

# Growth Performance and Mortality in Aquatic Macrobenthic Invertebrates

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*Growth performance and mortality are two topics related closely to  
population dynamics of benthic macroinvertebrates. A new measure of  
overall growth performance for benthic invertebrate populations, the index*

$\psi = \log(\text{maximum body mass}/\text{maximum age})$  is introduced. This index makes growth of populations and species comparable and is likely to be a species-specific feature. Differences in the index  $\psi$  among taxa and living modes as well as the relationship between growth performance and exploitation by man are analysed and discussed. Section 4 on mortality analyses the relationships between mortality and productivity in benthic invertebrate populations. An empirical model to estimate the natural mortality rate  $M$  of benthic populations from maximum body mass, maximum age and water temperature is constructed.

## 1. INTRODUCTION

Populations are the basic units of ecosystem trophic structure. Hence we have to learn about properties and dynamics of populations in order to understand the organization and dynamics of the whole system. Regarding ecosystem trophic flows, population consumption and production are the most significant parameters, which are in turn determined by processes such as recruitment, individual growth and population mortality.

A huge amount of information on macrobenthic population dynamics is scattered through the literature, each bit referring to a certain species at a certain location during a certain period of time. Many attempts have been made to collate this information in order to analyse the relationships among various population parameters (e.g. productivity and individual age) or between population parameters and other factors (e.g. growth and temperature). These analyses aimed either to identify principles underlying the observed relationships or to establish empirical relationships which might serve as substitutes for more extensive methods.

Here, I will follow the second procedure and use empirical data on benthic invertebrate populations to deal with two questions: how to estimate growth performance and how to estimate natural mortality rate from easy-to-obtain biotic and abiotic parameters.

## 2. METHODS

### 2.1. Data Sources

This review is based on a large-scale collection of data on the population dynamics of aquatic macrobenthic invertebrates. Data on the growth, mortality and production of 963 populations referring to 476 different

invertebrate species were extracted from 403 publications (see the references — population dynamics, (D)).

The data extracted were mostly from international journals, but a significant part had to be taken from unreferenced literature such as local journals, unpublished reports and Ph.D. theses (see the references — population dynamics, (D)).

### 2.2. Data Evaluation

Three sets of data on population dynamics were collected: (i) data on growth, i.e. maximum age, maximum body mass and growth function type and parameters; (ii) data on mortality, i.e. parameters of mortality function; and (iii) data on productivity, i.e. biomass, production,  $P/B$  ratio.

In many cases, parameters not provided directly in the publication, e.g. maximum body mass or growth function parameters, had to be derived indirectly from information given in figures and tables. All units were transformed to the following standards: the unit of time is the year, the unit of area is the inverse square metre, the unit of size is the millimetre, the unit of mass is the kilojoule and the unit of temperature is the kelvin. Mass units were converted to kilojoules using conversion factors provided in the literature (see the references — conversion factors, (C)) when necessary.

Additional parameters collected were taxonomic information, life mode, water depth and water temperature. Average annual water temperature at each location was inferred from various publications (see the references — temperature, (T)) when not provided by the original author. Obviously not all parameters mentioned here were available for all the populations included. All information is summarized in one data file (Microsoft Excel format), which is available on request from the author.

Note that data sources (D) and evaluation data (C and T) are not especially quoted in the text, where general (G) references are quoted.

### 2.3. Data Distribution

Table 1 indicates that data on growth ( $N = 887$ ) and productivity ( $N = 963$ ) are much more frequent than data on mortality ( $N = 103$ ). Mollusca and Insecta larvae have the highest share (about 30% each) in the data on growth as well as on productivity, whereas about two-thirds of the mortality data refer to molluscs.

The distribution of the data with respect to geographical latitude (77.5°S to 74.5°N, Figure 1a) and water depth (0–2900 m, Figure 1b)

Table 1 Distribution of benthic invertebrate data sets among taxa and topics.

Taxon	Species	Genera	Families/ orders	Data sets		
				Growth	Mortality	Productivity
Mollusca	151	94	39	337	65	325
Polychaeta	45	30	17	97	8	98
Crustacea	57	37	16	123	9	156
Echinodermata	35	26	6	38	18	51
Insecta larvae	175	111	10	273	3	309
Others	13	10	5	19	0	24
Sum	476	308	93	887	103	963

Data drawn from the bibliography – population dynamics.

indicates that the majority of the data refer to shallow waters (0–10 m water depth) in northern boreal regions (30°N to 60°N). Accordingly, the bulk of the data represent moderate temperature regimes with average annual temperatures between 280 and 290 K, although several populations living under “extreme” temperature conditions (minimum 271.2 K, maximum 303 K) are included, too.

From a purely statistical point of view, this uneven distribution of data with respect to taxon and abiotic parameters may limit the validity of any general conclusions drawn here. They reflect, however, the historical development as well as the actual distribution of research activities in benthic population dynamics, and there is no possibility of changing this situation in the foreseeable future. Hence we have to work with the data available.

#### 2.4. Statistical Analysis

Fitting of non-linear functions, e.g. growth functions, was carried out by the SIMPLEX algorithm (Nelder and Mead, 1965). One-way and multiple ANOVA was applied according to Sachs (1978) and Sokal and Rohlf (1981), and the Games-Howell test was used for *post hoc* comparisons of means. Multiple linear regressions were used according to Draper and Smith (1981).

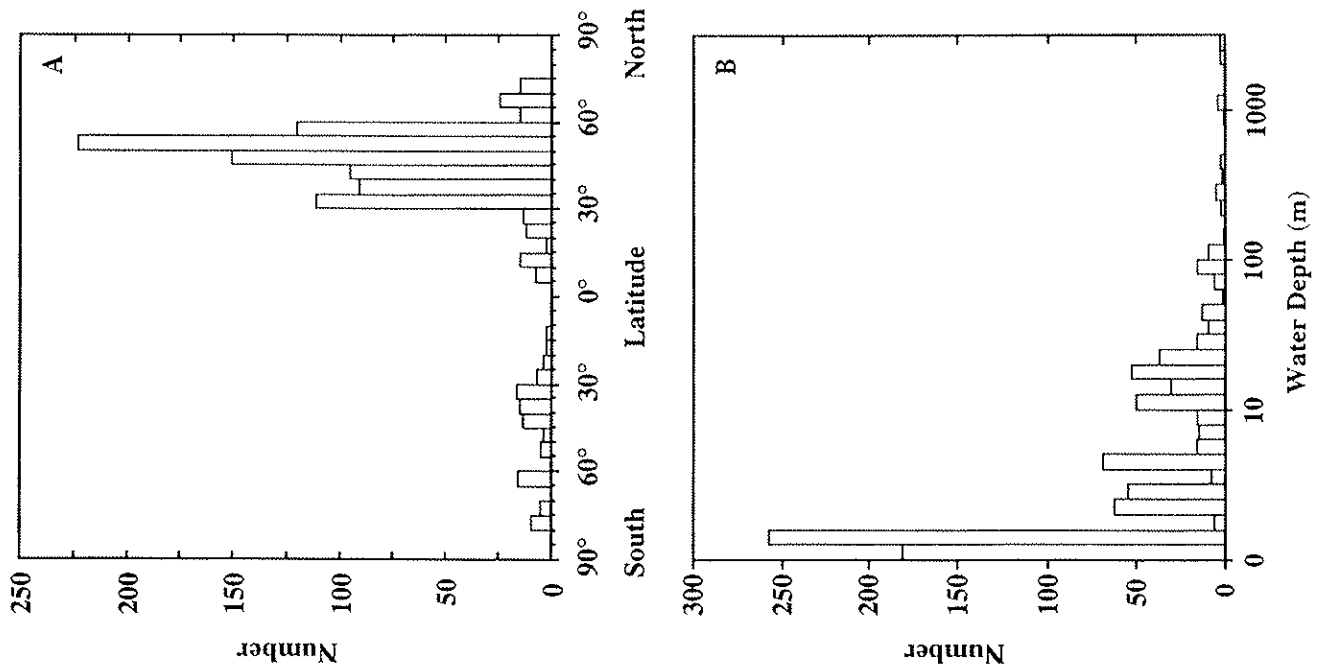


Figure 1 Distribution of the 963 data sets on benthic population dynamics with respect to (a) geographical latitude and (b) water depth.

### 3. GROWTH PERFORMANCE OF BENTHIC INVERTEBRATES

Growth of the individual is one of the main characteristics of most multicellular organisms and hence an important parameter in population dynamics. Environmental conditions, e.g. food availability, temperature or other physiological stress, can affect growth directly (see Taylor, 1960; Pauly, 1980; Brey and Clarke, 1993), and, conversely, growth will adjust to environmental conditions within species-specific limits. These interactions are likely to happen on evolutionary time scales, too. Substantial evidence that recent species are separated by differences in growth (e.g. DeAngelis *et al.*, 1985; Reiss, 1991; Pauly *et al.*, 1994) supports the idea of individual growth playing a significant role in the evolution of species. Systematic investigations of this topic, however, are lacking, especially concerning benthic invertebrates.

This section aims to develop tools which will enable us to compare growth between different taxa based on the concept of "overall growth performance" introduced for fish by Pauly (1979). Two questions are posed: (1) How can we measure growth performance of benthic invertebrates? (2) Is growth performance a species-specific feature?

#### 3.1. Growth and Growth Models

Individual growth is defined as the change of body mass  $M$  with time  $t$ . Growth can be positive as well as negative, e.g. during periods of starvation. Body mass  $M$ , body size  $S$  and body surface  $SU$  are related by  $M = a_1 S^b$  and  $SU = a_2 S^c$  ( $a$  and  $b$  are constants characteristic for a population) and hence growth can be described by changes in  $S$  and  $SU$ , too. To keep things simple, I will focus on positive growth in body mass  $M$ .

Growth of most benthic invertebrates follows the same principles as in other animals:

- There are species-specific limits of body mass  $M$ .
- Growth in  $M$  is a non-linear process. It accelerates during early phases of life, but will finally slow down with increasing age.

This general growth pattern may be explained by the different proportion of catabolism (breakdown of tissues) and anabolism (synthesis of tissues) to body mass. It seems that energy requirement increases at a higher rate with body mass than does energy intake, thus limiting maximum attainable body mass (see Ursin, 1967, 1979; Reiss, 1991). For the description of lifetime growth many different models of the type

$$M_t = M_\infty f(t) \quad (1)$$

where  $M_\infty$  is the asymptotic limits of body mass  $M$  and  $t$  is time, have been developed, which generally produce negative exponential or sigmoid growth patterns (e.g. Gompertz, 1825; von Bertalanffy, 1938; Richards, 1959; Pauly, 1979; Schnute, 1981). All of these models show excellent empirical capacities, but the von Bertalanffy growth function (VBGF) is the one most commonly used in marine ecology and fishery biology:

- Specialized VBGF (isometric growth):

$$M_t = M_\infty [1 - \exp\{-K(t - t_0)\}]^3 \quad (2a)$$

- generalized VBGF (allometric growth):

$$M_t = M_\infty [1 - \exp\{-K(t - t_0)\}]^p \quad (2b)$$

where  $M_\infty$  is the asymptotic limits of body mass  $M$ ,  $K$  and  $D$  are constants defining the velocity of approaching  $M_\infty$  and  $t_0$  is the theoretical age at which  $M_t = 0$ .

#### 3.2. Definition and Measures of Growth Performance

Individual growth is a non-linear process which has to be described by multiparameter non-linear models such as the VBGF. Therefore, it is difficult to compare growth among different organisms or taxa in a definite and statistically proper way. Several attempts have been made to solve this problem (e.g. the index  $\omega$  of Gallucci and Quinn, 1979), but Pauly (1979) was the first who developed a consistent concept of "overall growth performance" (OGP) to make individual growth comparable. OGP measures how "well" an organism grows, in a similar way to the use of acceleration as a measure of the performance of a car.

