

Brachiopods and climate change

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ABSTRACT: Animals can respond in three main ways to environments that change and deteriorate. They can cope with their inherent physiological flexibility, evolve or adapt to new conditions, or migrate away to areas consistent with survival. The main factors dictating survival are the rates of change and capacities of species to cope. Articulated brachiopods are known as a group that employ low energy solutions and exhibit slow rates in life histories characters, especially in growth and metabolic rates. This way of life carries with it a range of consequences, including poor abilities to raise metabolic rates to perform work. This brings with it poor abilities to cope with elevated temperature. Slow growth, deferred maturity and low feeding rates make them less likely to produce novel adaptations compared with other marine invertebrate taxa. Being largely restricted to hard substrata and low energy supply environments also makes it harder for them to migrate to new sites compared to other groups, because of the large geographic distances between colonisable areas. The only clear area they may have that gives them advantages is in the flexibility of their larval release strategies, where settlement can be from very short, millimetre-scale distances to hundreds of kilometres.

KEY WORDS: adaptation, aerobic scope, articulated brachiopods, growth, life history, metabolism, migration, survival

The current topic in biology that raises most interest with scientists, the public and politicians concerns how environments on Earth are changing, and how these changes are affecting, or going to affect life across the planet. The Earth has warmed over the last 100 years such that global air temperatures are presently around 0.75°C warmer than they were in the early part of the 20th century (Jones *et al.* 1999; IPCC 2001). There is also now wide acceptance that warming will continue, with predictions that air temperatures will rise by around 4°C, and sea temperatures by 2°C globally in the next 100 years (IPCC 2001). Warming will, perforce, be patchy, and some areas will warm more than this while others will see smaller changes. Other environmental characters are also changing, such as precipitation levels, and these will change further (MacCracken *et al.* 2003). For coastal zones and marine ecosystems global predictions are that sea level will rise, sea-ice cover will decrease and there will be changes in salinity, alkalinity, wave action and ocean circulation.

A major area where knowledge is lacking is in the ability for faunas to respond to change, and this is especially so for brachiopods. This review will evaluate the various mechanisms available to organisms to respond to change, and how brachiopods compare to other groups in their likely abilities to cope with change.

1. How can animals respond to changing environments?

There are three main ways in which animals can cope with change in the environment. These are (1) To use their own physiological capacity and flexibility to survive, including modifications of activity or behaviour; (2) To evolve or adapt to the new conditions by the production of, and selection for, genetic mutations consistent with survival; and (3) To migrate to new areas that are suitable for continued survival.



1.1. Using physiological capacity

Under normal conditions, organisms have a certain amount of capacity or flexibility available to meet biological requirements. As the environment varies, more or less of that capacity is needed to cope with these requirements (Fig 1a). Any capacity remaining above that required for essential functions can be viewed as excess capacity, or scope, which may be available for other requirements. When an environment changes, extra costs are incurred to survive that change which reduces the spare capacity remaining. These costs can be over a wide range of biological characteristics, including direct physiological, such as temperature forced increases in minimum metabolic rates, or ecological, such as higher activity costs to avoid temperature extremes during the day, or modifications to optimum foraging periods. As long as the total load stays within the overall biological capacity, long-term survival is not compromised (Fig 1b). However, if environmental requirements are moved beyond the limits of the biological capacity then survival becomes time limited (Fig 1c).

There is considerable debate suggesting that environmental change will occur in a non-linear fashion, and that climate variability will increase. Some recent models have tested this possibility and indicated that climate variability is currently increasing and may increase further in the coming decades (Schär *et al.* 2004). Increased variability alters the stresses on organisms and might be expected to take them outside their biological capacity range for shorter periods than a consistent change in conditions. Survival here depends on the organisms ability to sustain biological processes in markedly sub-optimal conditions. An analogy for this is where animals perform activity and can maintain aerobic conditions in their tissues until the activity increases to a point beyond the capacity of the oxygen delivery system. When this happens, anaerobic metabolism is recruited, but can only be sustained for short periods. In a changing environment scenario and over longer

