Ecology of tropical soft-bottom benthos: a review with emphasis on emerging concepts *

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Abstract: A review of the tropical soft-bottom literature reveals that several general concepts in benthic ecology, formulated mainly from temperate work, are either in need of modification or are not readily applicable to tropical benthic ecosystems. Several concepts emerge from the present tropical literature suggesting that in comparison with temperate communities: (1) species diversity and faunal densities are not necessarily greater in the tropics, (2) environmental stress (excluding anthropogenic input) is generally more severe, (3) infaunal communities are composed of proportionately more small opportunistic species (4) predation by demersal fishes and crustaceans is more intense, (5) microbes may be a carbon sink in some shallow-water habitats, notably mangroves, (6) production is generally high, but breeding and reproduction are frequently not continuous and, (7) the distribution and abundances of tropical benthos, like most other communities, reflect temporal and spatial mosaics of major regulatory factors (competition, predation, food supply, environmental disturbances).

Several tropical marine ecosystems such as mangroves and coral reefs are unique, and other environments such as continental shelves possess several common features which distinguish them to some degree from their temperate counterparts. To confirm, reject or modify these emerging concepts, several aspects of tropical benthic ecosystems require further study, including effects of wet season activity, physiological tolerances, nutrient recycling, secondary production, benthic-pelagic coupling and pollution. Such information and emerging conceptualizations are necessary to permit proper and informed conservation and management of these unique ecosystems.

Most research on benthic communities has been conducted in temperate, and to a lesser extent, subtropical and boreal latitudes (Gray 1981). Lack of benthic research in tropical regions is due to many reasons, including distance of major oceanographic centers from the tropics, lack of funding and inadequate facilities.

Research into tropical marine benthic ecosystems has, over the past four decades, been sporadic and, until recently, conducted mainly during short-term visits by workers from developed countries. Most early (pre-1970) work was necessarily taxonomic or consisted of compilations of faunal lists. Hence, little comprehensive work exists detailing factors affecting the distribution and abundance of soft-bottom benthic assemblages in the tropics (Longhurst & Pauly 1987).

Recent reviews of tropical estuarine and marine ecosystems (De La Cruz 1986; Alongi 1989a; Hatcher, Johannes & Robertson 1989) have clearly underscored the importance of these systems for the future of mankind, both as significant contributors to the global carbon cycle and as nursery grounds for commercially viable species. Indeed, as pointed out by Hatcher, Johannes & Robertson (1989), conservation and management of tropical soft-bottom systems is critical, but the information necessary to permit the development of proper conservation strategies is insufficient.

The purpose of this review is to briefly examine the existing tropical infaunal literature (but generally excluding mangroves and coral reefs, see review of Alongi 1989a) and to make evident how unique these communities are, to

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formulate a preliminary synthesis of ecological concepts presently emerging from the study of infaunal communities in the tropics.

Tropical Intertidal Assemblages

Abundances, community composition and intertidal zonation.

Table 1 provides a comprehensive, but not exhaustive, compilation of densities of meiofaunal and macroinfaunal assemblages in tropical intertidal habitats. Abundances of heterotrophic microbial communities are not included because nearly all microbial studies to date in the tropics have utilized antiquated techniques such as plate counts. Only recent studies have used modern, more reliable, techniques such as direct counts by epifluorescence microscopy and uptake of radionuclides to estimate microbial activity (Alongi 1988a.b). Data on tropical microalgal abundances (as chlorophyll *a*) does exist, but most of the information is incomparable because of lack of standardized units (e.g., μg Chl *a* per g^{-1} sediment dry weight, per g^{-1} sediment wet weight, per wet cc, per dry cc, etc). However, the comparable intertidal data, mostly from mangrove and coral reef sediments, suggests low (< 10 μg Chl*a* g^{-1} DW) microalgal densities (see review Alongi 1989a).

The data summarized in Table 1 must be considered with caution owing to the different sampling techniques and sieve sizes used, and sediment depths. In fact, many pre-1975 papers examined did not give sufficient information to assess densities per unit area or volume. Nevertheless, it is reasonably clear that the highest faunal densities occur in sheltered habitats, whereas the lowest densities are found in exposed, coarse sandy beaches. As reflected in the tables, most tropical intertidal studies have been conducted on sandy beaches.

Densities of meiofauna and small (< 5 mm) macroinfauna in tropical unvegetated tidal flats and beaches are generally greater than in mangroves where densities of both faunal groups average < 500 individuals 10 cm^{-2} and from < 10 to several hundred animals m^{-2}, respectively (Grelet *et al* 1987; Alongi 1989a). The lower densities in mangroves are probably due to a variety of factors, including possible negative effects of mangrove-derived tannins and lower concentrations of interstitial oxygen and surface microalgae. In contrast, infaunal abundances are greater in coral reef lagoons where sediments are rich in micro - and macroalgae and plant detritus (Grelet *et al.* 1987), and where environmental conditions are more quiescent.

