



## EFFECTS OF TEMPERATURE ON THE SIZE OF AQUATIC ECTOTHERMS: EXCEPTIONS TO THE GENERAL RULE

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**Abstract**—1. Of 61 studies of aquatic ectotherms, increased rearing temperature (apparently not stressful for growth and development) caused a reduction in organism size at a given developmental stage in 55 cases (90.2%) and an increase in only six (9.8%).

2. The six exceptions to the size-reduction rule included one diatom (*Phaeodactylum tricornutum*), one copepod (*Salmincola salmoneus*) and four species of mayfly (Ephemeroptera). The extent to which these exceptions could be explained by each of four mechanisms was investigated by comparing their life cycles and niches with those of other closely-related species.

3. No satisfactory explanation could be found for the response of *P. tricornutum*, but mechanisms consistent with the response of *S. salmoneus* were: reduced risk of oxygen shortage, low risk of ectotherm predation and seasonal constraints on the life cycle. The latter may also help explain the four mayfly exceptions.

**Key Word Index:** Temperature; body size, life history; ectotherms; growth; Ephemeroptera; Copepoda; *Salmincola salmoneus*; Bacillariophyta; *Phaeodactylum tricornutum*; phenotypic plasticity

### INTRODUCTION

The production of a smaller adult body at increased rearing temperatures is easily explicable if temperatures are stressfully high or resources are either in short supply or of poor quality so that individual growth rates are reduced (Brett, 1971; Cossins and Bowler, 1987; Moore and Folt, 1993). A more difficult problem is to explain why an organism's size at a given developmental stage should be reduced by increased rearing temperatures under conditions with abundant resources and when the temperature increase is observed or expected to increase an individual's growth rate. Yet this reduction in size has been observed in over 80% of ectotherms studied, including members of the Protista, four phyla and eight classes of animal, two families of plant and one bacterium species—from terrestrial and aquatic habitats (Atkinson, 1994). Earlier studies broadly support this finding (Bělehrádek, 1935; Ray, 1960; von Bertalanffy, 1960; Precht *et al.*, 1973).

Temperature can affect organism size at a given developmental stage by constraining growth (von Bertalanffy, 1960; Atkinson, 1994) or by altering the adaptive value of body size (Loosanoff, 1959; Culver, 1980; Roff, 1981; Myers and Runge, 1986; Chrzanowski *et al.*, 1988; Atkinson, 1994) or of developmental rate (Myers and Runge, 1986; Atkinson, 1994; Atkinson, 1995; Sibly and Atkinson,

1994). No single overriding physiological constraint or adaptive explanation has yet been found to account for the general size reduction.

One approach to identifying the causes of major variation in the temperature–size relationship is to compare life cycles and niches of species which are exceptions to the general rule with those of species which follow the rule, especially species which are otherwise closely related taxonomically and ecologically. This paper focuses on published phenotypic plasticity in organism size, rather than genetic variation related to temperature differences. Re-examination of existing data may not provide definitive explanations but can help narrow the range of hypotheses to be tested. Here, I consider the extent to which exceptions to the general rule from aquatic environments that have been reported in the literature can be explained by each of four mechanisms that relate temperature to size-at-stage. Any combination of the four mechanisms may operate on a given population.

#### *Mechanism 1: Oxygen limitation (carbon dioxide limitation for autotrophs)*

Increased temperature both reduces the amount of dissolved oxygen in water (Wilber, 1964) and increases respiratory activity and hence demand for oxygen. According to this mechanism, even if

individual growth rate is not immediately reduced at high temperatures, high temperatures may still correlate with future oxygen shortage in the organism's natural environment. For autotrophs, when nutrient and light levels are high, the amount of dissolved carbon dioxide (CO<sub>2</sub>) may become limiting (e.g. Fogg, 1965). In either case, temperature could thus act as a cue for future risks, and hence alter the optimal time to mature (Atkinson, 1994; Sibly and Atkinson, 1994). All else being equal, exceptions to the general temperature-size rule would thus be expected to come from environments in which high temperature was not normally associated with future shortage of oxygen (or CO<sub>2</sub> for autotrophs).

#### *Mechanism 2: Habitat loss*

For some habitats such as small seasonal ponds and streams, increased evaporation at increased temperatures can increase the likelihood of their drying out. Again, therefore, for organisms adapted to these habitats temperature might serve as a cue for future risks, and hence alter the optimal time to mature (Atkinson, 1994; Sibly and Atkinson, 1994), or to produce forms capable of either resisting desiccation or allowing dispersal to sites with more favourable conditions. According to this mechanism, exceptions to the general temperature-size rule would be more likely to come from environments not prone to desiccation at high temperatures rather than from ones that sometimes dried out.

#### *Mechanism 3: Risk of predation by other ectotherms*

Using adaptationist reasoning, many authors have predicted that, all else being equal, increased juvenile mortality should favour earlier maturation at a smaller size (Williams, 1966; Wilbur and Collins, 1973; Roff, 1981; Werner, 1986; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Kawecki and Stearns, 1993; Sibly and Atkinson, 1994). Feeding rates of ectotherm predators generally increase with increasing non-stressful temperature whilst endotherm predation may even be reduced (Atkinson, 1994). Thus, for organisms that mainly experience ectotherm predation, an increased temperature may serve as a cue for increased predation risks and hence favour earlier maturation even at the expense of time spent growing. I propose that among the species least likely to experience ectotherm predation are very large species—at least during the latter part of their development when they are protected by their large size. Increased temperature would be less likely to favour reduced adult size in these species than in those with higher predation risks.

