

Biodiversity of the Indian Ocean from the perspective of staghorn corals (*Acropora* spp)

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Received 1 April 2004, revised 11 October 2004

The Indian Ocean represents a vital link in the knowledge of where modern reef-building corals began existence, how they survived changes in the configuration of world oceans and how they will survive into the future. To address the central questions of the Census of Marine Life (CoML) for the Indian Ocean, we use the dominant modern reef-building coral genus *Acropora* as an exemplar, working from a large database of world-wide distributions. Previous biodiversity and biogeographic studies of this genus indicated a demarcation between Indian and Pacific Ocean faunas, despite predominantly widespread distribution ranges. From the distribution of modern and fossil *Acropora* assemblages, it is evident that the genus *Acropora* evolved in either the western Indian Ocean or Mediterranean regions of the late Tethys Sea, rather than the central Indo-Pacific as is often assumed from "centre of origin" models. In this paper, additional data on *Acropora* biodiversity from regions of the Indian Ocean is examined to give a preliminary indication of the nature and origin of their biogeographic relationships. The Indian Ocean has unique faunas particularly in the region of the Red Sea and Arabian Gulf. While it is open to influx of Pacific Ocean species via the Indonesian Throughflow current, there is little likelihood of migration of Indian Ocean species into the Pacific. In the event of continuation of global warming, southerly migration of coral species ranges may also take place. Monitoring for such changes could be built into a further detailed compilation of *Acropora* species composition from sites within the Indian Ocean, which will also lead to finer-scale resolution of the distribution patterns shown here.

[Key words: Indian Ocean; biodiversity; reefs; corals; *Acropora*; global warming]

Introduction

The Indian Ocean is home to a diverse array of ancient and unique faunal assemblages, and we propose that a powerful tool for understanding the past, present and future of these is to focus on a taxonomic subset of organisms, for which cumulative distribution information is available and can be supplemented by additional sampling.

This review will focus on the history and relationships of regional Indian Ocean faunas using a single group of reef-building corals, the genus *Acropora* (Oken 1815, Scleractinia; Astrocoeniina; Acroporidae). This is a highly diverse and functionally important group with more than 120 valid species worldwide^{1,2}, at least 84 of these occurring in the Indian Ocean³. Species of *Acropora* dominate the shallow parts of reefs and are involved in most issues relating to the ecology, conservation and management of coral reef environments: *Acropora* is thus an exemplar that is both accessible and relevant. While some Indian Ocean reefs are amongst the least disturbed in the world (e.g. some

central ocean atolls), they are still vulnerable to the impacts of climate change, with dramatic losses in coral cover, particularly for *Acropora*, being reported from Indian Ocean reefs during the 1997-98 coral bleaching events⁴. Other reefs, particularly fringing reefs associated with populated coastlines, are being degraded by human activities such as overfishing, runoff, pollution etc.

Acropora also provides an ideal opportunity to follow colonisation of the Indian Ocean through time, as the earliest fossil record of *Acropora* is dated at late Paleocene in NE Africa (65-54 my)⁵. The Indian Ocean, as defined for this census of Marine Life CoML-Indian Ocean workshop, contains the tectonically young regions of the Gulf and the Red Sea, ancient African reef sites, coastlines along the western edge of the Indo-Australian arc and composite landmasses, most notably India which has transferred its position from one side of the ocean to the other during the period from late Cretaceous to late Eocene in which corals were evolving (e.g. see Smith *et al.* ⁶). This ocean represents a vital link in the

knowledge of how and when reef-building corals began existence, how they survived vast changes in configuration and flow of the world oceans and how they will be placed to survive into the future.

The Indian Ocean (including the Red Sea and Gulf) provides the type localities for a significant proportion of the world's coral species, described by some of the great taxonomists, and description of new species continues to the present (see references in Wallace¹; Veron⁷). At least 85 species or about 23% of nominal species of *Acropora* were originally described from the Indian Ocean^{1,7}. Type specimens and other samples of corals from the Indian Ocean are maintained in good care and accessible conditions in numerous museums outside the region; such collections provide a source of information, for an Indian Ocean Biological Information System (IOBIS).

This paper begins by summarising our previously published data and hypotheses on the distribution and biogeography of *Acropora*. New data on the distribution of *Acropora* species in the Indian Ocean are then presented and a preliminary analysis made of the relationships of regions based on *Acropora* species composition. These preliminary findings are discussed and some predictions made about implications for the future composition and survival of Indian Ocean reef building corals, particularly in the event of persistent global warming.

