Chapter 2

COMMUNITY ECOLOGY OF PELAGIC COPEPODS IN TROPICAL COASTAL WATERS

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ABSTRACT

Tropical copepod communities are more diverse than those of temperate ecosystems, in large part due to the occurrence of multiple species of small copepods belonging to the families Oithonidae and Paracalanidae. We contrast the communities found in tropical estuaries, coasts and the epipelagic of shelf seas based on our own studies in Australian and Indonesian waters and compare these to other tropical systems. Trophic factors related to the predominance of microbial food webs in tropical seas are important in shaping tropical copepod communities, as are swarming and emergence behaviors. "Tropicalization" of plankton resulting from global warming may result in these communities becoming more widespread.

INTRODUCTION

Studies of the community ecology of copepods began in Europe and North America using sampling gear developed to better understand the distribution of keystone species such as *Calanus finmarchicus*, a key determinant of the recruitment success of herring and other commercially important fishes. Consequently, our knowledge of the ecology of pelagic copepods is largely based upon temperate ecosystems, with the calanoid genera *Calanus* and *Acartia* widely regarded as model copepods. Despite the tropical ocean comprising approximately 50% of the area of all open water and 30% of the total area of continental shelf [1], it is less well known than temperate and even polar regions. The copepod communities occurring in the tropics are more diverse than those in temperate regions and differ in species composition. Tropical copepods are small in comparison to the more widely studied copepods

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of temperate ecosystems, consistent with Bergmann's rule that states that body size is smaller in warmer climates both at the interspecific and intraspecific level [2]. Consequently, the use of sampling equipment developed for temperate plankton has meant that the smaller fraction of tropical plankton has been undersampled. Thus, the full diversity of tropical copepod communities has only become apparent since the use of fine mesh nets (<200 μm) has become more widely adopted.

In this chapter we review the community ecology of tropical planktonic copepods. Our purpose is two-fold. Firstly, we seek to describe the copepod communities of characteristic coastal marine ecosystems in the tropics, ranging from those occurring in turbid and turbulent ultra-trophic mangrove-dominated coastal systems to those of clear oligotrophic shelf waters. In the first instance this is based on our own work in tropical Australia (Figure 1) for which methods and taxonomic resolution are comparable, but we draw on comparable studies from elsewhere in the tropics where appropriate. Secondly, we briefly consider the behavioral and trophic factors that influence community structure. We confine ourselves to copepod communities in the epipelagic (<200 m depth) between the tropics of Cancer and Capricorn. Copepod populations in the field are dominated by juvenile stages: nauplii outnumber copepodites that in turn outnumber adults. However, since it is only possible to identify adult copepods to species, this review is based only on the adults.
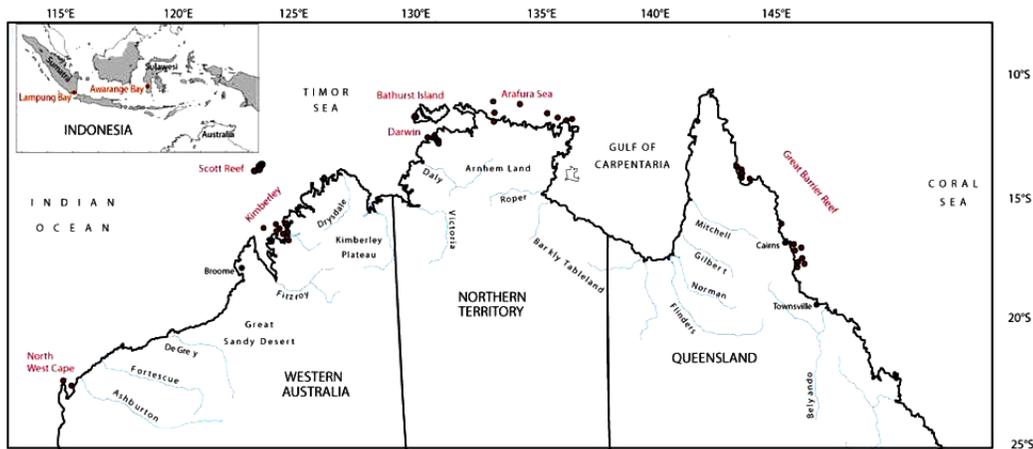

Figure 1. Location of Australian and Indonesian studies referred to in the present work.

TAXONOMIC MAYHEM

The importance of taxonomy cannot be understated when attempting to understand community composition. Unfortunately, tropical ecosystems tend to be understudied in comparison to those in temperate regions, and this is made worse by the small size of the common pelagic copepods: most are <800 μm in total length. Three families dominate tropical pelagic marine copepod communities: the cyclopoid families Oithonidae and Oncaeidae, and the calanoid family Paracalanidae. Indo-Pacific forms of Oithonidae are comparatively well described [3], though many of the smaller species (especially those in the *Paroithona* group) remain undescribed, and there seems little doubt that widely occurring

taxa such as *Oithona simplex*, amongst others, are plural. Epipelagic forms of Oncaeidae are also quite well known, e.g., [4]. This family is, however, characterized by tiny forms that become more diverse in the mesopelagic and for which the taxonomy is much less mature. The family Paracalanidae comprises superficially similar copepods belonging to a number of genera (*Paracalanus*, *Acrocalanus*, *Parvocalanus*, *Bestiolina*, *Delibus*, *Calocalanus*) in which there are many closely related species. Almost without exception, taxonomic descriptions are old and do not reach the standard or conventions of modern copepod taxonomy [5,6]. Consequently, there are many form variants and regional morphotypes that are difficult if not impossible to resolve using the available taxonomy, as a result of which recent taxonomic effort has been redirected toward the use of molecular tools [7]. For instance, *Paracalanus parvus* (Claus, 1863) was widely regarded as being a cosmopolitan species. With increasing frequency, new species have been erected to accommodate local variants of this "superspecies", usually on the basis of minor differences in character states and without consideration of the level of variation within the genus as a whole. For the Australian material of this keystone species, we have adopted the resurrection of the name *P. indicus* for material from New Zealand, which our specimens most closely match based on the comparison of collections from a range of locations [8]. We recognize, however, for this species and for others in the family, that there is an enormous range of regional variation that in all likelihood represent complexes of sibling species, as has been confirmed in molecular studies underway (Cornils, personal communication).

