Latitudinal Diversity of Sea Anemones (Cnidaria: Actiniaria)

DAPHNE GAIL FAUTIN*, LACEY MALARKY, AND JORGE SOBERÓN

Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045

Abstract. We sought to determine if the global distribution of sea anemones (cnidarian order Actiniaria) conforms to the classic pattern of biogeography—taxon richness at the equator with attenuation toward the poles—a pattern that is derived almost entirely from data on terrestrial plants and animals. We plotted the empirical distribution of species occurrences in 10° bands of latitude based on published information, then, using the Chao2 statistic, inferred the completeness of that inventory. We found the greatest species richness of sea anemones at 30–40° N and S, with lower numbers at tropical latitudes and the fewest species in polar areas. The Chao2 statistic allowed us to infer that the richness pattern we found is not due to particularly poor knowledge of tropical sea anemones. No 10° band of latitude has less than 60% of the theoretical number of species known, but for only about half of them could we reject the null hypothesis ($P = 0.05$) that information is complete; anemone diversity is best documented at high latitudes. We infer that the 1089 valid species currently known constitute about 70% of the theoretical total of about 1500 species of Actiniaria. The distribution pattern of sea anemone species resembles that of planktonic foraminiferans and benthic marine algae, although planktonic bacteria, marine bivalves, and shallow and deep scleractinian corals show the terrestrial pattern of equatorial richness attenuating with latitude. Sea anemone species richness is complementary to that of scleractinian corals at many scales; our findings affirm it at the global scale.

Introduction

High taxonomic diversity at the equator with attenuation toward the poles has been termed "one of the most funda-

mental" (Willig *et al.*, 2003, p. 273) or "one of the most pervasive" (Fuhrman *et al.*, 2008, p. 7774) global biological patterns. A "long and rapidly increasing list of taxa that exhibit a latitudinal gradient of increasing diversity from the poles toward the equator" was claimed by Fuhrman *et al.* (2008, p. 7775), but no examples supported that statement. Willig *et al.* (2003) asserted that the pattern generally holds regardless of taxon, biome, or time; this claim was erroneously stated by Konar *et al.* (2010) to apply only to the terrestrial environment. However, in a meta-analysis of 600 studies, Hillebrand (2004) did not find that pattern in about a third of the datasets. Most research supporting such a pattern of diversity has been on vertebrates and angiosperms (Hillebrand, 2004); many exceptions concern relatively short distances and vertebrates that are secondarily marine (Willig *et al.*, 2003).

Despite the land surface of the earth being about half that of the seas, far less research of this sort has been done with marine than with terrestrial organisms. Most research on marine invertebrate distribution has been limited in geographic extent: for example, along the Pacific coast of Chile (*e.g.*, Lancellotti and Vasquez, 1999; Valdovinos *et al.*, 2003) and in the North Atlantic (Clarke and Lidgard, 2000). The only global surveys of latitudinal patterns of species diversity of single higher marine taxa we found were by Kerswell (2006) (benthic marine algae) and Cairns (2007) (deep scleractinian corals); Stehli and Wells (1971) (shallow scleractinian corals) and Jablonski *et al.* (2006) (bivalves) provided them at the generic level, and planktonic members only were inventoried by Fuhrman *et al.* (2008) for bacteria, and Rutherford *et al.* (1999) and Brayard *et al.* (2005) for foraminiferans. Studies such as that of Mora *et al.* (2008) focus on knowledge of diversity, not spatial distribution of the taxon.

We assessed global latitudinal distribution in species of

sea anemones, which constitute the exclusively marine order Actiniaria (phylum Cnidaria). We used published occurrence records assembled in the online resource "Hexacorallians of the World" (Fautin, 2013) to determine the number of species (taxonomic, not nominal) occurring in 10° bands of latitude. The data are based on both observations and collections recorded in the literature, primarily that concerning taxonomy and biogeography, but also that of ecology, behavior, and pharmacognosy. Sea anemones are typical of marine taxa—they are not of commercial importance and most are not charismatic. We found a pattern reminiscent of that shown by Rutherford *et al.* (1999) and Brayard *et al.* (2005) for planktonic foraminiferans, and by Kerswell (2006) for benthic marine algae: lower diversity at equatorial latitudes than at mid-latitudes in both southern and northern hemispheres, and lowest diversity of all at polar latitudes.

To understand if this pattern was due to the inventory at equatorial latitudes being less comprehensive than at higher latitudes, we estimated the completeness of knowledge of sea anemone diversity, a topic that is beginning to be addressed (*e.g.*, Mora *et al.*, 2008, 2011; Costello *et al.*, 2011). Effort could not be determined directly from the data we used, a problem that Boakes *et al.* (2010), among others, has identified with use of historical data. We therefore used the Chao2 statistic, a method that extrapolates from the number of rare species in an assemblage to estimate the number of species in the assemblage that are undetected (Colwell and Coddington, 1994; Mao and Colwell, 2005). We infer that, overall, the 1089 known species of sea anemone constitute about 70% of total diversity; in general, knowledge is most complete where diversity is lowest—at highest latitudes. Despite its uncertainties, our analysis reinforces the pattern we inferred, of maximal diversity at mid-latitudes.

These data also allowed us to assess whether sea anemone distribution supports Rapoport's Rule (*e.g.,* Gaston *et al.*, 1998). We found no evidence for it, sea anemones living at high latitudes having no broader latitudinal extents, on average, than those living at low latitudes.

Materials and Methods

Occurrence data

Occurrence records, captured in a database and displayed in "Hexacorallians of the World" (Fautin, 2013), came from the publications in which the occurrences were initially reported (thus repetitions of previously published occurrences are not included). The data were assembled into species occurrences per 10° latitudinal band (17 total). Some coordinates (latitude and longitude) recorded in Fautin (2013) are from the published source of the records or in station lists for specimens collected on expeditions. The rest were georeferenced retrospectively from placenames. All

georeferenced records in Fautin (2013) are served to the Ocean Biogeographic Information System (OBIS: http://www.iobis.org), which passes them to the Global Biodiversity Information Facility (GBIF: http://www.gbif.org) and to the World Register of Marine Species (WoRMS: http://www.marinespecies.org).

Excluded from our analysis were occurrence records giving very general locations, such as Greenland or the Pacific Ocean, that were therefore assigned coordinates of low precision. We limited our analysis to records with a precision sufficiently high that the assigned coordinate would fall within one 10° band. All except a few poorly documented species of Actiniaria are benthic as adults (attached to firm substrata or burrowed into soft substrata); none of the data analyzed were from the planktonic larval stage of life.

