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Cold Adaptation in Marine Organisms [and Discussion]

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Cold adaptation in marine organisms

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Animals from polar seas exhibit numerous so called resistance adaptations that serve to maintain homeostasis at low temperature and prevent lethal freezing injury. Specialization to temperatures at or below 0 °C is associated with an inability to survive at temperatures above 3–8 °C. Polar fish synthesize various types of glycoproteins or peptides to lower the freezing point of most extracellular fluid compartments in a non-colligative manner. Antifreeze production is seasonal in boreal species and is often initiated by environmental cues other than low temperature, particularly short day lengths. Most of the adaptations that enable intertidal invertebrates to survive freezing are associated with their ability to withstand ariel exposure. Unique adaptations for freezing avoidance include the synthesis of low molecular mass ice-nucleating proteins that control and induce extracellular ice-formation.

Marine poikilotherms also exhibit a range of capacity adaptations that increase the rate of some physiological processes so as to partially compensate for the effects of low temperature. However, the rate of embryonic development in a diverse range of marine organisms shows no evidence of temperature compensation. This results in a significant lengthening of the time from fertilization to hatching in polar, relative to temperate, species. Some aspects of the physiology of polar marine species, such as low metabolic and slow growth rates, probably result from a combination of low temperature and other factors such as the highly seasonal nature of food supplies. Although neuromuscular function shows a partial capacity adaptation in Antarctic fish, maximum swimming speeds are lower than for temperate and tropical species, particularly for early stages in the life history.

1. Introduction

At high latitudes seawater remains in equilibrium with ice throughout the year at close to its freezing point of −1.9 °C. In addition to low temperature, polar marine ecosystems are subject to extreme seasonal cycles of light and primary productivity. In spite of these harsh conditions the Antarctic and Arctic Oceans contain an abundant and relatively diverse fauna. Present-day species are highly stenothermal and intolerant of temperatures more than a few degrees Celsius outside their normal range. Poly-A ribonucleic acid (RNA) analysis with Northern blot has shown that the gene for the heat shock protein (hsp 70) is transcribed at temperatures as low as 5 °C in Antarctic fish (Maresca *et al.* 1988). This degree of specialization to low temperature probably reflects the relative stability of environmental conditions over many millions of years (Clarke 1983).

Polar temperatures are lethal for all tropical and most temperate marine organisms. Adaptations that serve to extend the thermal range of a species are often referred to as resistance adaptations (figure 1*a*). For example, mammalian microtubules are 'cold-labile' and depolymerize at 0–4 °C, whereas tubulins from Antarctic fish assemble *in vitro* at −2 °C

