



# Patterns in marine hydrozoan richness and biogeography around southern Africa: implications of life cycle strategy

Mark J. Gibbons<sup>1\*</sup>, Emmanuel Buecher<sup>1</sup>, Delphine Thibault-Botha<sup>1,2</sup> and Rebecca R. Helm<sup>1,3,4</sup>

<sup>1</sup>Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa, <sup>2</sup>Aix-Marseille Université, CNRS, LOPB-UMR 6535, Laboratoire d'Océanographie Physique et Biogéochimique, OSU/Centre d'Océanologie de Marseille, Campus de Luminy, Case 901, Marseilles 13288, France, <sup>3</sup>Marine and Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Roggebaai 8012, South Africa, <sup>4</sup>80 Waterman Street, Box G-W, Brown University, Providence, RI 02912, USA

## ABSTRACT

**Aim** To examine patterns of marine hydrozoan richness around southern Africa and to test the hypothesis that patterns of biogeography become weaker with increasing dispersal ability.

**Location** The coastline of southern Africa from 21° S, 14° E to 28° S, 33° E, extending from the intertidal zone seawards a distance of 200 nautical miles.

**Methods** Published and unpublished information on the distribution of marine Hydrozoa was entered as presence/absence data onto a gridded coastline of the region. A similarity matrix between the species composition of grid squares was constructed using the Bray–Curtis index and visualized using non-metric multidimensional scaling ordinations. Separate analyses were conducted, and compared, on the three major life cycle groupings: holoplanktic, meroplanktic and benthic.

**Results** Over 450 species of marine Hydrozoa have been reported from the region, and species richness increases eastwards, in a manner at odds with the distribution of sampling effort. There was a significant correlation between the geographic structures of the resemblance matrices generated for the three life cycle groupings. In other words, all three groups showed similar patterns of biogeography around the region, and these were broadly similar to those reported by others. However, there were differences between them that reflect the resolution at which the data were examined. At a level of 40% similarity, there was no biogeographic structure to the holoplanktic fauna, the meroplanktic taxa were simply sub-divided into cool- and warm-temperate/subtropical elements, and in the case of benthic taxa, the cool-water fauna was further split into a southern Namaqua and a depauperate northern Namib component. Even at a resolution of 70% similarity, the holopelagic taxa could be separated only into cool-temperate and warm-temperate/subtropical faunas.

**Main conclusions** Holoplanktic taxa show comparatively less biogeographic structure than meroplanktic taxa, which in turn show less clearly defined biogeographic structure than benthic taxa. It is suggested that this is related to the interaction between oceanography and dispersive-stage duration. The role that the Agulhas Current plays in influencing the Benguela Current fauna is highlighted. This study has implications for conservation planning exercises based on protecting representative biotopes in different biogeographic regions.

## Keywords

Agulhas Current, Benguela Current, Cnidaria, dispersal, holoplankton, jellyfish, medusae, meroplankton, polyp, species richness.

\*Correspondence: Mark J. Gibbons, Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa. E-mail: mgibbons@uwc.ac.za

## INTRODUCTION

Southern Africa is bathed by the Agulhas Current on the east coast and by the Benguela Current on the west. The Agulhas Current is a classical western boundary current that transports warm equatorial water polewards: it is deep, narrow and fast and shows limited seasonal variability in position (Lutjeharms, 2006). It is characterized by low productivity, and biological communities exhibit high diversity but low biomass (Bustamante *et al.*, 1995; Gibbons & Hutchings, 1996). The Benguela Current is a typical eastern boundary current that is associated with coastal, seasonally variable, wind-driven upwelling: it carries cool water equatorwards as a broad, fairly shallow and sluggish current (Shannon, 1985). Productivity is high and biological communities are generally species-poor, although individuals can be very abundant (Bustamante *et al.*, 1995; Gibbons & Hutchings, 1996).

Both currents are topographically steered. The Agulhas Current lies close to shore in the north, moving progressively offshore as it travels westwards along the edge of the Agulhas Bank and then retroflects eastwards south of Cape Agulhas (Lutjeharms, 2006). This area of retroflexion is very dynamic, and eddies, rings and filaments are regularly shed that may move northwards into the South Atlantic (Duncombe Rae, 1991), frequently interacting with the Benguela Current as they do so (Duncombe Rae *et al.*, 1992). The Benguela Current tracks the edge of the shelf along the west coast of South Africa and Namibia, and is close inshore only at the major capes and peninsulas: Cape Point and Cape Columbine in South Africa, Lüderitz and Cape Frio in Namibia (Shannon, 1985). It moves progressively offshore northwards, and forms a pronounced front with the southward-flowing Angola Current that shifts latitudinally in both an intra- and an inter-annual manner (Meeuwis & Lutjeharms, 1990).

Given the geographic position of southern Africa and the marked changes in the physical environment it experiences, it is no wonder that the region has been the focus of biogeographic interest since before Ekman (1953). A number of studies have analysed the distribution patterns of a range of marine and estuarine organisms including (not exhaustively) mites (Procheş & Marshall, 2002), soft corals (Williams, 1992), decapods (Kensley, 1981), echinoderms (Thandar, 1989), ascidians (Primo & Vázquez, 2004), fishes (Turpie *et al.*, 2000) and algae (Bolton *et al.*, 2004). Although most of these studies have been directed at single taxa, a few have been more inclusive (e.g. Stephenson, 1944, 1948; Emanuel *et al.*, 1992; Bustamante *et al.*, 1997).

