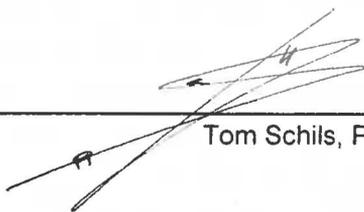


AN ABSTRACT OF THE THESIS OF Robert J. Tomasetti for the Master of Science in Biology presented July 25, 2007.

Title: Global biogeography of marine algae

Approved: _____


Tom Schiils, Ph.D., Chairperson, Thesis Committee

Aim To describe the global distribution patterns of marine benthic algae along latitudinal and longitudinal gradients, temperature, spatial scales, taxonomic gradients, and patterns of endemism. To determine the validity of species-to-genus ratio (SGR) patterns of algal diversity, which are contrary to SGR patterns of other organisms. Furthermore, to create a connectivity network for algae that allows for more accurate estimates of distances between localities for the purposes of similarity analyses. Finally, to qualitatively compare algal diversity patterns with those for corals and shore fishes.

Location Global distribution data, divided into 155 localities, were used.

Methods Global presence-absence records of marine algae were collected from online resources, scientific papers, and gray literature and compiled into a digital database of 131,400 records, with 52,680 unique species-locality records occurring after treatment with geographic and taxonomic filters. Records were grouped into 155 unique localities, which were further classified into three temperature regions (temperate, subtropical, and tropical) based on NOAA/NCEP sea-surface temperature data averaged since 1981. Localities were further subdivided into a grid of 5° x 5° mapped on a Plate Carrée Equirectangular Cylindrical Map Projection. The Tripartite Similarity Index (TSI) was used to measure percent similarity between all locality pairs (excluding the Antarctic and Arctic localities), with minimal distances between all localities in pair-wise combinations calculated by implementation of Dijkstra's algorithm for shortest path problems along a modeled connectivity network. Analyses of variance and covariance were used to ascertain differences in patterns revealed by regression analyses between locality records clustered along temperature, geographic, or

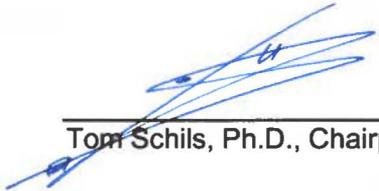
taxonomic gradients. Endemism metrics were calculated by a corrected weighted-measure using two methods: as the proportion of range-restricted species in each 5° x 5° cell (assuming the same species over the total cells of a given locality), and by localities alone.

Results The biogeography of marine algae is extremely complex, with multiple diversity patterns depending upon how data were filtered and analyzed. The results suggest that the three main algal systematic groups (Phaeophyceae, Rhodophyta, and Ulvophyceae) respond differently to temperature gradients and that each oceanic basin is statistically distinct. Algae have small, patchy range distributions with bimodal peaks in generic and species richness in middle latitudes. However, when the ratios of species-to-genus are analyzed, a unimodal peak in diversity occurs centered on the Philippines and the South China Sea region. Longitudinal diversity gradients are complex, with at least four peaks in diversity globally (western Pacific, Mediterranean, Caribbean, and the eastern Pacific). The Japanese islands of Honshu and Hokkaido have the greatest individual species (1504) and generic (459) richness globally of all localities analyzed. Endemicity patterns vary widely between traditional methods and range-restriction methods, with the current study finding many regions of high range restriction (weighted endemism) that have been ignored previously (*e.g.*, the eastern Pacific). Results verify some past findings and speculations, but conflict with others. Several possibilities are proposed to explain deviations from past results.

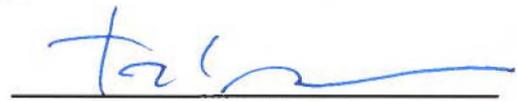
Main Conclusions TSI similarity analyses suggest that relatively few algal genera invaded the tropics from cooler waters but that these speciated rapidly, with more species per genus on average in the tropics compared to cooler regions. Marine algae have distinct diversity patterns compared to corals and shore fishes and separate techniques should be used for analyzing algae. Distinct differences between temperature regions and oceanic basins and differences between algal groups suggest that different algal phyla should not be grouped for analyses. The implementation of a connectivity network proves useful for geographic analyses in the marine realm (especially over large geographic regions) and should be used in place of geodesic or Euclidean distances to account for land barriers to distribution that are less conspicuous and widespread terrestrially. Endemism analyses reveal amphitropical peaks in range-restricted species and along the entire west coast of the Americas, regardless of temperature. In both endemism analyses, several isolated islands and archipelagoes had the highest proportion of range-restricted species: the Galapagos, San Juan and Felix islands in the eastern Pacific, the Chatham, Bounty, and Antipodes islands in the southwestern Pacific, the Cargados Carajos Shoals and Saya de Malha Banks in the Indian Ocean, and Tristan da Cunha in the Atlantic.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Robert J. Tomasetti presented July 25, 2007.



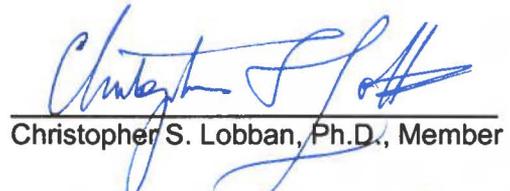
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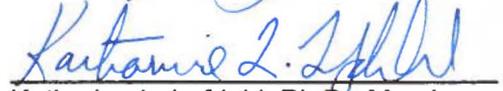
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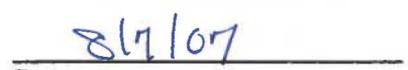


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Acting Coordinator, Office of Graduate Studies



Date

GLOBAL BIOGEOGRAPHY OF MARINE ALGAE

BY

ROBERT J. TOMASETTI

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

IN

BIOLOGY

UNIVERSITY OF GUAM

JULY 2007

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This study could not have been completed without the direction and guidance of my thesis committee, the members of which I acknowledge accordingly. My entire committee was instrumental in my academic growth, opening my eyes to a variety of subjects I was unaware of before starting this project. This project has been started and stopped at several points throughout the years, but the final push to analyze global algal records only occurred in the summer of 2006 due to the excitement and expertise of my committee. Truly, I owe a debt of gratitude to many, and I can only hope that one day I may repay the dedication (many times in the face of deadlines to help me accommodate specific research goals or for personal reasons) that my committee has shown to me over the years. Furthermore, my committee was extremely helpful and understanding when I had to change the focus of my thesis at nearly the last minute to accommodate a recently published work very similar in scope to my initial thesis outline. Yet I believe that the initial delay caused by Ailsa Kerswell's 2006 Global biogeography of algae manuscript helped to ultimately strengthen my thesis and develop interesting new concepts which I hope will have relevance for the larger scientific community. I can only hope to one day approach the authority of every single one of my committee members. While I realize that much will come with time and study, I also realize that I have been privileged to work with some truly great scientists.

Methodologically, I also received much help, and I wish to acknowledge specific methodological contributions of my committee and collaborators kind enough to aid me. Specifically, Dr. Tom Schils, my committee chairperson, was instrumental in the organization of my algal records into a uniform *MS Access 2004* database, from which I performed data manipulation, visualizations, and statistics through the *Mathematica 5.2* program provided by Dr. Alexander Kerr. Dr. Schils also contributed significantly to the Mathematica programming code that allowed for visualization of mapped grid-cell and latitude and longitude binned data, wrote the code for the calculation of Tripartite Similarity Analyses among localities, and provided access to his extensive database of Arabian Sea and Indian Ocean records. Dr.

Schils also visualized range extension data in *Statistica 6.0*. Dr. Schils frequently brought to my attention many key literature sources that guided my methodological approach, including Linder's (2001) weighted endemism paper as a counterpoint to more common endemism measures.

Dr. Terry Donaldson provided his expertise on fish biogeography, his critical reading skills, and several computer programs in the early stages of this project. Additionally, he provided meticulous corrections in a prompt manner and was kind enough to serve as my chair for over a year when I first reentered the UOG Marine Laboratory in January 2005 after a several-year hiatus. When Dr. Schils came to the UOG Marine Laboratory in 2006, Dr. Donaldson kindly suggested that Dr. Schils would be the appropriate chairperson to focus my thesis upon the specific problems of algal biogeography compared to Dr. Donaldson's specialty of fish biogeography.

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Dr. Christopher Lobban's Marine Botany course at the University of Guam provided the impetus for this project by introducing me to seaweeds, whereas my focus originally was on reef fishes, corals, and biogeography. Throughout the years, his love for seaweeds has become infectious, and he has always been supportive of my ideas.

Dr. Katharine Lofdahl provided a genetic perspective to my geographic work. Specifically, Dr. Lofdahl continuously provided an alternate perspective to genus-species concepts compared to traditional morpho-taxonomic methodologies. She was apt to point out

how cryptic speciation and differential speciation rates for separate algal groups may result in biases to analyses.

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INTRODUCTION

MARINE BIOGEOGRAPHY BACKGROUND

Biogeography aims to describe large-scale spatial patterns of biodiversity and the mechanisms driving such patterns. While the biogeography of terrestrial ecosystems has been studied for more than 150 years (see review in Rosenzweig 1995), marine biogeography is much less understood. Many marine organisms have similar patterns of diversity to terrestrial organisms (e.g., higher diversity in the tropics; Koleff *et al.* 2003), but the mechanisms driving such patterns remain unresolved. Numerous theories have been proposed to explain these patterns, focusing on either historical factors (e.g., center-of-origin hypotheses or climate-induced fragmentation of ranges: McCoy & Heck 1976; Briggs 1999, 2000), physical factors (e.g., oceanic current patterns, tectonic plate movements, or disturbance: Connell 1978; Rotondo *et al.* 1981; Jokiel & Martinelli 1992; Roberts 1997), or both (Buckley 1982; Wiley 1988; Rohde 1992; Fraser & Currie 1996; Cornell & Karlson 2000; Brooks & McLennan 2001; Mora *et al.* 2003). Recently, Hughes *et al.* (2002) and Price (2002) demonstrated that separate processes govern patterns of endemism and species richness.

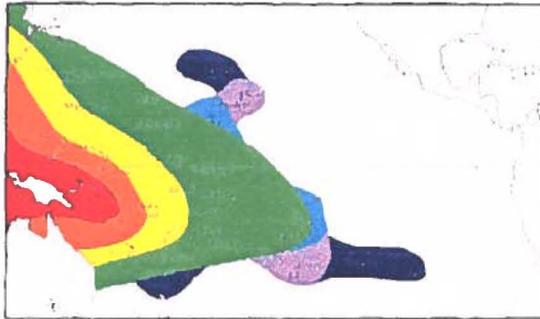
Among algae, Bolton (1994) found that polar regions had the lowest richness (< 200 total species per locality) and that only four localities had very high species richness: Southern Australia, the Mediterranean Sea, Japan, and the Philippines (all between 900-1100 total species per locality). Bolton (1994) stated that southern Australia, the Mediterranean Sea, Japan, and the Philippines are multiple areas of similarly high diversity. All other latitudes in Bolton's (1994) study had a mix of species poor and species rich localities, often at the same latitudes, highlighting the patchy nature of algal richness patterns. Bolton (1994) suggested that small islands with low richness were in line with island biogeography theory (MacArthur & Wilson 1967).

The Indo-West Pacific region, centered between the Philippines and Indonesia, is the center of highest marine biodiversity for corals and shore fishes (e.g., Briggs 1984; Rohde 1992; Stoddart 1992; McAllister *et al.* 1994; Veron 1995; Lieske & Myers 1996; Veron & Stafford-Smith 2000; Hughes *et al.* 2002; Allen & Adrim 2003; Bellwood *et al.* 2005; Carpenter & Springer 2005). Also, corals and shore fishes have the same pattern of diversity at multiple taxonomic levels (Figure 1). This is not the case for most marine benthic algae, at least at the generic level (Figure 2A; Kerswell 2006).