Pauly (1979) and Munro and Pauly (1983) introduced several closely related indices of OGP which are derived from the specialized VBGF to characterize growth of fish. The index  $P$  is proportional to the maximum rate of body mass increase during the lifetime, i.e. the mass increase at the inflexion point of the VBGF:

$$\begin{aligned} M_t &= M_\infty [1 - \exp\{-K(t - t_0)\}]^3 & (3) \\ \Rightarrow (\delta M / \delta t)_{\text{Max}} &= \frac{4}{3} K M_\infty \\ &= \frac{4}{3} \times 10^p \\ \Rightarrow P &= \log(K M_\infty) \end{aligned}$$

where  $K$  and  $M_\infty$  are parameters of the VBGF and  $(\delta M / \delta t)_{\text{Max}}$  is the instantaneous increase in body mass at inflexion point of VBGF.

Moreau *et al.* (1986) demonstrated that the index  $P$  and the closely related index  $\varphi$  developed by the same authors are suitable for statistical

comparisons of OGP. The index  $\omega$  of Gallucci and Quinn (1979) showed very poor statistical properties, making comparisons of OGP based on  $\omega$  (e.g. Appeldoorn, 1981; Duineveld and Jenness, 1984; Beukema and Meehan, 1985) less reliable.

### 3.3. Extended Measures of Growth Performance

Since the VBGF is a suitable model for the description of benthic invertebrate growth, OGP of these organisms can be characterized and compared by indices such as  $P$ . This concept could easily be extended to other growth models, because all common models describing growth in body mass have one (and only one) inflexion point. Therefore, the maximum rate of body mass increase  $(\delta M/\delta t)_{\text{Max}}$  could be used as a measure of OGP. For large-scale comparisons of OGP, however, a more general measure based on easy-to-obtain parameters is required, because analysis of growth in benthic invertebrates is a time-consuming and expensive approach.

In physics, performance is defined as labour/time. Labour is an equivalent of energy, and energy is an equivalent of mass. If we apply this concept to the ecological problem of OGP, then it is obvious that growth performance could be defined by the relationship between the maximum body mass observed,  $M_{\text{Max}}$  (kJ), and the time required to build up this body mass, i.e. the maximum age observed,  $A_{\text{Max}}$  (years). This approach would be valid for individuals as well as for populations:

$$\text{index of overall growth performance OGP} = f(M_{\text{Max}}, A_{\text{Max}}) \quad (4)$$

where  $M_{\text{Max}}$  is the maximum body mass and  $A_{\text{Max}}$  is the maximum age.  $M_{\text{Max}}$  and  $A_{\text{Max}}$  can be interpreted as being more or less equivalent to  $M_{\infty}$  and  $K$  of the VBGF, and hence an index  $\psi$  can be formulated accordingly from  $P = \log(KM_{\infty})$

$$\psi = \log(M_{\text{Max}}/A_{\text{Max}}) \quad (5)$$

The empirical comparison of  $\psi$  with  $P$  based on the data sets available indicates linear and highly significant relationships (Figure 2). Therefore,  $\psi$  is equivalent to those indices developed and tested for fish populations and can be used to measure growth performance in benthic invertebrates.

### 3.4. Is Growth Performance Specific for Species?

Many investigations show that individual growth of benthic invertebrate species can be extremely variable (e.g. Weymouth *et al.*, 1931; Taylor, 1960;

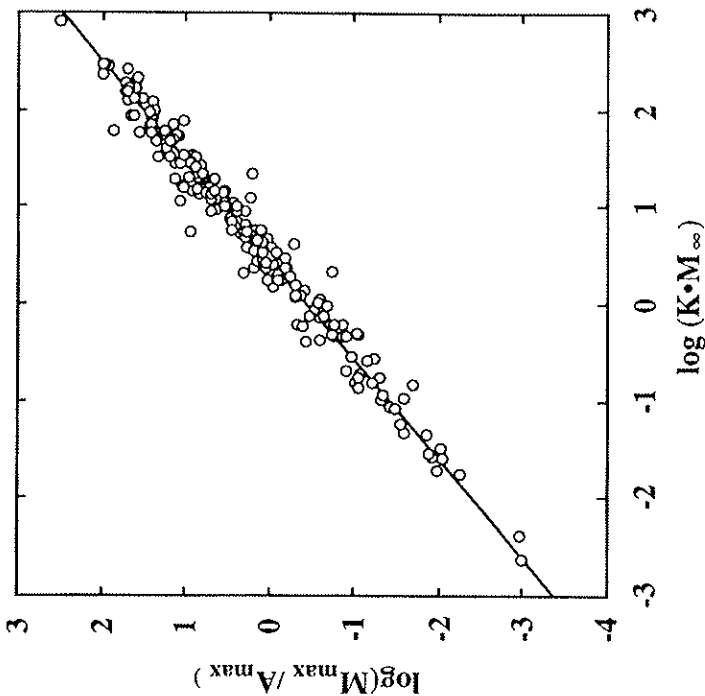


Figure 2 Index of growth performance  $\psi$ . Empirical relation between  $P = \log(KM_{\infty})$  and  $\psi = \log(M_{\text{Max}}/A_{\text{Max}})$  in benthic invertebrate populations.  $\log(M_{\text{Max}}/A_{\text{Max}}) = -0.452 + 0.980 \log(KM_{\infty})$ .  $N = 216$ ,  $r = 0.986$  and  $P < 0.001$ .

Gilbert, 1973; Appeldoorn, 1981; Beukema and Meehan, 1985). Differences in growth parameter values (e.g.  $K$  and  $M_{\infty}$  of the VBGF) or in maximum age  $A_{\text{Max}}$  and maximum body mass  $M_{\text{Max}}$  between populations of one species may easily exceed several hundred per cent. This variability is mainly caused by environmental factors such as temperature or food supply (e.g. Taylor, 1960; Ansell, 1968; Gilbert, 1973; Appeldoorn, 1983).

The data of Pauly (1979), Munro and Pauly (1983), Moreau *et al.* (1986) and — with restrictions — Vakily (1992) indicate that closely related species differ in overall growth performance (OGP, measured by the parameter  $P$ ) despite the high intraspecific variability in growth parameter values. Obviously the intraspecific variability of OGP is lower than the variability of single parameters of the growth model. This is a result of the antagonistic nature of the two basic parameters of growth models, i.e. the asymptotic limit of body mass (e.g.  $M_{\infty}$  of the VBGF) and the "speed"

parameter (e.g.  $K$  of the VBGF). Within a species there seems to exist a broad band of possible values of  $M_{\infty}$  and  $K$ . Statistically, high values of  $M_{\infty}$  combine with low values of  $K$ , and vice versa. Examples for benthic invertebrates are given by Taylor (1960), Ansell (1968), Gilbert (1973), Appeldoorn (1981) and MacDonald and Thompson (1988). The OGP indices are derived from the product of the two growth parameters, and hence their variability is lower.

If OGP is indeed consistently much less affected by external factors than the asymptotic limit of body mass ( $M_{\infty}$ ) and the "speed" parameter ( $K$ ), it can be interpreted as a species-specific feature and be used for the ecological characterization and separation of species. Moreover, one may ask whether OGP is not only species-specific but a genetically determined feature. In the following I will analyse whether the OGP index  $\psi$  is a species-specific parameter in benthic invertebrates.

As a first step the basic precondition for a species-specific feature, i.e. the intraspecific inverse relationship between  $1/A_{Max}$  and  $M_{Max}$ , has to be verified. The data in Table 2 referring to 24 species or genera indicate that the relationship between  $1/A_{Max}$  and  $M_{Max}$  is inverse in all taxa.

As a second step I analyse whether the OGP index  $\psi$  is species-specific or only a characteristic feature of higher taxonomic levels. The central problem of this investigation is the fact that a species is only the lowest level of the taxonomic hierarchy. If OGP is a species-specific, perhaps genetically fixed feature, then higher taxonomic levels (genus, family, etc.) will affect species OGP too, because taxonomic and evolutionary distance are closely related. Therefore we should expect, on the one hand, closely related species (e.g. from the same genus) to have similar OGPs. On the other hand, the intraspecific variability of OGP should be small enough to separate these species, especially if they are quite similar in many other features or if they live sympatrically (e.g. see Schoener, 1986). It has to be kept in mind, however, that less related species may also show similar or even identical OGPs owing to convergent evolutionary development in the feature of growth. Since we do not know the minimum taxonomic distance for convergence in OGP, the interspecific comparison of OGP data of many species is not sufficient to answer the above question. Many comparisons will show differences, many others, however, will not.

Therefore, a second approach aimed at the variability of OGP is required. If the previous assumptions are correct, the variability of OGP should increase with increasing taxonomic level; for example, variability should be low within a species, higher within the superior genus and higher again within the superior family, etc.

The appropriate statistical approach for this problem would be a nested ANOVA which compares OGP variability within taxa with variability among taxa. Our data, however, were not sufficient to allow for this kind

Table 2 Empirical relation between  $\log(1/A_{Max})$  and  $\log(M_{Max})$  in various benthic invertebrate taxa using linear regression:  $\log(1/A_{Max}) = a + b \log(M_{Max})$ . Species were summarized into genera, when a previous ANCOVA did not detect significant differences.  $N$  is the number of data sets.

Taxon	$N$	$a$	$b$	$r$	$P$
<i>Abra alba</i>	17	-0.388	-0.228	-0.624	0.0074
<i>Abra ovata</i>	6	-1.273	-0.694	-0.715	0.0339
<i>Corbicula</i> spp.	6	-0.232	-0.771	-0.724	0.0724
<i>Haliotis</i> spp.	5	0.843	-0.678	-0.812	0.0947
<i>Lymnaea</i> spp.	5	-0.099	-0.706	-0.876	0.1244
<i>Macoma</i> spp.	20	-0.842	-0.225	-0.457	0.0427
<i>Mytilus edulis</i>	10	-0.249	-0.331	-0.677	0.0316
<i>Nucula</i> spp.	13	-0.974	-0.383	-0.842	0.0003
<i>Spisula</i> spp.	9	-0.099	-0.336	-0.830	0.0057
<i>Venus</i> spp.	5	-0.563	-0.300	-0.948	0.0140
<i>Ampelisca brevicornis</i>	8	-0.461	-0.406	-0.950	0.0008
<i>Corophium volutator</i>	16	-0.383	-0.317	-0.940	0.0001
<i>Corophium</i> spp.*	11	-0.259	-0.233	-0.843	0.0011
<i>Diatylis radiata</i>	8	-0.328	-0.247	-0.767	0.0264
<i>Gammarus</i> spp.	15	-0.599	-0.822	-0.601	0.0179
<i>Ampharete</i> spp.	12	-0.678	-0.658	-0.472	0.1216
<i>Nephtys hombergii</i>	9	-0.358	-0.869	-0.660	0.0530
<i>Strongylocentrotus</i> spp.	4	0.394	-0.725	-0.999	0.0008
<i>Cricotopus</i> spp.	5	-0.764	-0.729	-0.795	0.1079
<i>Polyspatium</i> spp.	9	-2.977	-1.940	-0.574	0.1060
<i>Cheumatopsyche</i> spp.	8	-0.694	-0.590	-0.928	0.0009
<i>Diplectrona</i> spp.	8	-0.348	-0.379	-0.607	0.1105
<i>Hydropsyche</i> spp.	17	-0.098	-0.253	-0.904	0.0001
<i>Parapsyche</i> spp.	7	-0.054	-0.182	-0.776	0.0404
Mean slope			-0.519		

\*Without *C. volutator*.

of test. Therefore two hypotheses had to be tested separately:

1. Random distribution of  $\psi$ :  
 $H_0$  — the  $\psi$  values are distributed randomly and do not depend on taxon;  
 $H_A$  — the  $\psi$  values depend on taxon.
2. Variability of  $\psi$ :  
 $H_0$  — the variability of  $\psi$  within a taxon is independent of the position of this taxon in the taxonomic hierarchy;  
 $H_A$  — the variability of  $\psi$  increases with taxonomic level, i.e. in the direction species  $\rightarrow$  genus  $\rightarrow$  family  $\rightarrow$  order  $\rightarrow$  class.

Table 3 Comparison of overall growth performance  $\psi$  among taxa on various taxonomic levels using five separate one-way ANOVAs. Independent variable: (1) species, (2) genus, (3) family/order, (4) subclass/class and (5) substem/stem. Dependent variable: index  $\psi$ . Conditions: each ANOVA includes only those taxa that include  $\geq 4$  independent values of  $\psi$  and  $\geq 2$  taxa on the inferior taxonomic levels (except species).