All of these studies have tended to show three distinct biogeographic provinces. A tropical and subtropical east coast province extends to southern KwaZulu Natal on the east coast, and may be split further into a northern tropical and a southern subtropical component. A warm-temperate south coast province extends across the width of the Agulhas Bank to Cape Point, and a cold-temperate province extends up the west coast. Some authors (e.g. Emanuel *et al.*, 1992) have further split the cold temperate west coast area into two, divided by

the permanent upwelling cell at Lüderitz: the Namaqua Province in the south and the Namib Province in the north.

The faunas of the various major biogeographic areas are quite distinct and the boundaries are fairly sharp: they agree with what is known about the physical oceanography of the region. Although richness generally decreases from east to west as one moves from tropical towards cold-temperate waters, this pattern varies with taxon (Awad *et al.*, 2002). The extent of endemism also varies with taxon, although it now appears that many range-restricted taxa are associated with the boundaries to the various provinces (C.L. Griffiths, Zoology Department, UCT, unpublished data).

Although most of the taxa examined to date have been benthic, two bathymetrically stratified studies have been conducted on strictly pelagic taxa: euphausiids (Gibbons *et al.*, 1995) and siphonophores (Gibbons & Thibault-Botha, 2002). The results of these studies agree in broad detail with those conducted on benthic taxa, although the boundaries between adjacent provinces are not always in the same place. For example, the boundary between the warm- and cold-temperate provinces is not at Cape Point, but rather at Cape Columbine further up the west coast. These and other differences are not unexpected given the nature of the pelagic environment and the biology of the organisms concerned.

Only a single study has tried explicitly to address the role of life cycle strategy and biogeographic pattern in the region: Teske *et al.* (2006) examined the genetic structure within populations of three widely distributed regional estuarine micro-crustaceans displaying quite different dispersal abilities, namely *Upogebia africana* (planktic larvae), *Exosphaeroma hylecoetes* (adult rafting) and *Iphinoe truncata* (adult drifting). Their results indicate that some phylogeographic breaks in the former two species coincided with some of the well-recognized biogeographic breaks outlined above, but in the latter species phylogeography was argued to reflect persistent palaeographic patterns.

Hydrozoans display a wide diversity of life cycle strategies. The classical medusozoan life cycle is metagenic: there is (generally) a benthic polyp that reproduces asexually to produce free-swimming, sexually active medusae that in turn (effectively) produce ciliated planula larvae that settle and develop into polyps again. Such a strategy is displayed by many Anthoathecata and Leptothecata, and the medusae are regarded as meroplanktic. There is, however, considerable variation: some lineages lack a polyp (many Trachylina) or a medusa (many Anthoathecata and Leptothecata) stage. In other taxa, both polyps and medusa may be combined into extensively polymorphic individuals (Siphonophorae).

Our knowledge of benthic hydroids around southern Africa was much better than that for the rest of the world until the end of the 1970s, thanks to the efforts of Naomi Millard FRSSA. Her monograph on the regional fauna (Millard, 1975) is still widely used across the globe, and she synthesized her understanding about benthic hydroid distribution and geographical affinities in a paper published towards the end of her career (Millard, 1978). Her results broadly reflect those

summarized above for other benthic groups. Although some of our knowledge about planktic hydrozoans pre-dates Millard, thanks to the early European expeditions, it was not until Francesc Pagès' work at the end of the 1980s that we actually began to build a regionally comparable understanding regarding medusae. Here we attempt to combine the data of both Millard and Pagès, augmented with some of our own observations, in order to tease apart the role of life cycle strategy on distribution. It is anticipated that taxa without any extensive dispersive life cycle phase will show clear patterns of distribution closely akin to those of other benthic invertebrates, whereas those without any benthic life cycle phase will have much broader ranges and much less clear biogeographies. Those taxa with both life cycle phases will display patterns of distribution between the two extremes.

