

Comparative studies of beaches

BY J. H. STEELE

Department of Agriculture and Fisheries for Scotland, Marine Laboratory, Aberdeen

Over a period of six years, scientists from Scottish marine laboratories and universities worked for the winter season with colleagues in India on the ecology of Indian beaches. The intention was to compare the population dynamics with similar studies on west coast Scottish beaches. Microbial, invertebrate and vertebrate fauna were studied, in terms of population distributions and especially, by experimental work, in relation to energy flow. The results show that, for the microbial and invertebrate fauna, the rates of energy flow are very much greater on the Indian than on the Scottish beaches. Thus population biomass, which is similar for the two areas, is a poor indicator of the dynamics. For the fish populations, metabolic rates are very similar, indicating almost complete compensation to the difference in temperatures. These differences between different parts of the ecosystem lead to speculations about the factors determining adaptation in the different environments.

INTRODUCTION

Over a period of six years, 1968–73, five visits, for three-month periods, were made to the west coast of India by marine ecologists from various Scottish laboratories. Also scientists from the National Institute of Oceanography of India worked in the Scottish laboratories, participating in programmes of research on exposed beaches. The aim of the work, in India and Scotland, was to combine experiments with field observations so that some understanding could be obtained of the dynamics of natural beach populations in different environments. The results of the studies in both regions have been published, so this paper will emphasize the comparisons between the two regions and explore the reasons for observed differences.

THE ENVIRONMENTS AND BASIC FOOD WEBS

The beaches studied in India (figure 1) were exposed to the Indian Ocean and, during the monsoon period, suffered considerable erosion (figure 2), which is at least as great and often greater than that experienced during the winter by similarly exposed beaches in Scotland. Thus, in both areas, but especially in India, one can expect marked seasonal cycles in the biota associated with this aspect of the physical environment (Ansell *et al.* 1972*a*; McLusky, Nair, Stirling & Bhargava 1975). Two particular beaches have been studied in detail (Shertallai in India and Firemore in Loch Ewe, Scotland). Firemore is less exposed and this factor, together with a greater tidal range, gives it an intertidal zone of approximately 200 m compared with approximately 40 m for Shertallai. Table 1 compares other features during the productive seasons and shows that the surf water in India has higher nutrients, plant pigments and particulate organic carbon than in Scotland. The carbon attached to the sand grains was, approximately, the same for the two areas but the chlorophyll values indicate that the epipsammic flora was considerably poorer in Shertallai than in Firemore.

These aspects form the bases for the food webs in the two areas, figure 3. The detrital carbon

in both areas may be enriched by fragments of macrophytes and, in India, by organic wastes. In Loch Ewe studies of the interstitial food chain showed that the utilization by bacteria of soluble organic carbon from water flowing into the sand was the most important source of energy for this part of the ecosystem (McIntyre, Munro & Steele 1970), being about nine times greater ($45 \text{ g C m}^{-2} \text{ a}^{-1}$) than the contribution from photosynthesis by the epipsammic diatoms ($5 \text{ g C m}^{-2} \text{ a}^{-1}$). This food chain, moreover, appeared relatively self-contained, with little net output to the larger fauna. These larger organisms, mainly bivalves and polychaetes, feed from the organic matter in the water and in turn have their siphons and palps cropped by small flatfish (*O*-group plaice) which live in the immediate sublittoral and migrate inshore with the tide. This part of the food chain was studied intensively with the general conclusion that not only was food limiting to the plaice population but the plaice could in turn limit, in particular, the bivalve populations. Obviously these food chains are part of a much larger system extending seaward and including zooplankton and other predators.

