

Interactions of growth and mortality in benthic invertebrate populations: Empirical evidence for a mortality-growth continuum*

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Abstract

Data from unexploited populations confirm a continual relation between growth rate and mortality rate in benthic invertebrates. They indicate a limited range of mortality attributable to a given growth rate, which may reflect a "mortality-growth continuum" of predator-prey relations ranging from "low mortality" to "high mortality" strategies in prey populations. An index based on the empirical relation between growth and mortality can be used to determine the position of a population in the "mortality-growth continuum". This index expresses relative predation pressure and may also be used to check for potential overfishing in exploited stocks of benthic invertebrates, when more sophisticated measures are not available.

Kurzfassung

Wechselwirkungen zwischen Wachstum und Sterblichkeit in benthischen Evertebraten: Empirische Hinweise auf ein Wachstum-Sterblichkeits-Kontinuum

Empirische Daten zeigen, daß in Populationen benthischer Evertebraten eine stetige Beziehung zwischen individuellen Wachstum und Sterblichkeit besteht. Offensichtlich kann bei einer gegebenen Wachstumsrate die Sterblichkeitsrate nur innerhalb eines bestimmten Bereichs liegen. Dieser Bereich könnte ein "Wachstum-Sterblichkeits-Kontinuum" repräsentieren, das verschiedene Überlebensstrategien von Beutepopulationen reflektiert. Mit einem aus der empirischen Beziehung zwischen Wachstum und Sterblichkeit abgeleiteten Index kann die Position einer Population im "Wachstum-Sterblichkeits-Kontinuum" bestimmt werden. Dieser Index drückt den relativen Raubdruck auf die Population aus und kann auch dazu verwendet werden, Überfischung in genutzten Beständen anzuzeigen.

Resumen

Interacción entre crecimiento y mortalidad en invertebrados bentónicos: datos empíricos de un continuo crecimiento-mortalidad.

Datos procedentes de poblaciones no explotadas de invertebrados bentónicos, confirman una relación continua entre tasas de crecimiento y mortalidad. Ello indica un rango limitado de mortalidad, atribuible a una tasa de crecimiento dada, que puede reflejar un "continuo" en la relación mortalidad-crecimiento de las relaciones predador-presa, variando desde estrategias de baja hasta estrategias de alta mortalidad en las poblaciones de presas. Un índice basado en la relación empírica entre crecimiento y mortalidad, puede emplearse para determinar la posición de una población en el "continuo" mortalidad-crecimiento. Este índice expresa la presión de producción relativa y puede usarse también, cuando formas de medición más sofisticadas no pueden ser empleadas, para conocer la sobrecaptura en stocks explotados de invertebrados bentónicos.

Introduction

The fate of natural populations is controlled by the three processes of individual growth, mortality and recruitment, and the variability of these in space and time. Individual growth, i.e. the increase in body mass with time, is assumed to be an age- and size-dependent process taking place within species-specific, genetically determined limits (see e.g. Peters 1986, Reiss 1991). Nevertheless, growth is affected by environmental factors such as food availability and temperature, which can cause remarkable intraspecific variability in growth rates (e.g. Appeldoorn 1981, Gilbert 1973, Selin *et al.* 1992).

Mortality 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 to longevity, such as the more or less synchronous death of adults after reproduction; and (iii) the continuous decrease in number of an age class with time, a process caused e.g. by predation, parasitism and disease. The latter is the type of mortality we will deal with here.

Recruitment, i.e. the addition of young individuals to the population, depends on many factors such as age at first maturity, age structure of the population, individual reproductive capacity and larval mortality.

In a steady state the three processes of growth, mortality and recruitment are balanced in a way that the population shows stationary size and age distribution.

Theoretically, the mortality of a population with constant individual growth and a constant number of recruits per unit of time could range within wide limits without departing from a steady state. On the one hand, mortality will be close to zero if losses caused by predation, parasitism and diseases are negligible. On the other hand, mortality is limited by the requirement for a sufficient number of animals to reach maturity and reproduce, which in turn depends on how fast the animals grow. Obviously, there is a general positive relation between growth and mortality, which has been shown empirically for finfish by Beverton and Hold (1959), Pauly (1980) and others.

Table 1. 83 data sets of mortality rate Z and growth constant K of unexploited benthic populations. A: Amphipoda, B: Bivalvia, D: Decapoda, E: Echinoidea, G: Gastropoda, H: Holothuroidea, I: Isopoda, O: Ophiuroidea, P: Polychaeta.