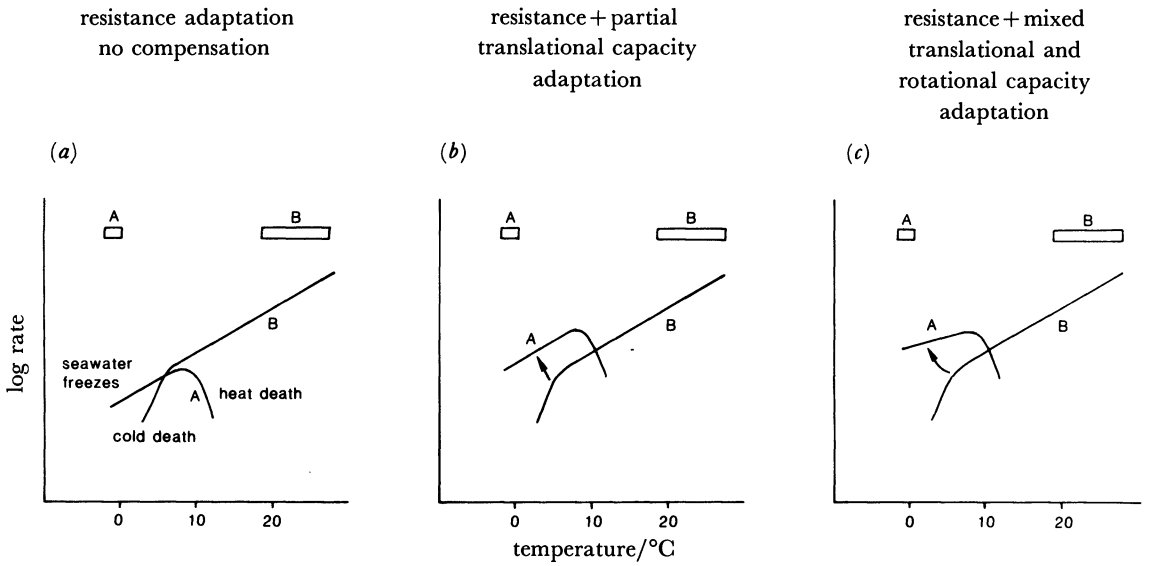

FIGURE 1. A diagrammatic representation of the patterns of temperature adaptation found in marine organisms. The effects of temperature on a rate process in a polar (line A) (environmental temperature −1.9 °C to +1 °C) and a tropical species (line B) (environmental temperature 16–25 °C are shown. (*a*) shows a resistance adaptation without temperature compensation, involving a shift in the upper and lower functional limits of the process without a change in the rate at any given temperature. (*b* and *c*) show resistance and partial capacity adaptations. The latter involves either a parallel (as in *b*) or a rotational shift (as in *c*) of line A along the temperature axis so as to increase the rate of the process over the normal temperature range of the species. This is referred to as a partial capacity adaptation, because at physiological temperatures the rate process is still significantly faster in the tropical than the polar species.

(Detrich & Overton 1988). Interestingly, the range of isoelectric points and amino acid compositions of bovine and Antarctic fish tubulins are only slightly different (the latter contain fewer glutamyl or glutaminyl residues). It has been suggested that amino acid sequences that are critical for function are highly conserved (Hochachka 1988).

Resistance adaptations are also evident in membrane properties. For example, the conduction of action potentials in peripheral nerves of tropical fish is readily blocked by low temperatures, whereas nerves from Antarctic fish remain active down to at least −5 °C. The temperature at which impulses are blocked by heat is lowered by about 12 °C in Antarctic fish, which suggests that the improvement at low temperature is achieved at the expense of membrane stability (Macdonald 1981). Brain synaptosomes isolated from cold-water fish contain a higher proportion of unsaturated fatty acids in membrane phospholipids than those in warm-water species (Cossins & Bowler 1987). This is associated with a compensatory increase in membrane fluidity at low temperature as measured by fluorescence polarization techniques (Cossins & Bowler 1987). Low temperature adaptations in Ca^{2+}-binding affinity and ATPase activity have been reported for sarcoplasmic reticulum from Antarctic fish (McArdle & Johnston 1980). As with brain synaptosomes, the fatty acid composition of the sarcoplasmic reticulum becomes more unsaturated in the rat, desert pupfish (28–34 °C) and arctic sculpin (0.5–2.9 °C). However, in this case the increase in fatty acid unsaturation index was not found to be associated with a decrease in membrane fluidity (Cossins *et al.* 1978).

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2. Freezing avoidance strategies

There is at least one example of an intertidal invertebrate that uses a freeze-avoidance strategy. The Antarctic limpet, *Patinigera polaris*, secretes a water-impermeable mucus containing glycoprotein thermal hysteresis factors that allow it to undercool to −10 °C (Hargens & Shabica 1973). Some polar fish such as the Antarctic liparid, *Paraliparus devriesii*, can undercool by 1 °C or more but are restricted to deep water where there is no possibility of contact with ice. Fishes living in ice-laden polar waters avoid freezing by lowering the freezing point of their body fluids. For example, *Pagothenia borchgrevinki* from McMurdo sound, antarctica has a blood freezing point of −2.7 °C compared with −0.8 °C for a typical marine teleost (DeVries 1988). This is partly the result of an increase in blood sodium chloride levels (NaCl) (40–70 % depending on species). The rest is largely due to antifreezes that lower the freezing point in a non-colligative manner. These are either relatively large glycopeptides (AFGP) or peptides (AFP). On a molar basis they depress the freezing point of the body fluids 200–300 times more than expected on the basis of colligative reactions alone (DeVries 1971). Five major classes of antifreeze compounds have been identified. Antarctic fish of the family Nototheniidae (suborder Notothenioidei) possess glycopeptides composed of repeating units of the tripeptide alanyl-alanyl-threonine with the disaccharide β-galactopyranosyl-(1-3)-2-acetamide-2-deoxy-α-D galactopyranose linked to threonine residues (figure 2). They occur in at least eight different size ranges (relative molecular mass, M_r 2600–34 000) and in the smaller ones, beginning at position 7, proline replaces the first alanine in the glycopeptide repeating sequence until the C-terminal is reached (DeVries 1988). The same eight glycopeptides have been isolated from the rock cod, *Gadus ogac*, from the near shore waters of Labrador in the northern hemisphere (Van Voorhies *et al.* 1978). A second class of antifreeze peptide is found in two other northern species, the winter flounder (*Pseudopleuronectes americanus*) (M_r, 3300) and the short-horned sculpin (*Myoxocephalus scorpius*) (M_r, 4000). These AFPs are in the form of a helical coil and 60 % of the amino acid residues are alanine with threonine, serine, arginine, leucine aspartine and glutamine accounting for the remainder (figure 2). Antarctic eel pout (family Zoarcidae) contain a third type of peptide antifreeze that has an extended structure with little helical or β-structure and polar residues appear to be randomly localized throughout