Materials and Methods

Acropora species distributions used in this paper include specimen-based records from the World-Wide *Acropora* Database, located at the Museum of Tropical Queensland, type localities of all valid species and their synonyms and reliable literature records. These data are recorded in Wallace¹, available electronically on the IOBIS website⁸ and illustrated graphically by Wallace⁹. For the Indian Ocean study, published data are supplemented by new and unpublished records added since 1999 to the World-Wide *Acropora* Database. These include species records from the Zoological Survey of India, (provided by Drs K.Venkataraman and C. Satyanarayana) and specimens from: Sri Lanka (A. Rajasurya); Mauritius (R. Moothian-Pillay); Yemen (E. Turak and L. Devantier); W. Thailand (N. Phongsuwan and our own collecting) and various other contributors (for a summary of localities see Table 1).

Regions used in the biogeographic analyses are defined and illustrated earlier^{1,10}. The sampling

locations within each region are summarised in Table 1. Comparisons between regions were based on Jaccard's similarity coefficient [Similarity = $a/(a+b+c)$, where a = number of species shared by two regions; b = number of species in region 1 and not region 2; c = number of species in region 2 and not region 1; note: a+b+c = total number of species in the two areas]. This measure was used for simplicity and because it is not sensitive to joint absences¹¹. Species interpretations are according to the world-wide revision in Wallace¹. Alternative interpretations of *Acropora* species published by Veron^{2,7} have not been incorporated into the database at this time.

Results and Discussion

The known: published interpretations of central Indo-Pacific *Acropora* distribution patterns.

Acropora occurs in all tropical oceans¹, three species exclusively in the Atlantic Ocean (*A. cervicornis*, *A. palmata* and *A. prolifera*) and the remainder in the Indo-Pacific. While the predominant

Table 1— Sampling locations within defined areas along with additional sampling required for further analyses (in **bold type**).

Region	Localities represented	Number of records
Red Sea	Yemen, Saudi Arabia, Eritrea, Egypt, Sudan /(Egypt, Sudan, Ethiopia)	226
Gulf	Kuwait, Saudi Arabia/ (Iran)	61
E. Africa	Kenya, S. Africa, Mozambique, Comoros, Madagascar, Yemen /(Somalia, Tanzania)	167
India & Sri Lanka	India (localities not specified), Sri Lanka, Bangladesh, Chagos, Maldives /(Lakshadweep Is)	469
Andaman Sea	W. Thailand, Malaysia/ (Andaman Is, Nicobar Is, Malaysia, Burma)	497
Indian Ocean West	Mauritius, Mascarene Arch., Seychelles, Chagos, / (more samples most localities)	244
Sumatra	Sumatra – Indian Ocean coast, Nias Is.	206
Indian Ocean East	NW Shelf, coastal W. Australia, Cocos Keeling, Christmas I.	509

Indo-Pacific distribution pattern is “widespread”, including the two oceans and the central region between them, various other patterns of narrower distribution have been identified¹. These include ranges restricted predominantly to either the Indian or Pacific oceans, often with some overlap into the Indonesian archipelago, ranges confined to single regions or two regions and ranges including both oceans but not the central region.

The highest *Acropora* biodiversity is recorded from the Indonesian archipelago (Fig. 1), the main component of a region sometimes referred to as the “coral triangle” or “centre of diversity”: however, species counts for individual regions within Indonesia never reach this total country biodiversity. A study of the similarity, biodiversity and distribution types of *Acropora* of six Indonesian regions (Fig. 2) showed four major patterns of deviation from a simple “centre of diversity” arrangement^{3,12}:

1. *A strong dual pattern, differentiating between Pacific and Indian Ocean fauna.* This was interpreted as indicating the two oceans were separated for some time in the past. Effective separations due to land and/or shallow water probably occurred during the mid Miocene, around 10 mya¹³ and the Pleistocene low sea stands¹⁴.
2. *The Pacific Ocean influence within Indonesia is stronger than the Indian Ocean influences-* This was interpreted as indicating that Pacific species are invading the central region. The mechanism proposed was dispersal of larvae via the

Indonesian Throughflow current, which is responsible for strong flow of the Pacific Ocean westwards into the Indian Ocean¹⁵ with little flow occurring in the opposite direction.

