Marine life at low temperatures - a comparison of polar and deep-sea characteristics

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Abstract: Temperature has been considered as the primary parameter determining the slow pace of ecological processes in low temperature environments. Results published during recent years have revealed this assumption to be correct for long-term developments. However, individual processes like growth and reproduction may be fast under particular circumstances, especially with high food and nutrient availabilities. The respective morphological, physiological and behavioral observations are summarized, and specific adaptations to low temperature on the molecular, cellular, species, and community levels are discussed.

Introduction

A symposium on extreme conditions for life certainly needs to include low (and high) temperatures, and we must ask for the specific characteristics of life in the large cold water ecosystems, the polar regions and the deep sea. They have the low temperature conditions in common, but they differ from each other in various other ecologically important factors. We need to consider species adaptations and the functioning of total communities. Energy availability is the dominant driving force of ecosystems, and we will discuss energetic aspects of life in cold environments, comparing life in polar regions with deep-sea life, and ask the question whether results from polar regions may help to explain the deep-sea system, or vice versa (see LIPPS and HICKMAN 1982). We are not attempting to present complete literature reviews of the different research disciplines considered. The referenced papers were selected arbitrarily, aiming at the assessment of general characteristics.

Definitions

Before going into further detail, some questions that refer to the focus of this symposium need consideration

- What is the true meaning of: Life under extreme conditions?

- Do extreme conditions in fact exist?

- Does any species live under extreme conditions?

- Who has defined the term "extreme conditions"?

This term originates from a non-marine homoiothermic species predominantly adapted to temperate zoogeographic regions. Life in the deep sea and in polar regions - in the opinion of the present authors - may not occur under extreme conditions concerning temperature, pressure, and energy. Generally, evolutionary processes have led species to adapt on different levels of organization - from cellular via individual to population levels - to a combination of conditions under which they can survive. Species have optima of ecological settings, presumably where production and recruitment reach maximum results, and they survive under boundary conditions at the limits of their distributional areas. These latter might be defined as "extreme" for a species. But, since boundaries exist everywhere, differ from species to species, and thus are spread out as a continuum, no ecotone or habitat may be defined as a generally extreme one.

Alternatively and more realistically, extreme conditions could be defined as those in which species can survive with reduced degrees of freedom. In that sense extreme conditions are those challenging special adaptational processes in the physiological, biochemical and behavioural design of an organism. Since tradeoffs will be involved, limiting the adaptational capacity of species, extremes are high or low values of abiotic factors allowing only a few species to thrive, namely those with a suitable design to adapt to such boundary conditions.

We should abstract from anthropocentric feelings and rather try to explain the different traits or developmental lines of adaptation to different ecosystems. Equivalent strategies to cope with the conditions of a specific ecological parameter, however effective in different ecosystems, may support our evaluations. This should increase the probability that our anthropogenic explanations interpret nature correctly.

In this context we should ask additionally whether life in the oceanic cold water sphere or in the warm water sphere demanded adaptation. This is an evolutionary question. The present situation developed from warmer environments in the Cretaceous to cold conditions nowadays, but original habitats and their temperatures are open to discussion. The onset of glaciation in the Antarctic, which also marks the onset of cooling in the deep sea, has been continuously redated and is now documented back to early Oligocene times 36 Ma ago (HAMBREY et al. 1990, 1991, EHRMANN and MACKENSEN 1992, ZACHOS et al. 1992). However, cooling of the South Polar Sea from late Eocene times (38 Ma), when Australia separated from Antarctica, to present only involved a decline of about 8°C which is equivalent to 0.003 °C, in a

thousand years (CLARKE 1990). As CLARKE states, on an evolutionary time scale this should not have posed a major challenge to the marine fauna, which has to cope with much more severe, short-term temperature fluctuations in most systems. Considering the volumes of water masses, cold environments are much more abundant today than warm ones. Regardless of where we draw the limits, at 10° C or at 4° C, in all instances the cold water sphere is much larger. The average ocean temperature is less than 4° C.

Limitations

For the polar regions we will predominantly draw on data from Antarctic waters. Knowledge of conditions and life in the Antarctic is broader than of the respective parameters in the Arctic, and the lower temperature as well as the relative independence from allochthonous influences allows more informative comparisons of deep-sea with Antarctic life.

A strongly seasonal migration of research fleets to the polar regions is observed, always during the months of high light intensity. This is the warmer and more productive time of the year, whereas the colder, dark months are rarely used for research. Therefore, many of the polar data may not allow extrapolation to full seasonal cycles.

Deep-sea research is conducted throughout the year, but substantial technical difficulties have to be overcome to sample and measure in the deep sea and to conduct experiments *in situ* or aboard the ship and in institute laboratories. For example, pressurized laboratory equipment as well as remotely controlled vehicles for deep-sea experimentation have rarely been used. Although the techniques for such equipment are available, the financial resources have rarely been approved. The long-term commitment through the provision of engineers has seldom been guaranteed.

Additionally, the questions asked and the results obtained for these large ecosystems deviate from each other. We therefore must accept limitations in the comparison of life in the deep sea and in polar regions.

Abiotic environmental conditions

Overall temperatures in both regions range from -1.5 °C to +2 - +4 °C. In the polar regions there are habitats close to freezing, and in the ice, organisms live in their frozen environment. Minimum temperatures in the Antarctic were given by PICKEN (1984) at -1.89 ° ±0.07 ° C. Salinity measures 34.6 - 34.9 % in Antarctic regions and in the abyssal seas, with more narrow ranges for the different water masses. However, salinity is likely not a key factor for regional

comparisons. Fluctuations of temperature and salinity are very small in Antarctic waters close to the continent, despite the local intrusion of "Warm Deep Water" (ARNTZ et al. 1992), and are almost nonexistent in the deep sea. Oxygen availability is below air saturation in the deep sea but sufficient in both regions (below the oxygen minimum layer in the deep sea) and will therefore be neglected in our considerations.

Other environmental conditions are highly different in the two regions. Pack ice covers large parts of the polar seas. The extension of the pack ice layer oscillates seasonally in accordance with air temperature and solar radiation. The sea ice system, mostly annual in Antarctic and multiannual in Arctic waters, is inhabited by characteristic communities (SPINDLER and DIECKMANN 1991), provides food and shelter for krill and other macrofauna (MARSCHALL 1988), and is an important resting place for penguins and seals. Fast ice close to the Antarctic shelf ice edge and in the inlets is of utmost importance for the reproductive biology of emperor penguins and Weddell seals. Life underneath the Antarctic ice shelves depends on lateral food advection and is largely reduced to a few motile macrofaunal species and fish, whereas bacteria occur in densities equal to those in non-polar habitats (DAYTON 1990). Around the Antarctic continent, anchor ice (DAYTON 1989) and the scraping, scouring, and ploughing effects of smashed ice, growlers, and icebergs contribute to disturbance in an otherwise rather constant environment (for further references cf. ARNTZ et al. 1994).