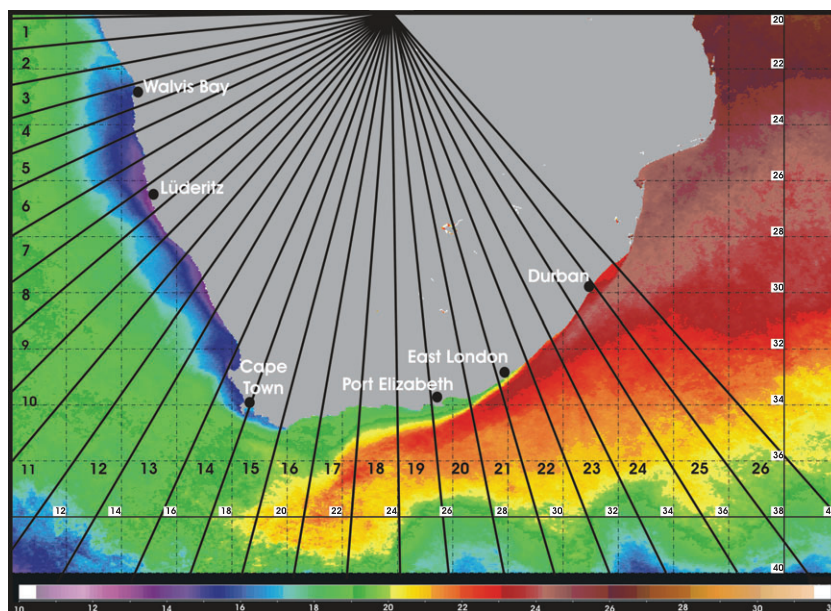
## MATERIALS AND METHODS

Information on the distribution of marine benthic hydroids and life cycle stages in the region is taken from Millard (1978), which is based largely on her regional monograph (Millard, 1975): there have been no subsequent studies of benthic hydrozoa from southern Africa to the best of our knowledge. The planktic data were collated primarily from the studies of Pagès (as detailed in Pagès *et al.*, 1992), Buecher & Gibbons (2000, 2003), Buecher *et al.* (2005), Gibbons & Buecher (2001), Sparks & Gibbons (2003), Gibbons & Thibault-Botha (2002) and Thibault-Botha *et al.* (2004). Additional records were obtained from Millard (1975), and from numerous sources in Kramp (1961). The most significant of these include Haeckel (1888), Vanhöffen (1911, 1912) and Kramp (1957, 1959) for medusae, as well as Moser (1925), Leloup (1934), Leloup & Hentschel (1935) and Totton (1941, 1954) for siphonophores. We recently examined a further 223 plankton samples that were collected in 2000 and 2001 from the area

between the Orange River mouth and Port Elizabeth, and these as yet unpublished data have also been included. The fully referenced dataset used here is shown in Appendix S1 in the Supporting Information. Taxonomy follows the recent monographic treatment of the group by Bouillon *et al.* (2006); systematic affinities follow Collins *et al.* (2008) and Cartwright *et al.* (2008).

For convenience we have divided the southern African coastline into 26 arbitrary sectors of approximately equal area following Millard (1978) (Fig. 1). The grid extends from c. 20° S along the west coast to c. 28° S on the east coast. The central point was chosen as 20° S, 24° E, from which a series of radii were drawn at 5° intervals starting through the Cape Peninsula. The seaward extent of the grid has been taken as 200 nautical miles from the coast. The geographic distribution of species around southern Africa was superimposed on the regional grid, by scoring records as either 1 (present) or 0 (absent). We have assumed that a species is present in gaps between positive records, but we have not extended the interpolation beyond the limits of the regional grid. Although we acknowledge that data exist for species beyond the region considered here, this knowledge is not consistent across all taxa. As a consequence, caution is needed in interpreting data from the extremes of the grid.

A similarity matrix between the species' composition of grid squares was constructed using the Bray–Curtis measure (Clarke & Warwick, 2001). Any species recorded from only one sector of the grid was removed from the dataset, unless it was found at either of the two coastal extremes (sector 1 or 26) or, in the case of benthic hydroids, has been recognized as endemic. Cluster analyses based on group-average sorting and non-metric multidimensional scaling (NMDS) ordinations (Field *et al.*, 1982) were then undertaken in order to visualize relationships between sectors. All analyses were conducted using PRIMER 6 software (Clarke & Gorley, 2006). In order to



**Figure 1** Satellite image (4-km resolution MODIS Aqua day-time SST: 11 micrometre product) of the southern African sub-region showing average sea surface temperatures for 2008. Also shown is the position of the sampling grid used here, adapted from Millard (1978).

determine how life cycle strategy influences the distribution of Hydrozoa in the region, we computed separate analyses for the different life cycle strategies: (1) benthic – those with primarily a benthic phase, including those with a benthic polyp and fixed gonophores or sporosacs, those with largely non-feeding eumedusoids or cryptomedusoids (mostly Anthoathecata, Leptothecata), and those with benthic medusae (Actinulidae and some Trachymedusae); (2) holoplanktic – those with a pelagic phase only, such as Trachymedusae, Narcomedusae and Siphonophorae; we have ignored neustonic species of Anthoathecata and Siphonophorae because of poor coverage; and (3) meroplanktic – those with both a benthic and a pelagic phase, namely mostly Anthoathecata, Leptothecata and Limnomedusae. Information on life cycle strategy has been taken from Bouillon *et al.* (2006). It is assumed that all species within a genus display the same life cycle strategy, and, in cases where the polyp stage of a taxon is unknown but presumed to exist, we have assumed species to be meroplanktic. We acknowledge that the former statement is not always accurate, as a number of hydroidoline genera are now recognized as being ‘polymorphic’ with regard to life history strategy and reproductive structure (e.g. Cunningham & Buss, 1993; Govindarajan *et al.*, 2006; Miglietta *et al.*, 2009), but the number of exceptions appears to be limited at this time and is thus unlikely to materially influence the results.

We compared the resemblance matrices between the different life cycle strategies in pairwise comparisons using the RELATE routine in PRIMER (Clarke & Gorley, 2006). This software computes Spearman rank correlations ( $\rho$ ) between the matching entries of the two resemblance matrices and effectively compares the results from those generated from 999 random permutations of the same. The null hypothesis is that there is no relationship between the two matrices ( $\rho = 0$ ).

