

Differences in energy flow through major components of subarctic, temperate and tropical marine shelf ecosystems

G. Høpner Petersen

Zoological Museum, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

Mark A. Curtis

Institute of Parasitology, MacDonald Campus of McGill University,
MacDonald College P.O., Quebec HOA 1CO, Canada

Abstract

Biological production is estimated here for some major components of marine shelf ecosystems from subarctic, temperate and tropical areas (Disko Bugt, the North Sea, and Phangnga Bay, Thailand). Included are values for the production of phytoplankton and herbivorous zooplankton, the production of benthic deposit feeders and filter feeders at the compensation depth, and the yield to man of pelagic and demersal fish.

Primary planktonic production increases from the subarctic to the tropics, but the transfer of this energy to higher trophic levels appears most efficient in the high latitude ecosystem. Although the zooplankton comprises a dominant link within the tropical food web, energy flow in the subarctic may be more equally partitioned between the benthos and the zooplankton. Consequently, pelagic organisms form the basis for a fishery in the tropical study area while demersal forms are of greater importance in the subarctic. The existence of such fundamental differences in the structure of marine ecosystems implies that management models developed for temperate waters may sometimes require substantial modification to serve a useful purpose in subarctic or tropical seas.

Introduction

In attempting to compare marine ecosystems from different areas of the world, it may be informative to examine how energy flow is channelled from the phytoplankton through pelagic and benthic components of the food web and since the relative importance of links between specific trophic levels varies considerably from place to place in the seas, it would seem appropriate to look for any general trends that may exist. To this end, the present paper reviews and synthesizes some existing information which relates to marine production for major ecosystem components of a subarctic, a temperate and a tropical region (Disko Bugt, the North Sea, and Phangnga Bay, Thailand).

Quantitative relationships between the abundance of marine fish and the availability of their food sources have been studied in the North Sea area since at least the classic work of C.G.J. Petersen on the food web of the Kattegat (Petersen, 1915, 1918, summarized in Thorsen, 1971). A more complete model and eco-

system structure for the North Sea has recently been developed by Steele (1974). Common to all such work is the difficulty in gathering adequate numerical data on primary producers, herbivores and carnivores, but despite this, contemporary estimates of food requirements versus food availability for important fish species appear to coincide fairly well (Jones, 1978).

We have recently completed studies on the life cycles and population characteristics of marine benthic bivalves and polychaetes from the Disko Bugt area of West Greenland (Curtis, 1977; Petersen, 1977a, 1978). This work, based upon seasonal samples, has led to estimates of infaunal benthic biomass and production. Here our results are placed within a generalized energy flow diagram and compared with similarly constructed models for temperate and tropical shelf areas.

Methods

In addition to our own data and that within the published literature, we have gathered relevant information through correspondence with a number of different institutions and investigators. As a guide in this research, an idealized scheme of a marine ecosystem has been used (Figure 1). This particular portrayal of energy transfer routes indicates where our limited data on production at certain ecosystem levels would fit into a more complete model and, conversely, it shows the position of some important food web components which have been omitted from the present study. Thus, for each of the three ecosystems considered here we have attempted to estimate the following; incident solar energy, phytoplankton production, production of herbivorous zooplankton, production of benthic deposit feeders and filter feeders, and the yield to man of pelagic and demersal fish. Due to lack of information, no reliable estimates could be arrived at for the production of benthic flora or of invertebrate predators in the plankton and benthos and for the same reason microbial decomposers could not be included in our models. In order to obtain comparative results, our efforts were confined to areas having a shallow continental shelf exposed to the open sea, with a sediment bottom within or just below the compensation depth.

Quantitative data on biomass and production are standardized here by applying the following approximations: 1 g wet weight of organic tissue = 0.25 g dry weight = 1 kcal; 1 g C in organic matter = 10 kcal (Steele, 1974). Information supplied by Brawn *et al.* (1968) and Atkinson and Wacasey (1976) indicates that 1 kcal · g⁻¹ is a reasonable estimate for the wet weight energy content of benthic polychaetes and bivalves (range of group means = 0.7-1.3 kcal · g⁻¹). To compensate for weight losses of dissolved organic matter and fluid, values for formaldehyde-preserved benthos and plankton are multiplied here by a factor of 1.2 to approximate fresh wet weight (Ellis, 1960). Production is expressed as kcal · m⁻² · yr⁻¹.