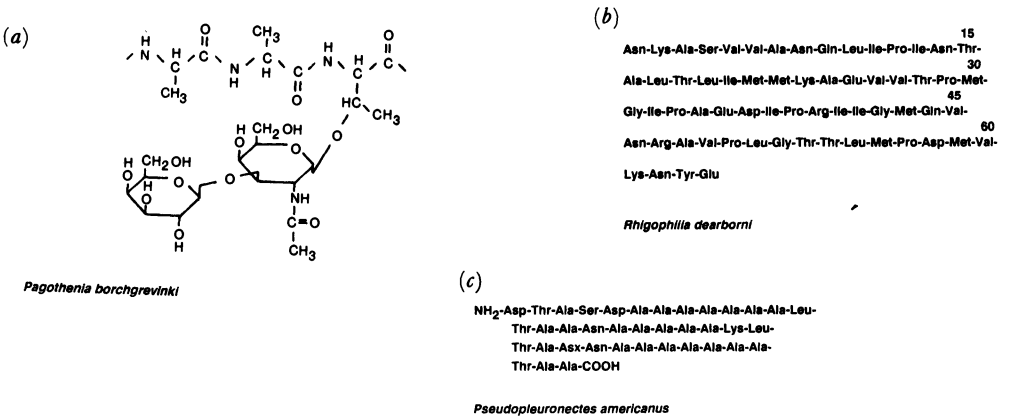

Figure 2. Structure of antifreezes found in the plasma of some polar fish (*a*) repeating unit of the glycopeptide from the Antarctic fish *Pagothenia borchgrevinki* (from DeVries 1988). (*b*) Primary structure of the antifreeze peptide from the Antarctic eel pout *Rhigophilia dearborni* (from DeVries 1988) and (*c*) primary structure of the antifreeze peptide from the winter flounder (*Pseudopleuronectes americanus*) (after Lin 1983).

the peptide (figure 2). A fourth type of AFP is found in another northern fish, the sea raven (*Hemitripterus americanus*). This peptide, approximate M_r 13000, has a modest amount of alanine (14%) and is distinguished from other fish AFPs by a relatively high half cystine content (6–7%) (Ng *et al.* 1986). A fifth class of AFP from the ocean pout (*Macrozoarces americanus*) adopts an expanded or random coil structure and it does not have a particularly high content of either alanine or half cystine residues (M_r 6000) (Hew *et al.* 1984).

AFGPs and AFPs are synthesized in the liver and secreted into the blood and most extracellular fluids. In Notothenioids AFGPs are not present in the cytosol, urine and endolymph but are only present in low concentrations in the ocular fluids (Turner *et al.* 1985; DeVries 1988). This is because the kidneys of Antarctic nototheniids are entirely aglomerular and therefore the antifreeze glycopeptides (2.6–32 kDa) cannot be filtered into the urine. The tissues surrounding urine and ocular fluids are fortified with antifreeze, which constitutes a barrier to ice propagation. The intestinal fluid is hyposmotic to plasma and contains AFGPs 7 and 8 to prevent it freezing. They are translocated from blood to bile via a paracellular route and evacuated at the anterior end of the intestine. Salt, water and digested foodstuffs are absorbed during passage down the intestine, concentrating the AFGPs. The loose anal sphincter is a potential point for ice entry, but at this point the intestinal tract freezes at −2.2 °C (O'Grady *et al.* 1982). Antifreeze peptides are also absent from the urine of the Antarctic eel pout (Eastman *et al.* 1979) and the short-horned sculpin (Fletcher *et al.* 1989), and it has been suggested that these species contain non-functional glomeruli. However, Fletcher *et al.* (1989) have recently reported that antifreeze peptides are found in the urine of winter flounder, sea raven, ocean pout and atlantic cod at concentrations that approached that of plasma. Thus in some species antifreeze peptides probably also increase the freezing resistance of urine.

Antifreezes are present all year round in Antarctic fish, but production is seasonal in northern species. The appearance of AFP in the plasma of winter flounder is suppressed by long days (over 15 h) and appears to be under the control of photoperiod, not low temperature. Similarly, in the Long Island (New York) population of tomcod (*Microgadus tomcod*) glycopeptide antifreeze appears in the plasma in November, in preparation for the winter, when water temperatures are only 7–9 °C (Reisman *et al.* 1984). In contrast, synthesis of AFGP in the Atlantic cod (*Gadus morhua*) is independent of photoperiod and it does not appear in the plasma until water temperatures drop to 0 °C (Fletcher *et al.* 1987). Exposure of winter flounder, *Pseudopleuronectes americanus*, to 10–12 °C results in a loss of blood antifreeze within 3 weeks. Synthesis is controlled at the level of DNA transcription and translation, as mRNA appears in the blood about 4 weeks before the peptide (Lin 1983).