Species	Taxon	Autor	K (y ⁻¹)	Z (y ⁻¹)
<i>Aega antarctica</i>	I	Wägele 1990	0.120	0.130
<i>Anodonta grandis</i>	B	Huebner <i>et al.</i> 1990	0.105	0.218
<i>Anodonta grandis</i>	B	Hanson <i>et al.</i> 1988	0.231	0.183
<i>Anodonta piscinalis</i>	B	Tudorancea and Florescu 1969	0.358	0.265
<i>Arctica islandica</i>	B	Brey <i>et al.</i> 1990	0.070	0.350
<i>Bivalvia gigantea females</i>	A	Thurston 1968,70	0.268	0.729
<i>Bivalvia gigantea females</i>	A	Bone 1972	0.154	0.889
<i>Bivalvia gigantea males+juv.</i>	A	Thurston 1968,70	0.371	0.801
<i>Bivalvia gigantea males+juv.</i>	A	Bone 1972	0.396	1.385
<i>Cardium corbis</i>	B	Taylor 1960	0.540	0.525
<i>Cardium corbis</i>	B	Taylor 1960	0.620	0.594
<i>Cardium corbis</i>	B	Taylor 1960	0.240	0.286
<i>Cardium corbis</i>	B	Taylor 1960	0.260	0.384
<i>Cardium corbis</i>	B	Taylor 1960	0.250	0.258
<i>Cardium corbis</i>	B	Taylor 1960	0.210	0.225
<i>Cardium edile</i>	B	Boydén 1972	0.699	0.990
<i>Cassidulus minis</i>	E	Freire <i>et al.</i> 1992	0.390	0.812
<i>Chamaelea gallina</i>	B	Ramón and Richardson 1992	1.162	4.687
<i>Chorismas antarcticus</i>	D	Gorny <i>et al.</i> 1993	0.348	0.731
<i>Cirrolana imposita</i>	I	Shafir and Field 1980	0.465	1.728
<i>Conus pennaceus</i>	G	Perron 1983	0.315	0.530
<i>Corbicula fluminea</i>	B	Marsh 1985	1.082	4.390
<i>Corbicula fluminea</i>	B	Marston 1977	0.340	1.739
<i>Dichelopandalus bonnier</i>	A	Al-Adhub and Bowers 1977	0.638	1.555
<i>Dichelopandalus bonnier</i>	A	Al-Adhub and Bowers 1977	0.557	1.569
<i>Donax incarnatus</i>	B	Ansell <i>et al.</i> 1972a,b	1.812	7.483
<i>Dosinia hepatica</i>	B	Hanekom 1986	0.489	0.568
<i>Echinus affinis</i>	E	Gage and Tyler 1985	0.100	0.236
<i>Exonolis mucronata</i>	P	Kemp 1988	0.768	1.948
<i>Halotis tris</i>	G	Sainsbury 1982	0.163	0.077
<i>Hyattella byssifera</i>	B	Petersen 1978	0.232	0.280
<i>Holothuria atra</i>	H	Ebert 1978	0.110	0.549
<i>Leatella pustulosa</i>	B	Gage 1991	0.500	0.426
<i>Lissarca notorcadensis</i>	B	Brey and Hain 1992	0.085	0.319
<i>Littorina africana</i>	C	McQuaid 1981	0.703	2.027
<i>Macoma balthica</i>	B	Green 1973	0.273	0.394
<i>Macoma balthica</i>	B	McGreer 1983	0.611	1.290
<i>Macoma balthica</i>	B	Chambers and Milne 1975	0.234	1.139
<i>Macoma balthica</i>	B	Katanov 1985	0.238	1.067
<i>Melina palmata</i>	P	Lastra <i>et al.</i> 1993b	0.749	1.996
<i>Mercenaria mercenaria</i>	B	Hibbert 1976, 77a,b	0.182	0.448
<i>Mercenaria mercenaria</i>	B	Kennish and Loveland 1980	0.169	0.520
<i>Mesodema arcuatum</i>	B	Brethes <i>et al.</i> 1986	0.234	0.263
<i>Modiolus modiolus</i>	B	Anwar <i>et al.</i> 1990	0.092	0.170

Species	Taxon	Author	K (y ⁻¹)	Z (y ⁻¹)
<i>Modiolus modiolus</i>	B	Anwar <i>et al.</i> 1990	0.079	0.238
<i>Mona atropes</i>	E	Moore and Lopez 1966	0.880	0.830
<i>Monodonta lineata</i>	G	Williamson and Kendall 1981	0.794	0.638
<i>Mya arenaria</i>	B	Feder and Paul 1974	0.048	0.114
<i>Mya arenaria</i>	B	Munch-Petersen 1973	0.297	0.640
<i>Mya truncata</i>	B	Petersen 1978	0.090	0.140
<i>Mya truncata</i>	B	Petersen 1978	0.065	0.250
<i>Mya truncata</i>	B	Petersen 1978	0.033	0.100
<i>Mytilus galloprovincialis</i>	B	Ceccherelli and Rossi 1984	0.660	0.969
<i>Nacella concinna</i>	G	Picken 1980	0.051	0.196
<i>Nacella delesserti</i>	G	Blankley and Branch 1985	0.197	0.343
<i>Notacmaea scutum</i>	G	Phillips 1981	1.278	2.050
<i>Nucella lapillus</i>	G	Hughes 1972	0.190	0.350
<i>Nucella turgida</i>	B	Warwick and George 1980	0.531	0.599
<i>Ophiocottus gracilis</i>	O	Gage and Tyler 1982	0.386	0.811
<i>Ophiocottus hexactis</i>	O	Morison 1979	0.160	0.397
<i>Ophiona ljungmani</i>	O	Gage and Tyler 1982	0.101	0.535
<i>Ophiona ljungmani</i>	O	Gage and Tyler 1981	0.101	1.146
<i>Parhyale hians</i>	A	Ali and Saliman 1987	1.493	1.200
<i>Parvicardium exiguum</i>	B	Lastra <i>et al.</i> 1993a	2.813	4.588
<i>Pecten maximus</i>	B	Baird 1966	0.431	0.232
<i>Pectinaria koreni</i>	P	Nicolaïdou 1983	3.183	7.300
<i>Psammochinus militaris</i>	E	Jensen 1969	0.170	0.190
<i>Saxidomus gigantea</i>	B	Paul <i>et al.</i> 1976	0.026	0.102
<i>Sevelis politica</i>	I	Lunmoore 1981, 82a,b, 85	0.366	0.626
<i>Scololepis gaucha</i>	P	Santos 1994	2.950	11.354
<i>Spisula sachalinensis</i>	B	Kang and Kim 1983	0.263	0.639
<i>Sterechinus antarcticus</i>	E	Brey 1991	0.017	0.070
<i>Strongylocentrotus droeb.</i>	E	Miller and Mann 1973	0.182	0.799
<i>Strongylocentrotus purpuratus</i>	E	Kenner 1992	0.326	1.227
<i>Talorchestia capensis</i>	A	Senus and McLachlan 1986	0.378	0.210
<i>Tapes philippinarum</i>	B	Yap 1977	0.913	2.406
<i>Tellina fabula</i>	B	Salzwedel 1979a,b	0.966	1.990
<i>Tellina fabula</i>	B	Salzwedel 1979a,b	0.631	1.725
<i>Unio tumidis</i>	B	Tudorancea and Florescu 1968	0.209	0.352
<i>Yoldia eightsi</i>	B	Nolan 1987, 88	0.062	0.130
<i>Yoldia eightsi</i>	B	Rabarts 1970	0.062	0.114
<i>Yoldia limatula</i>	B	Lewis <i>et al.</i> 1982	0.468	0.803

The purpose of this paper is to investigate the kind and the strength of the links between growth and mortality in marine benthic invertebrate populations. Subsequently we will discuss potential use of growth-mortality relations in interpreting the underlying processes in population dynamics and their ecological, as well as evolutionary background.