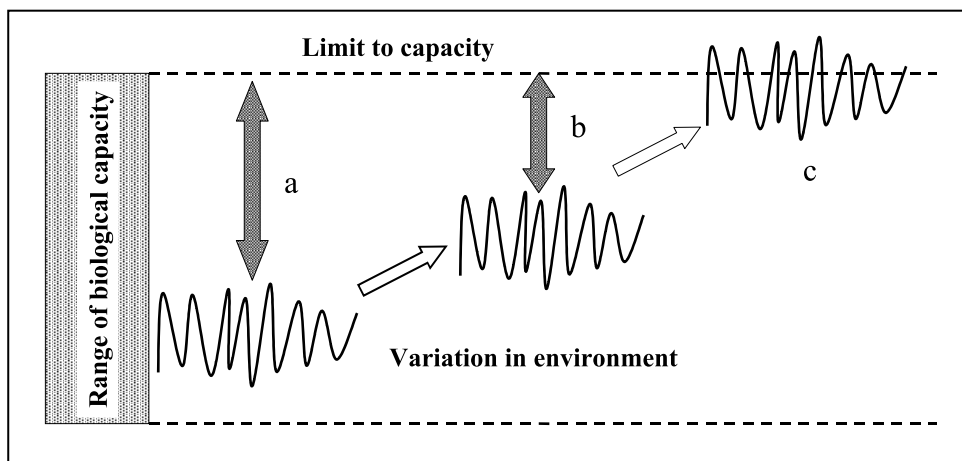


Figure 1 Schematic representation of the physiological cost to an organism incurred by varying environmental conditions: (a) Costs lie easily within the organism's range of capabilities, and significant spare capacity exists; (b) The environment has changed, increasing costs and decreasing remaining spare capacity; (c) Environmental change has reached the point that is beyond the organisms capacity, and survival is compromised. Figure modified from Peck (2005).

timescales, it may mean that in some seasons conditions preclude animals from breeding, but longer-term survival is possible because reproduction occurs in other years.

1.2. Evolving or adapting

The second way of coping with a changing environment is to produce an adaptation that alters the range of biological capacity to a new point that encompasses the costs of the new conditions (the upper limit to capacity in Fig. 1 is lifted up above the level of the new costs). This is effected either within individuals by adaptation, or from generation to generation via mutation and evolutionary processes. An evolutionary response depends on life history characters such as age at reproduction and numbers of embryos produced per breeding event (Peck 2005).

1.3. Migration

The third type of response to changing environments is to migrate to areas with favourable conditions. Most continents have long coastlines covering many degrees of latitude. Thus the Pacific coastline of South America ranges from around 7°N in Colombia to 55°S at the southern tip of Chile. Theoretically species can migrate away from warming environments to higher latitude, cooler sites consistent with continued survival. However, successful migration depends on many factors, including numbers of propagules produced, distances to, and size of, colonisable areas and the ability to establish on arrival at new sites (Hill *et al.* 2002; Siegel *et al.* 2003; Peck *et al.* 2006). For marine species, the strength and direction of oceanic currents has a major effect, as do large barriers such as major river estuaries. The Amazon estuary in Brazil, for example, produces a 1600 km-long downdrift mud shoreline and a freshwater lens that can extend over 120 km offshore (Gibbs & Konwar 1986). In periods of change the rate of change and stability of habitats are both important, because the time required to establish new communities, and the suitability of new sites, are affected by rate of change.

2. Brachiopod characteristics

2.1. Physiological flexibility and capacities

Current ideas on abilities to cope with change in environmental temperature in marine ectothermic (cold blooded)

species centre around the capacity to raise metabolic rate, usually as oxygen consumption, to cover the increased costs of raised body temperatures (Pörtner 2002; Pörtner *et al.* 2007). There are reliable data now from several species showing that oxygen supply failure is the proximate mechanism causing death in marine ectotherms when temperatures rise (Peck *et al.* 2002; Pörtner *et al.* 2004). Thus, on this criterion, the ability to raise metabolic rate is the crucial factor.