The action of these antifreezes remains unclear (see DeVries 1988). They decrease the temperature of ice nucleation but do not effect the melting point of frozen serum. Modification of almost any of the hydroxyl groups of the carbohydrate moiety of AFGPs and modification of glutamic and aspartic acid of AFPs leads to a loss of antifreeze effect. All the hydroxyl, carboxyl and amino groups of the antifreezes can potentially form hydrogen bonds with the oxygens or hydrogens in the ice lattice. Some AFPs have structures where the polar residue spacings are such that a lattice match can be recognized between the peptide and the oxygens along one of the axes of the ice crystal. However, this is not the case for the Antarctic eel pout AFP, which is also an effective antifreeze. One suggestion is that the adsorption of the antifreezes to ice crystals could lead to an increase in surface area with only a small increase in volume and hence result in a lowered freezing point (Raymond & DeVries 1977).

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3. Freezing tolerance in intertidal invertebrates

Animals in the intertidal zone can experience much colder and highly variable temperatures during aeriel exposure. In the Arctic and Antarctic the scouring action of ice makes the intertidal zone extremely hostile. Even in sub-polar regions the fauna of the intertidal zone shows low diversity and is dominated by a relatively few species of cold-hardy invertebrate (Aarset 1982).

During short ariel exposures the microclimate experienced by sessile invertebrates can be significantly warmer than ambient air temperatures because of the thermal inertia of the substrate. Seawater trapped inside the animal may also serve as a thermal buffer by reducing the rate of cooling. Most species undercool by only a few degrees below the freezing point of their body fluids. Survival times of 24 h or more are usually limited to -8 to -11 °C (Aarset 1982). A few species, such as the euryhaline nematode, *Ascolaimus elongatus* (Buetschli), can tolerate tempertures of -20 °C for at least 48 h (Farke *et al.* 1984). Freezing tolerance often increases towards the cold end of the geographical range of a species and is greater in winter than in the summer (Loomis 1985).

Intracellular ice formation is invariably lethal and for survival freezing must be restricted to the extracellular fluids. The formation of extracellular ice causes the rapid redistribution of water and solutes between the extracellular and intracellular fluid compartments. This results in dehydration and ion concentration, with potentially injurious effects on membrane and protein structure. The risk of structural damage to membranes is compounded by recrystallization, the tendency of small ice crystals to reform into larger ones with time. Freezing of the extracellular fluids also restricts the transport of oxygen, substrates, waste products and hormones. The metabolic activity of cells continues at a low level when the extracellular fluids are frozen. Freeze tolerant species must therefore maintain metabolic homeostasis in the face of anoxia, subzero temperatures, and high ion and solute concentrations.

Most of the adaptations that enable intertidal invertebrates to survive freezing are associated with their ability to withstand ariel exposure. For example, intertidal animals often have impressive abilities to survive anoxia due to metabolic rate depression and the use of anaerobic pathways with relatively high yields of adenosine triphosphate (ATP), which result in the accumulation of non-toxic waste products (succinate, alanine, acetate, proprionate, etc.) (De Zwaan & Putzer 1985). The tissues of intertidal invertebrates are also well adapted for dealing with osmotic stresses and have efficient mechanisms of cell volume regulation. However, as most species are osmoconformers they cannot use the accumulation of low molecular mass cryoprotectants to control freeze concentration. For example, barnacles *Balanus balanoides* contain only 1 mM glycerol, compared with an intracellular osmolarity of 1000 mosmol† in full-strength seawater (Cook & Gabbot 1970).

Some species, including bivalves (Aunaas 1982). and gastropods (Hayes & Loomis 1985), produce low molecular mass ice-nucleating proteins (INPS) during the winter. These function to induce and control extracellular ice formation thus minimizing osmotic stress during freezing. Thermal hysteresis proteins (THPS), which have a role in inhibiting ice recrystallization, have also been identified in *Mytilus edulis* (Theede *et al.* 1976). The synthesis of INPS and THPS probably represents the only unique adaptations for freezing tolerance in marine species (Storey & Storey 1988).

† One osmole contains one mole of osmotically active particles.

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The bivalve *M. edulis*, has a lethal limit of around 64% of tissue water as ice when adapted to both 50% and 150% seawater (Williams 1970). This suggests that the primary site of freezing injury is structural damage to membranes associated with shrinkage rather than stress imposed by high solute and ion concentrations. Increases in blood calcium concentration improve freezing tolerance in the bivalve, *Modiolus demissus*, perhaps by stabilizing membrane structure (Murphy 1983). Changes in the composition of membrane lipids have been reported to improve cold tolerance in barnacles (Cook & Gabbott 1972). However, a later study found no evidence for seasonal changes in the unsaturation index of either total phospholipid or the neutral lipid fractions (Tooke & Holland 1985).