A complicating factor is the possibility of size-dependent predation. For instance, in small plank-

tonic species, small size can provide protection from size-selective ectothermic predators such as fish and large insects (Zaret, 1980; Dodson, 1989; Stibor and Luning, 1994). This advantage of small size has been proposed to explain the general size reduction in some planktonic species at increased temperature (Culver, 1980; Chrzanowski *et al.*, 1988). Conversely, some invertebrate predators of planktonic species prefer small individuals (Zaret, 1980; Stibor and Luning, 1994). Data on size-selective predation are likely to be unavailable for the majority of populations for which temperature effects on size are known. In the present paper, therefore, I just consider whether exceptions to the general temperature-size rule include very large species.

#### *Mechanism 4: Seasonal effects*

Many organisms mature at particular times of year and use photoperiod as a seasonal cue (e.g. Masaki, 1978; Tauber *et al.*, 1986; Roberts and Summerfield, 1987; Nylin *et al.*, 1989; Ellis *et al.*, 1990; Scott and Dingle, 1990). In organisms reared under photoperiods that indicate that little time would normally be available in their natural environment before maturity must be reached (e.g. before food would normally deteriorate) faster juvenile growth at increased temperatures could lead to the production of larger rather than smaller adults since those from all temperature treatments would mature at similar times (or photoperiods). According to this mechanism, exceptions to the general rule would be found in species which must pass a particular developmental stage at a particular time of year and which are reared in the laboratory under photoperiods near to those at which the particular developmental event normally occurs.

### MATERIALS AND METHODS

Published studies of the effects of rearing temperature on size-at-stage of aquatic ectotherms were examined. Whilst some genetic evolution during the experiments may have been unavoidable in species with very short generation times (e.g. protists, bacteria), the rapidity of response even in some of these suggests that phenotypic plasticity was also observed (e.g. Margalef, 1954). The criteria for inclusion of studies in the review are summarized here and discussed more fully by Atkinson (1994).

In those studies deemed acceptable for inclusion, environmental conditions were controlled and the range of temperatures allowed the organisms to reach maturity but did not attain values so stressfully high that an increase was shown to reduce rates of individual growth or differentiation. Temperatures that were

obviously outside the range normally encountered by the species were also excluded as were temperatures so low that daily mortality rate was increased with reduced temperature, despite a presumed lower metabolic rate. Also studies were excluded if there was evidence that the amount of resources were limiting or the food provided was both unnatural and caused a reduction in growth rate below that on other foods. However, most studies lacked at least some relevant data (e.g. growth rates, photoperiod, food quality). Quality of data is taken into account in the analysis of exceptions to the general rule in the present paper. The review focused on studies of developmental stages near to reproductive maturity. In unicells, however, size at initiation of fission was only available from one study (Adolph, 1929). Therefore, to increase sample size of protists, less precise measures such as average size over a period of several generations were also included. Size measures included dry or wet weights, or correlates of organism weight such as body length or exoskeletal dimensions. Finally, only experiments in which statistically significant ( $P < 0.05$ ) effects of temperature on size had been found (by the authors or myself) were included in the review.

The present paper extends the preliminary work of Atkinson (1994) by examining the extent to which exceptions to the general rule can be explained by mechanisms 1–4. The following information was sought from published sources for those species for which the relevant mechanism was applicable:

- (1) Evidence that any oxygen (or  $\text{CO}_2$ ) limitation at high temperatures in the natural environment would be less than for other related aquatic species in the review (mechanism 1);

- (2) Evidence for an association between increased temperature and habitat drying out (mechanism 2);
- (3) Organism size (mechanism 3);
- (4) Evidence of an association between a particular stage of the life history and a particular time of year (mechanism 4). [It was not possible, however, to identify the extent to which juvenile developmental period was constrained by season.]

## RESULTS

Sixty-one studies of aquatic organisms satisfied the criteria for inclusion in the review (Table 1). The organisms included one bacterium, seven protists (five autotrophic, two heterotrophic), two rotifers, four molluscs, twenty-six insects, thirteen crustaceans, seven amphibians and one fish (Table 1). Whilst most species were from freshwater, eight were from saltwater environments.

Fifty-five studies (90.2%) showed a size reduction with increased rearing temperature, whilst only six (9.8%) showed a size increase (Table 1). These six exceptions to the general rule, described below, comprised one protist (Fawley, 1984), one copepod crustacean (Johnston and Dykeman, 1987), and four mayflies (Sweeney and Vannote, 1978; Vannote and Sweeney, 1980).

### *Exception 1: Phaeodactylum tricornutum (Bacillariophyta)*

At high light intensities, cell width and volume of this pennate marine diatom increased with each increase in rearing temperature over five treatments

