

Life cycle strategy, species richness and distribution in marine Hydrozoa (Cnidaria: Medusozoa)

Mark J. Gibbons¹*, Liesl A. Janson², Adiel Ismail³ and Toufiek Samaai²

¹Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, ²Marine and Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Roggebaai 8012, ³Department of Computer Science, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa

ABSTRACT

Aim Using the genus as the unit of analysis, we examine the relationship between richness, distribution and life cycle strategy for all currently recognized marine Hydrozoa.

Location The global marine environment.

Methods A global dataset detailing the number of species per genus and the mean date of first description (as a proxy for geographic range size) per genus was assembled for all currently recognized marine Hydrozoa. Differences in means per genus were examined by dominant life cycle strategy (holoplanktic, meroplanktic and benthic) using nonparametric ANOVA and resampling methods.

Results By comparison with benthic taxa, holopelagic genera are (on average) significantly less species rich and were described at a significantly earlier date. Taxa with meroplanktic life cycles have a richness and a date of first description that is mid-way between the two extremes.

Main conclusions Following from previous work showing that there is a negative relationship between the date of first description and geographic range size, our data indicate that holopelagic taxa not only have fewer species per genus but also have a wider distribution than benthic taxa. These quantitative results are in agreement with long-standing intuitions, and should be applicable to other taxa. They run counter to some recent genetic observations that suggest taxa having planktic larvae might nevertheless show restricted distributions; we argue that this inference reflects a lack of sampling of holopelagic taxa, and a call is made to provide empirical evidence from this realm.

Keywords

Benthic taxa, date of description, dispersal, global analysis, holoplankton, medusae, meroplankton, polyp, range size, 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

Free-living marine invertebrates occupy one of two environments as adults – the pelagos or the benthos. Many benthic animals nevertheless occupy the pelagos for a short period of time at some stage in their life, be it as gametes or developing larvae. These temporary components of the plankton are referred to as meroplankton, whilst organisms that remain in the plankton for the full duration of their life are known as holoplankton. The length of time that a life cycle stage is resident in the plankton is related to the trophic mode of that stage. Taxa with lecithotrophic larvae or non-feeding life cycle stages tend to be pelagic for relatively short periods of time,

and dispersal is comparatively limited (e.g. Scheltema, 1986). Others have planktotrophic larvae that feed whilst in the plankton, and these may be resident for prolonged periods of time during which they undergo extensive and sometimes complex development and can disperse over much greater distances (e.g. Scheltema, 1986; Avise *et al.*, 1987).

The evolution of benthic taxa, because of their obvious association with the seabed and their relatively restricted use of the pelagos, is thought to have been strongly influenced by tectonic and climatic events, and vicariance has been suggested to be the major mechanism leading to allopatric speciation (e.g. Springer, 1982; Heads, 2005). The diversity of the marine benthos is comparatively high, and relatively few species are

naturally widely distributed on a global scale. Although vicariant events such as the closure of the Isthmus of Panama and the establishment of the Antarctic Circumpolar Current have been invoked to explain some speciation events within the pelagos (e.g. van der Spoel, 1996; van Soest, 1998), the very nature of the environment is such that many have argued that processes linked to dispersal may be more important in plankton (e.g. Waters & Roy, 2004). The diversity of the marine holoplankton is low (Angel, 1993), and many taxa are very widely distributed (e.g. Kramp, 1961).

While it follows that taxa using the pelagos in a restricted way will be more limited in distribution and more diverse than holoplanktic forms, we have been unable to find any explicit, global examination of this in the literature. That said, there is certainly a large amount of support for a negative relationship between population genetic structure (Φ_{ST} , F_{ST}) and range size or dispersal ability in the marine environment (e.g. Kyle & Boulding, 2000; Bradbury *et al.*, 2008), as suggested by Avise *et al.* (1987). Here we set out to test the hypothesis that taxa that are permanently found in the marine plankton are less diverse and more widely distributed than those that are temporary members, using the monophyletic Hydrozoa.