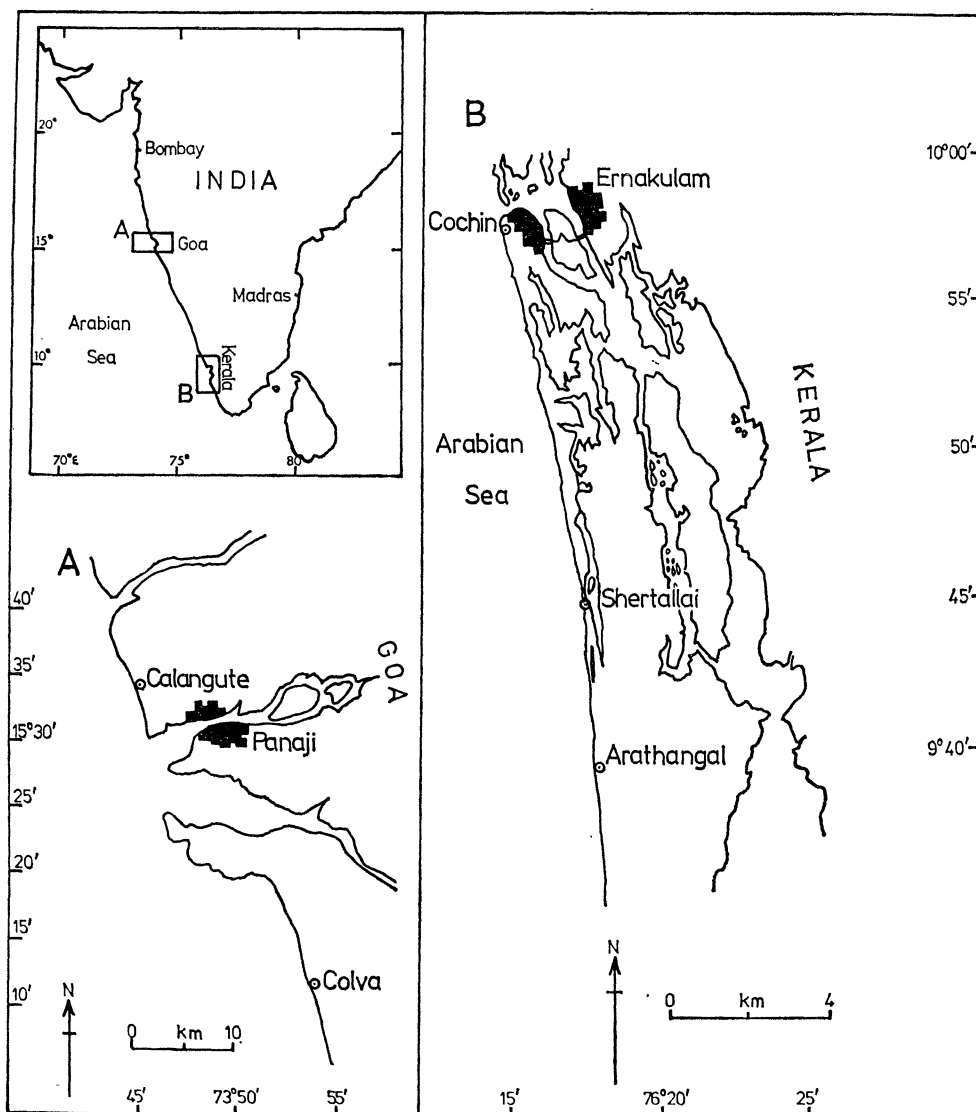


FIGURE 1. Location of beaches in India studied during I.B.P. The beach at Shertallai is considered in detail here.

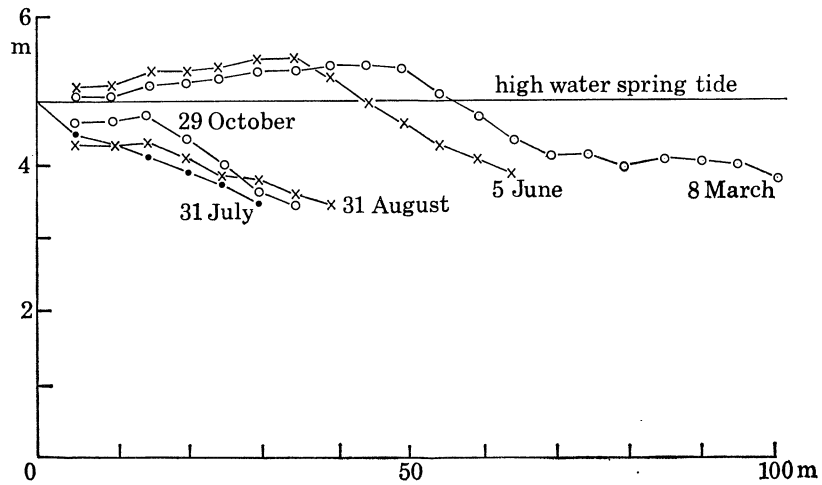


FIGURE 2. Beach profiles for Shertallai for different dates during 1968 (Ansell *et al.* 1972 a).

TABLE 1. ENVIRONMENTAL LEVELS DURING SPRING AND SUMMER IN FIREMORE (SOUTH) LOCH EWE AND DURING THE PRE-MONSOON PERIOD AT SHERTALLAI (KERALA) S. INDIA

	Firemore (south)	Shertallai
tidal range/m	3.2	1.0
width of beach/m	200	40
mean diam. of sand/ μm	230	175
temperature/ $^{\circ}\text{C}$		
sand	7-15	32-45
surf	7-13	31-34
salinity(‰)		
sand	23-34	34-35
surf	34	34
phosphate/($\mu\text{mol P/l}$)	0.1-0.7	0.8-2.7
chlorophyll		
sand/($\mu\text{g/g}$)	0.4-1.7	0.02-0.07
surf/($\mu\text{g/l}$)	1.0-3.0	2.2-13.3
carbon		
sand/($\mu\text{g/g}$)	200-300	200-400
surf/($\mu\text{g/l}$)	500-1000	900-3700

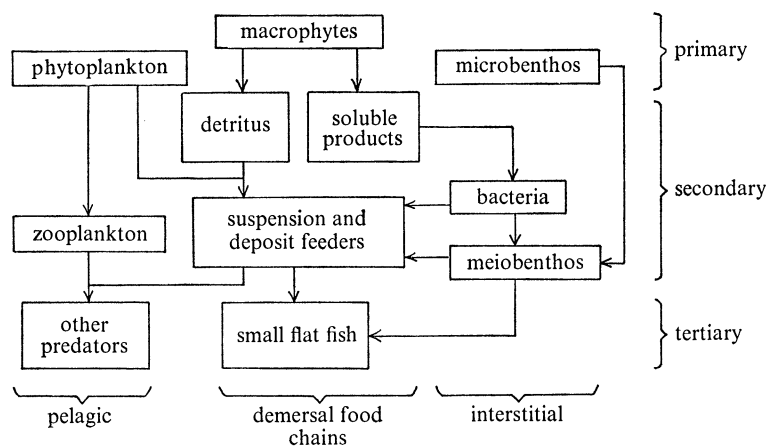


FIGURE 3. Generalized ecosystem for a beach and inshore area, divided broadly into three trophic levels and three main food chains.

The same basic components of the web are also present in India but with differing relative importance. The greater effect of surf on sand movement can provide a greater exchange of both particulate and soluble carbon between the interstitial water and the overlying surf, possibly providing a significant link between the food chain within the sand and that feeding at the surface. Bivalves form a dominant component of the fauna but predation on them is mainly by invertebrates such as crabs (and also by man) rather than by the small flatfish. These fish, sampled in India, live rather further from the beach than in Scotland, but also feed mainly on fauna such as polychaetes. (For technical reasons it was not possible to study the Indian sublittoral in any detail.)

Thus, although the same basic components of the food web occur in both regions, the importance of certain links differs, and these differences must be borne in mind when looking at the dynamics of particular species or groups.