4. Capacity adaptations

(*a*) *Does low temperature limit functional capacities?*

Reducing temperature slows the rate of diffusion of molecules and decreases enzyme reaction rates. In the absence of compensating mechanisms physiological processes would be expected to occur much more slowly in cold- than in warm-water organisms. The extent to which low temperature limits the physiology and behaviour of marine organisms is an important and largely unresolved question. Most enzyme-mediated processes exhibit a Q_{10} in the range 1.5–3.0. Rates significantly above those expected on the basis of extrapolating rates for temperate organisms down to low temperatures are usually referred to as capacity adaptations (figures 1*b*, *c*). Not all processes in the same organism show a similar degree of capacity adaptation. A few of the better studied examples are described below.

(i) *Rate of development*

Although the rate of development is under genetic control it is strongly influenced by temperature. The time taken for fish eggs to hatch in nine marine species at different temperatures is shown in figure 3*a*. Rates of development are clearly much slower in cold- than in warm-water species, with little evidence for temperature compensation. However, the situation is complicated by the trend for polar species to have larger diameter eggs that require more time for cleavage. The larvae of polar fish are large and advanced on hatching, enabling them to take maximum advantage of seasonally available prey. Bosch *et al.* (1987) found that the time to hatching of the ciliated blastulae of the Antarctic sea urchin, *Sterechinus neumayeri*, occurs around 140, 128 and 110 h after fertilization at −1.8, −1.0 and 1.5 °C, respectively. A curvilinear relation between temperature and the duration of embryonic development was found for a range of sea urchin species with planktonic larvae (figure 3*b*). Similar results from other marine poikilotherms also suggest little or no temperature compensation in the rate of development (figure 1*a*).

(ii) *Growth rate*

Although temperature is an important determinant of growth rate it is also strongly influenced by other abiotic and biotic factors, particularly food supply. For example, growth of the tellinid bivalve, *Macoma balthica*, in the Wadden Sea is confined to a period from March to June when temperatures rise from 4 to 16 °C and there is an abundant good quality food supply. However, in the autumn, when the temperature is also within the optimum range, the food supply is low and growth is negative (Beukema *et al.* 1985). Vahl (1980) found evidence

