Marine Biology of Polar Regions and Effects of Stress on Marine Organisms
Edited by J. S. Gray and M. E. Christiansen

INTRODUCTORY THEME PAPER

RESPONSES TO ENVIRONMENTAL STRESS: TOLERANCE, RESISTANCE AND ADAPTATION

B.L. Bayne

Natural Environment Research Council,
Institute for Marine Environmental Research,
Prospect Place, The Hoe, Plymouth PL1 3DH, UK

INTRODUCTION

Attempts to define the concept of "stress" in ecology have led to semantic confusion. On the one hand, the term has been applied to properties of the environment which impose a force on the organism; in this sense the stress is a stimulus. On the other hand, the term as used by Selye (1950) refers to the response by the organism to a potentially harmful environmental change; when used in this sense, the causative factor is called a stressor. In recent years, however, some agreement has been reached to confine the term stress to describe an environmental stimulus which, by exceeding a threshold value, disturbs normal animal function; the reaction of the organism is then termed the stress response. When used in this way and applied to organisms, there is an equivalence with the term as applied to ecosystems (Lugo, 1978; Ulanowicz, 1978).

The adaptedness of organisms represents a compromise between structural and functional constraints on the one hand and particular environmental challenges on the other. Environmental states exist to which organisms respond by expressing physiological (and other) attributes which may be 'adaptive', in the sense that they compensate, at least in part, for potential loss of performance, but which may be less than fully effective and so represent a reduction in fitness relative to the optimal condition. The practical aim of research into the effects of stress is to provide a quantitative appreciation of the environmental situations to which organisms respond by physiological and biochemical changes which may be adaptive, but with an efficiency that may be expressed as reduction in fitness.

In research into the stress responses of fish (Pickering, 1981) a distinction is made between primary responses (mostly neuro-hormonal in character) and secondary responses (the physiological consequences of the primary response, mostly changes to respiratory and metabolic processes). It is not currently possible to discuss the effects of stress in marine invertebrates in similar terms since virtually nothing is known of the hormonal aspects of the stress response in such animals. On the other hand, the physiological components of the stress response have been studied in detail in some species. Many such studies consider the stress response in terms of a balance between energy (and nutrient) gains and losses, and an environmental change is considered a stress when, in responding, the individual nevertheless suffers a reduction in net energy gain. This view of environmental stress and its effects is similar to Odum's (1967) concept of stress acting on ecosystems to divert potential energy away from doing useful work to increased expenditure on maintenance and repair. Some such equivalence in terminology and in approach is important if studies on individual organisms are to be set within the wider context of the effects of stress on populations, communities and ecosystems. Energy (and nutrient) flux can provide the common currency in such studies. In this paper, stress will be used to refer to the environmental stimulus and the response will be considered largely in terms of physiological energetics.

TOLERANCE AND RESISTANCE

The works of Fry (1947, 1971), Precht (1958), Prosser (1958), Brett (1958) and Kinne (1964) provide the theoretical framework for studies of the responses of poikilotherms to changes in the environment. Alderdice (1972, 1976) suggested a synthesis of these ideas which encompasses the notion of zones of tolerance and resistance and the concepts of capacity and resistance adaptations. Care is required in the use of the term adaptation, however, since it may refer either to the end-product of a physiological response which is considered to be of survival value or it may designate a change in the capacity of the species to respond to new environmental stimuli. In the former sense, no genetic change is implied; the response may simply reflect the physiological plasticity of the phenotype. In the latter sense, some degree of selection is inferred which causes differential mortality of phenotypes. Much of the research on responses to stress does not make this distinction and the adaptive nature of the response, if any, is assumed to reflect the innate homeostatic nature of physiological adjustments to changes in environment. In the present discussion physiological responses will be considered as 'acclimations' or 'compensations' and the term adaptation reserved for genotypic changes.

Following Alderdice (1972), capacity acclimations may be visualised as changes in the structure of contour diagrams in which a physiological response is plotted in relation to one or more environmental variables. By analysis of the structure of such diagrams (or "response surfaces") the various categories of acclimation (complete, partial, inverse etc.) can be evaluated. Resistance acclimations are represented as movements of the response surfaces along the axes of the environmental matrix. Fig. 1 shows the combined effects of temperature and salinity on a measure of activity in the hard clam, Mercenaria mercenaria, in March and in September (van Winkle et al., 1976). Resistance acclimation is evident as a shift in the response surface so that in September, maximum activity occurred at 15°C and 30 $^{0}/_{00}$, in contrast to 20°C and 25 $^{0}/_{00}$ in March.

A similar treatment can be applied to measurements that represent more directly the components of ecological fitness, such as growth efficiency and reproductive potential. Such response surfaces will identify combinations of environmental and intrinsic factors that evoke physiological responses in the organism that represent different degrees of adaptedness. These combinations may fall within the organism's zone of tolerance (Fry, 1947), in that they can be tolerated indefinitely by the individual, but they nevertheless stimulate altered physiological (or biochemical) states which are measurably different from the states typical of more optimal environmental conditions. Identifying the processes that are responsive to these sub-optimal environmental conditions and that are also relevant to attributes of fitness affords a powerful means for evaluating the current adaptive state of the individual. I will consider a few examples from studies of the growth of marine bivalve molluscs.