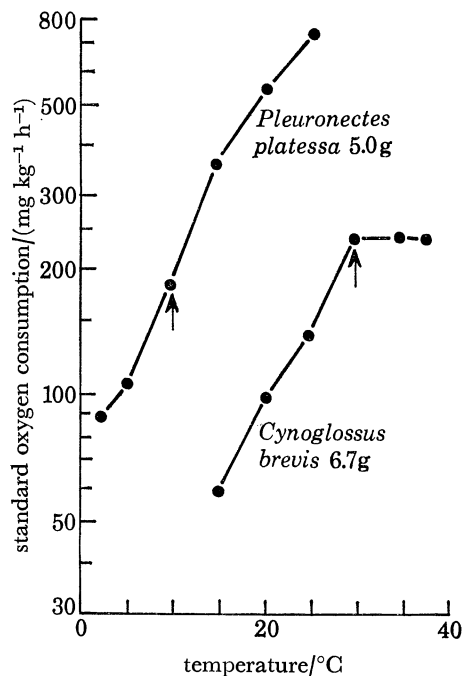


FIGURE 4. The effect of temperature on standard oxygen consumption of *P. platessa* and *C. brevis*. Arrows indicate environmental temperature (Edwards, Blaxter, Gopelan & Mathew 1970).

METABOLISM, FEEDING AND PRODUCTION

These relatively static pictures need to be supplemented by information on feeding and metabolic rates. Obviously, a major feature in such experiments is the effect of temperature and this is demonstrated in measurements of respiration rate. Taking the small flatfish, figure 4 summarizes the data from experiments in both areas with fish of approximately the same size. The main conclusion is the almost complete temperature compensation, so that respiration rates are almost equal for average temperature in each environment. This result is in general agreement with earlier work (Bullock 1955; Scholander, Flagg, Walters & Irving 1953). However, metabolic rate is affected not only by temperature but also by the rate of food intake. This is illustrated by feeding experiments in India with growing *Cynoglossus*, figure 5, where a

fourfold change in metabolic rate can occur with different feeding rates. In both regions (Edwards & Steele 1968; Edwards *et al.* 1971) examinations of stomach contents suggest that food is in limited supply for the younger fish and, as a possible consequence, growth rates of *Cynoglossus* during its first year are only 50 % higher than those of plaice (Krishnan Kutty 1967; Wimpenny 1953). Thereafter, *Cynoglossus* becomes sexually mature in its second year of life while plaice mature in their third or fourth year and achieve a greater final size. Thus the former fish will utilize energy for reproduction earlier in life than the latter. Again, these features, together with the more prolific speciation in *Cynoglossus*, are accepted differences between temperate and tropical fish.

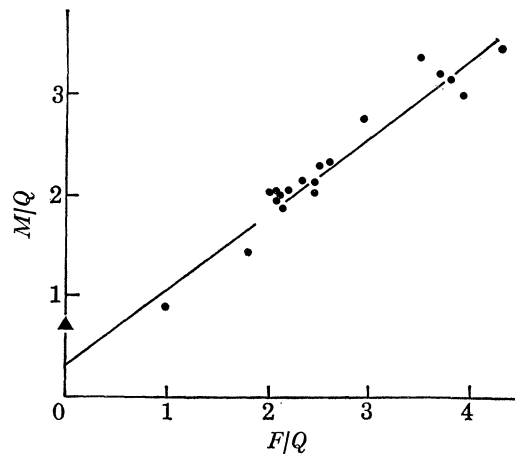


FIGURE 5. Relation of metabolic rate (M) to food assimilated (F) for growing *Cynoglossus* spp. M and F are divided by Q , the standard oxygen consumption, to eliminate the effects of differing mass of individual fish used in the experiment. \blacktriangle , refers to starved fish. (All quantities expressed in units of calories per gram dry mass per hour.) (Edwards *et al.* 1971.)

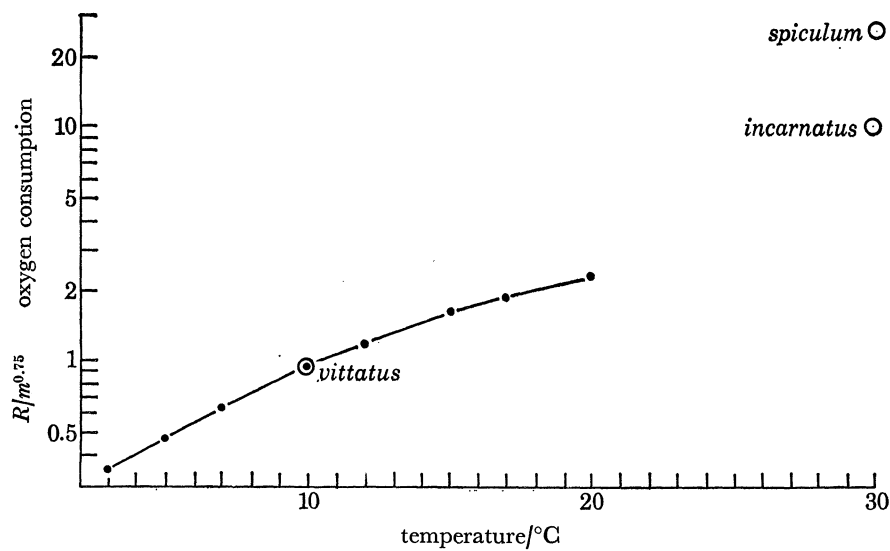


FIGURE 6. Respiration of temperate and tropical *Donax* spp. in relation to temperature. The measured respiration, R , is divided by the 'metabolic mass', $m^{0.75}$, to remove the effects of different masses of experimental animals (McLusky & Stirling 1975).