Hydrozoans are a diverse group of medusozoan cnidarians. They are found in all marine environments, and display a vast array of life cycle strategies (Bouillon *et al.*, 2006). The ancestral life cycle is likely to have been metagenic, as the possession of a 'medusa' is regarded as synapomorphic for Medusozoa (e.g. Collins, 2002; Marques & Collins, 2004), i.e. there is (generally) a benthic polyp that reproduces asexually to produce free-swimming, sexually active medusae which in turn produce ciliated planulae larvae that settle and develop into polyps again. Such a strategy is displayed by many Anthoathecata and Leptothecata. There is, however, considerable variation: some lineages lack a polyp or medusa stage (many Anthoathecata and Leptothecata; Cornelius, 1992). In other taxa, both polyps and medusa may be combined into extensively polymorphic individuals (Siphonophorae).

We use the number of species per genus as a measure of species richness. In the absence of data on geographic range size we have used the date (year) of first description. There is a well-established negative relationship between the date of first description and geographic range size for a diversity of terrestrial and aquatic animals (e.g. Blackburn & Gaston, 1995; Gaston *et al.*, 1995; Allsop, 1997; Collen *et al.*, 2004; Gibbons *et al.*, 2005). In other words, the earlier the date of first description, the wider the known distribution of the species. We discuss this premise below.

MATERIALS AND METHODS

A dataset containing all the known species of Hydrozoa, plus supplementary information on taxonomy, life cycle strategy and date of first description, was compiled from the recent encyclopaedic work of Bouillon *et al.* (2006), following the systematic revisions of Collins *et al.* (2008) and Cartwright *et al.* (2008). We have used only those marine species

considered by Bouillon *et al.* (2006) to be valid; all those regarded as doubtful, invalid or synonyms were excluded from the analyses (see Appendix S1 in Supporting Information). In order to look at the role of basic life cycle strategy on richness and date of first description (as a proxy for global range size), we have assumed that all species within a genus display the same life cycle strategy. We acknowledge that this is not always true (see Discussion), but the number of exceptions appears to be limited at this stage and is thus unlikely to materially influence the results. The three categories of life cycle strategy that we investigated were as follows. (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 (almost complete medusae with radial canals but rarely with tentacles; may have a short free pelagic life) and cryptomedusoids (more regressed stage than eumedusoid, without radial canals or tentacles; unusually free swimming), or those with benthic medusae (Actinulidae and some Trachymedusae). (2) Holoplanktic: those with a pelagic phase only, including Siphonophorae and some Anthoathecata (species in the Porpitidae and Margelopsidae). (3) Meroplanktic: those with both a benthic and a pelagic phase. We have ignored all cases where the polyp phase is at present unknown (c. 170 species in 96 genera; Bouillon *et al.*, 2006).

We have taken two approaches in our analyses. Firstly, we have compared the mean number of species per genus and the mean date (year) of first description in the three different life cycle categories using Kruskal–Wallis nonparametric ANOVA tests (Zar, 1996). Analyses were conducted in STATISTICA version 7 software (StatSoft, Inc., 2002), accepting 95% levels of significance.

Secondly, we have used simulation tests to determine whether the number of species per genus, and the mean date of first description of species per genus, in each life cycle category was significantly different from random samples of the overall data. It has been suggested that resampling methods have more statistical power than standard parametric tests when the data are not normally distributed (Crowley, 1992). An appropriate number of genera were selected at random and without replacement from the overall dataset, depending on the generic richness of each life cycle category. The mean, standard deviation and skewness of this sample were all calculated, 999 times, following Gaston & Blackburn (1994). If the distribution of species amongst genera is random (the null hypothesis) then the mean, standard deviation and skewness values from the simulated distributions should fall randomly about those calculated from the real distributions.

RESULTS

Table 1 provides a summary of species, genus and family richness in the Hydrozoa, as considered here. The overall richness of species in the three life cycle strategies considered here is clearly different (Table 1). There are not only fewer species in holoplanktic taxa but also fewer genera and families. Whilst benthic taxa have the greatest number of species and

Table 1 Summary of marine hydrozoan diversity by class, order and life cycle strategy.