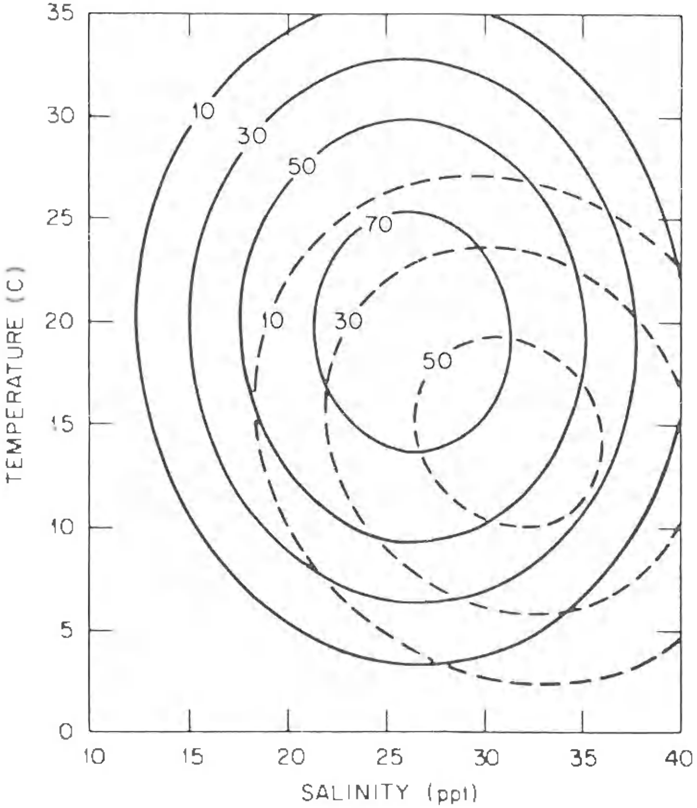

Fig. 1. Response surface for percentage activity of Mercenaria mercenaria (extension of siphons) at different temperatures and salinities (from van Winkle *et al*., 1976). Solid lines, March; dashed lines, August - September.

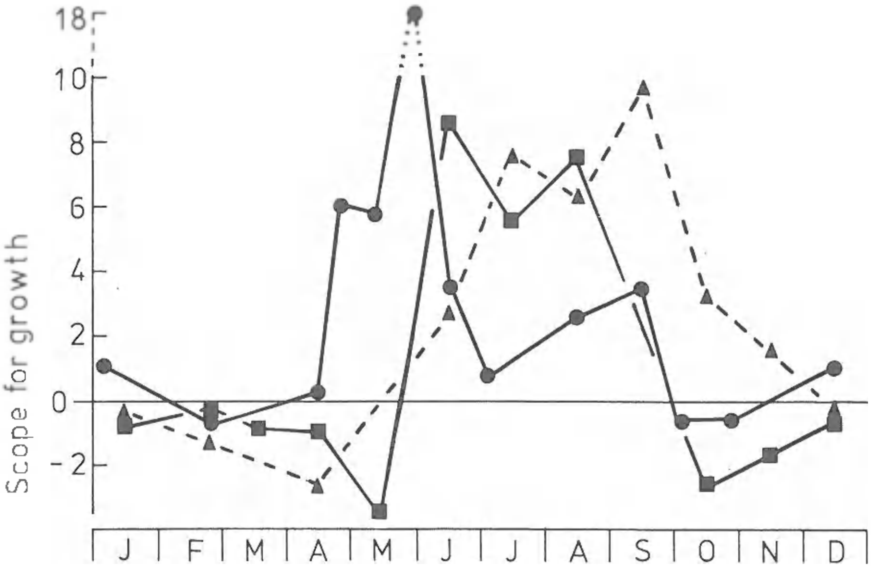

Fig. 2. The seasonal cycle in the scope for growth (see text) for three bivalves. ●, *Chlamys islandica* (Vahl, 1980); ▲, *Mytilus edulis* (Bayne and Widdows, 1978) - both as calories per hour; ■, *Mya arenaria* (Gilfillan *et al*., 1977) - as µg C 10^{-1} per hour.

GROWTH AND ITS PHYSIOLOGICAL COMPONENTS IN RESPONSE TO ENVIRONMENTAL CHANGES

The rate of growth of individuals may be extremely varied over a species' geographical range (e.g. Bachelet (1980), discussing *Macoma balthica*). In addition, even within narrow geographical limits, individuals may show marked seasonal differences in growth and may express reduced rates of growth under conditions of high temperatures and/or reduced rations that are frequently experienced in the normal environment (de Wilde, 1975; Beukema *et al*., 1977; Nichols and Thomson, 1982; all on *M. balthica*). Fig. 2 illustrates the seasonal growth patterns for three other bivalve species. In the light of these data, three predictions seem reasonable. Firstly, physiological and other responses to minimise these periods of reduced growth are to be expected. Also, given the usual allometric relationships between body size and the rates of such physiological processes as feeding and respiration, we might expect changes to occur in the seasonal growth pattern as the individuals increase in age. Finally, since reproduction in these species imposes high energy demands (e.g. Bayne *et al*., 1983), a close relationship is to be expected between seasonal cycles of growth and the annual reproductive cycle.

The three studies illustrated in Fig. 2 have one other feature in common viz. that growth was measured, not directly as a change in weight, but indirectly as the energy (or carbon) gains and losses in components of the energy budget - hence the term the "scope for growth". This procedure has the merit of analysing the growth process in terms of individual physiological mechanisms and so elucidating the physiological compensations which comprise the response to the environmental change.

PHYSIOLOGICAL RESPONSES TO ENVIRONMENTAL STRESS

This discussion will be limited to the three expectations suggested viz. the types of physiological compensations observed, the effects of body size and the relationships between the scope for growth and reproductive processes.

Physiological compensations. The components of the energy budget of an organism (food consumption, digestion, excretion, respiration, growth and the production of gametes) are functionally coupled so that changes in any one process have consequences for some or all of the others. A distinction between metabolism as comprising the "sum of the reactions which yield the energy the organism utilizes" and activity (including growth) as "what the organism does with the energy derived from metabolism" (Fry, 1971) is a useful one in this context. Changes in the components of the energy budget in response to changes in the environment often have apparent homeostatic properties, effecting a control over the amount of energy made available for growth and reproduction.

Many examples of the control properties of physiological flexibility in the energy budget exist (Calow, 1977). Hubbell (1971) and Calow (1976) consider such properties from a cybernetic (or "systems") perspective. Newell and Branch (1980) provide some examples from the marine invertebrates of apparent homeostasis in response to temperature (see also Bayne and Newell, 1983). I will illustrate the point with three related examples from work on bivalves.