The picture emerging from a comparison of temperate and tropical bivalves is quite different. A comparison, figure 6, of respiration rates of *Donax vittatus* in Scotland with the two species found in India, *D. spiculum* and *D. incarnatus*, shows no evidence of temperature compensation. In this case, unlike the flatfish, there appears to be an inverse relation between metabolism and longevity which is supported by data on *Donax* species from other areas (Ansell, personal communication).

TABLE 2. RATIOS OF PRODUCTION TO AVERAGE BIOMASS (IN CALORIFIC UNITS) FOR BIVALVES ON INDIAN AND SCOTTISH BEACHES

Indian	<i>Donax incarnatus</i>	5.9	} Ansell <i>et al.</i> (1972b)
	<i>Donax spiculum</i>	10.3	
Scottish	<i>Donax vittatus</i>	1.3	} Ansell (unpublished)
	<i>Tellina tenuis</i>	1966 0.4	
		1967 0.3	} Trevallion (1971)
		1968 0.9	

In consequence of differences in metabolism and life cycles, the ratios of yearly production to average biomass of the two beach populations, shown in table 2, are very different (*Tellina tenuis* is the common bivalve at Firemore (Loch Ewe) and on many other Scottish beaches). Thus, although the biomass per unit area may be similar on the Scottish and Indian beaches, the productivity of the latter is very much greater.

Underlying these differences in metabolism and production are significant differences in behaviour. Bivalves such as *Donax* and *Tellina* normally live buried in the sand on moderately exposed Scottish beaches but are absent on beaches with severe exposure. In India, *Donax* can migrate up and down the beach with the surf or tide, emerging into the incoming rush of the surf after it breaks and then burrowing rapidly into the sand before the backwash occurs (this region is called the swash zone). This allows them to survive on exposed beaches and also enables them, unlike *Tellina*, to feed continuously in the organically rich surf water. Such a behaviour pattern imposes much greater energy demands which, in turn, are supplied by the much higher rate of food intake. However, their aggregation on the sand surface in the swash zone also exposes them to predation (by man, crabs, etc.) at a much higher rate than is likely in *Tellina*. This behavioural adaptation of the tropical bivalves may thus depend as much on the available high food concentrations as on the increased temperature.

For the microbial populations attached to the sand grains it is not possible to express respiration directly in terms of the biomass of the organisms: the results, figure 7, are given instead per gram of sand (A. L. S. Munro, pers. comm.). However, the differences between winter and summer rates at Firemore are attributed to availability of food substrate rather than temperature or change in biomass (as indicated by carbon content of the attached organic material). Similarly, the higher respiration at ambient temperature in India ($0.65 \mu\text{g O}_2 \text{ g}^{-1} \text{ h}^{-1}$) compared with the range at Firemore (0.10–0.17) must be regarded as due to an increased rate per unit biomass since the attached carbon at Shertallai was only approximately 50% greater than that at Firemore. In turn, this requires an increased rate of intake of energy and this is made possible at Shertallai by the much greater flow of water through the sand compared with that measured at Firemore (Steele *et al.* 1970). In consequence, the estimated annual production of the microbial populations on the tropical beach is five times that of the temperate beach.

The interstitial meiofauna feeding on this microbial production has a biomass at Shertallai only one-tenth of that at Firemore. Unfortunately, there are no estimates of production of the meiofauna at Shertallai, but even if the turnover were several times greater in the tropical region this is still likely to leave the tropical production considerably lower than in the temperate region. The probable explanation (Munro, pers. comm.) is that the strong swash action at Shertallai removes much of the epipsammic growth from the sand grains. Thus, unlike the situation on the less exposed Scottish beaches, the interstitial production at Shertallai can contribute to the suspension-feeding macrofauna migrating with the swash. The strong surf action will tend to mix this material rapidly with the more offshore water so that it is not completely and solely available to the beach macrofauna. However, a comparison of the interstitial production ($72 \text{ g C m}^{-2} \text{ a}^{-1}$; Munro, pers. comm.) with the total macrobenthos food requirement ($30 \text{ g C m}^{-2} \text{ a}^{-1}$; Ansell *et al.* 1972*b*) indicates that it may make a significant contribution to the higher levels of particulate organic carbon in the water (table 1) and to the greater feeding rates of the fauna.

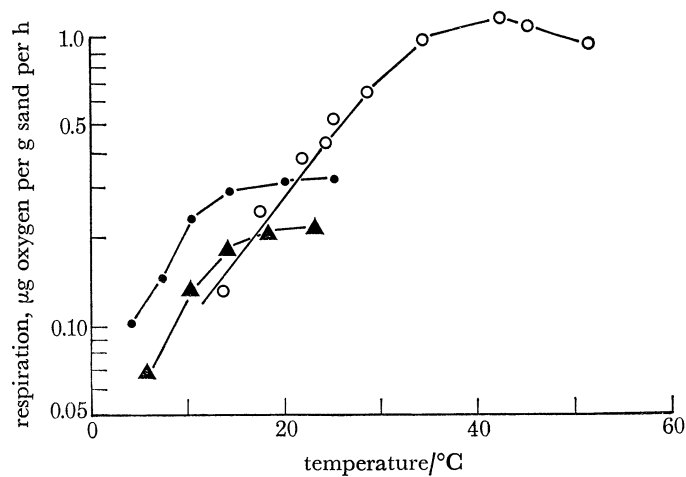


FIGURE 7. The effect of temperature on respiration by sand microflora. Winter (▲) and summer (●) at Firemore; pre-monsoon (○) at Shertallai.

These results indicate some of the differences in biomass, metabolism and productivity of three different trophic groups, heterotrophic micro-organisms, invertebrate filter feeders and small carnivorous fish. They also show how differences in these factors for the two regions are determined by adaptations to their environment. Adaptation of an organism to its environment is not a one-way process since the 'environment', in a general sense, consists of other organisms, as well as factors such as temperature, salinity or wave action which cannot readily be altered by living components of the system. There is a wealth of literature on the responses to changes in temperature and activity. In particular, the energy requirements at different temperatures have been studied experimentally for a wide range of organisms, both in terms of acclimation of a species from one environment to temperatures within and outside its normal range, and also by comparison of similar species from environments with very different temperatures. Much of this literature for marine organisms is summarized in Kinne (1970).