Table 1. Summary by taxon of effects of increased rearing temperature on aquatic organism size

| Kingdom              | Phylum          | Class        | Sub-class/Order<br>(for Arthropoda) | No. of reductions | No. of increases |
|----------------------|-----------------|--------------|-------------------------------------|-------------------|------------------|
| Monera<br>(Bacteria) |                 |              |                                     | 1                 | 0                |
| Protists             | Chlorophyta     |              |                                     | 4                 | 0                |
|                      | Bacillariophyta |              |                                     | 0                 | 1                |
|                      | Ciliophora      |              |                                     | 2                 | 0                |
| Animalia             | Aschelminthes   | Rotifera     |                                     | 2                 | 0                |
|                      | Mollusca        | Gastropoda   |                                     | 2                 | 0                |
|                      |                 | Pelecypoda   |                                     | 2                 | 0                |
|                      | Arthropoda      | Insecta      | Diptera                             | 17                | 0                |
|                      |                 |              | Ephemeroptera                       | 5                 | 4                |
|                      |                 | Crustacea    | Copepoda                            | 9                 | 1                |
|                      |                 |              | Decapoda                            | 2                 | 0                |
|                      |                 |              | Mysidacea                           | 1                 | 0                |
|                      | Chordata        | Amphibia     |                                     | 7                 | 0                |
|                      |                 | Osteichthyes |                                     | 1                 | 0                |
| Total                |                 |              |                                     | 55                | 6                |

from 14 to 23°C—a range considered optimal for population growth and photosynthesis (Fawley, 1984). At lower light intensities there was the risk of resource limitation affecting the results, and the increase in size with increase in temperature gradually became less pronounced with declining light intensity. Increased temperature increased the rate of carbon-fixation per cell per hour, and the rate of cell division up to 23°C. [A 25°C treatment—apparently stressful for rate of development—was excluded from the present review]. To reduce the risks of other variables affecting the interpretation of the results, the experiments used enriched artificial seawater and maintained a 14:10 hour light:dark regime throughout (Fawley, 1984).

The other four unicellular algae in this review were freshwater chlorophytes and had reduced cell sizes at increased temperatures (Appendix). Little information is available on the environmental conditions to which the experimental organisms were adapted, including any association between high temperature and oxygen or CO<sub>2</sub> limitation or habitat drying out (mechanisms 1 and 2). Mechanism 3 and 4 do not apply to these species since they are of microscopic size, can pass through several generations per week, and therefore a particular developmental stage is not associated with a particular time of year.

#### *Exception 2: Salmincola salmoneus (Copepoda)*

Adult trunk (body) length in this parasitic copepod, which was reared on gills of Atlantic salmon (*Salmo salar*) kelts under simulated natural day-lengths, was significantly greater at higher than at lower temperatures (Johnston and Dykeman, 1987). The other five species of copepod were free-living and each showed size reductions with increased temperature (Table 2). *S. salmoneus* was the only gill parasite present in the sample of 61 studies in the review, and would therefore, uniquely in this review, have had an oxygen supply modified by fish respiratory activity. This suggests the possibility that respiratory compensation by the fish at increased temperatures, to maintain amounts of oxygen entering the gills, may normally reduce, prevent or delay any increased risks of oxygen shortage for the parasite at increased temperatures (mechanism 1). However, the oxygen consumption requirements of *S. salmoneus* were not measured to allow this idea to be tested. Other factors that may affect the importance of oxygen shortage are considered in the Discussion.

No information on any association between high temperature and the drying up of the salmon kelt rivers (mechanism 2) is known.

In this example, any size-related protection from ectothermic predation (mechanism 3) depends not on

the size of the parasite but on that of the fish host. The Atlantic salmon kelts, measured to the tail fork, were 68–72 cm long (C. E. Johnston, unpublished data), and kelts are typically 2–6 kg in weight (e.g. Paton and Dunlop, 1898). They are therefore easily the largest organisms of the sixty-one included in this review (Appendix), and hence one of the least likely to have major risks of predation by other ectotherms. Consequently, an increased risk of predation at increased temperatures is unlikely to provide strong selection for rapid development of the parasite, even at the expense of size at the time of maturity.

Whilst temperature affected size under simulated natural photoperiods, no significant effects were observed when fish and parasites were kept under an “advanced photoperiod regime” in which the length of light period was increased from short day length in January to the longest (summer) day length in March. This maximum day length was maintained from March to 21 June and then declined naturally thereafter. Thus seasonal effects (mechanism 4) appear to interact with the effect of temperature. Moreover, at least in the life cycle of Scottish *S. salmoneus* described by Friend (1941), only adult parasites were present on salmon kelts by May, suggesting a strong association between adulthood and time of year. However, another of the copepods in the review, *Pseudocalanus minutus*, also shows a strong association between life-history stage and time of year: it has a strictly annual life cycle in Nova Scotia waters and spawns in the late winter (McLaren *et al.*, 1989). These results differ from those for at least three of the other copepods studied which were thought by Abdullahi and Laybourn-Parry (1985) and Laybourn-Parry *et al.* (1988) to reproduce throughout the year (Table 2).

#### *Exceptions 3–6: Four mayfly species (Ephemeroptera)*

Whilst five mayfly species had a reduced dry weight at adult emergence at increased temperatures, despite faster growth and development (Sweeney and Vannote, 1978, 1984; Vannote and Sweeney, 1980; Sweeney *et al.*, 1986; Söderström, 1988), another four had an increased dry weight (Sweeney, 1978; Sweeney and Vannote, 1978; Vannote and Sweeney, 1980). The recent discovery of a second species of *Isonychia* in the study stream of White Clay Creek (*I. circe*), whose small larvae closely resemble those of *I. bicolor* (B. W. Sweeney, unpublished data) suggests that the data on *Isonychia* (Sweeney, 1978) may refer to two species. These species have different life cycles (B. W. Sweeney, unpublished data; Table 3). [Other species and experimental treatments studied by these authors were not included in the review since they either lacked size differences between