Each occurrence record in the database is entered with the scientific name of the species given in the publication from which it came. However, if that is not the name currently considered valid for the species, or if a subsequent publication showed that the identification had been in error, that record is also associated in the database with the name currently considered to be valid (Fautin, 2009). Our analysis is limited to records for which a current valid name could be assigned, and so it is by species rather than by name to avoid the confounding effect of synonyms pointed out by, for example, May (1998). We also excluded records for the species of the genus *Urticina*, which are taxonomically and nomenclaturally confused.

For analyses concerning Rapoport's Rule, the latitudinal extent of a species was calculated from the low end of the band at one end to the high end of the band at the other, with the midpoint being the average value of the extent from one side to the other. Thus a species known in bands 20–30°N and 30–40°N would have a range of 20° and a midpoint of 30°N; a species known in bands 20–30°N and 40–50°N would have a range of 30° and a midpoint of 35°N. For species known from more than one band, we noted whether the records are in contiguous bands.

Environmental data

To test whether the pattern we found was an artifact of sampling, we compared the number of records with two parameters that might correlate with richness: ocean area (because sea anemones are marine, a band with a greater area of ocean might, for that reason alone, include a larger number of species) and coastline length (because the benthos of shallow water is more accessible than that of deep water, a band with more coastline might, for that reason alone, include a larger number of species). We recognize that such a simple comparison is cursory, but it provides a sense of whether these parameters might control the pattern; Stehli and Wells (1971, p. 117) characterized quantifying the amount of appropriate habitat as "insurmountable."
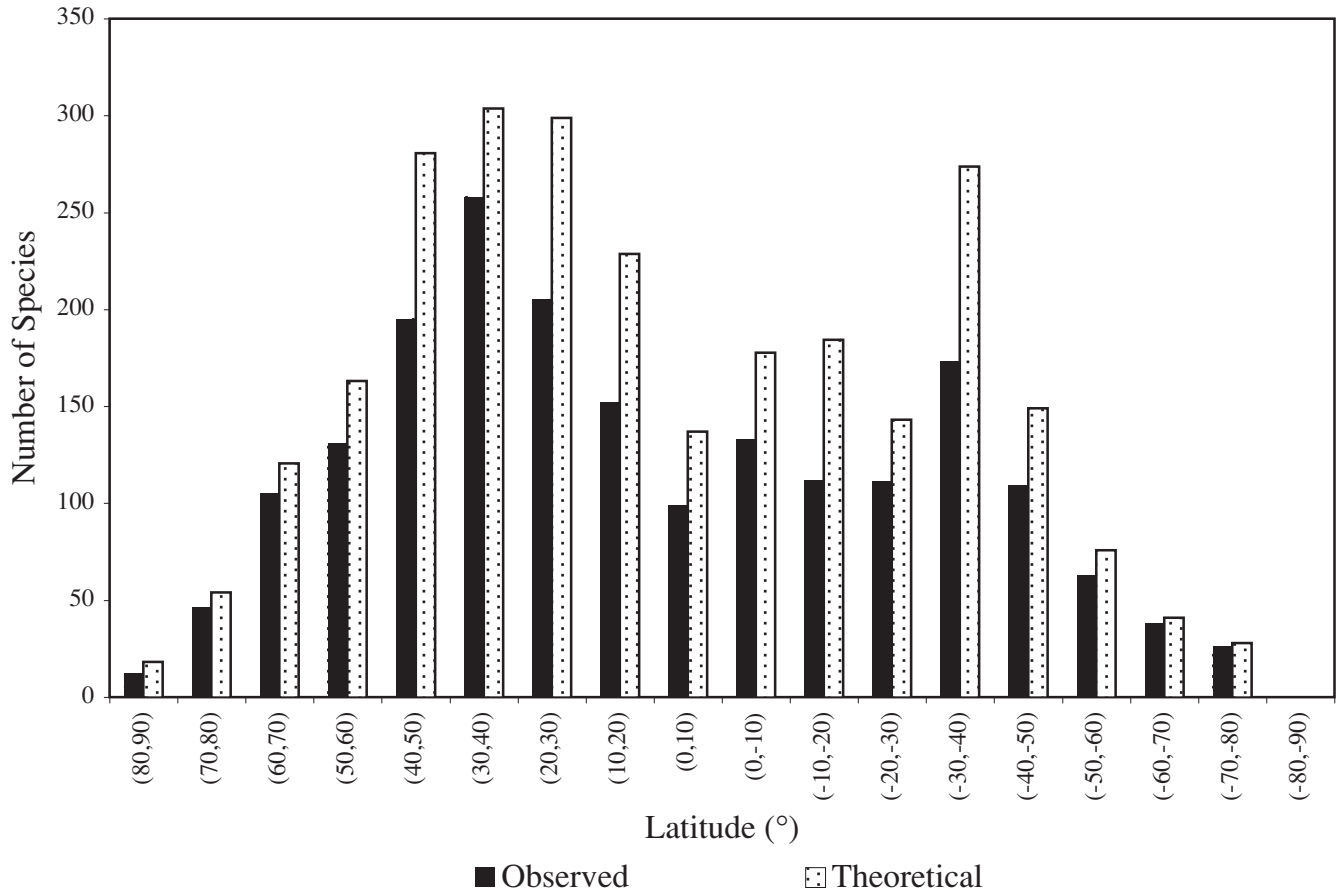
Figure 1. Number of observed and theoretical species of sea anemones as a function of latitude (the latter inferred using the Chao2 estimator). Species richness of both observed and theoretical numbers peak between 30° and 40° N and S.

"Hexacorallians of the World" is the taxonomic component of "Biogeoinformatics of Hexacorals" (Fautin and Budde-meier, 2006); the other component contains environmental data, including those we used to determine ocean surface area and coastline length.

Statistical analyses

$S*_2$ is the theoretically actual number of species according to the Chao2 estimator (Colwell and Coddington, 1994): $S*_2 = S_{obs} + (L^2/2M)$, where S_{obs} is the observed number of species in a sample, L is the number of species that occur in only one sample, and M is the number of species that occur in exactly two samples. We calculated $S*_2$ for each 10° band and for the world as a whole. The ratio of S_{obs} to $S*_2$ is the index of completeness (C) (Nakamura and Soberón, 2008). When $C = 1$, the inventory is complete; when $C = 0.7$, the inventory is 70% complete, *etc.* We evaluated the null hypothesis that the inventory is complete (H_0: $C = 1$), using the method in Nakamura and Soberón (2008), with a significance level of 0.05. Because we performed multiple

comparisons, we applied a Bonferroni correction to the 0.05 level, dividing it by 17, the number of bands.

