The Structure and Function of Arctic Benthic Communities: Are High-Latitude Ecosystems Different?

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ABSTARCT. The structure and function of marine ecosystems at high latitudes are thought to be different from low latitudes. Documenting such latitudinal gradients however is not easy; inferring their causes likewise remains elusive. The present review compares food webs from East Greenland down to the Caribbean. In this comparison, respiration and biomass are used to calculate mean residence time (= turnover rate) of functional components of the benthos. Tables of the mean size of individuals within functional groups of benthic communities suggest that each area can be characterized by a different "within-community" distribution of biomass. At high latitudes, the biomass is concentrated into larger forms for various reasons, some logical (e.g., Bergmann's Rule), some not. In uniformly cold environments characterized by a short growing season, heterotrophic bacteria can play a relatively minor role (the Pomeroy Principle), compared to low latitudes. An "accumulation" of biomass up the food chain would explain the importance of "fisheries" at high latitudes. It is proposed that enhanced Arctic warming could shift ecosystem function back toward that found at low latitudes, and thus may deleteriously affect available fish stocks. More CO_2 would be produced, and this feedback would enhance the gradual warming by the greenhouse gas effect.

Key Words: animal size, Arctic, benthos, climate change

Introduction

It has long been observed that large animals, such as whales, bears, etc., live principally at high latitudes. A rational and universally accepted hypothesis explaining this pattern is that the large size confers a smaller surface area to volume ratio, thus promoting heat conservation which would enhance survival in cold climates. Known as Bergmann's Rule (1847), this explanation applies only to warm blooded organisms that have to conserve heat efficiently. This idea has generated considerable study, some of which tends to refute the general pattern or its supposed causes (McNab 1971; Lindstedt and Boyce 1985; Geist 1987).

An increase in size of ectotherms (invertebrates and fishes) has also been observed to parallel a latitudinal gradient, however (Lindsay 1966; Golikov and Averincev 1974; Cushman *et al.* 1993; Atkinson 1994). Because conservation of heat is not at issue, the reasons for such a pattern must be sought elsewhere. There may be some adaptive significance of large size and long life. Rapid growth during a short summer season would provide stored resources for surviving a long winter. For example in the predatory chaetognath (arrow worm) *Sagitta elegans,* large size was thought to confer survival from lack of food (McLaren 1966). The increase in clutch size that accompanies body size might also enhance survival. The harpacticoid copepod *Scottolana canadensis* is also bigger in cold water (Lonsdale and Levinton 1985), as are many pelagic copepods (Huntley and Lopez 1992).

In some situations, the reverse can be true. For example, for European butterflies a decline in size with increasing latitude has been attributed to a decline in growth period. In such cases, it is

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assumed that size is directly proportional to development period and that this confers some advantage (Nylin and Svard 1991). Perhaps animals with complex life cycles that provide alternative mechanisms for "over-wintering" exhibit a different pattern from those with simple direct development.

Some explanations are based on animal reproductive physiology, usually relating animal size at maturity and time of reproduction. Temperature affects both growth (biomass, protein synthesis, cell size) and differentiation (cell number, DNA replication, cell division) in an often non-linear fashion (van der Have and de Jong 1996). For example the nematode Caenorhabditis elegans grows 33% longer at 10° than at 25°C. This species has an invariant number of eggs with each spawning, but both adult body size and egg size were larger at the low temperature (Van Voorhies 1996). Thus, the individual cells were larger too at low temperatures.

It has been well-documented that the biomass of deep-living macrofauna is higher at high latitudes (Rowe 1983), and a similar latitudinal gradient in biomass-depth profiles for the macro-zooplankton has been observed (Vinogradov 1968). The latter author suggested that cold and the pulsed nature of primary production causes lower utilization of particulate organics in the upper water column, and thus greater transfer of organic matter to depth. That is, the "biological pump" is more efficient at removing organics to depth than it is under warmer conditions (Rowe and Baldauf 1995).