3. *Endemicity to parts of the central region-* This was interpreted as indicating isolation of regions in the past. Deepwater basins within central and eastern Indonesia probably remained available for coral settlement throughout the Miocene to Recent in Indonesia (see for example Hall¹³). Patterns of genetic isolation of populations of gonodactyloid stomatopods associated with these basins¹⁶ support this hypothesis.
4. *Similarity between Central Sulawesi, Indonesia and New Britain, Papua New Guinea-* New Britain is a deep water basin similar to those within Indonesia and almost contiguous with the Central Sulawesi region (see Hall & Halloway¹³). This relationship is consistent with Paulay’s hypothesis¹⁷ of extinction of a previously more widespread Indo-Pacific molluscan fauna in all but the deepest basins due to Pleistocene low sea stands.

It was concluded that the high diversity of the “coral triangle” has multiple origins and that the simple concept of a circle of increasing diversity does not apply. The question still remains, however, as to the location of the origin of *Acropora* and possibly many other coral genera. This question can only be addressed with fossil evidence and this, at present, indicates Indonesia is extremely unlikely to be the point of origin.

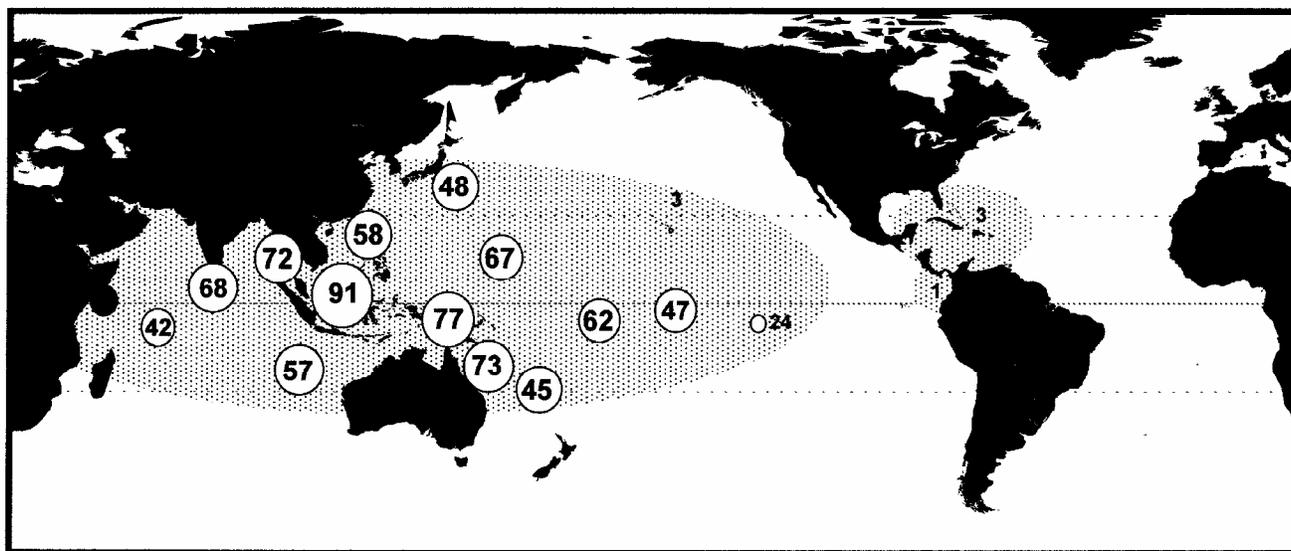


Fig. 1—Worldwide distribution of *Acropora* showing the number of species present in each region.