Class	Order	Life cycle strategy	No. families	No. genera	No. species	No. genera per family	No. species per genus	No. species per family	DOFD per species per genus
All	All	Benthic	47	215	2086	4.6	9.7	44.4	1924.9
All	All	Meroplanktic	46	102	733	2.2	7.2	15.9	1915.7
All	All	Holoplanktic	24	95	245	4.0	2.6	10.2	1900.2
Hydroidolina	All	All	89	359	2932	4.0	8.2	32.9	1917.9
Hydroidolina	Anthoathecata	Benthic	23	79	499	3.4	6.3	21.7	1940.2
Hydroidolina	Anthoathecata	Meroplanktic	28	61	458	2.2	7.5	16.4	1923.8
Hydroidolina	Anthoathecata	Holoplanktic	2	5	9	2.5	1.8	4.5	1859.9
Hydroidolina	Leptothecata	Benthic	17	120	1554	7.1	13.0	91.4	1912.4
Hydroidolina	Leptothecata	Meroplanktic	17	33	249	1.9	7.5	14.6	1902.4
Hydroidolina	Siphonophorae	Benthic	1	7	11	7.0	1.6	11.0	1931.1
Hydroidolina	Siphonophorae	Holoplanktic	15	54	152	3.6	2.8	10.1	1903.9
Trachylina	All	All	13	53	132	4.1	2.5	10.2	1910.5
Trachylina	Actinulidae	Benthic	2	2	11	1.0	5.5	5.5	1962.5
Trachylina	Limnomedusae	Benthic	3	5	8	1.7	1.6	2.7	1963.2
Trachylina	Limnomedusae	Meroplanktic	1	8	26	8.0	3.3	26.0	1908.5
Trachylina	Narcomedusae	Holoplanktic	3	11	36	3.7	3.3	12.0	1896.0
Trachylina	Trachymedusae	Benthic	1	2	3	2.0	1.5	3.0	1918.8
Trachylina	Trachymedusae	Holoplanktic	4	25	48	6.3	1.9	12.0	1902.3

DOFD, mean date (year to one decimal place) of first description.

Data derived from Bouillon *et al.* (2006), excluding all species they recognized as invalid or dubious, and all taxa with an incompletely known life-history strategy.

genera, they have only slightly more families than the meroplanktic taxa. This pattern is not consistent across the two classes.

The mean number of species per genus varies with life cycle strategy (Fig. 1a), and the species richness of holoplanktic genera is significantly less than that of benthic or meroplanktic genera [$H(2, n = 412) = 22.46, P < 0.0001$]. While the mean number of species per genus for taxa displaying meroplanktic life cycles is lower (7.1) than that observed for benthic taxa (9.7), this difference is not significant. Similar results are shown by the simulations (Table 2), from which it can be seen that the distribution of species amongst benthic and pelagic genera is not random. Not one of the 999 random samples from the overall dataset generated means (7.40, SD = 14.4) less than that observed for holoplanktic species, and only a single sample had a mean greater than that observed for the benthic taxa. On average, holoplanktic genera have fewer species, and benthic genera have more species, than would be expected by chance. Although the richness of genera with meroplanktic life cycles does not differ appreciably from expected (44.14% of the simulations generated means less than observed), the real distribution of species amongst genera tends to be narrower and more skewed to the right than those generated by the simulations (Table 2).

Although the first hydrozoans were described in the mid-1700s (Fig. 2), there was a general paucity of new descriptions until the early and mid-1800s. Thereafter the rate of description of new species has remained more or less constant for holoplanktic taxa, although the curve has been

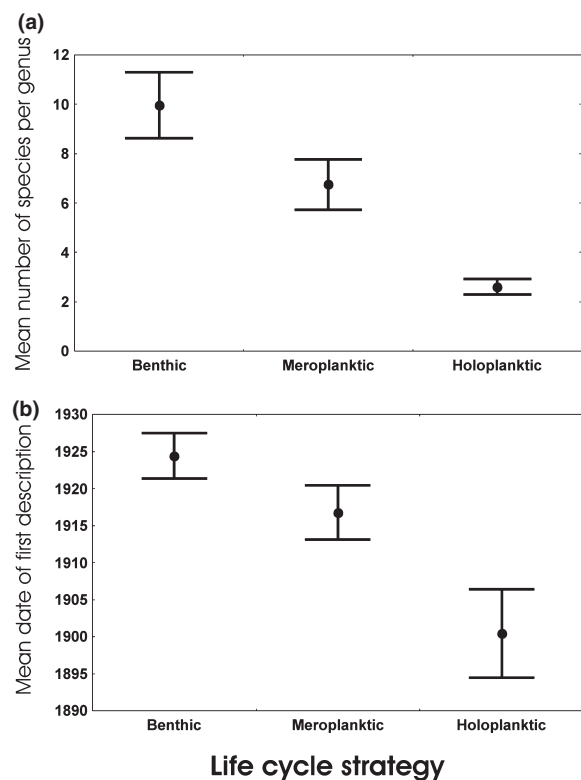


Figure 1 Whisker plots showing how the mean (and standard error) number of species per genus (a) and the mean date of first description of species per genus (b) vary with life cycle strategy in marine Hydrozoa.