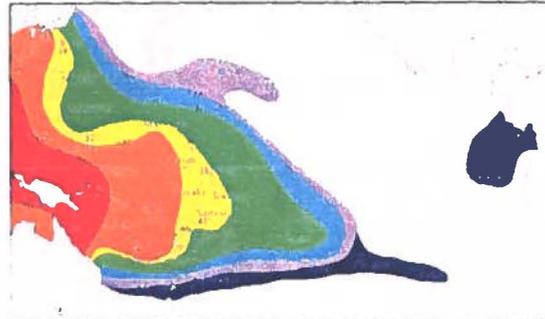
Boyero (2006) points out that speciation rates for many groups may be higher in the tropics because of higher habitat complexity for many tropical ecosystems compared to temperate counterparts. Tropical marine environments do represent greater habitat complexity for algae than temperate marine environments, largely because of high coral diversity in tropical regions and very few reefal developments in the latitudes where algae have their highest diversity. As habitat complexity increases as a function of increased coral diversity and percent cover, available habitat for algae decreases, as relatively few algae are able to use living coral as a growth substrate. In temperate regions, algae do not need to compete with corals, and therefore are able to use more habitat. The greater Australasian region has an enormous area available for benthic marine habitats as a result of high coastline complexity and a shallow continental shelf. As a result of peak coral diversity in Australasia, the theoretically high habitat availability in this region for algae is greatly diminished by corals.

Reconciling evolutionary processes underlying geographical diversity patterns is difficult (Jablonski *et al.* 2006). For instance, speciation rates are highest in the tropics for a variety of terrestrial and marine groups (Allen & Gillooly 2006; Weir & Schluter 2007), possibly as a result of increased mutation rates at elevated temperatures (Rohde 1992; Allen *et al.* 2006). More stable environmental conditions in the tropics may lessen overall speciation rates in algae.

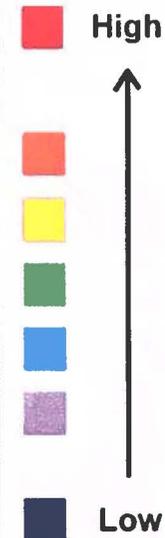
FAMILIES (reef fishes)



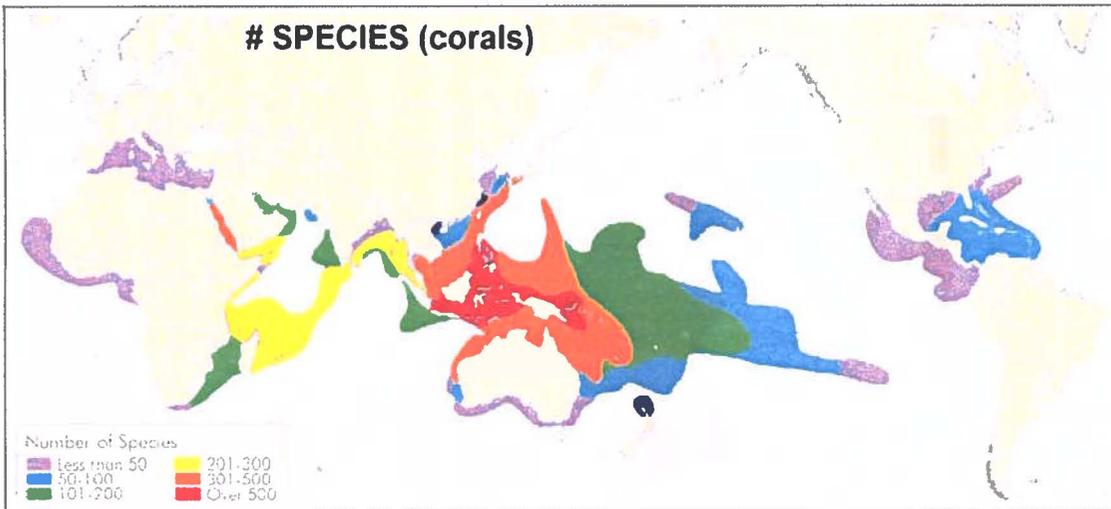
GENERA (corals)



RICHNESS



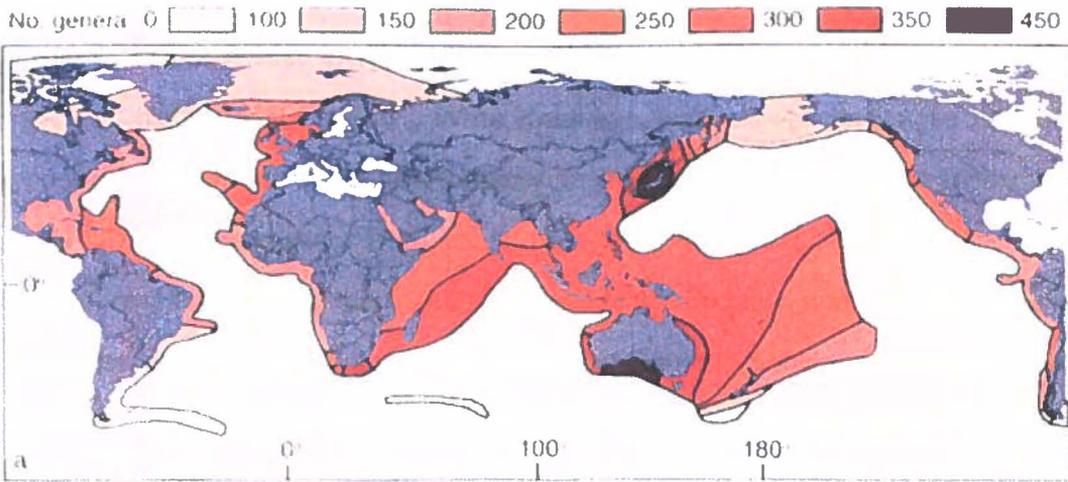
SPECIES (corals)



3

Figure 1. Biodiversity in terms of richness for reef fishes and corals across several taxonomic classes, adapted from the following sources: (upper left) Springer (1982), for family-level reef fish distributions in the tropical Pacific; (upper right) Coudray & Montaggioni (1983), for generic diversity of reef-building corals in the tropical Pacific; and (bottom) Veron & Stafford-Smith (2000), for global species diversity of corals, with additional data for New Zealand, Cambodia, and the central coastline of China from Wilkinson (2004). For global latitudinal diversity patterns of all shore fishes, see Rohde (1992). Colors have been changed from the original figures to reflect the same proportional diversity scale. The same color in all figures corresponds to the same relative level of diversity. In all figures, diversity is highest in the Indo-West Pacific triangle centered between Indonesia and the Philippines.

A



B

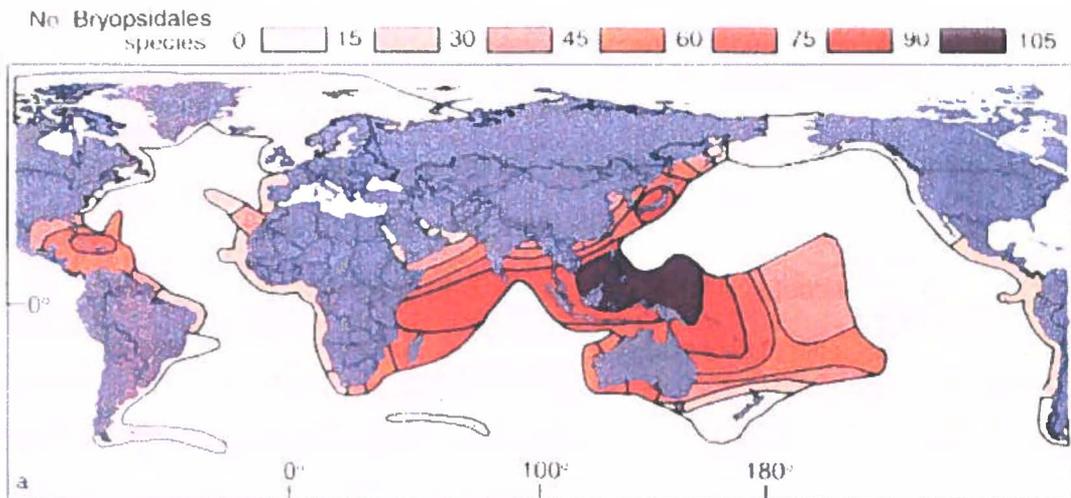


Figure 2. Global algal diversity (from Kerswell 2006) in terms of generic richness (A) and species diversity among the Bryopsidales (Ulvophyceae) (B).

Yet, recent work with birds and mammals has revealed an opposite trend, with genetic divergence of species greater at higher latitudes (Weir & Schluter 2007). Whether the same process applies to algae remains unclear. With birds and mammals, species richness is highest in the tropics. While Kerswell (2006) showed that algae within the Bryopsidales also have tropical species peaks in diversity, most algal groups (and genera overall) have temperate peaks in diversity (Bolton 1994; Kerswell 2006). Both Jablonski *et al.* (2006) and Weir and Schluter (2007) suggested that speciation and extinction rates are greatest for low diversity regions. If generally true, then one would expect algae to have higher speciation and extinction rates in both the tropics and polar regions, where algal richness is lowest.

While algae may have different patterns of diversity compared to hermatypic corals, they are functionally similar in that both are sessile organisms that rely on photosynthesis for growth. In contrast to corals and shore fishes, however, algae are most diverse in temperate waters (Bolton 1994; Santelices *et al.* 2006). Specific groups of algae can have tropical peaks in diversity (Figure 2B; Kerswell 2006), indicating that patterns of diversity and endemism in algae differ from those of corals and shore fishes (Santelices & Abbott 1987; Bolton 1994; Millar *et al.* 1999). Diversity patterns of algae can also differ depending on which region is examined (Santelices *et al.* 2006).

Marine algae have not received the same attention as corals and fishes in studies aimed to explain generalized global patterns of marine biodiversity on coral reefs. Yet, marine algae are a necessary and dominant component of all marine ecosystems including coral reefs (Coudray & Montaggioni 1983; Abbott 1999; Malakoff 2000) and their contrasting biogeographic patterns of diversity indicate that a single mechanism does not affect all diversity on coral reefs. Unfortunately, few algae leave a fossil record, so estimates of extinction rates might be impossible for algae. As a result, the mechanisms of speciation remain unclear for how certain genera within the tropics dispersed widely while the majority of algae have short dispersal capacities (Kinlan & Gaines 2003).

Understanding the differences in algal diversity patterns compared to corals or fishes is integral to defining processes driving coral reef biodiversity. Cheney (1977) found that the ratio between the richness of certain algal groups varied predictably between temperate and tropical regions of the Atlantic, but further work has shown that variation exists between different oceanic basins (Schils 2006). Biogeographical analyses of extensive data sets with a high taxonomic and geographic resolution linked to environmental data are essential to describe accurately the affinities among regions worldwide and indicate which factors are responsible for the patterns. For example, water temperature is not the sole factor determining global distribution patterns of algae (Hommersand 1986; van den Hoek *et al.* 1990).

As with corals (Veron & Stafford-Smith 2000), marine algae have distinct patterns in habitat and substrate zonation at local scales (Børgesen 1934; Zaneveld 1969). Only recently has the effect of upwelling been recognized as explaining disjunct biogeographic affinities of algae on an oceanic scale (*e.g.*, Schils *et al.* 2001; Schils & Coppejans 2003a, b; Schils 2006). Phycologists are beginning to recognize the role of cryptic genetic diversity among different species populations that are morphologically similar (*e.g.*, Kooistra *et al.* 1992; Zuccarello *et al.* 1999, 2002; Verbruggen *et al.* 2005a, b; De Clerck *et al.* in press). Given the small distribution ranges of most algae (Figure 3; Kinlan & Gaines 2003), species with large ranges may in fact be multiple cryptic species that are morphologically similar.