Empirical evidence

We collected data from the literature on the growth and mortality of 83 unexploited marine macrobenthic populations. The figures for growth were derived from the specialised von Bertalanffy function and for mortality, from the single negative exponential

model (Table 1). All populations were assumed to be in a steady state, which was quite likely, due to the persistence of most of the populations at the individual investigation sites over a period of several years. In several cases either the growth constant K or the mortality rate Z were not given directly and had to be computed from other information provided, such as growth curves and size frequency data. A log-log regression of the two variables (Fig. 1) showed a strong positive relation between the growth constant K and the mortality rate Z, which was almost linear:

$$\log(Z) = 0.339 + 1.037 \times \log(K) \quad r^2 = 0.695$$

Analysis of variance failed to detect any significant effects ($\alpha = 0.05$) of other parameters such as taxon (Mollusca - Crustacea - Echinodermata), living mode (infauna - epifauna, motile - sessile), feeding type (suspension feeder - deposit feeder - grazer - predator) or temperature on the above relation. The maximum variability of Z is about one order of magnitude for any given value of K.

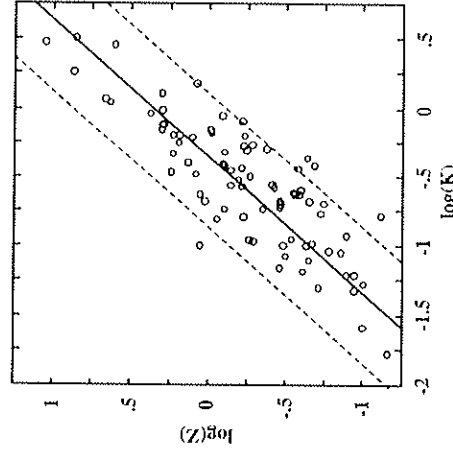


Figure 1: Empirical relation between growth constant K of the VBGF and mortality rate Z in 83 unexploited benthic invertebrate populations. Stippled lines indicate band of one order of magnitude width. Geometric mean regression according to Ricker (1973).

Discussion

Data base and data variability

Our data indicate that the positive relation between growth rate and mortality rate observed in finfish (e.g. Beverton and Hold 1959, Pauly 1980) also holds true for unexploited benthic marine invertebrate populations. Containing 83 populations and 60 species only, our data base may be rather small compared to the large number of benthic species inhabiting the world's waters. This may also explain why we could not detect significant effects of other parameters, such as asymptotic length L_{∞} and temperature (as found by Pauly 1980) on the mortality rate. However, degree of fit of Pauly's three-parameter-model ($r^2 = 0.717$) is not distinctly better than our one-parameter

ameter-model ($r^2 = 0.695$), and the range of residuals is the same in both cases (Pauly 1980: -0.9 to $+0.7$; this study: -0.7 to $+0.8$).

Additionally, our selection, although including all data available in the literature, is likely to be not very representative of the benthos in general. This is due to the preferences of investigators around the world which work e.g. mainly on molluscs and neglect polychaetes. The assumption of a steady state in all the populations may be problematic too. Although all of them have been persistent over longer periods of time, this does not necessarily indicate a steady state. Pooling of many populations, which may be in different stages of random fluctuation around a steady state may increase variability, but is unlikely to falsify the observed positive relation between growth and mortality.

The positive relation between growth rate and mortality rate itself may be a rather trivial observation. However, the distinct variability in this relation – for a given K , Z varies by approximately one order of magnitude (Fig. 1) – is likely to have some ecological significance.

Evolution and ecological strategies

If we interpret the variability of Z (in relation to K) in terms of ecological strategies, then the extreme cases of the mortality/growth relation may characterise two opposite strategies: On the one hand, "low mortality" populations are relatively well protected against predation and maximize population biomass by maintaining a large fraction of older specimens which, however, reduces ecological efficiency and turnover because a greater fraction of the assimilated energy is needed for body maintenance. On the other hand, "high mortality" populations are exposed to high predation pressure, but they maximize ecological efficiency, recruitment and rate of turnover. The empirical data (Table 1, Fig. 1) indicate a continuum extending from a high mortality/growth to a low mortality/growth relationship. In other words, there is a natural range of variability of Z associated with particular values of K , which seems to be in the range of one order of magnitude in macrobenthic populations. If these observations are generally valid, we can conclude stable predator-prey relationships can only exist within certain limits of exploitation of the prey population, no matter which benthic community, taxon, living- or feeding type of prey is being considered.

The limited data base does not allow us to decide whether environmental or evolutionary forces cause the variability in the relationship between K and Z . If the influences are evolutionary, this would provide some insight into the co-evolution of prey and predators in benthic communities. A mortality rate distinctly higher than predicted by the regression line, would indicate that this prey population is exposed to (with respect to all populations observed) higher-than-average exploitation by its predators. To maintain a steady state, this has to be compensated for by a comparatively higher recruitment rate, i.e. more recruits per adult specimen. This can be achieved by higher-than-average gonad productivity, lower age at maturity or enhanced larval survival. However, the limited variability of Z (Fig. 1) indicates that recruitment rate will not exceed certain limits in benthic populations; these limits may be determined either by physiological (e.g. individual reproductive effort) or by ecological (e.g. larval survival) parameters.

A mortality rate distinctly lower than predicted by the regression would indicate successful protection strategies. This may be achieved by protective body structures (spines, thick shells etc.), by chemical defences, or by living out of reach of predators, e.g. occupying a size range beyond any predators handling capacity, or hiding in deep burrows. Again, however, Fig. 1 indicates that there are limits to this strategy. Z will not be reduced deliberately, indicating that a certain amount of mortality always has to be accepted.

Both the lower and the upper empirical limit of the mortality - growth relation may well reflect the borders beyond which the corresponding strategies, "low mortality" strategy and "high mortality" strategy, are energetically too costly to be maintained under steady state conditions.

