

# Temperature and reproductive metabolism in macrobenthic populations\*

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**ABSTRACT:** Clarke (1987; Mar Ecol Prog Ser 38:89–99) analysed the effects of variation in maintenance metabolic costs with temperature on reproductive metabolism in poikilothermic animals. Based on model calculations, he concluded that annual mass-specific gonad production (GP) and the share of assimilated energy used for reproductive purposes (RE) are affected in opposite ways by temperature. In animals of similar size and ecology either GP will decrease with decreasing temperature if RE remains constant or RE will increase with decreasing temperature if GP remains constant. Empirical data on productivity of marine benthic invertebrate populations suggest that the evolutionary adaptation of gonad metabolism tends toward changing GP and maintaining RE independent of temperature.

**KEY WORDS:** Macrozoobenthos · Reproduction · Temperature

## INTRODUCTION

Temperature affects metabolism in poikilotherms, and many empirical investigations comparing species from different regions show basic metabolic rates to be positively related to ambient temperature (Musayeva & Shushinka 1978, Ivleva 1980, Robinson et al. 1983, and others). Empirical investigations dealing with the effects of this relationship on animal productivity have focused almost exclusively on somatic production (Banse & Mosher 1980, Plante & Downing 1989, Morin & Bourassa 1992 and others), largely ignoring that fraction of incoming energy used for reproductive purposes.

Clarke (1987) was the first to explore how the relation between temperature and basic metabolism may affect reproduction. He analysed 2 measures of reproductive metabolism: gonad productivity (GP), i.e. annual mass-specific gonad production, and reproductive effort (RE), i.e. the share of assimilated energy used for reproductive purposes. From model computations based on a few published individual energy budgets, Clarke (1987) concluded that GP and RE are

affected in different ways by temperature. In animals of similar size and ecology either GP will decrease with decreasing temperature if RE remains constant, or RE will increase with decreasing temperature if GP remains constant.

In this study I analysed the available data on population dynamics of marine benthic invertebrate populations to establish whether or not there are general trends in GP and RE related to temperature. The results are discussed in light of possible evolutionary strategies of adaptation to different temperature environments.

## The model

Clarke (1987) established the following model to describe the partitioning of assimilated energy into various sinks in a mature female animal:

$$A = P_s + R_s + R_{a-s} + P_g + R_g + R_{a-g} + R_b \quad (1)$$

where  $A$  is assimilation,  $P_s$  and  $P_g$  somatic and gonad production,  $R_s$  and  $R_g$  respiratory costs of somatic and gonad production,  $R_{a-s}$  and  $R_{a-g}$  respiratory costs of behavioural activity associated with somatic production and reproduction, and  $R_b$  is basic maintenance metabolism. He defined 2 measures of reproductive

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metabolism: (1) GP (called reproductive output, RO, by Clarke),

$$GP = P_g/M \quad (2)$$

(where  $M$  is mean body mass during the period of observation), i.e. GP is the mass-specific gonad production, and (2) annual reproductive effort RE,

$$RE = (P_g + R_g + R_{a-g})/A \quad (3)$$

i.e. the proportion of assimilated energy used for reproductive purposes.

Clarke (1987) concluded from his model calculations that, under certain assumptions, the differences in  $R_0$  for any 2 temperatures  $T_1 < T_2$  within the physiological range will result in either

Alternative A:  $RE_1 > RE_2$  if  $GP_1 = GP_2$

or

Alternative B:  $GP_1 < GP_2$  if  $RE_1 = RE_2$ .

### Empirical relations

Clarke (1987) confined his model calculations to the annual energy budget of a single sexually mature female. This model can be applied to populations, provided there are no intrinsic differences in the physiology of cold and warm water populations, such as an elevated basic metabolism at low temperatures (see Clarke 1991). Brey & Clarke (1993) and Arntz et al. (1994) gave evidence that differences in growth and productivity of benthic populations from different regions are mainly related to temperature and food availability, hence I assume the above model to be valid at the population level, too.