Early tropical studies of intertidal macroinfauna were concerned mainly with zonation of 'species associations', classifying low, mid and high intertidal zones on the basis of the dominant species (Dahl 1953; Gauld & Buchanan 1956; Berry 1964; McIntyre 1968; Vohra 1971). This reflects the application of Thorson's (1957) parallel-bottom community concept –dominant during this time period– to tropical intertidal habitats. Later studies (e.g. Dexter 1972, 1974, 1979; Shelton & Robertson 1981) focussed on comparing different intertidal habitats in terms of species composition, abundance, biomass and diversity.

It is clear that tropical intertidal habitats differ greatly in macrofaunal community composition from temperate intertidal assemblages. Tropical sandy beaches and sand flats are dominated by crustaceans, mainly crabs, and bivalve molluscs and tropical mudflats have a high proportion of polychaetes and microcrustaceans, whereas temperate intertidal habitats consist mainly of polychaetes and gastropod molluscs (see Swennen, Duiven & Spaans 1982; Vargas 1987). Why? Several behavioural studies have suggested that tropical crustaceans and bivalves are more motile and possess more rapid escape mechanisms than their temperate counterparts to avoid high temperatures, salinity and dessication in the tropics (Ansell & Trevallion 1969; McLusky *et al* 1975; Jones 1979). Ocypodid crabs and tellinid bivalves, especially of the genus *Donax* appear to be particularly well adapted to life in the tropical intertidal and several studies have documented their unique life histories (Wade 1967; Ansell & Trevallion 1969; Ansell & Trevallion 1969; Ansell *et al* 1972; McLusky *et al* 1972). However, differences do exist among tropical intertidal regions, as shown in the comparative studies of Dexter (1972, 1974, 1979) and Shelton & Robertson (1981) and must be taken into account before generalizations can be made.

Seasonality and effects of monsoons.

Many of the above-cited studies were conducted during only one season, further limiting

TABLE 1

Densities of meiofauna (No. Individuals 10 cm^{-2}) and macroinfauna (No. Individuals m^{-2}) in some tropical intertidal habitats $\bar{x}$ = mean; range

Locality	Habitat	Meiofauna	Macroinfauna	Reference
Gold coast. Africa	sandy beach		$\bar{x}$ = 4245;0-40,064	Gauld & Buchanan 1956
Porto Novo, India	estuarine sand bar	$\bar{x}$ = 2626; 420-3815	$\bar{x}$ = 1305; 176-3360	McIntyre 1968
	marine sandy beach	$\bar{x}$ = 1405; 395-1010	$\bar{x}$ = 2688; 2656-2720	
	moderately exposed sandy beach	$\bar{x}$ = 1307; 968-1960	$\bar{x}$ = 208; 127-368	
Lebanon	sandy beaches	$\bar{x}$ = 27; 7-68		Hulings 1971
Tunisia		$\bar{x}$ = 196; 101-409		
Morocco		$\bar{x}$ = 148; 29-570		
Shimmary Beach, Panama, Caribbean Sea	carbonate beach		$\bar{x}$ = 193; 25-463	Dexter 1972; 1974; 1979
Naos Is. Panama Pacific coast	quartz sandy beach		$\bar{x}$ = 2439; 1507-4067	
Singapore	sheltered sandy beach		$\bar{x}$ = 5614; 1678-9236	Vohra 1974
Andaman & Nicobar Island. Indian Ocean	sandflat	600-800		Rao 1975
Shertallai. India	sandy beach	$\bar{x}$ = 467; 215-1337		Munro, Wells & McIntyre 1978
Cebu. Phillipines	sandy beach	$\bar{x}$ = 739; 417-1142		Natividad 1979
Texas. USA	sandy beach		$\bar{x}$ = 2700; 335-6616	Shelton & Robertson 1981
Bay of Bengal. India	coarse sandy beach	$\bar{x}$ = 219; 118-381		Rama Sarma & Chandra Mohan 1981
Malaysia	mudflats			
	Sungei Bulok		$\bar{x}$ = 129	Broom 1982
	Kuala Selangor		$\bar{x}$ = 479	
Surinam, S. America	exposed mudflat		$\bar{x}$ = 245	Swennen, Duiven & Spaamo 1982
Mombasa. Kenya	sandy beaches	$\bar{x}$ = 1790; 1013-2560	$\bar{x}$ = 993; 592-2736	Ansari, Ingole & Parulekar 1984
Punta Morales, Gulf of Nicoya, Costa Rica	mudflat	$\bar{x}$ = 898; 653-1078		de la Cruz & Vargas 1987
Gulf of Aquaba. Arabia Sea	seagrass beds; fringing coral sands	$\bar{x}$ = 2369; 922-4239	$\bar{x}$ = 1547; 815-4106	Grelet *et al* 1987
Gulf of Nicoya, Costa Rica	mudflat		$\bar{x}$ = 13,827; 3787-41086	Vargas 1987
Queensland. Australia	sandflat	$\bar{x}$ = 841; 324-4000		Alongi 1988b

comparisons between and among intertidal habitats. Extensive studies conducted in the Indo-Pacific (Ganapati & Rao 1962; Trevallion *et al* 1970; Ansell *et al* 1972; Natividad 1979; Rama Sarma & Chandra Mohan 1981; Broom 1982; Harkantra & Parulekar 1985) have, however, examined seasonality and the effects of monsoons on intertidal infauna. Which season (or seasons) organisms exhibit their highest abundances appears to be dependent on whether the habitat in question is in the wet or dry tropics. Meiofauna and macroinfauna suffer increased mortality during monsoons in the wet tropics due to the fluctuations in salinity and sediment erosion. In the dry tropics, organisms usually attain peak densities in autumn and winter; lowest abundances occur in spring and summer when the absence of cloud cover results in sediments warming to $> 30^\circ$ C.