The relative distribution of biomass among the components of benthic communities varies geographically too (Mills 1975). While it is often presumed that levels of primary productivity control marine ecosystem structure (see Walsh 1988), it has been noted that fisheries landings can be remarkably different on opposite sides of the same ocean, even though primary production is about the same (Mills 1979). Is this a function of geology and physics, or do Mills' observations apply to some more specific ecological phenomena? From the perspective of this paper, are ectotherms really larger under "polar" conditions, and if so, why?

In this review a comparison is made of the major living components of a limited suite of "example" continental margin ecosystems. The function and structure of the coastal benthos is considered because new information has become available for low as well as high latitudes. Comparisons of coastal ecosystems have been made before, but with somewhat different approaches. For example, Walsh (1988) compared a variety of "typical" continental shelf ecosystem food webs using carbon budgets, but he presented the fluxes of carbon between stocks, without giving the stock sizes. Each of his shelf ecosystems was characterized by a large particulate detrital pool, much of which he presumed was exported to depocenters on an adjacent continental slope (Walsh et al. 1981). His polar example, the SE Bering Sea, was remarkably different: a large fraction of the spring bloom organic matter was consumed by a rich, productive macrofauna not encountered on any of the other shelves, even though the rates of new primary production were the same or less than elsewhere. The rich benthos had in effect replaced the detrital pool. It was puzzling however that sediment community oxygen demand in the sandy sediments was quite modest (Rowe and Phoel 1992). Walsh's explanation was that the Bering Sea shelf was so wide that physical export of particulate detritus was not possible. On the other hand, if organics are generally recycled on continental shelves rather than exported, as others contend (Rowe et al. 1986; Kemp et al. 1994), why was the Bering Sea sediment community respiration rather low (Rowe and Phoel 1992) and macrofaunal invertebrate biomass so high (Alton 1974)? If this apparent contradiction were true, was it a function of the "polar" environment? Again, is the "polar" benthic community in fact different?

In the following account, emphasis is put on biomass distribution, rather than fluxes between the stocks. This is intended to complement the "Walsh models" and thus allow some inferences about the ratios of fluxes to stocks under different conditions of temperature and food supply. It is this comparison of food supplies, standing stocks and energetic losses to respiration that I hope will allow us to better understand the fundamental differences between

"polar" and low latitude marine ecosystems.

Methods

This review will focus on the biomass of functional groups associated with marine sediments. Most of the information is not new, but has been generated by others. Standard techniques have been used, with slight and hopefully minor differences between the data sets. Quantitative samples were taken with a spade core, box core or van Veen grab. The samples near Alaska (Bering and Chukchi Seas) were sieved with 1 mm mesh sieves, whereas those off the east coast of North and Central America were sieved with a 0.25 mm sieve for macrofauna. The samples taken off Peru were sieved with a 0.42 mm mesh. All the macrofaunal samples were sorted to major taxa in the laboratory using a dissecting microscope. The samples were weighed wet and this value was converted to organic carbon using standard conversion factors (Rowe 1983). The megafauna and demersal fishes were sampled with bottom trawls, for the most part.

To assess the meiofauna, replicate (3) subsamples were taken with a plastic core liner or with 50 cc plastic hypodermic syringes modified to operate like a small piston corer. These were sieved with a 63 mM sieve and then counted using a dissecting microscope. Their biomass was determined by using an ocular micrometer to determine volumes and then converting volume to biomass (Rowe *et al.* 1988). Bacteria samples were taken with 20 cc or 5 cc syringes also modified to operate like a small corer. These were fixed with 2% glutaraldehyde or formalin. The bacterial densities were determined from direct counts under an epifluorescent microscope after staining with DAPI (Cruz Kaegi 1992).

Sediment community respiration was determined using benthic chambers described in Rowe *et al.* (1994). At depths greater than approx. 35 m, these were implanted with an autonomous lander or a submersible. Exceptions were the Mosquitia shelf (total community respiration was estimated from organism biomass, size and temperature by M. E.

Cruz Kaegi); the hypoxic area off the Mississippi River (remineralization was estimated by carbon dioxide fluxes into benthic chambers and S-35 labelled sulfate reduction incubations aboard ship (Morse and Rowe in press), rather than oxygen demand); and the anoxic sediments off Peru (remineralization was determined from labeled-sulfate reduction experiments aboard ship (Rowe and Howarth 1985)).