## RESULTS AND DISCUSSION

### Hydrozoan richness around southern Africa

Table 1 summarizes the species richness, by order and life cycle strategy, of marine Hydrozoa around the southern African grid examined here. If we exclude Limnomedusae, because only a single species is known from the region, and rank the remaining orders by species richness, the diversity of the southern African fauna reflects that of the global species pool (Bouillon *et al.*, 2006), being dominated by Leptothecata and, to a lesser extent, by Anthoathecata. However, if we look more closely at the data it is clear that the southern African fauna has proportionally more species than expected from global ratios in taxa that possess medusae, and proportionally fewer in taxa that lack a dispersive medusa (Table 1). There is a gradation to this relationship: less than 9% of the global benthic species are found in southern Africa, as opposed to *c.* 21% of those with meroplanktic life cycles and *c.* 50% of those that are holoplanktic. This is particularly obvious in the case of benthic Anthoathecata, for which only 23 species (4.7% of the global total) are described from the grid examined here.

Comparisons between our results and those of other areas are constrained by a general paucity of synthesized information. An equivalent dataset has been compiled only for the Mediterranean Sea, which is considered to be one of the best explored regions for Hydrozoa (Bouillon *et al.*, 2004). The pattern of richness observed there is broadly similar to that observed here, although this may be artificial because both sampling (especially in deeper water) and taxonomic effort have been lower around southern Africa.

A summary of our understanding of meroplanktic species richness around southern Africa is shown in Table 2, from which it can be seen that Millard (1975) described similar

**Table 1** Diversity of southern African, and global, marine Hydrozoa by order and life cycle strategy. N<sub>1</sub>: data considered here in our biogeographic analyses; N<sub>2</sub>: all data, including singletons. Data are also expressed as percentages of totals (middle panel), and regional faunas are shown as percentages of global fauna (right hand panel). Global data were extracted from Bouillon *et al.* (2006), ignoring all species regarded as doubtful, invalid or synonyms.

| Subclass     | Order         | Life cycle strategy | Number         |                |       | Percentage     |                |       | Percentage World |                |
|--------------|---------------|---------------------|----------------|----------------|-------|----------------|----------------|-------|------------------|----------------|
|              |               |                     | N <sub>1</sub> | N <sub>2</sub> | World | N <sub>1</sub> | N <sub>2</sub> | World | N <sub>1</sub>   | N <sub>2</sub> |
| Hydroidolina | Anthoathecata | Meroplanktic        | 59             | 92             | 465   | 15.7           | 20.3           | 15.2  | 12.7             | 19.8           |
| Hydroidolina | Anthoathecata | Benthic             | 21             | 23             | 492   | 5.6            | 5.1            | 16.1  | 4.3              | 4.7            |
| Hydroidolina | Anthoathecata | Holoplanktic        | 2              | 2              | 4     | 0.5            | 0.4            | 0.1   | 50.0             | 50.0           |
| Hydroidolina | Leptothecata  | Meroplanktic        | 51             | 62             | 247   | 13.6           | 13.7           | 8.1   | 20.6             | 25.1           |
| Hydroidolina | Leptothecata  | Benthic             | 144            | 154            | 1548  | 38.4           | 33.9           | 50.7  | 9.3              | 9.9            |
| Hydroidolina | Siphonophorae | Benthic             | 0              | 0              | 11    | –              | –              | 0.4   | –                | –              |
| Hydroidolina | Siphonophorae | Holoplanktic        | 68             | 86             | 155   | 18.1           | 18.9           | 5.1   | 43.9             | 55.5           |
| Trachylina   | Actinulida    | Benthic             | 0              | 0              | 11    | –              | –              | 0.4   | –                | –              |
| Trachylina   | Limnomedusae  | Benthic             | 0              | 0              | 7     | –              | –              | 0.2   | –                | –              |
| Trachylina   | Limnomedusae  | Meroplanktic        | 1              | 1              | 26    | 0.3            | 0.2            | 0.9   | 3.8              | 3.8            |
| Trachylina   | Narcomedusae  | Holoplanktic        | 14             | 15             | 36    | 3.7            | 3.3            | 1.2   | 38.9             | 41.7           |
| Trachylina   | Trachymedusae | Benthic             | 0              | 0              | 3     | –              | –              | 0.1   | –                | –              |
| Trachylina   | Trachymedusae | Holoplanktic        | 15             | 19             | 47    | 4.0            | 4.2            | 1.5   | 31.9             | 40.4           |