Table 2 Results of the simulations of the frequency distribution of (a) the number of species per genus and (b) the date (year) of first description of marine Hydrozoa, by life cycle strategy. The percentage of the 999 simulated distributions with mean, standard deviation or skewness values less than those of the real distribution are shown.

		Mean		Standard deviation		Skewness	
Life cycle strategy		Real	Simulations less (%)	Real	Simulations less (%)	Real	Simulations less (%)
(a)	Benthic	9.70	99.80	18.89	99.50	3.52	1.00
	Meroplanktic	7.19	44.14	11.11	13.61	4.99	84.38
	Holoplanktic	2.58	0.00	2.96	0.00	5.01	83.58
(b)	Benthic	1924.92	99.90	43.96	6.11	-0.89	17.42
	Meroplanktic	1915.70	36.84	38.60	1.60	-0.67	68.67
	Holoplanktic	1900.20	0.00	57.00	99.80	-0.44	90.69

more sigmoidal in the case of both benthic and meroplanktic taxa (Fig. 3). The mean date of first description varies significantly [$H(2, n = 412) = 13.98, P < 0.001$] with life cycle strategy (Fig. 1b). Holoplanktic species were on average described earlier (AD 1900) than benthic species (*c.* AD 1925), but there is no significant difference between the date of first description of species in genera displaying meroplanktic and either other life cycle type. Similar results are seen in the simulations (Table 2). On average, the species in holoplanktic genera were described earlier, and those from benthic genera were described later, than would be expected by chance. Although the date of first description of species in meroplanktic genera does not differ from expected (36.8% of the simulations generated means less than observed), differences in the standard deviation and skewness of simulated and real distributions are apparent. It is noteworthy too that the standard deviation about the date of first description of holoplanktic species is much larger than that generated by the simulations.

DISCUSSION

Our understanding of the diversity of life is biased, because the species that have been described are not a random subset of the total (Diamond, 1985; May, 1988). A number of factors have been shown to play a role in influencing the date of first description, although each varies in significance with the taxon under scrutiny. For terrestrial birds, mammals, beetles and butterflies, these factors include body size, population size, altitude, geographic location, behaviour and geographic range size (Blackburn & Gaston, 1995; Gaston *et al.*, 1995; Allsop, 1997; Collen *et al.*, 2004), with geographic range size usually being the most significantly correlated with the date of first description. In a meta-analysis of 18 orders of diverse marine zooplankton (including three hydrozoans), body size has been shown to be relatively unimportant as a predictor, but depth and especially geographic range size are significantly correlated with the date of first description (Gibbons *et al.*, 2005). The negative relationship between the date of first description and geographic range size therefore appears to cut across habitats and organisms. As a consequence, and until such point at

which the full distributional ranges of all species are known, the date of first description can be considered to represent a robust measure of geographic range size in comparative analyses such as these.

Although holopelagic taxa may have only half the number of families and genera as benthic taxa, species richness is an order of magnitude less than that of meroplanktic and benthic taxa. The absolute number of species with meroplanktic life cycles is *c.* 30% of that of benthic taxa, though the number of families is similar and the number of genera is *c.* 50% less (Table 1). If we recognize Bouillon *et al.*'s (2006) valid taxa with incompletely known life cycles (e.g. undescribed polyp) as meroplanktic, then both life cycle strategies are similarly diverse at the generic and familial levels, though benthic taxa still have twice as many species (data not shown). There is thus a decline in species richness with an increasing use of the plankton. This decline in species richness is matched by a corresponding increase in distributional range, if we use date of first description as a proxy for range size.