The morpho-taxonomic classification of corals has been recently questioned as phylogenetic studies reveal cryptic species and polyphyletic families (Romano & Cairns 2000; Kerr 2005). Some widespread algal species are likely multiple cryptic species given the low dispersal capacities of algae (Figure 3), and as phycologists investigate individual taxa, cryptic species are invariably found (Zuccarello *et al.* 2002; Tronchin *et al.* 2004; De Clerck *et al.* 2005; Saunders 2005; Saunders & Lehmkuhl 2005; Verbruggen *et al.* 2005a, b). When examined molecularly, one clade of *Halimeda* (Section *Halimeda*) was found to have "almost double the number of genealogical species than those currently recognized by

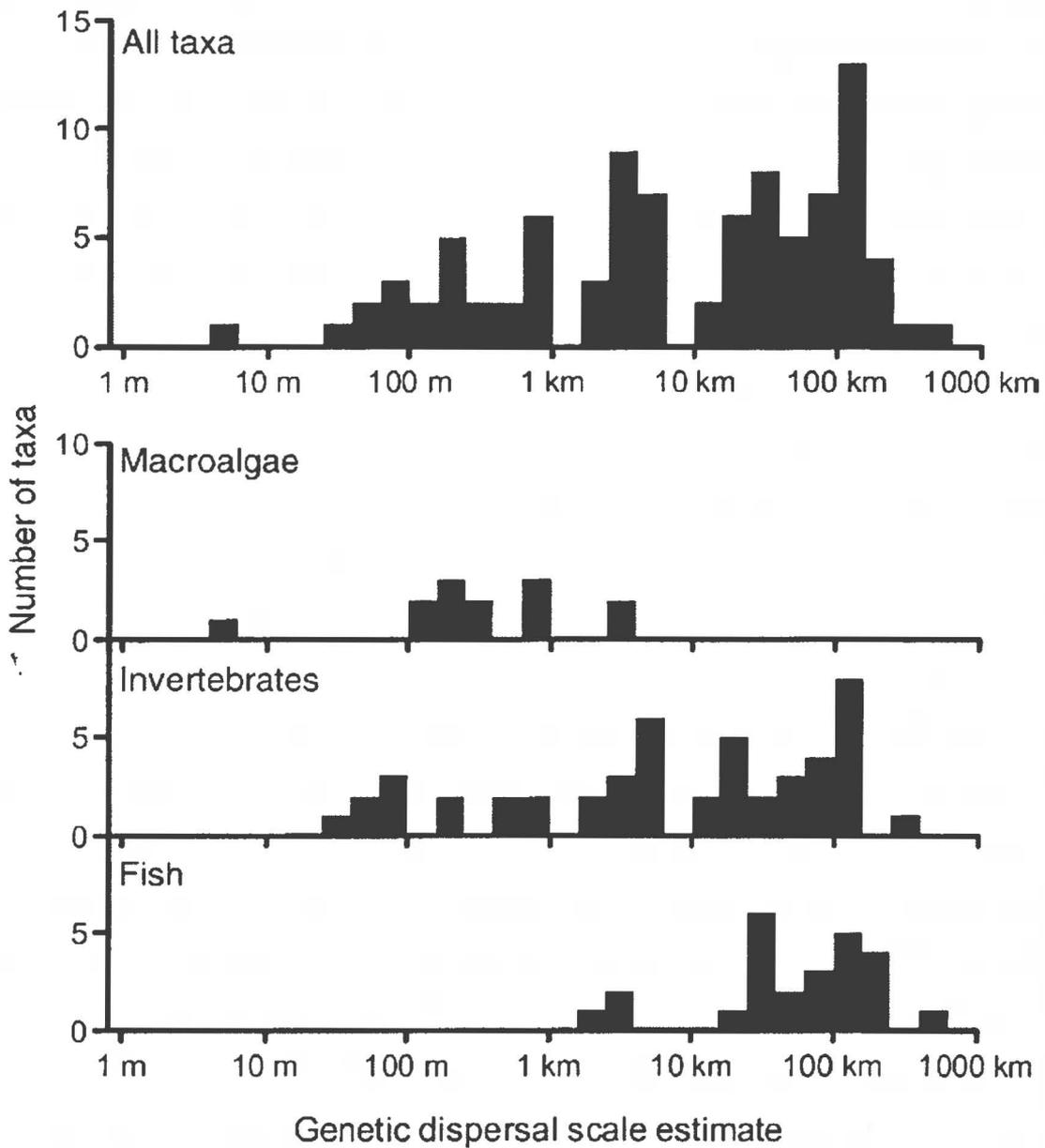


Figure 3. Distribution of mean dispersal distance estimates for marine benthic organisms with source data "based on a literature compilation of genetic isolation-by-distance slopes. Top panel: all taxa ($n = 90$). Bottom panel: sessile macroalgae ($n = 13$), sessile and sedentary invertebrates ($n = 48$), and demersal fish ($n = 25$). Bin size = $0.2 \log(\text{distance})$, distance measured in kilometers," where n refers to unique species analyzed. Figure from Kinlan & Gaines (2003).

classical, morphology-based taxonomy" (Verbruggen 2005). Too few studies have been performed to determine whether different rates of cryptic speciation occur among different algal classes or temperature regions, though so far most genera examined molecularly have cryptic species (T. Schils, pers. comm. 2007).

Verbruggen (2005) noted that while *Halimeda* spp. are suggested to vary in morphology with habitat, no one to date has carried out a detailed study of the environmental, geographic, and genetic factors in determining intraspecific morphological variation (Verbruggen *et al.* 2005). Often, morphologically similar species or varieties are misidentified. Also, debate surrounds some morphological forms (*i.e.*, whether they are separate species or ecotype varieties), with the case of *Caulerpa peltata* versus *Caulerpa racemosa* var. *peltata* a prime example.

Endemic species and localized diversity are major contributing factors to overall diversity in terrestrial systems (Hughes *et al.* 2002), but patterns of endemism have been shown to be non-concordant with overall numbers of species in corals and shore fishes (Hughes *et al.* 2002). The highest concentration of reef fish endemics occurs in the Philippines and central Indonesia (Mora *et al.* 2003), but much variation can exist in results depending on methodologies (compare Hughes *et al.* 2002, Roberts *et al.* 2002, and Mora *et al.* 2003). Kerswell (2006) showed that endemism is a relatively minor contributor to algal generic diversity, but is important at the species level in the Bryopsidales.

In the marine environment, high levels of endemism usually occur in isolated localities, though Hughes *et al.* (2002) found a peak in endemic species (for corals and fishes) in the Indo-West Pacific "triangle" of diversity between the Philippines and Indonesia. Roberts *et al.* (2002) found similar patterns for corals, fishes, marine snails, and lobsters. How endemism is defined has great repercussions on observed patterns of endemic richness (*e.g.*, compare Hughes *et al.* 2002 and Mora *et al.* 2003, where differences of taxonomic filters and the use of percent endemism versus total numbers of endemic species resulted in vastly different conclusions for the same geographic regions examined).

While many typically-analyzed reef fish families (Hughes *et al.* 2002; Roberts *et al.* 2002; Mora *et al.* 2003) do occur on non-coral substrates (Holbrook *et al.* 1994), one would expect that total numbers of endemics would be highest where diversity is highest. How localities are analyzed plays an important role in locating endemism hotspots. For instance, Hughes *et al.* (2002) ignores adjacent localities (<400 km apart), while Mora *et al.* (2003) include all localities and updated taxonomies, thus resulting in very different patterns of diversity within the Indo-West Pacific.

Corals have much lower endemism than previously thought (Hughes *et al.* 2002), in large part because of increased sampling effort, taxonomic knowledge, and whether individual taxonomists are splitters versus lumpers. Where endemic corals exist, localities are not only isolated geographically, but they are isolated by water currents as well, with the only notable peaks in coral endemism occurring in the Hawaiian Islands, Madagascar, and the Red Sea (Hughes *et al.* 2002). Many more localities have more endemic fishes than corals (Hughes *et al.* 2002), in part because corals are now thought to disperse over greater distances than fishes.

CURRENT UNDERSTANDING OF GLOBAL ALGAL BIOGEOGRAPHY

A major obstacle to describing global biogeographic patterns of marine algae continues to be a lack of uniform, high-resolution spatial data, and the inherent problems of attempting to fit marine algal distributional data into marine biogeographic regions defined previously upon studies of other groups of organisms. Occasionally, comparisons have been made among marine algae from selected regions at selected latitudes (Pielou 1977; Millar 1999; N'Yeurt & Payri 2004). Most algal studies to date are on an oceanic or regional scale (*e.g.*, Taylor 1960; Hollenberg 1968a, b; Pielou 1977; Lawson 1978; Lewis 1990; Cambridge *et al.* 1991; Silva *et al.* 1996; De Clerck 1999; Schils 2006). Considerable effort has been given to defining key biogeographic boundaries for algae in temperate waters (*e.g.*, Murray & Littler 1981; Yarish *et al.* 1984; Novaczek *et al.* 1989; van den Hoek & Breeman 1989), but

only a few attempts have been made to integrate global algal data (van den Hoek 1984; Lüning 1985; Bolton 1994; Adey & Steneck 2001; Kerswell 2006; Santelices *et al.* 2006). Perhaps because of a lack of thorough records, past biogeographic studies of algae have classified the entire tropical Indo-West Pacific (IWP) region, from eastern Africa to Easter Island, as one biogeographic region (van den Hoek 1984; Lüning 1985; Adey & Steneck 2001; Kerswell 2006).

The most thorough global study of marine macroalgae to date (Kerswell 2006) calculated range sizes of algae with methods used previously in studies of corals. This approach may be flawed because algae are shown to have much smaller dispersal capacities than other marine organisms (Figure 3; Kinlan & Gaines 2003), thus resulting in patchy patterns of diversity for algae (Bolton 1994). Much variation is seen in the richness of localities within the same geographic region (Bolton 1994) and a range extension approach where algae are assumed to occur at all places between their extreme limits of dispersal (e.g., Kerswell 2006) is inappropriate.

Patchy distributions do not necessarily suggest researcher bias. For example, *Pseudocodium cf. floridanum* is known only from Guam, Japan, Papua New Guinea, Oman, and eastern South Africa. While likely to be found at more localities, it is unlikely to occur at all localities within its large range. Santelices and Marquet (1998) found that range sizes of algae decreased towards regions of highest diversity regardless of temperature. In contrast, the IWP region of highest coral diversity is a region of high range-overlap in coral species, with nearly three-quarters of all hermatypic coral species occurring there and few endemics (Veron & Stafford-Smith 2000; Hughes *et al.* 2002). For marine algae the region of highest diversity for algae consists of the islands of Honshu and Hokkaido, Japan. This region has 1504 of 8057 known species, over 300 of which are found only on those two islands, and has less than 20% of all algal species occurring in their waters. Algal diversity patterns differ markedly from corals, and this suggests that methods borrowed from coral biodiversity studies may not be valid for use with algae.

Recently, phycologists have also combined multiple criteria to define biogeographic boundaries, but again on a regional scale only (Bolton *et al.* 2004; Price *et al.* 2006; Schiils 2006; Schiils & Wilson 2006). Oceanic basins differ in their physical characteristics and are bounded by landmasses in different ways which, coupled with the Earth's rotation, have important ramifications for circulation and upwelling patterns (Pipkin *et al.* 1977). These differences complicate efforts to generalize biogeographic patterns from one region to another. The description of biogeographic affinities is important for explaining processes that govern algal communities across spatial scales, and for linking the composition of disjunct taxa to prior speciation and radiation events (*e.g.*, the similarities of several disjunct algal communities in the Indo-Pacific were linked to relicts of a previously widespread flora in the Miocene; Hommersand 1986). Kerswell (2006) showed that algal genera are typically widespread and endemism is much greater at the species level. This finding suggests that biogeographic patterns for algae might differ depending upon taxonomic level (Price 2002).