Fig. 3 shows a relationship between the clearance (=feeding) rate and the respiration (=oxygen consumption) rate in Mytilus californianus (from Bayne et al., 1975); the relationship is exponential, so that increasing increments in clearance and the processes of feeding that this represents (the activity) require a disproportionate increase in respiration (an index of metabolism). The intercept of the curve with the ordinate estimates the metabolic rate associated with zero feeding activity in a satiated animal and may be compared with the measured metabolic rate of an inactive, starved individual (indicated by a triangle in the figure) and with the mean 'routine' respiration rate typical of an individual showing spontaneous activity. The histogram to the right of Fig. 3 shows features of the energy budget typical of one experiment. The absorbed ration A (i.e. the ingested ration corrected for absorption efficiency) was ~ 22.0 J.h^{-1} and mean respiratory energy losses ($R_{routine}$) were 11.2 J.h^{-1}, leaving a surplus available for growth of 10.8 J.h^{-1} (in this discussion other energy losses e.g. excretion, are ignored; this affects the quantitative argument, but

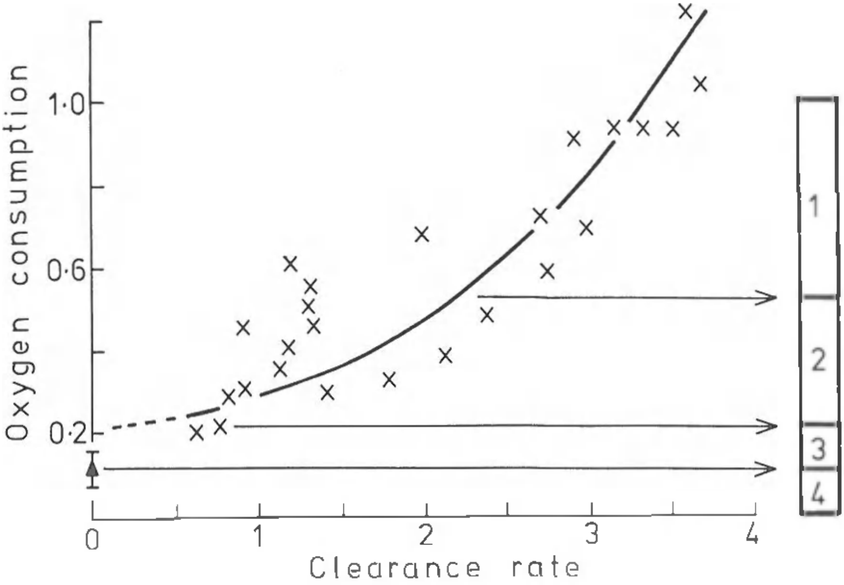

Fig. 3. A relationship between the rate of oxygen consumption (ml O_2 h^{-1}) and clearance rate (l h^{-1}) for Mytilus californianus (from Bayne et al., 1975). 1: Net energy gain. 2: Costs associated with feeding. 3: Costs of digestion. 4: Basal metabolic costs. See text for discussion.

not the main conclusions reached).

These results suggest a means for effective, albeit short-term, energy saving for bivalves during feeding. By transient cessation of feeding when the digestive tract is full and digestion is in progress, a reduction in metabolic expenditure is possible. In the longer term, however, the relationship in Fig. 3 acts rather to constrain physiological flexibility, since the individual must "accept" an exponentially increasing metabolic cost in order to fuel linear increases in feeding rate. Other features of control must be invoked by the individual to regulate net energy gain in the longer term, for example in response to changes in the food supply.

In a recent series of experiments with three bivalve species from two environments, one characterised by high concentrations of seston which was low in energy content and the other by low concentrations of seston high in energy content, Bayne, Klumpp and Clarke (unpublished data) related the physiological variables clearance rate, the rate at which food was passed through the digestive gland, the efficiency with which this food was absorbed and the rate of oxygen consumption, to the available ration. Not unexpectedly, higher rates of clearance (and hence of ingestion, since no pseudofaeces were produced) led to more rapid passage of food through the gut and to reduced absorption efficiency (Table 1; site B). Individuals feeding on the low quality diet showed reduced rates

TABLE 1. The feeding behaviour of *Perna perna* at two sites on the Cape peninsular, South Africa. At site A (low quality diet) ingestion rate is relatively slow, the residence time of food in the digestive gland (7 h) and the absorption efficiency are high; at site B (high quality diet) ingestion rate is more rapid, the residence time of food in the digestive gland (2 h) and the absorption efficiency are low. The result is a daily absorbed ration that is similar at both sites. A similar result was obtained for two other mytilid species. From Bayne, Klumpp and Clarke, unpublished).

Site	Seston concentration $mg \cdot l^{-1}$	Seston energy content $J \cdot mg^{-1}$	Available ration $J \cdot l^{-1}$	Clearance rate $l \cdot h^{-1}$	Time to max fullness of digestive gland h	Absorption efficiency	Number of digestive gland fillings per day	Absorbed ration $J \cdot d^{-1}$
A	7.11±0.6	2.4	17.3	2.5±0.5	3.5	0.65±0.10	3.4	316
B	3.27±1.2	6.4	20.4	3.3±0.8	1.0	0.40±0.05	12.0	312

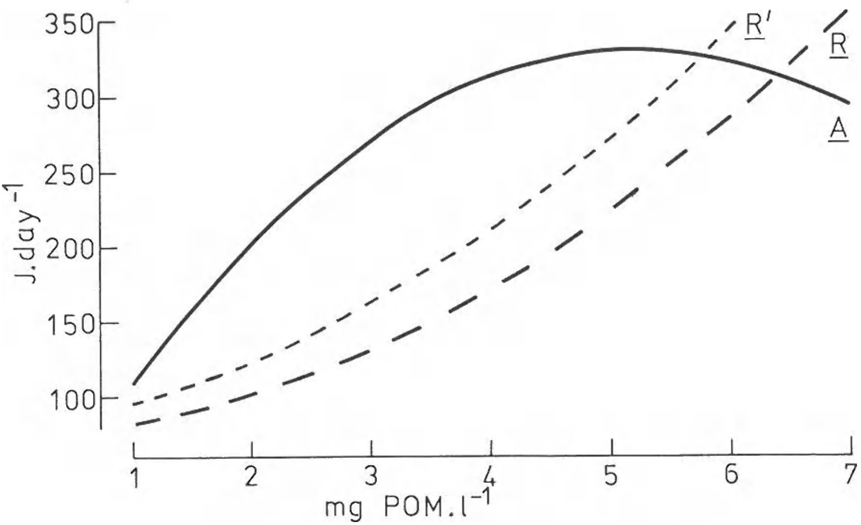

Fig. 4. Absorbed ration (A), calculated from data on residence time of food in the digestive gland and on absorption efficiency (see text), related to the concentration of particulate organic matter (POM) in suspension. Also plotted are two values for respiratory heat loss (R), calculated as an exponential function of clearance rate; R^1 is R x 1.20. The scope for growth is (A-R) or (A-R^1).

of clearance, slower rates of gut passage and higher absorption efficiencies (site A). When calculated on a daily basis, however, the absorbed ration was similar at the two sites, suggesting an effective compensation for differences in food supply.