Taxonomic problems are not confined to these families. We believe other common genera also contain cryptic species. There are new records of undescribed or poorly described species with each new study in a previously unstudied area of the tropics. Unfortunately, taxonomy is a dying art, and though molecular tools are improving our knowledge of diversity there appears no easy solution to resolving the routine identification of the basic units of ecosystems.

HABITAT DIFFERENCES IN COPEPOD COMMUNITY COMPOSITION

The community composition of tropical marine copepods varies depending on habitat. Inshore, shallow-water communities are characterized by high abundances but low diversity. For instance, in the mangrove-dominated macrotidal system of Bathurst Island, northern Australia, abundances of adult copepods are high ($>12,000$ adults m^{-3}) but are comprised of only 21 species, with three clear dominants (Table 1). In contrast, at Scott Reef, the location furthest offshore, abundance was low (730 adult copepods m^{-3}), but diversity was high (119 species). Though less oceanic in character, waters adjacent to Australia's North West Cape (NWC) had similar abundances to Scott Reef but had more species (136), probably as a result of the combined effects of greater sampling effort and smaller mesh size (73 μm net used compared to 100 μm net at Scott Reef).

Table 1. The proportion of copepods in total zooplankton, and the abundance (adults m^{-3}) of the 10 most abundant copepod species in 8 tropical environments. Where species reached this criterion in only one environment, they are listed at the bottom of the column, with their abundances in brackets

Species Name	Bathurst Island	Indonesia	Darwin Harbour	Arafura Sea	Kimberley	Great Barrier Reef	North West Cape	Scott Reef
Proportion adult copepods (%)	9	10	11	23	35	12	9	18
Proportion adult copepods + copepodites (%)	98	93	92	83	87	75	72	76
Total copepod abundance	12,235	12,719	5,112	3,692	1,620	1,655	1,092	731
Oithona simplex	1,391	1,697	278	259	138	292	73	118
Euterpina acutifrons	708	889	353	269	200	226	48	
Microsetella spp.	560	351	434	441		65	70	93
Oithona nana		1,723	43	1,021	186	359	126	121
Oithona attenuata	359		368	118	180	89	42	
Parvocalanus crassirostris	3,283	1,743	1,175			274	31	
Bestiolina similis	186		157			17		
Oithona aruensis	5,132	176	1,456					
Oithona rigida		4,706		74			76	
Paracalanus indicus	83					47	84	
Oithona plumifera				109				25
Oncaea spp.						108		108
Parvocalanus dubia		822					32	
Parvocalanus sp. 2				598	462			

Table 1. Continued

Species Name	Bathurst Island	Indonesia	Darwin Harbour	Arafura Sea	Kimberley	Great Barrier Reef	North West Cape	Scott Reef
	Acartia pacifica (189)	*Bestiolina* sp. (188)	*Acartia sinjiensis* (53)	*Oncaea clevei* (177)	*Acrocalanus gibber* (47)	*Ditricho-corycaeus dahli* (39)	*Oncaea waldemari* (32)	*Calocalanus* sp. 1 (19)
	Onychocorycaeus catus (102)	*Spinoncaea* sp. (127)	*Oithona nishidai* (663)	*Paracalanus aculeatus f:minori* (101)	*Bestiolina* sp. 1 (52)			*Calocalanus* sp. 2 (13)
					Canthocalanus pauper (35)			*Delibus* sp.(37)
					Parvocalanus sp. 1 (109)			*Oithona* sp. 4 (23)
								Oithona sp. T (15)

Copepod communities become more diverse with distance offshore. There are three patterns of rank abundance curves in Figure 2, indicating differences in community structure in mangrove, coastal and shelf environments. Mangrove estuaries in Indonesia and Darwin Harbour follow a similar pattern to those at Bathurst Island but are more speciose because of greater exchange with coastal waters. Coastal plankton communities of the Great Barrier Reef (GBR) and Kimberley are similar, but include a greater proportion (1/3) of rare species (i.e., those with abundances <1 m^{-3}), possibly as a result of mixing of offshore water. In contrast, shelf environments (NWC and Scott Reef) have more attenuated rank abundance curves and a much larger proportion (approximately half) of rare species. The Arafura Sea is a special case of coastal community, similar in pattern to the shelf communities but truncated in species number. By contrast, temperate coastal plankton, using the example of data from the L4 Station near Plymouth in the English Channel, has similar abundance of the most common species but is less diverse, though some genera have not been speciated [9].
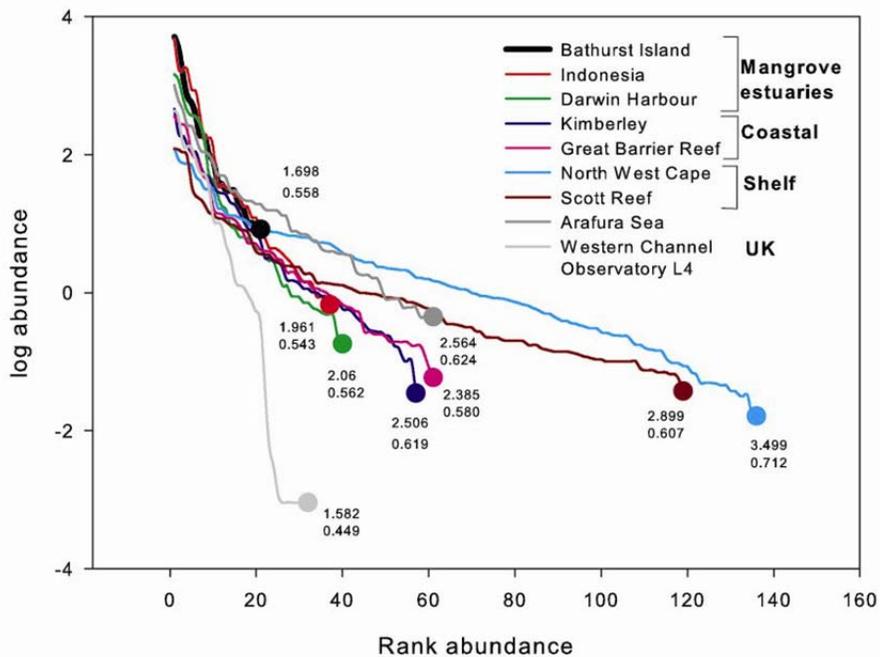

Figure 2. Rank abundance curves ("Whittaker plots") for adult copepods collected in the top 60 m of the water column at 8 locations in tropical Australia and Indonesia. Samples were collected with 73 μm plankton nets, except for the Arafura Sea, Kimberley and Scott Reef studies where 100 μm nets were used. For comparison with temperate communities, the corresponding pattern for 200 μm coastal plankton in the English Channel is included [9]. The top number adjacent to the terminal symbol of each line is the Shannon-Weiner diversity index (H'), and the bottom number is Pielou's evenness (J).