It should be noted that this pattern does not hold for all taxa (Table 1). For example, whilst most marine Trachylina lack a benthic polyp stage, some medusae are strictly benthic and/or inhabit the interstitial environment. This group includes all members of the order Actinulidae and the family Ptychogasteriidae (Trachymedusae). In these cases, the mean number of species per genus (*c.* 3.5) is much lower than that of other benthic taxa, yet the mean date of first description (*c.* AD 1941) is much more recent. Likewise all members of the siphonophore family Rhodaliidae are also considered to be benthic. The mean number of species per genus is even smaller (1.57) than that observed for holoplanktic species, but the date of first description is much later (*c.* AD 1931). We suspect that both results are artificial. In the case of Actinulidae and benthic Trachymedusae it probably reflects the fact that the benthic environment has been poorly sampled in an appropriate manner for hydrozoans, as nematodes and harpacticoid copepods are both considered to be comparatively diverse (Baguley *et al.*, 2006). In the case of rhodaliid siphonophores, the environment they occupy is bathyal and also undoubtedly poorly sampled. That said, however, the very homogeneity of the vast deep-sea landscape may allow widespread dispersal

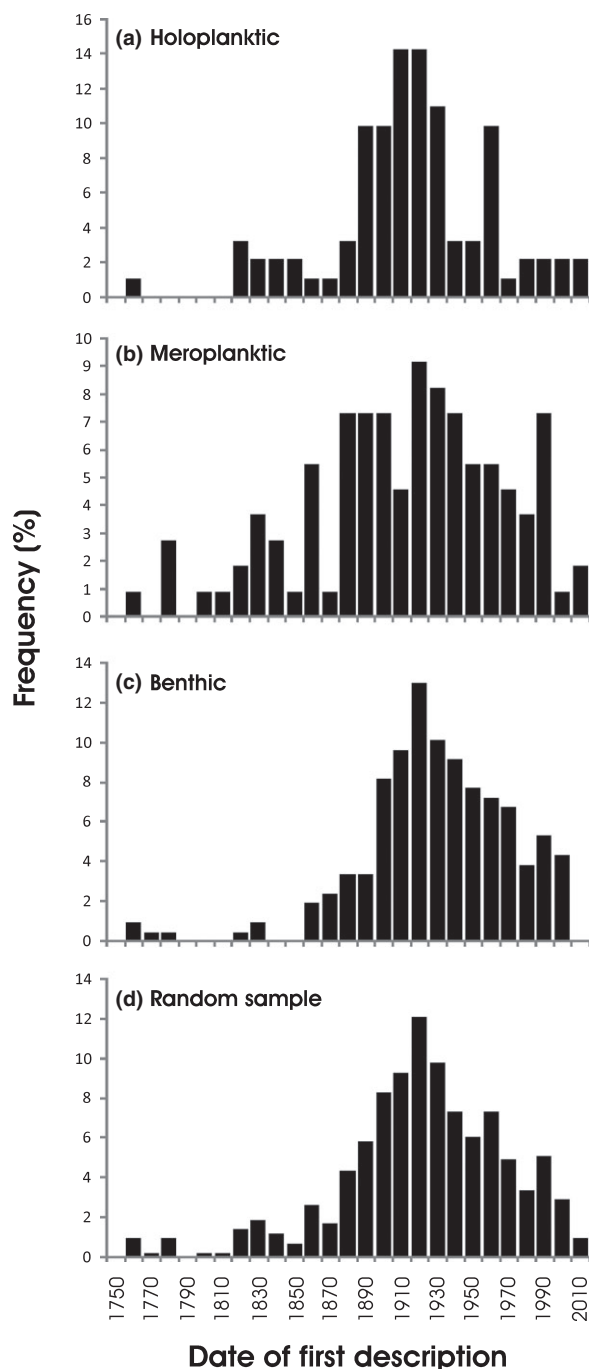


Figure 2 Histograms showing that the temporal pattern of species description (percentage per decade) of marine Hydrozoa varies with life cycle strategy: (a) holoplanktic taxa only ($n = 95$), (b) meroplanktic taxa only ($n = 102$), (c) benthic taxa only ($n = 215$) and (d) 999 random samples ($n = 215$, to match the number of benthic genera) of all the data. [Correction added after online publication, 5 November 2009: Figure 2 was originally published with an error on 29 October. This corrected version was published a week later.]

and encourage reduced richness, as has been observed for example in the fauna associated with the carcasses of baleen whales (Glover *et al.*, 2005).