The physiological flexibility suggested in Table 1 is based on balances between rates of clearance, the passage time of food in the digestive tract, and absorption efficiency, all responding to changes in ration. In Fig. 4 these relationships have been extrapolated over a wider range of available ration (as mg POM. litre^{-1}) to estimate absorbed ration (A; J.d^{-1}); a curve of respiratory heat loss (R) is also plotted, based on an exponential relationship between clearance rate and the rate of oxygen consumption (see Fig. 3). This extrapolation is a simplification, not least because the volume capacity of the digestive gland may itself be altered in response to long-term changes in ration. Nevertheless, the treatment serves to illustrate the range of ration over which the scope for growth, calculated simply as A-R, may be positive. Should the respiration rate be increased to R' by the action of some environmental factor (e.g. temperature) or by

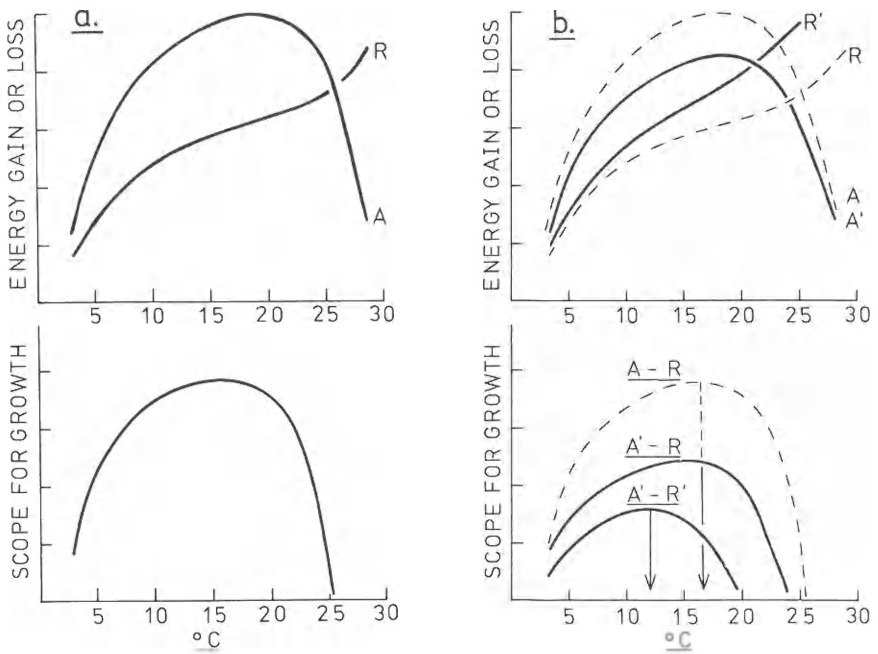

Fig. 5. a. Curves representing the absorbed ration (A), respiratory losses (R) and the scope for growth (A-R) for *Mytilus edulis* at different temperatures. b. As for a but with A reduced (A^1) and R increased (R^1) as discussed in the text. Temperature optima are indicated by arrows.

endogenous factors which might increase the energy demands of the animal (e.g. the onset of gametogenesis), the range of ration over which the scope for growth can be maintained positive will be reduced. These results indicate the flexibility in feeding response that allows these animals control over net energy balance in response to changes in food supply; they also demonstrate the likely impacts of certain stress factors which operate on the components of the energy budget to reduce overall physiological flexibility.

The natural environment for bivalves includes changes in temperature as well as changes in food supply. My final example in this section concerns responses to temperature by *Mytilus edulis*. Individuals of this species have been shown to acclimate with considerable efficiency to temperatures between 10° and 20°C (Widdows and Bayne, 1971; Bayne *et al*., 1973). Fig. 5a illustrates the acclimated rates of energy gain (A) and loss (R) in mussels fed a constant ration at different temperatures, and the resulting scope for growth calculated simply as A-R. Over a wide range of temperature, from ∿7 to 22°C, the scope for growth is maintained at high values, becoming negative at ∿25°C, which approaches the incipient lethal limit for the species.

In Fig. 5b two hypothetical situations of environmental stress are considered. In the first, a 15% reduction in the absorbed ration, A, is applied at all temperatures (A^1; this might result from a change in available ration or from a factor which suppresses feeding activity or reduces absorption efficiency). This results, of course, in a reduction in the scope for growth (A^1-R) and also reduces the temperature at which the scope for growth becomes negative, but does not affect the temperature optimum at which maximum energy is made available for growth (viz. 17°C). In the second hypothetical situation, an increase in respiratory heat loss is also introduced; however, whereas the original respiration rate (R) showed partial temperature acclimation (Q_{10} between 10° and 20°C of ∿1.3) the new rate (R^1) is taken as the sum of R and an increment which is fully temperature-dependent (Q_{10}=2). Such a change in respiration rate may follow, for example, from the stimulation of an activity or from the imposition of a chemical stress, where the normal mechanisms of temperature acclimation are not invoked. In these circumstances the scope for growth (A^1-R^1) is further reduced, as is the temperature of zero scope, and in addition the optimum for growth is shifted to a lower temperature (from 17° to 12°).

It is important to bear in mind that both the hypothetical changes considered in Fig. 5b, although representing 'deteriorations', at least in an energetic sense (and therefore being consistent with the concept of a stress imposing an "energy drain"), involve responses consistent with the normal physiological processes of compensation for normal environmental changes. There is no suggestion here of a maladaptive physiological response. Nevertheless, the implications for the individuals' fitness are considerable - a decline in the energy available for growth and reproduction, an increased vulnerability to temperature changes at the extremes of the normal ecological range and, more subtly but nonetheless damaging to an integrated metabolic strategy, a shift in the thermal optimum.