Currents are variable but generally stronger in the Antarctic than in the abyssal regions, although the so-called abyssal storms in some restricted areas of the deep sea lead to repeated erosion and resedimentation at other localities (HOLLISTER and MCCAVE 1984). Pressure varies with depth but is low in most of the polar regions and high in the deep sea. With its driving influence on biological processes, light becomes indirectly of utmost importance to distinguish between the two systems. Although light is strongly seasonal in the Antarctic and absent in the deep sea, the dependence of primary production on light and the fueling of the two systems by organic matter must be considered very important ecological parameters.

Metabolic cold adaptation

It is well known that biological processes, in principle, decelerate with decreasing temperature. Applying van't Hoffs law, reactions in polar and deep-sea animals should be reduced by factors between 4 and 9 compared with tropical species. However, this simple relationship applies to physiological laboratory experiments with individual species, but not necessarily to

the comparison of species living under different temperature regimes coinciding with other variations in environmental conditions and the respective adaptational strategies. These differences in lifestyle and performance adaptations between species from the same and also from other environments may overrule the basic dependence of physiological and biochemical processes on temperature; they must therefore be considered in a general evaluation of unifying adaptational principles. For species defined on morphological characteristics, we also have to consider genetic distances between populations adapted to various environmental regimes of abiotic and biotic factors.

Specific adaptations to polar regions include the biochemical and molecular antifreeze mechanisms and lipid storing organs, which have been developed in various groups. An increase in plasma osmolarity enables Antarctic fish (Notothenioidei) to survive subzero temperatures. These fish, as do Arctic cod (Gadidae), also produce antifreeze glycopeptides to remove spontaneously forming ice crystals. The concentration of these antifreeze substances decreases with depth, i.e. with increasing water temperature: fish species living in cold shallow water close to the Antarctic continent and pelagically, close to the surface, have higher concentrations of these substances than fishes living in the "Warm Deep Water" (WÖHRMANN 1992).

Lipid stores have been developed by many polar invertebrates, fishes, and warm-blooded animals to cope with low food availability during winter, to fuel reproduction, and as a protective mechanism against extremely low temperatures. The latter holds true for polar seals, whales, and penguins, which all have developed thick fat or blubber layers of triglycerids, partly due to the fact that their fur or feather coats lose their insulating properties in water (HAGEN 1995). The extreme case is the emperor penguin. The male withstands 4 months without food on the fast ice while brooding the only egg, losing about half of its body weight during this time.

Among invertebrates, particularly the copepods have been studied for lipid stores. Since most Antarctic species spend the winter at depth in diapause, it seems strange that they should deposit large amounts of lipids. However, they save most of this energy (which, in contrast to the lipids in seals and birds, are wax esters) during the diapause and spend it only in spring for reproductive purposes. *Calanus propinquus* is an exception; this species, which remains active in winter, stores triglycerides (HAGEN, loc. cit.). Antarctic krill *(Euphausia superba)*, contrary to former belief, also store lipids (triacylglyceroles) (SIEGEL and KALINOWSKI 1994).

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These adaptations, which appear special for polar animals, are no longer considered in the following, more general comparison of the physiology and biochemistry of polar and deep-sea animals.

Critical temperatures

Boundary conditions are traditionally defined in terms of the LD_{50} values indicating 50 % survival. Recently, critical thresholds for low and high temperatures (Tc) were identified for different species as being characterized by the transition to an anaerobic mode of metabolism (ZIELINSKI and PÖRT-NER 1995, SOMMER et al. 1995). Under these conditions it is not the availability of ambient oxygen that is limiting, but critical temperatures are caused by an insufficiency of circulatory and ventilatory systems to ensure adequate oxygen supply and/or by an insufficient capacity of aerobic pathways to meet energy. Critical temperatures are shifted depending upon seasonal adaptation. Low thresholds observed close to or above freezing in temperate zone species have obviously been eliminated during evolutionary low temperature adaptation (the price being a high sensitivity to high temperatures, i.e. a low upper Tc). The molecular mechanisms responsible for setting the Tc's are not known. Adaptational changes (for an overview of temperature adaptations see PROSSER and HEATH 1991) possibly responsible for the shift of the low Tc to below polar ambient temperatures would include among others a rise in aerobic capacity (combined with mitochondrial proliferation), improvement of muscle function and nervous conductivity, and adjustments of the metabolic machinery (for example enzyme quantities and kinetic properties), changes that overall may be summarized as "metabolic cold adaptation". This definition should be preferred over the historical definition which focusses on whether the adaptation to low temperature is associated with elevated energy expenditure.

Cold compensation in metabolic rate

Historically, the hypothesis of "metabolic cold adaptation" for species living in polar regions was based on an assumption already presented by KROGH (1916), elaborated by SCHOLANDER et al. (1953) as well as WOHL-SCHLAG (1960, 1964), and summarized by DUNBAR (1968). This concept assumed elevated rates of resting metabolism of cold-adapted ectotherms under low temperatures to ensure maintenance of vital functions. In recent years the concept of cold adaptation has been discussed and reviewed, e.g. by CLARKE (1983, 1987 a and b, 1988, 1991), and it requires new formulation. True resting metabolic rates (standard metabolic rates as redefined by PÖRT-NER and GRIESHABER 1993 excluding all levels of spontaneous activity and

all effects of external and internal stressors) are difficult to measure, since long periods of recovery from handling and stress effects during the measurement procedure may lead to a long-term elevation of metabolic rates, especially in animals from cold environments (for recent, more adequate analyses in polar fish see STEFFENSEN et al. 1994). The partitioning of energy also needs to be considered since, even with a complete exclusion of motor activity, a variable proportion will be channelled into growth or reproduction depending on the season. A strong seasonality in food availability as discussed by CLARKE will also influence standard metabolism in polar environments. Metabolic rate will change with fluctuating levels of excitation depending on whether food is available or not. Metabolism will increase during specific dynamic action in freshly fed animals. During periods of nutrient deficiency, metabolic depression may occur due to regulatory shifts in the organism. Whether such a shift to the slow lane of passive survival (suspended animation) truly occurs is unknown, as are the potential underlying mechanisms. However, phases of suspended growth activity and intermittent fast growth have been reported for polar fish and invertebrate species (see below). Research focussing on the regulatory mechanisms causing the switch between low and high energy turnover would have to follow similar lines as depicted for the down regulation of metabolic rate in invertebrate or vertebrate facultative anaerobes (including a role for intra- and/or extracellular pH, changing hormone or transmitter levels, enzyme phosphorylations, mechanisms of channel arrest; BUCK and HOCHACHKA 1993, PÖRTNER 1993, GRIESHABER et al. 1994, LUTZ 1992).