Results

Of the 1089 species of Actiniaria considered valid as of 1 April 2012 (Fautin, 2013), we analyzed data on 1053 (97%), for which the database contained 13,806 occurrence records. Excluded from analysis were 757 records of low precision and 314 records for *Urticina*; in addition, "Hexacorallians of the World" contains 1073 records that are not georeferenced (most because the placename is ambiguous or imprecise). Thus 11,662 records—84% of those available—were analyzed. These records cover 160° of latitude, from 78.5°S to 81.8°N. The statistical tool we used considers the number of species recorded exactly once and twice, allowing us to infer effort and thereby to calculate the number of species remaining to be discovered: valid species currently known are 73% of the theoretical total of 1497 species of Actiniaria on earth.

The dark bars in Figure 1 are the empirical data for the
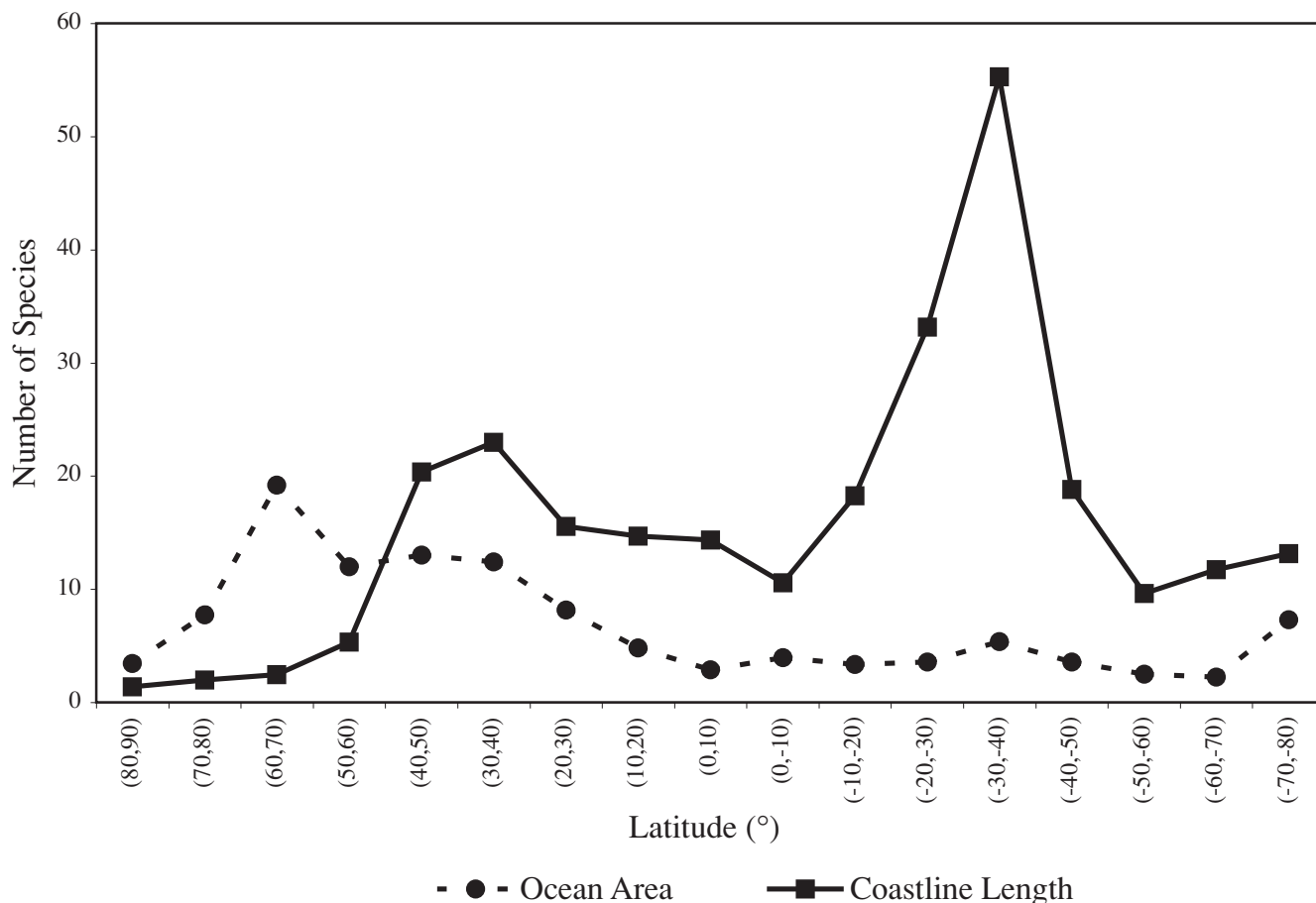
Figure 2. Observed species diversity as a function of latitude proportional to ocean area (10^6 km^2; dashed line) and to coastline length (10^5 km; solid line).

latitudinal distribution of sea anemone species: numbers peak between 30° and 40° N and S (258 species and 173 species, respectively), with richness decreasing toward the equator and poles. The light bars in Figure 1 are the theoretical values of species richness ($S*_2$) for each latitudinal band as determined by the Chao2 estimator. Figure 2 plots the observed number of species per band correlated with coastline length and ocean area. Completeness of the inventory (C) is depicted relative to observed species richness in a band (Fig. 3) and by latitude (Fig. 4). There is no relation between the number of species inventoried and completeness of the inventory ($r = -0.34$, $P = 0.185$) (Fig. 3). Nine points lie below the band of rejection of the H_0: $C = 1$ (Fig. 4); except for that centered at $-35°$ (the peak in the southern hemisphere), they are at middle latitudes.

The average number of localities per species is just over 11, but four species were recorded from more than 200 localities each: *Hormathia digitata* (431 records), *Metridium senile* (239 records), *Entacmaea quadricolor* (223 records), and *Hormathia nodosa* (213 records). Slightly more than 60% of species (641) are known from only one 10° band: of them, just over half (323 species) are

recorded from more than one locality in that band ("Band Unique" in Fig. 5); the 318 species that are known from only a single locality ("Globally Unique" in Fig. 5) represent 30.2% of species analyzed and 2.7% of occurrence records. Figure 6 plots the distribution of the 412 species known from more than one 10° band by latitudinal range: 265 are recorded in contiguous bands and 147 in noncontiguous bands. The latitudinal extent of all species is shown in Figure 7, the midpoint of the latitudinal distribution on the *x* axis, and the extent of the distribution on the *y* axis.