OBJECTIVES

This study describes the global biodiversity patterns of marine algae according to five metrics: latitudinal and longitudinal gradients, temperature, spatial scales from small-scale (localities) to large scale (oceanic basins), taxonomic class differences, and patterns of endemism. In a review of papers using the ratio of species to genera (SGR) in biogeography, Jarvinen (1982) found that the species richness increases faster than generic richness as area increases. Jarvinen (1982) concluded that SGR is a statistically biased metric and any results are a mathematical anomaly. Statistical tests were used to determine the significance of apparent species-to-genus ratio (SGR) patterns that preliminarily appeared contrary to SGR patterns of other organisms (*e.g.*, Enquist *et al.* 2002). One objective of this study was to determine if SGR is an accurate metric of algal diversity, even if it may not be for other organisms, or whether SGR is merely a sampling artifact as suggested by several past studies (reviewed in Jarvinen 1982). Qualitative differences in

algal diversity patterns compared to corals and shore fishes are described here to highlight the processes potentially governing diversity in each group.

Temperature was tested by examining differences in algal populations among varying sea-surface temperature (SST) classes: temperate, subtropical, and tropical (see Materials and Methods for classification scheme). Admittedly, temperature is tied tightly to latitude, but past research has shown that temperature is important in affecting distribution patterns of algae (Yarish et al. 1984), especially in regions of upwelling (De Guimaraens & Coutinho 1996; Diaz-Pulido & Garzón-Ferreira 2002; T. Schils pers. comm. 2007). Upwelling can cause a pseudo-high latitude effect, where algae from normally higher latitudes can occur, sometimes leading to disjunct distributions (Schils & Coppejans 2003a; Schils & Coppejans 2003b). Laboratory research has confirmed the importance of temperature in affecting distribution extents of algae at various life-history stages in the Northern Atlantic Ocean (van den Hoek & Breeman 1989; van den Hoek et al. 1990).

Beta diversity (turnover) is defined as the similarity between localities, with adjacent sites presumably sharing higher species and generic similarities in floristic composition compared to distant localities (MacArthur & Wilson 1967; Rosenzweig 1995). How turnover is defined and analyzed greatly affects similarity over distance (Koleff *et al.* 2003). While this study does not address turnover *per se*, it is an integral component of formulas within the Tripartite Similarity Index (TSI; Tulloss 1997), the similarity index used here. The most conservative definition of turnover addresses only the differences in taxonomic composition between adjacent localities (Koleff *et al.* 2003), while this study calculates differences in taxonomic composition between all pair-wise combinations of localities.

Traditionally, when determining distances between localities for similarity analyses, straight paths in Euclidean or Geodesic space are commonly used. In the marine environment, dispersal barriers such as land masses, current patterns, and different temperature regimes make straight-line distance calculations inappropriate. Recent attempts have tried to apply new metrics towards calculating distances between localities (Hennig &

Hausdorf 2006; Soininen *et al.* 2007), but these attempts still base their initial framework on straight-line distances between localities. When only regional or adjacent marine populations are considered (or for many terrestrial situations and some organisms like migratory birds), geodesic approaches might be applicable. In a global study, potential dispersal and connectivity pathways around dispersal barriers must be modeled to determine accurate distances between localities for similarity analyses (Urban & Keitt 2001).

With few exception (Williams & Tracey 1984), the precursor of connectivity networks in terrestrial biogeography is Croizat's panbiogeography theory (Gallo *et al.* 2007), first elaborated into graph theory spanning tree methodologies by Page (1987) and elaborated by others (Rapoport 1982; Page 1987; Platnick & Nelson 1988; Grehan 1994; Morrone & Crisci 1995), sometimes referred to as "spanning-tree biogeography" (Platnick & Nelson 1988). Unfortunately, controversy surrounding Croizat's original theory of panbiogeography (Grehan 2001) and concerns that modern revivals of the theory present a threat to cladistical biogeography theory (Craw 1988; Humphries & Seberg 1989; Page 1990) have limited its applications in biogeography. Because panbiogeography has been noted as the only historical biogeographic discipline to analyze spatial relationships (Grehan 2001), it is an important consideration when describing geographic affinities among floras.

Connectivity networks have only rarely been applied in the marine realm (*e.g.*, Bunt *et al.* 1982; Prud'homme van Reine 1988), and used mostly in food web theory (Urban & Keitt 2001), oceanographic current modeling, and fisheries biology. Recently, graph theory concepts have been integrated with metapopulation landscape ecology analyses (Urban & Keitt 2001). Renewed interest has integrated panbiogeography with modern marine analyses on larger geographic scales (Heads 2005; Gallo *et al.* 2007). A regional attempt at connectivity of pathways between algal communities in the Indian Ocean was used by Schils (2006), but only localities with stylized borders in contact with other localities were used for pathways and actual graph theory techniques were not used.

This study represents a first attempt to use connectivity networks for the marine environment in studying algae globally, but the purpose of this study is not to use connectivity networks to deduce historical patterns in marine algae. While using some of the techniques of panbiogeography theory, this study merely evaluates shortest distances between individual localities along a connectivity network using Dijkstra's algorithm (Dijkstra 1959) as implemented in *Mathematica 5.2*, without qualification of whether all taxa studied followed such routings.

Bolton (1994) stated "it is difficult, perhaps impossible, to correlate coastline length of regions with species diversity in seaweeds." This is because algal occurrence data is usually at the political level. While records of algae from islands almost always use the island's name, even when variations in spelling over time and among cultures are overcome, accurate coastline lengths for individual islands are often unavailable, especially in island-rich nations (*e.g.*, the Federated States of Micronesia, Indonesia, and the Philippines). Remote sensing coastline measurements are often restricted to greater than 1:250,000 scale, meaning many small islands (*e.g.*, most of Oceania) don't show up in global datasets.

Algal occurrence data does not allow for uniform determinations of taxonomic composition among grids of equal size, so non-corrected, traditional measures of endemism for algae also suffer potentially from unequal geographic sizes among localities. Patterns of endemism for algae (in terms of percent composition of endemics and overall numbers of endemic species) were compared qualitatively with patterns of endemism for corals and shore fishes.

Algal endemism was determined through a newer metric (which has not been used for corals and shore fishes), and because algal data were of a coarser scale to coral and fish data, some comparisons are not valid. Algal endemism patterns, as defined traditionally, were compared to patterns seen for corals and shore fishes. Patterns of algal endemism were also examined for concordance with patterns of species richness. In most approaches to calculating endemism, arbitrary range cutoffs are applied to define endemism. Linder's

(2001) approach solves the artificial bias of past methodologies by allowing the range extents of all species within a locality to contribute to a weighted measure of average range-extent of species for each locality or grid cell, while correcting for species richness.

HYPOTHESES

Latitudinal and Longitudinal Diversity Gradients

Because marine algae have their highest diversity outside of the tropics, algae were predicted to have an inverse relationship with latitudinal patterns for corals and reef fishes. Algal richness patterns were also expected to differ longitudinally. Specifically, it was hypothesized that algal diversity was higher in the Atlantic (including the Mediterranean) than comparative levels of diversity for corals and shore fishes from the same region (Figure 1). Since this difference was expected, it was predicted that multiple longitudinal differences would be seen between diversity patterns of algae compared to corals and shore fishes. Should the latitudinal and longitudinal gradients differ for marine algae, then a single process would be unlikely to govern overall marine diversification. SGR was predicted also to be a valid metric for algae. Global species richness patterns were examined to determine whether Kerswell's (2006) findings were applicable to all algal species.

The Effect of Temperature on Algal Diversity Patterns

Marine algal diversity patterns were examined to test whether a single hotspot of diversity occurs overall or whether multiple hotspots occur in each temperature region. Algae are known to have higher diversity in temperate regions and it was predicted that there would be separate peaks, or hotspots, in algal diversity in the northern and southern hemispheres. Northern and southern hemisphere temperate waters are separated by a vast tropical "barrier," meaning that equally high peaks in diversity should occur in each hemisphere. Should differences exist between hemispheres, the northern hemisphere is

expected to have higher diversity because of greater coastline area compared to the southern hemisphere (Figure 4).

The Effect of Spatial Scale on Algal Diversity Patterns

Marine algal diversity was tested also for variation in patterns with respect to changes in spatial scale. Most of the algal diversity data was collected at the political level, thus making quantification of algal diversity across uniform spatial gradients impossible. To standardize for large variation in the size of localities, algal species richness was tested for increases with increasing coastline length. Overall species richness was predicted to increase with increasing coastline distance, whereas overall patterns of biodiversity were predicted to remain the same across coastline lengths.

Variation in Diversity Between Algal Classes

By defining algal biodiversity patterns for of distantly related algal phyla (the Phaeophyceae, Rhodophyta, and Ulvophyceae), variation in patterns of algal hotspot diversity were tested across algal groups. Diversity patterns were also tested for variance at the species and genus levels, and as to whether the SGR of algae can be used to further elucidate patterns of algal diversity. The same pattern of diversity across taxonomic levels occurs in fishes and corals (two very different functional groups; Figure 1), so the null hypothesis was not expected to be rejected based upon the functional similarity between algae and corals. Should the three main algal classes vary in their biodiversity patterns, then grouping these classes may not be the best way to test biogeographic theories among algae. Conversely, using data for a single algal group to define the general diversity of algae as a whole (e.g., Kerswell 2006) may not be valid (Price *et al.* 2006).