As a corollary, it appears that early results suggesting a large degree of cold compensation in metabolic rate were erroneous. Careful measurements of the respiratory rates of invertebrates and fishes by HOLETON (1973, 1974), WHITE (1975), RALPH and MAXWELL (1977 a, b), WELLS (1987), and STEFFENSEN et al. (1994) have revealed no or very small increases of resting metabolic rates at low temperatures, if compared with species from temperate regions that have similar ecological characters and that have been cooled to low temperatures. Therefore, it appears tempting to deny the existence of metabolic cold adaptation, since the effect on metabolic rate is small and hardly detectable. Such a conclusion would appear even more valid for deep-sea species, although the combined effects of pressure and low temperature lower the temperature to which membrane functions have to adapt from true values of 2 °C to apparent values as low as -11 to -19 °C (SOMERO 1992). However, the selection of a low motor activity lifestyle in the deep sea and the associated biochemical design, at least in the pelagic, has led to overall metabolic rates even lower than in polar shallow-water species (see below, CHILDRESS 1995) and, therefore, may obscure any effect of metabolic cold

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adaptation. The real question is whether the compensatory strategies required to maintain cell and tissue function at low temperature or at a combination of low temperature and high pressure, are detectable by analysis of standard metabolic rate, considering the influences of different life styles and performance levels (see above). Even if this is not the case, metabolic cold adaptation will occur. The effect on metabolic rate may be small or compensated for by other adaptational features and, therefore, not be detectable in overall oxygen consumption measurements. In conclusion, the historical view of metabolic cold adaptation as a compensatory increase in metabolic rate, while certainly stimulating, should be abandoned and redefined as the multilevel adaptational process allowing survival in the cold with changing (rising or decreasing) rates of individual physiological processes.

Homeoviscous and enzyme adaptations

Within metabolic adjustment cold homeoviscous adaptation maintains membrane fluidity. Proliferation of mitochondrial and sarcoplasmic reticulum membranes as well as altered expression of membrane proteins support membrane-associated functions (PROSSER and HEATH 1991, HAZEL 1995). Generally, protein stability is higher at low temperature, but more (or less) protein may be required to maintain specific functions. In that sense, low temperature adaptation can be optimized by increasing enzyme activities (capacity adaptations) and/or varying kinetic parameters of enzymes (maintenance of regulatory capacity and flexibility = rate control adaptations); this includes a lower activation energy and lower Michaelis constants (Km values) along with effects by changing levels of activating or inhibiting metabolites (cf. HOCHACHKA and SOMERO 1984, PROSSER and HEATH 1991, for a recent example see VETTER 1995). Usually, these are long-term adaptational processes, if investigated in the same species under different temperature regimes. For example, the effect of temperature on the apparent Michaelis constant (Km) for pyruvate of muscle-type (M4) lactate dehydrogenase (LDH) was studied in fish from environments characterized by different temperature ranges. Whereas the Km values increase rather regularly with increasing temperature and within the natural temperature range, the values are similar for each species in the respective range of environmental temperature (HOCHACHKA and SOMERO 1984). Also, enzymes from cold-adapted shallow- and deep-living teleosts fall into the same range of Km values. Expression of various isozymes is seen to be responsible for the changes in kinetic parameters during temperature adaptation (e.g. LIN and SOMERO 1994). Compared to enzymes of metabolic pathways, digestive enzymes such as hydrolases and proteases are only poorly regulated. These enzymes are

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more strongly dependent upon factors other than temperature, e.g. hormones or food availability. Nonetheless, DITTRICH (1992) described kinetic properties of trypsin-like proteases to differ in polar and tropical benthic crustaceans. She found a pronounced cold adaptation of the Antarctic species, becoming evident in lowered activation energies of the protease and relatively high enzymatic activities.

Acid-base regulation

Adaptations in metabolic control and capacity to low temperature are supported by the adequate adjustments in the regulatory patterns of extra- and intracellular acid-base status, an aspect not very well understood at present. A basic and early hypothesis arose from the observation that pH in intra- and extracellular fluids of ectotherms frequently changes in a way that a constant protonation of histidine-imidazole groups (the most common buffer in biological fluids; these groups are also involved in substrate or coenzyme binding to enzymes) is maintained during temperature changes (alphastat hypothesis, REEVES 1977), thereby ensuring functional integrity. However, neither is this a unifying principle to the extent stated in many textbooks and reviews, nor are the mechanisms completely understood by which pH is adjusted to the respective values at different temperatures. pH changes occur due to passive and active mechanisms (e.g. SARTORIS and PÖRTNER 1995), but the mechanisms determining the new setpoints are unknown. Temperature-specific changes in pH may be a means contributing to integrate cellular and systemic functions and to readjust and regulate overall metabolic rate.

Energy savings and energy partitioning

HOCHACHKA (1988) discussed the adjustments of channels and pumps as determinants of metabolic cold adaptation strategies (Tab. 1). "Pumps" are active transport systems, i.e. highly conservative, ion-specific ATPases. "Channels" are ion-specific transmembrane proteins allowing passive ion fluxes to occur. Both ion fluxes are derived protein functions which must be kept in precise balance; temperature however, differentially affects these two processes. The capacity of ATP-dependent ion pumps declines in cold water because of high Q_{10}-values for this active process, whereas fluxes across the passive channel system are less sensitive to low temperature owing to the lower Q_{10} for physical processes. Two strategies appear possible: Firstly, if channel densities remain unchanged between high and low temperatures, then ATPase densities would have to be increased to compensate for the Q_{10} effect. This is metabolically more costly and appears as a strategy developed by organisms that maintain a high level of activity at low temperatures and

therefore depend upon high levels of nervous activity and on mechanisms able to rapidly restore any imbalance in ionic equilibria, such as may occur during muscular activity. According to HOCHACHKA, such a strategy could explain the metabolic cold adaptation found in Antarctic fish. Secondly, at constant ATPase densities a decrease in channel densities could allow the Q_{10} effect on ATPases to be fully expressed. The respective organisms would become hypometabolic, resting O_2 uptake rates would decrease, and the capacities of ion and osmoregulation would decrease accordingly. These are characteristics of many deep-sea fishes. The two opposite strategies for living in cold environments are contrasted in Table 1 (for a more detailed analysis of the effects of temperature on ion regulation see COSSINS et al. 1995). However, a tradeoff between both strategies can be seen in both polar and deep-sea organisms. The level of motor activity appears somewhat higher in Antarctic than in deep-sea species but does not reach the levels seen in temperate or tropical species at ambient temperatures. Therefore, metabolic cold adaptation (in the historical sense) does not fully compensate for the temperature-dependent decrease in metabolic capacity and scope for activity. The decisive question appears to be an ecological one: To what extent does the environment allow or enforce the full development of an energy saving strategy as derived for deep-sea species? Pressure and low temperature are constraints shared by all deep-sea ectotherms, and low temperature being a constraint shared by all polar ectotherms. It appears that low temperature is a common restriction explaining why polar or deep-sea ectotherms, on average, lead a life characterized by low energy turnover. In addition, limited food availability may also force especially deep-sea species to become as economic as possible and to compromise and choose the adequate levels of awareness and reactivity. The latter appears as a general trend governing the evolutionary selection of different, high or low energy turnover modes of life (cf. WIESER 1995). In the deep sea, even the marine ectotherms with the most costly life style, squid, convert to a lower activity mode of life characterized by special mechanisms of neutral buoyancy (WELLS 1994, VOIGHT et al. 1994).