Articulated brachiopods are characterised by low and variable metabolic rates (James *et al.* 1992; Peck *et al.* 1997; Peck 2001a). Their oxygen consumption rates are generally between 0.2 and 0.9 times those of similar sized bivalve molluscs from similar habitat temperatures (Peck 2001a) (Fig. 2). The ability to raise oxygen consumption is measured as the difference between the minimum (standard) rate of oxygen consumption and the maximum aerobic metabolic rate. This is called the aerobic scope, and is expressed as a factorial of the minimum rate. Thus a species that can double its metabolic rate to perform work has an aerobic scope of $\times 2$. For most taxonomically similar or ecologically similar species aerobic scopes are consistent across latitudes and groups. Because of this species with lower resting rates of oxygen consumption have less energy available for work than those with higher rates. Thus, on Figure 1 a brachiopod at 0°C with a resting oxygen consumption rate of $2 \mu\text{l O}_2 \text{ h}^{-1}$ that can double its metabolism for work has the equivalent of $2 \mu\text{l O}_2 \text{ h}^{-1}$ of energy for work. A bivalve at the same temperature with a resting rate of $10 \mu\text{l O}_2 \text{ h}^{-1}$ has $10 \mu\text{l O}_2 \text{ h}^{-1}$, or five times as much absolute energy available.

The problem for brachiopods appears even more extreme than this as their abilities to raise metabolic rates for biological work appear smaller than for most other groups. The concept of metabolic scope is harder to grasp for sessile than mobile species, because it is not possible to measure oxygen consumption under conditions of enforced activity such as for fish in swim tunnels. However, there are several other factors that raise metabolism other than exercise. The best studied of these for sessile marine species are feeding and temperature. Following feeding, metabolic rates of animals rise to a peak value and then decline back to the prefeeding level (Fig 3). This is called the specific dynamic action of feeding (SDA) or heat increment of feeding. At moderate to high feeding levels the peak is extended and becomes flattened. This has been argued to be a measure of the maximum metabolic rate for sessile species