Infaunal communities also respond differently depending upon the intensity and frequency of the monsoons. For example, in India where cyclones are very intense and prolonged, meiofaunal densities decrease rapidly. In northeastern Australia where monsoons are generally not as prolonged or as intense as those in Southeast Asia or on the Indian subcontinent, meiofaunal densities in tropical mangrove estuaries were most abundant during the summer wet season (Alongi 1989a). These contrasting results may reflect the fact that monsoons occur in different seasons in these different climatological zones. Interestingly, both meiofaunal and macroinfaunal communities appear to be able to repopulate quickly following climatological disturbances in the tropics. The magnitude of seasonal fluctuations is also dependent upon distance from the equator. Habitats bordering the equator, for instance, in Malaysia (Broom 1982) exhibit less seasonal variability than tropical assemblages closer to the poles, reflecting the fact that climate and its effect on intertidal and shallow subtidal benthos varies greatly within the tropics.

Tropical coastal assemblages (estuaries, lagoons, seagrass beds and nearshore subtidal).

Most studies of benthic communities in tropical estuaries and shallow (< 50 m) nearshore regions have been conducted in India (Table 2). Comparatively few comprehensive benthic studies of tropical seagrass beds are extant (Jackson 1973; Heck 1979; Young & Young 1982; Ibañez-Aguirre & Solís-Weiss 1986).

Despite variations in sieve sizes and sampling gear, it is clear that the eastern Indian coastline (e.g. Bay of Bengal) harbors a numerically rich infauna compared to the more highly polluted, stressed western coast (Datta & Sarangi 1986). As discussed later, species diversity is generally low reflecting the dominance of opportunistic species. Outside India, the data indicate poor to moderately rich infaunal assemblages (Wade 1972a,b) with numerical richness apparently related to various stresses such as low salinity and oxygen and low plankton production (Holm 1978).

The Indian studies reveal that tropical subtidal infauna respond negatively to freshwater inputs during the monsoons, but recolonize quickly and are dominated by small, surface deposit– and suspension-feeding polychaetes and bivalves. As with temperate benthos, coastal lagoons in the tropics have also been poorly studied with most studies comprised of faunal lists rather than information on density, biomass and species diversity (Moore *et al* 1968; Holm 1978). The study by Holm (1978) indicates a potentially rich epi- and infauna in moderately flushed lagoons lined with submerged vegetation. Densitites of macrofauna ranged from 1059 to 4700 per m^2 in a seagrass flat (Moore *et al* 1968). In other tropical lagoons not well flushed, high saline waters up to 300 $^0/_{00}$ are common. Jones, Price & Hughs (1978) found a moderately abundant macrofauna ($> 500\ m^{-2}$) in a saline lagoon on the Saudi Arabian coast of the Arabian Gulf. Diversity (as number of species) was low (< 15). These moderately high densities, despite the high salinity, were attributed to comparatively high primary production.

Not surprisingly, there is very little information on functional relationships among tropical subtidal assemblages. In one of the few such studies, Black & Peterson (1988) examined possible adult-larval interactions and competition between suspension-feeding bivalves and smaller infauna in Western Australia. They found that the suspension-feeding bivalves exhibited no evident competitive interactions with, or provided any positive enhancement of, the establishment of the smaller infauna. These results, if found in other tropical subtidal habitats, would help to explain the coexistence

TABLE 2

Densities of meiofauna (No. Individuals 10 cm^{-2}*) and macrofauna (No. m*$^{-2}$*) in some tropical shallow-water, coastal habitats (estuarine and marine)* $\bar{x}$ *= mean, range*