Differences and similarities in the biochemical and physiological design of deep-sea and polar organisms become obvious from comparisons of vertical distribution and metabolism of fishes living in Antarctic and California borderland waters (TORRES and SOMERO 1988 a). There are based on "minimum depth of occurrence" (CHILDRESS and NYGAARD 1973), which is de- fined as the water depth below which about 90 % of a population lives. Whereas oxygen consumption rates versus minimum depth of occurrence are rather similar when measured at ambient temperatures, the rate for species from off California decreases when calculated for Antarctic temperatures of

Tab. 1: Simplified differences in metabolic cold adaptation between polar and deep-sea fish, expressed by a balance of active and passive mechanisms of ion exchange on different levels and their energetic, morphological and behavioural consequences (modified after HOCHACHKA1988.)

Polar fish	Deep-sea fish
upward adjustment in ion pump densities	downward adjustment in ion channel densities
increased ATP demand of ion pumping and osmoregulation	reduced ATP demand of ion pumping (Q_{10} effect)
energetically expensive	energy saving
basic metabolic requirements higher	suppressed metabolic rates and capacities
body muscular skin firm	body flabby skin delicate
sluggish, but higher reaction capacity	sluggish, hovering around

0.5° C applying a Q_{10} value of 2. Thus, the Antarctic fish exhibit a higher respiration rate than expected from Q_{10} calculations, and this clearly reflects cold adaptation in the historical sense mentioned above. However, one must be careful not to generalize from these findings. Available measurements in marine invertebrates do not support such a generalization (HIRCHE 1984, CLARKE 1987). Actually, metabolic cold compensation seen in fishes may be typical for these hypoosmotic animals which, despite already elevated ion levels in the plasma of some cold water versus temperate zone species (e.g. GONZALEZ-CABRERA et al. 1995), are most likely to need some compensatory adjustment in pump densities to meet the requirements of osmoregulation and maintain ion gradients. Therefore, the historical concept of metabolic cold adaptation is likely to be valid for fishes, but certainly not to the extent originally published.

Additionally, TORRES and SOMERO (loc. cit.) analyzed intermediary metabolic enzymes in white skeletal muscle, lactate dehydrogenase (LDH) representing the anaerobic, and citrate synthase (CS) the aerobic potentials. The activities of white muscle enzymes are representative for the metabolic

rate of this tissue, which comprises the largest part of the fish body mass (CHILDRESS and SOMERO 1979). Whereas LDH levels are similar in both fish groups, CS activities are higher in Antarctic species and, therefore, support the conclusion of a higher aerobic metabolic rate in Antarctic compared with California species (cf. TORRES and SOMERO 1988 b). However, the results show decreasing respiration rates and enzymatic activities in white muscles with depth, but this decrease is not present in brain and heart enzymes (CHILDRESS and SOMERO 1979). Whereas differences in white muscle key aerobic enzymes are likely to reflect different baseline levels of motor and thus aerobic metabolic activity, the influence of the mode of life on brain and heart metabolism is less. These organs could be more dependent on sensory reactivity and body size, rather, than on mode of life, at least below a certain level of motor activity. Brain and heart seem unsuitable to be included in energy saving strategies in deep-living versus polar species.

Moreover, biochemical reactions may be altered by hydrostatic pressure and this needs to be considered when comparing processes in organisms and communities from shallow and deep cold environments. Generally, all processes involving a change in volume will be affected by pressure in a sense that those leading to volume reductions will be favoured. On the molecular level this will disturb the overall balance of metabolic pathways, with an effect on the total rate of metabolic activity (SOMERO 1991). Pressure effects are most important in the context of membrane-associated functions and modify membrane adaptations (SOMERO 1992) by increasing the extent to which homeoviscous adaptation is required (see above). They strongly affect (and call for an adaptation in) ATP-dependent ion pumping or, on a more complex level, nervous function. pH will also fall with increasing pressure. Some enzymes are modified to secure appropriate levels of the apparent Michaelis constant values. These alterations usually only involve minor changes in the primary structure of an enzyme. Opposite to the development of labile, very heat-sensitive protein in polar species, adaptations to high pressure are linked to a strengthening and an associated heat resistance of protein structure.

Much of the enzyme work has been conducted with skeletal muscle type (M_4) lactate dehydrogenase (LDH). For both shallow- and deep-living, cold-adapted fishes, Km of the cofactor nicotinamide adenine dinucleotide (NADH) increased for pressures between 1 and 68 atmospheres. The relative increase was stronger in shallow-water fishes and a further increase was observed to 476 atm. For deep-water species no additional increase was observed above 68 atm. Similarly, the Km values of pyruvate are pressure-dependent in shallow-living compared with deep-sea teleosts. Generally, enzymes purified from deep-living organisms appear less pressure sensitive

than those purified from organisms living in shallow waters. Comparing polar and deep-sea organisms reveals, however, that Km values usually fall in cold environments and is compensated for by an adaptational rise, whereas Km values will rise at increased pressures. The need to develop structural rigidity in the deep sea is combined with a loss in catalytic efficiency, an aspect which might contribute to the limited performance of deep-sea species. On the other hand, much of the decrease in enzyme and metabolic capacity occurs during the first 200 to 400 m of depth, suggesting that lifestyle rather than pressure per se is the primary determinant of metabolic rate (SIEBENALLER et al. 1982). As opposed to pelagic species, benthic deep-sea species show no such decline in metabolic rate, but this might also be related to the lower metabolic capacities of benthic species in general.

In addition to adaptational changes in individual biochemical and physiological mechanisms the partitioning of energy between physiological processes appears most relevant for the overall energy turnover of an organism. A low rate of protein synthesis would contribute to reducing the metabolic rate, possibly due to increased protein stability at low temperature which allows for a reduction in protein turnover and an uncompensated Q_{10} effect. Seasonal influences are considered by CLARKE (1987): Growth and gametogenesis should have the same requirements for protein synthesis, independent of the temperature regime, and it is the maintenance protein turnover which seems to be reduced owing to the Q_{10}. These lower maintenance costs and the associated low standard metabolism would be an energetic advantage, leaving room for an increase in growth and reproduction depending on nutrient availability. Cold adaptation may also exist in this respect, and according to the evaluation of the above data, standard metabolism in cold-adapted ectotherms consumes relatively less energy and represents an ecological advantage for organisms in polar and deep-sea regions.