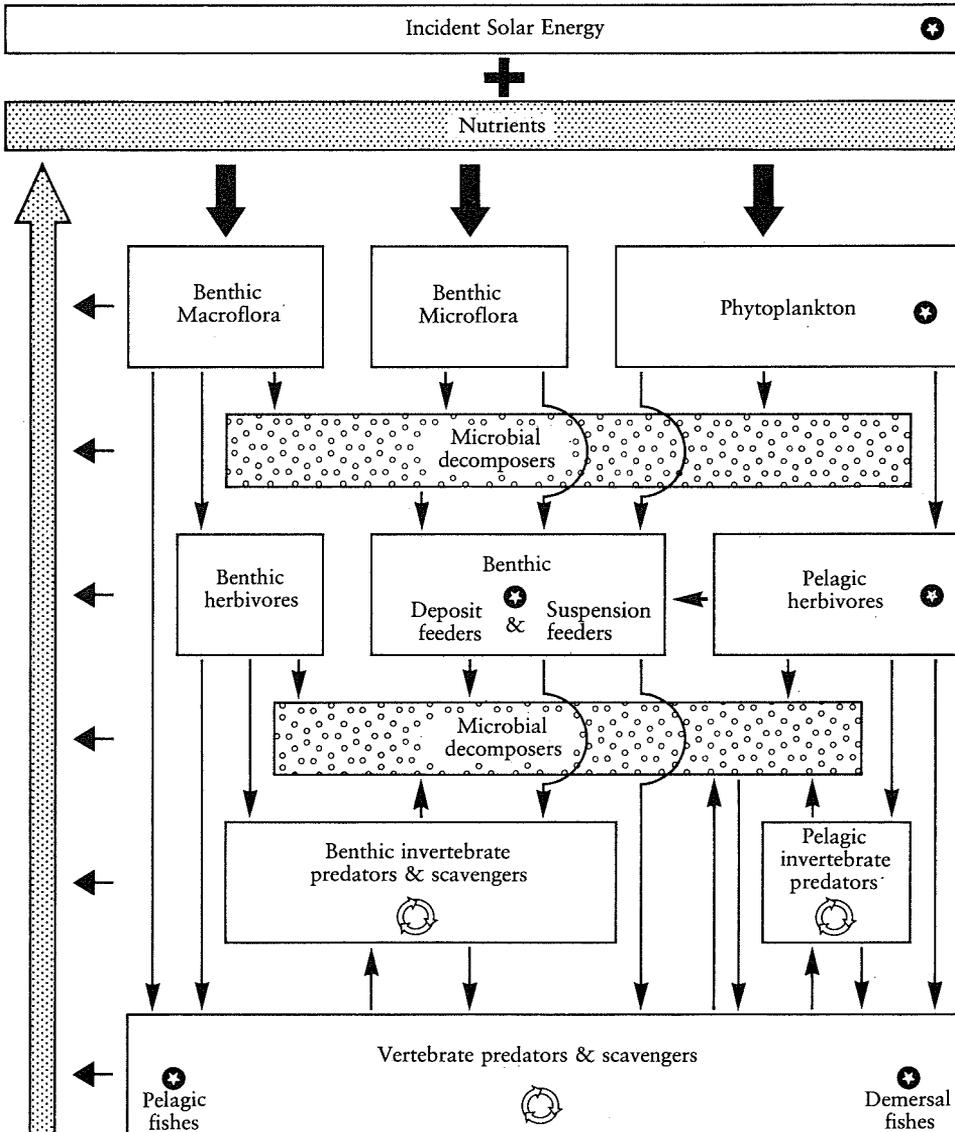
→
 Fig. 1. A simplified model of major components in a marine ecosystem. Three thick arrows signify the input of organic energy, while horizontal arrows depict the release of nutrients. A circle of arrows represents recycling within a component through predation and/or cannibalism. Remaining arrows indicate the primary transfer pathways. Ecosystem components for which we have obtained production estimates are marked with an asterisk.

Results

Disko Bugt, West Greenland

Solar insolation has been recorded at Godhavn during a significant part of the year and is estimated to be $5 \cdot 10^5 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Milan Petersen, Botanical Institute, University of Copenhagen, pers. comm.).

Phytoplankton production measured by the ^{14}C technique was estimated to be $36 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Petersen, 1964) but due to a change in standards (Steemann



Nielsen, 1965) this result must be multiplied by 1.45, yielding a corrected value of $522 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for primary production in the Disko Bugt area. O. Norden Andersen, Zoological Museum, University of Copenhagen (pers. comm.) obtained values ranging from $60\text{-}90 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for the years 1973-75. Phytoplankton production is therefore estimated to lie between 500 and $900 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

Mean annual zooplankton biomass has never been measured in the Disko region proper. However, for the Davis Strait area off West Greenland Zverea (1972) presents data indicating that the dry weight standing crop of zooplankton may be about $100 \text{ mg} \cdot \text{m}^{-3}$. By summing this over the upper 50 m, a value of $5 \text{ g} \cdot \text{m}^{-2}$ dry weight biomass is obtained. McLaren (1969) estimated that the production to biomass value for arctic marine zooplankton at 'Ogac Lake', adjacent to Frobisher Bay, equals about 3.0. Using these figures we arrive at a value of $60 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ as a rough approximation for herbivorous zooplankton production in the Disko Bugt area.