Table 2. Temperature-size relationships and selected habitat and life-cycle characteristics in six species of Copepod

| Species  | Temperature effect on size <sup>1</sup> | Habitat                                | Organism size <sup>2</sup>                     | Association of dev. stage with time of yr  | References   |
|--|---|--|--|--|--|
| <i>Acanthocyclops vernalis</i> (syn. <i>Cyclops vernalis</i> ) | Reduced                                 | Benthos of lakes, esp. eutrophic ones  | 1.62 mm<br>30 µg                               | Probably reproductive throughout year  | Coker (1933); Abdullahi and Laybourn-Parry (1985)                                      |
| <i>A. viridis</i> (syn. <i>Cyclops viridis</i> )               | Reduced                                 | Benthos of lakes, esp. eutrophic ones  | 53 µg  | Probably reproductive throughout year  | Coker (1933); Abdullahi and Laybourn-Parry (1985); Laybourn-Parry <i>et al.</i> (1988) |
| <i>Cyclops serrulatus</i>                                      | Reduced                                 | (No information)                       | 1.32 mm  | (No information)   | Coker (1933)   |
| <i>Macrocyclus albidus</i>                                     | Reduced                                 | Benthos of lakes, esp. eutrophic ones  | 44 µg  | Probably reproductive throughout year  | Abdullahi and Laybourn-Parry (1985); Laybourn-Parry <i>et al.</i> (1988)               |
| <i>Pseudocalanus minutus</i>                                   | Reduced                                 | Marine plankton                        | 1.01 mm  | Univoltine; Spawns in late winter  | Lock and McLaren (1970); McLaren <i>et al.</i> (1989)                                  |
| <i>Salminicola salmoneus</i>                                   | Increased                               | Gills of Atlantic salmon in freshwater | 4.82 mm (host probably > 70 cm long 2-6 kg wt) | Altered daylength regime prevents temperature-size response; only adults found by May in Scottish population | Johnston and Dykeman (1987); Friend (1941)   |

<sup>1</sup>Effect of increased temperature on size-at-stage.<sup>2</sup>Size measurements are means from the treatments and sex producing the largest sizes; weights are fresh weights (Abdullahi/Laybourn-Parry), lengths are body lengths (Coker, Lock/McLaren, Johnston/Dykeman).

Table 3. Temperature-size relationships and life-cycle characteristics in nine species of mayfly (Ephemeroptera)

| Species   | Temperature effect on size <sup>1</sup> | Organism size <sup>2</sup> | Association of developmental stage with time of year <sup>3</sup>  | References  |
|---|---|----------------------------|--|---|
| <i>Ameletus ludens</i>  | Reduced                                 | 3.85 mg                    | Univoltine; a winter-spring species  | Vannote and Sweeney (1980); B. W. Sweeney (unpublished)   |
| <i>Centropilum triangulifer</i> (syn. <i>Cloeon iri-angulifer</i> ) | Reduced                                 | 1.8 mg                     | Egg diapause April-August<br>3 + generations/yr; expt. used 13:11 LD regime and offspring of overwintering generation. | Sweeney and Vannote (1984)                                |
| <i>Leptophlebia intermedia</i>                                      | Reduced                                 | 3.70 mg                    | Univoltine; no egg diapause observed; adults emerge late March   | Sweeney <i>et al.</i> (1986); B. W. Sweeney (unpublished) |
| <i>Parameletus minor</i>  | Reduced                                 | 9.5 mm                     | Univoltine; emergence typically in June  | Söderström (1988); Söderström and Johansson (1988)        |
| <i>P. chetifer</i>  | Reduced                                 | 10.5 mm                    | Univoltine; emergence typically in June  | Söderström (1988); Söderström and Johansson (1988)        |
| <i>Caenis simulans</i>  | Increased                               | 0.5 mg                     | Possible egg diapause September-May; a summer species  | Vannote and Sweeney (1980); B. W. Sweeney (unpublished)   |
| <i>Isonychia bicolor</i> <sup>4</sup>                               | Increased                               | 15.9 mg                    | Bivoltine in White Clay Creek; summer generation examined  | Sweeney (1978)  |
| <i>Tricorythodes atratus</i>  | Increased                               | 1.72 mg                    | Possible egg diapause September-May; a summer species  | Vannote and Sweeney (1980); B. W. Sweeney (unpublished)   |
| <i>Eurylophella funeralis</i> (syn. <i>Ephemerella funeralis</i> )  | Increased                               | 4.42 mg                    | Univoltine in White Clay Creek; no egg diapause; a winter-spring species   | Vannote and Sweeney (1980); B. W. Sweeney (unpublished)   |

<sup>1</sup>Effect of increased temperature on size-at-stage.<sup>2</sup>Size measurements are those in the treatments and sex producing the largest sizes; weights are dry weights (Sweeney/Vannote); lengths are body lengths (Söderström).<sup>3</sup>Larvae of "winter-spring" species hatch from eggs in the autumn but grow mainly during winter and spring; in "summer" species most growth and resource exploitation is from May to September.<sup>4</sup>Study may have included specimens of *Isonychia circe* which has a short summer generation and probably egg diapause from September to May (B. W. Sweeney, unpublished).

temperatures that I was able to demonstrate were significantly different ( $P < 0.05$ ), grew slower at increased temperatures, or were provided with food of demonstrably inadequate quality]. In the work by Sweeney and Vannote, both cooling and warming, relative to ambient stream temperature of White Clay Creek, Pennsylvania, usually produced a reduction in size of emerging adults, which supported their concept of a thermal optimum at which body size and fecundity were maximal. *Eurylophella funeralis*, however, showed the opposite response (i.e. increased size) when temperature was raised above ambient (Table 4 in Vannote and Sweeney, 1980).