Conclusions

Cold temperatures in polar and deep-sea regions have caused adaptive evolutionary changes along similar lines, although temperatures reach significantly lower values in polar seas than in most of the deep sea. Low temperature appears as a common constraint limiting the overall energy expenditure of an organism. Hydrostatic pressure causes temperature adaptations of membrane-bound processes to be even more explicit in the deep sea, whereas protein adaptations are different at high pressures, nonetheless ensuring maintenance of adequate catalytic properties in both cases. Energy saving strategies on top of temperature-induced reduction of metabolism appear to be characteristic for deep-sea pelagic animals, these strategies being related

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to the more passive mode of life of deep-sea (at least pelagic) versus polar animals. In comparison, there is some evidence for a compensatory rise in metabolic rate in polar fishes, but this general trend, which is possibly related to the less temperature-dependent cost of osmoregulation in these hypoosmotic animals, may be compensated for by the even lower-activity lifestyle in deep-sea fish. Further research is required to elucidate to what extent metabolic cold adaptation, redefined as the summed adjustments of individual metabolic features to the cold, changes the partioning of catabolic energy into the various metabolic and physiological processes on the cellular and whole animal level. Furthermore, the regulatory patterns eliciting such changes and modifying overall metabolic rates in the cold and during additional seasonal fluctuations of environmental parameters, are not at all understood.

Characteristics of growth and production in polar regions and at great depth

It has long been held that processes of production such as growth of body and reproductive tissues are slow in polar and in deep-sea environments, and that this was related to large body sizes, late maturity, extended longevity, few and large yolky eggs, brooding of offspring, as well as no or short pelagic larval periods. These are typical of K-strategists, and the characteristics were partly related to low temperatures. However, a number of arguments have accumulated which seem to contradict these observations and the interpretation of cold-water environments as slow process systems.

Primary production

Contrary to what was believed before the BIOMASS programme (EL-SAYED 1994), Antarctic waters are characterized by low overall productivity, with high primary production being patchy and mostly confined to coastal regions (SAKSHAUG 1994). Although the permanently ice-free region of the South Polar Sea comprises, depending on season, between 40 and 85 % of the area, and the seasonally ice-free region between 10 and 45 %, and although nutrients in these areas are abundant throughout the year, these waters belong to the poorest primary production areas in the world's oceans (HOLM-HANSEN et al. 1977). On the other hand, shelf waters and the zone of melting sea ice have a fairly high production and may contribute as much as 40 % of the total pelagic primary production of the Southern Ocean, including most of the "new" production (SAKSHAUG, loc.cit.). During an algal bloom high primary production values were recorded by BATHMANN et al. (1991) in the Antarctic Coastal Current. "Bloom systems" dominated by diatoms are characterized by

short-term production pulses and high mortality resulting in important sedimentation events, whereas the low-biomass flagellate systems more typical of Antarctic waters maintain a low but steady production throughout most of the year (SCHAREK and NÖTHIG 1995). In the Barents Sea, pelagic primary production is much higher due to higher productivity in the ice-free areas and a relatively small extension of the ice-covered zones (SAKSHAUG, loc. cit.). These differences clearly cannot be explained by differences in water temperature. Various hypotheses are under discussion, including surface water stability and degree of vertical mixing, the availability of trace metals (in particular, iron), and grazing pressure (CULLEN 1991, LOCHTE and SMETACEK 1995).

TILZER and DUBINSKY (1987) studied primary production in Antarctic waters and concluded from their results that phytoplankton potential growth rates are not severely affected by the low temperature of the South Polar Sea. During short days with restricted energy supply or in times of deep water column mixing, phytoplankton survival is achieved through substantial reduction in respiration rates. Another type of adaptation is the lowering of the compensation point light intensity, i.e. many species become adapted to low light intensities for the dark time of the year (HEYWOOD and WHITAKER 1984). This indicates that the regulating parameter may be light intensity related to day length and surface layer stability. LOCHTE and SMETACEK (1995) also consider the lack of constant environment in the euphotic zone, not temperature, to be a major ecological factor for the low overall productivity of Antarctic waters. They argue that phytoplankton growth rates under Antarctic conditions do not differ greatly from those of temperate species, maximum growth rates at 0 °C being about half those at 10 °C. Even at sub-zero ranges, temperature cannot be the only limiting factor.

High production rates can also be found in the pack ice zone if the light can penetrate into the ocean to some extent between the ice floes. In contrast, the algae under fast ice are shade adapted and show a lower production, because not much light penetrates the ice and the often considerable snow cover. Experiments on sea ice microalgae have shown maximum uptake rates of nutrients close to ambient temperatures. Temperatures within the sea ice are often considerably below those of polar seawater, causing an enormous increase in salinity in the brine channels. Theoretically, salinity in these channels should be 140 ‰ at -10 °C, although the highest value measured *in situ* was 92 ‰. At any rate, sea ice communities must withstand the combined effects of both low temperatures and extremely high salinities (DAHMS 1993). The - often high - biomasses of these ice communities are dominated by pennate diatoms, dinoflagellates, and foraminiferans, but many other

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groups are also present (SPINDLER and DIECKMANN 1991). Despite the obviously harsh environment, which, however, is fairly constant during the polar winter (KIRST 1995), the algal biomasses (and those of the foraminiferan *Neogloboquadrina pachyderma*) exceed those in the water column by many times (SPINDLER and DIECKMANN, loc. cit.). Experimentally, growth of ice diatoms has been measured at -5.5 °C and a salinity of 95 ‰. Survival was observed at -10 °C and 145 ‰, and growth thereafter resumed at 34 ‰ (BARTSCH 1989).

Similarly, benthic microalgae depend on high energy and are less influenced by ambient temperatures. In Antarctic waters they showed a rapid response to the light increase following the breakup of the sea ice in November, and a production maximum was observed in December (GILBERT 1991 a and b).

In examining primary production at low temperatures, we must also consider the chemoautotrophic processes in the areas influenced by hydrothermal vents and cold seeps. Life at hydrothermal vents along tectonic spreading centres is mostly interpreted to occur at temperatures elevated well above ambient. This is certainly true, but at the outskirts of the vents the high bacterial production materializes at normal deep-sea temperatures, since a steep temperature gradient is observed around the hot core of ejected water. Bacterial chemoautotrophic production is based on the chemically reduced constituents in the vent water as energy sources and is specifically realized in symbioses with various invertebrates. Principally, the same processes characterize the communities cold seep. Again, this happens at deep-sea or slightly elevated temperatures (e.g. JANNASCH and WIRSEN 1983, HESSLER and SMITHEY 1984, JONES 1985, HECKER 1985, LAUBIER et al. 1986, JUNIPER and SIBUET 1987, KENNICUTT II et al. 1988).