Estimates of benthic production can be based on recent studies of bivalves and polychaetes (Curtis, 1977 and Petersen, 1978). According to Ellis (1960), bivalves and polychaetes comprise about 90 % of the macrobenthic biomass in the area and this is confirmed by our unpublished results. Data on average biomass and annual production (including gonad output) are given in Table 1, where the bivalve and polychaete species have been grouped according to feeding mode. The value for the suspension feeding bivalves (*Mytilus edulis*, *Serripes groenlandicus*, *Cardium ciliatum*, *Macoma calcarea*, *Hiatella byssifera* and *Mya truncata*) were calculated for each species from information on recruitment, growth, mortality and gonad development. Biomass and production for the deposit feeding bivalves (Nuculacea and Thyasiracea) were calculated by multiplying their densities ($\text{number} \cdot \text{m}^{-2}$) by mean weight and applying a P/B ratio of 0.1, a reasonable figure compared with the P/B range for other small Disko bivalves. The values for polychaete production are based on population studies of *Terebellides stroemii*, a deposit feeding species of average size having a P/B ratio of 1.9. Gonad production for polychaetes is estimated as 0.1 times mean biomass. Deposit feeding polychaetes dominate suspension feeders (primarily Sabellidae) in the area. The data for predatory polychaetes (Polynoidae, Sigalionidae, Phyllodocidae, Nepthyidae, Lumbrineridae) are listed separately in Table 1.

Of the four localities studied two (Fangsthytten and Tut) lie within Disko Fjord and exhibit the low levels of benthic biomass typical of such habitats, far less productive than areas exposed to the open sea (Thorson, 1971). One of the remaining sites (Godhavn Havn) is situated in shallow water (3-13 m) but the other (Lyngmarksbugt) is at intermediate depth and can be considered representative of a subarctic benthic community near the compensation depth. Production at Lyngmarksbugt is calculated to be $64 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for bivalves and polychaetes and is estimated at about $70 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for the total macrobenthos.

Detailed statistics on fish yield are not available for the Disko region, however, a total allowable catch of approximately $2\text{-}8 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ is specified in fishery negotiations for trawling in 200-500 m for deep water shrimp (*Pandalus borealis*) and Greenland halibut (*Reinhardtius hippoglossoides*) (Dr. P. Kannevorf, Green-

Table 1. Total biomass and annual production in $\text{kcal} \cdot \text{m}^{-2}$ for polychaetes and bivalves in the Disko area, illustrating the position of the study localities relative to depth and exposure.

Character of locality	Sheltered		Exposed		
Shallow	<i>Fangsthytten 3-18 m</i>		<i>Godhavn Havn 3-13 m</i>		
		Biomass	Production	Biomass	Production
	Suspension-feeding bivalves	36.0	15.2	313.0	64.2
	Suspension-feeding polychaetes	0.0	0.0	0.2	0.4
	Deposit-feeding bivalves	3.1	0.3	0.2	—
	Deposit-feeding polychaetes	0.8	1.6	97.1	194.2
Total	39.9	17.1	410.5	258.8	
Predatory polychaetes	2.8	5.6	15.3	30.6	
Deep	<i>Tut 80-107 m</i>		<i>Lyngmarksbugt 26-47 m</i>		
		Biomass	Production	Biomass	Production
	Suspension-feeding bivalves	0.6	0.1	40.0	8.6
	Suspension-feeding polychaetes	0.0	0.0	0.1	0.2
	Deposit-feeding bivalves	33.3	3.3	1.1	0.1
	Deposit-feeding polychaetes	6.6	13.2	27.7	55.4
Total	40.5	16.6	68.9	64.3	
Predatory polychaetes	2.1	4.2	3.8	7.6	