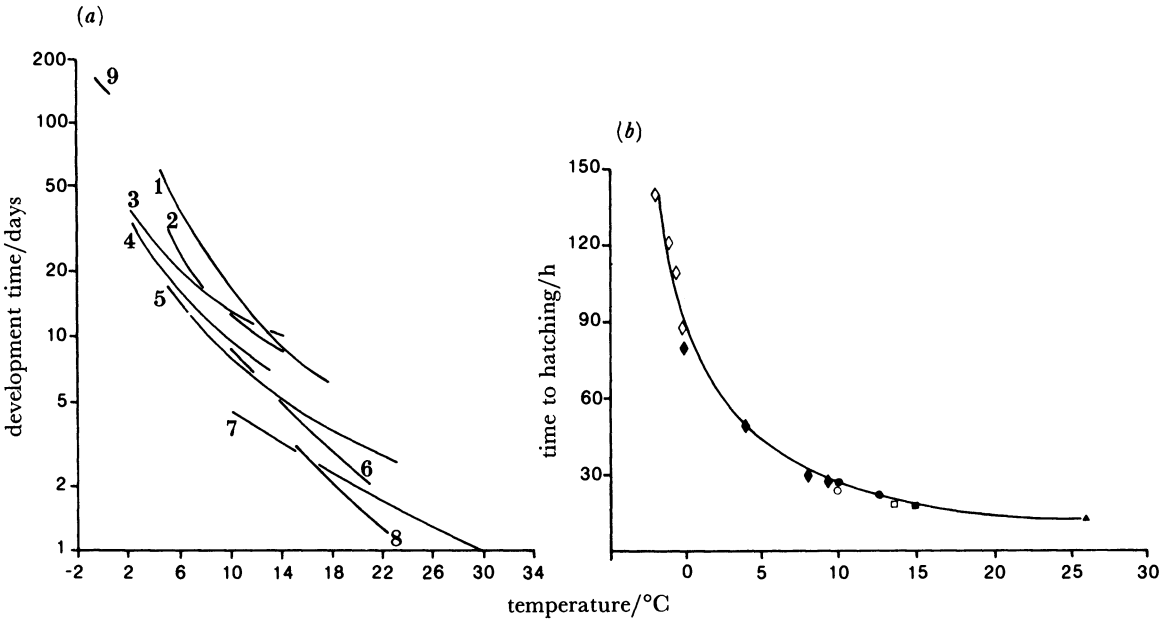

FIGURE 3. (*a*) The time from fertilization to hatching for nine species of marine teleost. 1, smelt *Osmerus eperlanus*; 2, Atlantic herring *Clupea harengus*; 3, plaice, *Pleuronectes platessa*; 4, Pacific cod *Gadus macrocephalus*; 5, rockling *Enchelyopus cimbrius*; 6, mackerel *Scomber scombrus*; 7, grey mullet *Mugil cephalus*; 8, striped bass *Morone saxatilis* (1–8 are from Blaxter 1988) and 9, *Harpagifer* spp. (from the South Orkney Islands, Antarctica is from P. Burren 1988 unpublished M.Sc. Thesis, University College of North Wales, Bangor). (*b*) The time from fertilization to hatching for sea urchin species with planktonic larvae within the families Echinidae (empty diamonds) and Strongylocentrotidae (filled-in diamonds). Hatching occurs at the ciliated blastula stage. From Bosch *et al.* 1987).

that seasonal variations in growth rate of the Iceland scallop, *Chlamys islandica*, were not due to variations in temperature or the amount or quality of phytoplankton. Instead, reduced growth rate could be explained by decreases in absorption efficiency with increasing dilution of particulate organic by inorganic matter, the scallop being unable to sort the trapped particles into organic and inorganic fractions.

Spies (1987) has shown that the growth rates of phytoplankton from the Weddell sea under optimal conditions of light and nutrient supply are high in spite of the low temperature. Maximum growth rates (0.4–1.3 divisions d^{-1}) and generation times (18–63 h $division^{-1}$) of the dominant diatom assemblages at -1 °C fall within the range observed for diatoms in temperate and tropical oceans (Spies 1987). Dayton *et al.* (1974) have also reported fast growth rates in the sponge, *Mycale acerata*, at McMurdo Sound, Antarctica. Thus low temperature *per se* is probably not a bar to high absolute growth rates in some phyla. However, molluscs, crustacea and fish from polar regions generally grow more slowly than species of similar ecology and maximum size from temperate latitudes (Clarke 1983). Growth is usually confined to the summer months even in animals occupying higher trophic levels. Clarke (1983) has argued that the evolution of life styles characterized by slow growth, deferred maturity, and the production of competitive young in polar animals is a response to the predictable pattern of food supply.

(iii) *Metabolic rate*

More than 70 years ago, Krogh proposed that cold-adapted animals would increase their metabolic rates to compensate for the retarding effects of low temperature (Krogh 1916).

Wohlschlag's (1964) observations that the resting metabolic rates of nototheniid fish from McMurdo Sound were higher than rates extrapolated from temperate fish cooled to Antarctic temperatures, gave support to this suggestion, termed 'metabolic cold adaptation' (MCA). However, these early studies have been criticised on methodological grounds, particularly for the failure to take adequate account of the effects of stress and activity on the measurements (Holeton 1974; Clark 1983). The resting metabolic rate of isopods as a function of temperature is shown in figure 4. This clearly shows that resting metabolic rates are generally lower in cold tolerant species. Clarke (1987) has argued that this partly reflects a reduced energy expenditure on protein turnover. On theoretical grounds some degree of metabolic cold adaptation would be expected in polar species, for example, associated with the cost of antifreeze synthesis in Antarctic fish. Indeed, the balance of evidence for Antarctic fish is that resting metabolic rates are probably around twofold higher than they would be for temperate species extrapolated to the same low temperature (Forster *et al.* 1987). As this is within the interspecific variation in resting metabolic rates for Antarctic fish, it is not possible precisely to quantify the effect.

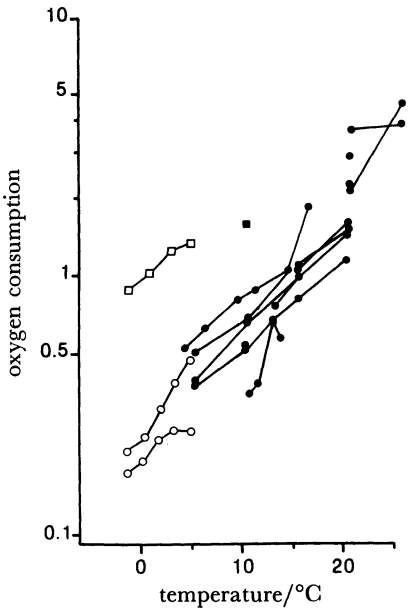

FIGURE 4. Relation between metabolic rate (μm O_2 h^{-1}) and temperature for 13 species of isopod from Antarctic (open symbols) and temperate (closed symbols) waters. The results have been corrected for scaling effects and represent the oxygen consumption of an isopod of 1 mg dry weight. Redrawn from Clarke (1983) and based on original data published Luxmoore (1984).