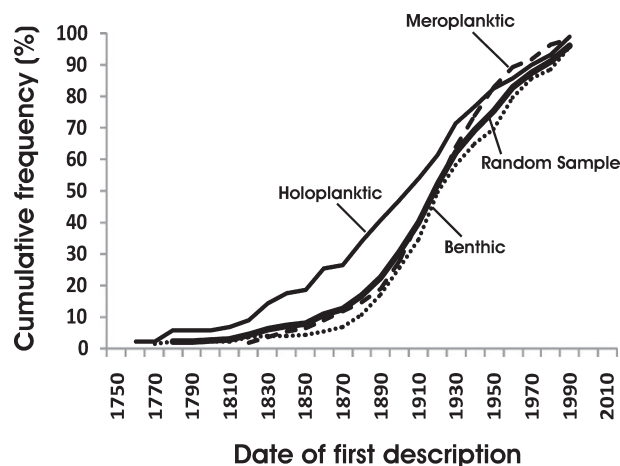


Figure 3 Cumulative species description curves for marine hydrozoan taxa with different life cycle strategies: $n = 95$ (holoplanktic genera), $n = 102$ (meroplanktic genera), $n = 215$ (benthic genera). Comparative information is also provided for 999 random samples ($n = 215$, to match the number of benthic genera) of all the data.

It is important to note that the greater numbers of benthic hydroids described (and hence the probability of an increased number of species per genus) could reflect the fact that they occupy environments that are relatively accessible. The argument that this would lead to more benthic species being discovered is difficult to counter, though plankton sampling has, especially in recent times, become extensive and it might then be expected that large numbers of holoplanktic taxa would be recently described. Although some are indeed recently described, this is not generally the case, hence the large standard deviation about the mean date of first description of holoplanktic taxa (Table 2). Further, it should be noted that the sampling of benthic environments at depths > 100 m has been very limited. Perhaps more relevant here is the fact that the polyp stages of many hydroids have a number of morphological features that allow ready discrimination. This is not the case for medusae, which are considered by many to have a small number of variable and taxonomically informative morphological characters (Dawson, 2004), and this may have led to the lumping of some lower taxa. The problem of lumping is not unique to hydrozoans, and it has been highlighted by Knowlton (2000) as occurring in a number of marine animal groups. While lumping leads to a reduction in richness, splitting leads to an increase in richness and crypsis (as an agent for splitting) has recently been reported for medusae (Dawson & Jacobs, 2001; Dawson, 2003). That said, it is important to stress that instances of crypsis have mostly been documented for medusae of taxa with meroplanktic life cycles (but see also Collins *et al.*, 2008). The effect of any new descriptions based on crypsis, in the present context, is that it leads to an increase in the number of species per genus, a recent date of first description and a reduction in distributional range size. While hidden genetic structure is apparent in other planktic taxa (e.g. Peijnenburg *et al.*, 2004; Goetze,

2005), few authors have gone so far as to actually define new species on this basis (see also Knowlton, 2000), and there is only limited evidence of crypsis within holoplanktic cnidarians thus far (Collins *et al.*, 2008).

The definition of many hydroidine genera has traditionally been based, in part, on the type of reproductive structure. The possession of a free-living medusa is generally considered to be synapomorphic for Medusozoa (Collins, 2002; Marques & Collins, 2004) and in many instances it has been secondarily lost through pedomorphosis, with a subsequent radiation of the more benthic descendants (Boero & Sarà, 1987). Thanks largely to molecular methods it is clear that the loss of medusae and the evolution of fixed gonophores/sporosacs can occur independently within closely related lineages, so that some genus-level groups are now considered artificial. This has been demonstrated within the anthoathecate family Hydractiniidae (Cunningham & Buss, 1993; Miglietta *et al.*, 2009), as well as the leptothecate family Campanulariidae (Govindarajan *et al.*, 2006).¹ The effect of this is likely to be a reduction in the size of some meroplanktic and benthic genera, so it is important that we remember the taxonomic framework within which the present analyses are conducted.