Data on most of the sediment communities came from published accounts of previous studies, all of which provide extensive descriptions of small variations in the basic methods described above. Some lumping and averaging has been done to make the categories as comparable as possible, and apologies are due the original authors for any mistakes that have resulted from these averagings and simplifications.

Results

Fourteen different areas are considered (Table 1); they range in latitude from 15° S to 80° N. Primary production at each site was taken from published accounts. These sites were chosen to provide a relatively wide range in primary production, bottom water temperature, latitude, sediment grain size and oxygen content of the bottom water. The 14 sites were confined to continental shelves to limit the effects of water depth. Estuaries and the intertidal were not included because of the effects of reduced salinities, terrestrial organics and ice scour.

Primary production, given in terms of g C m^{-2} y^{-1}, varied greatly (27 to 1,825 g C m^{-2} y^{-1}) across a large range of latitude (15° S. to 80° N. Lat.). Temperature ranged from -1.5° to 29°C. Oxygen concentration has a profound effect on the benthos, and two low oxygen examples were included to illustrate these effects on the relative distribution of biomass and metabolic fluxes: the Peru upwelling and the Mississippi River plume. These two examples were also characterized by the high rates of primary production. The top 7 sites in Table 1 are characterized by relatively constant, high temperatures through-

Table 1. Environmental variables in the sites compared along a latitudinal gradient (Primary production units: g C m^{-2})

Site	Temp.	Depth	Sediment	Prim. Prod.	Oxygen	Latitude
Mosquitia Coast (Hond.)[1]	26	50	Silty Sand (CaCO$_3$)	40	oxic	15
Upwelling (Peru, anoxic)[2]	14	300	Silty Clay	1,825	anoxic	15
Bay of Campeche (Mex.)[3]	22	75	Silty Sand (CaCO$_3$)	44.8	oxic	18
NW Africa (Mauritania)[2]	18	35	Fine Sand	730	oxic	22
Texas Shelf[1]	29	30	Silty Clay	185	oxic	30
Miss. R. Shelf(hypoxic)[1]	27	20	Silty Clay	1,080	hypoxic	30
NE USA Shelf[4]	10	70	Silty Clay	340	oxic	40
Conception Bay (Nfld.)[1,5]	-0.5	275	Silty Clay	151	oxic	47
SE Bering Sea[6]	1.0	50	Sandy Silt, no clay	156	oxic	57
St. Lawrence I. Polynya[6]	0.8	39	Silty Sand	100	oxic	64
Chukchi Sea[6]	-1.5	40	Fine Sand	324	oxic	66
NE Greenland Polynya[7]	-0.5	300	Silty Clay with Pebbles	29	oxic	78
Barents Sea (Shallow)[8]	0.29	114	Silty Sand	60	oxic	80
Barents Sea (Deep)[8]	1.11	382	Sandy Silt and Clay	80	oxic	80

1, M.L. Cruz Kaegi (unpubl. data); 2, Rowe (1985), Rowe &Howarth (1985); 3, Soto & Escobar (1995); 4, Rowe et al. (1988, 1991); 5, Pomeroy et al. (1991), M. Cruz Kaegi (unpubl. data); 6, Feder & Jewett (1988), Alton (1974), Bakkula (1981), Bakkula & Low (1983), Grebmeier & McRoy (1989), Grebmeier & Cooper (1995), Haflinger (1981), Highsmith & Coyle (1992), Jewett & Feder (1981), Stoker (1981); 7, Rowe et al. (1997); 8, Piepenburg et al. (1995); 9, Input to sea floor, not primary production

Table 2. Biomass (mg C m^{-2}) at the 14 study sites compared along a latitudinal gradient. Sediment oxygen consumption (SOC) units: mg C m^{-2} d^{-1}