No direct evidence is presented by Sweeney and Vannote to indicate that oxygen limitation (mechanism 1) at increased temperatures was greater for some of the study species from White Clay Creek than for others. However, exceptions to the general rule (excluding *E. funeralis*) were found among species or generations whose growth was confined mainly to the summer months of May to September, when mean stream temperatures were high, whereas those which followed the general rule grew mainly during the winter and spring (Sweeney and Vannote, 1978; Vannote and Sweeney, 1980; Table 3). High summer temperatures may lead to a reduction in oxygen content of the stream water. According to mechanism 1, an oxygen shortage at increased temperatures in summer, rather than in winter or spring, would favour rapid maturation and small adult size particularly in the summer-reared mayflies. Yet the increase in size of "summer" species at increased temperature runs counter to this prediction. However, neither the oxygen content of the water in the experiments nor the oxygen consumption requirements of the different species at different temperatures are known, and therefore any suggestion that mechanism 1 is unimportant in explaining the variation amongst the mayfly species must still be provisional.

Since the likelihood of drought will be highest during the summer months, selection for rapid maturity (and smaller size) would be predicted under mechanism 2 especially for "summer" species at increased temperatures. The fact that mayflies from White Clay Creek reared during the summer (and subject to natural summer photoperiods; B. W. Sweeney, unpublished data) attained larger, not smaller, sizes when reared at increased temperatures (Table 3) suggests that mechanism 2 is not the primary ultimate cause of the differences observed among these species. However, two species of *Parameletus*, which produced smaller adults at increased temperature (Söderström, 1988) were from

habitats including seasonal streams that in some years dried out causing major population losses (Söderström and Johansson, 1988).

The species that were exceptions to the general rule were not significantly different in size from those from the same river which showed size reductions at increased temperature ( $T = 12$ ,  $P > 0.1$ , Mann-Whitney test; Table 3), so there is no evidence that size-related protection from ectotherm predators (mechanism 3) caused the different responses to temperature.

The contrasting size responses to increased temperature between species growing mainly during the summer and those growing mainly during the winter and spring (Table 3) might be explicable if emergence had to be more synchronized around a particular time of year in the "summer" species or generations than in the "winter-spring" species or generations (mechanism 4). No information is available to me on whether emergence is more synchronized around a particular time of year in the "summer" species or generations.

## DISCUSSION

### A general rule

The reduction in size at a given developmental stage observed at increased rearing temperatures in 90.2% of studies occurred despite the exclusion from the review of studies and treatments in which growth rates were observed or expected to be reduced, rather than increased, with increasing temperature. It is of course possible that certain examples would turn out to be inadmissible if experimental protocols and effects on growth and mortality had been more fully recorded. Effects of gaps in the data set on the proportion of size reductions have been analyzed by Atkinson (1994) and found not to alter the general result.

The proportion of aquatic ectotherms showing a reduced size-at-stage when reared at increased temperatures is greater than the proportion found among terrestrial species, but not significantly so ( $P > 0.2$ ; Atkinson, 1994). In the absence of known fundamental physiological constraints on growth and size at the increased temperatures (Atkinson, 1994), explanations have recently been proposed which consider the optimal developmental period and adult size when temperature correlates with mortality and population growth as well as individual growth (Sibly and Atkinson, 1994). The four mechanisms proposed in the present paper to try to explain the occurrence of aquatic exceptions to the general rule relate environmental temperature to risks of increased mortality or reduced future growth. The extent to which

these mechanisms may explain the exceptions are discussed next.

#### *Photosynthetic protists*

Why was *Phaeodactylum tricornutum* but not the four other algal examples an exception to the general rule? The review provided insufficient information to allow evaluation of possible explanations.

Information on individual growth rate of cells at the different temperatures was not available for *Scenedesmus obliquus* (Margalef, 1954) or for the three species of *Chlamydomonas* (Ray, 1960), although rates of *Chlamydomonas* cell division did increase with increasing temperature (Ray, 1960). In *Phaeodactylum tricornutum* at high light intensities, increased temperatures up to 23°C increased rate of carbon-fixation per cell and rate of cell division (Fawley, 1984). Since cell size was increased too, growth rate per cell was presumably increased. Therefore, only for *P. tricornutum* was there evidence for increasing growth rates at increased temperatures. Hence the possibility that the other species were cultured under conditions which reduced growth with increasing temperature—inadmissible as examples illustrating the general temperature–size rule—cannot be ruled out.

Effects of energy supply (light intensity) on algae can complicate the interpretation of temperature effects on size in a way not found in studies of heterotrophs. Unlike heterotrophs whose growth is not limited by energy supply if excess high quality food is provided, individual algal growth is limited not only by low light intensities (insufficient energy), but also by very high light intensities. Moreover, the high light intensity at which growth retardation starts to occur can increase with increasing temperature, as was found in the cryptophyte *Cryptomonas erosa* (Morgan and Kalf, 1979). Thus for some species it may be impossible to find a single light intensity that will enable them to grow at each of several temperatures without energy supply limiting growth in at least one of them.

Fawley (1984) related his results to the observation that *P. tricornutum* thrives in light-limited, poorly-mixed mass-culture systems at temperatures below 20°C and are rarely found above this temperature. Increased cell size was associated with increased chloroplast size, especially at low light intensities, and both of these generally increase sinking rate (Eppley *et al.*, 1967; Walsby and Reynolds, 1980; Fawley, 1984). Thus a rapid rate of sinking at high temperature would reduce the abundance of the alga at least from near the water surface.