In short-term laboratory experiments, the energy requirements for increasing temperature or activity will be met from stores within the organism but in the longer term these must be balanced by the rate of food intake. Such longer-term experiments are fewer and, in the main,

have been carried out on fish. Brett and co-workers have carried out several experiments which show the interactions of food ration, temperature and growth. For example, as the daily ration for young sockeye salmon was changed from 1.5 to 6% of fish mass, the temperature at which maximum growth occurred rose almost linearly from 5 to 15 °C (Brett, Shelbourne & Shoop 1969). Further, growth as a fraction of the ration (gross growth efficiency) varied relatively slightly (21–25%) over this temperature range. Thus the optimum temperature for growth is closely related to food intake. Energy expended as metabolism varies not only with temperature and activity but also with quantity of food assimilated. In warm-blooded animals, this extra energy expenditure (specific dynamic action) over basal metabolism may be relatively small but, in poikilotherms feeding actively, the metabolism can be several times greater than the lowest values found near starvation. For the sockeye salmon at optimum temperature and ration, metabolism was approximately nine times that of starved fish at the same temperature (see also figure 5). The consequences are that for organisms in the laboratory acclimated, but not compensated, at higher temperatures, figure 8, maximum growth requires a food intake several times that of fish acclimated to low temperatures. The optimum food intake at the low temperature could result in decrease in mass at the high temperature.

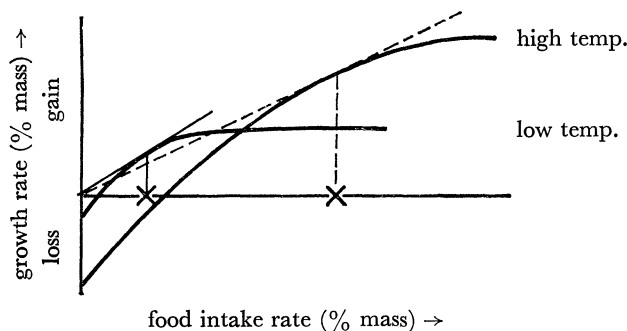


FIGURE 8. Representation of the effect of temperature acclimation on growth at different rates of food intake, indicating the food intakes required for maximum growth efficiency at different temperatures.

When these different metabolic requirements are studied in the laboratory, experimental design permits the various components, such as food ration, temperature and activity, to be varied independently. In the natural environment, such factors will interact with metabolic rate. For the individual organism food ration and activity can be closely linked. However, the main interaction may occur at the population level where the relative sizes of the population and of its food resource are often, but not always, interrelated. The availability of food, and the response of the population to this availability, are likely to determine the metabolic rate. In particular, the nature of the adaptations to different temperature régimes in different areas must be determined by the nature and quantity of the food resources available to the population since this sets limits on energy expenditure. On this basis, the differing compensations of similar species in the cold waters around Scotland compared with those in the warm water on the Indian coast need to be related to the ecological context in which the animals are living.

Differing exposure to wave action does not appear to provide a sufficient explanation of differences in beach fauna (Eleftheriou & Nicholson 1976). The fauna can differ considerably: bivalves are sufficiently mobile to survive on exposed tropical beaches but not on very exposed temperate beaches where only crustacea appear to have the requisite mobility. Wave action

affects not only the physical environment of the fauna but also determines the organic cycle in several different ways, supplying organic matter to the attached bacterial flora but also possibly removing that flora from the littoral area before it is eaten by the interstitial fauna. The measure of exposure is essentially the *rate* at which physical energy is dissipated on the beach. It is likely to affect directly other dynamic aspects involving 'biological' energy, such as rate of growth, rate of movement, or rate of predation, rather than the statics of the system – numbers or biomass. For this reason we can expect the physical environment of a beach to be an important factor in the metabolic adaptations of its inhabitants as well as in relation to animal numbers.

A further factor is the amount of seasonal change. There are many differences between the Indian monsoon and the Scottish winter, but both can produce marked physical disturbance of exposed beaches with effects on their populations. For various understandable reasons, studies have usually been done outside these periods of major disturbance, but the similarity in seasonal instability should be remembered.

It is not known what effect seasonal factors will have on the immediate sublittoral where the Indian fish populations were studied. In general, changes in littoral beaches produce consequent changes immediately offshore and such effects may be found off the Kerala beaches where the fish occurred. Also, upwelling during the monsoon can bring cool deoxygenated water to inshore areas (Banse 1968). Yet the effects are less than might be expected since the bivalve populations have a seasonal reproductive cycle as marked as their temperate counterparts, whereas the flatfish show evidence for a much longer or even year-round spawning period, quite unlike the short-season of the Scottish plaice and dabs. Thus the environment of the fish may approach the supposed seasonal uniformity often associated with tropical areas.

The lack of defined breeding periods in the tropical flatfish raises the main question about the effects of temperature and its importance both in terms of absolute differences between temperate and tropical regions, and also in relation to seasonal variations.

TEMPERATE CYCLES

In northern waters it is apparent that, in a very general sense, 'biological activity' is not in phase with the temperature cycle. The spring outburst of phytoplankton follows immediately after the winter minimum in sea temperature which is usually observed in late February or March. This outburst normally results from the initiation of the seasonal thermocline. That is, it depends on the formation of small temperature differences between the upper and lower layer, rather than on the average temperature throughout the water column. This growth of phytoplankton is followed rapidly by the growth of zooplankton populations and is associated with the pelagic larval stages of many fish and bottom fauna.