## METHODS

Only a very few publications on population dynamics of benthic invertebrates cover all parts of the energy budget. Respiration has been measured very infrequently, and no data including all components of total respiration could be found. Therefore only half of Clarke's (1987) evolutionary couplet, i.e. the relation between GP and temperature, can be analysed. On the population level, Clarke's measure of reproductive output,  $GP = P_g/B$  ( $B$  is population biomass) is a measure equivalent to the  $P_s/B$  ratio generally used to describe somatic productivity in benthic invertebrate populations. The hypotheses to be tested are:

$H_0$ : there is no positive relation between GP ( $= P_g/B$ ) and temperature; and

$H_A$ : there is a positive relation between GP and temperature.

Confirmation of  $H_0$  would indicate that 'Alternative B' is to be rejected, whereas confirmation of  $H_A$  would point towards rejection of 'Alternative A'.

GP was computed from published data on 88 marine benthic invertebrate populations inhabiting subtropical, boreal and polar environments (Table 1). All mass data were converted to kJ where necessary.

Temperature, mean individual body mass and main taxa (Mollusca, Crustacea, Echinodermata) were checked for significant effects on GP by analysis of covariance (ANCOVA). Subsequently, the relation between GP and temperature was analysed by Spearman rank correlation.

## RESULTS

Table 2 shows the results of the ANCOVA analysing the effects of  $T$ ,  $\log(M)$  and taxon (Mollusca, Crustacea, Echinodermata) on  $\log(GP)$ . There is no significant relation between  $M$  and GP nor any interaction between  $M$  and taxon (Table 2A). GP is significantly affected by temperature and the temperature effect differs significantly among taxa (Table 2B). Spearman rank correlations indicate a significant positive relation between temperature and GP for all data ( $\rho = 0.435$ ,  $p < 0.001$ ) as well as in Mollusca ( $\rho = 0.388$ ,  $p = 0.005$ ) and Crustacea ( $\rho = 0.595$ ,  $p = 0.032$ ) separately (Fig. 1). There is no significant correlation in Echinodermata ( $\rho = 0.332$ ,  $p = 0.148$ ); however, if the 2 data points referring to *Sterechinus neumayeri* are excluded, the correlation becomes highly significant ( $\rho = 0.638$ ,  $p = 0.009$ ). These results indicate  $H_A$ , that there is a positive relation between GP and temperature, has to be generally accepted.

## DISCUSSION

Many empirical investigations have demonstrated a strong negative relationship between individual body mass and mass-specific basic metabolic rates (see Ivleva 1980, Robinson et al. 1983, Calder 1985, and others) as well as derived parameters such as population  $P_s/B$  ratio (Banse & Mosher 1980, Schwinghamer et al. 1986, Plante & Downing 1989, Brey 1991, Morin & Bourassa 1992). Surprisingly there is no such relation between body mass and GP ( $= P_g/B$  ratio) detectable in the present data (Table 2). Thus, GP in benthic invertebrates seems to be independent of body mass, whereas annual gonad production is positively related to body mass, indicating that an increase in gonad output may be one of the evolutionary advantages of larger body size.

Table 1. The 88 data sets this investigation is based on (see 'Data Sources' for full citations). *M*: mean individual body mass (kJ); *T*: mean water temperature (K); GP: annual gonad productivity,  $P_g/B$  ( $\text{yr}^{-1}$ ) (see 'Methods')