What species characterize these environments? Table 1 lists the average abundance of adults for the 10 most abundant species in each environment, across a depth gradient from inshore to offshore environments. *Oithona simplex* occurred in all environments, and *O. nana* and the harpacticoids *Euterpina acutifrons* and *Microsetella* spp. were present in all but one. Of the 33 species that accounted for the 10 most abundant species in all habitats, 9 belonged

to the cyclopoid family Oithonidae, and 13 to the calanoid family Paracalanidae. In inshore environments, the dominance of *Parvocalanus crassirostris* is remarkable, with abundances up to 50,000 individuals m^{-3} [10]. *O. aruensis* is restricted to inshore environments, and *O. rigida* can reach very high abundances in seagrass dominated systems such as those in the Indonesian Bays. In the English Channel *Oithona*, *Oncaea* and *Paracalanus* are also the most abundant genera, but the importance of *Pseudocalanus* and *Calanus* is distinct from tropical communities. Overall, the abundance of adult copepods at L4 is approximately 1,400 individuals m^{-3}, which is similar to the coastal environments in tropical Australia (Table 1). In other respects, the abundant genera (*Ditrichocorycaeus*, *Acartia*, *Temora*, *Clausocalanus* and *Centropages*) are in common with tropical communities, but differ in usually being represented by only a single species.

Estuaries

In Australia, many tropical estuaries are inverse estuaries in the dry season (i.e., more saline in the inner regions of the waterway) and are dominated by tidal exchange [11]. The biodiversity of estuaries can be conceptualized as a Remane diagram in which the number of species changes along the salinity gradient from freshwater to marine, and in which the truly estuarine component is restricted to only a few species (Figure 3). This concept has recently been revised [12] to more realistically depict estuarine fauna rather than that of brackish seas.
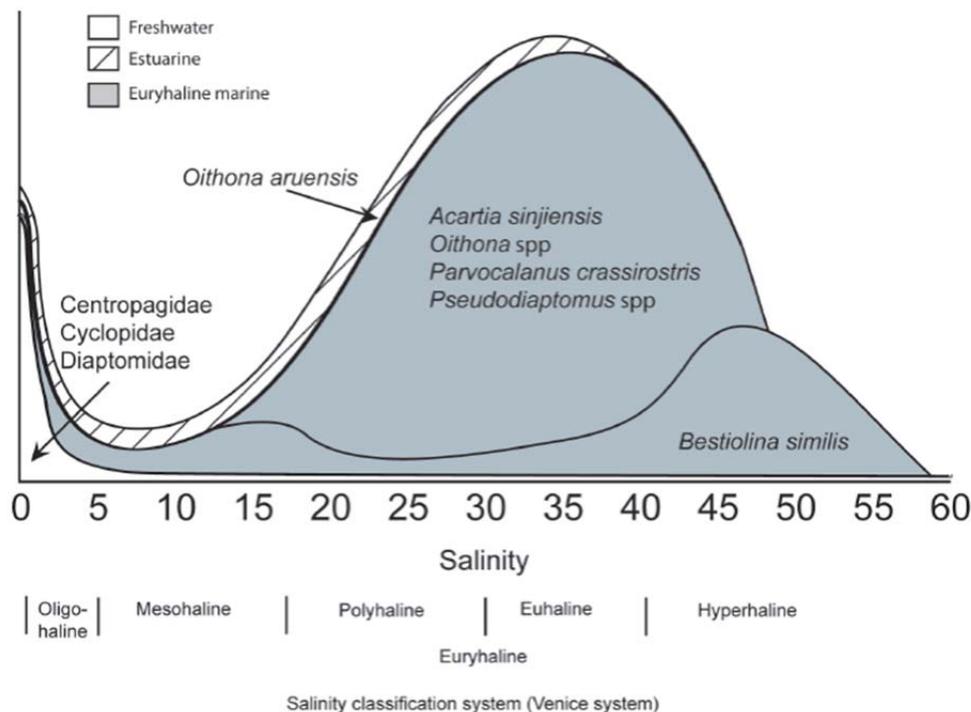

Figure 3. A modified Remane-style diagram [12] for copepod communities in the tropical estuaries of Australia, indicating the dominant species within each community.

There is little information on copepods in the oligohaline region of Australian estuaries (salinity <5), but Australian freshwater zooplankton is dominated by cyclopoid copepods of the family Cyclopidae and calanoid copepods of the family Centropagidae [13]. To our knowledge, cyclopoid communities of northern Australian freshwaters have not been studied. In northern Australia, freshwater calanoids are represented by the centropagids *Boeckella triarticulata*, *Calamoecia lucasi* and *C. canberra* [13]. *C. ultima* and *C. trifida* also occur, as well as the diaptomids *Eodiaptomus lumholtzi* and *Tropodiaptomus australis* [14]. In periods of flood, these species may be flushed into the upper reaches of estuaries, but there are simply too few studies to confirm this.

The mesohaline region (salinity 5–18) is dominated by the truly estuarine component of the fauna, typically *Pseudodiaptomus annandalei* and *P. griggae*, and small species of *Oithona* spp. In North Queensland and Darwin Harbour, the dominant oithonid was *O. nishidai* [10,15], but in Cape York rivers north of the McIvor River the dominant oithonid was *O. robertsoni* (as *Oithona* sp. 1 and *Oithona* sp. 2 respectively, [10]). Consequently, there appears to be a faunal divide in the mesohaline sections of Cape York estuaries, reflected not only in differences in dominant oithonids, but also in the occurrence of *Gladioferens pectinatus* south of the McIvor River [10], a species common in estuaries of SE Australia. Amazingly, *O. nishidai* extended its distribution to the oligohaline region of Darwin Harbour where it reached an abundance maximum of 23,000 individuals m^{-3} [15]. At salinities of 8–25 in Darwin Harbour, the truly estuarine *O. aruensis* was the most common oithonid, reaching densities higher than 6,000 individuals m^{-3} [15].