Site	SOC*	Macrof.	Megaf.	Fish	Bacti.	Meiof.	Total
Mosquitia Coast (Hond.)[1]*	71	368	8		382	551	1,309
Upwelling (Peru, anoxic)[2]	120	8	0	0	90,000	17.1	90,025
Bay of Campeche (Mex.)[3]	109	307	33	3.3	269	151	763
NW Africa (Mauritania)[2]	211	1,561	189		8,000		9,750
Texas Shelf[1]	294	721	40	4	2,992	147	3,904
Miss. R. Shelf(hypoxic)[1]	584	421	0.0	0.0	7,695	128	8,244
NE USA Shelf[4]	109	11,700	9.8	250	5,930	178	18,068
Conception Bay (Nfld.)[1,5]	88	2,586	15		5,227	1,230	9,058
SE Bering Sea[6]	56	2,475	218	658			3,351
St. Lawrence I. Polynya[6]	204	20,000	135				20,135
Chukchi Sea[6]	255	35,000	209				35,209
NE Greenland Polynya[7]	35	955	100		440	70	1,575
Barents Sea (Shallow)[8]*	21.8	3,744	873	5.1		35.4	4,658
Barents Sea (Deep)[8]	33.3	5,198	909	25.9		21.8	6,155

1, M.L. Cruz Kaegi (unpubl. data); 2, Rowe (1985), Rowe & Howarth (1985); 3, Soto & Escobar (1995); 4, Rowe et al. (1988, 1991); 5, Pomeroy et al. (1991), M. Cruz Kaegi (unpubl. data); 6, Feder & Jewett (1988), Alton (1974), Bakkula (1981), Bakkula & Low (1983), Grebmeier & McRoy (1989), Grebmeier & Cooper (1995), Haflinger (1981), Highsmith & Coyle (1992), Jewett & Feder (1981), Stoker (1981); 7, Rowe et al. (1997); 8, Piepenburg et al. (1995)

*All total SOC values determined from bottom incubation chambers, with the exception of the Mosquitia Shelf (*) and the shallow Barents Sea (*), which were determined from organism biomass and temperature

Table 3. Mean size of individuals of macrofauna at the sites in this study where abundance data were available. Sieve size was 0.25 mm in all cases except the Bering Sea, where a 1 mm sieve was used

Mosquitia Shelf	0.22 mg C ind.[-1]
Texas Shelf	0.24 mg C ind.[-1]
Miss. River Plume	0.12 mg C ind.[-1]
Conception Bay, Ffld.	1.34 mg C ind.[-1]
Bering Sea	2.49 mg C ind.[-1]
Northeast Greenland Polynya	0.23 mg C ind.[-1]

out the year (+10° to 29°C), whereas the bottom 7 sites are characterized by cold temperatures (-1.5° to +1.1°C) accompanied by ice cover for some fraction of the year, even though the latter latitudes vary quite appreciably (47° to 80° Lat.).

The size categories of the functional groups of sediment-associated organisms have also been tabulated in order of increasing latitude (Table 2). The highest total biomass was contained in the chemoautotrophic bacteria mats (*Thioploca* spp.) in "near anoxic" conditions at low latitudes (Rowe 1985). Under these conditions, the bacteria dominated the sediments; the metazoans were effectively eliminated by low-oxygen stress. A high biomass of bacteria was encountered in the hypoxic location near the Mississippi River outflow (Cruz Kaegi 1992). It should be noted that in both cases with low oxygen conditions, the metazoans were severely reduced. This is contrasted by the high biomass of macrofauna at intermediate latitudes and relatively high primary production (Chukchi Sea, Table 2).

