and the production predicted by Eq. (2)

$$\log P = 0.18 + 0.97 \log B - 0.22 \log W_{m} + 0.04\ T_{b} \\ - 0.014\ Tb \log (Z+1) \qquad (2)$$

(n = 123; R^2 = 0.86; F = 194; p < 0.0001), where all variables are listed in decreasing order of their partial significance (all have p < 0.001).

Analysis of covariance showed that the production of benthic populations in different types of environments differed significantly (p < 0.05). Residual analysis of Eqs. (1 & 2) shows that there was no significant difference between the production of intertidal and soft-bottom populations, but there was a significant difference (p < 0.05) between production rates of benthic populations found in shallow seagrass beds and those living in intertidal or soft-bottom environments (Table 1). The Tukey test reveals that there was no significant (p < 0.05) difference in the production of estuarine and

Fig. 3. Relationships between the residuals of the Brey (1990) model of marine invertebrate secondary production (Fig. 2A) and (A) the sea-surface temperature, (B) the water temperature at the bottom where the benthic organisms were living, and (C) the depth (Z; in m) of the water at each study site. Solid lines: least-squares linear relationships between the 2 variables

Table 1. Fit to the trend in Eq. (2) of populations living on different substrata. Fit is measured by the residuals from Eq. (2), considering the effects of biomass, body mass, bottom temperature and depth. n: number of populations; SD: standard deviation of the mean residual. The vertical line indicates no significant difference (p < 0.05) between the residuals of Eq. (2) for the bracketed categories

sure of the average temperature climate inhabited by populations, and is therefore much simpler to interpret than the surface temperature (see 'Discussion' in Plante & Downing 1989). For the sake of biological interpretability, we also fit a multivariate equation including T_b and its interaction with depth:

Substratum	Mean residual	n	SD
Intertidal	−0.067	36	0.264
Soft bottom	−0.024	74	0.072
Seagrass	0.347	11	0.132

Table 2. Fit to the trend in Eq. (2) of populations living in estuaries and open seas. Other: includes some peculiar environments such as hypersaline lagoons and fjords. Fit is measured by the residual from Eq. (2), considering the effects of biomass, body mass, bottom temperature and depth. n: number of populations; SD: standard deviation of the mean residual. The vertical line indicates no significant difference (p < 0.05) between the residuals of Eq. (2) for the bracketed categories

Substratum	Mean residual	n	SD
Estuarine	−0.015	62	0.349
Sea	−0.008	57	0.220
Other	0.497	6	0.080

Table 3. Fit to the trend in Eq. (2) of populations of different taxa. Fit is measured by the residual from Eq. (2), considering the effects of biomass, body mass, bottom temperature and depth. n: number of populations; SD: standard deviation of the mean residual; p: t-test probability associated with the null hypothesis that the mean residuals of each group do not differ from zero; ns: p > 0.05

Taxon	Mean residual	n	SD	p
Gastropoda	−0.408	6	0.110	<0.05
Anthozoa	−0.213	3	0.159	ns
Harpacticoidea	−0.158	1	−	−
Amphipoda	0.092	37	0.249	ns
Bivalvia	−0.059	40	0.291	ns
Polychaeta	−0.044	30	0.275	ns
Echinodermata	0.189	2	0.423	ns
Decapoda	0.452	3	0.261	ns
Leptostraca	0.458	1	−	--
Isopoda	0.453	3	0.275	ns

marine benthic species, once differences in biomass, body mass, temperature and depth had been accounted for (Table 2). Further, of the 10 taxonomic groups which were present in the data set, only a few populations of gastropods departed significantly from the general trend described by Eqs. (1 & 2) (Table 3).

DISCUSSION

Biomass is the most important variable explaining world-wide variation in marine secondary production. It alone is responsible for 77 % of the explained variation in Eq. (1). The coefficient associated with biomass is 0.96, which is not significantly different from 1, indicating that there is no demonstrable density-dependence of biomass turnover rate in this fauna. The same result was indicated by the analyses of Banse & Mosher (1980), Brey (1990) and Morin & Bourassa (1992). The finding of a coefficient close to unity suggests that the P/B ratio is constant with B for popula-

tions of equivalent body mass under similar environmental conditions.

Body mass is the second most important variable for determining marine secondary production. Our analysis confirms that the production of marine invertebrates is negatively related to body mass as $\propto W_m^{-0.21}$, where B is statistically held constant. This exponent is not significantly different (p < 0.05) from −0.25, the value suggested by general allometric theory (Peters 1983). The observed value also agrees with the exponent of −0.27 found by Brey (1990), and is statistically indistinguishable from the exponent found in the Plante-Downing freshwater model ($W_m^{-0.16}$). Our result, however, contrasts with Banse & Mosher's (1980) finding that production varies as $W_m^{-0.37}$. The differences among the exponents may arise from statistical fits that are influenced by variables that are unaccounted for in other models. For example, if we were to fit the bivariate relationship between production and body mass without considering W_m, T or Z, we would find an exponent of −0.16. Perhaps these apparent differences among exponents of production models are due less to real differences among the data sets than to statistical artifacts due to unexplained variation.