(a) ANOVA.

Taxonomic level	No. of taxa	No. of data	P
Species	35	242	<0.001
Genus	48	418	<0.001
Family/order	34	671	<0.001
Subclass/class	9	874	<0.001
Substem/stem	7	881	<0.001

(b) Post hoc comparison of means.

Taxonomic level	No. of pairwise comparisons	No. of significant different pairs ( $\alpha = 0.05$ )	As % of all combinations
Species	595	344	57.8
Genus	1128	545	48.3
Family/order	561	239	42.6
Subclass/class	36	22	61.1
Substem/stem	21	11	52.4

These two hypotheses were tested by one-way ANOVAs. Because of the somewhat inconsistent taxonomic definitions, I combined some taxonomic levels and used the following hierarchy: species, genus, family/order, subclass/class, substem/stem.

Table 3 indicates clearly that  $\psi$  is a taxon-specific feature. There are significant differences between taxa at all hierarchical levels. Moreover, on each level about 50% of all pair-wise comparisons indicate significant differences between taxa, much more than to be expected from purely random effects.

The results summarized in Table 4 show clearly that the variability of OGP within a taxon increases with increasing taxonomic level. It is lowest at the species level and highest when all invertebrate data (887 populations referring to 443 different species) are combined. These findings indicate strongly that in benthic invertebrates OGP, measured by the index  $\psi$ , is a species-specific feature.

Table 4 Comparison of the variability of overall growth performance  $\psi$  within taxa of various taxonomic levels using one-way ANOVA. Independent variable: taxon (species, genus, family/order, subclass/class, substem/stem). Dependent variable: standard deviation SD of index  $\psi$  within each taxon of the corresponding level.

(a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Taxonomic level	4	4.560	1.267	26.415	<0.001
Residual	128	6.018	0.048		

(b) Table of means and post hoc comparison of means.

Taxonomic level	N	Mean SD of $\psi$	SE	Family/order	Subclass/class	Substem/stem
Species	35	0.208	0.028	*	*	*
Genus	48	0.376	0.035	*	*	*
Family/order	34	0.587	0.042			*
Subclass/class	9	0.827	0.072			
Substem/stem	7	0.833	0.061			
All data†	1	1.022				

SE, standard error.

\*Significant difference,  $\alpha = 0.05$ .

†Not used in the test, because only one value of SD of  $\psi$ .

### 3.5. The Effect of Temperature on Growth Performance

Individual growth is based on physiological processes which depend on temperature. Therefore, it is likely that temperature affects one or both of the parameters ( $A_{Max}$  and  $M_{Max}$ ) used to construct the OGP index  $\psi$  and hence the index  $\psi$  itself. According to the general effects of temperature on physiological rates (Precht *et al.*, 1973; Peters, 1986; Regier *et al.*, 1990), we should expect an increase of OGP with increasing temperature. If OGP, however, is a species-specific parameter, the index  $\psi$  should be independent of temperature within the temperature range a species is adapted to; that is, possible effects of temperature on  $A_{Max}$  and  $M_{Max}$  should cancel out each other and leave the index  $\psi$  more or less unaffected at the species level.

Potential temperature effects can be tested by the Arrhenius equation, i.e. linear regression of  $\log(1/A_{Max})$ ,  $\log(M_{Max})$  and index  $\psi$  versus  $1/T$  (temperature in K). Based on all data sets with temperature data

( $N = 874$ , 443 species),  $\log(1/A_{\text{Max}})$  and  $1/T$  are significantly related (slope =  $-3022.978$ ;  $P < 0.001$ ), whereas  $\log(M_{\text{Max}})$  is not significantly affected by temperature ( $P = 0.705$ ). The relationship between the OGP index  $\psi$  and  $1/T$  is also significant, although the correlation is distinctly weaker than the one between  $\log(1/A_{\text{Max}})$  and  $1/T$ :

$$\psi = 9.164 - 2774.792/T \quad N = 874, r = 0.195, P < 0.001 \quad (6)$$

The temperature coefficient  $Q_{10}$  of the rate  $M_{\text{Max}}/A_{\text{Max}}$  derived from the above regression is between 2.1 and 2.3, close to the values found for many physiological processes and biological activities (Precht *et al.*, 1973; Regier *et al.*, 1990). These findings indicate that across a wide temperature range ( $-1.8$  to  $+30^\circ\text{C}$ ) and beyond species limits, increased physiological rates in warmer waters accelerate growth and hence shorten lifespan, but do not affect the maximum body mass attained during a lifetime.

At the species level, however, things look different. Table 5 shows the results of the same regressions for 20 species (all with  $N \geq 5$ ) and additionally for 20 genera (all with  $N \geq 8$ ). In 12 of the 20 species, the index  $\psi$  is not significantly affected by temperature. In four of the remaining species  $\psi$  is affected negatively by temperature, and only in four species (*Nephtys hombergi*, *Hyella azteca*, *Asellus aquaticus* and *Argopecten purpuratus*) is a positive effect equal to the one observed in the total data set detectable. At the genus level, the picture is similar: temperature does not affect  $\psi$  in 11 of 20 genera. The relationship is negative in five of the remaining nine genera and positive in four genera only (*Nephtys*, *Pontoporeia*, *Chironomus* and *Baetis*). Obviously there is no general and consistent positive effect of temperature on the index  $\psi$  at the species and genus levels. The relationship between temperature and OGP is either non-existent or rather variable and seems to depend on the taxon in question.

These findings indicate that OGP is more or less independent of temperature within the temperature range a species is adapted to. In the ideal case, the trends for  $A_{\text{Max}}$  and  $M_{\text{Max}}$  are in opposite directions with temperature, and consequently OGP remains constant. Examples are all species and genera in Table 5 where the relationship between  $A_{\text{Max}}$  and/or  $M_{\text{Max}}$  and temperature is significant, but the relationship between  $\psi$  and temperature is not significant. The overall positive relationship between  $\psi$  and temperature in the broad temperature range ( $+1.8$  to  $+30^\circ\text{C}$ ) and beyond species limits indicates that the OGP of species is adjusted to temperature. Each of the 443 different species included in the above regression went through an evolutionary adaptation to a certain temperature range. Obviously this adaptation included OGP, because the "average" OGP of a species depends on the temperature range that the species lives in. These results strongly support the hypothesis that OGP is a species-specific feature.

### 3.6. Growth Performance of Selected Taxa

ANOVA is used to compare  $\psi$  values of different taxa, and an auximetric grid (a plot of  $\log(1/A_{\text{Max}})$  versus  $\log(M_{\text{Max}})$ ) *sensu* Pauly (1979, 1984) is used for data representation. Figure 3a presents an auximetric grid of all OGP data included in this study.  $\psi$  values of benthic invertebrates range between  $-3$  and  $+2$ , well below the range of  $P$  values found in fish,  $0$  to  $+7$  (modified after Froese and Pauly, 1996). Figure 3b indicates that, as expected from the above analysis, there is considerable overlap in OGP between major taxonomic groups. In the following, I compare OGP at various taxonomic levels within the groups Bivalvia, Crustacea and Insecta larvae, where sufficient data are available.

#### 3.6.1. Bivalvia

At the superfamily/family level, the Pectinacea show by far the highest average growth performance (mean  $\psi = 1.36$ , Table 6, Figure 4). The residual families fall into one group with intermediate OGP ranging from  $\psi = 0.20$  to  $0.47$  (Cardiacea, Myacea, Mactracea, Veneracea, Unionacea and Mytilacea), and a second group with low OGP values between  $\psi = -0.61$  and  $-1.61$  (Nuculacea, Lucinacea, Pisidiidae, Tellinacea and Nuculanacea). These results indicate that the evolutionarily more primitive taxa such as Nuculacea and Nuculanacea (both subclass Ctenidiobranchia) and Lucinacea (primitive Veneroidea) have low OGP values. The highest OGP values are found in "modern" taxa (see Allen, 1985), i.e. Pectinacea, Mytilacea and Unionacea. All of these are highly efficient suspension feeders which have developed special adaptations: the Pectinacea can swim (to escape from predators), the Mytilacea are able to generate large banks using byssus threads (possibly for resistance to currents and wave impact) and the Unionacea successfully colonized fresh waters (for less competition).

3.6.1.1. *Species of the superfamily Tellinacea* The taxon Tellinacea is the only superfamily with sufficient data (20 species, 87 OGP values) for a comparison of growth performance among several species. The data contain one suspension-feeding surf clam (*Donax vittatus*) and seven deep-burrowing species with long, thin inhalant siphons used for surface deposit feeding and facultative suspension feeding (Brafeld and Newell, 1961; Olafsson, 1989). Among the Tellinacea species *D. vittatus* distinctly shows the highest growth performance (mean  $\psi = -0.04$ ; Table 7 and Figure 5). If all data referring to the genus *Donax* are considered (five species, nine values), the average OGP is even higher ( $\psi = +0.13$ ). Mean  $\psi$  values of the remaining species range between  $-1.56$  (*Abra ovata*) and  $-0.73$  (*A. alba*) without a clear ranking. These data indicate that surf



Table 5 Linear regression of  $\log(1/A_{\max})$ ,  $\log(M_{\max})$  and of overall growth performance  $\psi$  versus  $1/T$  (K) on the level of species (all species with  $N \geq 5$ ) and genus (all genera with  $N \geq 8$ ), respectively.

Taxon	N	Slope	P	$\log(1/A_{\max})$	Slope	P	$\log(M_{\max})$	Slope	P	index $\psi$
<i>Nephtys hombergi</i>	9	-	NS	-	-	NS	-	-	NS	0.041
<i>Amphiarete acutifrons</i>	10	-	NS	-	-	NS	-	-	NS	-
<i>Owenia fusiformis</i>	5	-5897	0.000	10 554	0.002	4 657	0.031	-	NS	0.031
<i>Cardium edule</i>	5	7188	0.028	-	-	-	NS	-	NS	NS
<i>Mytilus edulis</i>	10	-8078	0.004	-	-	-	NS	-	NS	NS
<i>Argopecten purpuratus</i>	5	-3301	0.011	-	-	-	NS	-	NS	0.037
<i>Flacopecten magellanicus</i>	8	-	NS	-	-	-	NS	-	NS	NS
<i>Abra alba</i>	17	-	NS	-	-	-	NS	3 204	0.090	NS
<i>Macoma balthica</i>	18	-	NS	-	-	-	NS	-	NS	NS
<i>Tellina fabula</i>	5	-	NS	-	-	-	NS	-	NS	NS
<i>Mercenaria mercenaria</i>	6	-	NS	-	-	-	NS	-	NS	NS
<i>Ampeletisca brevicornis</i>	8	-	NS	5 685	0.019	3 881	0.004	-	NS	NS
<i>Corophium volutator</i>	8	-3994	0.057	16 402	0.023	12 408	0.033	-	NS	0.004
<i>Hyalella azteca</i>	5	-2147	0.001	-757	0.064	-1 390	0.020	-	NS	0.020
<i>Diasyllis rathkei</i>	8	-	NS	-	-	-	NS	-	NS	NS
<i>Asellus aquaticus</i>	8	-	NS	-	-	-	NS	-9 755	0.020	NS
<i>Corydalis cornutus</i>	5	756	0.012	-	-	-	NS	-	NS	NS

<i>Diplectrona modesta</i>	8	-	NS	-	-	-	NS	-	NS	NS
<i>Macroneuma carolinu</i>	7	-4726	0.001	-	-	-	NS	-	NS	NS
<i>Parapsyche caridis</i>	7	-	NS	-	-	-	NS	-	NS	NS
<i>Nephtys</i>	11	-	NS	-	-	-	NS	-6 284	0.093	NS
<i>Ampharete</i>	12	-	NS	-	-	-	NS	-	NS	NS
<i>Pectinaria</i>	9	-	NS	-	-	-	NS	-	NS	NS
<i>Spisula</i>	9	-7360	0.021	-	-	-	NS	-	NS	NS
<i>Nucula</i>	13	-6046	0.001	13 614	0.001	7 567	0.006	-	NS	0.006
<i>Pisidium</i>	8	-	NS	-	-	-	NS	-	NS	NS
<i>Abra</i>	40	-	NS	3 906	0.008	4 495	0.004	-	NS	0.004
<i>Macoma</i>	21	-	NS	-	-	-	NS	-	NS	NS
<i>Tellina</i>	9	-	NS	-	-	-	NS	-	NS	NS
<i>Anodonta</i>	8	-1389	0.021	-	-	-	NS	-	NS	NS
<i>Ampeletisca</i>	23	-	NS	-	-	-	NS	-	NS	NS
<i>Corophium</i>	11	-	NS	6 061	0.045	6 031	0.013	-	NS	0.013
<i>Gammarus</i>	16	-4607	0.004	5 816	0.002	-	NS	-	NS	NS
<i>Pontoporeia</i>	8	-5292	0.022	-	-	-	NS	-7 577	0.013	NS
<i>Chironomus</i>	11	-9734	0.001	-	-	-	NS	-11 747	0.001	0.001
<i>Polydora</i>	9	-5470	0.059	2 157	0.003	-	NS	-	NS	NS
<i>Tanytarsus</i>	8	-	NS	-	-	-	NS	-	NS	NS
<i>Baetis</i>	10	-3851	0.051	-	-	-	NS	-6 317	0.002	NS
<i>Cheumatopsyche</i>	8	-2851	0.018	5 126	0.001	2 275	0.006	-	NS	0.006
<i>Hydropsyche</i>	17	-1793	0.001	5 779	0.001	3 985	0.001	-	NS	0.001

P, probability of error; NS, not significant ( $P \geq 0.05$ ).

