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REPORT

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Estimates of species diversity of free-living marine isopod crustaceans on coral reefs

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Abstract A core group of isopod crustacean genera appears to be present at many coral reef sites. Within these genera, however, species show high local endemicity. Based on the estimated percentage of endemism for the Atlantic (19% for individual sites, 90% for the tropical western Atlantic as a unit), the Indian Ocean (50%), the eastern-central Pacific (80%), and the western Pacific (40%), it is estimated that there are some 5,000 to 13,000 isopod species in the world's coral reefs, and that some 2,000 to 6,000 of these are endemics. (At present, approximately 4,400 species of marine and 560 species of freshwater isopods have been described.) Based on the crudely estimated relative abundances of other peracaridan crustaceans in coral reefs (compared to isopods), the total diversity of reef amphipods, tanaidaceans, cumaceans, and mysidaceans is approximately 54,500 species.

Key words Isopod · Crustaceans · Diversity · Endemism

Introduction

Faunal diversity on coral reefs has received much attention, and there is frequent talk of its equivalancy to tropical rain forests with regard to richness of species (e.g., Dauget 1995; Reaka-Kudla et al. 1996). Measures of reef biodiversity are most frequently based on macro-components like corals, bryozoans, fishes, large mollusks, and crabs. Largely ignored for lack of data and the difficulty of quantitative sampling, are the hordes of cryptic microfauna, almost exclusively invertebrates, that constitute a major component in the food chain and biomass of reefs. For example, the peracaridan crustaceans (amphipods, isopods, tanaids, mysids, cumaceans) are abundant and diverse on reefs, but few published reports and even fewer quantitative studies are available (see Kensley 1983; Briggs 1994).

There are about 4500 valid described species of marine isopods (Kensley and Schotte 1995). Isopods, exclusive of the primarily terrestrial Oniscidea, occur in most marine habitats, from the tropics to the poles, from the high intertidal to the abyss. Early published reports seemed to imply a greater isopod diversity in temperate regions than in the tropics. Early reports also indicated considerable diversity in the deep sea (Beddard 1886); later deep-sea benthic studies increasingly confirm the high diversity of deep-sea benthos (Lambshead 1993), including the Isopoda (Hessler and Sanders 1967; Hessler et al. 1979; Poore and Wilson 1993). The diversity of isopods in the tropics, however, and especially on coral reefs, has been more slowly revealed. Fine-scale collecting of microhabitats on reefs has demonstrated a high diversity of peracaridan crustaceans in general, including isopods (Roman 1970; Kensley 1983). Sampling by trapping on reefs has also revealed speciose guilds of scavenging crustaceans whose presence was previously unsuspected (Keable 1995). Bruce (1994) gives preliminary numbers of cirolanid isopods from Madang, Papua New Guinea, and notes that there are more species at this single site than in the entire Caribbean. Sampling of microhabitats at reef sites in the Western Atlantic, tropical Indian Ocean, and Great Barrier Reef has given rise to an impression of a pattern of high specific endemism in a number of almost ubiquitous genera. Additionally, the occurrence of a suite of co-occurring genera seemed predictable, regardless of reef locality. Surprisingly, this pattern has not been confirmed for the Hawaiian and Galapagos archipelagoes which, although well collected for some crustacean groups such as the decapods, are still poorly known with respect to other groups. Thus, only 16 species of free-living shallow

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water isopods have been recorded to date from Hawaii, and only 17 from the Galapagos (Brusca 1987).

Several questions can be posed, relating to the diversity and distribution of isopods on coral reefs:

1. Do certain taxa co-occur so that there is a predictable suite of isopod genera that may be found at almost any coral reef site?
2. What is the composition of the species within these co-occurring genera, i.e. do they include both endemic and widespread species?
3. Can isopods provide a rough quantitative basis for predicting the order of magnitude of microfaunal biodiversity?

Materials and methods

In an attempt to provide some data to address these questions, the isopod fauna from six island reef localities were listed by genus, with the number of species within each noted, and endemicity indicated (Table 1). Records included were strictly from reefs; species from nearby mangroves, seagrass beds, and lagoonal sandy habitats were not included.