Together with the seasonally high phytoplankton production occurring at certain sites in polar regions, this demonstrates that primary production is not necessarily low at low temperatures. Wherever hydrographic stability prevails in low temperature environments (and, of course, nutrients are available), primary production may be high. In this respect it is important to note that these observations do not imply permanently high production levels. Peak phytoplankton production is restricted to short periods of time and the yearly average is low. In the deep sea, venting may be an intermittent process, on average with low emanations of warm or hot water and reduced chemical energy availability.

Heterotrophic bacteria

Similar results have been found for bacterial secondary production. Bacteria may have high doubling rates in the deep sea when energy is fueled into

the system. Experiments under high pressure with relatively fresh phytodetritus from the seafloor or with aged and sterilized detritus prepared from seston which was filtered out of central oceanic surface waters stimulated high growth rates in heterotrophic bacterial assemblages from sediment samples collected at about 4550 m depth (LOCHTE and TURLEY 1988, TURLEY and LOCHTE 1990). Fast reactions were also demonstrated with ^{14}C-labelled cyanobacteria as nutrient supply (LOCHTE 1992). Further observations of high growth rates were reported by ALONGI (1990) in detritus-rich samples from about 2400 m and 4000 m and by POREMBA (1994) at 4550 m.

Experiments demonstrate that organic matter degradation by psychrophiles occurs faster at temperatures somewhat above ambient (DEMING and BAROSS 1993), and there is a strong dependence on the quality and quantity of the organic material. BOETIUS and LOCHTE (1994) investigated the potential hydrolytic activities of extracellular enzymes in 15-day incubations of deep-sea sediments from 4500 m. They concluded that enzyme production by natural, mixed microbial assemblages directly depends upon the supply and the quality of organic matter. For a depth transect from the shelf to 3500 m in the Arctic Ocean, BOETIUS (unpubl. manuscript) came to the same conclusion about bacterial activities as derived from microbial extracellular enzymes.

These methods, applied to total sediment samples, cannot distinguish between bacteria, fungi, protozoans, and meiofauna. However, compartmentalization of sediment oxygen demand showed (see below) that 60 - 80 % of the oxygen were respired by bacteria, i.e. the above results should be attributable mainly to bacterial activities.

Under the aspect of temperature adaptation, the psychrophilic bacteria exhibit optimal growth at low, polar ambient temperature and the psychrotrophic species are cold tolerant but grow best at somewhat elevated temperatures. For our comparison with the abyssal environment we must recognize the ability of psychrophiles to react rapidly to organic matter input by retaining high-affinity active-transport systems (KARL 1993). Polar temperatures do not limit these bacteria. KOTTMEIER and SULLIVAN (1990) report on algal and bacterial biomass and production rates in Antarctic pack ice. They discovered very high densities and production rates in surface ice ponds, which may warm up by a few degrees during summer but nonetheless remain cold water habitats. Overall these authors conclude that the bacteria are very important for the production cycle in the pack ice region. This is corroborated by HELMKE and WEYLAND's (1995) studies on bacteria in the ice and the adjoining water column.

Protozoa

In their experiments with natural and artificial detritus from surface waters LOCHTE and TURLEY discovered an opportunistic flagellate of the genus *Bodo*. The species bloomed together with the bacteria, feeding on their high stocks (TURLEY et al. 1988, LOCHTE and TURLEY 1988, TURLEY and LOCHTE 1990). Very little is known about protozoan life and production in the deep sea, but foraminiferans are an ecologically important component (THIEL 1975, 1983, ALTENBACH and SARNTHEIN 1989, GOODAY and TURLEY 1990, GOODAY et al. 1992). In the Norwegian and Greenland Seas, benthic foraminiferans not only from abyssal depths but also from cold water continental slope habitats, showed fast responses to organic matter that was added to undisturbed sediment samples collected with a multiple corer from 1240 m depth and incubated at 0 °C, the ambient temperature. ALTENBACH (1992) registered an increase of 88.7 % of organic carbon in foraminiferans three days after detritus application. HEEGER (1990) demonstrated their high food particle uptake by cytological studies and observations from life. Particulate matter was assembled outside their aperture within a day of phyto-detritus sedimentation and, later on, particles of this material were accumulated in their vacuoles. According to LINKE (1989), metabolic rates of foraminiferans and heat production show fast reactions to sedimentation events. ATP turnover was kept rather constant at relatively high rates for a rapid response to energy income, but ATP content was increased from the AMP-pool. After some time the total adenosine nucleotide level had increased, which indicates the growth of foraminiferal biomass (GRAF and LINKE 1992).

A fascinating observation on the growth of a xenophyophorian was reported by GOODAY et al. (1993). The high-speed version of a film produced from single shots by a time-lapse camera revealed episodic growth of an upright standing, leaf-like structure. Although no observational material is available, the authors assume degradable organic matter being caught at the obstacle protruding above the sediment surface and supplying organic matter for consumption.

Comparable seasonal data on foraminiferal growth and sediment compound reactions are not available from polar regions. The pronounced seasonality of primary production allows the assumption of fast reactions by the Arctic and Antarctic systems as well. In shallow waters the relative organic matter input to water layers below the euphotic zone and to the seafloor is quantitatively and qualitatively higher than in deep water.

Thus, the unicellular organisms capable of rapid reactions to food supply can show periods of fast responses even under cold-water conditions in polar and deep-sea habitats. These results were confirmed by measurements of community activity in central oceanic regions. Although not studied within a single year, a seasonal cycle can be compiled for ATP concentrations as a measure of metabolic activity, total adenylates as a measure of benthic biomass, and the ratio of ATP:ETS (electron transport system) as an index for that part of respiration used for ATP production. The seasonal response to phytodetritus sedimentation was determined by chloroplastic pigment equivalents in the sediment. In the central Northeast Atlantic the peak in primary production occurs in May and the detritus arrives at the sea floor about 4 - 6 weeks later, stimulating the summer increases in metabolic activities and growth (THIEL et al. 1988/89, PFANNKUCHE 1992, 1993).

Based on measurements of sediment community oxygen consumption and applying the experimentally derived rates for microbial respiration and growth by LOCHTE and TURLEY (1988) and TURLEY and LOCHTE (1990), PFANN-KUCHE (1992) estimated that 60-80 % of the energy from phytodetritus mass sedimentation is consumed by bacteria. This largely explains the seasonal increases of benthic activities.