Discussion

We infer that the peaks in abundance at mid-latitudes of both northern and southern hemispheres are even greater than indicated by the data we analyzed. Figure 1 shows that, in general, the more species occur in a 10° band of latitude, the less well-known the fauna: inventories appear to be mostly complete at higher latitudes, in the northern hemisphere from 50°N and in the southern from 40°S (Fig. 4). The northernmost band has a very high variance; the fact
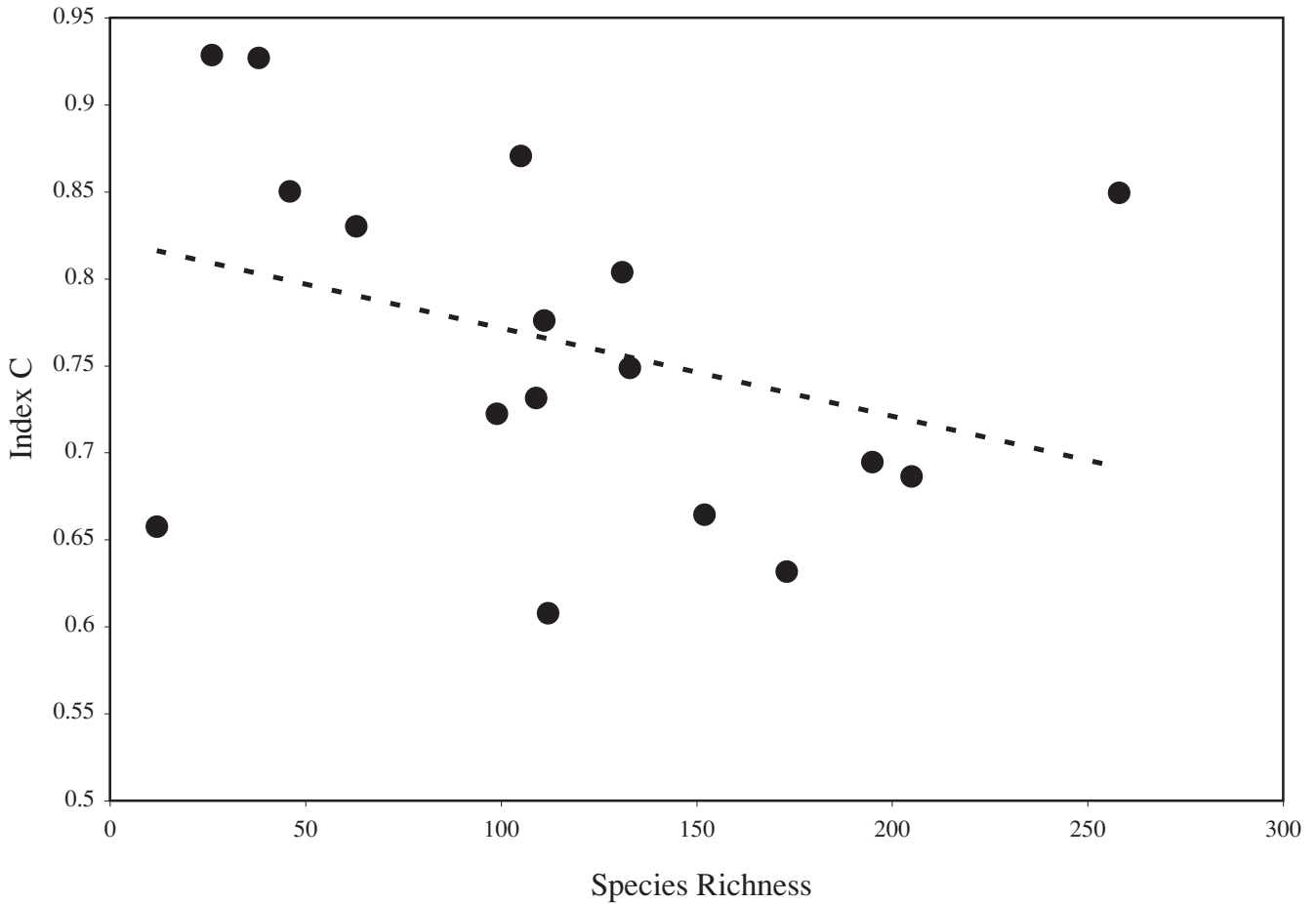
Figure 3. Completeness of inventory (y axis: $C = S_{obs}/S^*$) as a function of species richness (x axis: S_{obs}). H_0 $C = 1$ cannot be rejected at $P = 0.05$. The slight negative trend ($r = -0.4975$, $P = 0.0422$) means that in bands with fewer species, the sea anemone fauna is more completely known.

that H_0 is not rejected for that region may be an artifact of the method we used, which is based on a first-order approx-
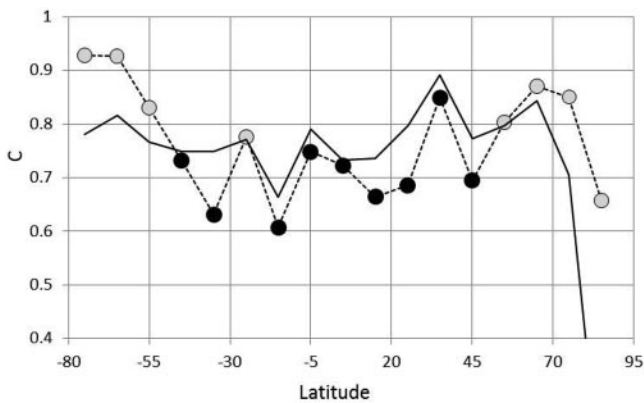
Figure 4. Completeness of inventory ($C = S_{obs}/ S^*$) as a function of latitude. The solid line is the threshold for the H_0: $C = 1$ at $P = 0.05$, with a Bonferroni correction; if C is below the line, H_0 is rejected (black circles). With one exception, rejection occurred only at middle latitudes.

imation (Nakamura and Soberón, 2008).We recognize that for the value of $C = 0.7$, the H_0 of a complete inventory is rejected, meaning that at the resolution we report, actinarians in some parts of the world are still not well inventoried at the species level, and that at the coarse spatial resolution we used (10°), the assumption of uniform detection probability underlying the Chao2 method is likely violated (Chao, 1987). We therefore suggest that Figure 4 be used mostly for comparison among bands. The completeness of knowledge, shown in Figures 3 and 4, is reflected in nearly a third of the species being known from a single locality (Figs. 5, 6), but we took advantage of the attribute of rareness to infer how many species have not been recorded at all. Despite these caveats, we are confident that the accuracy of our estimates is based on the most comprehensive database in existence for the taxon and on methods that have been found robust in comparative studies (Walther and Moore, 2005).