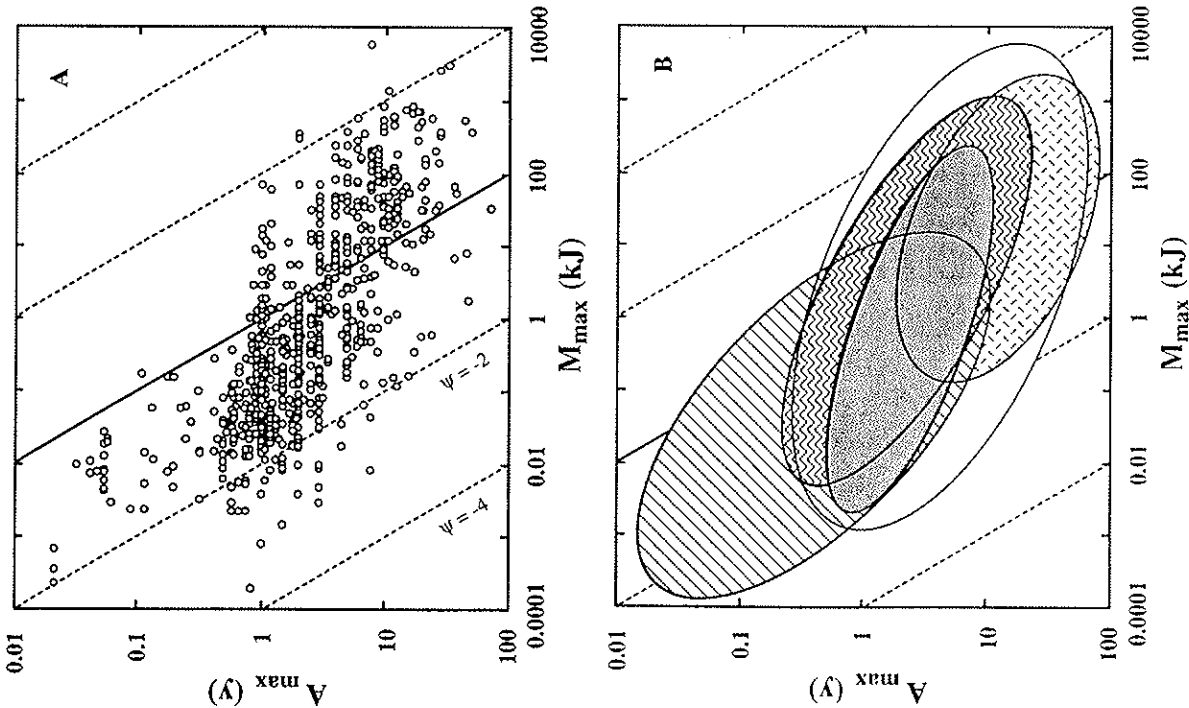


Figure 3 Auximetric grid comparing OGP in benthic invertebrates. Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ . (a) Data for 887 populations. (b) Approximate range of OGP in major taxonomic groups: □, Mollusca; ▨, Polychaeta; ▩, Crustacea; ▧, Insecta larvae; ▩, Echinodermata.

Table 6 Comparison of the OGP index  $\psi$  of 11 bivalve superfamilies/families using one-way ANOVA,  $N = 236$  (bivalve superfamilies/families with  $<5$  OGP data are excluded). Independent variable: superfamily/family. Dependent variable: OGP index  $\psi = \log(M_{Max}/A_{Max})$ .

(a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Taxon	11	134.763	12.251	29.058	<0.001
Residual	228	94.441	0.414		

(b) Table of means and *post hoc* comparison of means.

Superfamily/family	N (species/data)	Mean $\psi$	SE	2	3	4	5	6	7	8	9	10	11	12
1 Cardacea	4/10	0.197	0.114	*	-	-	*	-	*	*	*	*	*	*
2 Lucinacea	3/5	-1.427	0.256		*	*	*	*	*	*	*	*	*	*
3 Macracea	7/12	0.433	0.186			*	*	*	*	*	*	*	*	*
4 Myacea	4/9	0.322	0.305				*	*	*	*	*	*	*	*
5 Mytilacea	7/22	0.674	0.120				*	*	*	*	*	*	*	*
6 Nuculacea	5/13	-1.613	0.122				*	*	*	*	*	*	*	*
7 Nuculanacea	5/8	-0.607	0.356				*	*	*	*	*	*	*	*
8 Pectinacea	11/30	1.356	0.081				*	*	*	*	*	*	*	*
9 Pisidiidae	12/20	-0.956	0.248				*	*	*	*	*	*	*	*
10 Tellinacea	20/87	-0.722	0.065				*	*	*	*	*	*	*	*
11 Unionacea	9/18	0.466	0.038				*	*	*	*	*	*	*	*
12 Veneracea	11/25	0.442	0.138				*	*	*	*	*	*	*	*

SE, Standard error.  
\*Significant difference,  $\alpha = 0.05$ .

clams have an exceptionally high OGP among the Tellinacea. Again, as discussed above at the superfamily level, the taxon with the highest OGP shows special features which separate it from related taxa. Owing to their burrowing technique and mobility (e.g. Ansell and Trevallion, 1969) *Donax* species are adapted to high-energy beaches, especially in upwelling areas, where primary production and hence food supply is exceptionally high, and competition by other suspension feeders is low.

3.6.1.2. *Species of the superfamily Pectinacea* Scallops show a generally high OGP, but Figure 6 indicates some differences between species. The data are not sufficient for appropriate statistical testing at the species level, but the OGP of species of the genus *Chlamys* is distinctly lower (mean  $\psi = 0.898$ ) than that of species belonging to the various

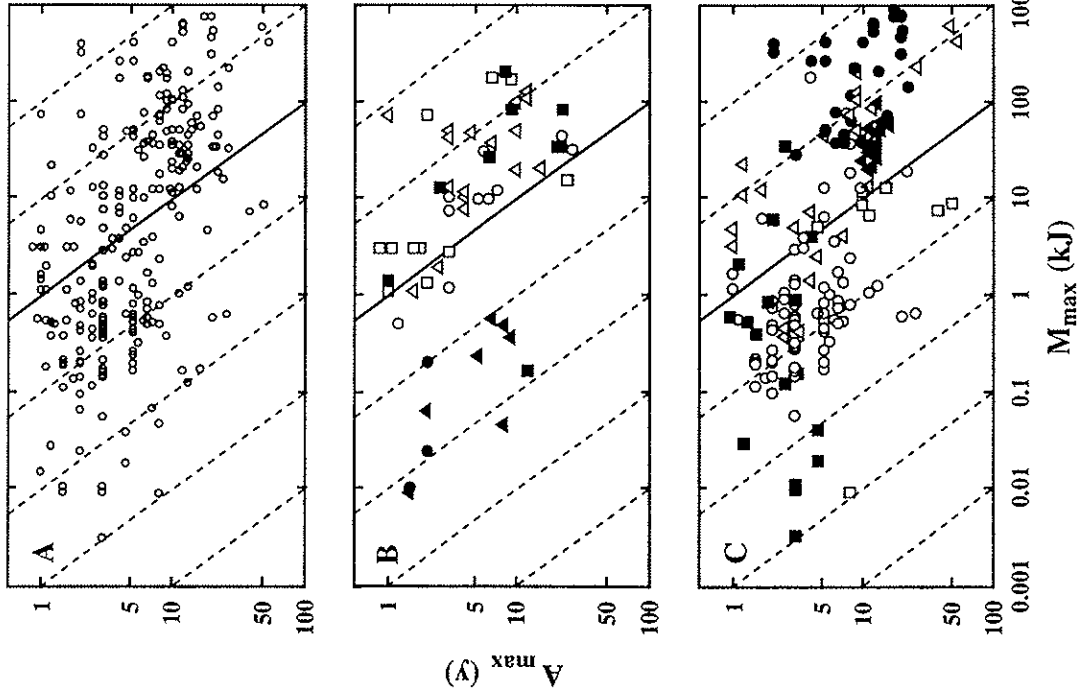


Figure 4 Auximetric grid comparing overall growth performance (OGP) in the class Bivalvia ( $N = 286$ , mean  $\psi = -0.139$ ). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ . (a) All data (236 populations). (b) Cardacea (○), Lucinacea (●), Mactracea (◻), Myacea (◼), Mytilacea (△) and Nuculanacea (▲). (c) Pectinacea (●), Pisiidae (◼), Tellinacea (○), Unionacea (▲), and Veneracea (△).

Table 7 Comparison of the OGP index  $\psi$  of eight bivalve species of the superfamily Tellinacea using one-way ANOVA,  $N = 69$  (species with  $<3$  OGP data are excluded). Independent variable: species. Dependent variable: OGP index  $\psi = \log(M_{\text{Max}}/A_{\text{Max}})$ .

(a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Taxon	7	5.886	0.841	10.169	<0.001
Residual	61	5.044	0.083		

(b) Table of means and *post hoc* comparison of means.

Species	N (data)	Mean $\psi$	SE	2	3	4	5	6	7	8
1 <i>Abra alba</i>	17	-0.731	0.062	-	*	-	*	*	*	*
2 <i>A. nitida</i>	14	-0.950	0.058	-	*	-	*	*	*	*
3 <i>A. ovata</i>	6	-1.563	0.089	-	*	-	*	*	*	*
4 <i>A. prismatica</i>	3	-1.172	0.098	-	*	-	*	*	*	*
5 <i>Donax vittatus</i>	3	-0.036	0.033	-	*	-	*	*	*	*
6 <i>Macoma balthica</i>	18	-0.833	0.093	-	*	-	*	*	*	*
7 <i>Tellina fabula</i>	5	-1.076	0.142	-	*	-	*	*	*	*
8 <i>T. tenuis</i>	3	-0.999	0.069	-	*	-	*	*	*	*

SE, standard error.

\*Significant difference,  $\alpha = 0.05$ .

*Pecten* genera (mean  $\psi = 1.657$ ). The highest OGP values recorded ( $\psi \approx 2.2$ ) refer to the Peruvian scallop *Argopecten purpuratus* during an El Niño event, when coastal surface water temperatures at the Peruvian coast are extraordinarily high (Mendo and Jurado, 1993).

### 3.6.2. Crustacea

Most of the 121 OGP data from the substem Crustacea refer to the suborder Amphipoda ( $N = 88$ ) and only very few to other taxa (Cumacea, 8; Decapoda 12; Isopoda, 15). Despite this, the data indicate a clear and significant ranking in OGP (Figure 7). Decapods show the highest growth performance (mean  $\psi = 0.898$ ), Cumacea (mean  $\psi = -0.676$ ) and Isopoda (mean  $\psi = -0.796$ ) hold intermediate positions, whereas amphipods show the lowest values (mean  $\psi = -1.143$ ).