That holopelagic taxa are more widely distributed than benthic taxa comes as no surprise given the dynamic (surface) and extensive (bottom water) nature of the environments occupied. The low species richness and wide distribution of holopelagic hydrozoans is matched in other planktic groups (Gibbons *et al.*, 2005) and a number of general explanations have been put forward to account for this (Angel, 1993; May, 1994). These include a general homogeneity in the physical and chemical composition of the pelagic environment, the absence of any structural architecture and the effects of physical mixing and water flow, as well as the nature and organization of the food webs.

These data are also in broad agreement with more general literature on dispersal ability or distributional range and genetic diversity (as an indicator of speciation potential) of marine invertebrates. Taxa with a brief planktic larval stage have more genetic structure than those that remain within the plankton for longer periods of time (e.g. Todd *et al.*, 1998; Uthicke & Benzie, 2003), and those without planktic larvae at all tend to be more genetically subdivided still (Kyle & Boulding, 2000). However, there are a growing number of exceptions to this pattern (see references in Heads, 2005), and it has been shown that some widely distributed benthic taxa having planktic larvae might show restricted distributions because of, for example, local recruitment behaviours (Thresher & Brothers, 1985). While pronounced genetic structure has also been noted in some widely distributed zooplankton (e.g. Peijnenburg *et al.*, 2004; Goetze, 2005; Papetti *et al.*, 2005), it has not been observed in others (e.g.

Bucklin *et al.*, 2000; Darling *et al.*, 2000). It has not as yet been recorded in medusozoans, presumably because of a lack of study, though crypsis in some meroplanktic species (not holoplanktic) has been observed, as noted above. Goetze (2005) discusses in some detail the patterns observed in the plankton and comments on the likely lack of genetic structure in eurytolerant species that can maintain viable populations in oligotrophic, open ocean waters. Most holopelagic hydrozoans attain their highest diversity in such waters (Bouillon, 1999) and many display a very wide vertical distribution (Mackie *et al.*, 1987).

Although there are species of marine Hydrozoa with relatively wide distribution ranges that lack dispersive larval stages, they are limited only to 'some several dozen species' (Cornelius, 1992, p. 253). Such distributions have been attributed to polyp rafting on seaweed and other flotsam (Miglietta *et al.*, 2009), and Cornelius (1992) argued that survival of polyps in transit and after arrival at a remote location will be greater than that of their medusa or planulae. In the latter regard it is worth noting that the total life span of planulae of benthic species is generally less (3–4 days) than that of species with medusae (2–10 days) (Sommer, 1992); both life cycles seemingly limit dispersal. Once at a remote location, Cornelius (1992, p. 258) speculated that 'there may be little preventing a rapid evolution of a medusa-suppressed lineage', which in turn would be free to raft to other areas. Such an argument could, in part, account for the wide distribution of some genera amongst island faunas and their high species diversity.

The results presented here are inferential, and are based on the use of proxies: numbers of species per genus as an index of diversity and date of first description as an index of geographic range size. Both have intrinsic errors, and are very dependent on our understanding of species identity, taxonomy and systematics. In particular, the delimitation of higher taxa is incomplete (Cartwright *et al.*, 2008; Collins *et al.*, 2008) and it remains in part a subjective endeavour. Yet regardless, the patterns that emerge here are strong. Whilst the approach taken here is novel, the conclusions are not and they support long held generalizations. If these disagree with recent results (e.g. Heads, 2005), they only do so because few others have attempted to include extremely dispersive (holopelagic) taxa in their analyses (as also noted by Bradbury *et al.*, 2008). We urge molecular systematists and population geneticists to take up the challenges posed by unravelling processes of speciation in the open ocean, and to add empirical data that will improve our understanding of the role of dispersal in pelagic biogeography.

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¹The genus *Obelia* has a particularly intriguing medusa that has been suggested to have arisen from a rare evolutionary reversal (Boero *et al.*, 1996), though prevailing thought and evidence suggests that medusae are more likely to be lost than gained in evolution.

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SUPPORTING INFORMATION

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

Appendix S1 Mean date of first description and number of valid species of marine Hydrozoa, by taxonomy and life cycle strategy.

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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. He has worked quite extensively in both pelagic and benthic environments but recently has focused on zooplankton, particularly gelatinous zooplankton.

Author contributions: M.J.G. conceived the ideas; L.J. and M.J.G. collected and consolidated the data; A.I. developed the resampling algorithm; M.J.G., L.J. and A.I. analysed the data; M.J.G., L.J. and T.S. led the writing.

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