P/B can be considered an indicator of the maximum limit of sustainable exploitation of populations. Because P/B declines with W_m (Fig. 5), small species can be exploited at greater rates than large ones, since their renewal rates are high and they can replace their
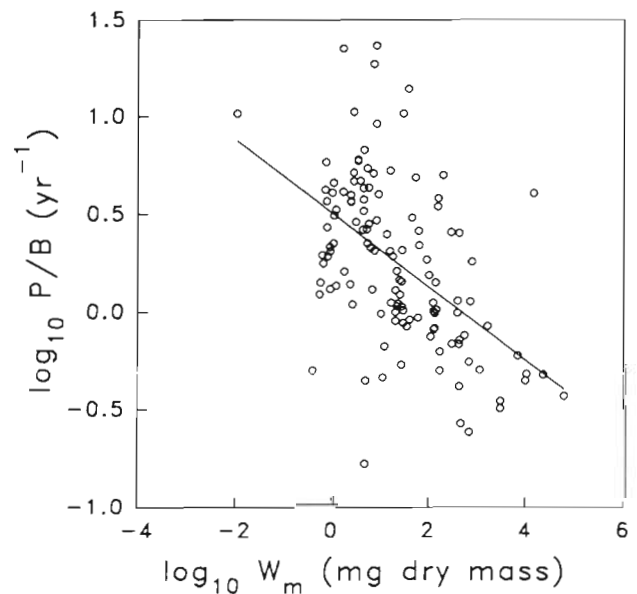

Fig. 5. Relationship between the biomass turnover rate (P/B) and the average body mass of the individuals in the largest size class of each population. Solid line: the least-squares linear relationship between these 2 variables [$\log_{10}(P/B) = 0.504 - 0.188 \log_{10} W_m$, $r^2 = 0.27$, n = 126, p < 0.001]

biomass in a short time. This characteristic also allows small species to be more resilient to environmental perturbations and consequently to be more successful at counterbalancing overexploitation. On the other hand, larger species of invertebrates such as some species of bivalves, decapods or echinoderms show a lower P/B, which indicates less capacity to survive overexploitation. This consideration is of obvious importance when the species considered represents a source of human food. Further, this analysis predicts that marine biodiversity will first be lost in the largest organisms when communities are perturbed or environmental conditions degraded. This result agrees with the general concept that severe reduction in numbers constitutes a greater problem for larger bodied vertebrates due to their lower intrinsic population growth rates (Belovsky 1987, Godman 1987, Pimm et al 1988), which leads them to be extremely vulnerable to extinction (Fenchel 1993) and to rebound slowly after a catastrophic decline (Peters 1983).

Ours is the first study to seek general patterns in the combined effects of biological and environmental characteristics on the secondary production of a broad variety of populations of marine invertebrates. Since production is the result of metabolic processes, it is not surprising that temperature has an influence on it. Ecologists have known for many years that temperature influences biological activities (Downing 1984). For example, increased temperature can decrease egg development time, and increase voltinism, rates of population growth and feeding The aggregate effect of these factors is to augment growth and reproduction, leading to increased production. The effect of temperature on production that we found is not significantly different from that found in analyses of freshwater invertebrate production. Neither of the coefficients in Eqs. (1 & 2) (0.03, 0.04) are, in fact, significantly different from 0.05 (Plante & Downing 1989), showing that the temperature dependences of production of marine and freshwater organisms are substantially similar. The Q_{10} indicated by the fitted coefficients in Eqs. (1 & 2) are between 2 and 2.5, very close to the standard Q_{10} found for many physiological rates (Hardy 1973). This finding suggests that the influence of temperature on secondary production may be the result of increased physiological rates in warmer waters.

The negative coefficient associated with depth in Eq. (1) indicates that production is highest near the sea surface and decreases rapidly in deeper waters. Since Eq. (2) adjusts statistically for the influence of bottom temperature, the effect of depth on secondary production is not simply due to lower temperatures at great depth. In fact, Eqs. (1 & 2) show that a given biomass of a population of a given body mass, living at any given
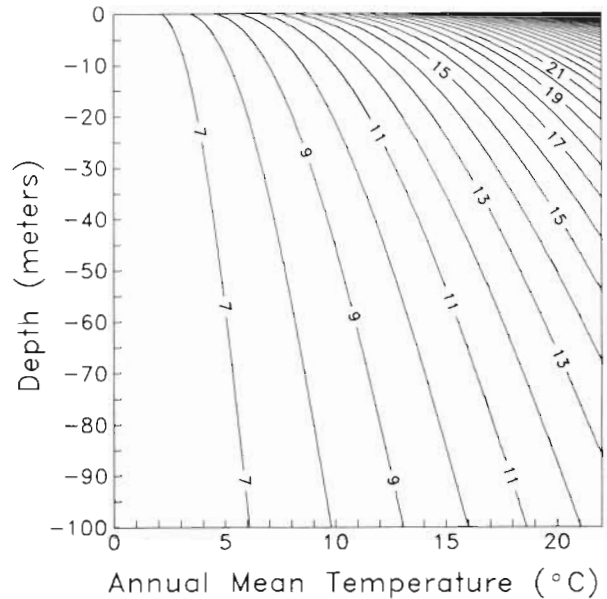