Locality	Habitat	Depth (m)	Meiofauna	Macroinfauna	Reference
Kingston Harbor, Jamaica	marine muds	6-16		$\bar{x}$ = 240; 148-433	Wade 1972a
Shatt-al-arab, Arabian Gulf	carbonate muds	7-15	$\bar{x}$ = 227; 24-599		Saad & Arlt, 1977
Karwar, central west coast of India	estuarine muddy sands and mud	6-8	$\bar{x}$ = 1098; 1022-1250		Ansari 1978
Madovi, Cumbarjua Zuari estuaries, Goa, India	estuarine sand to mud	4-7		$\bar{x}$ = 1653; 492-4382 (total) $\bar{x}$ = 528; 93-2120 (monsoonal)	Parulekar, Dhargelkar & Singbal 1980
Narmada Estuary, India	estuarine sand to mud	3-19	$\bar{x}$ = 53; 0-3164	$\bar{x}$ = 592; 0-4049	Varshney, Govindan & Desai 1981
Krishna, Godavari, Mahanadi, Hooghly rivers, E. coast India	marine muds	15-50	$\bar{x}$ = 813; 502-2149	$\bar{x}$ = 1529; 90-4785	Ansari *et al* 1982
Carrie Bow Cay, Belize	*Thalassia* meadows	1-2		$\bar{x}$ = 12, 167	Young & Young 1982
Carrie Bow Cay, Belize	bore sand	1-2		$\bar{x}$ = 16, 750	Young & Young 1982
Gautami-Godavari estuaries, India	estuarine muddy sands	< 10	$\bar{x}$ = 1386; 245-2194		Kondalarao 1983
South Gujarat estuaries, India	estuarine sands to mud	< 10	$\bar{x}$ = 138; 0-5334	$\bar{x}$ = 122; 0-880	Govindan, Varshney & Desai, 1983
Vellar Estuary, Porto Novo, India	estuarine sand	2-5	$\bar{x}$ = 90; 33-213 $\bar{x}$ = 51 (premonsoon) $\bar{x}$ = 87 (monsoon) $\bar{x}$ = 46 (postmonsoon)	$\bar{x}$ = 94; 78-112 $\bar{x}$ = 80 (premonsoon) $\bar{x}$ = 99 (monsoon) $\bar{x}$ = 75 (postmonsoon)	Fernando, Khan & Kasinathan 1983
Gulf of Nicoya, Costa Rica	marine muddy sands + mud	6-65		$\bar{x}$ = 1269; 0-8744	Maurer & Vargas 1984
Goa, Coast, India	estuarine muddy sands	10		$\bar{x}$ = 1703; 475-310 (premonsoon) $\bar{x}$ = 810; 71-1495 (postmonsoon)	Harkantra & Parulekar 1985
West Bongal, India	estuarine sands	< 10		$\bar{x}$ = 620; 100-2420	Datta & Sarangi 1986

of surface suspension-and deposit-feeders in tropical seafloors.

Tropical continental shelves

Benthic information on tropical continental shelves have likewise been obtained mainly by Soviet and Indian scientists working in the Indian ocean (Table 3). Consequently, the same problems regarding sieve sizes and sampling procedures (different sediment depths; dry weight *vs.* wet weight biomass) prevail, limiting inter-shelf comparisons. Macroinfaunal densities naturally vary widely depending upon sediment type and water depth. There is very little information on meiofaunal densities and biomass on tropical shelves (Table 3).

Despite the lack of data, there appear to be several characteristics common to most if not all tropical shelves which distinguish them, to a limited degree, from temperate continental shelves:

1. Faunal composition appears to be dominated by large epibenthos, lancelets (e.g.

TABLE 3

Densities (No. 10 cm^{-2}) and biomass (mg DW 10 cm^{-2}) of meiofauna and macroinfauna (No. m^{-2} and g DW or g WW m^{-2}) on some tropical continental shelves. $\bar{x}$ = mean; range

		Meiofauna		Macroinfauna		
Locality	Depth (m)	Density	Biomass	Density	Biomass	Reference
Guinea & Senegal shelves, West Africa	20-350			15-1386	1.5-74.2	Longhurst 1958,1959
Mozambique Channel, S.E. Africa	< 31			32-333	5.8-25	Makarov & Averin 1968
N.W. Indian shelf	20-350				$\bar{x}$ = 20; 10-100 (WW)	Neyman 1969
S.W. Indian shelf	20-350				$\bar{x}$ = 5; 0-10 (WW)	
West Pakistan shelf	20-200			196-224	10-15	Savich 1970
Persian Gulf	20-50				$\bar{x}$ = 25 30-35 (WW)	Neyman & Kondritskiy 1974
Bay of Bengal	20-170	$\bar{x}$ = 163; 13-963	$\bar{x}$ = 2.5; 0.2-13	$\bar{x}$ = 517; 58-1644	$\bar{x}$ = 92; 0.06-36.5	Ansari *et al* 1977
Cap Blanc, Spanish Sahara	30-1830			$\bar{x}$ = 8124; 1635-35200	$\bar{x}$ = 26.3; 2.4-94.4 (WW)	Nichols & Rowe ,1977
Goa Coast, India	20-840	$\bar{x}$ = 1217 250-2925				Ansari, Parulekar &
West Indian shelf	10-70			$\bar{x}$ = 708; 543-985	$\bar{x}$ = 11.5; 5.5-24.5 (WW)	Jagtap 1980
Andaman Sea, Indian Ocean	10-200	$\bar{x}$ = 248; 68-438	$\bar{x}$ = 14; 3.6-32.8 (WW)		$\bar{x}$ = 10; 1-37 (WW)	Parulekar & Ansari 1981
Malacca Strait, Indian Ocean	80-320	$\bar{x}$ = 149; 7-200	$\bar{x}$ = 9; 1-27 (WW)	$\bar{x}$ = 258; 118-528	$\bar{x}$ = 15; 0.2-71 (WW)	Ansari & Parulekar 1981
Arabian Sea	10-250		$\bar{x}$ = 1.4 (DW)		$\bar{x}$ = 0.9 (DW)	Rodrigues,
Andaman Sea	10-250		$\bar{x}$ = 0.9 (DW)		$\bar{x}$ = 0.8 (DW)	Harkantra,
Bay of Bengal	20-150		$\bar{x}$ = 0.2 (DW)		$\bar{x}$ = 1.8 (DW)	Parulekar 1982
Hong Kong Shelf	13-23			$\bar{x}$ = 101; 55-183	$\bar{x}$ = 35; 12-155 (WW)	Shin & Thomspon 1982
East African Shelf (12-17°N)	10-100				$\bar{x}$ = 3.5; 0.5-17.6 (DW)	Domain 1982
Peru shelf	35-350				$\bar{x}$ = 45.3; 1-247 (WW)	Rosenberg *et al* 1983
Java, Indian Ocean	5-30			$\bar{x}$ = 463; 330-739		Warwick & Ruswahyuni 1987