3.6.2.1. *Genera of the suborder Amphipoda* The seven genera compared in Table 8 and Figure 8 can be separated into three groups: *Bovallia*,

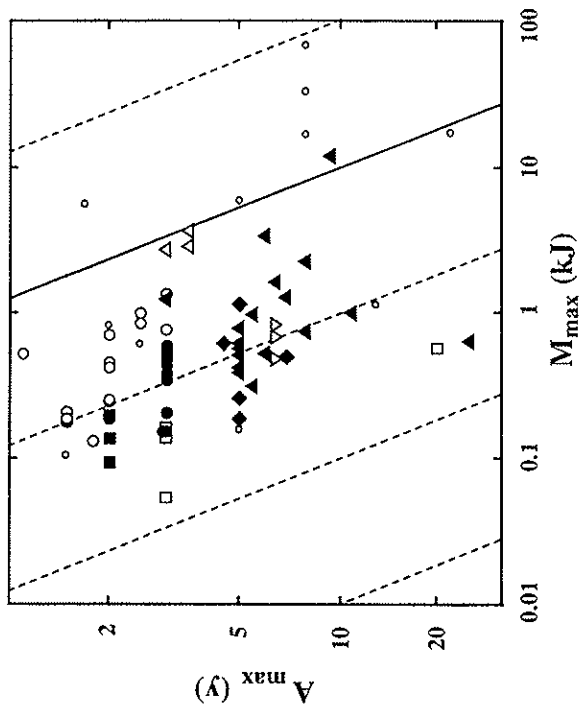


Figure 5 Auximetric grid comparing overall growth performance in eight species of the family Tellinacea ( $\geq 3$  data points per species). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ . Small circles represent all species with  $< 3$  data points.  $\circ$ , *Abra alba*;  $\bullet$ , *A. niitida*;  $\square$ , *A. ovata*;  $\blacksquare$ , *A. prismatica*;  $\Delta$ , *Donax vittatus*;  $\blacktriangle$ , *Macoma balthica*;  $\blacklozenge$ , *T. fabula*;  $\nabla$ , *T. tenuis*.

with the single Antarctic species *B. gigantea*, shows by far the highest OGP (mean  $\psi = +0.285$ ); the *Gammarus* species show intermediate values (mean  $\psi = -0.690$ ); and the remaining genera, *Ampelisca*, *Corophium*, *Hyalella* and *Pontoporeia*, show similar low OGP with average  $\psi < -1$ . The genus *Gammarus* is a good example for a small range of OGP values ( $\psi$  between  $-1.187$  and  $-0.041$ , Figure 8) despite a large variability in  $A_{\max}$  (0.3–8.5 years) and  $M_{\max}$  (0.10–4.14 kJ).

3.6.2.2. *Species of the genus Ampelisca* This genus is of particular interest, because five of the seven species included in the analysis (*A. armoricana*, *A. brevicornis*, *A. sarsi*, *A. tenuicornis* and *A. typica*) occur sympatrically (Bay of Morlaix, Dauvin, 1988a,b,c,d, 1989). There should exist distinct differences in the OGP of at least some of these species, if growth performance has any function in species separation. An ANOVA comparing the three species with sufficient data shows that OGP is significantly ( $P < 0.001$ ) different among *A. brevicornis* (mean  $\psi = -0.928$ , *A. tenuicornis* (mean  $\psi = -1.547$ ) and *A. sarsi* (mean  $\psi = -1.990$ ). The

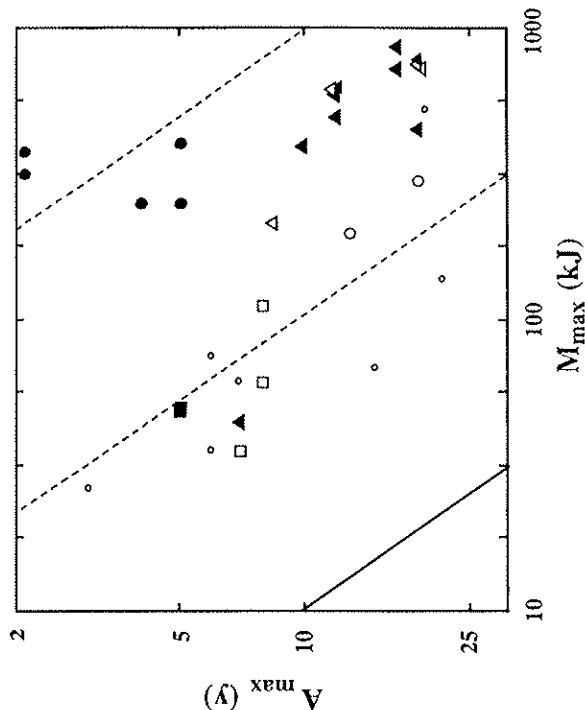


Figure 6 Auximetric grid comparing overall growth performance in six species of the family Pectinacea ( $\geq 2$  data points per species). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ . Small circles represent all species with  $< 2$  data points.  $\circ$ , *Adamussium colbecki*;  $\bullet$ , *Argopecten purpuratus*;  $\square$ , *Chlamys patagonica*;  $\blacksquare$ , *Chlamys varia*;  $\Delta$ , *Patinopecten carinus*;  $\blacktriangle$ , *Placopecten magellanicus*.

remaining two species have intermediate OGP values close to *A. sarsi* (Figure 9). The Pacific species *A. auracana* shows a  $\psi$  value similar to *A. brevicornis*, whereas *A. agassizi* from Georges Bank falls in the group with intermediate OGP. This example demonstrates clearly that OGP can play a significant role in the ecological separation of closely related species. Moreover, it may indicate "character displacement" of OGP (*sensu* Brown and Wilson, 1956) among the sympatric species.

### 3.6.3. Insecta Larvae

In terms of abundance, biomass and energy flow, larvae of pterygote insects are one of the most important groups of freshwater benthic communities. In the marine environment, they are restricted to brackish water areas, and hence have been neglected in most previous comparative studies on benthic population dynamics. The average OGP of insect larvae

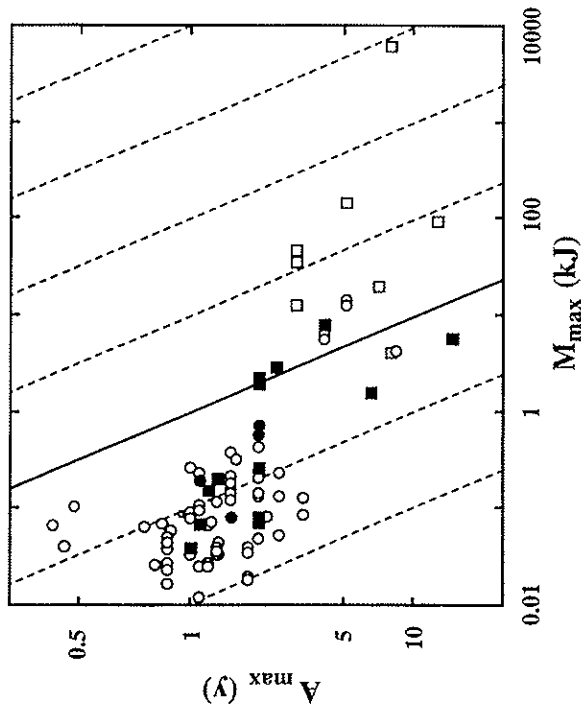


Figure 7 Auximetric grid comparing overall growth performance in the sub-stem Crustacea ( $N = 110$ , mean  $\psi = -0.859$ ). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ , Amphipoda;  $\bullet$ , Crustacea;  $\square$ , Decapoda;  $\blacksquare$ , Iso-poda.

is low (mean  $\psi = -1.104$ , see Figure 10). Two orders, Megaloptera (mean  $\psi = 0.726$ ) and Odonata (mean  $\psi = -0.330$ ), show significantly ( $P < 0.001$ ) higher OGP than the Trichoptera (mean  $\psi = -0.962$ ), Plecoptera (mean  $\psi = -1.043$ ), Ephemeroptera (mean  $\psi = -1.056$ ) and Diptera (mean  $\psi = -1.401$ ). The latter group has the lowest OGP values among the Insecta. The data available contain a vast number of insect species, but only very few of them provide sufficient OGP values for statistical comparisons. Even at the level of genera, only the order Diptera fulfils minimum requirements for testing.

3.6.3.1. *Genera of the order Diptera* Figure 11 indicates that the Diptera cover a wide range of OGP values between  $-4$  and  $0$ . The nine genera compared statistically (Table 9) fall into three groups: the genera *Procladius* (mean  $\psi = -0.607$ ) and *Chironomus* (mean  $\psi = -0.816$ ) show comparatively high OGP values, whereas *Tanytarsus* (mean  $\psi = -2.138$ ) and *Cladotanytarsus* (mean  $\psi = -1.964$ ) show exceptionally low values. Further separation of the remaining genera is omitted by the low number of data (Table 9).

Table 8 Comparison of the OGP index  $\psi$  in six genera of the suborder Amphipoda using one-way ANOVA,  $N = 67$  (genera with  $< 4$  OGP data are excluded). Independent variable: genus. Dependent variable: OGP index  $\psi = \log(M_{\max}/A_{\max})$ .

## (a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Taxon	5	15.234	3.045	36.632	<0.001
Residual	61	5.074	0.083		

(b) Table of means and *post hoc* comparison of means.

Genus	N		Mean $\psi$	SE							
	(species/data)				2	3	4	5	6		
1 <i>Ampelisca</i>	7/23		-1.406	0.089			*	*	*	*	*
2 <i>Bovallia</i>	1/4		0.285	0.075							
3 <i>Corophium</i>	2/11		-1.337	0.065			*	*	*	*	*
4 <i>Gammarus</i>	5/16		-0.690	0.046							
5 <i>Hyalella</i>	1/5		-1.636	0.022							*
6 <i>Pontoporeia</i>	2/8		-1.410	0.063							*

SE, standard error.

\*Significant difference,  $\alpha = 0.05$ .

## 3.7. Growth Performance of Different Living Types

A further interesting question is whether OGP is related to the living mode of the species in question. All data were grouped according to three parameters, (i) feeding (four categories: suspension feeder, grazer, deposit feeder and predator/scavenger); (ii) mobility (two categories: motile and sessile) and (iii) position (two categories: infauna and epifauna), and tested by full-interaction ANOVA. According to Table 10, OGP is affected by all three parameters. Suspension feeders show the highest OGP (mean  $\psi = -0.046$ ), followed closely by predators/scavengers (mean  $\psi = -0.128$ ). The OGP of grazers is distinctly lower (mean  $\psi = -0.592$ ), and deposit feeders show by far the lowest values (mean  $\psi = -1.027$ , Table 10b). The significant interaction between feeding and position refers to suspension feeders only, where OGP is higher in infaunal species (mean  $\psi = 0.052$ ) than in epifaunal species (mean  $\psi = -0.102$ ). Mobile species (mean  $\psi = -0.785$ ) show significantly lower OGP than sessile species (mean  $\psi = -0.262$ ). This difference is affected by position (Table 10c), although epifauna and infauna do not differ significantly for all data levels.