Euryhaline marine species are important in tropical estuaries, especially during the dry season. In polyhaline and euhaline waters (salinity 18–40) the oithonid species *Oithona simplex*, *O. nana*, and *O. attenuata* co-occur with *O. aruensis*, and the family Paracalanidae (mostly represented by *Parvocalanus crassirostris* and *Bestiolina similis*) clearly dominates the calanoid community. In euhaline waters *P. crassirostris* is generally more abundant than *B. similis* [10]. However, *B. similis* appears to be more euryhaline than *P. crassirostris* since it is found in salinities lower than 3 [15] and is dominant in hyperhaline waters [16]. In addition, the calanoid *Acartia sinjiensis* is widely distributed in tropical Australian estuaries, occurring in salinities as low as 8 in Darwin Harbour [15], and though not generally numerically dominant is often one of the most common copepods, especially as juveniles [10].

The copepod composition of Australian tropical estuaries is broadly similar in structure to that of tropical regions in other parts of the world, based on studies where nets of similar mesh size have been used. Small species of *Oithona* are usually the most abundant copepods, though the species composition depends on the location and may change seasonally. The ubiquity of *Parvocalanus crassirostris* is remarkable, and other paracalanids are common. Though *Acartia sinjiensis* is characteristic of northern Australian estuaries, elsewhere the genus is represented by other species, such as *A. spinicauda* in Malaysia [17] and *A. lilljeborgi* in Brazil [18].

In Indian estuaries, many of the calanoid copepods are marine in origin, reflecting high rates of exchange with coastal waters especially during the dry season [19]. In total, 67 species occur, which may be an underestimate because many studies used coarse mesh nets (> 300 μm). Ten species of Diaptomidae occur in oligohaline waters [19], but the most significant difference between Indian and Australian estuaries is the diversity of Acartiidae and Pseudodiaptomidae. The family Acartiidae has 14 representatives in Indian estuaries. In

the Cochin Backwater of Kerala, India, 9 species of Acartiidae co-occur, with their co-existence facilitated by catastrophic change associated with seasonal flooding preventing the competitive exclusion of "fugitive species" that find refuge in marginal environments [20]. By contrast, the Acartiidae of Australian tropical estuaries is generally represented by one species (*A. sinjiensis*), though others can occur (*A. pacifica*, *A. erthyraea* and *A. fossae*) [15]. The genus *Pseudodiaptomus* is extremely speciose (79 species) [21] and has species that range from fully marine waters to freshwater; 12 species occur in Indian estuaries alone [19] and 5 in northern Australia [15]. Because of its strongly demersal behavior, *Pseudodiaptomus* is generally under-represented in plankton samples collected during the day. Few studies sample widely at night, but some indication of the presence of the genus can be gauged by the occurrence of the nauplii, which are distributed throughout the water column and are distinctive in body form. Similarly, *Temora turbinata* is a common constituent of estuarine zooplankton, and is abundant and sometimes dominant in mangrove estuaries in Brazil [18,22]. This species was also common in plankton samples collected in mangrove estuaries of SE Queensland [23], but in Australia the occurrence of *T. turbinata* is ephemeral.

Coral Reefs

Early coral reef researchers noticed that resident zooplankton communities within coral reefs are different from those in surrounding waters, as a result of the removal of the larger organisms such as larvaceans and large copepods [24,25]. This is because each cubic meter of water that passes over a reef face is visually inspected by *ca.* 500 planktivorous fishes [26], and results in the removal of most of the larger planktonic organisms. Consequently, there is an almost complete absence of large copepods within the waters immediately downstream from coral reefs. However, some copepod species have developed behaviors to avoid the intense predation on coral reefs, including swarming, emergence, bottom avoidance and surface aggregation. Swarming and emergence are not necessarily limited to coral reef environments and we discuss those phenomena in the Behavior section below.

Numerous studies have described patterns in zooplankton abundances near coral reefs such as near-bottom depletion [27], bottom avoidance [28] and surface accumulation [29]. However, these studies have not identified copepods further than to the level of Order, and the distribution of specific taxa has not yet been described. The relative importance of copepods in waters immediately adjacent to coral reefs varies abruptly depending on time of day. Copepods comprised 72–83% of the zooplankton at a fringing reef at Moorea, Tahiti, during the day, but only 26–49% during the night [29]. In the coral reef lagoons of the Laccadives, copepod communities were dissimilar to those of surrounding seas, and abundances were greater at night because of the emergence of copepods from the sediments [30]. Dominant copepods differed between lagoons, with *Dioithona oculata*, *Acartia dweepi* and a species of *Calanopia* most abundant in net tows. In emergence traps, the calanoid *Pseudocyclops* spp. was important [30]. On Caribbean reefs, *Oithona colcarva* is the dominant copepod [31], but is seldom reported where nets with mesh >200 μm are used.

Most coral reefs of the GBR are located within the GBR "lagoon", which is partially isolated from the open waters of the Coral Sea. *Parvocalanus crassirostris* was the most abundant copepod in the plankton at Davies Reef, a mid-shelf platform reef [32]. The reef associated plankton at this location closely resembled that of open water plankton elsewhere

within the lagoon of the GBR [33]. However, the occurrence of swarming species such as *Dioithona oculata*, *Acartia australis* and *Centropages orsinii* caused the community structure within the lagoon to be distinct from that in surrounding waters during summer. The latter two species occur widely in inter-reefal waters, but their increased abundance within Davies Reef lagoon may be the result of some environmental cue that caused them to form swarms [32]. Since swarms form during the day and disperse at night, light cues have been frequently invoked to explain their occurrence [34, 35]. At Davies Reef, emergent taxa such as *Pseudodiaptomus* spp., *Pseudocyclops* sp. and *Stephos* sp. are also present [32].

The presence of small copepods such as *Parvocalanus crassirostris* and species of *Acartia* and Oithonidae are characteristic of the coral reef associated zooplankton in the Indian Ocean, Indo-Pacific and Caribbean Sea, with demersal species of genera such as *Pseudodiaptomus*, *Stephos* and *Pseudocyclops* further distinguishing these communities from those of surrounding waters.