Branchiostoma) and large Foraminifera such as *Marginopora* and *Alveolinella* (Buchanan 1958; Longhurst 1958; Gosselck 1975);

2. Across shelf variations are due to several factors, including gradients in depth, carbonate production and sedimentation, infringement of water movement and lack of seasonal water-column turnover (Bukatin *et al* 1982; Longhurst 1983; Alongi 1989b);
3. Infaunal communities are composed mainly of small (< 5.0 mm) opportunists that are surface deposit-and suspension-feeders. This appears to be an adaptive strategy to respond quickly to erratic inputs of nutrients,

low water content (i.e. high compaction) of mostly quartz and carbonate sand and generally warm (> 20°C) sea temperatures (Longhurst 1959: Harkantra *et al* 1980; Alongi 1989b);

4. One common feature of subtropical and tropical shelves is an abundant demersal fisheries, including penaeid prawns and shrimps (Ghana, Buchanan 1958; Sierra Leone, Longhurst 1983; India, Harkantra *et al* 1980; Georgia Bight, Hanson *et al* 1981; Gulf of México, Yingst and Rhoads 1985; central Great Barrier Reef, Alongi 1989b), Demersal populations are probably abundant on these shelves due to the predominantly shallow sandy bottoms and abundant epibenthic and surface infaunal prey;
5. Tropical continental shelves are generally shallow, driven by intermittent intrusions of upwelled, nutrient-rich water and by estuarine outwelling of detritus (probably of low nitrogen content) and input of reef detritus of generally higher nutritional quality. Benthic communities thrive in tropical upwelling regions off Panama (Lee 1978), Peru (Tarazona *et al.* 1988) and northeast Africa (Nichols & Rowe 1977), and in areas of massive estuarine outwelling such as off India (Neyman 1969; Ansari *et al.* 1977). Interestingly, these shelves are commonly subjected to anoxia (with deleterious effects on the benthos) if estuarine inputs and upwelling events occur on a massive scale, too frequently, or occur simultaneously with periods of stagnant water mass, for instance, off the Amazon (Aller & Aller 1986) and off Peru (Rosenberg *et al* 1983).

Comparison of two tropical benthic regimes: the Amazon and central Great Barrier Reef continental shelves.

The comprehensive studies of Aller and Aller (1986) on the Amazon shelf and by Alongi (1989b) on the central Great Barrier Reef shelf provide a rare opportunity to compare and contrast tropical benthic biocoenoses from different biogeographical provinces. The inner Amazon shelf is dominated by massive runoff and sedimentation from the Amazon river and near the river mouth, resulting in an unstable seabed causing either very low or totally absent infaunal communities. Away from the mouth, however, densities of bacteria, meiofauna and macroinfauna are comparatively high due to a more stable seafloor and sedimentation of phytoplankton blooms caused by nutrient runoff from the Amazon (Table 4). Aller & Aller (1986) concluded that the high degree of physical disturbance coupled with low food inputs appear to be the major factors regulating benthic infauna on the Amazon shelf.

In contrast, densities of the major groups are higher on the central Great Barrier Reef shelf probably due to the more stable seabed and greater food input, particularly from export of detritus from individual reefs of the GBR on the outer shelf. Alongi (1989b) concluded that intermediate levels of food input and physical disturbances from trawling and storms regulate benthic standing crops and processes on the central shelf.

Although sedimentary organic carbon and nitrogen concentrations on the Amazon shelf are on average much higher than on the central GBR shelf (Table 4), the amounts are low compared to levels on temperate shelves and other tropical shelves influenced by upwelling (Longhurst & Pauly, 1987). Detrital food limitation and moderate to high levels of physical disturbance appear to be common features of the benthic regimes of both of these tropical continental shelves.