Lowest total sediment community biomass was encountered in the areas of low mean rates of primary production, the Northeast Greenland polynya (NEWP), the Mosquitia shelf and the SW Gulf of Mexico. At these sites, all categories contained rather modest biomass. However, the "cold" sites were to some extent higher in biomass and individual animal size (Table 3) than areas with "warm" bottom water, such as the SW Gulf of Mexico and the Mosquitia shelf. The Texas and the Mississippi River plume shelves were characterized by substantial biomass and high temperatures, but the biomass was to a large degree bacteria, rather than meta-
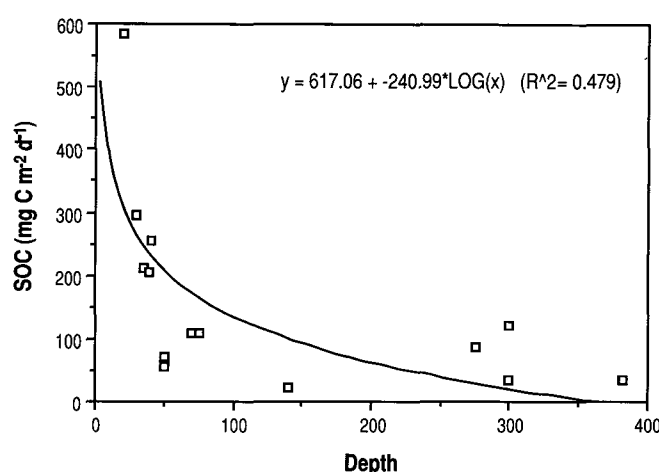

Fig. 1. Sediment oxygen demand, expressed as carbon remineralization (mg C m^{-2} day^{-1}) as a function of depth. Station data in Tables 1 and 2. Carbon fluxes based on oxygen demand calculated using an RQ of 0.85.
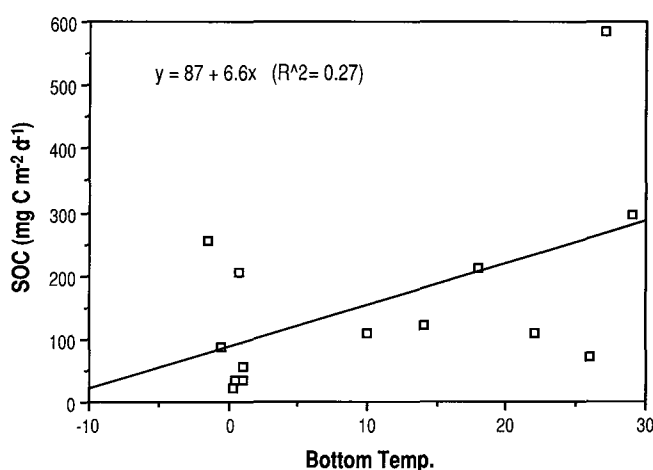

Fig. 2. Sediment oxygen demand (mg C m^{-2} day^{-1}) as a function of temperature. Station data in Tables1 and 2. Carbon fluxes based on oxygen demand calculated using an RQ of 0.85.

zoans. The Gulf of Mexico hypoxic area (Miss. R.) was characterized by another group of chemoautotrophic bacteria (*Beggiatoa* spp.) (Cruz Kaegi 1992), but with much less biomass than that off Peru.

Meiofauna was universally low compared to the other categories. The same can be said for the megafauna and the bottom living fishes: they had low values compared to the bacteria and the macrofauna in most regions. Sampling for these groups was inconsistent however between the sites being compared.