The mortality - growth continuum

There seem to be some connections between our "mortality - growth" -continuum and the well-known r - K continuum of population strategies (MacArthur and Wilson 1967, Pianka 1970, Stearns 1976). The r - K continuum is based on opposite strategies of population growth. At the one end of the r - K continuum there are the "opportunistic type" populations with emphasize fast increase of population size by high rate of increase r ($dN/dt = r \cdot N$), whenever and wherever conditions are favourable. At the opposite end are the "climax type" populations, which emphasize maximum exploitation of the carrying capacity K ($dN/dt = r \cdot ((K-N)/K) \cdot N$) of their habitat. Characteristic features of "opportunistic type" life histories include fast individual growth to maturity, short generation time and high recruitment rate (Stearns 1976). These are in turn always associated with high mortality, provided the time scale of observation is sufficiently long to assume steady state. Species with "climax type" life histories tend to maintain high population biomass. According to Stearns (1976), they exhibit later maturity, longer lifespan and low recruitment rate, which is partially caused by intraspecific competition (e.g. Jarayabhand and Newkirk 1989, Peterson 1982).

The connections between the r - K continuum and the mortality - growth continuum are obvious, but our investigation is limited to populations in steady state and meeting certain conditions of growth and mortality. Hence we deal only with a small aspect of the whole theory of the r - K continuum. In contrast to the r - K continuum, however, the position of a population in the "mortality - growth" continuum can be determined mathematically by means of the empirical relation between K and Z (Fig. 1). It can be expressed as the deviation from the common $\log(Z)$ - $\log(K)$ regression line on a logarithmic scale:

$$\Delta Z:K = \log(Z_{\text{measured}}/Z_{\text{predicted}}) \quad -\infty < \Delta Z:K < \infty$$

where $\log(Z_{\text{predicted}})$ is computed by inserting K_{measured} in the common regression equation:

$$\log(Z_{\text{predicted}}) = 0.339 + 1.037 \times \log(K_{\text{measured}})$$

$\Delta Z:K$ is a measure of relative predation pressure. Negative values of $\Delta Z:K$ indicate a lower than average mortality-to-growth ratio, positive values indicate a higher than average relation for the population in question. Those species with the largest deviation included here, *Haliotis iris* and *Ophura ljunghmani*, would have $\Delta Z:K$ values of -0.627 and -0.759 , respectively. This measure can be applied in various ways:

Table 2. 22 data sets of mortality rate Z and growth constant K of exploited benthic populations. Taxa abbreviations see Table 1.

Species	Taxon	Author	K (y ⁻¹)	Z (y ⁻¹)
<i>Anusium pleuronectes</i>	B	Del Norte 1988	0.930	7.200
<i>Anusium pleuronectes</i>	B	Nigranad 1988	1.300	7.200
<i>Anadara granosa</i>	B	Ng 1986	0.600	4.060
<i>Anadara granosa</i>	B	Ng 1986	0.550	3.240
<i>Anadara granosa</i>	B	Ng 1986	0.790	4.120
<i>Anadara granosa</i>	B	Ng 1986	0.780	3.660
<i>Anadara granosa</i>	B	Ng 1986	0.870	2.930
<i>Cancer polyodon</i>	D	Wolff and Soto 1992	0.570	1.850
<i>Cancer polyodon</i>	D	Wolff and Soto 1992	0.540	2.560
<i>Cardium edule</i>	B	Boyden 1972	0.660	0.990
<i>Chlamys opercularis</i>	B	Taylor and Venn 1978	0.508	0.504
<i>Chlamys varia</i>	B	Conan and Shatee 1978	0.454	0.543
<i>Egeria radiata</i>	B	Etim and Brey 1993	0.828	2.030
<i>Fisurella crassa</i>	G	Bretos 1980	0.159	0.465
<i>Fisurella maxima</i>	G	Bretos 1982	0.315	0.860
<i>Mesodema donacium</i>	B	Arniz et al. 1987	0.380	2.500
<i>Perna perna</i>	B	Berry 1978	0.960	4.618
<i>Perna perna</i>	B	Berry 1978	0.960	4.799
<i>Perna picta</i>	B	Shatee 1992	0.552	1.366
<i>Placopecten magellanicus</i>	B	Posgay 1979	0.370	0.800
<i>Turbo sarmaticus</i>	G	McLachlan and Lombard 1980	0.271	0.810
<i>Venus antiqua</i>	B	Clasing et al. 1994	0.183	0.664

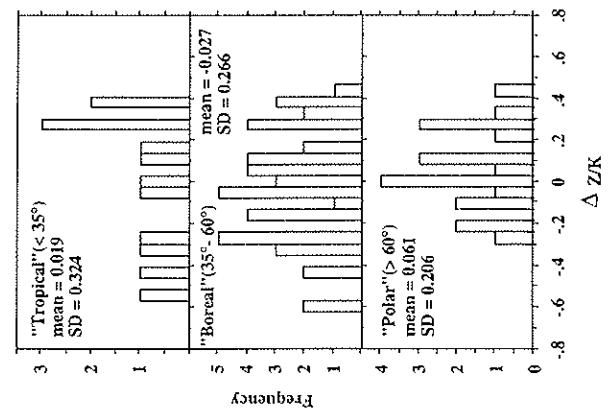


Figure 2. Comparison of $\Delta Z/K$ in tropical ($N = 13$), boreal ($N = 45$), and polar ($N = 20$) benthic invertebrate populations. Deep sea (> 500 m) populations are excluded.

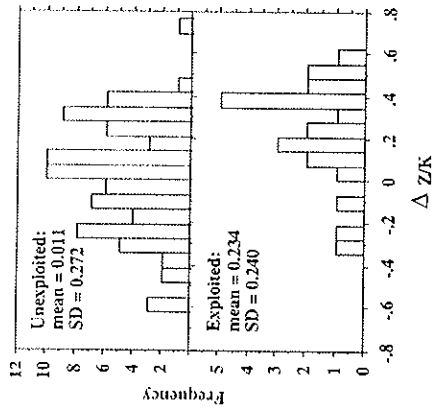


Figure 3. Comparison of $\Delta Z/K$ in 83 unexploited and 22 exploited benthic invertebrate populations.