Two of the individual higher marine taxa for which global latitudinal diversity has been studied show the terrestrial pattern—shallow and deep scleractinian corals
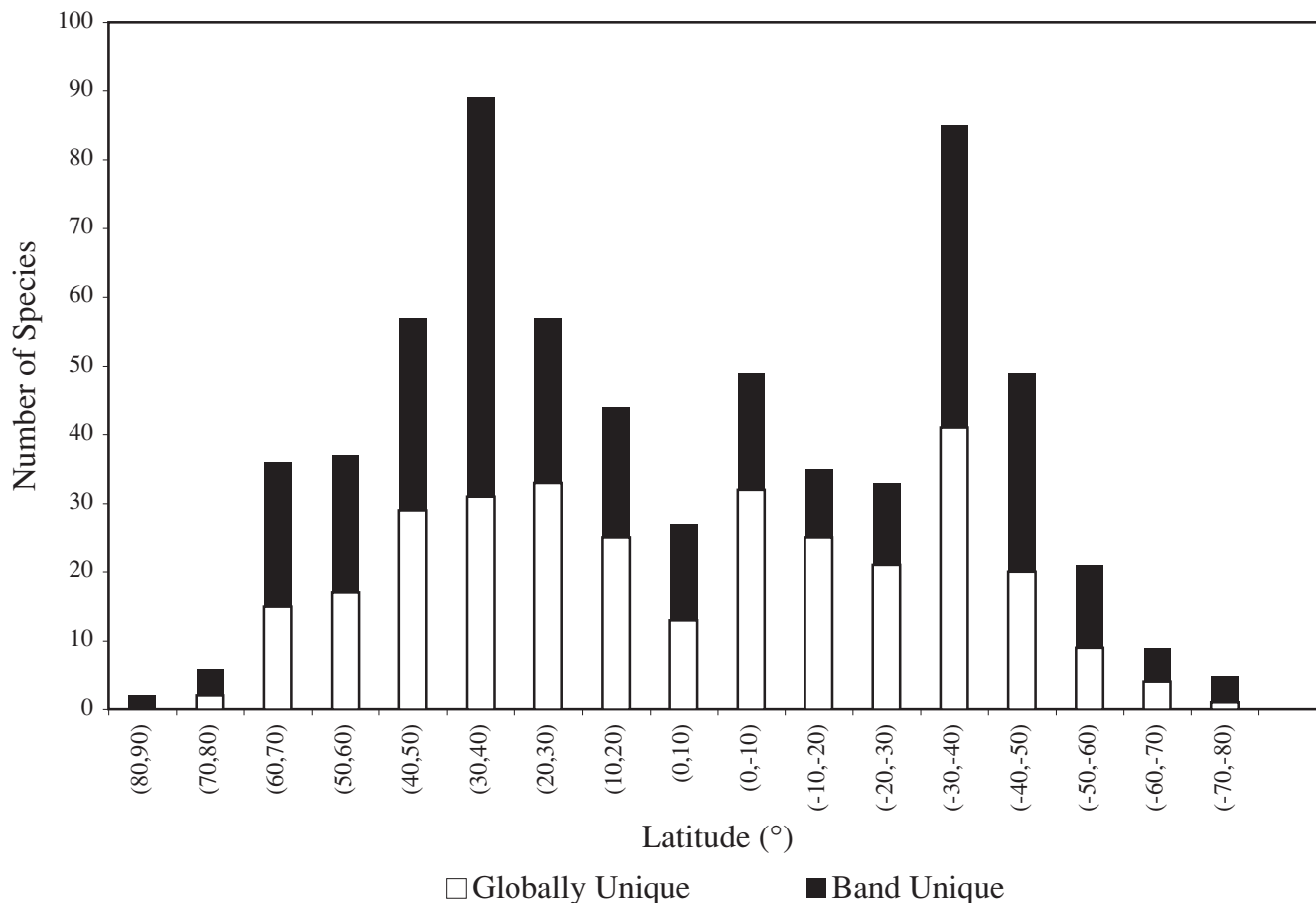
Figure 5. Distribution of the 641 species of sea anemones occurring in only one 10° band of latitude. Dark bars indicate species for which there is more than one record in that band (Band Unique), and light bars indicate species for which only a single record exists (Globally Unique).

(Stehli and Wells, 1971; Cairns, 2007, respectively) and bivalves (Jablonski *et al.,* 2006)—as does a portion of another—planktonic bacteria (Fuhrman *et al*., 2008). By contrast, the biogeographical pattern we found in sea anemones is much like that of portions of two taxa—planktonic foraminiferans (Rutherford *et al*, 1999; Brayard *et al.*, 2005) and benthic algae (Kerswell, 2006). Kerswell (2006, p. 2485) declared "benthic marine algae an exceptional group," but that pattern may actually be the typical one, as hinted at in the study by Tittensor *et al.* (2010) on 13 of what are termed "major species groups," or "taxonomic groups," or "taxa" of marine organisms. Five of the groups analyzed do not represent taxonomic units (mangroves is a functional group; coastal fishes and oceanic and non-oceanic sharks are habitat-defined subsets of taxa; and tunas and billfishes has elements of both). It is unclear what Tittensor *et al*. (2010) meant by "corals," a taxonomically ambiguous term (Fautin and Buddemeier, 2009); Stehli and Wells (1971) and Cairns (2007) had shown the terrestrial pattern in scleractinian corals. "Foraminifera," the only phylum-level group, lacks a latitudinal pattern. Six of the 13

groups—euphausiids, cetaceans, squids, non-squid cephalopods, pinnipeds, and seagrasses—appear more diverse at higher than lower latitudes. These groups include organisms that are primarily pelagic (the first three) and primarily benthic (the last three); Foraminifera has members of both.