Sediment oxygen consumption (SOC) was a function of depth, even though the depths were limited more or less to the continental shelf (Fig. 1). SOC was only marginally dependent on temperature (Fig. 2),
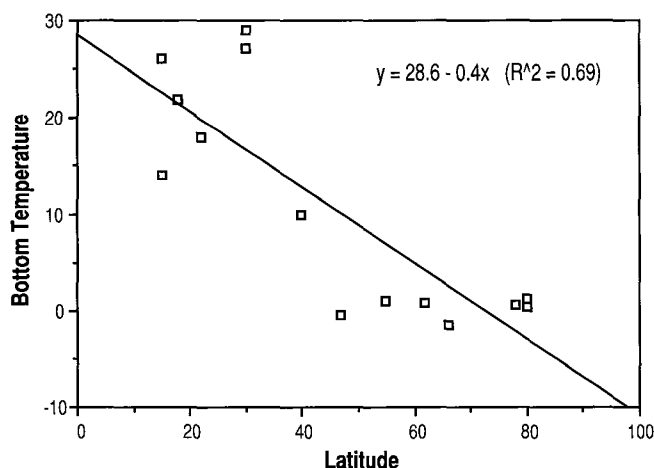
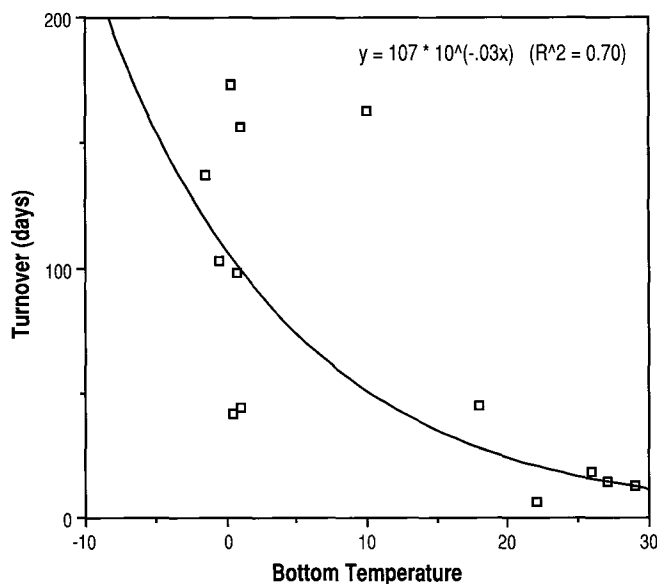Fig. 3. Bottom temperature as a function of latitude, based on the information in Tables 1 and 2.

Fig. 4. Sediment community biomass turnover time (t=days) as a function of bottom water temperature. Turnover time calculated by dividing the total biomass in the sediment (macrofauna, meiofauna and bacteria, from Table 2) by the sediment oxygen consumption (Table 2). The anoxic site off Peru dominated by sulfide oxidizing Thioploca sp. bacteria is not included (t=750 days).

even though temperature was apparently related to latitude (Fig. 3).

Sediment community "turnover time" can be calculated by dividing the standing stock by the community respiration rate (Rowe et al. 1991). Turnover time appears to be directly related to latitude (Fig. 4), if the one site subjected to anoxia, the Peru upwelling, is left out of the regression. Thus, carbon turns over rapidly in warm semi-tropical environments because the respiration rates are high and the biomass is low, but organic matter is cycled slowly at high latitudes because the 'per unit mass' respiration rates are low. If a calculated turnover time for the anoxic condition is realistic (t=750 days), this is probably somehow related to the chemoautotrophic process.

Discussion

Low total biomass was encountered where the temperatures were high. Likewise, biomass of the bacteria tended to be low when input of organic matter was low, but high where sediment organics could be focused or accumulating due to regional geology or currents, such as the fjord-like Conception Bay, regardless of temperature. The regional gradients of both respiration and biomass off Alaska are thought to be a function of currents (Gregmeier and Cooper 1995). Bacterial abundances would be expected to be

high in the fine grained sediments of the offshore depositional areas of the Chukchi Sea. However, bacteria and meiofauna have not yet been counted in the Bering and Chukchi Sea sediments.

The abundance and size of the bacteria and the meiofauna may be influenced by grain size. Most of the sediments at the sites reviewed contained silt and clay sized particles, with the exception of the St. Lawrence Island polynya, SE Bering, SE Chukchi and the Barents Sea, which all contained fairly substantial sand fractions (Feder and Jewett 1988; Grebmeier and Cooper 1995; Piepenburg et al. 1995). Again, it is unfortunate for this comparison that bacteria were not counted in any of these sediments.

The longest turnover times were located in the coldest environments (with the exception of the chemoautotrophic bacteria in the Peru upwelling, t=750 days). This is because the biomasses were high and respiration rates were low. High or rapid rates of turnover occurred at sites with high temperatures accompanied by high community oxygen demand and relatively low biomass.