Fig. 6. Contour plot showing the general relationship between water depth, bottom temperature and secondary production found by multiple regression and shown in Eq. (2). Predictions are for a population of average biomass ($B = 19$ g m^{-2}), and maximum individual body mass ($W_m = 1162$ mg dry mass), shown over the range of environmental conditions where data coverage was most dense. The extreme upper left and lower right corners are extrapolated

temperature, has significantly lower production if it lives in a deeper habitat. This may be due to the fact that a much greater proportion of primary production reaches the bottom in shallow coastal waters than in deep oceans (Mann 1988). Benthic organisms at deep sites depend primarily on low-quality food such as fecal pellets, crustacean exuviae, organic detritus with a scarce phytoplanktonic component that is degraded during sedimentation (Ferrante & Parker 1977, Urrère & Knauer 1981) and thus decreases in quantity and quality with increased depth (Honjo 1980, Pomeroy et al. 1984, Roman & Tenore 1984). This interpretation is bolstered by the significant interaction term in Eq. (2), which shows that production decreases much more rapidly with increasing depth in warm waters (Fig. 6), where the breakdown of sedimented organic matter would be most rapid.

Likewise, there are apparently differences in the secondary production of different types of marine environments. The data suggest that seagrass beds support higher production than soft bottoms and intertidal zones (Table 1). The average residual in logarithmic form for soft bottoms and intertidal zones is -0.0381 while it is 0.347 for seagrass beds. This suggests that for a given biomass, body mass, temperature and depth, secondary production in seagrass beds is on average $10^{0.385}$ times, or 2.4-fold, that found in other

environments. This conclusion is, however, based on only 11 observations in seagrass beds and, thus, must be interpreted with caution. This agrees with Phil (1986), however, who found secondary production to be greater in vegetated areas than in unvegetated areas of the Swedish west coast, probably due to greater food availability in seagrass beds (Virnstein et al. 1983).

Our analyses predict that biomass-specific production levels for animals of a given body mass decrease systematically from low latitudes through subarctic zones, and decrease, regardless of latitude, from shallow waters to the ocean depths (Fig. 6). The effect of temperature is strongest in shallow waters and becomes progressively weaker as depth increases. Our analyses therefore predict a stronger effect of depth in warm waters at low latitudes and subtropical zones. Biomass-specific production rates appear to be highest in those populations with small individual body mass living in shallow, warm waters, and lowest in populations with large individual body mass living in cold, deep waters. This result leads us to speculate that drastic changes in population biomass levels could endanger the viability of species and populations with high individual body mass living in deep, subarctic areas. Average mass-specific renewal rates (P/B) vary from >10 in small animals living in warm, shallow environments (biomass renewed 10 times annually), to <0.3 in large resource organisms like Arctica islandica living in cold, deep environments. Fishing mortality should therefore be carefully adjusted according to renewal rates in order to avoid resource depletion and extinction. Large species living in deep, cold environments therefore appear to be the most vulnerable species, because they are the slowest in compensating for perturbations like the overexploitation of edible species, the accidental overexploitation of non-commercial species taken as bycatch, or increased mortality due to environmental pollution (Upton 1992).

Empirical analyses such as Eqs. (1 & 2) reveal the form of global trends in secondary production, while analysis of the characteristics of populations that fail to fit these trends may suggest other important factors influencing production as well as avenues for future research. For example, analysis of the residuals of Eq. (2) shows that the production of populations from Chesapeake Bay, USA, are on average 60% higher than that predicted by Eq. (2). Chesapeake Bay is a highly eutrophic estuary. Further precision may therefore be had in future models by accounting for differences in food availability or ecosystem productivity, factors that can often limit benthic populations (Marsh & Tenore 1990). Unfortunately, this task may be difficult because differences in food availability arise from the interaction of many factors, including community

structure and interspecific competition (Sarvala 1986), which may assume differential importance depending upon trophic level and feeding behaviour. Others (e.g. Robertson 1979) have hypothesized that population structure may also play a role, and that production may be influenced by the numerical dominance of young or senescent individuals. Our analysis underscores the importance of considering both environmental and population characteristics in studies of the secondary production of marine benthic invertebrates.

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