Global analyses for marine species are increasingly possible by mining large datasets that are becoming available through initiatives such as OBIS and WoRMS. However, the data assembled from such a diversity of sources may not be directly useful in deriving patterns of distribution: Boakes *et al.* (2010), using data for a group of birds, pointed out some potential biases concerning space and time in large datasets. In our analysis, the number of species in each band was not proportional to sea surface area and coastline length (Fig. 2) for that band, from which we concluded that those factors are not responsible for the pattern we uncovered. Because our data come from a variety of sources, gathered during more than 200 years, on expeditions and idiosyncratically, effort was one of the greatest potential biases; we used completeness of the inventory to assess effort, the ratio of observed number of species to (calculated) true number
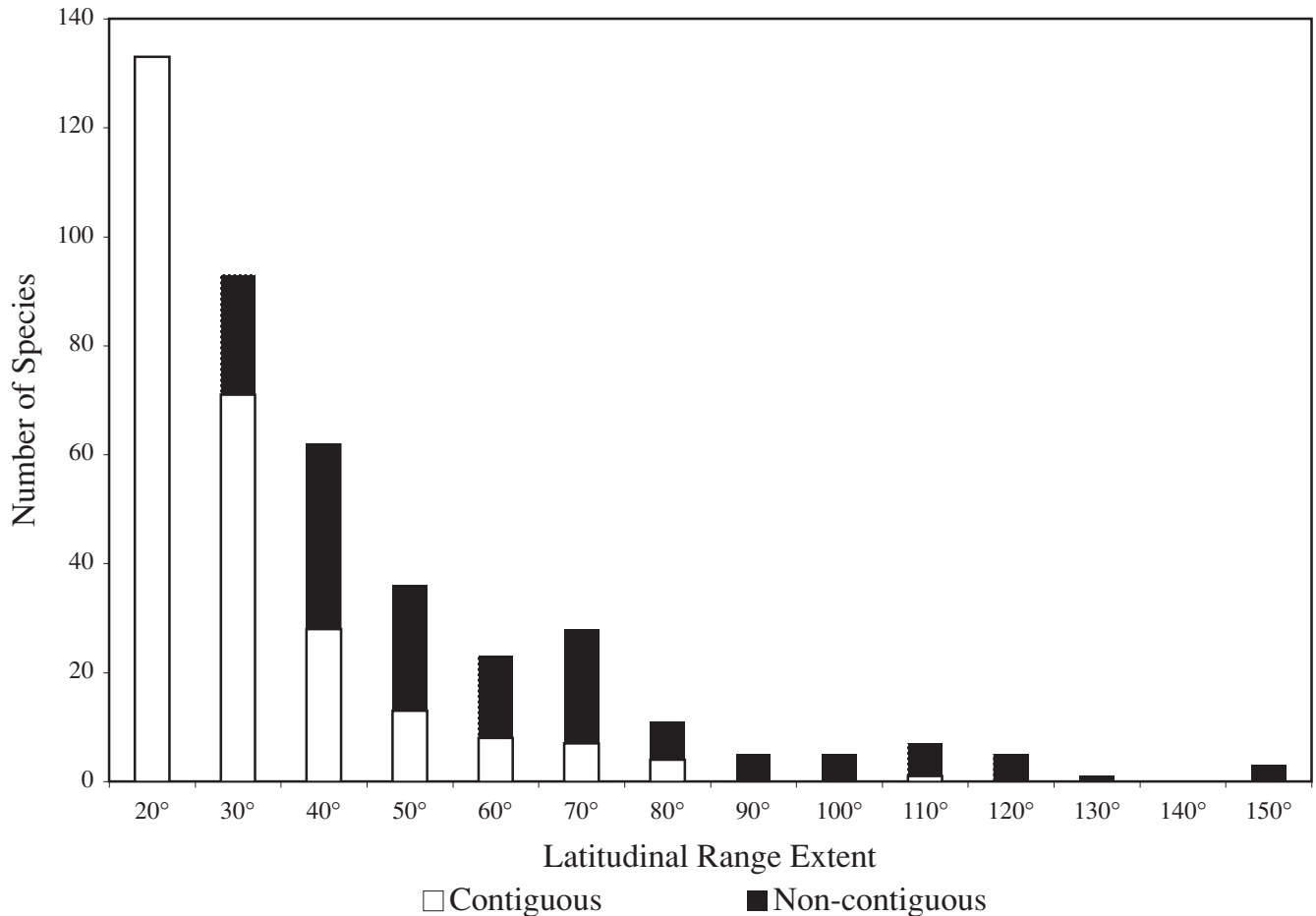
Figure 6.   Latitudinal range of the 412 species of sea anemones occurring in more than one 10° band. Light bars indicate species for which records are in contiguous bands, and dark bars indicate species for which records are in non-contiguous bands.

being a metric of the completeness (Nakamura and Soberón, 2008).

We estimate, using the pooled value from the Chao2 statistic, that the completeness of the species inventory for actiniarians is about 70%, which means, given that we did not have data for all valid species, that the actual total number of species is about 1500. Few analytical approaches to assessing completeness of knowledge currently exist. Recent assessments of the completeness of knowledge of the marine fauna are strikingly varied: Mora *et al.* (2008), using a database and accumulation-curve methods similar to ours, estimated that the global marine fish inventory is almost 80% complete; Mora *et al.* (2011) inferred that 91% of marine species await description; and Costello *et al.* (2011) inferred that 24%–31% of species are undescribed. Cairns (1999, p. 8) cited three disparate figures for the proportion of scleractinian coral species remaining to be described: he inferred by one method that it amounts to 10%, he cited a published inference that it is as many as half, and, "on a purely intuitive basis," he estimated it to be

37%. Intuition appears to be commonly used for estimating completeness of inventories of marine species. It is the basis of the estimate for most groups by Appletans *et al.* (2012) that one-third to two-thirds of marine species are known.

For fishes, Mora *et al.* (2008, p. 149) found that "censuses of species were particularly incomplete in tropical areas," and Mora *et al.* (2011, p. 5), addressing some issues that have to do with sampling, inferred, based on the literature, that current records "are biased towards conspicuous species with large geographical ranges, body sizes, and abundances." We conclude, on the basis of this and the fact that 60% of species are known from only a single 10° band (Figs. 5, 6), that the record in Actiniaria is not biased in favor of species with large geographical ranges. Conspicuousness seems also not to be a factor in sea anemones: for example, our database contains many records for burrowing species, and 46 are for the very small, inconspicuous anemone *Triactis producta*.