The work of Stoker (1981) dealt specifically with the size of organisms in Bering/Chukchi Seas. He

sieved samples with a 3 mm mesh and a 1 mm mesh. He caught three times as many individuals on the small sieve (3471±792 ind. m^{-2}) compared to the larger one (1134±313 ind. m^{-2}). However, most of the biomass was taken on the large sieve (10,700 mg C m^{-2} versus 820 mg C m^{-2}). Thus, most of the macrofauna biomass was tied up in animals with a mean weight of 9.4 mg C ind.$^{-1}$. Horikoshi (1981) found an increase in mean size of benthos on entering the western Bering Sea.

A comparison of individual mean size (Table 3) suggests that mean sizes on temperate continental shelves are about the same, e.g., on the order of 0.2 mg C ind.$^{-1}$. At Conception Bay, which also had low temperatures and high overall biomass, the average macrofaunal individual had a mean value of 1.3 mg C ind.$^{-1}$. At higher latitudes individual size seems to increase, unless the levels of primary production are limitingly low, as in the Northeast Greenland polynya, which had individual sizes of 0.23 mg C ind.$^{-1}$ (calculated from Rowe et al. 1997). Variations between sites may be a function of sieve size, and until that is standardized, gradients such as that in Table 3 remain suspect.

The literature is replete with references to the high biomass that occurs at high latitudes, both in terms of the size of individuals (Table 3) and the integrated biomass of the total community (Table 2). The limited data presented here comparing low and high latitude sediment-associated communities appear to confirm this comparison. The question is why energy is partitioned differently under these contrasting situations (Levinton and Monahan 1983; Levinton 1983).

The large size at cold temperatures has been accounted for on several levels. A biophysical explanation documents that cells are larger during development, the result being bigger adults. But it remains to be seen whether this contributes to survival. Quite to the contrary, warm-blooded taxa at low latitudes have developed a vast array of physiological and morphological strategies to get rid of excess heat generated by metabolic reactions (Schmidt Nielsen 1984). Perhaps large-bodied endotherms live at high latitudes in order to get rid of heat, rather than conserve it.

Is enhanced survival value accrued to larger sizes because additional biomass provides energy reserves necessary to survive overwintering? If so, then large size among the ectotherms at high latitudes results from natural selection. If and when endotherms and ectotherms have been observed to lose weight during the overwintering period, it might be concluded that they had to have their original large size to survive. Although time-dependent simulations predict biomass declines during overwintering under the ice (Rowe et al. 1997), it remains to be demonstrated with data and energy budget calculations that the bigger organisms do in fact use stored reserves to survive the winter.

In the discussion of why high latitudes are different from lower latitudes (Dunbar 1968; Petersen and Curtis 1980; Ambrose and Renaud 1995), it is generally proposed that polar ecosystems allow organic particulates from the upper water column to sink or otherwise be transported to the deep zooplankton (Vinogradov 1970) and benthos (Dayton and Oliver 1977; Rowe 1983; Walsh and McRoy 1986). One result is higher benthic biomass (Grebmeier and McRoy 1989), but this does not explain why the individuals are larger in size, if indeed they are.

A related issue is the role of the bacteria in the ecosystem. Pomeroy and Deibel (1986) have suggested that low temperatures inhibit microbial activity more than should be expected due to the Arrhenius or Q_{10} effect. This was supported by the measurements by Jody Deming (in Rowe et al. 1997) in the Northeast Greenland polynya (Table 1). The sediment bacteria had relatively low biomass, and low rates of substrate incorporation. An exception appears to be the cold sediments of Conception Bay, Nfld., where bacteria dominated the biomass due both to large cell size and numbers (Table 2, Cruz Kaegi, unpublished data). Although bacteria were not included in the studies off Alaska, the sediments are relatively coarse compared to those in Conception Bay. Rowe et al. (1988) found substantially more bacteria in fine-grained sediments compared to sand-sized material off New England. Likewise, the coarse grained studies of our low lati-

tude (Mosquitia shelf, SW Gulf of Mexico) sites generally had low bacterial fractions. Thus, the bacteria may play a minor role in the Chukchi and Bering Sea sediments, but this remains to be demonstrated. The role of polar bacteria under conditions of high and low organic supplies, and in different sediment types, remains an important issue for future work.