Emerging concepts

It is hoped that the reader has developed, at this stage, some appreciation of tropical seafloor habitats, the assemblages that live in them, and how general concepts in benthic ecology (diversity, stress, disturbances, see Gray 1981) may have evolved with fewer misconceptions and to a more advanced state, if tropical information was obtained and/or considered earlier. In this section, I discuss how some major preconceptions in temperate benthic ecology, when applied to the tropics, are either in need of modification or are not valid.

1. *Species diversity and faunal densities are not greater in the tropics.* The tropics is not a homogenous part of the biosphere. Thus it is not surprising that the greatest range of faunal densities and species diversity occurs here. Older ecological studies conducted primarily in rainforests and on coral reefs indicated highest

TABLE 4

Comparison of major infaunal groups and sedimentary characteristics on the Amazon (Aller & Aller 1986) and central Great Barrier Reef (Alongi 1989b) continental shelves

	Amazon	GBR
Depth range (m)	0-52	15-46
Bacteria (g^{-1} DW)	$\bar{x} = 7.5$; $1.3\text{-}21 \times 10^9$	$\bar{x} = 1.5$; $0.4\text{-}2.7 \times 10^{10}$
Meiofauna (No. 10 cm^{-2})	$\bar{x} = 282$; 0-2045	$\bar{x} = 1520$; 810-3255
Macroinfauna (No. m^{-2})	$\bar{x} = 1038$; 59-3953	$\bar{x} = 2530$; 2060-5406
organic C (%DW)	$\bar{x} = 0.6$; 0.07-0.84	$\bar{x} = 0.25$; 0.05-0.71
organic N (%DW)	$\bar{x} = 0.10$; 0.01-0.14	$\bar{x} = 0.06$; 0.02-0.13
C/N ratio	6.0	4.2
Major sources of detritus	intermittant phytoplankton blooms; river runoff of plant detritus	river runoff of mangrove + terrestrial debris; low phytoplankton input; reef detritus + mucus
Seafloor	unstable, fluid muds to mid shelf; a high physical disturbances from larger river discharges: inner shelf muds to outer shelf quartz sand	stable, compacted sand with low H_2O content; across-shelf gradient of terrigenous to carbonate facies; physical disturbances from trawling and cyclones; river input limited to inner shelf

species richness per habitat in the tropics, especially in the Indo-Pacific region (see MacArthur 1972). Sanders (1968, 1969) hypothesized that physically stable, benign environments such as the tropics favor development of more complex, species-rich communities compared with stressed and/or younger environments where physical factors dominate in regulating community evolution. Even earlier, Thorson (1955, 1957) suggested that species richness increases markedly toward the equator for epifauna of hard-bottoms, although not for infaunal assemblages.

These hypotheses have had their detractors (e.g. Abele & Walters 1979), but modification and refinement of the stability-time idea by Huston (1979) has attained a general level of acceptance. Huston's hypothesis is not centered around comparisons of temperate-tropical species diversity, but in predicting variations in within-habitat diversity as caused by varying levels of disturbance. The model is latitudinally independent and has provided some relief from the old ideas of tropical *vs.* temperate diversity gradients.

I propose that benthic habitats in the tropics are subjected to a wider range of environmental disturbances than temperate habitats, accounting for the wider variation in species diversity of tropical benthos. For instance, in my experience, intertidal regions in the tropics are fairly inhospitable places, where organisms are commonly subjected to very high (>30° C) temperatures, desiccation, low dissolved oxygen levels, low food supply, chemical plant defenses and monsoons. These conditions are generally not borne by temperate organisms. Indeed, Alongi (1987) found low to moderate species diversity and low number of species per habitat for free-living nematodes in mangrove sediments in northern Australia, supporting Hilary Moore's (1972) earlier contention that tropical intertidal organisms are, on average, subjected to greater physical stress than their temperate counterparts. Other benthic studies have found low or moderate species diversity in the tropics again depending on degree of physical stress (Johnson 1970; Wade 1972a,b; Spight 1977; Maurer & Vargas 1984; Warwick & Ruswahyuni 1987).

2. *Environmental stress is generally greater in the tropics.* In addition to the evidence cited above, other examples can be provided to

support this supposition. Shallow inshore communities in regions of intense wet season activity and upwelling are frequently smothered by massive riverine sedimentation (Aller & Aller 1986) or by erosion of estuarine mudbanks (Seshappa 1953). They are frequently stressed by low salinity (Goodbody 1961) and by anoxia caused by the impingement of coastal water masses during heavy continental runoff and subsequent diatom blooms (Harper *et al* 1981; Nichols 1976a,b: Rosenberg *et al* 1983). It is of interest to note that most physiological studies have indicated that tropical organisms are generally not more tolerant to environmental stress than temperate organisms (Mayer 1914; Scholander *et al* 1953).