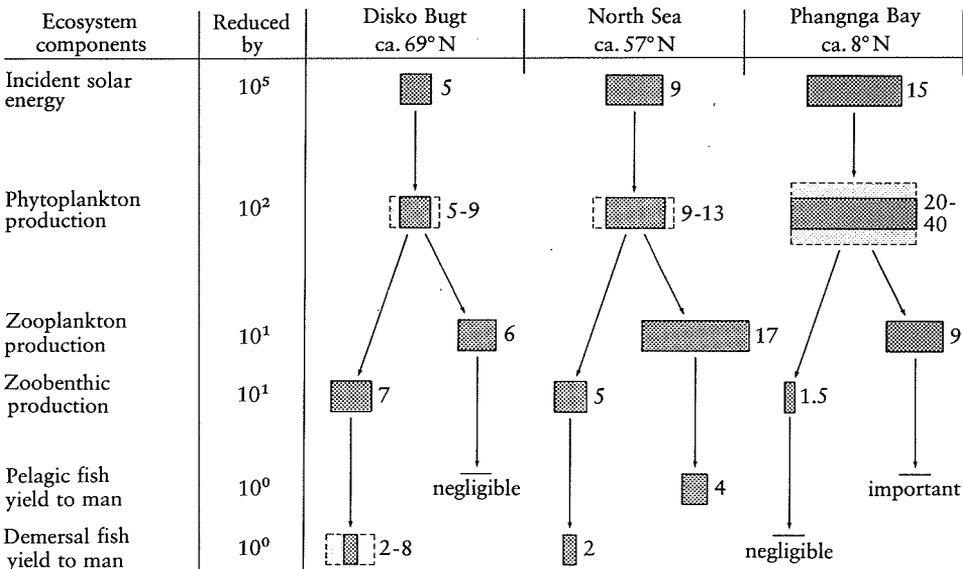


Fig. 2. Incident solar energy, phytoplankton production, secondary planktonic and benthic production, and fish yield to man for food webs from Disko Bugt, the North Sea and Phangnga Bay. All values expressed as $\text{kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. In fishery statistics 'demersal' means 'caught near to the bottom'; in biology it means 'feeding at or in the bottom'.

land Fishery Investigations, pers. comm.). The sustainable yield of demersal fish of the shallow shelf would probably exceed that value. This fishery consists of a commercial long line operation in 20-100 m (Disko Bank) for wolffish (*Anarrhicas lupis*), cod (*Gadus morhua*), and halibut (*Hippoglossus hippoglossus*), and a near-shore fishery by jig and longline for the local consumption of uvaq (*Gadus ogac*), sculpin (*Acanthocottus scorpius*), cod (*Gadus morhua*), and long rough dab (*Hippoglossoides platessoides*). The pelagic fish catch is mainly dependent on capelin (*Mallotus villosus*), on arctic char (*Salvelinus alpinus*) and on salmon (*Salmo salar*) and the yield of the pelagic fishery is presently very small in comparison to that of the demersal fishery.

On the basis of the above comments and calculations, a quantitative energy flow diagram for selected levels of the Disko Bugt food web is presented in Figure 2.

The North Sea

Incident solar energy for the central North Sea is taken to be the same as that measured at Copenhagen. This amounts to $9 \cdot 10^5 \cdot \text{kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Kr. Holst, the Royal Danish Veterinary School, pers. comm.).

The remaining values for an analysis of ecosystem components in the North Sea are derived from the model presented by Steele (1974), which we have simplified somewhat in Figure 2. His estimate of benthic production is supported by more recent data on biomass in the central North Sea (Petersen, 1977b).

Phangnga Bay, West Thailand

This tropical area has been selected because one of us (G.H.P.) has surveyed the benthos off Phuket Island (8°0'N, 98°10'E) using the same methods as in Greenland and because some information on other trophic levels was available. Such data are difficult to obtain from other tropical localities.

A value of $15 \cdot 10^5 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for incident solar energy at Cochin (Qasim, 1973) may be taken to be roughly equivalent to that for the west coast of Thailand. Cochin is situated on the west coast of India at approximately the same latitude as Phuket.

Phytoplankton production off Thailand's west coast is estimated by Cushing (1973, p. 477) to be about $200 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. S. Wium Andersen, University of Copenhagen (pers. comm.) has determined the level of primary production off Phuket Island to be $300\text{-}400 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The range of phytoplankton production is therefore taken to be $2000\text{-}4000 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

Zooplankton production in the upper 200 m off Thailand's west coast is estimated at about $12 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Cushing 1973) on the basis of mean biomass and a P/B ratio of 8. For our locality, with the bottom averaging 30-50 m, zooplankton production may be in the order of $9 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ($90 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$).

Benthic production has not yet been studied in the area, but some results on biomass are at hand in a preliminary report on 420 grab samples taken off Thailand's west coast (Seidenfaden *et al.*, 1968 p. 254-260). Fully 80% of the grab hauls yielded wet weight biomass values of between 0 and $10 \text{ g} \cdot \text{m}^{-2}$ and only 3% exceeded $50 \text{ g} \cdot \text{m}^{-2}$. Polychaetes comprised 73% of the specimens while shrimp

and decapod crustaceans accounted for most of the remainder of the sampled bottom fauna. The meiofauna is described as extremely poor. The findings of Seidenfaden *et al.* (1968) correspond well with the senior author's survey off Phuket where grab samples with a 0.1 m² van Veen contained very few animals. Dredge samples yielded many more invertebrates, but when kept in aquaria they were seen to be relatively fast moving forms. Apparently, sedentary infaunal animals confined to the top 10 cm of the sediment bottom are generally rare although deep burrowing forms could be present. The biomass and production of corals were not estimated, but they are seemingly important in shallow depths (from tidal zone to 20 m). Results from the Gulf of Thailand and from the Andaman Sea (Tamaiyavanish, Chulalongkorn University, pers. comm.) together with data on patterns of variation for benthic biomass in the Indian Ocean (Neyman *et al.*, 1973) tend to confirm the above observations. Estimating a benthic biomass of 3 g · m⁻² at the compensation depth and a P/B of about 5 (about twice that of temperate waters) gives a production value of about 15 kcal · m⁻² · yr⁻¹.