Six island sites were chosen, based on my familiarity with their fauna, and/or the existence of reliable records of reef isopods for them (Table 1). In the case of those areas which I sampled, often repeatedly, (Carrie Bow Cay, Cuba, Aldabra Atoll, Lizard Island), the sampling technique has been the same, enhancing the level of comparability of these sites. This sampling includes bagging smaller coral rubble accumulations in situ, along with large lumps of dead coral, the latter being broken up later on shore. All rubble and coral pieces are immersed in seawater with a few drops of formalin added, and oxygen depletion allowed to proceed. The sample was then repeatedly washed in clean seawater, the rubble and dead coral pieces discarded, and the remnant fixed and preserved for later detailed sorting. The six sites were as follows:

1. Carrie Bow Cay, Belize (records taken from Kensley and Schotte 1989).
2. Cuba (based on material from two collecting trips in April 1994 and June 1995).
3. Turks and Caicos Islands (records taken from Schotte et al. 1991).
4. Aldabra Atoll, Indian Ocean (records taken from Kensley 1988, but also based on unpublished material collected during five field seasons).
5. Lizard Island, Great Barrier Reef, (records taken from Bruce 1986, Cohen and Poore 1994; Harrison and Holdich 1982a, b, 1984; Kensley 1982; Poore 1975, 1978; Poore and Kensley 1981; and Poore and Lew Ton 1985, 1986, 1988a, b, c, d, 1990, as well as unpublished records from two collecting trips by the author).
6. Society Islands, Pacific Ocean (records taken from Müller 1989a, b, c, 1990a, 1991a, b, c, 1992a, b, 1993a, b, as well as unpublished data of W. Moore).

Results and discussion

The level of endemism for individual sites in the broad Caribbean area (sites 1–3) is lower than that of the Pacific or Indian Ocean sites. However, for the three sites combined, all but seven (8.5%) of the 82 species (*Paradella dianae*, *Mesanthura pulchra*, *Carpias triton*, *Carpias minutus*, *Paracerceis caudata*, *Amakusanthura magnifica*, *Xenanthura brevitelson*) are endemic, i.e., not occurring outside the Caribbean region. There is thus a 91.5% level of endemism for coral reef-dwelling isopods of the Caribbean region. Although evidence is lacking, regional endemism may also be the norm for large areas like the Great Barrier Reef and the large archipelagos of Indonesia and the Philippines.

Core genera

Of the 45 genera listed in Table 1, 18 occur on coral reefs in all three oceans. The anthurideans are particularly well represented on reefs, with 23 genera, of which eight are found in all three oceans. Perhaps the slender cylindrical body form is particularly well suited to the multitude of crevices, hollows, burrows, empty tubes and shells found in reefs, while the variety of feeding types demonstrated by the group, including scavenging, microherbivory, micropredation, and sucking herbivory, all demonstrate how the habitat has been exploited. Free-living marine isopods, along with the rest of the peracaridans, are characterized by low egg production (seldom more than 100 eggs per marsupium, more usually less than ten), and direct development of young with no planktonic dispersal stage. Given these characteristics, the widespread presence of core genera in all three tropical oceans suggests a long history of dispersal with tectonic plates, with localized speciation accounting for regionally high endemism.

Estimating diversity

The following attempt at making this estimate starts with actual numbers of species at several sites, then makes a number of assumptions based on these numbers. With each level of assumption, the reliability of the numbers obviously decreases. The resulting indication of the order of magnitude of the numbers of species thus needs to be treated with suitable caution.

Let us assume, on the basis of the divisions made by the Revised Sixth Edition of the National Geographic Atlas of the World (1992), that there are 16 tropical island-groups in the western Pacific, and 24 island groups in the eastern-central Pacific. The line of division between these Pacific regions is the western edge of the Pacific Plate. Let us also assume 19 tropical island groups in the Indian Ocean. The entire Caribbean region is treated as a single large archipelago.