The consequences of this can be seen in specific groups of animals or parts of the ecosystem. Thus, copepods taken from natural populations display maximum oxygen consumption in April and by June or July the rates have fallen to those observed in March (Marshall 1973). Measurements of the masses of the copepods showed a similar seasonal pattern but this accounts for only part of the seasonal variation in respiration. Mullin & Brooks (1970) have shown that the masses of copepods at particular stages in their development depend on the food concentration in which they have been kept. Thus food supply appears the determining factor.

For benthic community respiration in Loch Thurnaig, a part of Loch Ewe, Davies (1975)

has shown that the oxygen uptake of the mud sediment begins to increase in March and reaches a maximum in June, following the increase in primary production rather than the seasonal temperature change from 7 to 13 °C. The Q_{10} , determined experimentally, was 1.9 and this is insufficient to explain the fivefold increase in the *in situ* respiration rate. Davies considers that these observations imply that, for this muddy bottom, the benthic community metabolism is regulated by the food supply.

These examples show the interrelation between food, metabolism and growth which is independent of the main temperature cycle but dependent on the food supply. For the zooplankton, it must be remembered that the food intake by each individual depends on food concentration which, in turn, depends on food intake by the whole population. For the benthos, the relations are not so clear-cut since the input of energy as organic matter from the water column is independent of the benthic population size, although the rate of utilization obviously does depend on this factor.

FOOD AS A LIMITING FACTOR

Beach ecosystems, because of their peripheral position in the marine environment, are more likely to depend on sources of food completely outside their control. Thus, the interstitial bacterial flora of the sand derives its energy from the organic matter in the water flowing through the sand. Similarly, the macrofauna feeding from the water close to the sand surface will derive its energy from the same source directly or through the bacterial production. On the other hand, the evidence suggested that the O-group plaice population in Loch Ewe, derived its food from certain components of the benthic macrofauna and in so doing could affect the energy balance of this fauna (Steele, Munro & Giese 1970). Thus, certain parts of the ecosystem were, in a broad sense, limited by food resources without affecting the concentrations of these resources, whereas at least one other component, the young fish, were both limited by, and played a part in, limiting their food resource. For the bivalve *Tellina tenuis* comparisons between populations in Loch Ewe and in the more eutrophic Clyde Sea Area (McIntyre 1970) show some improvement in growth in the latter region but mainly a great increase in population density. Similarly, tank experiments in which O-group plaice were provided with different densities of *Tellina* as food, showed that the fish could survive at low food concentrations with very slow growth rates although, in the sea, they grow at rates near the maximum found in the tanks. Production size in the sea varied from year to year, probably through predation, to maintain this near-maximum rate in relation to fluctuations in their limiting food supply.

These observations accord well with the general sense that, in undisturbed ecosystems, the observed natural growth rate of any species is much nearer to the optimum which can be determined experimentally than to a minimum at which the organism can manage to survive. Explanations of this in evolutionary terms are fraught with difficulty but the general conclusion is useful in considering the overall adaptations within a community.

Especially, in this context, the adaptations which one might expect could be very different for those species whose source of food is outside the community, for example *Tellina* or *Donax*, than for those species where the rate of feeding of the population has some effect on the food concentration.

From the studies on the Indian beaches, it would appear that in relation to food supply the bacterial flora and the bivalve macrobenthos resemble those Scottish populations with which they have been compared. For the small flatfish, the environments are different and no

information could be obtained for the Indian stocks on the details of their interaction with their food supply. From the available information on stomach contents and from a general comparison with similar systems it is not unreasonable to assume that there are interactions with their food supply comparable, in principle, with those observed at Loch Ewe.

These metabolic relations for poikilotherms are expressed in a summarized form through the formula of McNeill & Lawton (1970):

$$P = 0.64R^{0.85}, \quad (1)$$

where P and R are the production and respiration rates of any population expressed on an areal basis. Further, as shown in the metabolic studies of fish and invertebrates, R can usually be expressed as,

$$R = f(T)NM^a, \quad (2)$$

where N is the number in the population, M is the average mass, and a is a constant between 0.6 and 0.8. $f(T)$ defines the temperature dependence and will contain any adaptation effects. If we take rate of food assimilation as F then

$$F = P + R. \quad (3)$$

It follows from (1) and (3) that if rate of food supply on an areal basis is constant then R has to be constant. If temperature is increased with no temperature adaptation then from (2) either population numbers or the mass of individuals must decrease to balance the increase in $f(T)$. However, for the 'individual' fish with a higher metabolic rate compared with that of its neighbour, the food concentration would need to be higher if it is to maintain a production proportional to its respiration. This would place it at a competitive disadvantage. Thus in the limiting food situation a decrease in metabolism appears the appropriate solution.

On the other hand, if food concentration is not affected by population density then an increase in R can be associated with an increase in production. Again, this does not imply that for each tropical animal an increased respiration rate over the rate of a similar temperate organism is the only response since, from (2), population biomass could increase. However, for the Indian bivalve populations, the conclusion from Ansell, Sivadas, Narayanan & Trevallion (1972*b*) is that biomass compared with temperate beaches is smaller rather than greater, but the respiration and therefore the production per unit biomass has increased markedly.

These speculations depend for verification on details of the actual behaviour of the organisms since there are still problems concerning the ability of the individual to acquire the energy to meet both growth and metabolism. This is obviously most critical for the *Donax* populations on the Indian beaches. Ansell *et al.* (1972*a*) have described how the Indian bivalves are tidal migrants living in the surf zone and thus having available a continual supply of food from water which has a high content of organic matter. The benthic bivalves on temperate beaches remain in one position and therefore are in the surf zone for only a fraction of their time. At other times there is either no supernatant water or the water is relatively calm probably with an organic matter content several times less than that of the surf (see Steele & Baird (1968) for data from Loch Ewe).