(i) It may be used at the species level, i.e. to compare different populations of a certain species. Due to the lack of appropriate data we cannot give an example here.

(ii) It can be used to compare ecosystems or regions (see Dobzhansky 1950 and MacArthur and Wilson 1967). Fig. 2 gives one example, where the data (Table 1) are roughly grouped into "polar", "boreal", and "tropical" populations. According to Dobzhansky (1950) tropical populations should tend more towards "climax type" life histories than boreal ones, i.e. they should have lower $\Delta Z/K$ values. The results do not indicate significant differences between the three regions (ANOVA, $P = 0.4555$), but this may be due to insufficient and unevenly distributed data.

(iii) Another potential application may be the use of $\Delta Z/K$ as a simple indicator of overfishing in exploited stocks of benthic invertebrates. Fig. 3 shows a comparison of $\Delta Z/K$ values of 22 exploited populations (Table 2) and $\Delta Z/K$ values of the unexploited populations in Table 1.

The mean $\Delta Z/K$ of exploited stocks (0.234, $SD = 0.240$) is significantly ($P < 0.001$) higher than the mean $\Delta Z/K$ of unexploited stocks (0.011, $SD = 0.272$). This clearly indicates that exploitation by man puts a comparatively high pressure on the fished invertebrate populations, i.e. the potential fishery induced increase in growth rate does not compensate for the increased mortality level.

The above examples demonstrate how the $\Delta Z/K$ concept can be used in ecological as well as resource management investigations. However, results derived from the actual regression equation using only 83 data sets (Table 1), should be interpreted with care. The data are heavily biased towards molluscs and echinoderms; greater taxonomic diversity and more data sets are required to improve the validity of this relation.