Let us assume (conservatively, based on Table 1) the presence of 50 reef species per western Pacific island site, 36 species per eastern-central Pacific site, 40 species per Indian Ocean site, and 30 species per Atlantic site. To provide some sense of range, a maximum and minimum of 20 species above and below the actual species numbers (Table 1) are also used. It is reasonable to expect some sites to have as many as 70 species,

Table 1 Numbers of species of Anthuridean, Asellotan, Flabelliferan, and Gnathiidean isopod genera from the reefs of 6 island sites. For each site, the first figure represents the number of species known, the second figure represents the number of endemic species (i.e. only recorded from that locality) of that genus

	CBC		Cuba		T and C		Aldabra Atoll		Lizard Island		Society Islands	
ANTHURIDEA												
[a]Accalathura	2	1	1	–			2	2	3	1	1	–
Aenigmathura									1	1		
[a]Amakusanthura	2	–	2	–	1	–	1	1	4	1		
Anthomuda							1	1	1	–	1	1
[a]Apanthura	1	–			2	–	1	1	3	–	2	2
Apanthuroides	1	–					2	1			1	1
Bourbonanthura											1	1
Chalixanthura	1	1										
Colanthura s.l.					1	1	1	–			2	1
[a]Eisothistos	1	–	1	1	1	–	1	1	1	1	1	1
Galziniella											1	1
Haliophasma									1	–		
[a]Kupellonura	1	–					1	1	2	–	1	1
Leptanthura							2	1	1	–		
Licranthura	1	1			1	1						
[a]Mesanthura	5	–	6	1	4	1	1	1	6	?		
Minyanthura	1	–	1	–							1	1
Neohyssura							1	–				
Panathura							1	–	1	–	2	1
[a]Paranthura	2	–					1	1	1	1	1	1
[a]Pendanthura	2	–	1	–	1	–	2	2	1	1	2	1
Sauranthura									1	1		
Xenanthura					1	–						
ASELLOTA												
[a]Carpias	3	1	3	–	4	–	1	–	1	1		
Halacarsantia											1	1
[a]Joeropsis	2	–	3	2	1	–	4	1	1	1	4	4
Mexicope					1	–	1	1				
[a]Munna	1	–	1	–	2	–	1	1	1	1	1	1
Munnogonium											1	1
Pleurocope	1	–	1	–	1	–			1	1		
Prethura							1	1	1	1		
[a]Santia	1	–	1	–	1	–	1	–	1	1		
[a]Stenetrium s.l.	6	–	3	–	4	1	3	1	4	4	5	4
Stenobermuda					1	–	1	1				
FLABELLIFERA												
Cilicaeopsis									1	–		
[a]Cirolana	2	–	1	–	1	–	3	1	4	2	1	1
[a]Cymodoce	1	–	1	–			1	–	1	–		
Dynamenella	2	–	2	–					2	–		
[a]Eurydice	1	–	1	–			1	–	1	–		
[a]Metacirolana	3	2	2	–	2	–	1	1	1	–	2	2
Neonaesa									1	–	1	–
Paracerceis	3	1	1	–	2	–						
Paracilicaea							1	–				
Paradella			2	–					1	–	1	1
GNATHIIDEA												
[a]Gnathia s.l.	3	1	3	–			3	3	3	2	2	2
Totals	49	8	37	4	32	4	41	24	52	21	36	30
% endemics		16		11		13		58		40		83

[a] Occurring in Atlantic, Pacific, and Indian oceans. CBC, Carrie Bow Cay, Belize, T and C, Turks and Caicos Islands

while others (obviously very small or degraded localities) may have as few as 10 species.

Assume a level of endemism (i.e. species restricted to a single island group, and based on Table 1) of 40% for the western Pacific, 80% for the eastern-central Pacific, 50% for the Indian Ocean, and 90% for the Caribbean Atlantic. Table 2 summarizes these numbers.