The scope for aerobic activity of Arctic copepods (Hirche 1987) and Antarctic fish (Forster *et al.* 1987) are no higher than for temperate species of similar size and locomotory habit. It therefore follows that maximum aerobic activity levels must be constrained in these species. There is a tendency for slow muscles in Antarctic fish to contain higher densities of mitochondria than muscles in comparable temperate species (Johnston 1987). For example, mitochondria occupy around 56% of slow fibre volume in the sluggish Antarctic silverfish, *Pleuragramma antarcticum* (Johnston *et al.* 1988). High densities of muscle mitochondria may partially compensate for the detrimental effects of temperature on enzyme reaction and diffusion rates. However, if temperature compensation of aerobic metabolism relies to a large

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extent on changes in the quantity rather than the quality of mitochondria this may place a severe constraint on the degree of capacity adaptation attainable.

(iv) *Burst swimming activity*

The selective pressure on free-swimming polar animals to escape predation or catch prey is presumably as great as that for temperate species. In some cases the major predators are homeothermic. In fish, the power required to swim increases as a cubed funcion of speed. During burst swimming, fish fast-muscle fibres must undergo rapid cycles of contraction and relaxation, increasing their rate of adenosine triphosphate (ATP) utilization more than 100-fold from rest. This large increase in ATP flux makes the fast motor system of fish an ideal model for investigating any constraints in behaviour imposed by low temperature. Studies on the effects of temperature on the mechanical properties of isolated muscle fibres have recently been reviewed (Johnston 1989). Skinned fast-muscle fibres from Antarctic fish generates 5–10 times higher maximum tensions at 0 °C than fibres from tropical species (figure 5*a*). Measured at their normal body temperatures, tension is still slightly higher for polar than warm-water species, that is, force generation shows a perfect or slight overcompensation to temperature (Johnston & Altringham 1985). In contrast, ATPase activity exhibits no compensation to temperature, such that the economy of isometric contraction decreases in the series Antarctic > North Sea > Tropical species (Altringham & Johnston 1986). Maximum contraction velocity has a Q_{10} of 1.5–2.0 and is significantly faster in cold- than in warm-water species (figure 5*b*). Finally, twitch contraction times, which are a major determinant of tail-