Metazoa

In the larger organisms seasonal responses are dampened, although some indications were presented by SOLTWEDEL et al. (1996) that nematode sizes increase during the year. This result stems from a multiple-year, combined seasonal study and needs further data to be verified. Meiofaunal densities in the southeastern Weddell Sea (211-2080 m depth) were found to be in the range of other deep marine environments but were higher than in the warm, oligotrophic deep-sea sediments of the Mediterranean and the Red Sea (HER-MAN and DAHMS 1992, VANHOVE et al. 1995).

Macro- and megafaunal benthic densities and biomasses are higher in the Antarctic than in the Arctic and much higher in both areas than in the deep sea (DAYTON 1990, ARNTZ et al. 1994). A finer distinction can be made for Antarctic macrofauna. In littoral communities the fauna is extremely scarce due to heavy ice impact (DAYTON 1990, GAMBI et al. 1994, BARNES 1995 a, CLARKE in press). Most shelf and upper slope communities are distinctly richer than comparable boreal and subtropical communities (BREY and CLAR-KE 1993); the authors relate this particularly to the low maintenance energy associated with the low ambient temperature. However, epifaunal communities at these depths (STARMANS 1993, BARNES 1995 b) are richer in most of the Antarctic than the endofaunal benthos (e.g. GALLARDO et al. 1977, VOSS

1988, GALERON et al. 1992, GERDES et al. 1992), although locally endo-benthos may be of greater importance (MÜHLENHARDT-SIEGEL 1988, 1989). Below 1000 m, Antarctic and non-Antarctic biomass levels do not seem to differ much (ARNTZ et al. 1994).

Production of most macrobenthic species investigated so far in Antarctic waters is very low, although there are a few exceptions such as the scallop *Adamussium colbecki* (see review by BREY and CLARKE 1993, BREY 1995). In general, also P/B values of Antarctic benthic invertebrates are significantly lower than those of their temperate counterparts; taking the effects of tempe-rature and depth into consideration, however, removes these differences in productivity (BREY and CLARKE, loc. cit.). A few indirect estimates of Ant-arctic benthic community production (EVERSON 1970, SCHALK et al. 1993) and of energy flow to and within the benthic system (JARRE-TEICHMANN et al. in press) reveal low overall production, slow turnover rates, but relatively efficient cycling considering the seasonal limitations in food supply.

Slow overall growth rates have been described for most Antarctic macro-benthic species studied to date (see summary by ARNTZ et al. 1994). However, a few species of Porifera, Ascidia, and Bivalvia were found to grow consid-erably faster than related species in cold and temperate environments (DAYTON et al. 1974, DAYTON 1989, RAUSCHERT 1991, EVERSON 1977). In order to evaluate general growth performances, BREY and CLARKE (1993) compared growth characteristics of 36 polar populations of various inverte-brates (26 Antarctic, 10 Arctic) with 327 populations living in non-polar regions. Based on production: biomass (P/B) ratios for molluscs, crustaceans, polychaetes, and echinoderms and taking into account mean individual body mass, latitude, water depth, and ambient temperature, they concluded that a broad variability exists in all latitudinal zones, but that average growth in polar populations is significantly slower than in lower latitudes.

Similarly, CLARKE and NORTH (1990) and HUBOLD (1992) pointed out for Antarctic fish species that average growth is slow, but larval growth rates may be faster when food is abundant. Growth of notothenioid fish from the high Antarctic is mostly slower than in the seasonal pack ice zone and around the islands north of it. However, *Dissostichus* spp. both from the high and low Antarctic grow at rates comparable to North Sea cod; *Notothenia rossii* compares to Atlantic cod from West Greenland and saithe from the North Sea, and growth of many other species is comparable to ecologically related species in the North Atlantic. This supports results from physiological studies in that some compensation either for low temperatures or other important ecofactors such as food limitation may have evolved in Antarctic fishes (KOCK 1992).

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Growth of organisms is not a continuous process, but may be broken up into a number of phases. Development may be interrupted by a diapause to bridge seasonally occurring adverse conditions. But before or during the next productive season, species may exhibit rapid development to secure optimum food supply for the larvae. *Thysanoessa inermis* and *T. raschii* exhibit such varied growth rates. CLARKE and PECK (1991) cite examples of fast growth in copepods and GLIWICZ (1990) demonstrates the dependence of growth rates in cladocerans on the available energy. *Euphausia superba* grows much slower than was supposed a decade ago, growing to an age of 5-7 years and attaining sexual maturity only in the 3rd summer. Growth in this species is restricted to the summer half of the year (SIEGEL and KALINOWSKI 1994). Examples for caridean shrimps were presented by CLARKE (1983) and GORNY et al. (1993). They demonstrate that phases of fast growth are interrupted by phases of slow or no growth, and that rapid growth is correlated with periods of high food availability. It is important to note that contrary to food availability, temperatures hardly change at all during the Antarctic year, and that low temperature does not prevent fast growth.

Growth and growth rates for the deep sea are summarized by GAGE and TYLER (1991). Only for a few species have growth estimates been achieved, not allowing a profound deep versus shallow comparison. Although some growth curves seem similar to shallow-water species, most deep-sea species seems to grow slowly. However, deep-sea species with r-strategic characters of development are also known. Larvae of the wood-boring Xylophaginae settled on wood in the bathyal in great numbers and exhibited rapid development and growth (TURNER 1973). This, too, may rather have been a result of available food, but it shows that accelerated life cycles may occur under cold water conditions in the deep sea.

As for primary production, we conclude that the secondary production processes of bacteria and larger organisms - unicellular species to megafauna - alternate between low and high level activities. Little information exists on interannual variations. Decisive in respect to this paper is the fact that cold water species and presumably assemblages have the ability to react rapid at optimum production conditions.

Thorson's rule

For polar regions and for the deep sea some traditional views on life history modes, which can be generally summarized as K-strategies, have evolued. They originate from observations on macro- and megafauna and include:

slow growth

extended longevity

large final size

low fecundity, large yolky eggs

mostly non-pelagic development

slow embryonic development

brooding, brood protection, viviparity

These life strategies, which are often cited as "Thorson's rule" (cf. PEARSE et al. 1991) have been found frequently in polar waters of both hemispheres, although they seem to occur more regularly in the Antarctic (see review by ARNTZ et al. 1994) and the deep sea (GAGE and TYLER 1991) than in the Arctic (THORSON 1950). They are certainly related to polar and deep-sea conditions but not necessarily to the low temperatures in these environments. Thus, it makes sense to avoid a long pelagic life in polar regions because food is extremely scarce in the water column during winter. However, the principal reason for this scarceness is not water temperature (which hardly changes between summer and winter in these areas) but lack of light during the winter season, with its impact on the total energy flow through the system. Temperature is involved indirectly in that it causes the formation of the pack ice and its snow cover, which in turn reduces light penetration even more, particularly in early spring and late autumn. There seems to be an additional temperature effect on the developmental period of eggs and larvae, which lasts particularly long in most polar invertebrates and fishes (e.g., see ARNTZ et al. 1994 and KOCK 1989, 1992). Latitudinal clines in egg number and size occur in Antarctic caridean shrimps (GORNY et al. 1992) and isopods (WÄGELE 1987, CLARKE and GORE 1992), but again the reason may not be the lower temperatures but increased food limitation towards the high Antarctic.