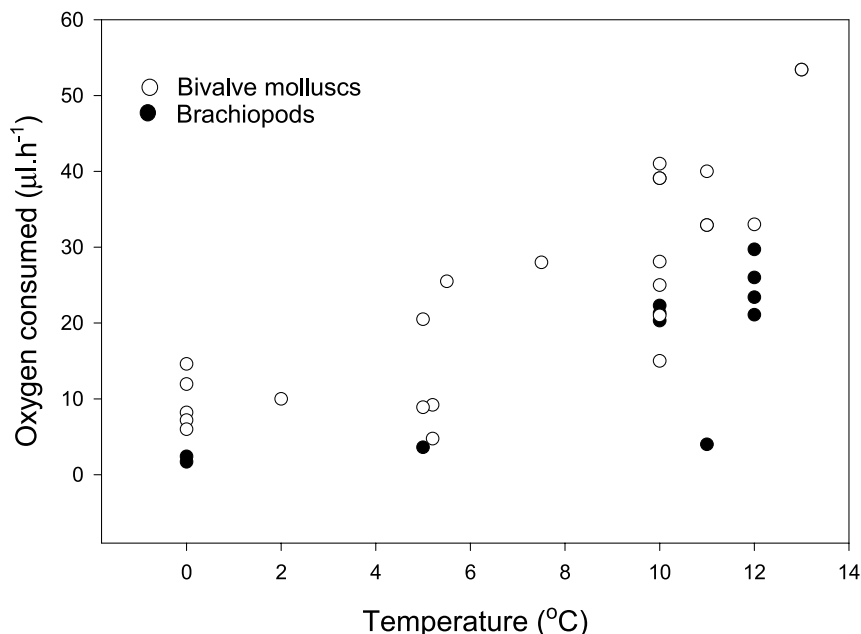


Figure 2 Routine oxygen consumption rates ($\mu\text{l O}_2 \text{ h}^{-1}$) for some temperate and polar brachiopods (●) and bivalve molluscs (○) measured at their normal habitat temperatures. Data are for a 50 mg ash-free dry mass brachiopod and a 50 mg tissue dry mass bivalve mollusc. These are both measures of the organic content of an animal, and different measures are used for articulated brachiopods and bivalve molluscs because of the presence of caeca in the shells of many brachiopod species (see Peck *et al.* 1987; Curry *et al.* 1989). A 50 mg ash-free dry mass articulated brachiopod is usually around 20–25 mm length. Figure modified from Peck (2001a) including further data for bivalve molluscs from Peck & Conway (2000). Articulated brachiopod species used in the figure are: *Neothyris lenticularis*, *Terebratella inconspicua*, *Terebratella sanguinea*, *Terebratalia transversa*, *Terebratalia unguicula*, *Laqueus californianus*, *Hemithyris psittacea*, *Terebratulina retusa* and *Liothyrella uva* (all from James *et al.* 1992). Bivalve species used are: *Mytilus edulis*, *Mytilus californianus*, *Chlamys varia*, *Argopecten irradians*, *Chlamys islandica*, *Yoldia eightsi*, *Gaimardia trapesina* (all from Peck 2001b, based on data in James *et al.* 1992); *Laternula elliptica*, *Cyclocardia astartoides*, *Gaimardia trapesina*, *Cerastoderma glaucum*, *Donax variabilis*, *Donax vittatus*, *Macoma balthica*, *Arctica islandica*, *Tellina tenuis* and *Scrobicularia plana* (from Peck & Conway 2000).

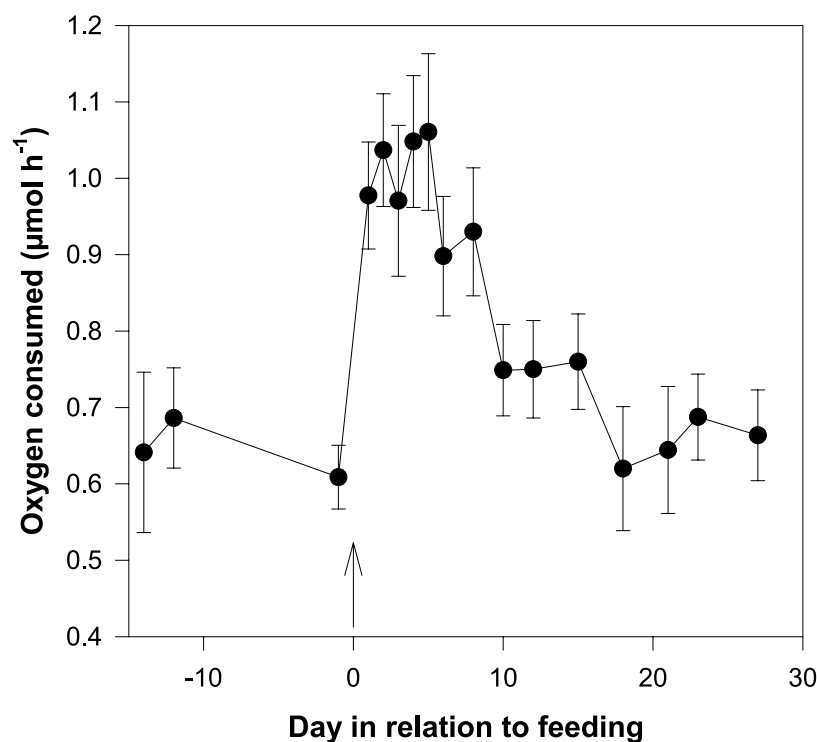


Figure 3 The effect of feeding on metabolic rate (measured as oxygen consumed) for the Antarctic articulated brachiopod *Liothyrella uva*. Brachiopods were held at 0°C in a 12 h light:12 h dark light regime. Oxygen consumption rises 1.6 times after feeding, and metabolism stays elevated for around 15 days after feeding. (From Peck 1996, fig. 1, p. 224).

Table 1 SDA peak elevations (factorial rise over prefeeding starved levels) and duration (days) in oxygen consumption for Antarctic ectotherms. Modified and updated from Peck (1998).