Size-related physiological changes. The rates of feeding and of respiration can usually be related to body size (the dry weight of soft tissues, W) by the allometric equation:

$$y = a.W^b$$

where a and b are fitted parameters. In the majority of studies with bivalves the exponent b takes higher values for respiration rate than for feeding (reviewed by Bayne and Newell, 1983). Sebens (1982) explored some of the implications of this difference for aspects of growth and reproduction. In Fig. 6 some data are plotted for *Mytilus edulis*. At low ration levels (bottom panel) the exponents for absorption, A and A^1, and for respiration, R and R^1, were 0.38 and 0.65, respectively. At 10°C the levels of absorption and respiration (i.e. the values for a in the allometric equations) were such that the scope for growth (A-R) was positive over all measured sizes, from 0.1 to 2.0 grams dry flesh weight. With a rise in temperature to 22.5°C, however, A declined (to A^1) and R increased (R^1), though the weight exponents b did not change; at this temperature (A^1-R^1) was positive only for individuals less than ∿0.6 g dw. When calculated as net energy flux (i.e. $(A-R).W^{-1}$) values declined over the entire weight range, at both temperatures. In these circumstances, then, small individuals were at an energetic advantage in responding to the high temperature.

At a higher ration (Fig. 6, top panel) the exponent value for absorption was unchanged but the $\underline{b}$ value for respiration was reduced to ∿0.4 (Widdows, 1978). The scope for growth at both temperatures now increased with increase in body size although, as before, if calculated per unit body weight the net energy gain declined in the larger individuals. These findings are relevant to the observed seasonal cycle of growth. As ration conditions decline in the winter months (e.g. *Chlamys islandica*; Vahl, 1980) or at high summer

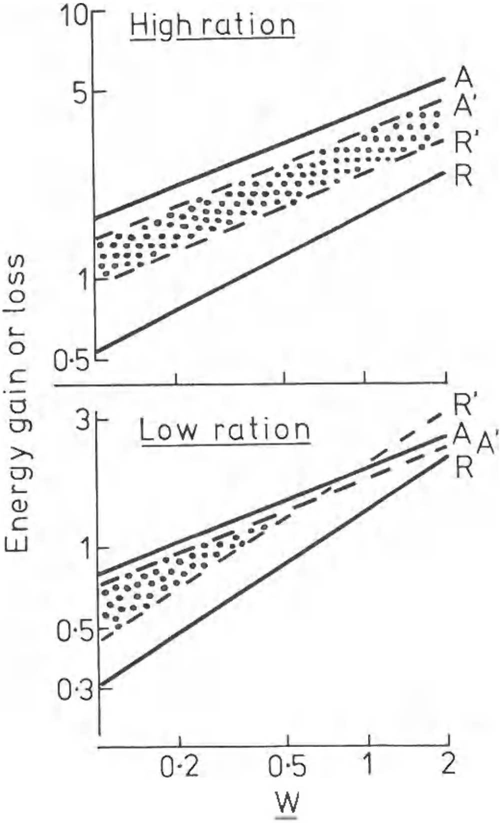

Fig. 6. Regression lines representing the absorbed ration (A) and respiratory losses (R) for *Mytilus edulis* of different size (W; grams), at two ration levels and at two temperatures. Solid lines, 10°C; dashed lines, 22.5°C. Both axes are logarithmic. The stippled area represents the scope for growth at 22.5°C.

temperatures (e.g. *Macoma balthica*; see also *Chlamys varia*, Shaffee and Lucas, 1982) larger individuals may be more severely affected and periods of negative growth may be of longer duration than for smaller individuals.

This analysis somewhat exaggerates the energetic advantages available to smaller individuals (and ignores any ecological disadvantages of small size; Paine, 1976). Small mussels, for example, have a higher maintenance energy requirement (as % body weight per day) than larger mussels and they lose weight more rapidly during starvation than do larger individuals. Also, small individuals store less energy as a reserve against periods of food shortage than do larger animals and consequently catabolise more protein in surviving starvation. Nevertheless, the indications are that less extreme environmental stresses can be expected to have a greater impact on the larger individuals; since these larger individuals are the major contributors to the reproductive potential of the population (see below), such stresses can have an exaggerated effect on aspects of population growth and survival.

Effects on reproduction. The graphs in Fig. 6 do not include the full energy losses to the individual, for gamete production can be considered a potential net export of energy that is not then available for somatic growth and body maintenance. The energy allocated to gametes by bivalves (Pr) increases with increase in body size according to an exponent b=1.0 (at least to a first approximation; Bayne *et al*., 1983). As the individual grows, a greater proportion of the available energy is used for gamete production i.e. the reproductive effort increases (Fig. 7). Two questions arise: to what extent does this increasing investment in reproduction occur at the expense of energy that would otherwise be used for repair and body maintenance? and to what degree are these reproductive processes vulnerable to environmental change?

The extent to which the energy demands of reproduction compete with those of maintenance may be represented in an index proposed by Calow (1979):

$$C = 1 - \left[(A - Pr)/R^{*} \right] ,$$

where A is the absorbed ration and R* is the energy demand of maintenance activities. Negative values for C indicate that reproduction, Pr, does not occur at the expense of maintenance; C=0 when reproduction and maintenance together demand all the available absorbed energy. This index has been calculated for *Mytilus* by Bayne *et al*. (1983); it takes negative values over most of the size range but increases to reach zero as the individual approaches its maximum body weight. The results suggest that energy allocations between maintenance, growth and reproduction are such as to result in a high rate of somatic growth in small individuals and an increasing rate of gametogenesis, with consequent reduction in somatic growth, as the individual grows in size; eventually, the sum of the energy made available to reproduction and the maintenance energy requirement equals the absorbed ration, at the animals' maximum body size. Environmental factors that decrease the total net energy gain might be expected to result in suppression of gamete production,