Source	Species	Taxon	<i>M</i>	<i>T</i>	GP
Otto (1976)	<i>Ancylus fluviatilis</i>	Mollusca	0.0074	280.0	0.569
Griffiths (1977), Griffiths & King (1979)	<i>Aulacomya ater</i>	Mollusca	11.9886	288.5	0.865
McLachlan et al. (1979)	<i>Bullia rhodostoma</i>	Mollusca	0.4963	292.0	0.500
Moore & Lopez (1969)	<i>Chione cancellata</i>	Mollusca	1.1103	299.0	0.414
Vahl (1981a, b)	<i>Chlamys islandica</i>	Mollusca	26.6370	280.0	0.123
Shafee & Conan (1984)	<i>Chlamys varia</i>	Mollusca	22.8026	285.0	0.067
			17.4043	285.0	0.151
Griffiths (1981a, b)	<i>Choromytilus meridionalis</i>	Mollusca	4.1797	292.0	5.288
			4.6529	292.0	2.908
			4.0241	292.0	4.338
			4.9919	292.0	5.063
Aldridge & McMahon (1978)	<i>Corbula manilensis</i>	Mollusca	5.0187	293.9	0.485
Dame (1972a, b, 1976)	<i>Crassostrea virginica</i>	Mollusca	4.7709	292.0	0.327
Ansell et al. (1972)	<i>Donax incarnatus</i>	Mollusca	0.1919	301.0	0.408
Barkai & Griffiths (1988)	<i>Haliotis midae</i>	Mollusca	1093.3330	287.0	0.326
			950.0000	292.0	0.558
Richardson (1979)	<i>Lissarca miliaris</i>	Mollusca	0.0066	272.2	0.114
Brey et al. (1993)	<i>Lissarca notorcadensis</i>	Mollusca	0.0198	272.0	0.128
			0.0202	272.0	0.115
Gaten (1986)	<i>Lymnaea peregra</i>	Mollusca	0.3845	283.0	4.820
Hummel (1985)	<i>Macoma balthica</i>	Mollusca	0.8017	282.3	0.162
Hibbert (1976, 1977a, b)	<i>Mercenaria mercenaria</i>	Mollusca	7.2510	285.0	0.332
Bréthes et al. (1986)	<i>Mesodesma arctatum</i>	Mollusca	2.4790	278.5	0.240
Kuenzler (1961)	<i>Modiolus demissus</i>	Mollusca	27.6442	294.0	0.054
Thompson (1984a, b)	<i>Mytilus edulis</i>	Mollusca	23.7180	279.1	0.595
Picken (1980)	<i>Nacella concinna</i>	Mollusca	2.1085	272.2	0.080
Nolan (1987)	<i>Nacella concinna</i>	Mollusca	3.6630	272.2	0.093
Hughes (1972)	<i>Nucella lapillus</i>	Mollusca	3.6160	280.0	1.802
Rachor (1976)	<i>Nucula nitidosa</i>	Mollusca	0.0654	282.0	1.424
			0.0594	282.0	1.341
			0.0577	282.0	0.603
			0.0918	282.0	1.044
Davis & Wilson (1985)	<i>Nucula turgida</i>	Mollusca	0.0933	283.5	0.481
Wright & Hartnoll (1981)	<i>Patella vulgata</i>	Mollusca	11.0881	282.0	0.272
			8.9263	282.0	0.280
MacDonald & Bourne (1987)	<i>Patinopecten caurinus</i>	Mollusca	107.9790	281.5	0.054
			602.1310	283.0	0.097
Berry (1978)	<i>Perna perna</i>	Mollusca	0.7842	294.0	1.297
			1.3066	294.0	1.010
Shafee (1992)	<i>Perna picta</i>	Mollusca	2.5182	291.0	0.576
Cheung (1993)	<i>Perna viridis</i>	Mollusca	4.7516	296.8	0.596
Seager (1978)	<i>Philine gibba</i>	Mollusca	1.7561	274.5	0.679
Holopainen (1979), Holopainen & Hanski (1979)	<i>Pisidium casertanum</i>	Mollusca	0.0018	280.0	0.180
			0.0013	277.5	0.250
MacDonald & Thompson (1986)	<i>Placopecten magellanicus</i>	Mollusca	507.6315	278.0	0.236
			221.5000	280.0	0.144
Hughes (1970a, b)	<i>Scrobicularia plana</i>	Mollusca	2.7752	285.0	0.455
Paine (1971)	<i>Tegula funebris</i>	Mollusca	1.4734	282.1	0.032
Salzwedel (1979)	<i>Tellina fabula</i>	Mollusca	0.0118	283.0	0.179
			0.0293	283.0	0.343
Trevallion (1971)	<i>Tellina tenuis</i>	Mollusca	0.5750	281.5	0.395
			0.4830	281.5	0.245
			0.3220	281.5	0.046
Clasing et al. (1994)	<i>Venus antiqua</i>	Mollusca	7.1276	284.0	0.028
Hastings (1981)	<i>Ampelisca brevicornis</i>	Crustacea	0.0172	285.0	0.253
			0.0250	285.0	0.208
Gorny et al. (1993)	<i>Chorismus antarcticus</i>	Crustacea	3.1280	272.0	0.021
Johnson (1976a, b)	<i>Cirolana harfordi</i>	Crustacea	0.1857	288.0	0.304
Shafir & Field (1980a, b)	<i>Cirolana imposita</i>	Crustacea	0.0388	287.0	0.857