Species	Peak elevation	Time to reach peak (days)	Total SDA duration (days)	Source
Invertebrates				
<i>Liothyrella uva</i> (Brachiopoda)	1.6	1–5	17	Peck (1996)
<i>Parborlasia corrugatus</i> (Nemertea)	1.8		20–25	Clarke & Prothero-Thomas (1997)
<i>Nacella concinna</i> (Gasteropoda)	2.3	6–7	8–12	Peck & Veal (2001)
<i>Glyptonotus antarcticus</i> (Isopoda)	2.2	3–4	7	Robertson <i>et al.</i> (2001)
<i>Waldeckia obesa</i> (Amphipoda)	4.0	1	4	Chapelle <i>et al.</i> (1994)
Fish				
<i>Notothenia coriiceps</i>	2.0	2	5	Brodeur <i>et al.</i> (2002)
<i>Notothenia coriiceps</i>	2.0–2.3	2–3	9	Johnston & Battram (1993)
<i>Harpagifer antarcticus</i>	2.1–2.5	2–3	10–15	Boyce & Clarke (1997)

of brachiopods, because the peak elevation matches the maximum metabolic rates obtainable for other factors raising metabolism such as elevated temperature (Peck 1998).

Although data are sparse for SDA in articulated brachiopods, the indication is that they have poor abilities to raise metabolism and poor metabolic scopes. The Antarctic *Liothyrella uva* can only raise its metabolic rate $\times 1.6$ over prefeeding standard metabolic rates when fed large meals, and the SDA lasts for around 15 days (Fig. 3) (Peck 1996). This is the lowest factorial SDA rise reported for an Antarctic ectotherm, and *L. uva* also has the lowest resting metabolic rate of all the species studied (Peck 1998) (Table 1). From this data we would expect brachiopods to be less capable than most other groups when dealing with short-term temperature changes. For Antarctic species this would seem to be the case. In a system where temperatures were raised at 1.5°C intervals from -1.5°C upwards and allowed to acclimate at each temperature step, *L. uva* failed to survive above $+4.5^\circ\text{C}$, whereas the limpet *N. concinna* survived up to 9°C (Peck 1989). Failure at 4.5°C is one of the poorest abilities to cope with rising temperature reported for Antarctic marine species, with only one species reported as being as sensitive (Peck 2005).

2.2. Evolution and adaptation

The ability to produce adaptations to new environments depends on several life history characters, the main ones of which are: (1) The mutation rates of genes in the genome; (2) The numbers of successfully fertilised embryos at each reproductive event; (3) Survival through larval phases and successful recruitment and establishment; and (4) The generation time, which includes growth rates to reproductive size and minimum reproductive sizes.

There is little or no information on the mutation rates of articulated brachiopods compared to other groups, and most of the molecular biology currently conducted on brachiopods is aimed specifically at identifying taxonomic positions (e.g. Lüter & Cohen 2002). Comparisons of the likely mutation rate responses of brachiopods to other groups are, therefore, not possible. Views on evolution rates of brachiopods from classical palaeontological evidence are also rare, but those that exist suggest that they produce adaptations slowly and evolve only slowly to new conditions (Stanley 1979; Gould & Calloway 1980). However, it should be noted that this conclusion is based on observations of slow changes in morphology of fossils, and this need not automatically translate into slow mutation rates.

Articulated brachiopods were thought to be highly restricted in their reproductive strategies, producing few developmental types (Valentine & Jablonski 1982), and only having

short duration, non-feeding lecithotrophic larvae, with a significant occurrence of brooding (Jablonski & Lutz 1983; Curry *et al.* 1989). However, recent work has shown that at least some species of articulated brachiopods have significant flexibility in some areas of their reproductive strategies. Both the Antarctic *Liothyrella uva* (Meidlinger *et al.* 1998) and the temperate *Calloria inconspicua* (Chuang 1996) have broods that contain embryos over a very wide range of developmental stages. They also release larvae of markedly variable developmental stages from early gastrula to fully competent three-lobed larvae. This gives them a remarkably flexible ability to colonise available sites over differing spatial scales. In *L. uva*, competent larvae settle immediately, usually on the parent or close by shells, whereas less developed larvae spend more time before settling and early gastrulae released may spend as much as 80 days in the water column before reaching settlement competence (Peck *et al.* 2001).