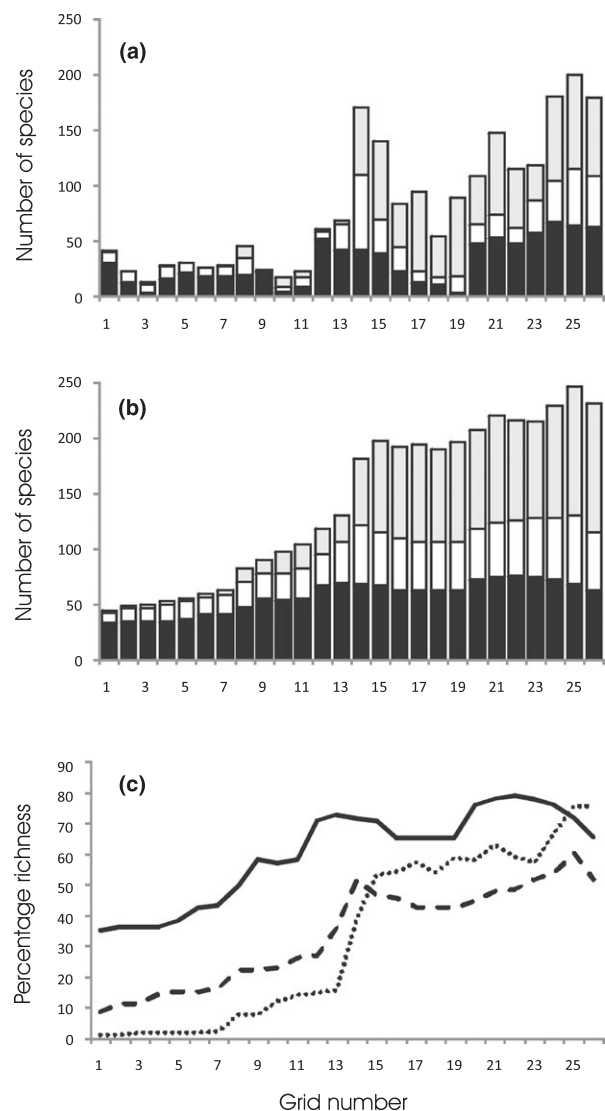
**Table 2** Number of marine hydrozoan species with meroplanktic life cycles that have been described from plankton samples, benthic samples or both sample types: (a) data used here in the biogeographic analyses, (b) all data (including singletons).

| Samples  | Anthoathecata | Leptothecata | Limnomedusae |
|----------|---------------|--------------|--------------|
| (a)      |               |              |              |
| Plankton | 43            | 37           | 1            |
| Benthos  | 15            | 13           | 0            |
| Both     | 1             | 1            | 0            |
| (b)      |               |              |              |
| Plankton | 71            | 45           | 1            |
| Benthos  | 15            | 16           | 0            |
| Both     | 6             | 1            | 0            |

numbers of hydroids belonging to Anthoathecata and Leptothecata. The number of benthic hydroids is dwarfed by the number of medusae identified in plankton samples, and indeed only seven species are recorded from both the benthos and the plankton. This lack of congruence in the two sets of data reflects a lack of knowledge about the identity of all life cycle stages, and is a world-wide problem. The data in Bouillon *et al.* (2006) would suggest that there are almost as many valid genera of Anthoathecata, Leptothecata and Limnomedusae with an unknown (but presumed) polyp stage (*c.* 107 genera, *c.* 166 species) as there are genera with a known meroplanktic life cycle (*c.* 121 genera, *c.* 765 species). Despite these differences, it is clear that discrepancies between the two sampling methods in the study region are marked. Part of this discrepancy may reflect issues of sampling: plankton samples are rarely caught in very shallow water, where many of these species are likely to occur. However, part must also arise from the fact that some hydrozoans are not easy to identify, either as medusae or as polyps. Unfortunately, we are unlikely to resolve this issue until we start to incorporate molecular and genetic data into our taxonomies.

From the proportions of species represented in the regional fauna (Table 1), the waters off southern Africa are home to a substantial number of marine Hydrozoa, despite their representing a relatively small proportion of the global ocean. This number is (relatively) greater for holoplanktic and meroplanktic taxa than it is for those without extensive planktic stages, which is in agreement with the data detailed for other marine organisms (Gibbons *et al.*, 1999). For example, 57% of the global number of euphausiids (holoplanktic crustaceans) are found in the region, whereas only 6% of gammarid amphipods (largely benthic crustaceans that protect developing young within marsupia) are so located: both groups are relatively well known from South Africa (Gibbons, 2000). Although this undoubtedly reflects the wide distribution of holoplanktic species (Kramp, 1961; Gibbons *et al.*, 2005) and their low diversity (e.g. Angel, 1993), it is likely also to reflect the relatively dynamic and varied oceanography of the region.

The richness of hydrozoan communities along the east coast of southern Africa is substantially higher than that observed along the west coast (Fig. 2). This is apparent whether we look



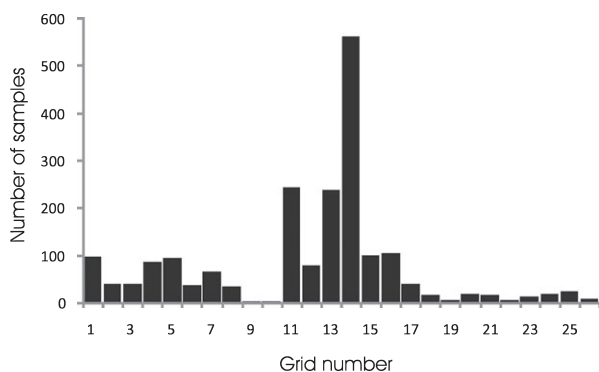
**Figure 2** Changes in (a,b) the species richness and (c) the percentage species richness of marine Hydrozoa around South Africa: (a) all data, including singletons; and (b,c) interpolated data, excluding singletons. Holoplanktic species, black shading, solid line ( $n = 99$ ); meroplanktic species, white shading, dashed line ( $n = 111$ ); benthic species, grey shading, dotted line ( $n = 165$ ). Grid numbers follow those in Fig. 1.