The reef systems of major tropical islands and continental coastlines are frequently more extensive (in terms of spread and total volume of microhabitats

Table 2 Total number of species and endemic species, for Western Pacific, Eastern/Central Pacific, Indian Ocean, and Caribbean island groups

For 24 Eastern/Central Pacific island groups, and an 80% level of endemism:		
Maximum	$24 \times 56 = 1344$ total species	1075 endemic species
Actual	$24 \times 36 = 864$	691
Minimum	$24 \times 16 = 384$	307
For 16 Western Pacific island groups, and a 40% level of endemism:		
Maximum	$16 \times 70 = 1120$ total species	448 endemic species
Actual	$16 \times 50 = 800$	320
Minimum	$16 \times 30 = 480$	192
For 19 Indian Ocean island groups, and a 50% level of endemism:		
Maximum	$19 \times 60 = 1140$ total species	570 endemic species
actual	$19 \times 40 = 760$	380
Minimum	$19 \times 20 = 380$	190
For the Caribbean as a unit, and a 90% level of endemism:		
Maximum	68	61 endemic species
actual	48 total species (for Carrie Bow Cay)	43
Minimum	28	22

Table 3 Estimates of number of island–equivalents, based on rough estimates of tropical coastline lengths

Pacific Ocean	
Pacific Central and South America	10
Indonesia	20
Philippines	20
Papua New Guinea	10
South-east Asia (Burma, Thailand, Malaysia, Viet Nam)	20
Northern Australia	10
Total	90
Indian Ocean	
Northern Indian Ocean (Red Sea, Arabia, India, Pakistan, Sri Lanka)	25
Tropical East Africa and Madagascar	15
Northwestern Australia	10
Total	50
Atlantic Ocean	
Tropical West Africa	10
Total	10

available) than those of smaller islands. For the marine isopods of these reefs, there are almost no data available similar to those described already for smaller island sites. Bruce (1994) trapped 100 isopod species at Madang, Papua New Guinea, geographically a major island. This number is about 2.5 times the number of species recorded on smaller island groups of the Pacific, Indian, and Atlantic oceans. To calculate the diversity of isopods for these major-island and continental coastline reefs, a factor of 2.5 'island-equivalents' is thus used, while acknowledging that this is an extremely flimsy basis for any calculations of diversity. Table 3 summarizes the 'island-equivalents' for the Pacific, Indian and Atlantic Ocean regions. Table 4 provides estimates of total species and endemic species for these three regions.

Thus, for the restricted habitat of coral reefs, and only for free-living isopods, there may be an estimated total of 5072 (sum of these minima) to 13472 (sum of these maxima) species, of which about 2230 to 6269 are endemics. Even accepting that some species are habi-

Table 4 Estimates of total numbers of species, and numbers of endemic species, for the Pacific, Indian, and Atlantic regions

For 90 western Pacific Ocean island equivalents, at a 40% level of endemism		
Maximum	$90 \times 70 = 6300$ total species	2520 endemic species
Actual	$90 \times 50 = 4500$	1800
Minimum	$90 \times 30 = 2700$	1080
For 50 Indian Ocean island equivalents, at a 50% level of endemism:		
Maximum	$50 \times 60 = 3000$ total species	1500 endemic species
Actual	$50 \times 40 = 2000$	1000
Minimum	$50 \times 20 = 1000$	500
For 10 Atlantic Ocean island equivalents, at a 19% level of endemism (based on individual western Atlantic island sites):		
Maximum	$10 \times 50 = 500$ total species	95 endemic species
Actual	$10 \times 30 = 300$	57
Minimum	$10 \times 10 = 100$	19

tat-generalists and occur in several habitats, adding the number of isopods from mangroves, seagrass beds, rocky shores, sandy lagoonal areas, one may easily add 1000–2000 further species.

Extrapolating from the isopod numbers to the rest of the peracaridan crustacean orders, and based on a sense of relative abundances gained from sorting many samples taken in coral reef habitats, in very broad terms the amphipods are about five times more diverse than the isopods, the tanaidaceans about one-third, the cumaceans about one-third, and the mysidaceans about one-fifth as diverse.

Based on the 9272 isopod species (the sum of the 'actual' these numbers), it is estimated that in coral reef habitats there are approximately: 46400 amphipodan, 3100 tanaidacean, 3100 cumacean, and 1850 mysidacean species. Estimates of levels of endemism are not possible for some of these groups, given the present state of knowledge.

In conclusion, for the peracaridan crustaceans of coral reefs, the order of magnitude of number of species is approximately 46000 and number of endemic species 1800. The high levels of endemicity found in often small island localities suggests that degradation or destruction of such localities could lead to large-scale loss of species diversity.

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