References

- Al-Adhub, A.H.Y.; Bowers, A.B., 1977: Growth and breeding of *Dichelopandalis bonnieri* in Isle of Man waters. J. Mar. Biol. Ass. U.K. 57: 229-238.
- Ali, M.H.; Salman, S.D., 1987: Growth and production of the amphipod *Polydora basensis* (Talitridae) in the Shatt al-Arab region. Mar. Ecol. Prog. Ser. 40: 231-238.
- Allen, K.R., 1971: Relation between production and biomass. J. Fish. Res. Board. Can. 28: 1573-1581.
- Ansell, A.D.; Sivadas, P.; Narayanan, B.; Sankaranarayanan, V. N.; Trevallion, A., 1972a: The ecology of two sandy beaches in south west India. I. Seasonal changes in physical and chemical factors, and in the meiofauna. Mar. Biol. 17: 38-62.
- Ansell, A.D.; Sivadas, P.; Narayanan, B.; Trevallion, A., 1972b: The ecology of two sandy beaches in South West India. III. Observations on the population of *Donax incarnatus* and *D. spiculorum*. Mar. Biol. 17: 318-332.
- Anwar, N.A.; Richardson, C.A.; Seed, R., 1990: Age determination, growth rate and population structure of the horse mussel, *Modiolus modiolus*. J. Mar. Biol. Ass. U.K. 70: 441-457.
- Appeldoorn, R.S., 1981: Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principal component analysis and the omega parameter of the von Bertalanffy equation. Fish. Bull. U.S. 81: 75-84.
- Arntz, W. E.; Brey, T.; Tarazona, J.; Robles, A., 1987: Changes in the structure of a shallow sandy-beach community in Peru during an el Niño event. In: Payne, A.I.; Galwin, Sales (eds.): The Benguela and comparable ecosystems. S. Afr. J. Mar. Sci. 5: 645-658.
- Baird, R.H., 1966: Notes on an scallop (*Pecten maximus*) population in Holyhead harbour. J. Mar. Biol. Ass. U.K. 46: 33-47.
- Berry, P. F., 1978: Reproduction, growth and production in the mussel, *Perna perna* (Linnaeus), on the east coast of South Africa. Invest. Rep. Oceanogr. Res. Inst., Durban 48: 1-28.
- Beverton, R.J.H.; Hold, S.J., 1959: A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: Wolstenholme, G.E.W.; O'Connor, M. (eds.): Ciba foundation colloquium on ageing: the lifespan of animals. London: Churchill, p. 142-177.
- Blankley, W.O.; Branch, G.M., 1985: Ecology of the limpet *Nacella deloesseri* (Philippi) at Marion Island in the sub-Antarctic Southern Ocean. J. Exp. Mar. Biol. Ecol. 92: 259-281.
- Bone, D.G., 1972: Aspects of the biology of the Antarctic amphipod *Borealia gigantea* Pfeffer at Signey Island, South Orkney Islands. Br. Antarct. Surv. Bull. 27: 105-122.
- Boyden, C. R., 1972: Relations of size to age in the cockles *Cerastoderma edule* and *C. glaucum* from the river Crouch estuary, Essex. J. Conchology 27: 475-489.
- Bréthes, J.-C.; Desrosiers, G.; Fortin, G., 1986: Croissance et production du bivalve *Mesodesma arctatum* (Conrad) sur la côte nord du golfe du Saint-Laurent. Can. J. Zool. 64: 1914-1919.
- Bretos, M., 1980: Age determination in the keyhole limpet *Fissurella crassa* Lamarck (Archaeogastropoda: Fissurellidae), based on shell growth lines. Biol. Bull. 159: 606-612.
- Bretos, M., 1982: Biología de *Fissurella maxima* Sowerby (Mollusca: Archaeogastropoda) en el norte de Chile. I. Caracteres generales, edad y crecimiento. Cah. Biol. Mar. 23: 159-170.
- Brey, T., 1991: Population dynamics of *Sterechnis antarcticus* (Echinodermata: Echinoidea) on the Weddell Sea Shelf and slope, Antarctica. Antarct. Sci. 3: 251-256.
- Brey, T.; Arntz, W.E.; Pauly, D.; Rumohr, H., 1990: *Arctica (Cyprina) islandica* in Kiel Bay: Growth, production, and ecological significance. J. Exp. Mar. Biol. Ecol. 136: 217-235.
- Brey, T.; Hain, S., 1992: Growth, reproduction and production of *Lissarca noronadensis* (Bivalvia: Philobryidae) on the Weddell Sea shelf, Antarctica. Mar. Ecol. Prog. Ser. 82: 219-226.
- Ceccherelli, V.U.; Rossi, R., 1984: Settlement, growth and production of the mussel *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 16: 173-184.
- Chambers, M.R.; Milne, H., 1975: The production of *Macoma balthica* (L.) in the Ythan estuary. Estuar. Coast. Mar. Sci. 3: 443-455.
- Clasing, E.; Brey, T.; Stead, R.; Navarro, J.; Asencio, G., 1994: Population dynamics of *Venus antiqua* (Bivalvia: Veneracea) in the Bahía de Yaldad, Isla de Chiloe, southern Chile. J. Exp. Mar. Biol. Ecol. 177: 171-186.
- Conan, G.; Shafiq, M.S., 1978: Growth and biannual recruitment of the black scallop *Chlamys varia* (L.) in Lanveoc area, Bay of Brest. J. Exp. Mar. Biol. Ecol. 35: 59-71.
- Dobzhansky, T., 1950: Evolution in the tropics. Am. Nat. 38: 209-221.
- Ebert, T.A., 1978: Growth and size of tropical sea cucumber *Holothuria (Halodeima) atra* Jäger at Enewetak Atoll, Marshall Islands. Pac. Sci. 32: 183-191.
- Etim, L.; Brey, T., 1994: Growth, productivity, and significance for fishery of the bivalve *Egeria radata* (Donacidae) in the Cross River, Nigeria. Arch. Mar. Fish. Res. 42: 63-75.
- Feder, H. M.; Paul, A. J., 1974: Age growth and size-weight relationships of the soft-shell clam, *Mya arenaria*, in Prince William Sound, Alaska. Proc. Nat. Shellfish Ass. 64: 45-52239.
- Freire, C.A.; Santos, P.J.P.; Fontoura, N.F.; Magalhaes, R.A.O.; Grohmann, P.A., 1992: Growth and spatial distribution of *Cassidulus minis* (Echinodermata: Echinoidea) on a sandy beach in southeastern Brazil. Mar. Biol. 112: 625-630.
- Gage, J.D., 1991: Biological rates in the Deep Sea: A perspective from studies on process in the benthic boundary layer. Rev. Aquat. Sci. 5: 49-100.
- Gage, J.D.; Tyler, P.A., 1981: Re-appraisal of age composition, growth and survivorship of the Deep-Sea brittle star *Ophiothrix luingmani* from size structure in a sample time series from the Rockall Trough. Mar. Biol. 64: 163-172.
- Gage, J.D.; Tyler, P.A., 1982: Growth strategies in deep-sea ophiuroids. In: Lawrence, J.M. (ed.): Proceedings Int. Echinod. Conf. Tampa Bay. Rotterdam: Balkema, p. 305-311.
- Gage, J.D.; Tyler, P.A., 1985: Growth and recruitment of the deep-sea urchin *Echinus affinis*. Mar. Biol. 90: 41-53.
- Gage, J.D.; Tyler, P.A., 1981: Re-appraisal of age composition, growth and survivorship of the Deep-Sea brittle star *Ophiothrix luingmani* from size structure in a sample time series from the Rockall Trough. Mar. Biol. 64: 163-172.
- Gilbert, M.A., 1973: Growth rate, longevity, and maximum size of *Macoma balthica* (L.). Biol. Bull. 145: 119-126.
- Gorny, M.; Brey, T.; Arntz, W.E.; Bruns, T., 1993: Development, growth and productivity of *Chorismus antarcticus* (Crustacea: Decapoda: Natantia) in the eastern Weddell Sea, Antarctica. J. Exp. Mar. Biol. Ecol. 174: 261-275.
- Green, R.H., 1973: Growth and mortality in an arctic intertidal population of *Macoma balthica* (Pelecypoda, Tellinidae). J. Fish. Res. Bd. Canada 30: 1345-1348.
- Hanekom, N., 1986: Growth and somatic production estimates of *Dosinia hepatica* (Lamarck) (Mollusca: Bivalvia) in the Swartkops Estuary, South Africa. S.-Afr. Tydskr. Dierkd. 21: 325-330.