at the raw data (including species recovered from single grids, but excluding interpolations; Fig. 2a) or at the interpolated data (excluding singletons, Fig. 2b). The latter dataset, which is used in our analyses of biogeography (see below), indicates that overall richness is uniformly low along the west coast to grid 7 and increases slightly through grids 8–13 before increasing quite markedly at grid 14 and stabilizing thereafter (Fig. 2b). This pattern is largely independent of life history strategy (Fig. 2c). Holoplanktic species show a gradual increase in richness eastwards, with slight increases at grids 12 and 20, whereas species with a benthic life history, especially those without a medusa phase, increase in numbers to the east of

grid 14 (Fig. 2c). The decline in species richness in grid 26 is an artefact of the lack of interpolation beyond this point and should be ignored.

Although most analyses of the distribution of faunal richness in the region have not extended into Namibia, the overall pattern for southern African Hydrozoa observed here (Fig. 2) closely resembles that shown by many other groups of marine organisms. In the case of marine Hydrozoa, the low levels of richness in all taxa with a benthic life cycle phase along the north-west coast of South Africa and Namibia undoubtedly reflect the sedimentary nature of the substrates present off the region and the absence of suitable hard substrata for polyp attachment (Sparks & Gibbons, 2003), although a number of other explanations could also be proposed. Taxa that typically increase in richness into the subtropical regions influenced by the Agulhas Current are those that have a diverse Indo-Pacific component, such as fishes (Turpie *et al.*, 2000) and echinoderms (Thandar, 1989). The situation is similar for those Hydrozoa associated with the benthos: Millard (1978) herself noted the '...heavy invasion of tropical species from the Indo-West Pacific region, [which] form the major component of the fauna of the east coast' (p. 182). Interestingly, not all groups of marine organisms display an increase in richness eastwards, and Awad *et al.* (2002) and Bolton & Stegenga (2002) have documented some taxa that reach peak richness along the south coast. These include octocorals, amphipods, isopods and red algae, although many others show greatest levels of endemism across this same region (Awad *et al.*, 2002). Although there are relatively few endemic species with medusae (Pagès *et al.*, 1992), Millard (1978) noted c. 33% endemism amongst benthic hydroids, and these too were mostly recorded from the south coast, despite the greater overall richness of benthic hydroids on the east coast.

In examining the distribution of richness across the region, we need to contextualize it in terms of sampling effort. Figure 3 shows the distribution of relative sampling effort in



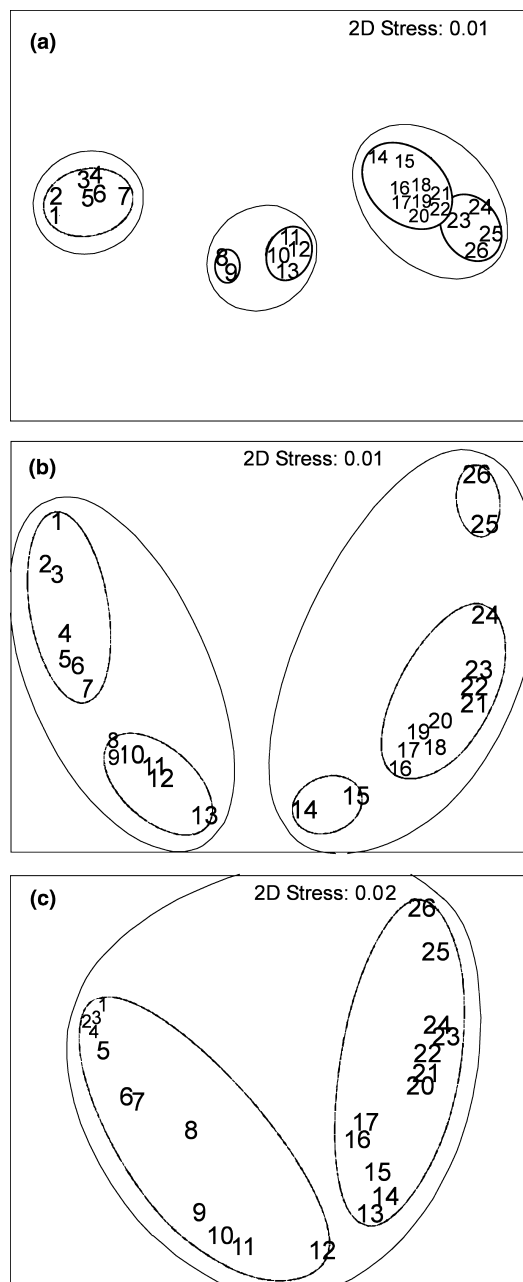
**Figure 3** Approximate distribution of sampling effort around southern Africa. These data reflect the number of plankton samples analysed, and assume that benthic sampling has been evenly distributed (see text):  $n = 2046$ . Grid numbers follow those in Fig. 1.