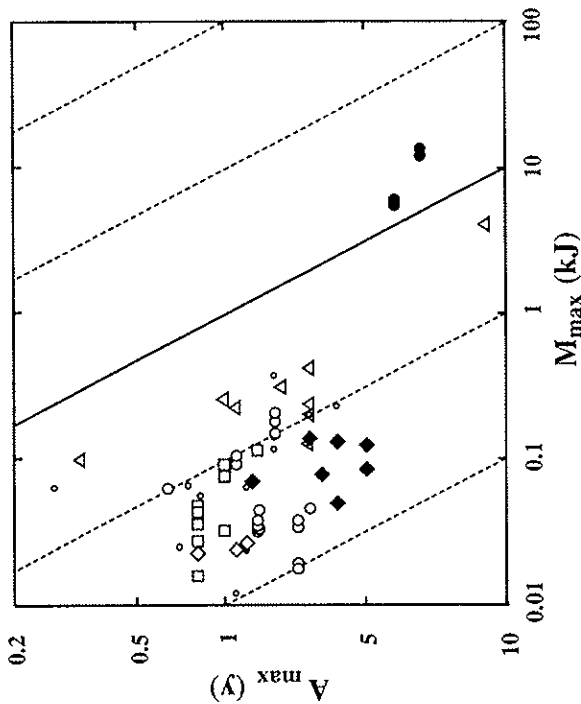


Figure 8 Auximetric grid comparing overall growth performance in six amphipod genera ( $\geq 4$  data points per genus). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ . Small circles represent all genera with  $< 4$  data points.  $\circ$ , *Ampelisca*;  $\bullet$ , *Bovallia*;  $\square$ , *Corophium*;  $\Delta$ , *Gammarus*;  $\diamond$ , *Hyalella*;  $\blacklozenge$ , *Pontoporeia*.

The parameters feeding and motility used here suffer from a certain extent of subjectivity, because the classification of many taxa into one or another category may be questionable (compare with the classification of Jumars and Fauchald (1977)). Nevertheless, the results indicate a certain ranking of OGP according to living mode. The overall OGP spectrum ranges from sessile suspension feeders such as mussels and clams to motile infaunal deposit feeders such as capitellid polychaetes. Two factors, energetic efficiency of food intake and costs of mobility, may play significant roles here.

### 3.8. Growth Performance and Exploitation

Table 11 summarizes the 30 species showing the highest OGP values. As expected from the previous discussion, molluscs (12 bivalves and seven gastropods) form the majority of these species. Twelve out of the 30 species (40%) are exploited by man, either on a commercial or on an

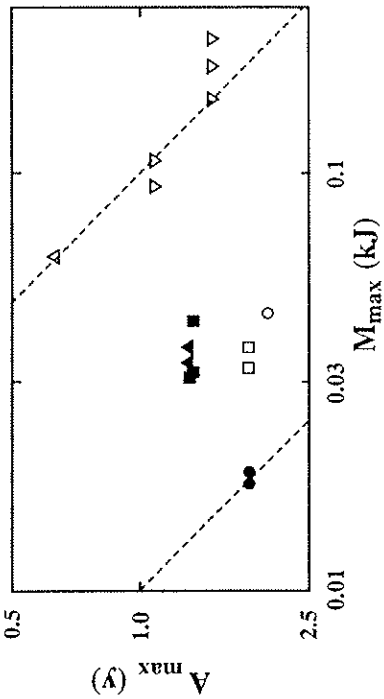


Figure 9 Auximetric grid comparing overall growth performance in seven species of the genus *Ampelisca*. Diagonal lines indicate equal values of  $\psi$ .  $\circ$ , *A. agassizii*;  $\square$ , *A. auracana*;  $\Delta$ , *A. auracana*;  $\nabla$ , *A. brevicornis*;  $\bullet$ , *A. sarsii*;  $\blacktriangle$ , *A. tenuicornis*;  $\blacktriangle$ , *A. typica*.

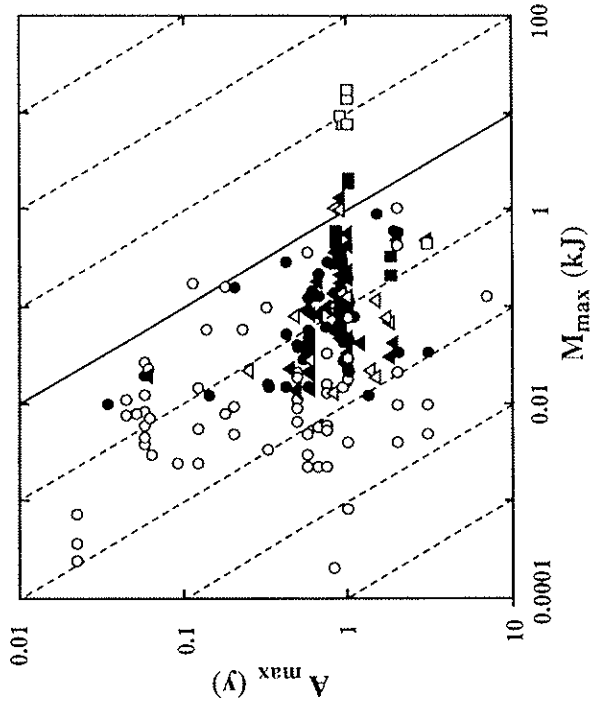


Figure 10 Auximetric grid comparing overall growth performance in six orders of the Insecta ( $N = 273$ , mean  $\psi = -1.104$ ). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ .  $\circ$ , Diptera;  $\bullet$ , Ephemeroptera;  $\square$ , Megaloptera;  $\blacktriangle$ , Odonata;  $\Delta$ , Plecoptera;  $\blacktriangle$ , Trichoptera.

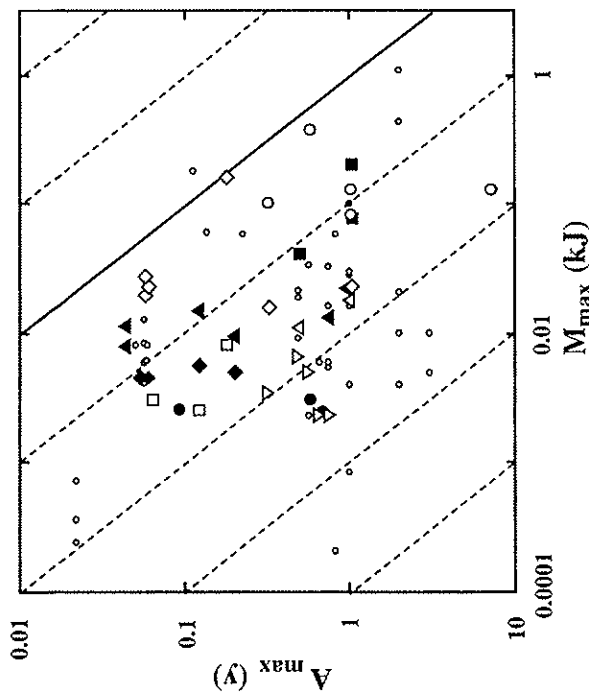


Figure 11 Auximetric grid comparing overall growth performance in nine genera of the order Diptera ( $\geq 4$  data points per genus). Diagonal lines indicate equal values of  $\psi$ . Solid diagonal line:  $\psi = 0$ . Small circles represent all genera with  $< 4$  data points.  $\circ$ , *Chironomus*;  $\bullet$ , *Cladotanytarsus*;  $\square$ , *Cricotopus*;  $\triangle$ , *Glyptotendipes*;  $\blacktriangle$ , *Limnochironomus*;  $\blacklozenge$ , *Procladius*;  $\diamond$ , *Simulium*;  $\nabla$ , *Tanytarsus*.

artisanal basis, compared with about 5% of all 477 species. If all 887 populations included here are ranked according to the index  $\psi$ , all exploited populations are situated in the top 20% of the data. This indicates a strong tendency of human exploitation towards species with high OGP, i.e. high OGP is likely to coincide with potentially high yield. Therefore, OGP may be a useful tool for the identification of potential benthic resources; likewise, species with low OGP are not potentially suitable for exploitation.

#### 4. MORTALITY IN BENTHIC INVERTEBRATES

Mortality is one of the processes regulating size and structure of a population. It may be separated into three categories: (i) episodic events of more or less simultaneous mass mortality induced by habitat disturbances; (ii) mortality caused by genetic limits of longevity such as the

Table 9 Comparison of the OGP index  $\psi$  in nine genera of the order Diptera using one-way ANOVA,  $N = 59$  (species with  $< 4$  OGP data are excluded). Independent variable: genus. Dependent variable: OGP index  $\psi = \log(M_{\text{Max}}/A_{\text{Max}})$ .

(a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Taxon	8	14.471	1.889	9.517	$< 0.001$
Residual	50	9.503	0.190		

(b) Table of means and *post hoc* comparison of means.

Genus	N (species/data)	Mean $\psi$	SE	2	3	4	5	6	7	8	9
1 <i>Chironomus</i>	4/11	-0.816	0.199	*	-	-	*	-	-	*	*
2 <i>Cladotanytarsus</i>	3/4	-1.964	0.238	-	-	-	-	-	-	*	-
3 <i>Cricotopus</i>	2/5	-1.406	0.069	-	-	-	-	-	-	-	*
4 <i>Glyptotendipes</i>	2/4	-1.004	0.101	-	-	*	-	-	-	-	*
5 <i>Limnochironomus</i>	2/4	-1.679	0.022	-	-	-	-	-	*	*	*
6 <i>Polypetillum</i>	5/9	-1.169	0.136	-	-	-	-	-	-	-	*
7 <i>Procladius</i>	2/7	-0.607	0.236	-	-	-	-	-	-	-	*
8 <i>Simulium</i>	3/7	-1.197	0.076	-	-	-	-	-	-	-	*
9 <i>Tanytarsus</i>	6/8	-2.138	0.079	-	-	-	-	-	-	-	*

SE, standard error.  
\*Significant difference,  $\alpha = 0.05$ .

more or less synchronous death of adults after reproduction; and (iii) the monotonous decrease in number of an age class with time, a process caused by, for example, predation, parasitism and diseases. The last is the type of mortality we will deal with here.

With respect to energy flow within an ecosystem, the energy/matter transfer from a prey to a predator population is proportional to prey mortality caused by the predator. Hence, natural mortality is an approximate measure for the amount of energy/matter transferred from the prey population to those populations feeding on it. With regard to populations exploited by man, mortality has basically the same significance. Moreover, fishing mortality (caused by man) and natural mortality (caused by other predators) are both parameters required for the successful management of exploited stocks.

Table 10 Effects of living mode on the OGP index  $\psi$  using three-way, full-interaction ANOVA,  $N = 883$  (significant sources are shown only). Independent variables: feeding (suspension feeder, grazer, deposit feeder, predator/scavenger), mobility (sessile, motile) and position (infauna, epifauna). Dependent variable: OGP index  $\psi = \log(M_{\text{NEW}}/A_{\text{NEW}})$ .

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Feeding	3	54.454	18.151	22.191	<0.001
Mobility	1	27.682	27.682	33.843	<0.001
Feeding $\times$ position	2	16.884	8.442	10.321	<0.001
Mobility $\times$ position	1	8.209	8.209	10.037	0.002
Residual	874	714.898	0.818		

Feeding type	N (data)	Mean $\psi$			
		1	2	3	4
1 Suspension feeder	258	-0.046	0.066	*	*
2 Grazer	123	-0.592	0.102	*	*
3 Deposit feeder	412	-1.027	0.038	*	*
4 Predator/scavenger	90	-0.128	0.089		

(b) Feeding: table of means and *post hoc* comparison of means.

\*Significant difference,  $\alpha = 0.05$ .

(c) Interaction between mobility and position.

Mobility type	Position type		Epifauna	Infauna	All
	$\psi$	SE			
Motile	$\psi$		-0.590	-1.071	-0.785
	SE		0.054	0.061	
	N		328	223	
Sessile	$\psi$		0.061	-0.490	-0.262
	SE		0.092	0.064	
	N		137	195	
All	$\psi$		-0.398	-0.800	-0.588

SE, standard error.

In the following sections I will analyse two questions related to mortality which are of ecological as well as of fishery biological interest: (1) How are mortality and productivity related empirically? (2) Is it possible to estimate natural mortality from other population parameters?

#### 4.1. Mortality and Mortality Models

Mortality of a population is the result of all processes causing the death of single individuals. Mortality of an individual can be defined statistically as the probability of death for this individual. Concerning a group of individuals with synchronous life history, e.g. an age class, total mortality corresponds to the sum of individual mortalities. The curve describing decrease in number with time can show various shapes which correspond to different mortality models (e.g. see Krebs, 1984).