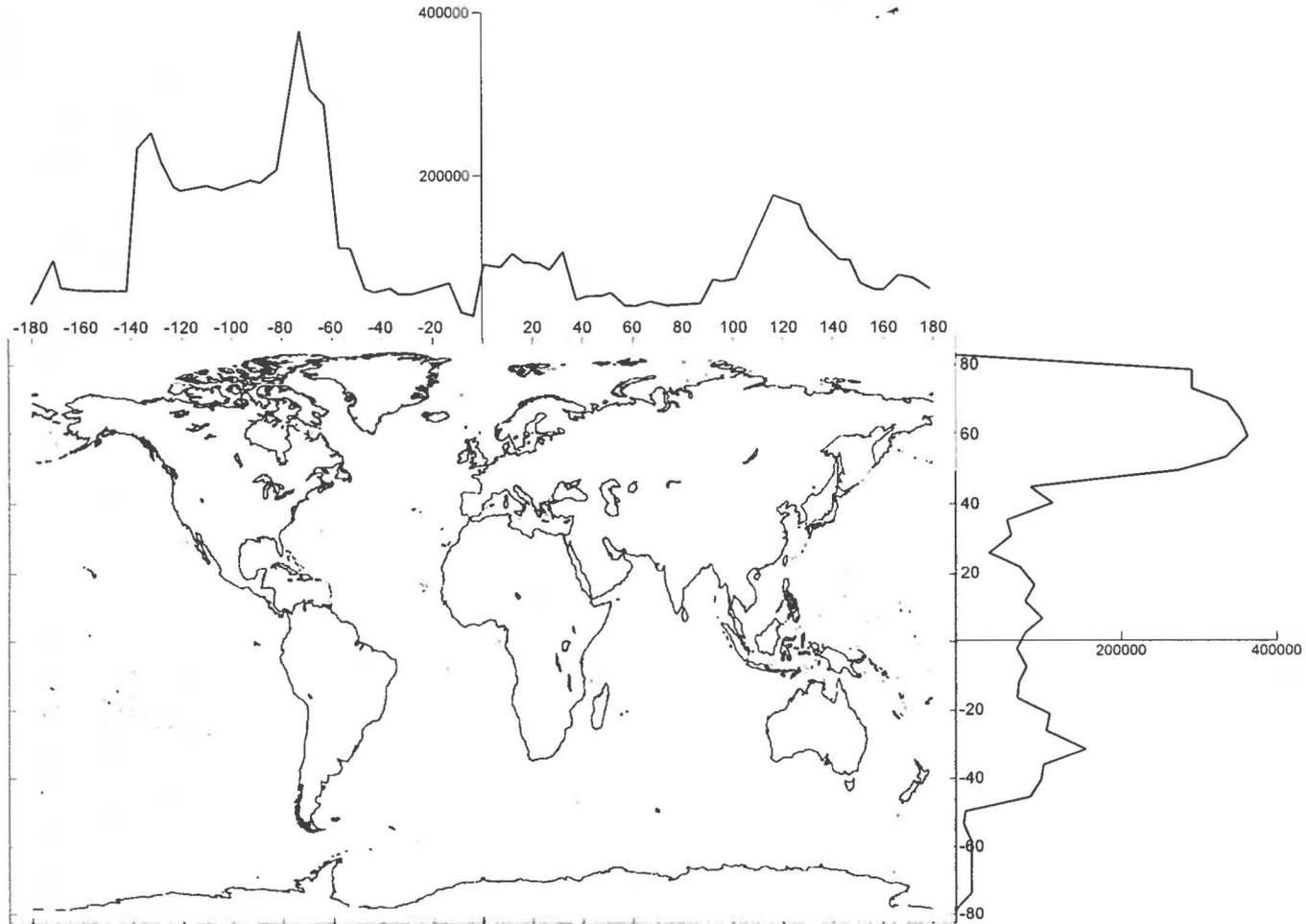


Figure 4. Total coastline per 5° bin for latitude and longitude assuming total coastline measurements of individual localities for all 5° bins such localities occur. Latitude coastline measurements (km) as total accumulated coastline (km) per 5° bin of latitude (Y-axis, -90 = 90°S, 90 = 90°N). Longitude coastline measurements (km) as total accumulated coastline (km) per 5° bin of longitude (X-axis, -180 = 180°W, 180 = 180°E). Note that scales are inappropriate in this Plate Carrée Equirectangular Cylindrical Map Projection because the globe is plotted along a 5° x 5° latitude-longitude grid with all degree lengths equal in size.

Patterns of Endemism Among Algae

Overall, algal diversity patterns were expected to differ from those of corals and fishes because of the explicit temperate affinities of algae. Nevertheless, patterns of endemism were expected to follow other marine groups, in part because of Kerswell's (2006) findings for algal genera. Endemism is generally low for all marine organisms (Hughes *et al.* 2002; Mora *et al.* 2003; Kerswell 2006), and tends to be high in isolated regions (MacArthur & Wilson 1967). While diversity of algae was expected to be richest in temperate regions, endemism was predicted to be generally low overall, with minor peaks in isolated regions. Because many subtropical and temperate islands are isolated and are beyond the latitudinal range of corals, algae were expected to also have peaks at isolated temperate localities. Algal endemism was not expected to be concordant with algal richness, although some increase of endemic species was expected with increased species richness, but endemism was predicted to make a minor contribution to the overall composition of a region.

Despite the prediction that overall algal diversity patterns would differ from those of corals and shore fishes, algal endemism patterns were expected to follow those of other marine groups in that isolated localities were thought to have the most endemics, both in absolute and proportional numbers. As with corals and fishes, endemism was predicted to play a relatively minor role in overall algal diversity. Kerswell (2006) found that endemism contributed negligibly to overall richness at the genus level, but that it potentially contributed more significantly in some localities for species of the Bryopsidales. The generality of Kerswell's (2006) findings for all algal species was tested. The Bryopsidales species had peaks in richness in the tropics (Kerswell 2006), while most algae have temperate peaks. It was predicted that endemism would generally contribute poorly to overall species richness. Should algal endemism patterns deviate significantly from those of corals and/or fishes, algae were predicted to have fewer overall endemics than the latter groups, in part because regions of high coral and fish endemism are noted as having almost no algal endemics (e.g., Papua New Guinea; Coppejans & Millar 2000).

Biogeographic Connectivity Network

In the marine environment, the interconnectedness of communities rely on water currents, with land (e.g., continents) acting as obstructions. It is assumed that computing distances between marine communities by following current pathways around landmasses will be more accurate than just taking geodesic straight-line distances between localities (which ignores land masses and other boundaries). To test this assumption, a comparison was made between outputs of similarity analyses using distance measurements between localities for both methodologies. Specifically, it was predicted that some localities in the short and medium range distances from each other in the geodesic straight-line analyses would shift towards longer distances as a result of having to route around continents.

MATERIALS AND METHODS

This study involved the creation of several databases to standardize algal occurrence data globally for analytical treatments and visualizations, illustrated in the following pictogram (Figure 5).

DATABASE DESIGN AND MANIPULATION

Algal Records Database

Presence-absence data of algal records were collected for marine waters globally, with the exclusion of landlocked waters or seas (e.g. 131,400 algal records from nearly 5,000 unique localities worldwide). All records were entered into a standardized format within the database program *MS Access 2004* (Microsoft Corporation, Redmond, WA, USA). After taxonomic filtering (see the Taxonomic Database section below) and selection of well-studied algal groups (green algae, or the Ulvophyceae; brown algae, or the Phaeophyceae; and red algae, or the Rhodophyta), 52,680 species-locality records were retained for analysis. Several major sources were used to create the algal database.

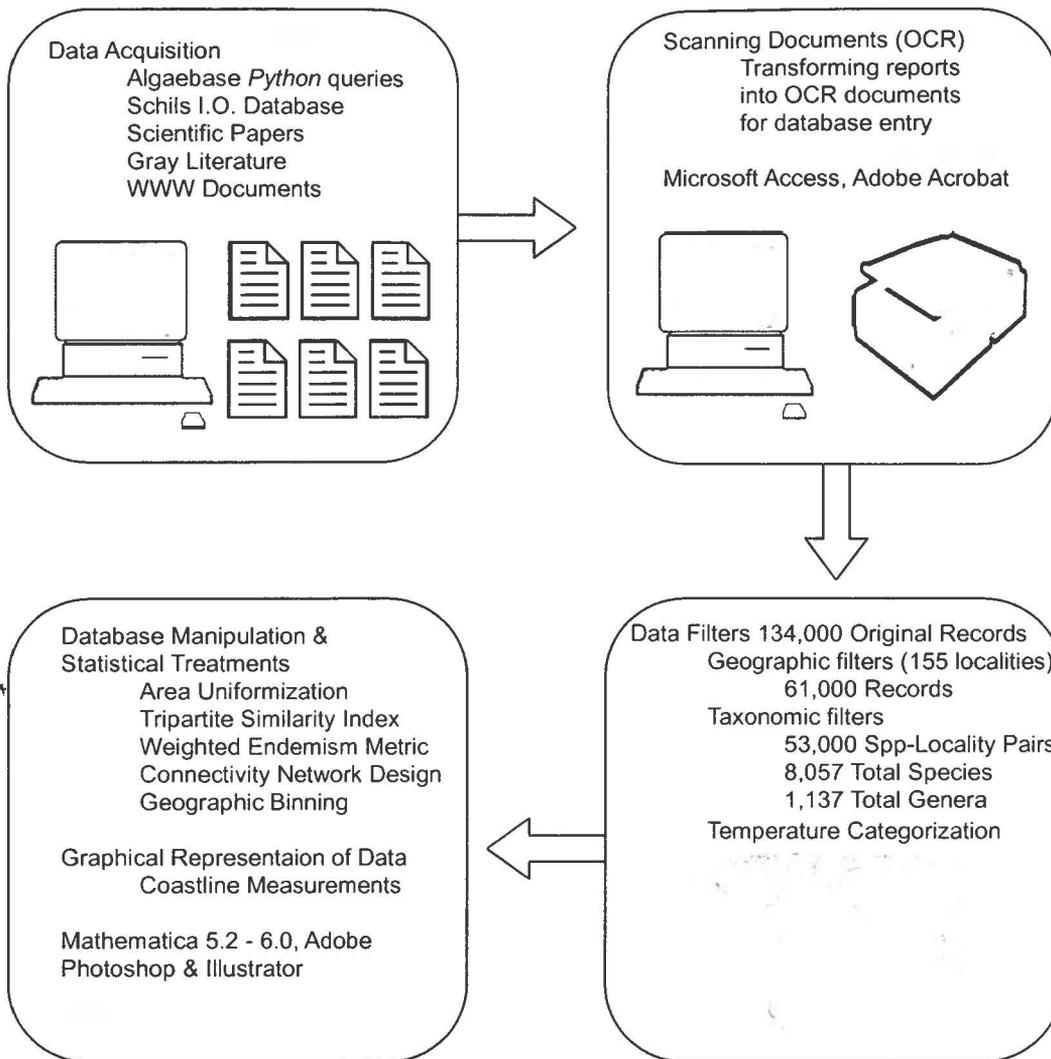


Figure 5. Methodology flowchart for the acquisition and processing of data, representing a schematic diagram of the various steps taken from data acquisition to final conclusions. Under data acquisition (upper left), “Schiis I.O. database” represents the Indian Ocean database of Tom Schiis, based on Silva *et al.* 1996 and updated with scientific literature and gray literature through 2007. Under scanning documents (upper right), “OCR” stands for *Optical Character Recognition*, a process whereby scanned documents allow selectable text. Under data filters (lower right), numbers represent individual algal records (locality and species data) after subsequent filtering, with eventually 53,000 species paired into 155 uniquely designated localities. Individual computer programs are designated where appropriate.

AlgaeBase (Guiry & Guiry 2006), the largest online resource of many global algal records, was queried semi-automatically using Structured Query Language (SQL) contained within an unpublished *Python 2.4.3* (Python Software Foundation, Ipswich, MA, USA) script written by Pieter Provoost (Netherlands Institute of Ecology [NIOO-KNAW], Yerseke, The Netherlands). Queries were made between July and September 2006, but individual algal data records were incorporated until February 2007. The records extracted as American Standard Code for Information Interchange (ASCII) text were adapted to build the algal database used in this study by manipulation in *MS Word* and *Excel 2002* (Microsoft Corporation, Redmond, WA, USA) programs.

Records of algal distributions not given in AlgaeBase (Guiry & Guiry 2006) were added in several stages. One stage included adding higher-resolution data for localities within regions included in AlgaeBase (Guiry & Guiry 2006) at a lower resolution than desired for data analysis (e.g., Micronesia, Australasia). The majority of these records were from localities such as China, Indonesia, Japan (especially the Ryukyu and Ogasawara Islands), Mexico, Micronesia, Melanesia, Polynesia, and various small islands elsewhere.

For Indian Ocean data (including the Persian Gulf, the Gulf of Oman, and the Arabian Sea, but excluding the Red Sea), the Indian Ocean Catalog of Silva *et al.* (1996) was used as a base. Previously omitted or recent sources (especially within Tanzania, South Africa, Malaysia, Thailand, and the Arabian Peninsula, including much gray literature) were added following methods described in Schils and Wilson (2006, updated since publication by Schils, unpublished data). Data for the shores and surrounding islands of West Africa were extracted from an unpublished checklist compiled by Prud'homme van Reine (2006). This checklist was based largely upon John *et al.* (2004), and supplemented with Prud'homme van Reine's unpublished data that included additional records for collections made through April 2005. For South Africa, high-resolution data collected along 50-km blocks of coastline (from Bolton *et al.* 2004) were used to supplement data from the Indian Ocean and West Africa database components. Additions to the South Africa records

since Bolton *et al.* (2004) were made by Schils and Wilson (2006), and by Schils (unpublished data) since then.