The implications from the work on burrowing (Ansell & Trevallion 1969) is that there is a Q_{10} effect on rate of burrowing so that very rapid burrowing does not appear to occur at lower temperatures and the ability to move with the surf zone is likely to be a feature of animals living in warmer waters.

Despite these differences in response to their environments there are similarities between the bivalves and the flatfish in terms of life span. As Ansell *et al.* (1972*b*) and Edwards *et al.* (1971) point out, life spans of the tropical species are much shorter than their temperate counterparts; and this is a fairly common feature of tropical organisms. Yet this is achieved in different ways. The life span can be taken to consist of two different phases: the immature, rapidly growing animal and the slow growing, reproducing adult. For the first phase there are significant differences between the bivalves and the flatfish. The rapid growth of the tropical *Donax* sp. allows them to reach sooner a mass at maturity comparable to their temperate relatives. The flatfish grow at a similar rate in both latitudes but the tropical species mature at a smaller size. Thus, the relation of R/m to longevity for bivalves (Ansell, personal communication) would not hold for the flatfish species. In turn, this would suggest that the short life span in the tropics is not *simply* a result of temperature effects on growth.

It is of interest to explore the ecological consequences during the adult phase. The length of this phase is critical for population survival since in general there must be a sufficiently long period of reproduction to ensure adequate recruitment. Murphy (1968) has pointed out that, as one would expect, there is a relation, in pelagic fish species, between number of spawning generations and variability in recruitment. For *Tellina* in Scottish waters, McIntyre (1970) has shown that successful recruitment may occur only at intervals of several years and this corresponds to a life span of six or more years. Further, McIntyre showed that there were different age distributions in different areas, indicating that each population depended predominantly on local recruitment. From the studies at Loch Ewe (Steele & Baird 1968) and in more productive areas in the Clyde (Steele *et al.* 1973) it can be concluded that food supply is one important factor limiting successful spawning by *Tellina*. Demersal species of fish in the waters around Scotland have very large variations in recruitment and this is an important factor in proper management. For the gadoids (Jones 1973) and for the flatfish (Steele & Edwards 1970), it is probable that variations in food supply during the early stages of life are the critical factors in determining recruitment.

If the Indian populations of fish and bivalves studied here are to have the more regular recruitment required by their short adult life span, then it is likely that food supply must be more regularly available than in temperate areas. In northern temperate areas much of the critical food supply is associated with the spring outburst and this can be variable in timing and in quantity (Cushing 1959; Steele 1974). It is possible that in tropical areas such as the west coast of India there is a longer and more regular productive season, covering much of the period outside the monsoon, and that this ensures an adequate food supply for the adult bivalves or, in the case of the flatfish, permits a long period of spawning and the almost continual recruitment noted by Edwards *et al.* (1971). As described earlier *changes* in temperature play a major role in the spring outburst and temperature is likely to be significant in the productive cycle in the tropics, but these could be effects on variation in food supply rather than a direct factor determining life span.

CONCLUSIONS

Within the context of the five visits made during the I.B.P., the results obtained have illuminated a range of questions but left many problems still to be explored. The great advantage of these comparisons of very different environments is that they increase also our understanding of each environment separately. Comparison of different areas in terms of

biomass of populations is known often to be inadequate and this is very much the case here, where great differences in the production/biomass ratios for bivalves alter completely the picture of the ecosystems derived from population estimates. Severe exposure on temperate beaches can eliminate the bivalve populations but such populations adapt to this on the Indian beaches studied here and they may benefit from the effect of surf action in transferring organic matter from the interstitial sand to the supernatant water. Lastly, and most significantly, there are the differing effects of temperature, ranging from almost complete compensation, to effectively none. It seems likely that these differences, observed in laboratory experiments, will require a considerable range of field observations for their explanation. It is possible that:

(1) High temperatures sometimes but not always correspond to higher metabolic rates and activity.

(2) These higher rates would in turn require higher rates of food intake by each individual.

(3) Populations which have a limited food supply would then have to decrease numbers to increase the food concentration per individual and this would place them at a competitive disadvantage.

(4) Temperature compensation in their metabolic rate is one solution to this problem. (There are obviously other solutions such as development of niches. This hypothesis has the advantage that it operates by selection at the level of the individual.)

(5) Where a population density has no, or small, effect on the density of available food, then higher temperatures can lead to other strategies such as the increase of activity to increase food intake and so permit more rapid growth.

These speculations are built on a minimal number of case histories and even for these the evidence is sometimes circumstantial. They do, however, illustrate the need for ecological information in interpreting the results of physiological experiments.

The areas chosen for investigation, beaches, are marginal to true marine ecology. They have had the advantage of providing very different communities in terms of the nature of the energy input. Also, they are areas where the effects of man can be considerable both through attempts to improve our utilization of the resources and also through possible deterioration in the environment. The results from Loch Ewe indicated that the young plaice were utilizing their available food resources effectively during a critical phase in the life cycle and so no greater production was likely to be achieved by simply increasing their density (Steele & Edwards 1970). The Indian data on *Cynoglossus*, although sparse, imply that these populations are not inherently more productive. On the other hand, the much greater productivity of the bivalves can explain, in part, why these are harvested successfully on many beaches. For both groups, the much shorter life span is likely to make the populations more susceptible to the effects of reproductive failure arising from natural causes, as with the anchovy off Peru, or from contamination of the shore. The bivalve populations, however, are already subject to great environmental stress from beach erosion and might be expected to have greater resilience.

These problems, of overfishing or pollution, usually have arisen in temperate regions. If they extend to their tropical counterparts, there can be a temptation to extrapolate from the former to the latter conclusions about the resilience or fragility of the ecosystems at risk. Such extrapolations would be dangerous, or possibly over-cautious, if they were based solely on general ideas about the differences between temperate and tropical ecosystems. The interpretations proposed here, although requiring much more work, show that the responses of parts of these

ecosystems can be very different, with temperature as only one factor which needs to be related to all the other ecological variables and their interactions.