- Hanson, J.M.; Mackay, W.C.; Prepas, E.E., 1988: Population size, growth, and production of an unionid clam, *Anodonta grandis simpsoniana*, in a small, deep boreal forest lake in central Alberta. *Can. J. Zool.* 66: 247-253.
- Hibbert, C.J., 1976: Biomass and production of a bivalve community on an intertidal mudflat. *J. Exp. Mar. Biol. Ecol.* 25: 249-261.
- Hibbert, C.J., 1977a: Energy relations of the bivalve *Mercenaria mercenaria* on an intertidal mudflat. *Mar. Biol.* 44: 77-84.
- Hibbert, C.J., 1977b: Growth and survivorship in a tidal-flat population of the bivalve *Mercenaria mercenaria* from Southampton water. *Mar. Biol.* 44: 71-76.
- Huebner, J.D.; Malley, D.F.; Donkersloot, K., 1990: Population ecology of the freshwater mussel *Anodonta grandis grandis* in a precambrian shield lake. *Can. J. Zool.* 68: 1931-1941.
- Hughes, R.N., 1972: Annual production of two Nova Scotian populations of *Nucella lapillus* (L.). *Oecologia* 8: 356-370.
- Jarayaband, P.; Newkirk, G.F., 1989: Effects of intraspecific competition on growth of the European oyster, *Osstrea edulis* Linnaeus, 1750. *J. Shellfish Res.* 8: 359-365.
- Jensen, M., 1969: Age determination of echinoids. *Sarsia* 37: 41-44.
- Kafanov, A.I., 1985: Growth and production of the bivalve mollusc *Macoma balthica* in Nabil' lagoon (North-eastern Sakhalin). *Sov. J. Mar. Biol.* (English translation) 11: 313-320.
- Kang, Y.J.; Kim, C.K., 1983: Studies on the structure and production processes of biotic communities in the coastal shallow waters of Korea. 3. Age and growth of *Spisula salicincta* from the eastern waters of Korea. *Bull. Korean Fish. Soc.* 16: 82-87.
- Kemp, P.F., 1988: Production and life history of a deposit-feeding polychaete in an atypical environment. *Estuar. Coast. Shelf Sci.* 26: 437-446.
- Kenner, M.C., 1992: Population dynamics of the sea urchin *Strongylocentrotus purpuratus* in a central California kelp forest: recruitment, mortality, growth, and diet. *Mar. Biol.* 112: 107-118.
- Kennish, M.J.; Loveland, R.E., 1980: Growth models of the northern quahog, *Mercenaria mercenaria* (Linne). *Proc. Nat. Shellfish Ass.* 70: 230-239.
- Lastra, M.; Sánchez-Mata, A.; Mora, J., 1993a: Population dynamics and secondary production of *Parvicardium exiguum* (Gmelin, 1790) in the Santander Bay (N of Spain). *J. Moll. Stud.* 59: 73-81.
- Lastra, M.; Sánchez-Mata, A.; Palacio, J.; Mora, J., 1993b: Dinámica temporal y producción secundaria de *Melina palmata* Grube, 1870 en la Bahía de Santander (N de España). *Cah. Biol. Mar.* 34: 43-53.
- Lewis, J.B.; Saleh, S.; Reiswig, H.M.; Lalli, C.M., 1982: Growth, production and biomass of the burrowing protobranch mollusc *Yoldia limatula* in the Bidford River, Prince Edward Island, Canada. *Mar. Biol.* 70: 173-179.
- Luxmoore, R.A., 1981: The ecology of Antarctic Serolid isopods. Ph.D. thesis, British Antarctic Survey, Nat. Environ. Res. Council. 231 pp.
- Luxmoore, R.A., 1985: The energy budget of a population of the Antarctic isopod *Serolis pöhlta*. In: Siegfried, W.R.; Condy, P.R.; Laws, R.M. (eds): Antarctic nutrient cycles and food webs. Berlin: Springer, p. 389-396.
- Luxmoore, R.A., 1982: Moulting and growth in serolid isopods. *J. Exp. Mar. Biol. Ecol.* 56: 63-85.
- Luxmoore, R.A., 1982: The reproductive biology of some serolid isopods from the Antarctic. *Polar Biol.* 1: 3-11.
- MacArthur, R.H.; Wilson, E.O., 1967: The theory of island biogeography. Princeton: Princeton Univ. Press.
- Marsh, P.C., 1985: Secondary production of introduced Asiatic clam, *Corbicula fluminea*, in a central Arizona canal. *Hydrobiologia* 124: 103-110.
- McGreer, E.R., 1983: Growth and reproduction of *Macoma balthica* (L.) on a mud flat in the Fraser River estuary, British Columbia. *Can. J. Zool.* 61: 887-894.
- McLachlan, A.; Lombard, H.W., 1980: Growth and production in exploited and unexploited populations of a rocky shore gastropod, *Turbo sarmaticus*. *Veliger* 23: 221-229.
- McQuaid, C.D., 1981: Population dynamics of *Littorina africana knysnaensis* (Philippi) on an exposed rocky shore. *J. Exp. Mar. Biol. Ecol.* 54: 65-75.
- Miller, R.J.; Mann, K.H., 1973: Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. *Mar. Biol.* 18: 99-114.
- Moore, H.B.; Lopez, N.N., 1966: The ecology and productivity of *Moira atropes* (L.). *Bull. Mar. Sci.* 16: 648-667.
- Morrison G.W., 1979: Studies on the growth of the sub-antarctic ophiuroid *Ophionotus hexacis*. Ph.D. thesis, Univ. London. 213 pp.
- Morton, B.S., 1977: The population dynamics of *Corbicula fluminea* (Bivalvia: Corbiculacea) in Plover Cove Reservoir, Hong Kong. *J. Zool.* London 181: 21-42.
- Munch-Petersen, S., 1975: An investigation of a population of the soft clam (*Mya arenaria* L.) in a Danish estuary. *Meddel. Danm. Fisk.-og Havunders.* N.S. 7: 47-75.
- Nicolaïdou, A., 1983: Life history and productivity of *Pectinaria koreni* Malmgren (Polychaeta) Estuar. *Coast. Shelf Sci.* 17: 31-43.
- Ng, F.O., 1986: Growth and mortality of the Malaysian cockle (*Anadara granosa* L.) under development of small scale fisheries. BOBP/WP/47, *file* Vakily 1992. 21 pp.
- Nolan, C.P., 1987: Calcification and growth rates in Antarctic molluscs. British Antarctic Survey, Cambridge, AD6/2H/1987/N8. 8 pp.
- Nolan, C.P., 1988: Calcification and growth rates in Antarctic molluscs. British Antarctic Survey, Cambridge, AD6/2H/1988/N8. 12 pp.
- Norte, A.G.C. del, 1988: Aspects of the growth, recruitment, mortality and reproduction of the scallop *Amusium pleuronectes* (L.) in the Lingayen Gulf, Philippines. *Ophelia* 29: 153-168.
- Nugranod, J., 1988: Preliminary report on the growth, mortality and recruitment of the Asian moon scallop *Amusium pleuronectes* in Koh Chang (Koh Kood area), eastern Gulf of Thailand. Unpublished report, *file* Vakily 1992.
- Paul, A.J.; Paul, J.M.; Feder, H.M., 1976: Age, growth, and recruitment of the butter clam, *Saxidomus gigartea*, on Porpoise Island, Southeast Alaska. *Proc. Nat. Shellfish Ass.* 66: 26-28.
- Pauly, D., 1980: On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.* 39: 175-192.
- Perron, F., 1983: Growth, fecundity, and mortality of *Comus penicillatus* in Hawaii. *Ecology* 64: 53-62.
- Peters, R.H., 1986: The ecological implications of body size. Cambridge: University Press. 329 pp.
- Petersen, G.H., 1978: Life cycles and population dynamics of marine benthic bivalves from the Disko Bugt area of West Greenland. *Ophelia* 17: 95-120.