(Table continued on next page)

Table 1 (continued)

Source	Species	Taxon	M	T	GP
Mathias (1971)	<i>Crangonyx richmondensis</i>	Crustacea	0.0128	282.0	0.042
			0.0114	281.0	0.056
LaFrance & Ruber (1985)	<i>Gammarus mucronatus</i>	Crustacea	0.0048	281.0	0.440
Marchant & Hynes (1981)	<i>Gammarus pseudolimnaeus</i>	Crustacea	0.0246	281.0	0.065
Mathias (1971)	<i>Hyalella azteca</i>	Crustacea	0.0038	282.0	0.368
			0.0035	283.0	0.252
Willows (1987)	<i>Ligia oceanica</i>	Crustacea	0.4461	282.5	0.164
Kemp et al. (1985)	<i>Rhepoxynius abronius</i>	Crustacea	0.0062	283.5	0.361
Luxmoore (1981, 1982, 1985)	<i>Serolis polita</i>	Crustacea	0.3835	272.3	0.051
Dayton et al. (1974)	<i>Acodontaster conspicuus</i>	Echinodermata	1355.6380	271.2	0.195
Singletary (1971)	<i>Amphioplus coinortodes</i>	Echinodermata	0.4489	298.0	0.203
O'Connor et al. (1986)	<i>Amphiura filiformis</i>	Echinodermata	0.6822	284.0	0.467
Lane (1977)	<i>Mellita quinquesperforata</i>	Echinodermata	4.5992	298.6	0.424
			8.3727	298.6	0.367
Singletary (1971)	<i>Micropholis gracillima</i>	Echinodermata	0.4941	298.0	0.484
Moore & Lopez (1966)	<i>Moira atropes</i>	Echinodermata	6.1745	299.0	0.375
Dayton et al. (1974)	<i>Odontaster validus</i>	Echinodermata	23.7790	271.2	0.157
McClintock et al. (1988)	<i>Odontaster validus</i>	Echinodermata	28.8570	271.2	0.107
Singletary (1971)	<i>Ophionephtys limicola</i>	Echinodermata	1.5114	298.0	0.268
Morison (1979)	<i>Ophionotus hexactis</i>	Echinodermata	1.0106	274.5	0.137
			0.5623	274.5	0.200
			1.4590	274.5	0.066
Greenwood (1980)	<i>Parechinus angulosus</i>	Echinodermata	7.4525	286.0	0.251
			17.2774	287.0	0.129
Dayton et al. (1974)	<i>Perknaster fuscus</i>	Echinodermata	199.2800	271.2	0.241
Brey (1991)	<i>Sterechinus antarcticus</i>	Echinodermata	2.3019	272.0	0.098
Brey et al. (in press)	<i>Sterechinus neumayeri</i>	Echinodermata	89.4137	271.2	0.426
			110.6756	271.2	0.434
Miller & Mann (1973)	<i>Strongylocentrotus droebachiensis</i>	Echinodermata	2.6690	279.0	0.156

As indicated by Fig. 1, the relation between  $T$  and GP is scattered, but nevertheless significantly positive in Mollusca, Crustacea and the pooled data of all 3 taxa. Within the Echinodermata, the significance level of the correlation depends on whether the 2 data points of *Sterechinus neumayeri* are included or not.

It remains unclear why this species shows a distinctly higher gonad productivity than other echinoderms living under similar temperature conditions. Altogether there is substantial evidence for a positive correlation of GP with  $T$  in macrobenthic populations of the 3 taxa (Fig. 1). Consequently, within Clarke's model, true RE is likely to be independent of temperature. Hence, there seems to be a tendency toward Clarke's 'Alternative B',  $GP_1 < GP_2$  and  $RE_1 \approx RE_2$  for  $T_1 < T_2$  in benthic invertebrate populations.