Taxonomic Database

After all species were entered into the Algal Records Database, they were validated for taxonomic accuracy in AlgaeBase (Guiry & Guiry 2006). A database was created in *MS Access 2004* (Microsoft Corporation, Redmond, WA, USA) to verify the validity of all genus and species names in the Algal Records Database and to assign old names to their appropriate synonyms. First, a complete list of genera was created by copying manually AlgaeBase's (Guiry & Guiry 2006) Taxonomy Browser function. Second, all genera outside of the scope of this study (all algae except the marine representatives of the Ulvophyceae, Phaeophyceae, and Rhodophyta) were flagged so that database queries could remove such records.

Out of the more than 134,000 initial Algal Database records, after all exclusions of groups outside of the study scope and corrections for errors in the genera list were made, approximately 12,200 unique species (varietals, forms, subspecies, ecomorphs, etc. were ignored) needed to be verified taxonomically. While many of the records in question represented valid species, some species were either typographical errors (often from the original source), invalid, or synonymous with other species.

Each species name (pending verification) was then queried through *SQL* from AlgaeBase (Guiry & Guiry 2006) using a second unpublished *Python 2.4.3* script written by P. Provoost. All currently valid species were linked with the 12,200 species pending verification in the Taxonomy Database. The *Python* script could not verify typographical errors of species names not already in AlgaeBase (Guiry & Guiry 2006) or species where multiple author names were attached to the same genus and species epithet. These records were noted and checked manually on AlgaeBase (Guiry & Guiry 2006) and valid names were linked to the Taxonomy Database.

Midway through the course of the taxonomic data filtering, it was discovered that while AlgaeBase (Guiry & Guiry 2006) is very complete in the number of sources included, algae listed for geographic localities were under the original names cited by authors, even if such names were invalid or later synonymized. As a result of this inconsistency, all AlgaeBase (Guiry & Guiry 2006) records were revalidated before inclusion in the final taxonomic database. While this validation was completed manually by the authors of the aforementioned database components that focused on the Indian Ocean, South Africa (T. Schils, unpublished data), and West Africa (Prud'homme van Reine, unpublished data), for the sake of consistency these data were also inspected for name changes or typographical errors.

A list of genera and species that did not occur in the Indian Ocean, South Africa, or West Africa database components (but occurred elsewhere in the database) was generated to determine whether any non-valid or non-applicable species had somehow been missed through prior taxonomic filtering. After processing these species names through the Taxonomy Database filters, the list consisted of six types of data: typographic errors, either through optical character recognition (*OCR*) errors made when copying and scanning records from the literature into the database, or through typesetting errors in the original publication; original publication errors (*i.e.*, author misidentifications or typographical errors); valid species and genera that do not occur in the Indian Ocean, South Africa, or West Africa components; species outside of the scope of the study (*e.g.*, cyanobacteria); invalidly described species or invalidly cited authors; and, old names that usually have been synonymized with other species.

Geographic Database

Each of the 131,400 records in the Algal Records Database were assigned geographic localities according to 2 methods. Data entered manually were given locality names based upon original notes by the authors of the studies referenced, while data from

database components were assigned localities based upon original database notes. After all locality designations were noted, data were sorted by locality name, yielding 4,987 unique localities noted for all algal records (which including spelling variations of the same localities). These unique database localities were grouped into higher-level entities based on geographic proximity and known algal affinities. In cases where algae were sampled poorly within a given area, localities were joined with adjacent localities. Final grouping of the 4,987 original locality records yielded 167 distinct localities that were defined as having the finest scale of resolution for use in this study.

Of the 167 distinct localities, 12 were excluded from analyses because they either fell outside of the study parameters (Terrestrial = algae from terrestrial, freshwater, and landlocked seas) or were too general for any analyses below the regional level (e.g., Australasia, Indonesia, the Caribbean, East Africa, the Mascarene Islands, the Mediterranean Sea, the Federated States of Micronesia, China, the Persian Gulf, the Red Sea, and West Africa). For data with locality information that was too general, original sources were checked whenever practically possible so that specific survey locations could be determined. No further locality information was available for algal records assigned in these 11 categories, and therefore, such records could not be placed into specific localities in the Geographic Database. Only rarely were species records not included for localities, as in the case where a taxon was only noted for too general a geographic region and not noted in higher spatial-resolution checklists.

The remaining 155 localities formed the basis of the highest resolution geographic analyses carried out in this study. Geographic coordinates in latitude and longitude to four decimal places were collected for each locality from a combination of sources: ReefBase's (The WorldFish Center, Penang, Malaysia) online *GIS* program, government sources, the online encyclopedia Wikipedia, atlases, The New Pacific™ Fourteenth Edition Map of Pacific Oceania, and various other online resources.

Coordinates were taken from three points within a locality: the maximal and minimal latitude and longitude, as well as a coastline midpoint. The midpoint measurement was not the midpoint between the maximal and minimal measurements, but rather a best attempt at characterizing the midpoint along a locality's coastline. For islands and peninsulas, however, the midpoint was usually represented as a center of mass, and often fell inland for small localities. The midpoints of island archipelagos were represented as an approximate midpoint within the range extents of such island groups. Occasionally, for triangular-shaped coastlines that could not be subdivided further for algal record purposes (e.g., India), the midpoint was taken as the peak of the coastline. Coastlines of individual localities were compiled from government sources, especially the 2006 CIA factbook (Central Intelligence Agency, Washington, DC, USA), ReefBase, Wikipedia (Wikimedia Foundation Inc., St. Petersburg, FL, USA), and several other online sources.

Individual geographic coordinates were not available for all algal occurrence records within each locality, so algae were assumed to occur over the entire range of each locality. Algal ranges were not extended artificially to all points between disparate locality occurrences, so that the patchy or disjunct distributions of many species could be portrayed accurately. The coastal range extents of algae within a locality were taken as the calculated coastline length of each locality. The total coastal range of each species was calculated as the sum of coastline lengths of all localities where an individual species was noted as occurring. All records from the Arctic and Antarctic oceans were excluded from such calculations because of the particularly poor geographic resolution of polar occurrence records coupled with the long coastlines of landmasses within each ocean (e.g. arctic Canada, arctic Russia, and Antarctica).

To compare thoroughly results to known patterns for shore fishes and corals, localities were grouped into three temperature classes: tropical, subtropical, and temperate. An annualized averaged global sea surface temperature (SST) map was created from National Oceanic and Atmospheric Administration (NOAA) and National Centers for

Environmental Prediction (NCEP) data collected for the months of January and July from 1981-2005 (Figure 6). Tropical localities are defined as having a monthly SST greater than 20°C in both winter and summer and a peak monthly SST above 25°C. Subtropical localities are defined as having a sustained SST greater than 20°C for at least 6 months of the year and only dropping below 15°C on rare occasions (not annually). Portions of the Arabian Sea that have seasonal subtropical upwelling temperatures, but peak SSTs in the range of the tropics were considered subtropical. Temperate localities are all localities that did not fall into either the tropical or subtropical classifications, and include Arctic and Antarctic waters.

ANALYSIS

Removing Residual Effects of Coastline on Algal Diversity

Coastline measurements per 5° x 5° cell were not available for all localities at the same spatial resolution were completely unavailable for most Pacific islands. Coastline measurements were not divided by the number of cells a locality occupied due to variations in rugosity and coastline cover per cell. Coastline measurements per 5° bin were taken by assuming full coastline measurements per cell that a locality occurred because richness values per cell were also assumed to represent richness values for an entire locality. The intersection of all localities per 5° latitudinal or longitudinal bin was calculated and all coastline km summed (Figure 4). While this approach overestimated coastline length per bin, the overestimation was of the same kind as assuming all species occurring at all points along an individual locality.

To account for the effect of coastline on species richness (and Jarvinen's 1982 proposition that species richness increases mostly as a function of area), the regression of log richness over log coastline for binned data was calculated with respect to latitude and longitude. The residual effect of coastline was removed by determining deviation of actual versus expected (regression) richness values with respect to coastline distance. Residual values were back transformed from log (base 10). Data were scaled to raw richness data

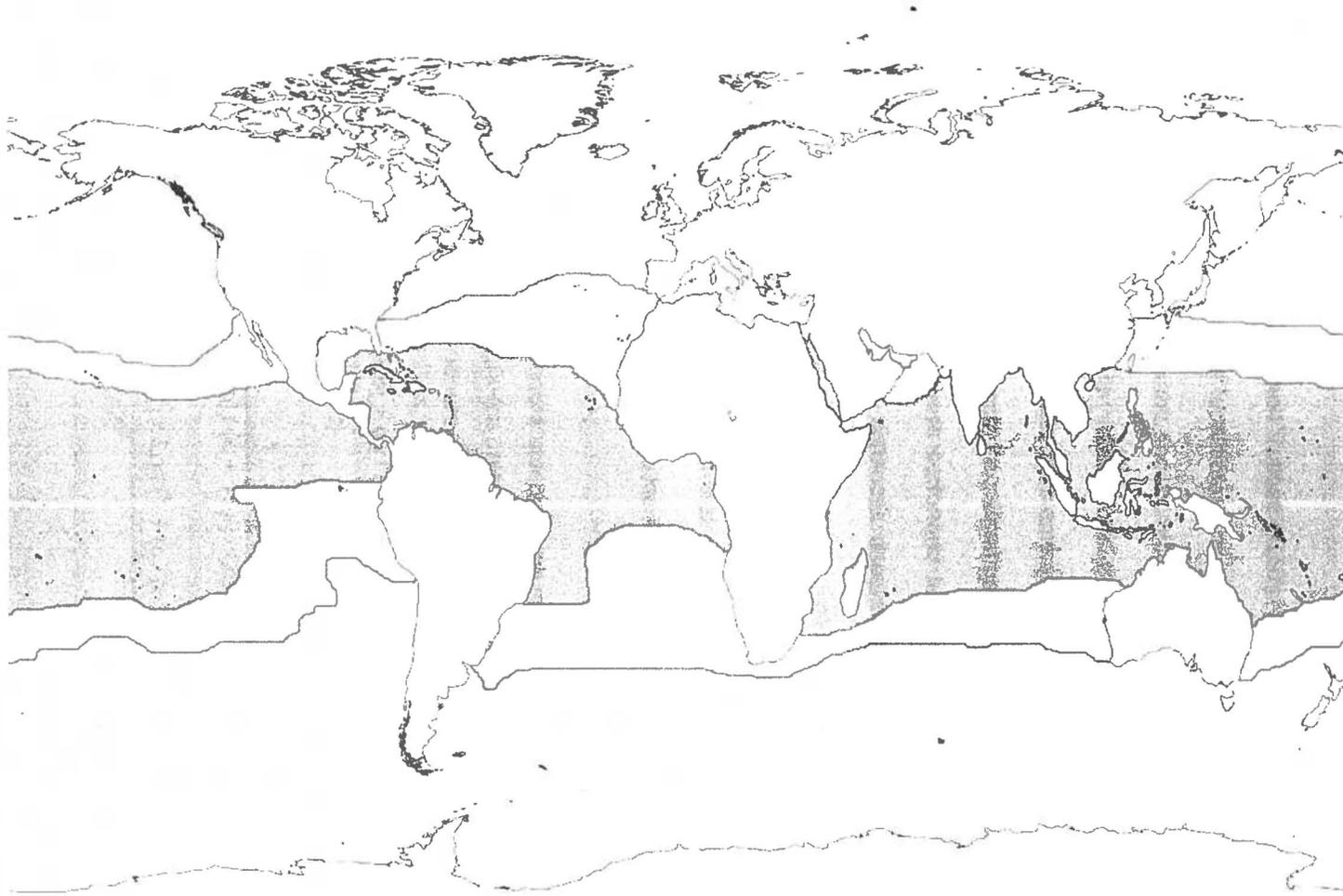


Figure 6. Boundaries between temperate, subtropical, and tropical waters with tropical waters (dark gray) defined as having a sea surface temperature (SST; determined from NOAA and NCEP data collected from 1981-2005) greater than 20°C year-round and a summertime SST above 25°C; subtropical waters (light gray) defined as having a SST over 20°C during at least 6 months of the year and only dropping below 15°C on rare occasions; and waters outside of these boundaries defined as temperate (white), including Arctic and Antarctic waters. Black areas demarcate coastlines. Note that in this Plate Carrée Equiarectangular Cylindrical Map Projection, while the globe is plotted along a 5° x 5° latitude-longitude grid, with all degree lengths equal in size, scales are inappropriate.

with respect to coastline (km) per bin by multiplying all residual values by a constant that would make residual and raw richness data equal at 0° latitude or longitude.