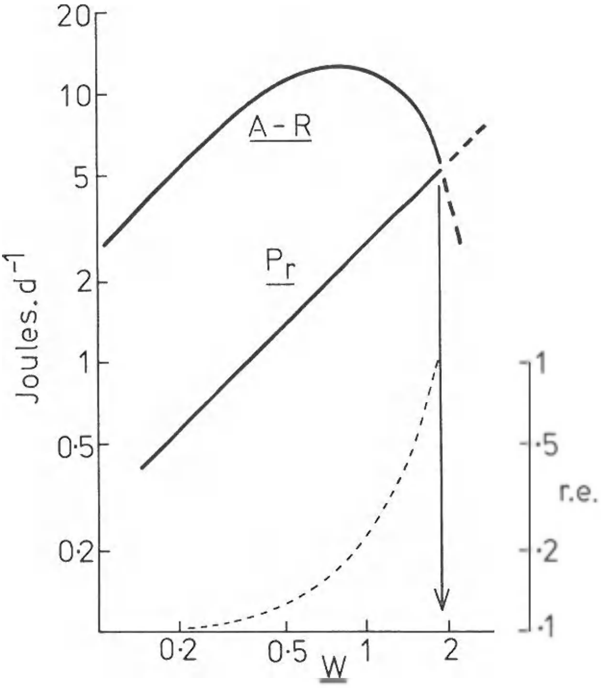

Fig. 7. The scope for growth (A-R) for Mytilus edulis plotted against body size (W; grams), together with gamete production (Pr). The reproductive effort or r.e. [Pr/(A-R)] is also plotted as a dashed line and the maximum attainable body size is identified by an arrow.

particularly in larger individuals in which tissue maintenance (and therefore survival) might be at risk.

There is evidence for the suppression of gamete production under environmental stress. Experiments reported by Bayne et al. (1978) demonstrated that, with reduced scope for growth, fecundity (numbers of eggs released) declined in direct proportion but the size (weight) of the eggs released, and the reproductive effort represented, remained at high values to ca. 70% reduction in scope, below which both declined sharply. A reduction in egg size would have a marked, deleterious effect on the survival and growth of the larvae (Kraenter et al., 1982) and therefore on overall fitness. These results resemble recent evidence from field studies that suggest, for some bivalves (see also Sutherland, 1972, on limpets) a maintenance or an increase in reproductive effort with increased exposure to air (e.g. Choromytilus meridionalis, Griffiths, 1981; Geukensia demissa, Jordan and Valiela, 1982) although, at the upper limits of their distribution on the shore reproductive effort may be reduced (Mytilus edulis, Rodhouse, pers.comm.).

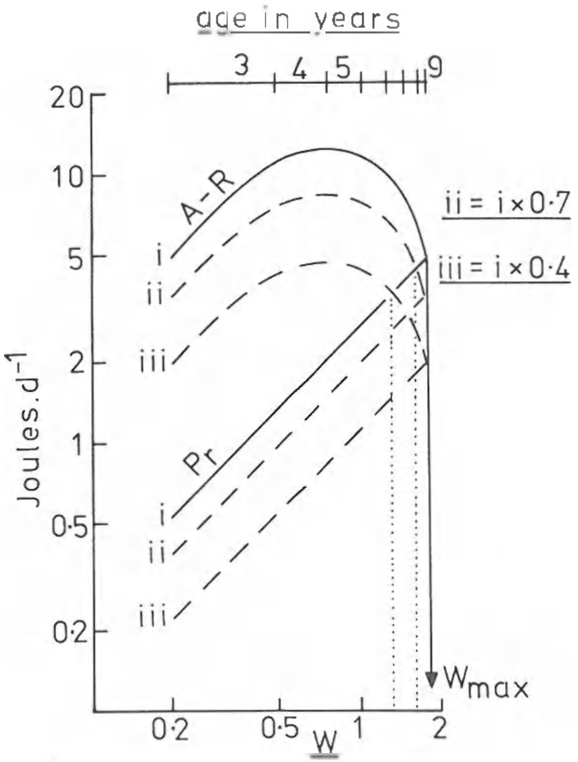

Fig. 8. Hypothetical curves of the scope for growth (A-R) and gamete production (Pr) for Mytilus edulis of different sizes (W; grams). A scale of age in years is also indicated. W_{max}; maximum attainable body size. See text and Table 2 for discussion.

Fig. 8 re-plots the curves of (A-R) and Pr against body weight, from Fig. 7. In addition, curves representing a 30% and a 60% reduction in each of these variables are shown. For any one condition, the intercept between (A-R) and Pr represents a size beyond which further gamete production would demand more energy than is concurrently available from the net energy balance (W_{max} in Fig. 8). It is assumed that growth ceases at a weight (on the abscissa) equivalent to this intercept. In response to a reduction in the net energy gain (e.g. (A-R) x 0.7) gamete production may decline in proportion, holding reproductive effort constant, or Pr may remain at its former value, representing an increase in reproductive effort.

If the former of these two 'options' is adopted, egg production will be possible up to the maximum body size suggested in Fig. 8 (W_{max}); if the second option is taken, however, egg production will cease at a size equivalent to the new intercept between Pr and the

TABLE 2. Life-time egg production by *Mytilus edulis* related to different levels of energy gain (A-R) and to various 'options' for gamete production (Pr) and reproductive effort. See text and Figure 12.

Variable	Option	Life-time egg production x 10^6
(A-R)	Pr	14.6
(A-R) x 0.7	Pr	8.8
	Pr x 0.7	8.0
(A-R) x 0.4	Pr	4.2
	Pr x 0.7	4.5
	Pr x 0.4	5.9

reduced (A-R). In Table 2 these various options have been considered in terms of a life-time production of eggs, assuming growth according to the age-scale inset in Fig. 8 and a weight-related fecundity given by the equation:

$$\text{Eggs per annum } (10^6) = 60.W^{1.0}$$

Given a 30% reduction in net energy balance (i.e. option ii in Fig. 8), life-time production is maximized if reproductive effort is increased whilst accepting a reduction in maximum body size. This response has features similar to the reports for bivalves living at different heights on the shore. If the reduction in energy balance is more severe (i.e. (A-R) x 0.4) the optimal response for egg production may be to keep the reproductive effort at the original level. However, under an environmental stress as severe as this, net energy gain is likely to approach the demands of maintenance and require a reduction in Pr in order to keep the cost index, *C*, below zero.