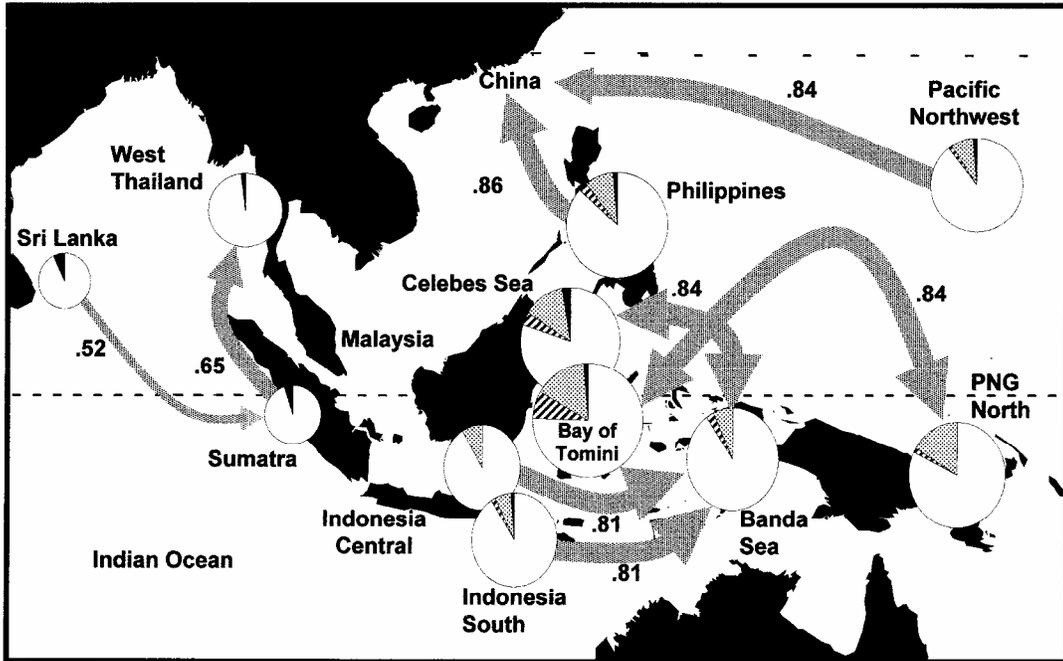


Fig. 2—Biogeographic relationships of six regions within Indonesia and surrounding Indian and Pacific Ocean regions. For each region the relative *Acropora* species diversity is indicated by the size of the pie diagram while the breakdown of distribution types is indicated as: widespread Indo-Pacific (white); shared with Pacific Ocean (stippled); shared with the Indian Ocean (black) and endemic (stripes). Each region is connected to its most similar region (Jaccard's) by an arrow: thickness indicates similarity.

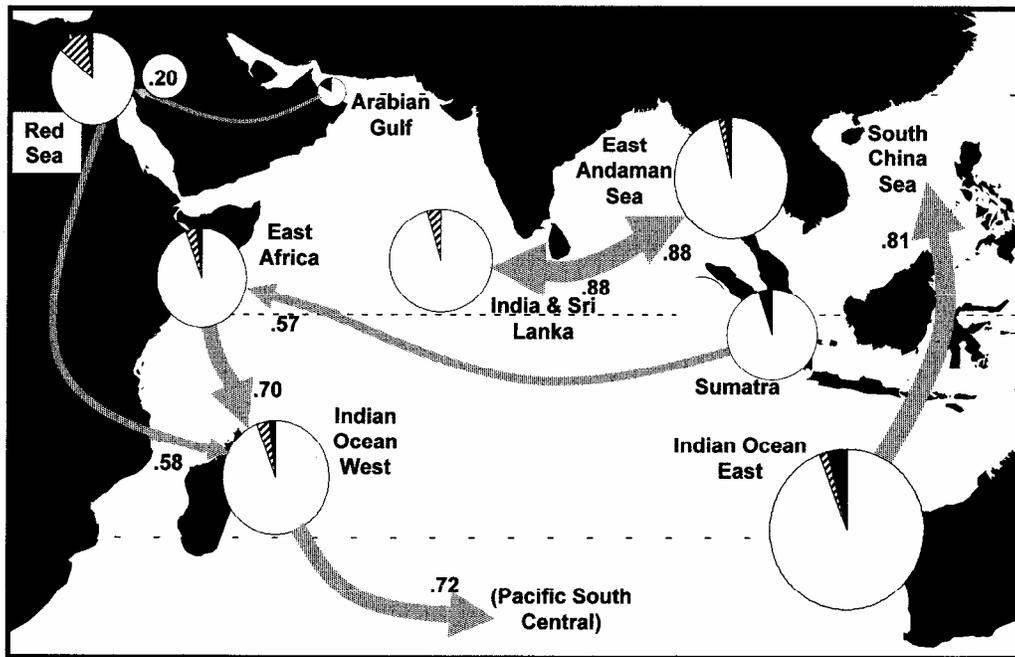


Fig. 3—Biogeographic relationships of regions of the Indian Ocean based on data currently available in the Worldwide *Acropora* database^{1,8} and unpublished records from the Museum of Tropical Queensland. Records are most numerous from Indian Ocean East and the Andaman Sea, however, all regions are incompletely surveyed at present. For each region the relative *Acropora* species diversity is indicated by the size of the pie diagram while the breakdown of distribution types is indicated as: widespread Indo-Pacific (white); shared with the Indonesian archipelago (black) and endemic (stripes). Each region is connected to its most similar region (Jaccard's) by an arrow: thickness indicates similarity.