Coastal and Shelf Waters

Copepods account for the majority of the mesozooplankton abundance in open seas of the tropics, though 42% of the zooplankton in the Gulf of Guinea were cladocerans and in the Indian Ocean a similar proportion were ostracods [36]. Overall though, copepods comprise 70% of the abundance and 30% of the biomass of zooplankton in the open tropical ocean [36]. The prevalence of pelagic tunicates such as salps and larvaceans account for a larger proportion of non-copepod zooplankton community biomass in the tropics than in the temperate ocean, probably since these mucous-net feeders are better able to feed on the dominant picoplankton. Moreover, this conclusion [36] was based on plankton samples from the top 250 m of the ocean as sampled by nets with meshes of 200–300 µm. The conclusions therefore ignore the fact that tropical copepods are small, and that in many cases the dominant copepod taxa in tropical waters pass through a 200 µm mesh. The effects of plankton net mesh size on various aspects of copepod community composition were tested in the South China Sea [37], and the abundance estimated with a 100 µm mesh net was more than two-fold higher than that estimated with a 200 µm mesh net. Surprisingly, there were no substantial differences in the abundances of most adult copepods, despite an earlier study finding that up to 92% of oithonids passed through 333 µm mesh nets [38]. There is a widespread lack of appreciation in the literature of the role of small copepods in marine pelagic ecosystems [39,40], particularly cyclopoid copepods such as *Oithona*. The family Oncaeidae is particularly important in tropical waters and is thought to be closely associated with larvaceans. Oncaeid copepods are mostly tiny, with most species having body lengths larger than 400 µm, and are most abundant in the mesopelagic. To fully account for all copepods living in the tropical ocean, fine mesh nets are required, and the use of nets of 50 µm mesh has been recommended [41].

Table 2. Composition of tropical coastal copepod communities

	Bay of Bengal [42]	South China Sea [37]	Jamaica [44]	Straits of Malacca [45]	Great Barrier Reef [46]	North West Cape [33]	Average
Mesh (µm)	200	100	64	140	73	73	
No. of copepod species	17	78	69	117	60	122	
Abundance (ind. m^{-3})	1,151	382	2,450	2,238 – 2,927	1,847	1,092	
% Abundance by Order							
Calanoida	73	67	42	33	28	35	46
Cyclopoida	19	29	53	41	53	51	41
Harpacticoida	8	5	2	14	18	10	10
% Abundance by Family							
CALANOIDA							
Acartiidae	2	5	*	2	1	1	2
Calanidae	2	6	2		1	1	2
Candaciidae		2	1		*	*	1
Centropagidae	4	1	*		1	2	1
Clausocalanidae	2	17	15			*	9
Eucalanidae	1	2	*	2	1	1	1
Lucicutiidae		4	*		*	1	1
Mecynoceridae		0	7		*	1	2
Metridinidae		2	1				2
Paracalanidae	49	25	14	28	21	19	26
Pontellidae	5	1	*		0	1	2
Pseudodiaptomidae	*			*		2	1
Temoridae	8	1	2		2	3	3
Tisbidae							

Table 2. Continued

	Bay of Bengal [42]	South China Sea [37]	Jamaica [44]	Straits of Malacca [45]	Great Barrier Reef [46]	North West Cape [33]	Average
CYCLOPOIDA							
Oithonidae	8	3	26	27	43	34	23
Corycaeidae	6	18	11	2	4	4	8
Oncaeidae	5	7	16	12	6	12	10
HARPACTICOIDA							
Ectinosomatidae	*	4	2	1	4	6	3
Euterpinidae	2	*		11	14	4	6
Miraciidae	6	1	*	2		*	2

Families are only listed where they constituted 2% of the community in at least one habitat, and where species were present but in less than 1% of total copepod abundance they are indicated by *.

To summarize the composition of coastal copepods in various regions of the tropics, we have made a comparison of 6 regions (Table 2). Such comparisons are always prone to bias because of methodological differences, taxonomic biases and differences in oceanographic regimes between environments. All 6 of the studies we have chosen used fine mesh nets (< 200 μm) except in the case of the Bay of Bengal. Copepod abundance was low in the South China Sea because this study spanned coastal and open sea communities, but has been retained because the multivariate analyses in that study demonstrated that the community composition in these environments was similar [37].

Overall, in these 6 examples calanoids comprised 46% of copepod communities, and cyclopoids 41% (Table 2). Calanoids dominated the copepod community in the Bay of Bengal and South China Sea, whereas cyclopoids were equally or more abundant elsewhere. Harpacticoids were most abundant in the GBR, primarily as a result of the prevalence of *Euterpina acutifrons* (Euterpinidae). The Paracalanidae and Oithonidae were the most important families, comprising 26% and 23% of the copepod community on average. The Paracalanidae were most important in the Bay of Bengal [42], where they comprised almost half the total copepod abundance, and even so are probably under-represented in that study because genera such as *Parvocalanus* and *Delibus* are not efficiently sampled by the 200 μm mesh net used. The comparatively high abundances of Clausocalanidae and Corycaeidae in the South China Sea and Caribbean Sea (Jamaica) are probably a reflection of the more open water environments in these studies. In the Makassar Strait of Indonesia, copepods comprised 41% of the fraction of the coastal zooplankton larger than 200 μm [43]. Here, calanoids constituted 66% of the coastal copepod community, and 89 species were recorded. The Paracalanidae accounted for more than 60% of the coastal calanoid community and included over 14 species. The Temoridae were also important, constituting 17% of the calanoid fauna.

The east and west tropical coasts of Australia differ markedly in nature, but their copepod communities are similar. Unusually, both have poleward flowing boundary currents, in the west the Leeuwin Current, and in the east the East Australian Current. The west coast has an extensive shallow shelf and is macrotidal (up to 11 m in tidal range), whereas the east is characterized by the GBR and is mesotidal (up to 5 m tidal range). Shelf waters on the west are strongly physically forced, well mixed and turbid, whereas the waters of the GBR are comparatively clear. Amazingly, given these environmental differences, mean adult copepod abundances on each side of the continent are virtually identical (GBR 1,660 individuals m^{-3}, Kimberley 1,620 individuals m^{-3}). The highest mean copepod abundances from our campaigns occurred in the Arafura Sea (3,690 individuals m^{-3}; McKinnon unpublished), and the lowest at Scott Reef (731 individuals m^{-3}). There appear to be some regional differences in communities however, with the GBR having a richer corycaeid community. Overall, this family constituted more than 20% of the total copepod count in surface waters of the GBR lagoon [47]. From our studies, *Onychocorycaeus agilis*, *O. pacificus*, *Corycaeus speciosus* and *Farranula carinata* occurred in the GBR, but not in Western Australia or the Arafura Sea.