- Peterson, C.H., 1982: The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecol. Monogr. 52: 437-475.
- Phillips, D.W., 1981: Life-history features of the marine intertidal limpet *Notoacma scutum* (Gastropoda) in central California. Mar. Biol. 64: 95-103.
- Pianka, E.R., 1970: On r- and K-selection. Am. Nat. 104: 592-597.
- Picken, G.B., 1980: The distribution, growth and reproduction of the antarctic limpet *Nacella (Patnigera) concinna*. J. Exp. Mar. Biol. Ecol. 42: 71-85.
- Posgay, J.-A., 1979: Population assessment of the Georges Bank sea scallop stocks. In: Thomas, H.J. (ed.): Population assessment of shellfish stocks. Rapp. P.-V. Réun. CIEM 175: 288 pp.
- Rabarts, I.W., 1970: Physiological aspects of the ecology of some Antarctic lamellibranchs. British Antarctic Survey, Cambridge, AD6/2H/1970/AN12. 21 pp.
- Ramón, M.; Richardson, C.A., 1992: Age determination and shell growth of *Chamaelea galatina* (Bivalvia: Veneridae) in the western Mediterranean. Mar. Ecol. Prog. Ser. 89: 15-23.
- Reiss, M.J., 1991: The allometry of growth and reproduction. Cambridge: University Press. 182 pp.
- Ricker, W.E., 1973: Linear regression in fishery research. J. Fish. Res. Bd. Canada 30: 409-437.
- Sainsbury, K.J., 1982: Population dynamics and fishery management of the paupa, *Haliotis iris*. I. Population structure, growth, reproduction, and mortality. N.Z. J. Mar. Freshw. Res. 16: 147-161.
- Salzwedel, H., 1979: Energy budgets for two populations of the bivalve *Tellina fabula* in the German Bight. Veröff. Inst. Meerestorsch. Bremerh. 18: 257-287.
- Salzwedel, H., 1979: Reproduction, growth, mortality and variations in abundance and biomass of *Tellina fabula* (Bivalvia) in the German Bight in 1975/76. Veröff. Inst. Meerestorsch. Bremerh. 18: 111-202.
- Santos, P.J.P., 1994: Population dynamics and production of *Scololepis gaucha* (Polychaeta: Spionidae) on the sandy beaches of southern Brazil. Mar. Ecol. Prog. Ser. 110: 159-165.
- Solin, N.I.; Gogolev, A.Y.; Buvanovskii, A.I., 1992: Local latitudinal variation in linear growth of bivalve mollusk *Modiolus kuzilensis*. Russian J. Mar. Biol. (Engl. Transl.) 17: 152-157.
- Senus, P. van; McLachlan, A., 1986: Growth, production, and a partial energy budget for the amphipod, *Talorchestia capensis* (Crustacea: Talitridae) in the eastern Cape, South Africa. Mar. Ecol. 7: 165-179.
- Shafee, M.S., 1992: Production estimate of a mussel population *Perna picta* (Born) on the Atlantic coast of Morocco. J. Exp. Mar. Biol. Ecol. 163: 183-197.
- Shafir, A., Field, J.G., 1980: Population dynamics of the isopod *Cirrolana imposita* Barnard in a kelp-bed. Crustaceana 39: 185-196.
- Stearns, S.C., 1976: Life history tactics: A review of ideas. Quart. Rev. Biol. 51: 3-47.
- Taylor, C.C., 1960: Temperature, growth, and mortality - The Pacific cockle. J. Cons. Int. Explor. Mer 26: 117-124.
- Taylor, A. C.; Venn, T.J., 1978: Growth of the queen scallop, *Chlamys opercularis*, from the Clyde Sea area. J. Mar. Biol. Ass. U.K. 58: 687-700.
- Thurston, M.H., 1968: Notes on the life history of *Borallia gigantea* (Pfeffer) (Crustacea, Amphipoda: Br. Antarct. Surv. Bull. 16: 57-64).
- Thurston, M.H., 1970: Growth in *Borallia gigantea* (Pfeffer) (Crustacea: Amphipoda: In: Holdgate, M.W. (ed.): Antarctic Ecology Vol.1. London: Academic Press, p. 269-278.
- Tudorancea, C.; Florescu, M., 1969: Aspecte ale producției și energiei populației de *Azodonta piscinaria* Nilsson din Balta Crapina (zona inundabilă a Dunării) Studii și Cerc. Biol. Seria Zool. 21: 43-55.
- Tudorancea, C.; Florescu, M., 1968: Considerations concerning the production and energetics of *Unio tumidus* Philipsson population from the Crapina marsh. Trav. Mus. Hist. Nat. Grigore Antipa 8: 395-409.
- Vakily, J.M., 1992: Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas. Manila: ICLARM, ICLARM contr. 801. 125 pp.
- Wägele, J.-W., 1990: Growth in captivity and aspects of reproductive biology of the Antarctic fish parasite *Aega antarctica* (Crustacea, Isopoda) Polar Biol. 10: 521-527.
- Warwick, R.M.; George, C.L., 1980: Annual macrofauna production in an *Abria* community. In: Collins, M.B.; Banner, F.T.; Tyler, P.A.; Wakefield, S.J.; James, E. (eds.): Industrialized embayments and their environmental problems. Oxford: Pergamon Press, p. 517-538.
- Williamson, P.; Kendall, M.A., 1981: Population age structure and growth of the trochid *Monodonta lineata*, determined from shell rings. J. Mar. Biol. Ass. U.K. 61: 1011-1026.
- Wolff, M.; Soto, M., 1992: Population dynamics of *Cancer polyodon* in La Herradura Bay, northern Chile. Mar. Ecol. Prog. Ser. 85: 69-81.
- Yap, W.G., 1977: Population biology of the Japanese little-neck clam, *Tapes philippinarum*, in Kanoehe Bay, Oahu, Hawaiian Islands. Pac. Sci. 31: 223-244.

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