Whilst cell division is often inhibited at extremely high temperatures, resulting in the production of

large cells (Lloyd *et al.*, 1982) cell division was observed to accelerate with increasing temperature up to 23°C in *P. tricornutum*, thereby precluding this explanation. No other physiological constraints permitting large *P. tricornutum* cell sizes only at increased temperatures are known to the author. Nor is the adaptive significance of increased sinking rates at high temperatures clear, especially in open water where cells could be completely removed from the euphotic zone. If increased sinking rate was an adaptive response to stressful conditions then the stress at these higher temperatures and light conditions was not seen as reduced rates of cell growth and division. No data were available to test if mortality rates were increased with increased temperature.

Studies not included in the Appendix—because of risks of light intensities inhibiting growth only at certain temperatures, or possible genetic adaptation to the experimental treatments, or lack of significant effects of temperature—contained two species which followed the general temperature–size rule (Morgan and Kalf, 1979; Meeson and Sweeney, 1982) and two species whose sizes were not significantly affected by temperature (Yoder, 1979; Meeson and Sweeney, 1982).

In conclusion, further research is required to establish the extent to which photosynthetic protists follow the temperature–size rule described by Atkinson (1994). Satisfactory explanations are also still required for the relationships so far observed between temperature and cell size.

#### *Copepods*

At least three of the four mechanisms—oxygen limitation, ectotherm predation risk and need to complete particular life-cycle stages by particular times of year—could help explain why the gill parasite *Salmincola salmoneus* was the only exception among thirteen crustacean studies (Tables 1 and 2). No information is available to allow mechanism 2—the risk of habitat drying out—to be rejected.

Other mechanisms, besides or instead of respiratory compensation by the salmon, may reduce the risk of oxygen shortage for *S. salmoneus*. Atlantic salmon, which have a high oxygen requirement, appear in nature to avoid conditions with low levels of dissolved oxygen (Priede *et al.*, 1988). Moreover, since the parasitic copepod is sedentary, it is unlikely to have a high respiratory demand and is therefore unlikely to suffer oxygen shortage at the oxygen concentrations experienced while the host remains alive. Further studies on gill parasites, especially when compared with non-gill parasites on the same fish would help identify how important, if



at all, are fish gills in affecting the size response to temperature.

It has now been well established that selection pressures from size-specific predation can be powerful enough to cause phenotypically plastic changes in life history in aquatic ectotherms including crustacea. Stibor and Lüning (1994), for example, showed that waterborne cues released by predators that prefer large adults of the cladoceran *Daphnia hyalina* caused the daphnids to reproduce at a smaller size whereas cues released from predators preferring small juvenile *D. hyalina* caused reproduction at increased size. Phenotypically plastic shifts in adult size due to differences in predation risk at different temperatures have not yet been studied.

Indirect evidence was found to support the idea that seasonal constraints force *S. salmoneus* to complete maturation before a particular time of year (mechanism 4). The strength of these constraints could not be ascertained but the fact that a change in photoperiod can remove the effect of increasing temperature on size suggests that further investigation of this phenomenon would be worthwhile.

#### Mayflies

Only one of the mechanisms—an association between life-history stage and time of year—showed the predicted relationship between temperature and size. Generally, exceptions to the temperature-size rule were confined to species whose growth occurred mainly during the summer months. But information on whether dates of emergence for these “summer” species were under greater constraint than for those for “winter-spring” species is not known. Moreover, *Eurylophella funeralis* proves an exception to this relationship since it was a “winter-spring” species which produced larger adults at increased temperatures.

An alternative explanation is provided by Sweeney and Vannote (1978) and Vannote and Sweeney (1980) who applied the concept of an optimal thermal regime to mayfly populations. This regime was typically found in rivers near the latitudinal centre of the species' geographic range, and maximized adult size and fecundity. Thus for species whose geographic range approximately centred on White Clay Creek (WCC), maximal adult size was generally found at ambient WCC temperatures. These authors account for the increased size of *E. funeralis* at temperatures higher than WCC by noting that this species has a more southern distribution than the others (Sweeney and Vannote, 1978) and thus is adapted to waters warmer than WCC. The concept of an optimal thermal regime is thus capable of explaining all the mayfly exceptions to the general rule shown in

Table 3. However, it is also evident from these studies that the optimal thermal regime for maximizing adult size is usually cooler than that which maximizes individual growth rate (Vannote and Sweeney, 1980; Atkinson, 1994).