Natural populations of mussels show signs of considerable variance in reproductive potential (Bayne *et al*., 1983). Presumably the 'plasticity' that this represents is potentially adaptive, enabling the individual to survive periods of stress (e.g. by nutrient limitation) whilst also being able to maximize reproductive output when conditions are more favourable. As with aspects of physiological compensation discussed earlier, however, responses occur which can be considered compensatory in direction, but which are on a curve of reducing efficiency. A detailed analysis of energy allocations between growth and reproduction allows some understanding of the range of responses available to these animals in resisting environmental stresses.

CONCLUDING REMARKS

The examples that have been discussed illustrate certain general features of the physiological effects of stress. In response to a stimulus that exceeds a certain threshold, acclimation is incomplete and although some compensation results (i.e. the balance of physiological procesess is partially restored) net energy gain is reduced and there is a decline in certain attributes of fitness (e.g. growth efficiency, reproductive potential). Importantly, the physiological flexibility of the individual is impaired under stress, illustrated in these examples as reduced thermal tolerance, a narrower range of ration level for growth, reduced maximum body size and restrictions on age-related fecundity. A feature of these stress responses not illustrated in the same detail, but implicit in the discussion, concerns the increasing 'depth' of response intensity, from behavioural responses (comprising, in bivalves, shell closure and escape responses by burrowing etc.) through aspects of physiological compensation and acclimation to modifications to reproductive processes, and eventually to differential mortality. These responses are unlikely to be linear with increasing intensity of stress, but the existence of different degrees of response provides an effective means for assessing the performance and state of adaptedness of an organism to a change in environment.

In making this assessment, however, it is important to consider not just the environmental factor itself, but the selection force that it might represent (Bock, 1980). The relationship between genetic and physiological variability amongst populations of the same species is critical in this evaluation, but relevant investigations are few. In recent years studies with Mytilus edulis by Koehn and his colleagues (see Koehn et al., 1980) have linked allele frequency differences at one locus (LAP 1 or aminopeptidase) with salinity changes in the environment and with physiological processes of volume regulation. Other studies by Gartner-Kepkay et al. (1980, 1983) demonstrate genetic differentiation between populations of mussels in spite of an apparent ease of gene flow, through larval recruitment, over the area studied. If selection is occurring in these situations, the environmental factors involved seem rather subtle when placed in the context of the eurytopic nature of the overall phenotype of the species. There is a challenge here for the ecologist to reconcile the physiological plasticity of the individual with the selective forces in the environment.

This requirement for careful evaluation of the selective forces represented by particular environmental stresses is even more urgent when attention is directed to comparisons between species. The same intensity of an environmental change may be "predictable" (in the sense of Grassle and Grassle, 1977) for one organism, and so invoke a physiological response, but be "unpredictable" for a different organism, leading to local extinction. Eurytopic, tolerant species are the correct objects of physiological and biochemical attention if we wish to assess how individual organisms are responding to environmental change, including pollution, since this tolerance is often based on physiological flexibility, which can be measured. However, if the objective is to detect community responses to stress such organisms are possibly inappropriate and attention should rather be focussed on organisms responding to other selection forces (e.g. Gray, 1982). It would be a mistake to confuse these two, and possibly of limited value to engage in detailed physiological studies of species (or of "species complexes") which are more likely to respond to the particular stress by genetic than by physiological change.

ACKNOWLEDGEMENTS

I am grateful to many colleagues at IMER, and to Dr Erich Gnaiger (University of Innsbruck) for discussion of these topics. The Institute for Marine Environmental Research is a component laboratory of the U.K. Natural Environment Research Council.

REFERENCES

Alderdice, D.F., 1972. Factors combinations, in Marine Ecology, vol. 1. Environmental factors, Part 3 (Ed. O. Kinne). Wiley-Interscience, London.

Alderdice, D.F., 1976. Some concepts and descriptions of physiological tolerance: Rate-temperature curves of poikilotherms as transects of response surfaces. J. Fish Res. Bd Can., 33, 299-307.

Bachelet, G., 1980. Growth and recruitment of the tellinid bivalve Macoma balthica at the southern limit of its geographical distribution, the Gironde estuary (S.W. France). Mar. Biol., 59, 105-117.

Bayne, B.L., and Newell, R.C., 1983. Physiological energetics of marine molluscs, in The Mollusca, Vol. 4, Physiology, Part 1 (Eds. A.S.M. Saleuddin and K.M. Wilbur). Academic Press, New York.

Bayne, B.L., and Widdows, J., 1978. The physiological ecology of two populations of Mytilus edulis L. Oecologia (Berl.), 37, 137-162.

Bayne, B.L., Thompson, R.J., and Widdows, J., 1973. Some effects of temperature and food on the rate of oxygen consumption by Mytilus edulis L., in Effects of temperature on ectothermic organisms (Ed. W. Wieser). Springer-Verlag, Berlin.

Bayne, B.L., Bayne, C.J., Carefoot, T.C., and Thompson, R.J., 1975. The physiological ecology of Mytilus californianus Conrad. 1: Aspects of metabolism and energy balance. Oecologia (Berl.), 22, 211-228.

Bayne, B.L., Holland, D.L., Moore, M.N., Lowe, D.W., and Widdows, J., 1978. Further studies on the effects of stress in the adult on the eggs of Mytilus edulis. J. mar. biol. Ass. U.K., 51, 659-668.

Bayne, B.L., Salkeld, P.N., and Worrall, C.M., 1983. Reproductive effort and value in different populations of the marine mussel, Mytilus edulis L. Oecologia (Berl.), 59, 18-26.

Beukema, J.J., Cadee, G.L., and Jansen, J.J.M., 1977. Variability of growth rate of Macoma balthica (L.) in the Wadden Sea in relation to availability of food, in Biology of benthic organisms (Eds. B.F. Keegan, O'Ceidigh, and P.J.S. Boaden). Pergamon Press, Oxford.

Bock, W.J., 1980. The definition and recognition of biological adaptation. Amer. Zool., 20, 217-227.

Brett, J.R., 1958. Implications and assessment of environmental stress, in Investigation of fish-power problems (Ed. P.A.

Larkin). H.R. Macmillan Lectures in Fisheries, University of British Columbia.