The GBR is 2,300 km in length and up to 330 km in width and extends over 15° of latitude (9 – 24°S). Approximately 90% of the shelf area comprises lagoonal habitat [48], which means exchange with the open ocean is limited by the matrix of coral reefs. The GBR thus provides a good model for pelagic copepod communities of a coastal shelf system. Over 200 species of pelagic copepods have been recorded within this ecosystem [46], and their ecology has been the subject of a number of studies [46,47,49-52]. The study of the Great

Barrier Reef Expedition of the 1920's is focused on the area around Low Isles and includes samples taken adjacent to the outer margin of the GBR, where copepod communities are the most diverse [49]. More recent work concentrated on inshore waters and used 73 μm mesh nets that allow a better account of the smaller fraction of the community [46]. However, the most complete areal coverage of copepod communities is contained in an unpublished study that aimed to parameterize the relationship between zooplankton biomass/abundance and chlorophyll on the GBR, for which an underway pumping system was developed where water was pumped from 2 m below the surface through a 200 μm mesh net [47]. Overall, copepod abundances were patchy (Figure 4), and were positively correlated with chlorophyll concentration. This study was unable to demonstrate any latitudinal change or seasonal change in copepod abundances. However, in the Central zone of the GBR off Townsville, there was a pronounced cross-shelf gradient in abundance: the geometric mean abundance inshore was 543 copepods m^{-3}, on the inner shelf 273 copepods m^{-3}, outer shelf 130 copepods m^{-3}, and in the Coral Sea 73 copepods m^{-3}. We believe these cross-shelf patterns are typical of tropical copepod communities.

All studies to date have identified similar patterns of community structure in waters of the GBR lagoon based on multivariate analyses of species abundances. In each case a distinctive inshore community has been identified, juxtaposed against an offshore (outer GBR or Coral Sea) community, and sometimes (depending on the study) one or two transitional communities in between. Most pertinently, during the wet season, the inshore community extends further out into the GBR lagoon [52,53], abruptly changing the mid-shelf community composition. Similarly, the abundance of zooplankton doubled 16 days after floods associated with the passage of a tropical cyclone [47].

The percentage of total zooplankton attributable to trophic role changes with position across the GBR shelf (Figure 5). On average, copepods constituted 80% of the zooplankton in that study, but the pronounced difference in the proportion of herbivores inshore was attributed to small herbivorous copepods (mostly Paracalanidae) and larvaceans [47]. The higher proportion of omnivores mid-shelf was attributable to increased abundance of *Acartia australis* and *Centropages orsinii*, both of which are associated with coral reefs (see Behavior section). The higher proportion of carnivores in the Coral Sea resulted from an increased abundance of Corycaeidae.

Copepod communities of tropical coastal waters vary in their structure depending upon location, but the overwhelming importance of two families, the Paracalanidae and the Oithonidae is characteristic of all. Each of these families comprise mostly small copepods that are not efficiently sampled by nets of 200 μm or more, which has led to an under-appreciation of the nature of tropical zooplankton, which in turn has compromised our understanding of ecosystem function [54]. In general, tropical coastal plankton communities show little seasonal pattern compared to those in temperate latitudes but can change markedly depending upon events such as flooding and cyclonic activity.
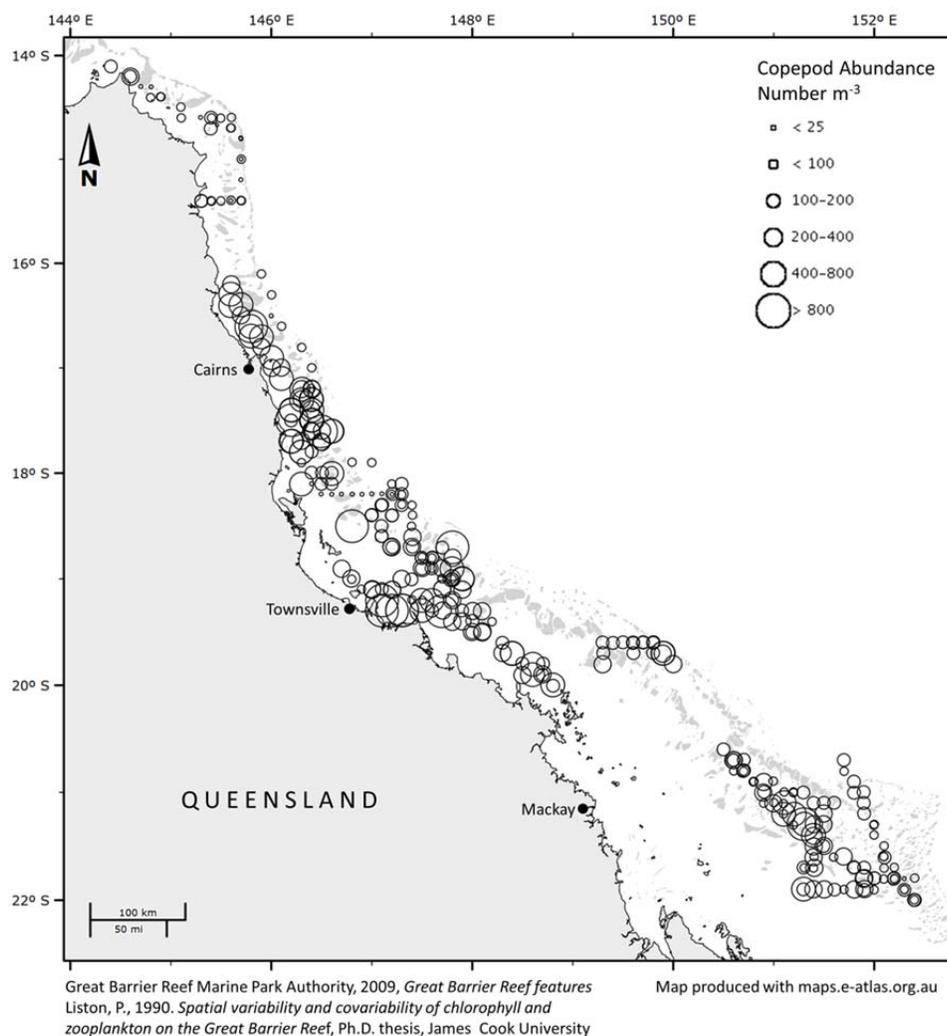
Figure 4. The relative abundance of copepods in the waters of the GBR lagoon [47].