This brings us back to the question of organism size and why high latitude ectotherms tend to be larger than those at low latitude. Are there reasons beyond the purely differential biophysical responses of differentiation and growth that are related to survival (Dunbar 1968; Piepenburg et al. 1995)? The creation of size spectra of individuals of dominant species might give greater insight into how and why individual species grow and differentiate under polar conditions. Little is known about top down or bottom up control of size distributions. Predators would tend to prey on larger sizes, and perhaps some polar ecosystems lack predation pressure on the larger sizes.

Bergmann (1847) suggested that endotherms increase volume to surface area at the poles to conserve heat. Perhaps a somewhat opposite phenomenon has occurred with the ectotherms. Perhaps small size and the resultant increase in the surface to volume ratio ameliorates the exchange of metabolic substrates and by-products required by higher temperatures. Some groups appear to have invaded lower latitudes from the poles (Menzies et al. 1973), and such a trend would have resulted in higher rates of metabolism in warm shallow water. Small size would be an advantage therefore at low latitudes.

One might also question what might happen to size distributions with global climate warming. If "warm" ecosystems are dominated by "respiration" over production, at what temperature would the biota "switch" from the production system with high biomass and efficient food chain transfers to the respiring system in which considerably more carbon is lost to respiration? If this switching point is very sensitive, then extensive loss of biomass might accompany even very slight global warming at the poles. If such a shift occurs, then organic matter

now ending up in the fisheries could be shunted into carbon dioxide. Global warming would then feed on global warming with a deleterious positive feedback (Rowe and Baldauf 1995).

How is energy, carbon, etc., transferred to really big, terminal components of polar food chains, that is, to those levels that first attracted the attention of Bergmann and which, for generations, have supported prodigious polar fisheries? The western Bering and Chukchi Sea sediments are characterized by large individuals, many of which are suspension feeders that filter phytoplankton directly from the water column (Grebmeier and McRoy 1989). Among these are the tubicolous amphipods *Ampelisca macrocephala*, which is fed upon by grey whales (Highsmith and Coyle 1991; 1992; Coyle and Highsmith 1994). In addition, many of the nearshore molluscs are fed on by birds (Divoky and Springer 1988). The SE Bering is characterized by large molluscs, sea stars and crabs (Jewett and Feder 1981). Detailed qualitative linkages between the benthos and terminal predators is available (Haflinger 1981; Feder and Jewett 1981). The creation of well-constrained budgets should be possible because the areal densities and the growth rates of the major prey such as bivalve molluscs appear to be well established (Weymouth and McMillan 1931; McDonald, Feder and Hoberg 1981). Quantitative information is also available on consumers such as groundfishes (Bakkala 1981; Bakkala and Low 1983; Raymond 1988) and mammals (Frost and Lowry 1988). A major difficulty is connecting the quantitative linkages between the lower levels of polar food chains (Schell et al. 1988; Hameedi 1988) with terminal end-members (Walsh 1988; Welch et al. 1992). Until this can be accomplished with some degree of confidence, we will not understand how or why polar ecosystems differ from those at lower latitudes.

Conclusions

The relative distribution of biomass among size groups of heterotrophic benthos is demonstrably

different at high latitudes in the Arctic than at low latitudes, with much greater development of biomass in the 'megafauna' or large infauna species (> 1 cm diameter and > approx. 0.5 g wet weight). The high temperatures of the tropics favor the development of smaller forms, in particular the heterotrophic bacteria. Whether or not this pattern obtains in the Antarctic remains to be demonstrated (Dayton and Oliver 1977).

It appears that a combination of low (approx. -1 to +2°C), fairly constant temperatures favors the development of high biomass. High temperatures favor respiration over production, thus preventing the development of biomass. At high temperatures, or under conditions of stress such as low oxygen, a substantial fraction of available organic matter is shunted through heterotrophic bacteria. A relatively small portion of the microbial production is available to higher trophic levels, however. The most prevalent theoretical explanation for the development of high biomass in benthic invertebrates at high latitudes is a general elevation in the "growth to respiration" ratio, an endogenous feature of each species in question.

Acknowledgements

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