Fish yield can only be described in broad qualitative terms. Thorson (in Seidenfaden *et al.*, 1968) remarks that it would be difficult for bottom feeding fishes of the flounder type to find enough food and that the trawl hauls showed such fish to be very scarce. This is in accordance with observations on trawl fisheries in the area where pelagic fish and squids constitute the major part of the catch.

Comparative results

According to the summary of information in Figure 2, phytoplankton production obviously increases when going from subarctic to temperate and tropical conditions. Of greater significance, however, is the manner in which the relative importance of zooplanktonic and benthic components of the ecosystems appears to change with latitude. This is most clearly shown by the ratio of zooplankton production to benthic production in each of the three ecosystems. For Phangnga Bay, this ratio is approximately 6:1; for the North Sea, 3:1; and for Disko Bugt, 1:1. This pattern suggests that while the zooplankton comprises a dominant link of the tropical ecosystem, energy flow through the subarctic ecosystem is more equally partitioned between benthos and zooplankton. In the temperate marine habitat, zooplankton production is proportionately greater than benthic production but the magnitude of the difference is less than that found in the tropical ecosystem. The relationship between the yield of pelagic and demersal fisheries for each of the three study areas appears to support conclusions based on benthic and zooplanktonic production. Data on fish yields indicate that demersal fish, which are important in the subarctic ecosystem, are comparatively unimportant in the tropics. In the North Sea, where both pelagic and demersal fish are commercially important, the pelagic catch is of greater size.

By summing the production of benthic and planktonic consumers and relating this value to phytoplankton production at each locality, we arrive at the following transfer coefficients: Disko Bugt, 12-26 %; North Sea, 17-24 %; Phangnga Bay, 3-5 %. Although these transfer coefficients (Cushing, 1973) may be no better than

guidelines, they seem to indicate that the utilization of primary production by consumers is more efficient in subarctic and temperate habitats than in the tropics. This may account for the somewhat surprising observation that zooplankton production may be higher in the North Sea than in Phangnga Bay, although the latter region has a much greater phytoplankton production.

Discussion

In attempting to compare our data on the Disko Bugt food web with that of the North Sea and the west coast of Thailand we have tried to utilize production estimates that are as nearly compatible as present knowledge allows. A few of the problems involved should, however, be mentioned. Data obtained for each study area were not measured contemporarily and only some represent annual means. Variations in production from year to year are known to occur, but we are forced here to accept values for many of the levels as representative for those localities over an average period. Reliable values for primary production are notoriously difficult to come by, especially when estimating annual production by integrating mean daily figures for ^{14}C fixation. (For further discussion see Platt & Rao, 1975). Caloric equivalents for wet and dry weights among various taxonomic groups may vary and it is difficult to arrive at a good compromise figure appropriate for complex assemblages of invertebrates like the plankton and benthos. The highly different techniques applied to estimate production may also introduce a bias. Estimates of the annual P/B ratios sometimes amount to little more than guesswork, although general relationships are beginning to emerge (Waters, 1969; Allen, 1971). Another difficulty can be the existence of predation (including cannibalism) within any single component of the generalized food web used here, especially when a single P/B ratio is applied to crude biomass estimates that are not sufficiently broken down into trophic levels. A common result is that the same energy transfer may be erroneously counted and summed two or three times. For the Disko material it is possible to establish that the biomass of predatory polychaetes amounts to about 5% (4-7%) of the total biomass of detritus- and suspension-feeding polychaetes and bivalves at each of the study localities.

Because of the nature of our information sources it has been especially difficult to quantify the pelagic and zooplanktonic components of the subarctic ecosystem. It may be argued that the yield of pelagic fish in the Disko Bugt area is presently small only because exploitation there is not effectively carried out. The pelagic fish in subarctic waters may in the future form the basis for commercial fisheries, but they will according to the views developed here not achieve the same relative importance to the overall fishing effort as is the case for temperate ecosystems.