In assessing the diversity of plants in politically defined regions such as counties or states, Moerman and Estabrook
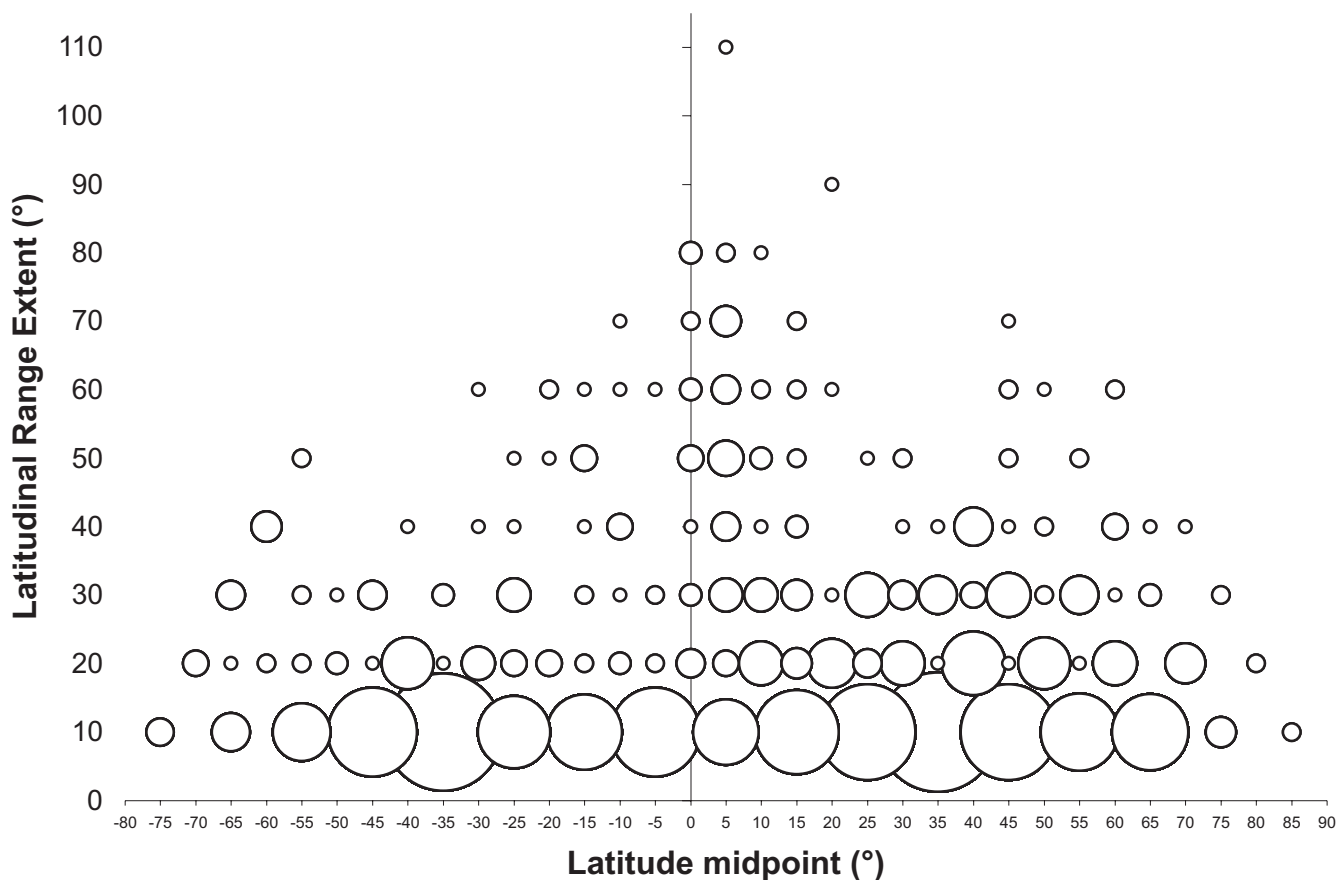
Figure 7. Latitudinal range and midpoint of occurrence of the 1053 species of sea anemones analyzed; size
of the spot is proportional to the number of species. Most species occur in only one 10° band of latitude, and
the greatest number of those are at mid-latitudes north and south.

(2006), among others, described what they termed "the
botanist effect," which states that more species are known
where there are more botanists. This effect was discredited
by Pautasso and McKinney (2007), and it does not appear to
explain what we found, either. Two of the most prominent
of the relatively few students of sea anemones were Eng-
lishman P. H. Gosse and Welshman T. A. Stephenson, who
published volumes on British sea anemones (Gosse, 1860;
Stephenson, 1928, 1935) [another such regional guide for
the United Kingdom is by Manuel (1981)]. Despite this
attention, the band 50–60° N (which contains nearly all of
the UK) is not unusually rich—at 131 species, it has fewer
than the band to its south (202) and more than the band to
its north (106)—and the estimate of its unknown species
follows the expected pattern (79% *vs.* 87% and 72%, re-
spectively) (Fig. 1).

Another potentially confounding factor is the use of
names (*e.g.*, Kerswell, 2006; Fautin, 2009). In the publica-
tion entitled "Global patterns and predictors of marine bio-
diversity across taxa," Tittensor *et al.* (2010) analyzed only
13 higher "taxa" for which appropriate taxonomic checking
was possible; Costello *et al.* (2011), analyzing all marine

taxa, considered synonyms and effort; and Vanden Berghe
et al. (2010) offered no explanation of how their diversity
analysis was done. In an analysis of the global distribution
of macroalgae, Kerswell (2006) dealt with the potential
problem inherent in use of scientific names, so that her
analysis, like ours, was by taxa, not by names. Kerswell's
analysis was of a slightly greater number of taxa than ours,
by genus for members of three classes, and by species for a
taxonomically well-resolved order of one of the classes.
Because many sea anemone genera and families may not be
monophyletic (*e.g.*, Daly *et al.*, 2007; Rodríguez *et al.*,
2012), analysis of sea anemones by taxa higher than species
could be misleading.

Rapoport's Rule was not supported by our data: we found
no correlation between latitudinal range and extent (Fig. 7).
This contrasts with Kerswell (2006, p. 2484), who found
that "genera and species of Bryopsidales with large latitu-
dinal extents cluster near the equator [whereas] small-rang-
ing genera cluster in both northern and southern hemi-
spheres," the opposite of Rapoport's Rule.

Ours is an empirical test of whether sea anemone diver-
sity varies with latitude, and if so, how. We do not seek

causes. Much research on the subject of latitudinal gradients focuses on the cause(s) of the pattern (*e.g.,* Gaston, 2000; Willig *et al.*, 2003; Kerswell, 2006; Mittelbach *et al.*, 2007; Furhman *et al.*, 2008; Konar *et al.*, 2010; Kraft *et al.*, 2011). The many proposed explanations for the conventional pattern of equatorial richness attenuating toward the poles number 30 according to Brayard *et al.* (2005) and are divided into three types by Mittelbach *et al.* (2007). However, the pattern we found reveals a strong correlation. One of the earliest global analyses of marine organisms was for genera of shallow-water scleractinian corals, which are very diverse in the equatorial tropics and diminish in diversity with latitude, so there are few to no representatives in polar seas (Stehli and Wells, 1971); species of deep-water scleractinians have a remarkably similar distribution pattern (Cairns, 2007). The pattern we found is complementary to that, consistent with the generalization of Fautin (1989) that distribution of sea anemones complements that of other anthozoans at multiple scales.

Acknowledgments

Literature Cited

Appletans, W., S. T. Ahyong, G. A. Anderson, M. V. Angel, T. Artois, N. Bailly, R. Bamber, A. Barber, I. Bartsch, A. Berta *et al*. 2012. The magnitude of global marine species diversity. *Curr. Biol.* **22:** 1–14.

Boakes, E. H., P. J. K. McGown, R. A. Fuller, C.-Q. Ding, N. E. Clark, K. O'Connor, and G. M. Mace. 2010. Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biol.* **8(6):** e1000385.

Brayard, A., G. Escarguel, and H. Bucher. 2005. Latitudinal gradient of taxonomic richness: combined outcome of temperature and geographic mid-domain effects? *J. Zool. Syst. Evol. Res.* **43:** 178–188.

Cairns, S. D. 1999. Species richness of Recent Scleractinia. *Atoll Res. Bull.* **459:** 1–12.

Cairns, S. D. 2007. Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bull. Mar. Sci.* **81:** 311–322.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43:** 783–791.