BEHAVIOR

Copepod behavior can greatly influence the community composition of tropical planktonic copepod communities. The formation of swarms (dense aggregations of individuals not organized by orientation) is a feature of some tropical copepod species [34]. *Dioithona oculata* occurs both in coral reef and mangrove environments, where it forms swarms with densities up to 91,000 individuals l^{-1}, apparently in response to light cues [55]. In the mangroves of Belize, swarms of *D. oculata* form in light shafts between mangrove prop roots, whereas on the GBR *D. oculata* forms discrete ball-shaped swarms behind coral heads [32,56]. To maintain position in swarms, *D. oculata* swims at speeds up to 2.0 cm s^{-1}, corresponding to 25 body lengths s^{-1} [55]. A number of tropical species of the calanoid genus *Acartia* have been observed forming swarms. These include *A. (Acanthacartia) spinata*, *A.*

(Acanthacartia) tonsa, *A. (Acanthacartia) fossae* (as *A. hamata*), *A. (Odontacartia) bispinosa* and *A. (Odontacartia) australis* [34]. On the GBR, *A. australis* forms a blanket in shallow well-lit waters over coral sand on the bottom of the reef lagoon [32,56]. In addition, *Centropages orsinii* forms near-bottom swarms [32]. There is circumstantial evidence to suggest that *Dioithona rigida* also forms swarms, based on highly overdispersed plankton counts, especially in seagrass habitats such as beds of *Enhalus* in Indonesia [57].
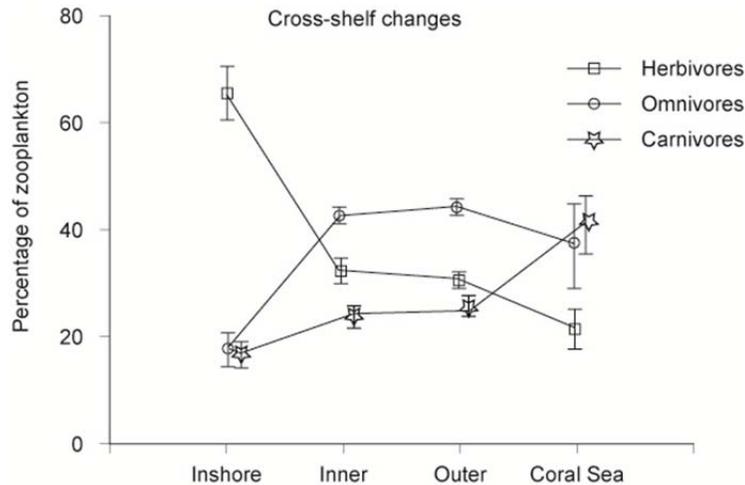

Figure 5. Cross shelf differences in the proportion of zooplankton attributable to three trophic types [47].

Patterns of vertical migration are subtle in most tropical copepods, and there has generally been insufficient sampling at scales fine enough to detect the vertical movement of any but the most obvious migrators, species of *Pleuromamma* in particular. On the GBR, there are only significant day-night differences in abundances of the larger copepod taxa (*Canthocalanus pauper*, *Undinula vulgaris*, *Temora turbinata*) [46]. It is likely that the small copepods dominating shallow water tropical communities do not have sufficient swimming power to overcome bottom-generated mixing and turbulence. Our knowledge of the fine scale vertical distribution of small copepods is limited by the small number of studies where sampling has been undertaken at sufficient resolution to resolve the comparatively small amplitudes of migratory movements. When a Longhurst Hardy Plankton Recorder was used to map distribution of copepods in oceanic waters of the eastern tropical Pacific it was demonstrated that a large number of tropical pelagic copepods have distinct depth preferences and that there are detectable day-night differences in the depth of maximum abundance [58]. In oceanic waters, small amplitude vertical migrations have been demonstrated for a number of taxa, and can also extend to an amplitude of approximately 80 m in the case of *Triconia conifera* [59]. At Scott Reef, depth stratified sampling indicated that some small copepod taxa (5 species of *Oncaea* and 2 of *Triconia*) were undertaking diel migrations [60].

The most pronounced vertical movement of copepods in shallow tropical waters is the emergence of copepods from sediments into the water column. At Heron Reef in the southern GBR, four emergent species of *Stephos* and 3 emergent species of *Pseudodiaptomus* occur [61]. Because these animals are seldom caught using conventional plankton sampling techniques, only one species of each of these genera was previously known to science (*S.*

tropicus and *P. colefaxi* respectively). The behavior of emergent species is complex, depending on substrate preferences, the stage of the moon and seasonal differences [61,62]. The genus *Pseudodiaptomus* demonstrates emergent behavior in a wide range of habitats [63]. In addition, the harpacticoid *Metis holothuriae* and the calanoid *Pseudocyclops* spp. also showed emergent behavior at Heron Reef [62]. In the tropical southwestern Atlantic, *Calanopia americana* shows pronounced patterns of emergence [64]. Overall, emergence appears strongly under the control of light, as emergence and reentry patterns are cued by nightfall and appear stronger on non-moonlit nights [65].

TROPHIC DETERMINANTS OF COMMUNITY COMPOSITION

Most primary production (> 80%) in tropical marine waters originates from cells < 2 μm in size, i.e., the picophytoplankton [66]. Cells of this size range are too small to be consumed by copepods. Though copepods, especially many of the small calanoids, are traditionally regarded as herbivores, this is unlikely to be the case in tropical environments because phytoplankton cells sufficiently large to be grazed on by copepods only occur in ephemeral blooms such as those arising from upwelling or storm activity. Consequently, the most important grazers of picoplankton production are the protistan community (heterotrophic nanoflagellates, ciliates and hetero/mixotrophic dinoflagellates), in combination grazing 75% of primary production in the tropics [67]. It is these organisms that constitute most of the diet of pelagic copepods. However, there are a couple of other linkages that are very important for the trophic ecology of tropical pelagic copepods. Firstly, because of the dominance of microbial food webs in tropical seas, mucous net feeders, especially pelagic tunicates, are very important. Larvaceans are at times as equally abundant as copepods and have fast growth rates. They discard multiple houses each day, which are rich in organic matter and form the basis of aggregates that are colonized by a wide range of microbiota, from bacteria to ciliates. Many species of copepods are known to utilize these resources, but particularly the family Oncaeidae [68], which is most abundant in the tropical mesopelagic zone. Secondly, and related to the first, is the predominance of marine snow in the water column, which combines small particles into aggregates of sufficient size to be fed upon by mesozooplankton. The importance of this detritus in the diets of tropical pelagic copepods has yet to be fully understood but is likely to be significant.