For the arctic habitats of Northeast Greenland and the northern parts of the Canadian archipelago the lack of pelagic fish is even more pronounced, with none at all which depend upon the plankton for their food. In a high arctic fjord on Ellesmere Island zooplanktonic production has been estimated at $2.6 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ from a P/B = 1.6 (Cairns, 1970), while benthic production may be in the order of $15 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (polychaete biomass $15 \text{ g} \cdot \text{m}^{-2}$, bivalve biomass $2 \text{ g} \cdot \text{m}^{-2}$ at

25-30 m; M.A. Curtis unpublished data). For this estimate of benthic production the P/B ratios for Disko Bugt have been reduced by 50 per cent. Even by such conservative treatment, the resulting ratio between zooplanktonic and benthic production for Tanquary Fiord would be 1:6, a complete reversal of the values obtained for Phangnga Bay.

From the Russian works (Neyman *et al.*, 1973, Zenkevitch, 1963) where standard techniques seem to have been used, it can be seen that benthic biomass in the northern Russian Seas is much higher than in the Indian Ocean. On the shallow shelf of the Barents Sea the biomass is often several hundred $\text{g} \cdot \text{m}^{-2}$. Zenkevitch (1963) claims that an icefjord on Novaya Zemlya holds the record with more than 3000 $\text{g} \cdot \text{m}^{-2}$. In the Indian Ocean the biomass is usually only a few $\text{g} \cdot \text{m}^{-2}$, and also within the Indian Ocean the biomass is smallest in the tropical zone and increases north and south of this. In all the seas the trend is that the biomass decreases with increasing depth.

Thorson (1971) demonstrated that the biomass is much higher in the East Greenland fjords than in the Persian Gulf, and that in both cases the biomass decreases with increasing distance from the open sea.

Our suggestion that benthic production is proportionately greater in high latitudes is also supported by the observations that those marine mammals and birds which prey almost exclusively on the benthos occur in the subarctic and arctic but not in the tropics. The increased importance of pelagic fisheries in temperate and tropical marine areas lends further credence to the hypothesis that the zooplanktonic and pelagic components of marine ecosystems in lower latitudes account for a proportionately greater share of energy flow.

In the Baltic several ecosystem models have recently been developed (Ankar, 1977; Jansson & Wulf, 1977), but they have mainly benthic plants as the primary producers and the systems studied are very limited in size. The Baltic has many biological and hydrographical features in common with the North Atlantic and arctic fjords, but the data at hand do not yet allow comparisons to be made between such localities. For similar reasons the food web described by Rosenberg, Olsson and Olund (1977) for the Swedish Byfjord, an oxygen deficient estuary, cannot be very meaningfully compared with the general result reported here.

Conclusions

We may consider here some possible reasons for the evident predominance of benthic links in the subarctic food web. The bottom temperatures at depths of 40-50 m in Disko Bugt are below 0 °C more than six months a year (Petersen 1964) and only in shallow water do they reach about 8-10 °C in the short summer period. Such low temperatures may reduce metabolism and thus conserve organic matter, giving the subarctic benthos an energy bonus in comparison with warmer seas. Off the west coast of Thailand the temperatures are 25-30 °C in the upper 50 m during the whole year. The metabolism of the tropical phytoplankton may be so high that only little of the measured primary production is available as food for the herbivores. In turn, the metabolism of the herbivores may be too high to give

any large yield to the predators. Scholander *et al.* (1953) found that the metabolism of arctic species is four to ten times lower than the metabolism of the tropical forms at their normal habitat temperature. The relative metabolic adaption appears when the results are extrapolated according to Krogh's normal curve. In this hypothetical case (the animals die) the metabolism of the arctic species should be thirty to forty times lower than that of the tropical species. Thus the high tropical pelagic metabolism might actually diminish the yield available for transfer to other trophic levels, even though gross rates of carbon fixation are quite high. Food chains are affected by this process when only a small part of the produced organic matter ultimately leaves the photic zone to become food for such organisms as benthic animals below and sea birds above this zone. It is also probable that the role of microbial decomposition is diminished within the tropical ecosystem because so little is left to decay.

There may be an advantage for subarctic organisms at higher trophic levels to depend upon the benthos because it (and possibly also the detritus food pool) is more stable in this seasonal abundance and is less subject to extreme annual fluctuations than are the planktonic and pelagic components of the subarctic ecosystem. Furthermore, the greater longevity and generally larger size of subarctic bottom invertebrates may make feeding more efficient for predators than is the case in lower latitudes. The sea bottom of the subarctic may be envisaged mainly as a habitat for filter feeders and detritus feeders and their predators, while in the tropics it serves to a greater extent as a habitat where suprabenthic animals hide and rest between feeding excursions to the water mass above.