3. *Tropical infaunal assemblages are composed of proportionately more opportunistic, small-sized species.* Nearly all of the benthic studies cited earlier suggest that conditions on tropical seafloors commonly lead to the development of pioneering seres and retardation of the establishment of large, equilibrium assemblages. Low food supply (oligotrophy), freshwater input, heavy sedimentation or erosion, anoxia, pollution, compaction of carbonate sediments and climatic disturbances (cyclones and monsoons) are generally more typical of subtropical and tropical shelves and coastal areas than in temperate latitudes. Pioneering assemblages are well adapted to respond quickly to patchy food inputs as well as to repopulate after disturbance, that is, they exhibit a high degree of resiliency. The fact that many such organisms are surface or water-column feeders suggests advantages in competing for the limited food supply depositing to the seafloor. The relative abundance of surface infaunal feeders can lead to greater rates of predation by epifauna and demersal organisms. Indeed, as mentioned earlier, demersal fishing industries are reasonably well developed on most shallow, warm water shelves (Longhurst & Pauly 1987).

4. *Predation is more intense in the tropics.* This early ecological paradigm (MacArthur 1972) appears to hold true for tropical benthos. Nearly all of the evidence is circumstantial and based on studies of predation pressure on intertidal gastropods (Bertness *et al.* 1981 and references within). Vermeij (1978) argued that narrow or occluded apertures, thickened shells, low spires and more pointed sculpture on mollusc shells increases from temperate to tropical seas. Experiments conducted in Panama and New England clearly indicate that shell-crushing predation of intertidal gastropds is greater in the tropics. Interestingly, greater predation appears to modify behaviour of tropical intertidal gastropods, such as curtailing their foraging time (Bertness, Garrity & Levings 1981).

Only one similar experiment has been conducted with tropical mudflat infauna (Vargas 1988), the results of which suggest that the role of macropredators (birds, crabs, fish) in controlling community structure is relatively minor. However, a large body of correlative evidence indicates a positive relationship between infaunal biomass and total fish catch on many subtropical and tropical shelves (Longhurst 1959; Savich 1971; Harkantra *et al* 1980; Rosenberg *et al*. 1983; Tarazona *et al.* 1988). Additional circumstantial evidence is provided by the greater proportion of predatory nematodes in coral reefs and mangroves in Australia (Alongi 1987, 1989b) in comparison with temperate nematode communities.

Other trophic relationships such as competition, commensalism and amensalism remain too poorly understood for tropical infauna to elucidate patterns and to compare with trophic interactions among temperate infauna.

5. *Microbes may be a sink for carbon in some tropical shallow-water benthic systems.* Recent carbon flux models of mangrove and coral reef benthos suggest an enormous rate of recycling between microbes and sedimentary carbon pools, implying that microbes are a sink or long-term shunt for carbon in these systems (Stanley *et al* 1987; Alongi 1988a,b,c; 1989b; Boto, Alongi & Nott 1989). This sink hypothesis (Alongi 1988c) evolved from a large body of circumstantial evidence obtained mainly from mangroves in tropical Australia: (1) bacterial standing crop is very large and productivity is high, often exceeding the rate of total primary production, (2) microalgal biomass is low to moderate, (3) the biomass of protozoans, meiofauna and small (< 5 mm) infauna are low compared to other benthic systems, (4) the above- and below-ground particulate carbon pools are large, but the below-ground DOC pool is low to moderate in size, (5) correlative evidence reveals relationships of

bacterial numbers and growth rates with organic carbon, but not with supposed grazers, and, (6) amino acid and DOC fluxes across the sediment-water interface are negligible unless the benthos is poisoned. After poisoning, fluxes of amino acids and DOC from tropical mangrove sediments are large, ranging from 0.08 to 0.2 and from 0.3 to 2.4 g C. m^{-2} d^{-1}, respectively. This latter evidence indicates no net export but large internal recycling of nutrient pools by microbenthos.

In addition, β-glutamic acid, a non-protein amino acid found in some anaerobic bacteria but not derived from mangrove root hairs, leachates, detritus or bacteria damaged during porewater extraction, is a major component of the interstitial dissolved free amino acid pool, suggesting that this amino acid may be a marker for natural bacterial mortality and recycling of bacterial intracellular pools. In fact, the composition of major amino acids found free in pore waters in mangroves and coral reefs and those found in intracellular pools of some sulfate-reducing bacteria are very similar (Alongi 1988c).

If protozoa and meiofauna consume large quantities of bacteria, replenishment of the DOC pool would have to depend on contribution from bacterial consumers. However, based on the above information, this might suggest that the entire microbial-meiofaunal food chain is, in turn, a sink for carbon particularly in subsurface sediments where consumer densities decline rapidly in the absence of biogenic structures (tubes, burrows, some oxidized root hairs). This raises two questions: to what extent are protists and meiofauna consumed by higher organisms? How productive are they and their potential consumers?

6. *Bacterial and infaunal production in the tropics is high, but breeding and reproduction are frequently not continuous.* Valid estimates of benthic secondary productivity exist only for the two most size-divergent groups, bacteria and macroinfauna. Many workers have indirectly estimated meiofaunal productivity using annual turnover rates and mean biomass values.