Calow, P., 1976. Biological Machines: a Cybernetic Approach to Life. Edward Arnold, London.

Calow, P., 1977. Ecology, Evolution and Energetics: A study in metabolic adaptation, in Advances in Ecological Research (Ed. A. Macfadyen). Academic Press, London.

Calow, P., 1979. The cost of reproduction - a physiological approach. Biol. Rev., 54, 23-40.

Fry, F.E.J., 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55, Publ. Ont. Fish. Res. Lab., 68, 1-62.

Fry, F.E.J., 1971. The effect of environmental factors on the physiology of fish, in Fish Physiology. Vol. 6. Environmental relations and behaviour (Eds. W.S. Hoar and D.J. Randell). Academic Press, New York.

Gartner-Kepkay, K.E., Dickie, L.M., Freeman, K.R., and Zouros, E., 1980. Genetic differences and environments of mussel populations in the maritime provinces. Can. J. Fish. Aquat. Sci., 37, 775-782.

Gartner-Kepkay, K.E., Zouros, E., Dickie, L.M., and Freeman, K.R., 1983. Genetic differentiation in the face of gene flow: A study of mussel populations from a single Nova Scotian embayment. Can. J. Fish. Aquat. Sci., 40, 443-451.

Gilfillan, E.S., Mayo, D., Hanson, S., Donovan, D., and Jiang, L.C., 1977. Reduction in carbon flux in Mya arenaria caused by a spill of No. 6 fuel oil. Mar. Biol., 37, 115-123.

Grassle, J.F., and Grassle, J.P., 1977. Life histories and genetic variation in marine invertebrates, in Marine organisms: genetics, ecology and evolution (Eds. B. Battaglia and J.A. Beardmore). Plenum Press, London.

Gray, J.S., 1982. Effects of pollutants on marine ecosystems. Neth. J. Sea Res., 16, 424-443.

Griffiths, R.J., 1981. Production and energy flow in relation to age and shore level in the bivalve Choromytilus meridionalis (Kr.). Estuar. Coast. Shelf Sci., 13, 477-493.

Hubbell, S.P., 1971. Of sowbugs and systems: the ecological energetics of a terrestrial isopod, in Systems Analysis and Simulation in Ecology (Ed. B.C. Patten). Academic Press, New York.

Jordan, T.E., and Valiela, I., 1982. A nitrogen budget of the ribbed mussel, Geukensia demissa, and its significance in nitrogen flow in a New England salt marsh. Limnol. Oceanogr., 27, 75-90.

Kinne, O., 1964. The effects of temperature and salinity on marine and brackish water animals. 1. Temperature. Oceanogr. mar. Biol. Ann. Rev., 1, 301-340.

Koehn, R.K., Newell, R.I.E., and Immerman, F., 1980. Maintenance of an aminopeptidase allele frequency cline by natural selection. Proc. Natn. Acad. Sci., 77, 5385-5389.

Kraenter, J.N., Castagna, M., and Van Dessel, R., 1982. Egg size and larval survival of Mercenaria mercenaria (L.) and Argopecten irradians (Lamarck). J. exp. mar. Biol. Ecol., 56, 3-8.

Lugo, A.E., 1978. Stress and ecosystems, in Energy and *environmental stress in aquatic systems* (Eds. J.H. Thorp and J.W. Gibbons). Technical Information Centre, U.S. Department of Energy, Virginia.

Newell, R.C., and Branch, G.M., 1980. The influence of temperature on the maintenance of metabolic energy balance in marine invertebrates. *Adv. mar. Biol.*, 17, 329-396.

Nichols, F.H., and Thompson, J.K., 1982. Seasonal growth in the bivalve *Macoma balthica* near the southern limit of its range. *Estuaries*, 5, 110-120.

Odum, H.T., 1967. Work circuits and systems stress, in *Symposium on primary productivity and mineral cycling in natural ecosystems* (Ed. H.E. Young). University of Maine Press, Orono.

Paine, R.T., 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology*, 57, 858-873.

Pickering, A.D., 1981, (Ed.). *Stress and Fish.* Academic Press, London.

Precht, H., 1958. Concepts of temperature adaptation of unchanging reaction systems of cold-blooded animals, in *Physiological adaptations* (Ed. C.L. Prosser). Ronald Press, New York.

Prosser, C.L., 1958. General summary: the nature of physiological adaptation, in *Physiological adaptations* (Ed. C.L. Prosser). Ronald Press, New York.

Sebens, K.P., 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology*, 63, 209-222.

Selye, H., 1950. Stress and the general adaptation syndrome. *Br. med. J.*, 1, 1383-1392.

Shaffee, M.S., and Lucas, A., 1982. Variations saisonnières du bilan énergétique chez les individus d'une population de *Chlamys varia* (L.): Bivalvia, Pectinidae. *Oceanologia Acta*, 5, 331-338.

Sutherland, J.P., 1972. Energetics of high and low populations of the limpet *Acmaea scabra* (Gould). *Ecology*, 53, 430-438.

Ulanowicz, R.E., 1978. Modelling environmental stress, in *Energy and environmental stress in aquatic systems* (Eds. J.A. Thorp and J.W. Gibbons). Technical Information Centre, U.S. Department of Energy, Virginia.

Vahl, O., 1980. Seasonal variations in seston and in the growth rate of the Iceland scallop, *Chlamys islandica* (O.F. Müller) from Balsfjord, 70°N. *J. exp. mar. Biol. Ecol.*, 48, 195-204.

Widdows, J., 1978. Physiological indices of stress in *Mytilus edulis*. *J. mar. biol. Ass. U.K.*, 58, 125-142.

Widdows, J., and Bayne, B.L., 1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. *J. mar. biol. Ass. U.K.*, 51, 827-843.

Wilde, P.A.W. de, 1975. Influence of temperature on behaviour, energy metabolism and growth of *Macoma balthica* (L.), in *Proc. Fifth Europ. Mar. Biol. Symp.* (Ed. H. Barnes). Aberdeen University Press, Aberdeen.

Winkle, W. van, Feng, S.Y., and Haskin, H.H., 1976. Effect of temperature and salinity on extension of siphons by *Mercenaria mercenaria*. *J. Fish. Res. Bd Can.*, 33, 1540-1546.