the region and assumes that Millard's (1978) sampling of the benthos was evenly distributed around the coast. Although this assumption is likely to be false (Naomi Millard was based at the then South African Museum in Cape Town), it is not possible to correct for this in the absence of appropriate metadata, and the picture that emerges is therefore dominated by plankton sampling effort. By contrast to the distribution of species richness around the sampling grid (Fig. 2), most of the sampling effort has been focused along the west and south-west coasts of southern Africa (Fig. 3). There is no relationship between effort and raw species richness (including species recovered from single grids, but excluding interpolations, Fig. 2a) for either all species or only those species with a planktic component in the life cycle, as determined using Spearman rank correlations ( $P > 0.05$ ). Most of the species that were recorded from single grids were meroplanktic Anthoathecata (Table 1) recovered from plankton samples. This suggests that the patterns of richness are real, and that we are underestimating richness in the east. These results contrast with some recent observations of Medd (2007) and unpublished data of C. L. Griffiths (Zoology Department, UCT), which show a strong bias in the distribution of species records by proximity to local centres of marine biological research. It should be noted that the relative scarcity of samples along the east coast of South Africa (and presumably the high likelihood that we have missed species there) constrains our understanding of the geographic affinities of that fauna.

### Biogeographic structure

There is a clear biogeographic structure to the regional hydrozoan fauna (Fig. 4, Appendix S2), and this structure is broadly independent of life cycle strategy. The results of the RELATE analysis in PRIMER indicate that all resemblance matrices are highly and significantly correlated ( $P < 0.001$ ) with each other: the  $\rho$ -value for the pairwise comparison of similarity matrices between holoplanktic and meroplanktic hydrozoans was 0.89; between holoplanktic and benthic species it was 0.92; and between benthic and meroplanktic species,  $\rho$  was 0.89.

Although patterns in the biogeography of the different life cycle groupings are very similar, there are some differences and these differences are informative. In the case of taxa that are very closely linked to the benthos (Fig. 4a), the patterns of biogeography are broadly similar to those seen for most other groups of benthic marine organisms (e.g. Emanuel *et al.*, 1992). At 40% similarity, the subtropical and warm-temperate province extends along the east (subdivided at Port St Johns – grid 22) and south coast of South Africa to somewhere between Cape Point and Cape Columbine (grid 14), where it is replaced by a cool-temperate Namaqua Province (*sensu* Emanuel *et al.*, 1992), which in turn is replaced by a Namib Province at Lüderitz (grid 8). In the case of the meroplanktic species, we can see a subtropical and warm-temperate province that extends along the east and south coasts to grid 14, where it is replaced with a cool-temperate province stretching up the



**Figure 4** Non-metric multidimensional scaling (NMDS) plots showing the similarity (Bray–Curtis measure) between geographic grids around southern Africa: stress values are shown in the upper right corner: (a) benthic species; (b) meroplanktic species; and (c) holoplanktic species. Grid numbers follow those in Fig. 1. The different lines encircling various grids reflect different levels of similarity: solid, 40%; dashed, 72%. Note that some points have been offset slightly to ease interpretation.

entire west coast (Fig. 4b). Although both Namaqua and Namib provinces can be discerned in the cool-temperate province, this is only clear at a high level of similarity. Most telling of all, however, is the absence of any comparable geographic structure for holoplanktic forms (Fig. 4c), which can only really be separated into a cool-temperate and a warm-

temperate/subtropical fauna (to the south of the Orange River mouth – grid 11) at a high level of similarity.

In the case of those taxa with a benthic polyp, it is largely unnecessary to explore the links between biogeographic pattern and oceanography in the region because of the many studies on benthic groups that have already done so, and we have essentially summarized these above. The role of the Agulhas Current in influencing these patterns is largely restricted to the east and, to some extent, south coasts, because it retroflects offshore between grids 15 and 16 (Lutjeharms, 2006). Its impact on the benthic fauna of the west coast is going to be strictly limited, as any rings or filaments that are shed at the point of retroflexion simply move further offshore into the South Atlantic (Lutjeharms, 2006). Although some of these features may subsequently move closer to the shelf as they pass northwards (Duncombe Rae, 1991), the survival and eventual successful settlement and metamorphosis of expatriated larvae (given their short residence time) is likely to be limited in the absence of appropriate physiological and behavioural traits (at least). The Agulhas Current does appear to play a more significant role in the biogeography of holoplanktic taxa, however, with its influence on the biota being felt up the west coast (Pagès & Gili, 1992) almost to the Orange River. Similar observations were made by Gibbons & Thibault-Botha (2002) for the regional siphonophore fauna, irrespective of underlying bathymetry.