These estimates must be considered highly questionable if not invalid because of the wide variation of P/B ratios for meiofauna and the fact that this information was derived from temperate organisms. Bacterial production rates are high in the tropics, ranging from 0.01 to 5 g C m^{-2} d^{-1} (Alongi 1989b,c). Production estimates for bacteria in tropical sediments have been considered in another review (Alongi 1989b) and will not be detailed further. Needless to say, lower infaunal biomass and generally warmer temperatures are probably at least two reasons for the higher bacterial standing crop and productivity in the tropics.

Several studies have estimated production of tropical macroinfauna (see review of Steele (1976) for the IBP results, Ansell *et al* 1978; Parulekar, Dhargalkar & Singbal 1980). The study by Ansell *et al* (1978) indicates macrofaunal turnover rates nearly ten times greater in SW India than in Scotland with annual P/B ratios ranging from 6 to 136. They suggest that these higher turnover rates reflect a lack of temperature compensation (as suggested by early physiological studies) and higher rates of predation on tropical organisms.

A larger volume of data indicates that in comparison with temperate counterparts, tropical species exhibit greater metabolism and growth rates on a per weight basis, and shorter lifespans and greater mortality (Nayer 1954; Edwards *et al* 1970; Lewis 1971; McLusky & Stirling 1975; Epifanio & Dittel 1982; Parulekar 1984; Richardson 1987). Breeding and reproductive activity are not continuous for most tropical benthic species with the life cycle of most organisms interrupted by wet season activity or excessive heat (i.e., mortality, hibernation or encystment) (Penzias 1969; Ansell *et al.* 1972a,b; Govidan *et al.* 1972; Vohra 1971) and lunar cycles (DeVries *et al.* 1983a). Tropical crustaceans, for example, *Callinectes* spp., frequently undergo one or more reproductive peaks superimposed on a year-long background of continuous, low-level breeding (DeVries *et al.* 1983b).

7. *The distribution and abundances of infaunal benthos reflect temporal and spatial mosaics of the major regulatory factors.* It is interesting to observe arguments in the literature concerning whether competition, predation or disturbance is the major factor regulating communities. Such views are groundless and intuitively unrealistic to any ecologist who works in the natural environment. Recent papers (e.g.

Dayton 1984, Menge & Sutherland 1987) have adopted more realistic portrayals of the interplay between regulating forces under varying environmental conditions. Not surprisingly, many of these ideas have developed from field experiments conducted in tropical rocky intertidal areas where the relative ease and success of simple manipulations have yielded concrete results (Menge & Lubchencho 1981; Garrity, Levings & Caffey 1986; Menge *et al.* 1986: Ansell & Morton 1987).

One of the more recent attempts to realistically model community regulation is the model of Menge & Sutherland (1987). Applicable to all habitats, the model predicts that, (1) predation and competition are absent or weak in stressful environments, (2) in moderate habitats, predation pressure is still weak, but sessile animals are less affected by stress leading to population densities great enough to initiate competition, and (3) predation ameliorates excessive competition for space (excluding 'predator bottlenecks') in benign environments. Testing in soft-bottom environments is needed to accept, reject or modify the model, but it is an important first step in realistically grappling with food web interactions as affected by changes in the environment. Many of these changes can be as ephemeral as a tidal cycle, further accentuating the concept of communities regulated and structured by a patchwork of many factors constantly changing in time and space.

CONCLUSIONS AND RECOMMENDATIONS

This review was written to provide counter-generalizations and examples to concepts ingrained in the general soft-bottom literature-concepts formulated from often unreliable data (poor methodology, lack of site, sample and season replication) and mostly from temperate information - concerning the structure and dynamics of infaunal assemblages. It is probable, that these counter-generalizations and emerging concepts will be modified or proven wrong to some degree in the future or, in the opposite vein, be uncritically accepted as fact. They are oversimplifications, but the potential benefits of attempting to improve upon general concepts in benthic ecology by considering the tropical component, outweigh the risks.

Another danger is that summarizing the tropical literature mainly by considering abundance data ignores the fact that species may function disproportionately as predicted from their abundances or biomass. In any event, one cannot expect tropical and temperate benthic ecosystems to be similar anymore than temperate deciduous forests are similar to tropical rainforests.

Listed below are topics in urgent need of more study:

1. effects of freshwater discharge, storms and other climatic disturbances;
2. benthic-pelagic coupling on continental shelves, including rate of detritus sedimentation;
3. nutrient recycling (C,N,P) and geochemistry;
4. microbial biomass and productivity;
5. physiological tolerances, especially to temperature and salinity;
6. effects of pollution on community structure and function;
7. secondary production of meiobenthos and macroinfauna;
8. trophic studies particularly demersal fish feeding and interactions among benthic groups; and
9. multidisciplinary, system-level studies combining analyses of water mass movement with sediment chemistry, geology and ecology. Studies of the entire benthic regime are rare.

With increasing population growth and anthropogenic input to coastlines in tropical countries, accurate information on benthic communities is urgently needed for informed and proper management and conservation of these unique ecosystems.

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