Tranter (1973) in his study on time lag in the response of zooplankton populations to changes in phytoplankton production found basic biological differences between the tropical and subtropical zones, but found them difficult to interpret. In his considerations on recycling mechanisms Tranter suggests that zooplankton in the tropics plays an important role in nutrient mineralisation without any appreciable time lag. In the subtropics where algal supply varies more, grazing may result in less immediate nutrient excretion, thus perpetuating the time lag between phytoplankton and zooplankton. Oscillation and the following time lag effect is still more accentuated when going to the higher latitudes, a situation in which the benthic animals may better cope than the zooplankton. Benthic animals can accumulate gonadal products and spawn synchronously with the phytoplankton bloom, while the zooplankton may be too slow during the spring in building up a population that can fully utilize the phytoplankton. The rapid and efficient recycling of nutrients between phytoplankton-zooplankton links in the tropics described by Tranter also supports the contention that it may be difficult to establish energy transfer routes leading to other ecosystem components, the food chains becoming shortened and having relatively small outputs to higher trophic levels, as the transfer coefficients calculated here indicate.

Mills (1975) has used the North Sea model of Steele for comparison with the continental shelf off Argentina, and he also has compared the subarctic and antarctic benthos. He concluded that the different shelf benthos communities may have very different structures both with regard to taxonomic groups and to feeding

modes and suggested that more than one basic pattern of energy flow exists. Such an interpretation could be supported by the more general results of the present study. Arnaud (1977) in his comparison of antarctic with arctic benthos stresses the importance of historical development, a matter also for serious consideration. Tiews (1973) describes the difficulties in management of the demersal fish stock in the Gulf of Thailand. The trawl fishery was introduced in 1962-64 and already in 1971 the catch per unit effort had decreased to one quarter of the original. Pauly (1978) states that the demersal fishing grounds in the S.E. Asia may be much less productive than was previously assumed.

If it is true that a relatively greater proportion of the assimilated energy is lost via contemporary metabolism in the tropical seas, and a relatively greater proportion of energy flow is channelled through the benthos in high latitudes, this could be used as a functional hypothesis in evaluating some general problems in marine ecology. The model may for instance help to explain why it has been difficult to establish level bottom communities in tropical shallow waters, why symbiosis between algae and animals (an ultrashort food chain) is commonly found among tropical species, and why the accumulation of toxins through the food chain seems to be more pronounced in high latitude ecosystems. It also seems implicit from material presented here that large scale management models developed for temperate waters may have to be substantially modified if they are to serve a useful purpose in arctic or tropical seas.

Acknowledgements

This paper could only be completed because many colleagues readily gave us unpublished information and valuable criticism. We wish to thank the following for their kind cooperation: O. Norden Andersen, S. Wium Andersen, P. Milan Petersen (all from the University of Copenhagen), K. Holst (Royal Danish Veterinary School, Copenhagen), P. Kanneworf (Greenland Fishery Investigations) and Suthicacae Tamiyavanich (Chulalongkorn University, Bangkok). Dr Eric Mills (Dalhousie University, Halifax, Canada) and Professor Max J. Dunbar (McGill University, Montreal, Canada) kindly commented on an earlier draft of this manuscript.

References

- Allen, K. R., 1971: Relation between production and biomass. *J. Fish. Res. Bd. Canada*, 28: 1573-1581.
- Ankar, S., 1977: The Soft Bottom Ecosystem of the Northern Baltic Proper with Special Reference to the Macrofauna. Contributions from the Askö Laboratory, University of Stockholm, Sweden. No. 19: 62 pp.
- Arnaud, P. M., 1977: Adaptions within the Antarctic Marine Benthic Ecosystem. In: George A. Llano (ed.) 1977. Adaptions Within Antarctic Ecosystems, Proceedings of the Third SCAR Symposium on Antarctic Biology. Washington. D.C. August 26-30, 1974.
- Atkinson, E. G. & J. W. Wacasey, 1976: Caloric values of zoobenthos and phytobenthos from the Canadian arctic. Environment Canada. Fisheries and Marine Service Technical Report No. 632. 24 pp.
- Brawn, V. M., D. L. Peer & R. J. Bentley, 1968: Caloric Content of the Standing Crop of Benthic and Epibenthic Invertebrates of St. Margaret's Bay, Nova Scotia. *J. Fish. Res. Bd. Canada*, 25: 1803-1811.
- Cairns, A. A., 1970: Seasonal Cycles, Population Dynamics, and Production of Copepoda in the Arctic. Ph.D. Thesis, McGill University.
- Curtis, M. A., 1977: Life cycles and population Dynamics of Marine benthic polychaetes from the Disko Bay Area of West Greenland, *Ophelia*, 16: 9-58.