Successful recruitment and establishment of populations depends on a range of factors, e.g. early growth rates, competition, predation and environmental stress (Dayton 1971). The timing of settlement in relation to availability (seasonality) of resources may also be of critical importance (Todd & Doyle 1981; Bowden 2005). Articulated brachiopods grow slowly and are thought to be poor competitors for space (Peck 2001b). Both of these factors militate against a strong ability to recruit and establish in new sites. Finally, articulated brachiopod distributions are mainly in areas of low resource supply, in fiords, caves, the polar regions and deep sea, although exceptions exist such as New Zealand and the Northern Pacific coast of the United States. Being restricted to low energy resource areas has been argued to suggest poor flexibility in life history to cope with change (Curry *et al.* 1989), and this is seen especially in the markedly reduced metabolic rates. This may be generally true, but reduced metabolic rates also confer the advantage of survival in periods when food supplies become unpredictable and long periods of low resource availability need to be endured.

In terms of generation time, articulated brachiopods appear to be slow. This is a consequence of their slow growth rates. Age at maturity has not been measured for many species, but in the Antarctic *Liothyrella uva*, the smallest brooding specimen found was 37 mm in length, which equates to an individual of well in excess of 20 years (Meidlinger *et al.* 1998).

Thus, on most criteria, articulated species appear to have poorer abilities to produce successful adaptations in changing environments, but in some areas, such as variation in developmental stage at larval release and time spent as larvae in the water column, they may be remarkably flexible.

2.3. Migration

The concept here is that as environments warm, species will adapt their ranges into new and cooler areas (e.g. Maschinski *et al.* 2006). The question arises as to how articulated brachiopods will perform in their abilities to migrate to areas consistent with survival. Curry *et al.* (1989) argued that articulated species are restricted because of their lack of variety in lifestyle. Whereas molluscs inhabit soft and hard substrata and have pelagic groups and are filter, deposit and predatory in their trophic relationships, articulated brachiopods are exclusively filter feeding and predominantly animals of hard substrata. This limits the areas that articulated species can colonise, and is reflected in their distributions. Two major zones where articulated species are common are in the deep sea and Antarctica. In both of these areas it is unlikely that there will be geographic gradations in the warming process. The deep sea is fed from cold water at the poles. As this warms, very large areas of the deep sea are likely to warm consistently. The only areas available for migration would be into shallower sites, and these are predominantly warmer. In Antarctica, the Southern Ocean is cohesive around the continent. To move polewards away from a warming event would be impossible for species like brachiopods because the route to higher latitude is blocked by land. Other problems exist for fiordic environments because they are often isolated oceanographically from similar but cooler sites, and migration would not be a simple movement along a coastline.

2.4. Consequences of large scale loss of brachiopods

Articulate brachiopods currently have large dense populations in some fiordic, polar, continental shelf and deep-sea environments (James *et al.* 1992). In some areas they occur in densities over 1000 m⁻² and they dominate communities (Kowalewski *et al.* 2002). Here they may act as a significant sink for carbon and as a substratum for many other benthic-dwelling groups including sponges, bryozoans and polychaetes (Barnes & Peck 1996; Rodland *et al.* 2004). A widescale loss of brachiopods would have effects, not only for local communities (as they form a large area of hard substratum used by other groups), but could also have wider consequences. They are also one of the main consumers of sedimenting biomass in fiordic and some polar and deep-sea areas. Should brachiopods fail in these habitats, consequences could, at least in the short-term, include local eutrophication when sedimenting organic material is not consumed and processed by them. Such eutrophication could lead to other groups encountering significant problems from reduced oxygen conditions, and this in turn could markedly change the ecological balance in benthic ecosystems in fiordic, polar, cave and other cryptic sites where articulate brachiopods.

3. Conclusions

Current models of the Earth's climate predict a general warming over the coming centuries. Different groups of animals have differing abilities to cope with change. The major articulated brachiopod attributes of slow growth, low metabolism, obligate filter feeding and being largely restricted to hard substrata appear to make them less capable of responding to the change in a way that will make them more likely to survive than other taxa. Some of their attributes, however do show significant flexibility, such as the developmental stage of larval release and potential for flexibility in dispersal. Many of the characters necessary for such assessments (e.g. metabolic scopes, larval dispersal distances and geneflow across populations, age at first reproduction, numbers of larvae produced

per year, levels of success in recruitment and establishment) are poorly understood for articulated brachiopods and further data are urgently needed. Despite all of these data suggesting brachiopods may be poor in dealing with changing environments, we should remember they have survived mass extinction events in the past and predicting who will fail and who will succeed is an exercise with great uncertainty.

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