The 2 parameters GP and RE may be interpreted as measures of alternative strategies in the evolutionary adaptation of reproductive metabolism to different conditions. If we compare 2 environments with different temperature, then the first strategy would result in more or less constant reproductive output, but at the cost of having less energy available for other metabolic demands at lower temperature. The second strategy would result in a more or less con-

Table 2. Analysis of covariance (ANCOVA) of the effects of  $T$ ,  $\log(M)$  and Taxon on  $\log(GP)$ ;  $T$  temperature;  $M$ : mean individual body mass. The analysis is based on the 88 data sets shown in Table 1

	df	SS	MS	F-value	p-value
<b>(A) M, T and Taxon as independent factors</b>					
$T$	1	2.371	2.371	12.442	0.0007
$\log(M)$	1	0.027	0.027	0.139	0.7100
Taxon	2	0.812	0.406	2.129	0.1257
$T$ [Taxon]	2	0.835	0.417	2.190	0.1187
$\log(M)$ [Taxon]	2	0.372	0.186	0.997	0.3809
Residual	79	15.056	0.191		
<b>(B) M excluded</b>					
$T$	1	3.120	3.120	16.4151	0.0001
Taxon	2	1.349	0.674	3.491	0.0351
$T$ [Taxon]	2	1.357	0.678	3.512	0.0344
Residual	82	15.838	0.193		

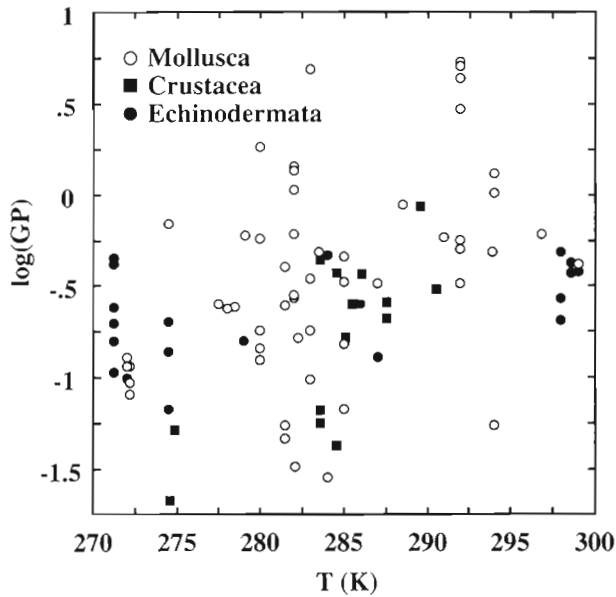


Fig. 1. Relation between gonad productivity GP ( $= P_g/B$ ) (see 'Methods') and temperature (T) in Mollusca, Crustacea and Echinodermata. Spearman Rank Correlation for Mollusca:  $\rho = 0.388$ ,  $p = 0.005$ ,  $n = 54$ ; Crustacea:  $\rho = 0.595$ ,  $p = 0.032$ ,  $n = 14$ ; Echinodermata:  $\rho = 0.332$ ,  $p = 0.148$ ,  $n = 20$ ; All:  $\rho = 0.435$ ,  $p < 0.001$ ,  $n = 88$

stant share of gonad metabolism in total metabolism, accepting a lower gonad productivity at lower temperature. The present results are evidence that the former strategy is not common among benthic invertebrate populations. They tend to maintain the proportion of energy invested in reproduction, irrespective of temperature while gonad productivity is reduced.

This is of particular interest for the understanding of evolutionary adaptations of reproductive strategies to low temperature environments. The widely accepted opinion is that cold water species in general are characterized by features summarized under 'Thorson's rule', such as low fecundity, large eggs, non-pelagic development and brooding, although many exceptions are known (see e.g. White 1984, Pearse & McClintock 1991, Arntz et al. 1994). However, my analysis indicates that the evolution of these cold water reproductive strategies does not affect the relative energy investment in reproduction. Evolution seems to affect mainly the mode of reproduction, rather than the basic energetics.

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