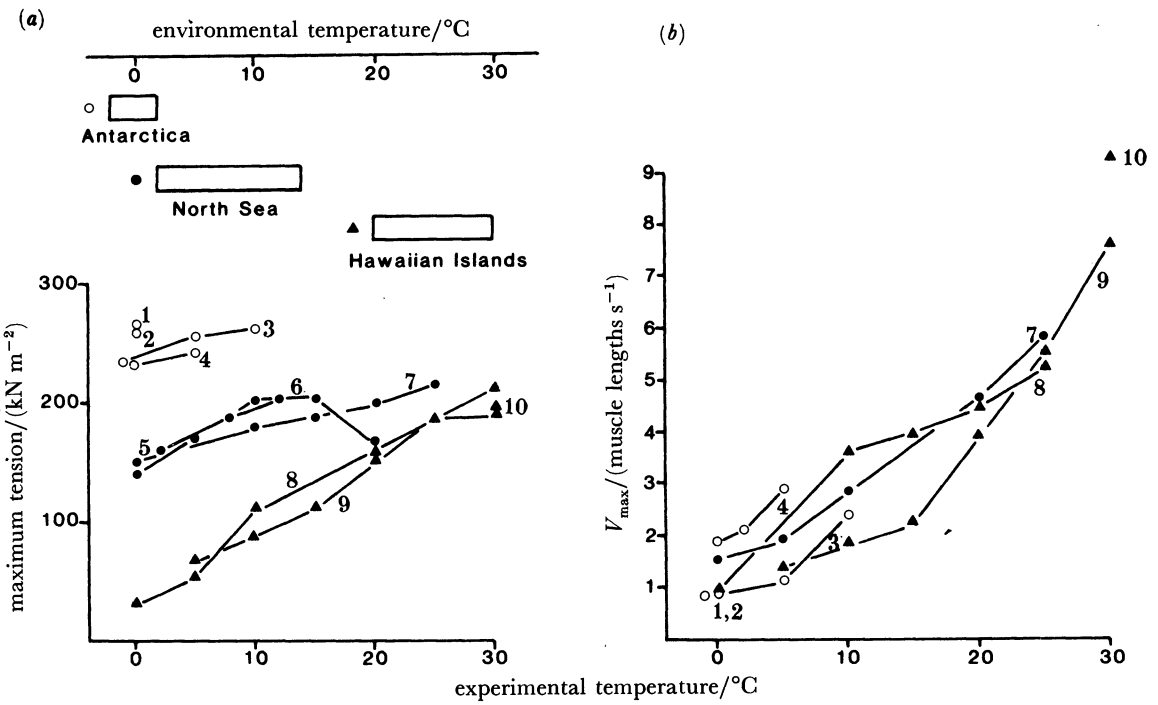

FIGURE 5. Effects of temperature on the contractile properties of skinned fibres isolated from the fast myotomal muscles of marine fish. (*a*) Maximum isometric tension and (*b*) unloaded contraction velocity (V_{max}) plotted against experimental temperature. Antarctic species from the south Orkney. Islands: 1, *Trematomus hansoni*; 2, *Notothenia rossii*; 3, *Chaenocephalus aceratus*; 4, *Notothenia neglecta*. North Sea species: *Gadus morhua* L., *Myoxocephalus scorpius* L., *Platichthys flesus* L. Tropical species: 8, *Maikaira nigricans*; 9, *Carangus melampygus* Wakiya; 10, *Euthynnus affinis*. (after Johnston, 1989).

beat frequency, only show a limited capacity adaptation. During swimming, muscle fibres undergo cyclic contractions and the power output is influenced by the amplitude of the length changes, the number and timing of nerve impulses, and by the period of each cycle (Johnston & Altringham 1988). Power output during swimming can be modelled by studying force transients in isolated muscles subject to sinusoidal length changes and periodic stimulation (Altringham & Johnston 1989). These experiments highlight the importance of 'matching' the timecourse of the force transient to the period of the locomotory movement. The slower twitch contraction kinetics of muscle fibres in Antarctic fish is likely to result in a lower maximum power output than for warm-water species, produced at a lower tail-beat frequency. Variations in the amplitude of the locomotory movements or the number and timing of stimuli may partially compensate for these effects (see below). Maximum swimming speeds have only been measured in two species of Antarctic fish; *Pagothenia borchgrevinki* (Montgomery & Macdonald 1984) and *Notothenia neglecta* (Archer & Johnston 1989). For 29 cm *N. neglecta* at 1–2 °C, maximum speed is 4.3 bodylengths per second/($L\ s^{-1}$) at a tail-beat frequency of 6.6 Hz (Archer & Johnston 1989). This is towards the lower end of the range reported for temperate species. However, differences in body shape, ecology and methodology complicate direct comparisons. Of more significance is the modest swimming performance of juvenile specimens (7 cm bodylength). Juveniles have a maximum speed of only 6.8 bodylengths s^{-1}, which is achieved at a higher tail-beat amplitude than in adults (0.29 L versus 0.20 L). Maximum tail-beat frequency in juveniles (8.9 Hz) is very modest, and not significantly higher than for adults (Archer & Johnston 1989). The greater amplitude of the locomotory movements in juveniles may help to partially compensate for the relatively low tail-beat frequency. This contrasts with studies of temperate species, such as the rainbow trout, which show that tail-beat amplitude is independent of swimming speed and that tail-beat frequency is highly scale dependent (Webb *et al.* 1984). These results suggest that maximum locomotory performance is probably limited by low temperature in Antarctic fish, particularly in larval and juvenile stages as they normally have much higher tail-beat frequencies than the adults.

Macdonald and co-workers have carried out elegant studies on the vestibular–ocular reflex in Antarctic fish. An optoelectronic movement transducer was used to measure rapid eye movements (saccades) in *P. borchgrevinki* (Montgomery & Macdonald 1985). At −2 °C, the fastest saccades were about 110° s^{-1}, about half the saccade velocity of a temperate fish at its acclimation temperature of 14 °C, but much faster than temperate saccades extrapolated to −2 °C. This is consistent with experiments on myotomal muscles and may represent the limit of temperature compensation that can be achieved in neuromuscular systems.

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Discussion

A. Clarke (*British Antarctic Survey, Cambridge, U.K.*). Dr Johnston has presented two examples of metabolic processes in polar marine organisms that show differing degrees of compensation for temperature: embryonic development, which shows very little compensation; fish swimming performance, which shows extensive, but not perfect compensation. Where in the spectrum does Dr Johnston feel the bulk of cellular processes (ATP production, protein, synthesis and so on) might fall?

I. A. Johnston. There is now good evidence that muscle contraction and swimming

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performance in polar fish shows a partial capacity adaptation to low temperatures. I would expect there to be matching between capacities for ATP utilization and ATP production. Thus, in the case of muscle, I would expect most metabolic processes to also show a partial capacity adaptation. However, this may not be the case for other tissues or even for muscles in other groups of animals. Much more research is needed before Dr Clarke's question can be answered.

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