Tripartite Similarity Index

Following Schils (2006) and Tulloss (1997), the tripartite similarity index (TSI) was used to evaluate the similarity of localities across spatial or temperature gradients. The TSI was developed to account for many shortcomings of other similarity indices, especially with occurrence data (Tulloss 1997). Distances between localities were calculated using Dijkstra's algorithm for shortest path problems (Dijkstra 1959) through implementation in *Mathematica* 5.2 (Wolfram Research, Inc., Champaign, IL, USA). Regressions and analysis of covariance (ANCOVA) tests were performed to ascertain whether separate processes governed algal similarities across distances depending on oceanic basin or temperature region analyzed.

Species or generic compositions were compared between locality pairs using values for shared, unique, and total species/genera. The TSI value for each pair-wise comparison of localities was calculated in *Mathematica* 5.2 using the following formulas, where Min = minimum and Max = maximum:

a = Total # species or genera unique to the most diverse locality

b = Total # species or genera unique to the least diverse locality

c = Total # species or genera shared by both localities

$$U = \frac{\text{Log} [(1 + ((\text{Min}[a,b] + c) / (\text{Max}[a,b] + c)))]}{\text{Log}[2]}$$

$$S = \frac{1}{\sqrt{ (\text{Log} [2 + (\text{Min}[a,b] / (c + 1))]) / \text{Log}[2])}}$$

$$R = \frac{(\text{Log} [1 + (c / (c + a))]) \times \text{Log} [1 + (c / (c + b))])}{\text{Log}[2]^2}$$

$$T = \sqrt{ (U \times S \times R) }$$

Measures of Endemism

Because species richness and locality size often vary greatly, traditional measures of endemism (e.g., in terms of 10% smallest ranged species or species only occurring in an individual locality) were deemed inappropriate. Instead, a corrected weighted index of endemism was used (after Linder 2001) that allowed for the accumulation of a higher percent composition of range-restricted species free from the effects of species richness (Crisp *et al.* 2001). This allowed for a more accurate determination of whether endemism patterns for algae are concurrent with species richness patterns. Because Linder's (2001) approach is not widely used in the marine realm, endemism was also calculated with a traditional measurement, whereby only species occurring in a single locality were considered endemics. The pattern of endemism revealed through the corrected weighted index of endemism was compared to the traditional measure of endemism to determine if localities are missed with traditional definitions of endemism.

Endemism was determined through two variations on Linder's (2001) corrected weighted endemism metric, measured as the proportion of range-restricted species in each 5° x 5° cell. When species are assumed to occur over the entire range of a locality (as in the occurrence data used in this study), the ranges of species from large localities may be overestimated. In both methods, because occurrence data were used, species were assumed to occur over the entire coastline of a locality. In the first method, the total number of cells occupied by each species was calculated, whereas in the second method, locality size was ignored and endemism values were calculated based on the number of localities a given species occurred. First, the total number of grid cells or localities (range) of each species was counted. Then, the summed inverse values of the ranges of all species within a given grid cell or locality were calculated (dividing 1 by the total number of grid cells or localities a species occurred) and divided by the total number of species occurring within each cell or locality. All of the species in a given grid cell or locality contributed to a calculation of endemism by generating an average proportion of range extents for the

species found in a given cell or locality. Cells or localities with a higher proportion of range-restricted species have a higher value than cells or localities with a higher proportion of widespread species, and thus can be considered cells or localities with a higher degree of endemism.

Geographic Distance Measurements

Traditionally, similarity index values are plotted as a function of Euclidean or geodesic distance between localities. For global comparisons, geodesic space is more appropriate. With the exception of adjacent localities, few pair-wise distances in the marine realm can be calculated as straight-line paths over the spherical surface of the Earth. Instead, land masses, currents, and temperature act as barriers to distribution. To calculate realistic distances between locality pairs for the TSI analyses, connectivity networks were constructed. A connectivity network was created between most localities (except the Arctic and Antarctic, which were excluded from most analyses). Localities were designated as nodes or vertices and paths between localities were designated as edges. Vertices were defined as the geographic midpoints of localities. Pathways were established in *Mathematica 5.2* using modern temperature, land mass, current patterns, and when applicable, known dispersal routes of algae (Figure 7).

Crossing of temperature regions (temperate, subtropical, and tropical) was allowed in the model only at adjacent localities, generally along continents and not across open water. Dijkstra's algorithm was used to calculate shortest-path routes for each pair-wise comparison, with the length of individual edges calculated using geodesic distances. Antarctic and arctic localities were excluded from analyses because of poor species richness and relatively few studies over large coastal distances.

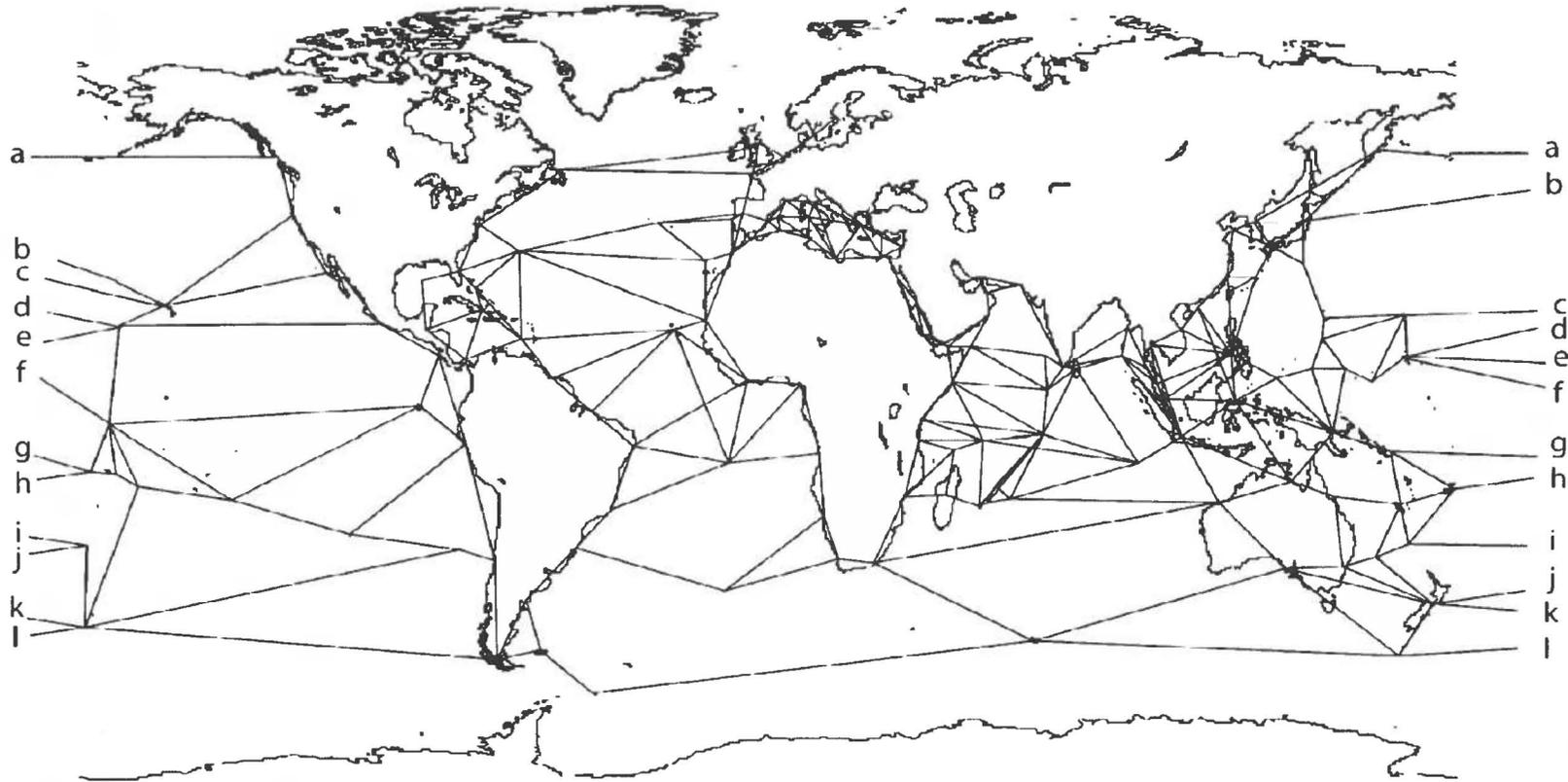


Figure 7. Global biogeographic marine connectivity network. Letters represent adjacent pathways across the Pacific, which is divided in this map projection. Crossing of temperature regions (temperate, subtropical, tropical) were only allowed in the model at adjacent localities, generally along continents and not across open water. Antarctic and arctic localities are excluded from pathway calculations. Edge length of pathways were calculated using Geodesic distances. Note that in this Plate Carrée Equirectangular Cylindrical Map Projection, while the globe is plotted along a $5^\circ \times 5^\circ$ latitude-longitude grid, with all degree lengths equal in size, scales are inappropriate.

Statistics and Graphical Representation of Data

Maps were created using *Mathematica 5.2* from 1:5,000,000 scale coastline data obtained through the National Geophysical Data Center (NGDC/NOAA) Marine Geology & Geophysics Shoreline and Coastline Data website. The NGDC/NOAA source data were processed syntactically in *MS Word 2004* to aid *Mathematica 5.2* manipulation. The globe was projected in *Mathematica* on a Plate Carrée Equirectangular Cylindrical Map Projection with a square grid of five degrees latitude and longitude, with all degree lengths equal throughout the map projection. Localities were assigned to five degree squares with an effort made towards minimizing overlap. Where individual localities overlapped within a grid cell, the locality with most coverage within that cell was used as the sole representation of algal richness. Rarely, two or three localities overlapped equally and these localities were sufficiently restricted in their coastline ranges that omitting their data from specific grid cells would misrepresent true diversity. In such cases, algal records were combined and the total numbers of unique species among pooled localities were used in graphical representations of algal diversity.

Algal diversity was mapped according to several metrics: generic richness, species richness, and species-to-genus ratio (SGR). Diversity was represented for individual localities along a continuous gray-scale gradient on a scale from lowest diversity (white) to highest diversity (black). Species and genus richness for individual grid cells was calculated from zero to one, with one representing the highest diversity cell value for each metric, and all other cells represented as a ratio of highest diversity. Graphical representation of grid cells and binned diversity data was achieved with a *Mathematica 5.2* routine (T. Schils, unpublished) based on collected geographic coordinates for all localities and through linking with the collated algal records, taxonomic, and geographic databases. Grids were linked with produced maps using *Adobe Illustrator 10* (Adobe Systems, Inc., San Jose, CA, USA).