If the ambient thermal regime generally produces maximal adult size in mayflies, to what extent might this explain temperature-size relationships in other taxa in this review? Rempel and Carter (1987) found that temperatures higher than ambient produced smaller adult dipterans, which is consistent with both the idea of the optimal thermal regime and the general temperature-size rule. Other studies generally used fixed temperatures and constant rather than naturally varying photoperiods, but at least one found that reductions in size with increased temperature were only observed at the upper end of the range of temperatures normally encountered in nature (Nayar, 1969). Another even found that a size increase was observed with increasing temperature at the lower end of the range, at the bottom of which mortality was also particularly high (Johns, 1981). If we expect the optimal thermal regime to be at temperatures away from extremes of the range normally encountered in nature, these examples appear to support the idea of the optimal thermal regime. Yet many others do not. In these others the range of temperatures over which a significant reduction in size was observed was the full range of temperatures stated by the authors to be normally encountered by the population in nature (Lock and McLaren, 1970; Pourriot, 1973; Abdullahi and Laybourn-Parry, 1985; Marian and Pandian, 1985; Chrzanowski *et al.*, 1988; Laybourn-Parry *et al.*, 1988; Hanazato and Yasuno, 1989). I suggest that the association between ambient water temperature and maximal adult size found by Sweeney and Vannote should apply to species in which the timing of maturation is tightly constrained by season and under conditions (e.g. photoperiods) which indicate these constraints to the growing organism. The tighter these constraints the more likely is synchronous maturation among treatments expected and an increased size in individuals at higher temperatures due to their faster growth. For species adapted to conditions warmer than the ambient conditions at a particular site (e.g. *Eurylophella funeralis* above) these time constraints are likely to be particularly acute. These constraints would be relaxed in species normally less constrained by season, or if photoperiods indicate plenty of time is available to complete juvenile development. In these cases, factors that have been predicted to produce the general size reduction at increased temperatures could make delayed maturation and larger size in the slower growing individuals reared at lower

temperatures adaptive. These factors include increased risks of mortality or reduced future growth at increased temperature—associated with faster ageing, more ectotherm predation, risks of oxygen shortage or habitat drying (Atkinson, 1994; Sibly and Atkinson, 1994).

In conclusion, the small number of aquatic exceptions to the widespread temperature–size rule observed in ectotherms belong to three main taxonomic groups. Whilst rigorous tests of mechanisms that might explain these exceptions were not possible using existing published data, a comparison of life cycles and niches among exceptions and non-exceptions to the rule that were otherwise closely related taxonomically and/or ecologically enabled me to highlight those mechanisms worthy of further investigation. This was particularly helpful in the identification of mechanisms likely to produce the exceptional response to temperature by the parasitic copepod, *Salmincola salmoneus* and in four mayflies species.

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## APPENDIX

### *Effects of Increased Temperature on Size-at-stage*

R denotes significant ( $P < 0.05$ ) size reduction; I denotes a significant size increase. Criteria for acceptance of studies are given in the Materials and Methods.

| KINGDOM                |                                  |         |        |                                  |
|------------------------|----------------------------------|---------|--------|----------------------------------|
| PHYLUM                 |                                  |         |        |                                  |
| Class                  |                                  |         |        |                                  |
| No.                    | (Sub Class/Order)                | Species | Effect | Reference                        |
| <b>BACTERIA</b>        |                                  |         |        |                                  |
| <b>(MONERA)</b>        |                                  |         |        |                                  |
| 1                      | <i>Pseudomonas</i> sp.           |         | R      | Chrzanowski <i>et al.</i> (1988) |
| <b>PROTISTA</b>        |                                  |         |        |                                  |
| 2                      | <i>Chlamydomonas reinhardi</i>   |         | R      | Ray (1960)                       |
| 3                      | <i>Chlamydomonas</i> sp. 1       |         | R      | Ray (1960)                       |
| 4                      | <i>Chlamydomonas</i> sp. 2       |         | R      | Ray (1960)                       |
| 5                      | <i>Scenedesmus obliquus</i>      |         | R      | Margalef (1954)                  |
| <b>BACILLARIOPHYTA</b> |                                  |         |        |                                  |
| 6                      | <i>Phaeodactylum tricornutum</i> |         | I      | Fawley (1984)                    |
| <b>CILIOPHORA</b>      |                                  |         |        |                                  |
| 7                      | <i>Colpoda</i> sp.               |         | R      | Adolph (1929)                    |
| 8                      | <i>Tetrahymena gelei</i>         |         | R      | Ray (1960)                       |
| <b>ANIMALIA</b>        |                                  |         |        |                                  |
| <b>ASCHELMINTHES</b>   |                                  |         |        |                                  |
| <b>Rotifera</b>        |                                  |         |        |                                  |
| 9                      | <i>Brachionus calyciflorus</i>   |         | R      | Pourriot (1973)                  |
| 10                     | <i>Philodina roseola</i>         |         | R      | Lebedeva and Gerasimova (1985)   |
| <b>MOLLUSCA</b>        |                                  |         |        |                                  |
| <b>Gastropoda</b>      |                                  |         |        |                                  |
| 11                     | <i>Crepidula fornicata</i>       |         | R      | Pechenik (1984)                  |
| 12                     | <i>Lymnaea japonica</i>          |         | R      | Imai (1937)                      |
| <b>Pelecypoda</b>      |                                  |         |        |                                  |