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REFERENCES (Steele)

- Ansell, A. D. & Trevallion, A. 1969 Behavioural adaptations of intertidal molluscs from a tropical sandy beach. *J. exp. mar. Biol. Ecol.* **4**, 9–35.
- Ansell, A. D., Sivadas, P., Narayanan, B., Sankaranaryanan, V. N. & Trevallion, A. 1972a The ecology of two sandy beaches in South West India. I. Seasonal changes in physical and chemical factors, and in the macrofauna. *Mar. Biol.* **17**, 38–62.
- Ansell, A. D., Sivadas, P., Narayanan, B. & Trevallion, A. 1972b The ecology of two sandy beaches in South West India. III. Observations on the population of *Donax incarnatus* and *D. spiculum*. *Mar. Biol.* **17**, 318–332.
- Banse, K. 1968 Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. *Deep Sea Res.* **15**, 45–79.
- Brett, J. R., Shelbourne, J. E. & Shoop, C. T. 1969 Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *J. Fish. Res. Bd Can.* **26**, 2363–2394.
- Bullock, T. H. 1955 Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.* **30**, 311–342.
- Cushing, D. H. 1959 The nature of production in the sea. *Fish. Inv. London, Ser. 2*, **22**, (6) 40 pp.
- Davies, J. M. 1975 Energy flow through the benthos. *Mar. Biol.* **31**, 353–362.
- Edwards, R. R. C. & Steele, J. H. 1968 The ecology of O-group plaice and common dabs at Loch Ewe. I. Population and food. *J. exp. mar. Biol. Ecol.* **2**, 215–238.
- Edwards, R. R. C., Blaxter, J. H. S., Gopelan, U. K. & Mathew, C. V. 1970 A comparison of standard oxygen consumption of temperate and tropical bottom-living marine fish. *Comp. Biochem. Physiol.* **34**, 491–495.
- Edwards, R. R. C., Blaxter, J. H. S., Gopelan, U. K., Mathew, C. V. & Finlayson, D. M. 1971 Feeding, metabolism and growth of tropical flatfish. *J. exp. mar. Biol. Ecol.* **6**, 279–300.
- Eleftheriou, A. & Nicholson, M. D. 1976 The effects of exposure on beach fauna. *Cahiers de Biologie Marine*. (In Press.)
- Jones, R. 1973 Density dependent regulation of the numbers of cod and haddock. *Rapp. P-v. Reun. Cons. perm. int. Explor. Mer.* **164**, 156–173.
- Kinne, O. (ed.) 1970 *Marine ecology*. Vol. 1, Pt. 1. *Environmental factors*. London: Wiley-Interscience.
- Krishnan Kutty, M. 1967 Observations on the growth rate of the large-scaled tongue sole, *Cynoglossus macrolepidotus* (Bleeker). *Proc. natn. Inst. Sci. India* **33**, 94–110.
- McIntyre, A. D. 1970 The range of biomass in intertidal sand with special reference to the bivalve *Tellina tenuis*. *J. mar. biol. Ass. U.K.* **50**, 561–575.
- McIntyre, A. D., Munro, A. L. S. & Steele, J. H. 1970 Energy flow in a sand ecosystem. In *Marine food chains* (ed. J. H. Steele), pp. 19–31. Edinburgh: Oliver & Boyd.
- McLusky, D. S., Nair, S. A., Stirling, A. & Bhargava, R. 1975 The ecology of a central West Indian beach, with particular reference to *Donax incarnatus*. *Mar. Biol.* (In the Press.)
- McLusky, D. & Stirling, A. 1975 The oxygen consumption and feeding of *Donax incarnatus* and *Donax spiculum* from tropical beaches.
- McNeill, S. & Lawton, J. H. 1970 Annual production and respiration in animal populations. *Nature, Lond.* **225**, 472–474.
- Marshall, S. M. 1973 Respiration and feeding in copepods. *Adv. mar. Biol.* **11**, 57–120.
- Mullin, M. M. & Brooks, E. R. 1970 The effect of concentration of food on body weight, cumulative ingestion and rate of growth of the marine copepod, *Calanus helgolandicus*. *Limnol. Oceanogr.* **15**, 748–755.
- Murphy, G. I. 1968 Patterns in life history and the environment. *Am. Nat.* **102**, 391–404.

- Scholander, P. F., Flagg, W., Walters, V. & Irving, L. 1953 Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* **26**, 67-92.
- Steele, J. H. & Baird, I. E. 1968 Production ecology of a sandy beach. *Limnol. Oceanogr.* **13** (1), 14-25.
- Steele, J. H. & Edwards, R. R. C. 1970 The ecology of O-group plaice and dabs in Loch Ewe. IV. Dynamics of the plaice and dab populations. *J. exp. mar. Biol. Ecol.* **4**, 174-187.
- Steele, J. H., McIntyre, A. D., Edwards, R. R. C. & Trevallion, A. 1970 Interrelations of a young plaice population with its invertebrate food supply. In *Animal populations in relation to their food resources* (ed. A. Watson), pp. 373-387. Oxford: Blackwell.
- Steele, J. H., Munro, A. L. S. & Giese, G. S. 1970 Environmental factors controlling the epipsammic flora on beach and sublittoral sands. *J. mar. biol. Ass. U.K.* **50**, 907-918.
- Steele, J. H., *et al.* 1973 Pollution studies in the Clyde Sea Area. *Mar. Poll. Bull.* **4**, 153-157.
- Steele, J. H. 1974 *The structure of marine ecosystems*. Harvard University Press. 128 pp.
- Trevallion, A. G. 1971 Studies on *Tellina tenuis* Da Costa. III. Aspects of general biology and energy flow. *J. exp. mar. Biol. Ecol.* **7**, 95-122.
- Wimpenny, R. S. 1953 *The plaice*. London: Edward Arnold.