The Oithonidae are usually regarded as raptorial carnivores, with a preference for ciliate prey [69], but can also be herbivorous [70], carnivorous [71], detritivorous [72], and coprophagous [73]. Generally, *Oithona* appears to be broadly omnivorous [54]. Similarly, paracalanid copepods have been regarded as herbivorous [74] but can also be carnivorous [75], and we therefore conclude that the broad dietary preferences shown for *Oithona* are also likely to be the case for other common small copepods such as *Parvocalanus crassirostris*. The dominance of these taxa in turbid and detritus-rich mangrove environments supports their close linkage to microbial foodwebs associated with the breakdown of organic material originating from the forests. Pelagic harpacticoids of the genera *Macrosetella*, *Miracia* and *Oculosetella* graze on the cyanobacterium *Trichodesmium* in the Caribbean [76], and we believe this is also the case for *Microsetella* in waters of the GBR. *Trichodesmium* forms huge surface slicks in the waters of the GBR [77], and zooplankton samples in these

conditions are dominated by *Microsetella* (McKinnon, pers. obs.). There are some small copepods, however, such as the Corycaeidae, which appear to be purely carnivorous [78, 79].

The nature of tropical copepod communities, then, is determined by the predominance of microbial and detrital food webs, in contrast to the stronger influence of the "classical" food web in temperate regions and the greater importance of herbivory within these.

THE "TROPICALIZATION" OF TEMPERATE COPEPOD COMMUNITIES

Marine plankton are useful indicators of climate-driven changes in marine ecosystems, and calanoid copepods in particular have proven useful in demonstrating changes in distribution primarily attributable to effects of warming [80]. In temperate seas such as the Northeast Atlantic, warm-water species such as *Calanus helgolandicus* have extended their range at the expense of cooler water congeners such as *C. finmarchicus* [81]. In the Northeast Pacific, subtropical species (*Acartia danae*, *Candacia bipinnata*, *Clausocalanus* spp., *Corycaeus* spp., *Mesocalanus tenuicornis*, *Pleuromamma abdominalis* and *Undeuchaeta major*) are becoming more prevalent [82]. It stands to reason, therefore, that in a warming ocean, tropical copepods should become more widespread. Unfortunately, there are few time series of sufficient duration to demonstrate the increased range of tropical species, though there are tantalizing suggestions that this may be occurring.

Parvocalanus crassirostris is primarily a tropical and subtropical species [21], but its range may be extending. There are increasing numbers of reports of *P. crassirostris,* and it is unclear whether this is occurring because of real changes in distribution and abundance patterns, or is a result of the more widespread use of fine mesh nets. *P. crassirostris* is known to occur in the Mediterranean [21], but has been newly recorded in the Adriatic [83] where it occurs at densities up to 28,000 individuals m^{-3}. Oddly however, the peak abundance occurs in cool months (October–December). *P. crassirostris* is now dominant in the East China Sea [84], despite it not being recorded in the area in the 1960's [85,86]. Each of those studies recorded cyclopoid species of similar size as *P. crassirostris*, so this is not simply an effect of plankton net mesh size. The increased abundance of *Temora turbinata* in China may be evidence of a poleward extension of a warm-water species attributable to global warming [87].

In Australia, there is evidence that warm-water "signature" species are moving southward into Tasmania [88]. This conclusion was based on *Acartia danae*, *Pleuromamma gracilis*, *P. quadrangulata*, *Subeucalanus crassus*, *Temora turbinata*, *Sapphirina* spp., and *Corycaeus* spp. contributing to the discrimination of a cluster of samples in an ordination analysis belonging to warm years. However, all these species have distributions well into temperate areas and even the subantarctic [21].

The phenomenon of "tropicalization" of temperate plankton communities has potentially important ecosystem consequences. Since warm water copepods have less food value than cold water species, food chains may be impacted, resulting in loss of "societal value" [82]. Range extension is directly attributable to climate-driven warming, and is distinct from other more directly anthropogenic effects such as invasions of alien species [89] and changes from large to small species as a result of eutrophication [90], each of which occur independently of ambient water temperature.

CONCLUSION

We commenced this review by remarking on how much our knowledge of not only the community ecology of pelagic copepods, but of their ecology in general, is shaped by the long tradition of research in temperate ecosystems. However, our increasing knowledge of subtropical and tropical zooplankton together with the more widespread use of fine mesh nets, leads to the inescapable conclusion that small copepods, together with larvaceans, are the most important metazooplankton in tropical waters. In all the environments considered in this review, the dominance of Oithonidae and Paracalanidae is striking. For instance, on the shelf of NW Australia 15 species of Paracalanidae (31% of total copepod abundance) and 11 Oithonidae (50% of total copepod abundance) co-occur [33]. It remains a mystery how so many species of these families co-exist, and how their ecological niches are distinct.

Consequently, if we were to choose a model copepod representative of subtropical and tropical marine waters, rather than *Calanus* or *Acartia*, it should be a representative of the Oithonidae or Paracalanidae. The genus *Oithona* is ubiquitous and abundant in a wide range of habitats, but is represented by different species in each. In contrast, *Parvocalanus crassirostris* dominates numerically in many tropical coastal waters, though admittedly molecular taxonomy may yet demonstrate that this species is plural. If we were to choose a single species to be a model tropical copepod, then what better candidate than *P. crassirostris*? To date, however, there is not a single study on the biology of this species and we can only guess at the ecological role of *P. crassirostris* based on studies of other larger, temperate paracalanids. Realistically, however, conventional experimental methods used for copepod research become challenging when dealing with one of the smallest calanoid copepods , as *P. crassirostris* is only about 500 μm long as an adult.

Tropical pelagic copepods grow and thrive in environments characterized by warm temperature and low chlorophyll, and in which microbial food webs predominate. Temperature drives fast metabolic rates, and in most tropical coastal environments the particle field is dominated by detritus, whether in the form of marine snow in coral reefs and shelf environments, or as resuspended particulate material in mangrove systems and in turbulent macrotidal coastal environments. The same environmental factors influence the predators of copepods in these systems, i.e., chaetognaths, ctenophores, medusa and larval fish in the plankton, as well as a vast array of benthic suspension feeders. Copepods are caught in the crossfire between finding sufficient food to fuel fast metabolic rate, yet avoiding intense predation. We have much to learn to understand how these competing factors combine to shape community structure.

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