continued—

## Appendix—continued

| KINGDOM<br>PHYLUM<br>Class |                                    |         |        |                                     |
|----------------------------|------------------------------------|---------|--------|-------------------------------------|
| No.                        | (Sub Class/Order)                  | Species | Effect | Reference                           |
| 13                         | <i>Mytilus edulis</i>              |         | R      | Pechenik <i>et al.</i> (1990)       |
| 14                         | <i>M. edulis</i>                   |         | R      | Bayne (1965)                        |
|                            | ARTHROPODA                         |         |        |                                     |
|                            | Insecta                            |         |        |                                     |
|                            | (Diptera)                          |         |        |                                     |
| 15                         | <i>Ablabesmyia mallochi</i>        |         | R      | Rempel and Carter (1987)            |
| 16                         | <i>Aedes aegypti</i>               |         | R      | van den Heuvel (1963)               |
| 17                         | <i>Ae. aegypti</i>                 |         | R      | Galliard and Golvan (1957)          |
| 18                         | <i>Ae. nigromaculis</i>            |         | R      | Brust (1967)                        |
| 19                         | <i>Ae. pseudoscutellaris</i>       |         | R      | Marks (1954)                        |
| 20                         | <i>Ae. taeniorhynchus</i>          |         | R      | Nayar (1969)                        |
| 21                         | <i>Ae. vexans</i>                  |         | R      | Brust (1967)                        |
| 22                         | <i>Chaoborus flavicans</i>         |         | R      | Hanazato and Yasuno (1989)          |
| 23                         | <i>Conchapelopia aleta</i>         |         | R      | Rempel and Carter (1987)            |
| 24                         | <i>Culex nigripalpus</i>           |         | R      | Nayar (1968)                        |
| 25                         | <i>Culicoides variipennis</i>      |         | R      | Mullens and Rutz (1983)             |
| 26                         | <i>C. variipennis</i>              |         | R      | Akey <i>et al.</i> (1978)           |
| 27                         | <i>Culiseta inornata</i>           |         | R      | Brust (1967)                        |
| 28                         | <i>Nilotanypus fimbriatus</i>      |         | R      | Rempel and Carter (1987)            |
| 29                         | <i>Parametrioctenemus lundecki</i> |         | R      | Rempel and Carter (1987)            |
| 30                         | <i>Polypedilum aviceps</i>         |         | R      | Rempel and Carter (1987)            |
| 31                         | <i>Stempellinella brevis</i>       |         | R      | Rempel and Carter (1987)            |
| 32                         | <i>Ameletus ludens</i>             |         | R      | Vannote and Sweeney (1980)          |
| 33                         | <i>Caenis simulans</i>             |         | I      | Vannote and Sweeney (1980)          |
| 34                         | <i>Cloeon triangulifer</i>         |         | R      | Sweeney and Vannote (1984)          |
| 35                         | <i>Ephemerella funeralis</i>       |         | I      | Vannote and Sweeney (1980)          |
| 36                         | <i>Isonychia bicolor</i>           |         | I      | Sweeney (1978)                      |
| 37                         | <i>Leptophlebia intermedia</i>     |         | R      | Sweeney <i>et al.</i> (1986)        |
| 38                         | <i>Parameletus minor</i>           |         | R      | Söderström (1988)                   |
| 39                         | <i>P. chelifier</i>                |         | R      | Söderström (1988)                   |
| 40                         | <i>Tricorythodes atratus</i>       |         | I      | Vannote and Sweeney (1980)          |
|                            | Crustacea                          |         |        |                                     |
|                            | (Copepoda)                         |         |        |                                     |
| 41                         | <i>Acanthocyclops vernalis</i>     |         | R      | Coker (1933)                        |
| 42                         | <i>A. vernalis</i>                 |         | R      | Abdullahi and Laybourn-Parry (1985) |
| 43                         | <i>A. viridis</i>                  |         | R      | Abdullahi and Laybourn-Parry (1985) |
| 44                         | <i>A. viridis</i>                  |         | R      | Coker (1933)                        |
| 45                         | <i>A. viridis</i>                  |         | R      | Laybourn-Parry <i>et al.</i> (1988) |
| 46                         | <i>Cyclops serrulatus</i>          |         | R      | Coker (1933)                        |
| 47                         | <i>Macrocyclops albidus</i>        |         | R      | Abdullahi and Laybourn-Parry (1985) |
| 48                         | <i>M. albidus</i>                  |         | R      | Laybourn-Parry <i>et al.</i> (1988) |
| 49                         | <i>Pseudocalanus minutus</i>       |         | R      | Lock and McLaren (1970)             |
| 50                         | <i>Salmincola salmoneus</i>        |         | I      | Johnston and Dykeman (1987)         |
|                            | (Decapoda)                         |         |        |                                     |
| 51                         | <i>Callinectes sapidus</i>         |         | R      | Leffler (1972)                      |
| 52                         | <i>Cancer irroratus</i>            |         | R      | Johns (1981)                        |
|                            | (Mysidacea)                        |         |        |                                     |
| 53                         | <i>Neomysis mercedis</i>           |         | R      | Johnston and Northcote (1989)       |
|                            | CHORDATA                           |         |        |                                     |
|                            | Amphibia                           |         |        |                                     |
| 54                         | <i>Pseudoacris ornata</i>          |         | R      | Harkey and Semlitsch (1988)         |
| 55                         | <i>Rana pipiens</i>                |         | R      | Smith-Gill and Berven (1979)        |
| 56                         | <i>R. sylvatica</i>                |         | R      | Ray (1960)                          |

continued—

## Appendix—continued

| KINGDOM      |                               |         |        |                             |
|--------------|-------------------------------|---------|--------|-----------------------------|
| PHYLUM       |                               |         |        |                             |
| Class        |                               |         |        |                             |
| No.          | (Sub Class/Order)             | Species | Effect | Reference                   |
| 57           | <i>R. sylvatica</i>           |         | R      | Berven and Gill (1983)      |
| 58           | <i>R. sylvatica</i>           |         | R      | Berven and Gill (1983)      |
| 59           | <i>R. sylvatica</i>           |         | R      | Berven and Gill (1983)      |
| 60           | <i>R. tigrina</i>             |         | R      | Marian and Pandian (1985)   |
| Osteichthyes |                               |         |        |                             |
| 61           | <i>Paralichthys olivaceus</i> |         | R      | Seikai <i>et al.</i> (1986) |