The known: records of early fossil *Acropora* distribution

While by no means thoroughly documented, the fossil record for *Acropora* is represented in various museum collections, especially in Europe. The earliest fossils were from around the Mediterranean and NE Africa, as well as the western Atlantic¹. Several species of *Acropora* have been recorded from reefs and assemblages from late Paleocene (NE Africa only) and throughout the Eocene (especially mid Eocene), during which time a Tethys Seaway is hypothesised to have flowed in a westerly direction. In the middle Eocene, this included a passage north of the Indian continent and through the Mediterranean region, with no separation of the Indian and Atlantic oceans. Although no records of *Acropora* from this time have been found from India, it is possible that there were *Acropora* on reefs to the north of India and that these played a role in seeding the European reefs. The earliest fossil records of *Acropora* in the Indonesian region were in the Oligocene (33.7-23.8 mya).

The knowable: preliminary analysis of Indian Ocean distributions

Our analysis of regional *Acropora* biodiversity and relationships of regions, based on the identified *Acropora* collections listed in Table 1, is presented in Fig. 3. Both the Red Sea and the Gulf have a high proportion of endemic and narrowly distributed species. The Gulf is most similar to the Red Sea, but at a low level of similarity. This is a region with a unique endemic fauna and supporting only a few widespread species, possibly limited to those most tolerant of the high temperatures and salinities of the region¹⁸⁻²⁰. Use of published species records from this region is difficult because of confused identifications. For more accurate future analyses, collections and data from Iran are required. The relationships of the Red Sea and Gulf to the immediately adjacent Arabian Sea and gulfs of Oman and Aden will become more clear when further collections on hand (e.g. from Socotra) are identified and additional collections made.

The Red Sea and Eastern Africa are most similar to the Indian Ocean West region. This may reflect similarities in shared widespread Indo-Pacific species with very broad ranges. The Indian Ocean West, however, is most similar to a remote region external to the Indian Ocean, the Pacific South Central. This is one of the regions of the Indian Ocean where the data

is incomplete and therefore this similarity may not be significant. However, it is possible that it reflects an intriguing “unique shared fauna”¹ between these two regions, including at least one species *Acropora retusa*, which is not represented in any other regions. This finding merits further investigation and it would be informative to examine whether it is duplicated in other taxonomic groups.

Additionally the biodiversity and regional relationships of East Africa could be interpreted differently, based on species described from the African coastal reefs by Reigl²¹. Comparing Reigl’s material with specimens in the Worldwide *Acropora* Collection, we interpreted these according to Wallace¹ as synonyms of existing valid species, contrary to Reigl^{21,22} and Veron³. It would be valuable to the Indian Ocean biodiversity study to address such questions of species limits further, using genetic material.

Not surprisingly, greatest similarity is shown between India/Sri Lanka and the Andaman Sea. Both of these adjacent regions have high *Acropora* biodiversity and at least two species are endemic to the combined region. These regions include “some of the most diverse, extensive and least disturbed reefs in the Indian Ocean”²³, yet some reefs in these regions have barely ever been investigated. Our material (totalling less than 1,000 identifications from these two regions to date) undoubtedly under-represents their overall species composition. Additionally, further studies on material on hand in the collections of the Zoological Survey of India is required to differentiate amongst different parts of India, information which was not available for this study.

We used the “Sumatra” region from the previous Indonesian study^{1,3}: this relatively small region could possibly be combined, either with the Andaman Sea locations or with the Indian Ocean East region. In the analysis this region showed a low level of similarity to the East African region. This is probably not significant, although it could reflect similar habitats as both regions are dominated by fringing reefs. This raises the prospect that future analyses of Indian Ocean *Acropora* biodiversity could include some data on reef type so as to address habitat-related versus biogeographic influences.

Lastly, the Indian Ocean East region is most similar to a region outside the Indian Ocean, the South China Sea (a region to the west of the Philippines region shown in Fig. 2). This relationship

would be predicted on the basis of the findings of the Indonesian study³, which related a pattern of distribution of Pacific species through central Indonesia to the influence of the Indonesian Throughflow current.

These results are based on limited sampling of most of the regions. Further sampling, using established protocols¹⁰ will undoubtedly increase the biodiversity records of all regions. However, even these preliminary results indicate major influences on regional Indian Ocean species composition from past history, present circulation and reef type or available habitat. Following the closure of the Mediterranean connection between the Indian Ocean and the Atlantic (completed gradually during the Miocene period 28.3-5.3 mya), and the docking of the Indian sub-continent with Asia, the Indian Ocean is now land-locked to the north and northwest. The Red Sea and the Arabian Gulf have opened up separately and independently of the previous Tethys connection. Circulation of the tropical Indian Ocean is influenced by the Pacific Ocean input. Reef types vary throughout the Indian Ocean but on the whole fringing reef types are found on the continental peripheries while atoll and barrier reefs dominate the centre. All of these influences can be seen in this preliminary study.