Colonization of virgin sediments

Colonization experiments with defaunated substrates, admittedly with rather small areas, at bathyal and abyssal depths have demonstrated fast and opportunistic arrival of some species but very slow reestablishment of the former community structure. Artificially and naturally increased organic matter content of these sediments increased the process of community development in its different phases (GRASSLE 1977, DESBRUYERES et al. 1980, 1985, LEVIN and SMITH 1984, GRASSLE and MORSE-PORTEOUS 1987, KAMINSKY et al. 1988, SNELGROVE et al. 1992). From Antarctic waters, very few colonization experiments have been published. GERDES (pers. comm.) recovered a settling plate array from 670 m after one year without any visible

colonization. DAYTON (1989) registered practically no settlement on colonization plates exposed in McMurdo Sound from 1974 to 1983, but heavy settlement of many groups in 1984. A similar observation, combined with fast growth of ascidians, was made by RAUSCHERT (1991) at King George Island. Both observations, which seem to be exceptions to the normal, slow community development (see also DAYTON and OLIVER 1977 for infaunal benthos), refer to the particularly heavy ENSO (El Nino Southern Oscillation) cycle 1982-84, which caused changes in Antarctic hydrographic conditions (DAYTON 1989).

Giantism and dwarfism

Large size and extended longevity are often reported as characteristics for cold environments, and these are supposed to be related to slow growth and late maturity. The question is whether they are related to low temperature. In fact, giants and dwarfs do exist side by side in the deep sea and in polar regions; however, we have to ask whether "metabolic size" correlates with morphological size. The general rules of allometry suggest that giants have the advantages of lower metabolic rates per mass unit and of being able to cover larger distances, but nonetheless need larger food quantities. Additionally, they could be expected to be able to survive longer periods of starvation. The active body or tissue mass is certainly rather small in giant isopods and pygnogonids. Holothurians and asteroids may attain large size, holothurians reaching up to 50 cm in length, but this is by no means the rule (GUTT 1991). Antarctic and deep-sea sponges may be large in their spicule structure, but the living tissue comprised only a small amount.

BROYER (1977) presented an analysis of giantism and dwarfism in the Antarctic and deep-sea benthos compared to other regions. Whereas the Antarctic benthos is inhabited by a comparatively high number of giants (11.7 %) and few dwarfs (1.0 %), the opposite is the case in the tropics (0.4 % and 22.4 %, respectively) and the deep sea (3.3 % and 15.2 %, respectively).

The above are observations on macro- and megafauna species levels compared to congeners from other regions. An overall ecological comparison requires considering communities through all size classes. This has rarely been done. Plankton and nekton research has been mainly restricted to meso- and macrozooplankton and nekton. According to ANGEL (1989), pelagic organisms increase in size with depth. We might relate the trend to increase in size to the decrease in temperature, but for the benthos the opposite seems to be true. For the deep-sea benthos the hypothesis was suggested that with increasing depth, and accordingly decreasing temperature, a shift to smaller organisms occurs (THIEL 1975, 1983). For pelagic organisms, larger size may

be advantageous in maintaining buoyancy and covering a larger ambit by swimming in search of food with a broad size spectrum. *Eurythenes gryllus* (Amphipoda) is a benthopelagic to pelagic species with a large biomass, measuring up to 12 cm in length. Fish probably have a maximum size at medium depths (HAEDRICH and MERRETT 1992), but benthic organisms may predominantly have a small average size. All these observations have a poor basis for comparison. Most deep-sea research has been restricted to bathyal and continental slope depths, whereas few data have been accumulated from abyssal depths and central oceanic areas. Benthos studies in the polar regions mainly concentrated on macro- and megafauna, and the size distribution throughout the benthos cannot be evaluated. However, assuming that these observations give correct size distributions, which differ for plankton, nekton, and benthos, temperature cannot be regarded as the main but only one of the steering parameters.

Perspectives

The selected observations presented in this paper are certainly far from a complete summary. However, the examples from life processes in polar and deep-sea regions reveal that there is a general retardation of life in these low-temperature environments. Nonetheless, on all different levels of organization fast processes do exist (although they are certainly not dominant).

These deviations from the generally expected lifestyles, along with certain fast processes under low temperature conditions, suggest that, although some kind of restriction mostly prevails in these cold environments, this limitation is not obligatory and can only partly be referred to temperature.

Therefore,

- temperature can be considered an ecological factor limiting the level of physiological performance, but

- temperature is obviously not the overall forcing parameter that structures assemblages and governs their dynamics.

If temperature does not play an exclusive role in shaping the communities and their dynamics in permanently cold environments we must seek other explanations. CHILDRESS (1995) presented a summary and arguments concerning the decline of metabolic rates with increasing depth. He argues against the exclusive importance of temperature, pressure, oxygen concentration, and food availability, but emphasizes the importance of light conditions and visibility as the prime reason for the decrease in locomotory activities and associated differences in protein content and enzyme capacities of deep-sea

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animals. This is an appealing hypothetical construction, but most of the data on which it is based originate from pelagic environments between the surface and the mesopelagic and may not be valid for life at greater depths or for benthic communities. Future research efforts must investigate the extent to which the various parameters, together with the related adaptational processes discussed above, have a share in structuring life in cold ocean environments.

Temperature certainly has a decisive influence on life, modulating the processes on molecular, cellular, individual, and population levels. The various morphological, physiological, and behaviorial adaptations must be investigated under the aspects of energy input to derive consistent explanations. For faunal communities, the effects of seasonal limitation of food availability have been stressed by various authors (e.g., CLARKE 1988). Coupling to and uncoupling from this parameter by different trophic groups in the Antarctic benthos has been discussed comprehensively by ARNTZ et al. (1994).

In this context, one adaptational trait needs further exploration: survival during extended diapauses or dormancies. Polar environments, to some extent also deep-sea regions, are governed by pronounced seasonal cycles of energy production and long periods of very limited energy availability. Adaptations of organisms to long-term suspended animation seem to be important and need consideration and investigation. Furthermore, a combination and interaction of ecological and physiological research efforts will be required for a causal understanding of the fundamental processes shaping marine life at low temperatures.

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