In his comprehensive review of the Agulhas Current, Lutjeharms (2006) notes that between 10 and 50% of the volume flux in the upper 1000 m of the Benguela Current is derived from the Agulhas Current. Importantly, at intermediate depths, the 'greater part of the waters in the Cape Basin is supplied from the Indian Ocean, with minor direct flow from the Atlantic Ocean' (Lutjeharms, 2006, p. 190). The Cape Basin effectively extends along the west coast of South Africa and Namibia, its northern boundary being delimited by the Walvis Ridge. Lutjeharms (2006) also notes that the northward-flowing jet current in the Benguela system (Shannon, 1985) is seasonally strengthened, in part by an increased injection of Agulhas ring water on the offshore side of the jet. During periods of relaxation in the upwelling wind stress along the west coast, the jet weakens and offshore water can be moved onshore during downwelling (Gibbons & Hutchings, 1996), which can result in a temporal increase in the diversity of the nearshore fauna (Pagès & Gili, 1992). So not only does the Agulhas Current influence the biota of the deeper water off the west coast (an environment occupied by some holoplanktic hydrozoans) but it is also likely to have a profound effect on the distribution of the epipelagic fauna.

In their earlier, geographically coarser, analyses of regional siphonophores and euphausiids, neither Gibbons & Thibault-Botha (2002) nor Gibbons *et al.* (1995) identified separate Namib and Namaqua provinces. This is in agreement with the results presented here for holoplanktic taxa and reflects the fact that the Lüderitz upwelling cell, which marks the boundary between the two provinces for taxa having benthic polyps,

provides only a partial cross-shelf barrier to holozooplankton and other pelagic organisms (Gibbons & Hutchings, 1996; Duncombe Rae, 2005; Lett *et al.*, 2007). Indeed, its significance as a barrier can be hypothesized to be related to the length of time that species remain in the plankton, being less influential for meroplanktic than for polyp-only forms (Fig. 4), and not at all for holoplanktic taxa. That said, differences are likely to be apparent in the numerical composition of assemblages (as Barange *et al.*, 1992) that reflect differences in system functioning.

We set out to test the hypothesis that the biogeography of marine Hydrozoa around southern Africa was correlated with life cycle strategy. Based on the above RELATE statistics it is clear that there is a strong commonality in biogeography between the various life history groupings. However, it is also clear that there are differences (Fig. 4). Holoplanktic taxa do show less biogeographic structure than meroplanktic taxa, which in turn show less clearly defined biogeographic structure than benthic taxa. This is likely to be related to the interaction between oceanography and dispersive stage duration.

Conservation planning exercises are often based on trying to protect representative biotopes in different biogeographic provinces (Lombard & Strauss, 2004). However, it is clear that the delimitation of a biogeographic province in the marine environment (Spalding *et al.*, 2007) varies with life cycle strategy. Although this needs to be taken into consideration when designing and implementing conservation plans, and suggests perhaps that the pelagos requires less protection than the benthos, we should not assume that all potential pelagic reserves are equal just because they contain similar organisms. The analyses conducted here have been based on presence/absence data, which fail to capture important information relating to abundance, biomass and system functionality (as Longhurst, 1998). Although there may be over 80% similarity in the species composition of the cold-temperate holoplanktic fauna either side of Lüderitz (see Appendix S2), it would be a mistake to assume that the northern and southern Benguela ecosystems are similar (Brown *et al.*, 2001) and that a single reserve would cater for both!

## CONCLUSIONS

There is a link between dispersal ability in the marine environment and genetic/species diversity (e.g. Bradbury *et al.*, 2008; Gibbons *et al.*, 2009). Taxa that lack a pelagic and dispersive life history phase or that have a short-lived planktic stage are often characterized by a higher diversity than those that spend a prolonged period of time in the water column (e.g. Bradbury *et al.*, 2008). Because of their close association with the benthos, the evolution of shallow-water taxa without a dispersive life history stage is thought to have been strongly influenced by climatic and tectonic events: allopatric speciation reflecting vicariant processes (e.g. Heads, 2005) has given rise to numerous, geographically restricted forms. If the regional pattern of distribution of such benthic taxa around southern Africa can be viewed as representative from this

relatively coarse study, then local biogeography appears to reflect quite accurately the prevailing oceanography at the mesoscale. By contrast, the biogeography of widely distributed holopelagic taxa reflects local oceanography only at the macroscale, perhaps because speciation and localized adaptation are effectively limited by 'dispersal'. Of particular interest here are those taxa that possess both benthic and pelagic life cycle phases, as they display intermediate patterns of geographical affinity. Although this makes sense at one level, it is nevertheless intriguing and suggests a need for further research to look at the disparate roles of the benthic and pelagic life cycle phases on speciation and distribution.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Data matrix used in the biogeographical analyses of marine Hydrozoa around southern Africa.

**Appendix S2** Dendrograms showing percentage similarity (Bray–Curtis measure) between the hydrozoan fauna of grids around southern Africa: (a) benthic species, (b) meroplanktic species, (c) holoplanktic species.

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## BIOSKETCH

**Mark J. Gibbons** is a lecturer in ecology and marine biology at the University of the Western Cape in South Africa, with an interest in biological oceanography. He is particularly fascinated by pelagic cnidarians and ctenophores, and his like-minded coauthors are now extending their experiences elsewhere in the world following study visits to South Africa.

Author contributions: M.J.G. conceived the ideas; M.J.G., E.B., D.T.B. and R.R.H. collected the data; M.J.G. analysed the data; and M.J.G. led the writing.

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