- Cushing, D.H.*, 1973: Production in the Indian Ocean and the transfer from the primary to the secondary level. In Zeitschel, B. (ed.) 'The Biology of the Indian Ocean' p. 475-486. Chapman & Hall, London.
- Ellis, D.V.*, 1960: Marine infaunal benthos in Arctic North America. Arctic Inst. of North America, Tech. Pap. No. 5: 1-53.
- Jansson, B.-O. & F. Wulf*, 1977: Ecosystem Analysis of a Shallow Sound in the Northern Baltic. Contributions from the Askö Laboratory, University of Stockholm. Sweden. No. 18: 160 pp.
- Jones, R.*, 1978: Further observations on the energy flow to the major fish species in the North Sea. International Council for the Exploration of the Sea. C.M. 1978/Gen:6 (Symp.). 18 pp.
- McLaren, I.A.*, 1969: Population and production ecology of Zooplankton in Ogac Lake, a landlocked fjord on Baffin Island. J. Fish. Res. Bd. Canada, 26: 1485-1559.
- Mills, E.L.*, 1975: Benthic Organisms and the Structure of Marine Ecosystems. J. Fish. Res. bd. Canada, 32 (9): 1657-1663.
- Neyman, A.A., N.N. Sokolova, N.G. Vinogradova & F.A. Pasternak*, 1973: Some patterns of the distribution of bottom fauna of the Indian Ocean. In Zeitschel, B. (ed.) 'The Biology of the Indian Ocean' p. 467-474. Chapman & Hall, London.
- Pauly, D.*, 1978: Theory and Management of Tropical Multi-Species Stocks. Unpublished.
- Petersen, C.G. Job.*, 1915: A preliminary result of the investigations on the valuation of the sea. Report from the Danish biological Station, 23: 29-32.
- 1918: The Sea bottom and its production of Fish-food. A survey of the work done in connection with valuation of the Danish waters from 1883-1917. Report from the Danish biological Station, 25: 1-62.
- Petersen, G. Høpner*, 1964: The hydrography, primary production, bathymetry and 'Tagsaq' of Disko Bugt, West Greenland, Meddr Grønland 199(10): 1-45.
- 1977a: General Report on marine benthic investigations near Godhavn, West Greenland, Ophelia, 16: 1-7.
- 1977b: The Density, Biomass and Origin of the Central North Sea Bivalves, Meddr Danm. Fisk.- og Havunders., N.S. 7: 221-273.
- 1978: Life cycles and population dynamics of marine benthic bivalves from the Disko Bugt Area of West Greenland. Ophelia 17(1): 95-120.
- Platt, T. & D.V. Subba Rao*, 1975: Primary production of marine microphytes. In: Cooper, J.P. (ed.): Photosynthesis and productivity in different environments p. 249-280. International Biological Programme 3. Blackwell Scientific Publications, Oxford.
- Quasim, S.Z.*, 1973: Productivity of backwaters and estuaries. In Zeitschel, B. (ed.) 'The Biology of the Indian Ocean' p. 143-154. Chapman & Hall, London.
- Rosenberg, R., J. Olsson & E. Ölundh*, 1977: Energy Flow Model of an Oxygen-Deficient Estuary on the Swedish West Coast. Marine Biology, 42: 99-107.
- Scholander, P.F., W. Flagg, V. Walters & L. Irving*, 1953: Climatic adaption in arctic and tropical poikilotherms. Physiol. Zoöl, 26: 67-92.
- Seidenfaden, G., T. Smitinand & G. Thorson*, 1968: Report on the Fifth Thai-Danish Expedition 1966. The Natural History Bulletin of the Siam Society (Bangkok), 22: 245-261.
- Steele, H.*, 1974: The Structure of Marine Ecosystems, Blackwell Scientific Publications. Oxford. 128 p.
- Stemann Nielsen, E.*, 1965: On the determination of the activity in ¹⁴C ampoules for measuring primary production. Limnol. Oceanogr., 10(Suppl. R.) 247-252.
- Thorson, G.*, 1971: Life in the Sea. 256 pp. World University Library. Weidenfeld & Nicolson, London.
- Tiews, K.*, 1973: Fishery development and management in Thailand. Archiv für Fischereiwissenschaft. 24(1-3): 271-300.
- Tranter, D.J.*, 1973: Seasonal studies of a pelagic ecosystem (Meridian 110° E). In Zeitschel, B. (ed.) 'The Biology of the Indian Ocean' p. 487-520. Chapman & Hall, London.
- Waters, T.F.*, 1969: The turnover ratio in production ecology of fresh-water invertebrates. Amer. Nat. 103: 173-185.
- Zenkevitch, L.*, 1963: Biology of the Seas of the U.S.S.R. 955 pp. George Allen & Unwin Ltd. London.
- Zvereva, Zh.A.* (ed), 1972: Geographical & Seasonal Variability of Marine Plankton. Akademia NAVKSSSR zool. Institut. Israel Programme for Scientific Translations 1975, 303 p.