It has been predicted that some shift of tropical faunal distributions to higher latitudes will take place in the event of continuation of global warming and this may be coupled with biodiversity loss in the tropics, at least on local scales, should frequent and persistent coral bleaching events become the norm. In a global warming scenario, the only refuge within the Indian Ocean would be to the south. There are currently no reliable predictions of the speed of this change, but monitoring for change could be built into a research program for an IOBIS. Such changes would impact on temperate habitats as well as coral reefs.

Global warming is probably the most dramatic predicted future change but numerous other human-induced impacts are regularly being reported from various coral reefs throughout the Indian Ocean and in many cases these could be linked to elements identified by this study, i.e. habitat and geographic influence. We propose that knowledge of patterns of biodiversity relationships as outlined above would reduce “the unknowable” by contributing data valuable for understanding and managing biodiversity and predicting change.

In conclusion we can relate our preliminary findings to the following hypotheses under the headings of the three questions posed by the CoML:

“What did live (in the Indian Ocean)?”

It is likely that an early *Acropora* fauna was shared between the Mediterranean region and the early Indian Ocean and that several species groups survived the closure and desiccation of the Mediterranean and the formation of the Indian Ocean. Thus the Indian Ocean may hold the key to *Acropora* origins. Further research on early fossil material, particularly from northern India and NE Africa, would help to test this. In combination with studies at molecular level, these would provide information vital to calibrating a molecular clock for corals.

“What does live (in the Indian Ocean)?”

We have shown how one taxon, a diverse coral genus, can be used to indicate biodiversity and biogeographic patterns. While we are not as yet able to present a complete picture of the distribution and biodiversity of *Acropora* throughout the Indian Ocean, our data set and preliminary results are already allowing us to indicate different biodiversity categories, e.g. centres of unique as well as overlapping faunas in the Red Sea and Gulf, disjoint faunas between the western Indian Ocean and the eastern-central Pacific, and a Pacific-influenced fauna in the eastern Indian Ocean.

We propose that these results indicate that it will be useful to expand this exemplar study of an Indian Ocean taxon by further sampling of *Acropora* in under-represented locations. We suggest that relationships amongst Indian Ocean regions and between those regions and others outside the Indian Ocean may resolve some issues and help to propose broader questions regarding Indo-Pacific biodiversity and how it might best be managed to preserve world ocean biodiversity.

“What will live (in the Indian Ocean)?”

Changes in distribution, extinctions and range contractions will become a focus of marine monitoring programs over the coming years. The Indian Ocean is unique amongst the three great world oceans spanning the equator in that it is partially landlocked and lacking a north temperate zone. Our results indicate that the Red Sea and Gulf are

important sites of endemics and may be at risk in a global warming scenario although heat tolerance may protect the species occurring there. Should range extension of tropical species to more southerly latitudes take place, coastlines, particularly in E. Africa and W. Australia, will provide the major recruitment sites and an impact on temperate faunas can be expected also. It is worth considering possible taxa for inclusion in regular monitoring programs so that latitudinal migration can be detected.

In the case of other threats to Indian Ocean biodiversity, we propose that taxonomic exemplars such as *Acropora*, carefully monitored within an IOBIS or other program, will provide indicators of change and a practicable approach to environmental management.

Our results also indicate that the Indonesian Throughflow current will play a role in future Indian Ocean composition, possibly providing both a source of recruiting larvae and a diluting influence on the Indian Ocean biodiversity. The time scales associated with these factors may be different. Unique elements of the Indian Ocean fauna, on the other hand, may remain in this ocean, due to the lack of flow in the other direction. Some of these unique elements, or more importantly, the locations of concordant biodiversity for a number of taxa, could be given greater protection if identified.

In conclusion we see a role for detailed study of particular taxa in accelerating knowledge of the patterns of biodiversity within the Indian Ocean and for planning future monitoring and management.

Acknowledgement

Numerous colleagues from the countries studied provided specimens and field assistance and we thank the organisers, sponsors and participants of the Indian Ocean Biodiversity Conference for the opportunity to develop and discuss the ideas in this paper. We thank Zoe Richardson for advising on the text.

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