Empirical evidence shows that, as in many other groups of aquatic and terrestrial animals, mortality of many benthic invertebrate populations can be described by one model, the single negative exponential mortality model (SNEMM):

$$\begin{aligned} \delta N/\delta t &= -Z N_t \\ \Leftrightarrow N_t &= N_0 e^{-Zt} \end{aligned} \quad (7)$$

where  $Z$  is the instantaneous rate of mortality, and  $N_t$  and  $N_0$  are the numbers at time  $t$  and time zero, respectively. This model indicates that the rate of mortality  $Z$  is constant over time. Regarding exploited populations, fishing mortality  $F$  (caused by man) is separated from natural mortality  $M$  by

$$Z = F + M \quad (8)$$

#### 4.2. The Relationship Between Mortality and Productivity

It is obvious that there are relationships between mortality and production of a population. In a steady state, the amount of energy/matter transferred to predators will equal the amount of energy/matter newly produced (i.e. elimination = production, see Crisp, 1984). Allen (1971) analysed the mathematical relationships between the mortality rate  $Z$  and somatic production/biomass ratio  $P_s/B$  in steady-state populations on the basis of various mortality and growth models. He found that

$$Z = P_s/B \quad (9)$$



Table 11 The 30 species with the highest OGP index  $\psi$ , sorted according to maximum index value.

Species	Group	Region	Index $\psi$	Exploited
<i>Cancer polydon</i>	Crustacea	P, Chile	2.874	Yes
<i>Argopecten purpuratus</i>	Bivalvia	P, Peru	1.697-2.248	Yes
<i>Gorgonia</i> sp.	Cnidaria	A, USA	1.581-2.104	No
<i>Haliotis tuberculata</i>	Gastropoda	A, Europe	1.702-1.994	Yes
<i>H. midae</i>	Gastropoda	A, South Africa	1.975-1.982	Yes
<i>Evechinus chloroticus</i>	Echinodermata	P, New Zealand	1.409-1.938	No
<i>Ferna viridis</i>	Bivalvia	Hong Kong	1.017-1.859	Yes
<i>Physa gyrina</i>	Gastropoda	FW, USA	1.720	No
<i>Placopecten magellanicus</i>	Bivalvia	A, USA	1.375-1.718	Yes
<i>Holothuria atra</i>	Echinodermata	P, Marshall Islands	1.715	No
<i>Turbo sarnaticus</i>	Gastropoda	I, South Africa	1.711	Yes
<i>Echinus esculentus</i>	Echinodermata	Europe	1.409-1.652	No
<i>Egeria radicata</i>	Bivalvia	Nigeria	1.623	Yes
<i>Patinopecten caurinus</i>	Bivalvia	P, USA	1.399-1.573	Yes

<i>Mesodesma donacium</i>	Bivalvia	P, Peru	1.558	Yes
<i>Folinites duplicatus</i>	Gastropoda	A, USA	1.519	No
<i>Orconeces limosus</i>	Crustacea	FW, Poland	1.445	No
<i>Spirula sachelinensis</i>	Bivalvia	Sea of Japan	1.261-1.431	Yes
<i>Crassadoma gigantea</i>	Bivalvia	P, USA	1.421	No*
<i>Scapharca naequivalis</i>	Bivalvia	Mediterranean	1.405	No
<i>Mya arenaria</i>	Bivalvia	A	0.642-1.394	No
<i>Haliotis iris</i>	Gastropoda	P, New Zealand	1.388	Yes
<i>Neris virens</i>	Polychaeta	A, Europe	0.526-1.386	Not
<i>Thais chocolata</i>	Gastropoda	P, Chile	1.351	Yes
<i>Mercenaria mercenaria</i>	Bivalvia	A	0.835-1.331	No
<i>Merchimis angulosus</i>	Echinodermata	A, South Africa	1.325	No
<i>Allocentrotus fragilis</i>	Echinodermata	P, USA	1.247	No
<i>Mellita quinqueperforata</i>	Echinodermata	A, USA	1.194-1.224	No
<i>Corydalis cornutus</i>	Insecta larvae	FW, USA	0.888-1.243	No
<i>Venerupis decussata</i>	Bivalvia	Mediterranean	0.924-1.239	No

A, Atlantic Ocean; I, Indian Ocean; P, Pacific Ocean; FW, fresh water.  
 \*Recreational fishery only (MacDonald *et al.*, 1989).

†Bait fishery.

provided that mortality can be described by the SNEMM and growth by the VBGF, by a negative exponential model or by a linear model. Other combinations of mortality and growth models, however, did not result in equally simple relationships. (The same holds true for Richard and Gompertz growth functions (personal observation), which were not analysed by Allen (1971).) The data from benthic invertebrate populations from the SNEMM and VBGF confirm the linear relationship between  $Z$  and  $P_s/B$  empirically:

$$Z = 0.020 + 1.036 P_s/B \quad N = 67, r = 0.961, P < 0.001 \quad (10)$$

$$P_s/B = 0.063 + 0.890 Z \quad N = 67, r = 0.961, P < 0.001$$

The intercept and slope are not significantly ( $\alpha = 0.05$ ) different from 0 and 1, respectively. This relationship is extremely helpful in situations when only one of these parameters is known.

Very often, however, growth of a benthic population is either not known or does not follow the VBGF model. Therefore I will analyse whether the approximation  $Z \approx P_s/B$  can be used to estimate the mortality rate from productivity and vice versa. An ANCOVA (Table 12) shows that the growth model does affect the relationship between  $Z$  and  $P_s/B$ , although at a rather low level of significance ( $P = 0.044$ ). Despite this effect, the variability of the relationship between  $Z$  and  $P_s/B$  seems to be sufficiently low (Figure 12) to establish general linear regressions which may be used to estimate one parameter from the other:

$$Z = 0.082 + 0.925 P_s/B \quad N = 103, r = 0.961, P < 0.001$$

$$P_s/B = 0.036 + 0.997 Z \quad N = 103, r = 0.961, P < 0.001 \quad (11)$$

#### 4.3. Natural Mortality Rate

The natural mortality rate  $M$  is an important parameter in population dynamics, especially in exploited stocks.  $M$  is required to estimate the part of mortality caused by man (i.e.  $F$ , see Ricker (1975), or for practical applications in benthic invertebrates see Clasing *et al.* (1994) and Etim and Brey (1994)).  $M$  is required for multispecies stock assessment models too (e.g. Jarre *et al.*, 1991). These models integrate several trophic levels, i.e. natural prey-predator relationships, and hence do not function without information on natural mortality (e.g. Anonymous, 1993).

Unfortunately,  $M$  is very difficult to calculate for exploited populations (see Ricker, 1975; Pauly, 1980). Therefore, any empirical approach to the estimation of natural mortality would be extremely helpful. For fish, Pauly

Table 12 Comparison of the effects of growth model type on the relation between  $Z$  and  $P_s/B$  using two-way nested ANOVA,  $n = 103$ . Independent variables: productivity  $P_s/B$  and growth model (VBGF, 67; Gompertz, 8; unknown, 28). Dependent variable: mortality rate  $Z$ .

Source	Degrees of freedom	Sum of squares	Mean square	F	P
$P_s/B$	1	16.657	16.657	75.132	<0.001
Growth model	2	0.008	0.004	0.017	0.983
$P_s/B$ (growth model)	2	1.430	0.715	3.225	0.044
Residual	97	21.507	0.222		

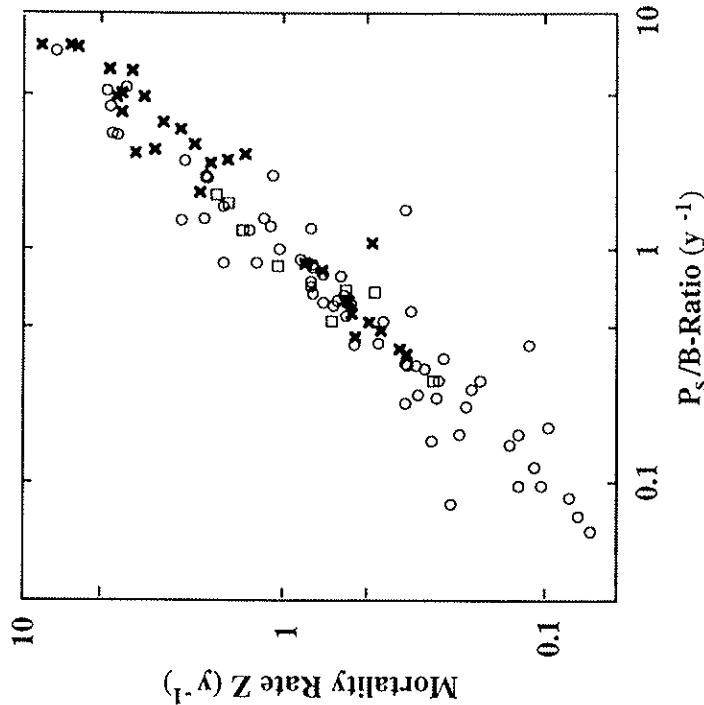


Figure 12 Relation between the mortality rate  $Z$  and productivity  $P_s/B$  in benthic invertebrates. Growth models: O, VBGF; □, Gompertz; ×, unknown. Note the logarithmic scales on both axes.

$$Z = 0.082 + 0.925 P_s/B \quad N = 103, r = 0.961, P < 0.001$$

$$P_s/B = 0.036 + 0.997 Z \quad N = 103, r = 0.961, P < 0.001$$

Table 13 Investigation of the relation between various parameters and the natural mortality rate  $M$  in unexploited populations using five-way, full-interaction ANOVA,  $N = 92$  (significant terms shown only). Independent variables:  $\log(M_{\text{Max}})$ ,  $\log(1/A_{\text{Max}})$ ,  $1/T$ ,  $\log(D+1)$  and taxon (substem/system). Dependent variable: natural mortality rate  $\log(M)$ .

## (a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
$\log(1/A_{\text{Max}})$	1	10.732	10.732	265.009	<0.001
$\log(D+1)$	1	0.574	0.574	14.161	<0.001
$(1/T) \log(D+1)$	1	0.581	0.581	14.343	<0.001
$\log(1/A_{\text{Max}}) \log(D+1)$	1	0.186	0.186	4.582	0.035
Residual	87	3.523	0.041		

(b) Model coefficients ( $N = 92$ ,  $r = 0.921$ ).

Variable	Coefficient	SE	P
Intercept	0.687	0.058	<0.001
$\log(1/A_{\text{Max}})$	1.129	0.069	<0.001
$\log(D+1)$	4.050	1.076	<0.001
$(1/T) \log(D+1)$	-1139.373	300.850	<0.001
$\log(1/A_{\text{Max}}) \log(D+1)$	-0.140	0.065	0.035

SE, standard error.

(1980) found an empirical relationship between  $M$  and parameters of the VBGF as well as temperature which can be used to estimate  $M$  in exploited populations. In the following I will analyse whether or not similar empirical relationships exist for benthic invertebrates.

## 4.3.1. Direct Estimation of Natural Mortality Rate

Based on Pauly's (1980) approach and the correspondence of the VBGF parameters  $K$  and  $M_{\infty}$  to the parameters  $A_{\text{Max}}$  and  $M_{\text{Max}}$  (see Section 3), I used a multiple linear model to analyse the relationship between the mortality rate  $M$  and various parameters. The resulting model is highly significant ( $N = 92$ ,  $r = 0.921$ ), but rather complex with interactions between  $1/A_{\text{Max}}$ , temperature and water depth which are not easy to interpret (Table 13). In contrast to Pauly's (1980) model, no effect of body mass ( $M_{\text{Max}}$ ) was detectable. The plot of fitted versus measured values of the mortality rate  $M$  (Figure 13) indicates considerable variance, which

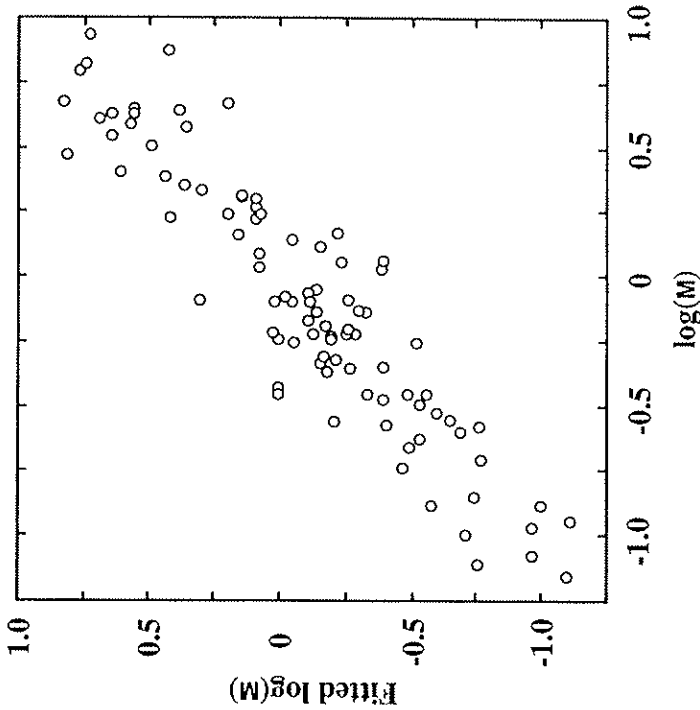


Figure 13 Natural mortality rate  $M$ . Fitted values (model in Table 13) versus measured values.

makes any estimate of natural mortality by this empirical model rather doubtful. More data on mortality are required to improve the performance of this model.