Clarke, A., and S. Lidgard. 2000. Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. *J. Anim. Ecol.* **69:** 799–814. doi: 10.1046/j.1365–2656.2000.00440.x

Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial

biodiversity through extrapolation. *Philos. Trans. R. Soc. Lond. B* **345:** 101–118.

Costello, M. J., S. Wilson, and B. Houlding. 2011. Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Syst. Biol.* doi: 10.1093/sysbio/syr080

Daly, M., M. R. Brugler, P. Cartwright, A. G. Collins, M. N. Dawson, D. G. Fautin, S. C. France, C. S. McFadden, D. M. Opresko, E. Rodriguez, S. L. Romano, and J. L. Stake. 2007. The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa* **1668:** 127–182.

Fautin, D. G. 1989. Anthozoan dominated benthic environments. Pp. 231–236 in *Proceedings of the Sixth International Coral Reef Symposium,* Vol. 3, R. H. Bradbury, ed. Townsville, Australia, 8–12 August 1988. Springer, Berlin.

Fautin, D. G. 2009. Biodiversity of reefs: inferring from sparse data. Pp. 1346–1349 in *Proceedings of the Eleventh International Coral Reef Symposium,* Vol. 2, Fort Lauderdale, FL, 7–11 July 2008. [Online]. Available: http://www.reefbase.org/resource_center/publication/icrs.aspx?icrs=ICRS11 [2013 April 1].

Fautin, D. G. 2013. *Hexacorallians of the World.* [Online]. Available: http://geoportal.kgs.ku.edu/hexacoral/anemone2/index.cfm [2013 February 10].

Fautin, D. G., and R. W. Buddemeier. 2006. *Biogeoinformatics of Hexacorals.* [Online]. Available: http://www.kgs.ku.edu/Hexacoral/index.html [2013 February 10].

Fautin, D. G., and R. W. Buddemeier. 2009. Coral. Pp. 197–203 in *Encyclopedia of Islands,* R. Gillespie and D. A. Clague, eds. University of California Press, Berkeley.

Fuhrman, J. A., J. A. Steele, I. Hewson, M. S. Schwalbach, M. V. Brown, J. L. Green, and J. H. Brown. 2008. A latitudinal diversity gradient in planktonic marine bacteria. *Proc. Natl. Acad. Sci. USA* **105:** 7774–7778. doi: 10.1073/pnas.0803070105

Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* **405:** 220–227. doi:10.1038/35012228

Gaston, K. J., R. M. Blackburn, and J. I. Spicer. 1998. Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* **13:** 70–74.

Gosse, P. H. 1860. *A History of the British Sea-anemones and Corals.* Van Voorst, London.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *Am. Nat.* **163:** 192–211.

Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314:** 102–106.

Kerswell, A. P. 2006. Global biodiversity patterns of benthic marine algae. *Ecology* **87:** 2479–2488.

Konar, B., K. Iken, G. Pohle, P. Miloslavich, J. J. Cruz-Motta, L. Benedetti-Cecchi, E. Kimani, A. Knowlton, T. Trott, T. Iseto, and Y. Shirayama. 2010. Surveying nearshore biodiversity. Pp. 27–41 in *Life in the World's Oceans: Diversity, Distribution, and Abundance,* A. D. McIntyre, ed. Wiley-Blackwell, Chichester.

Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson *et al*. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* **333:** 1755–1758. doi: 10.1126/science.1208584

Lancellotti, D. A., and J. A. Vásquez. 1999. Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *J. Biogeogr.* **26:** 1001–1006.

Manuel, R. L. 1981. *British Anthozoa: Keys and Notes for the Identification of the Species.* Academic Press, London.

Mao, C. X., and R. K. Colwell. 2005. Estimation of species richness: mixture models, the role of rare species, and inferential challenges. *Ecology* **86:** 1143–1153.

May, R. M. 1998. The dimensions of life on Earth. Pp. 30–45 in *Nature*

and Human Society: the Quest for a Sustainable World, P. H. Raven, ed. National Academy Press, Washington DC.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Mush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios *et al.* 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10:** 315–331.

Moerman, D. E., and G. F. Estabrook. 2006. The botanist effect: counties with maximal species richness tend to be home to universities and botanists. *J. Biogeogr.* **33:** 1969–1974.

Mora, C., D. P. Tittensor, and R. A. Myers. 2008. The completeness of taxonomic inventories for describing the global diversity and distribution of marine fishes. *Proc. R. Soc. B* **275:** 149–155.

Mora, C., D. P. Tittensor, S. Adl, A. G. B. Simpson, and B. Worm. 2011. How many species are there on earth and in the ocean? *PLoS Biol.* **9(8):** e1001127. doi: 10.1371/journal.pbio.1001127

Nakamura, M., and J. Soberón. 2008. Use of approximate inference in an index of completeness of biological inventories. *Cons. Biol.* **23(2):** 469–474. doi 10.1111/j.1523–1739.2008.01116.x

Pautasso, M., and M. L. McKinney. 2007. The botanist effect revisited: plant species richness, county area, and human population size in the United States. *Conserv. Biol.* **21:** 1333–1340.

Rodríguez, E., M. Barbeitos, M. Daly, L. C. Gusmão, and V. Häussermann. 2012. Toward a natural classification: phylogeny of acontiate sea anemones (Cnidaria, Anthozoa, Actiniaria). *Cladistics* **28:** 375–392. doi: 10.1111/j.1096-0031.2012.00391.x

Rutherford, S., S. D'Hondt, and W. Prell. 1999. Environmental controls on the geographic distribution of zooplankton diversity. *Nature* **400:** 749–753.

Stehli, F. G., and J. W. Wells. 1971. Diversity and age patterns in hermatypic corals. *Syst. Zool.* **20:** 115–126.

Stephenson, T. A. 1928. *The British Sea Anemones*, Vol. I. The Ray Society, London.

Stephenson, T. A. 1935. *The British Sea Anemones*, Vol. II. The Ray Society, London.

Tittensor, D. P., C. Mora, W. Jetz, H. K. Kotze, D. Ricarad, E. Vanden Berghe, and B. Worm. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* **466:** 1098–1101. doi: 10.1038/nature09329

Valdovinos, C., S. A. Navarrete, and P. A. Marquet. 2003. Mollusk species diversity in the Southeastern Pacific: Why are there more species towards the pole? *Ecography* **26:** 139–144. doi 10.1034/j.1600–0587.2003.03349.x

Vanden Berghe, E., K. I. Stocks, and J. F. Grassle. 2010. Data integration: the Ocean Biogeographic Information System. Pp. 333–353 in *Life in the World's Oceans: Diversity, Distribution, and Abundance*, A. D. McIntyre, ed. Wiley-Blackwell, Chichester.

Walther, B. A., and J. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* **28:** 815–829.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Syst.* **34:** 273–309.