## 4.3.2. Indirect Estimation of Natural Mortality Rate

As shown above (equation (11)), the annual mortality rate  $Z$  and the annual  $P_s/B$  ratio of benthic invertebrates are linearly related. Hence, we can use  $P_s/B$  as a substitute for the indirect estimation of the mortality rate  $M$  from other population parameters. This approach may benefit from the much higher number of  $P_s/B$  data available.

Previous models of this kind established by Warwick (1980), Hoenig (1983) and Etim and Brey (1994) used only one independent variable,  $A_{\text{Max}}$ , to estimate the annual  $P_s/B$  ratio. Here, the combination of the parameters  $A_{\text{Max}}$ ,  $M_{\text{Max}}$  and temperature resulted in a highly significant

Table 14 Investigation of the relation between various parameters and the annual  $P_s/B$  ratio in unexploited populations using five-way, full-interaction ANOVA,  $N = 837$  (significant terms shown only). Independent variable: annual productivity ratio  $\log(P_s/B)$ . Dependent variables:  $\log(M_{Max})$ ,  $\log(1/A_{Max})$ ,  $1/T$ ,  $\log(D+1)$  and taxon (substem/stem).

## (a) ANOVA.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
$\log(1/A_{Max})$	1	85.980	85.980	1655.421	<0.001
$\log(M_{Max})$	1	0.656	0.656	12.635	<0.001
$1/T$	1	0.268	0.268	5.156	0.023
Residual	833	43.265	0.052		

(b) Model coefficients ( $N = 837$ ,  $r = 0.935$ ).

Variable	Coefficient	SE	P
Intercept	1.684	0.466	<0.001
$\log(1/A_{Max})$	0.993	0.024	<0.001
$\log(M_{Max})$	-0.035	0.010	<0.001
$1/T$	-303.904	133.837	0.023

SE, standard error.

multiple model (Table 14). Variability (Figure 14) is slightly lower than in the above model used to estimate  $M$  directly but much lower than in the previous models using only  $A_{Max}$  to estimate  $P_s/B$ .

The relation between mortality rate and productivity is highly significant (equation (12)), and these two models are suitable for estimations of the natural mortality rate  $M$  in benthic invertebrate populations. Confidence limits of the estimate of  $M$  can be computed according to Draper and Smith (1981). A problem remaining with intensely exploited populations is correctly estimating of  $A_{Max}$  and  $M_{Max}$ , because heavy fishing tends to remove all large specimens from the population. In those cases, independent estimates of  $A_{Max}$  and  $M_{Max}$ , i.e. from unexploited populations or from pre-exploitation times, may be required.

An Excel spreadsheet containing calculation routines for estimating population parameters is available from the author.

#### 4.4. Mortality and Taxonomic Position

Mortality rates may be typical for a certain species, but in contrast to overall growth performance they cannot be interpreted as a species-

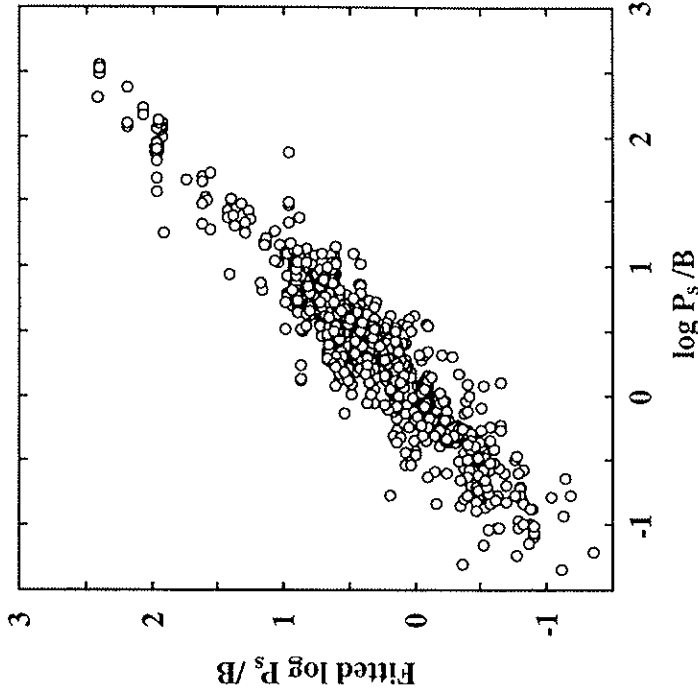


Figure 14 Annual  $P_s/B$  ratio. Fitted values (model in Table 14) versus measured values.

specific feature. Mortality is the product of "outside" forces such as predation which act within the limits given by prey population parameters such as growth and recruitment, that is, to maintain a steady state, the mortality suffered by a population cannot exceed the level determined by the productivity of the population (see above), which in turn depends on the growth and recruitment rates. Therefore, the mortality rate is related to various population parameters, e.g.  $A_{Max}$  and  $M_{Max}$  (see above) or the growth constant  $K$  of the VBGF (Brey and Gage, 1997). It is, however, not subject to the evolution of the species by itself, but the levels of mortality observed in natural populations are the products of the coevolution of prey and predator species.

Nevertheless we are able to identify taxon-specific differences in mortality. Figure 15 indicates clearly that although there is a wide variability of productivity ( $\approx$  mortality) values within each taxonomic order/subclass, taxa consisting mainly of small, short-lived species (e.g.

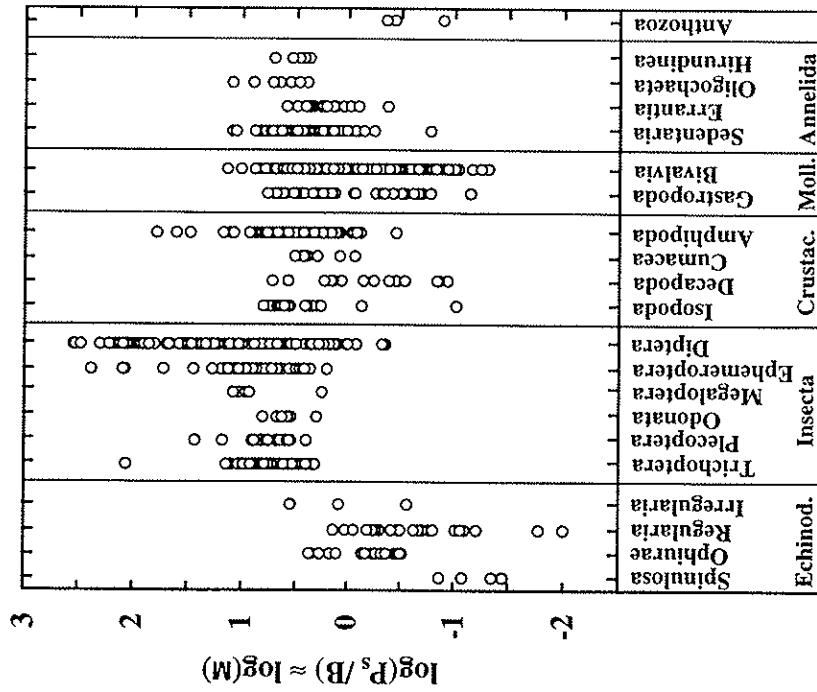


Figure 15 Annual  $P_s/B$  ratio ( $\approx$  natural mortality rate  $M$ ) in various benthic invertebrate orders/subclasses.

orders/subclasses of the Insecta) are separated from taxa consisting of large, long-lived species (e.g. orders/subclasses of the Echinodermata).

**5. RELATIONSHIPS BETWEEN GROWTH PERFORMANCE, MORTALITY AND PRODUCTIVITY**

The previous section showed that the mortality rate  $Z$  and somatic productivity  $P_s/B$  are mathematically and statistically (equations (10) and

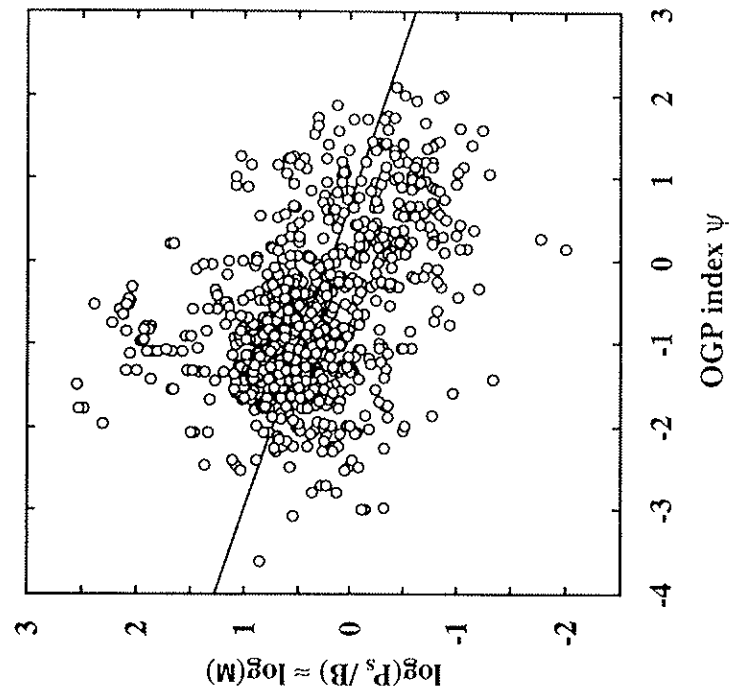


Figure 16 Empirical relation between the index of overall growth performance  $\psi$  and the annual  $P_s/B$  ratio in benthic invertebrate populations.

$\log(P_s/B) = 0.193 - 0.269 \psi \quad N = 860, r = -0.411, P < 0.001$

(11)) closely related. For populations in a steady state we can assume that  $Z \approx P_s/B$ . On the other hand,  $P_s/B$ , and hence  $Z$ , do not correlate well with the overall growth performance index  $\psi$ .

$\log(P_s/B) = 0.193 - 0.269 \psi \quad N = 860, r = -0.411, P < 0.001$  (12)

The relationship is not only weak, but also negative (Figure 16). This discrepancy is related to the well-documented negative relationship between the population  $P_s/B$  ratio and individual body mass (e.g. see Barse and Mosher, 1980; Schwinghamer *et al.*, 1986; Plante and Downing, 1989; Brey, 1990; Morin and Bourassa, 1992; Brey and Clarke, 1993; Tumbiolo and Downing, 1994; for theoretical background, see Schmidt-Nielsen, 1984; Peters, 1986; Reiss, 1991). Populations with a high  $P_s/B$  ratio

consist of fast-growing but small individuals, a combination which cannot result in high values of OGP (equation (5)).

Obviously, maximizing OGP and maximizing  $P_s/B$  are different if not opposite ecological strategies. Remarkably, the interest of human exploitation focuses on those species with high OGP (see Section 4) and not on those with a high  $P_s/B$  ratio, although these populations would offer a higher maximum sustainable yield. Concerning this choice of food, however, humans fit well into the general picture of positive correlation between predator and prey size (see Krebs, 1984). Man just seems to follow the ecological principle of maximizing foraging efficiency by concentrating on larger prey species.

#### ACKNOWLEDGEMENTS

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