Algal latitude and longitude records were each binned by five degrees and all unique records within a bin were summed by the same richness metrics as above: generic richness,

species richness, and the species-to-genus ratio. Binned outputs were visualized in *Mathematica 5.2* and combined with the mapped figures using *Adobe Illustrator 10*. An algal record was determined to occur within a given bin through determining the maximal latitude and longitude extents of individual localities and assigning such ranges to all genera and species found within those localities. All unique genera and species within each band were calculated to create an average SGR for each bin. When values for each bin were plotted, latitudinal and longitudinal gradients in diversity were compared for algal genera, species, and the ratio of species to genera (SGR).

To test the robustness of the taxonomic filters, and to ascertain differences in species-genera relationships because of algal group or temperature, regressions of log-transformed data were performed similar to Enquist *et al.* (2002). Linear regression analyses, analysis of variance (ANOVA), and posthoc Tukey's Honestly Significant Difference tests were performed using built-in functions within *Mathematica 5.2*. Coefficients of determination (R^2 values) were calculated between the log number of species of algae to the log number of genera of algae (see Enquist *et al.* 2002), as an entire group and for the Ulvophyceae, Phaeophyceae, and Rhodophyta individually. R^2 values were also calculated for the species-to-genus relationship of all algae within each temperature region. Planned orthogonal analyses of covariance (ANCOVA) were performed with the aid of programming code written in *Mathematica 5.2* following Zar (1999) to compare multiple linear regression equations for each log-log plot produced. Because both X and Y variables (species and genera) are subject to error, the data represented a Model II ANCOVA situation. However, because data could be log-transformed, resulting in a linear relationship between both variables, and because ANCOVA analyses of regression lines were performed for predictive purposes, Model I ANCOVA linear regression techniques were used (Zar 1999).

Depending on the data, ANCOVA linear regression analyses were performed for slopes $k = 2$ (two regression lines) and $k = 3$ (where three regression lines were compared). For cases where slopes were determined to not be statistically different, common slope

equations were calculated and elevations (Y-intercepts) of each population regression equation in question (either individual algal classes or temperature regions) were analyzed for significant differences according to the appropriate linear regression ANCOVA formula. In cases of $k = 3$, where a significant difference was discovered, a Tukey test for multiple comparisons among elevations was used to determine where significant differences occurred. For cases of $k = 3$ where slopes were initially determined to be significantly different, an adapted Tukey test for multiple comparisons among slopes was performed. For pair-wise comparisons of the Tukey tests that proved not significant contributors to overall variation in slopes among all three regression equations compared, ANCOVA for comparisons of elevations were performed as described above. Using ANCOVA in this manner tested for homogeneity of the Y-intercepts by testing the null Hypothesis that there were no differences among sample means when these were adjusted for a common Mean-X and a common regression line (after Zar 1999 Section 18.5). Such tests were not performed on significantly different slope-pairs as per the requirements of ANCOVA. In cases of $(k) = 2$, the same flowchart was used, but ANCOVA-adapted Student's t-tests were used.

Alpha diversity was calculated for each locality as the species and generic richness per locality (Whittaker 1972). Beta diversity, while used traditionally as a measurement of turnover (Whittaker 1972), can also be applied to tripartite similarity index (TSI) analyses between localities because turnover in species and generic composition between localities was calculated in the process of the TSI analyses. The similarity of all pair-wise locality comparisons was calculated, as opposed to only a comparison of adjacent localities, as used by conservative measurements of beta diversity. Gamma diversity was calculated as richness within latitude and longitude bins, as well as between temperature regions. No similarity or turnover analyses were performed, as is commonly performed with beta-diversity calculations. Gamma diversity can also be calculated as the global richness (Whittaker 1972) of algae overall and for each algal group. These examples are outlined here, but because of the potential ambiguity of interpretation with this terminology, focus on such

labels is not given in the discussion of results. For instance, even locality data (the finest resolution analyzed) is comprised of multiple studies and smaller localities within. Therefore, each locality datum can be considered a measure of gamma diversity itself.

The statistical package program *Statistica 6.0* (StatSoft, Inc., Tulsa, OK, USA) was used to illustrate Whisker-Box plots for range distributions of algal groups and for algae as a whole according to temperature regions based upon range values calculated in *Mathematica 5.2*.

METHODOLOGIES USED FOR HYPOTHESES

The latitudinal and longitudinal diversity gradients for algae were compared qualitatively to corals and fishes. Comparisons with corals were restricted to the latitudinal extent of their ranges. Overall algal diversities of several broad temperature classes (tropical, subtropical, and temperate) were compared to each other as well as dividing each temperature class into northern and southern hemisphere components. ANCOVA linear regression analyses were performed to ascertain significant differences.

Changes in algal diversity patterns with spatial scale were tested in two ways. First, range extents of species richness were calculated as total coastline distance. Second, range extents of species were evaluated for differences in diversity patterns with respect to algal group or temperature. In both cases, range extent was plotted as percent of total coastline distance. Variation in patterns of diversity across taxonomic levels was tested by comparing algal richness at the species, genus, and class levels to determine whether spatial gradients or diversity peaks changed depending upon the level examined.

Endemism was calculated in two variations of Linder's (2001) weighted endemism metric: measuring range by number of grid cells, assuming species occurred in all 5° x 5° grid cells of a locality; and measuring range by number of localities only. While the Linder (2001) methodology used uniform grid cells, range extents were also calculated as numbers of localities because some localities occupied many grid cells, artificially affecting range-

extent calculations, with endemism favoring small localities. Uniform area cells were not available (a prerequisite of Linder's 2001 methodology), so the results of each adaptation were compared to traditional measurements of endemism (species only occurring in a single locality). Patterns of endemic diversity were compared with those of species richness to test whether increased endemism is concordant with increased species richness, as conflicting results exist in the literature (see Hughes *et al.* 2002 and Mora *et al.* 2003).

ANCOVA linear regression analyses were performed on the species-to-genus ratios (SGRs) of individual algal groups and temperature classes to determine whether SGR is an accurate metric of algal diversity. A previous study of other taxonomic groups has shown SGR to be biased statistically and that it increases with increasing species richness or sampling effort (Jarvinen 1982).

ANCOVA analyses were used also to compare regression lines between similarity analyses of straight-line geodesic distances compared to connectivity network shortest-path routes. While connectivity network results were considered more accurate, the results of straight-line geodesic distances were evaluated for their accuracy in approaching connectivity network results.

ADDRESSING SOURCES OF ERROR

Multiple sources of error and bias were identified in the data. Localities of varying sizes were used, and even localities of similar sizes could have varying coastline lengths, and thus varying levels of habitat available to species. This study aimed to discover global algal biodiversity patterns at a coarse scale, and since multiple geographic entities were clustered into individual locality designations, the use of varying locality sizes was sufficient for this purpose.

Previous attempts to calculate algal range sizes (e.g., Kerswell 2006) have generated ranges of individual algal species and genera that assume occurrence at all points intermediate of an alga's range limits. Algae generally have patchy distributions, small

ranges (Kinlan & Gaines 2003) and usually occur in a narrow band along coastlines. This study calculated algal ranges as the total coastline occupied by a given algal species and genera, which reduces error from overestimating algal range size.

Algae were assumed to occur over the entire coastline of a locality, while ideally range extent would be calculated within each five degree grid cell individually. This approach created a complication for calculations of endemism based on methods given in Linder (2001). Using Linder's unmodified formula on occurrence data where uniform locality sizes were not used over-represented small localities, as range restriction values were calculated based on the total number of cells an individual species occurred. For very long coastlines (*e.g.*, Antarctica), the potential arose that even if a species only occurred in the Antarctic, its range was considerable.

A correction was applied to Linder's (2001) original formula, whereby endemism values were calculated for individual localities first then those values were applied to all 5° x 5° cells a given locality occupied. For the several cells occupied by overlapping localities, endemism values of individual localities were averaged. Given the generally small size of overlapping localities, little additional error was expected in this approach. The use of Linder's (2001) approach minimized error associated with arbitrarily considering only species occurring in a given number of cells or only at a single locality because the corrected weighted endemism metric includes all species, regardless of range size, in its calculation. As such, much of the error associated with previous calculations of endemism is overcome through the use of this metric. Species compositions for uniform cells would ideally be used in applications of Linder's (2001) methodology.

Connectivity networks were used to lessen error in similarity analyses by representing more accurate dispersal route distances compared to basic geodesic distances between locality pairs without considering land masses and other barriers. The Tripartite Similarity Index (TSI; Tulloss 1997) was chosen as a measurement of similarity between localities because it overcomes many of the mathematical problems associated with other

similarity indices, especially when calculating similarities between localities with greatly differing numbers of taxa (Tulloss 1997; Schils 2006), as is the case with algae. Separate TSI analyses were performed for genera and species, grouped by oceanic basin and temperature regions. TSI values for pair-wise locality comparisons were accompanied by calculated minimum distances between locality pairs, as determined through implementations of Dijkstra's algorithm (Dijkstra 1959) for shortest-path problems along a modeled connectivity network.

Sampling effort is known to play an effect on species-area curves (Hill *et al.* 1994), with larger areas potentially having more species due to greater sampling effort as opposed to ecological processes. Part of this error is mitigated by relying solely on presence-absence data over generally larger areas. Smaller areas were grouped into larger locality entities in an effort to mitigate sampling error as well. Any study that includes data from multiple sources makes certain assumptions about the validity of original data. By performing taxonomic validations of all species and by removing uncertain taxa in a uniform way, error was reduced as much as possible. The assumption was also made that a thorough record of all algal studies globally was used, which is impossible (especially for the thousands of gray-literature reports).

Collection bias was minimized by referring to regional compilations of data whenever possible and by including multiple database components that were themselves the results of the efforts of hundreds of researchers. It is certain that studies were missed given the limited time for data collection, but it is believed that this database is the most complete global dataset of its kind, even if finer-resolution regional databases exist elsewhere. Also, by more than tripling the number of occurrence records from the previously most complete study (Kerswell 2006; in large part because this study focused on genera, while the present study also includes all species), more accurate conclusions can be made about algal diversity patterns on a global scale, even if Kerswell (2006) has finer resolution data for a few localities (*e.g.*, Arctic Canada).

RESULTS

SPECIES-GENUS RELATIONSHIPS

Several patterns of algal diversity were discovered depending on how diversity was analyzed or whether algae were examined as a whole or by separate classes. While there is a slight relationship between species richness with coastline length (Figure 8), the R^2 is low and just as many speciose regions have long coastlines as short ones and some regions with long coastlines have only moderate species diversity.

Analysis of variance (ANOVA) and analysis of covariance (ANCOVA), performed on the calculated regression equations of the relationship between genera and species within three temperature regimes (Figure 9) for all marine algae and by individual algal classes, revealed significant differences with respect to temperature and algal class (Table 1).

The general pattern seen among all algal groups was that whenever significant differences occurred in ANCOVA analyses, temperate algal populations were always involved (Table 1). Sometimes, the subtropics were significantly different from the tropics, but where such cases occurred, there was always an example where temperate regions were significantly different from one of the other temperature zones. Individual patterns were revealed when different algal groups were analyzed, suggesting that no algal group can act as a proxy for other algal groups.

Temperate regions had fewer species per genus than other temperature zones. The tropics generally had the highest average number of species per genus for any given locality (Figure 9), as indicated by its lower slope (Figure 9). For all algal classes, the Y-intercepts of temperate algae were always the highest, while Y-intercepts of subtropical algae always the lowest (Figure 9). Subtropical algal slopes were almost always steeper than those of tropical algae (except for the Ulvophyceae, Table 1).

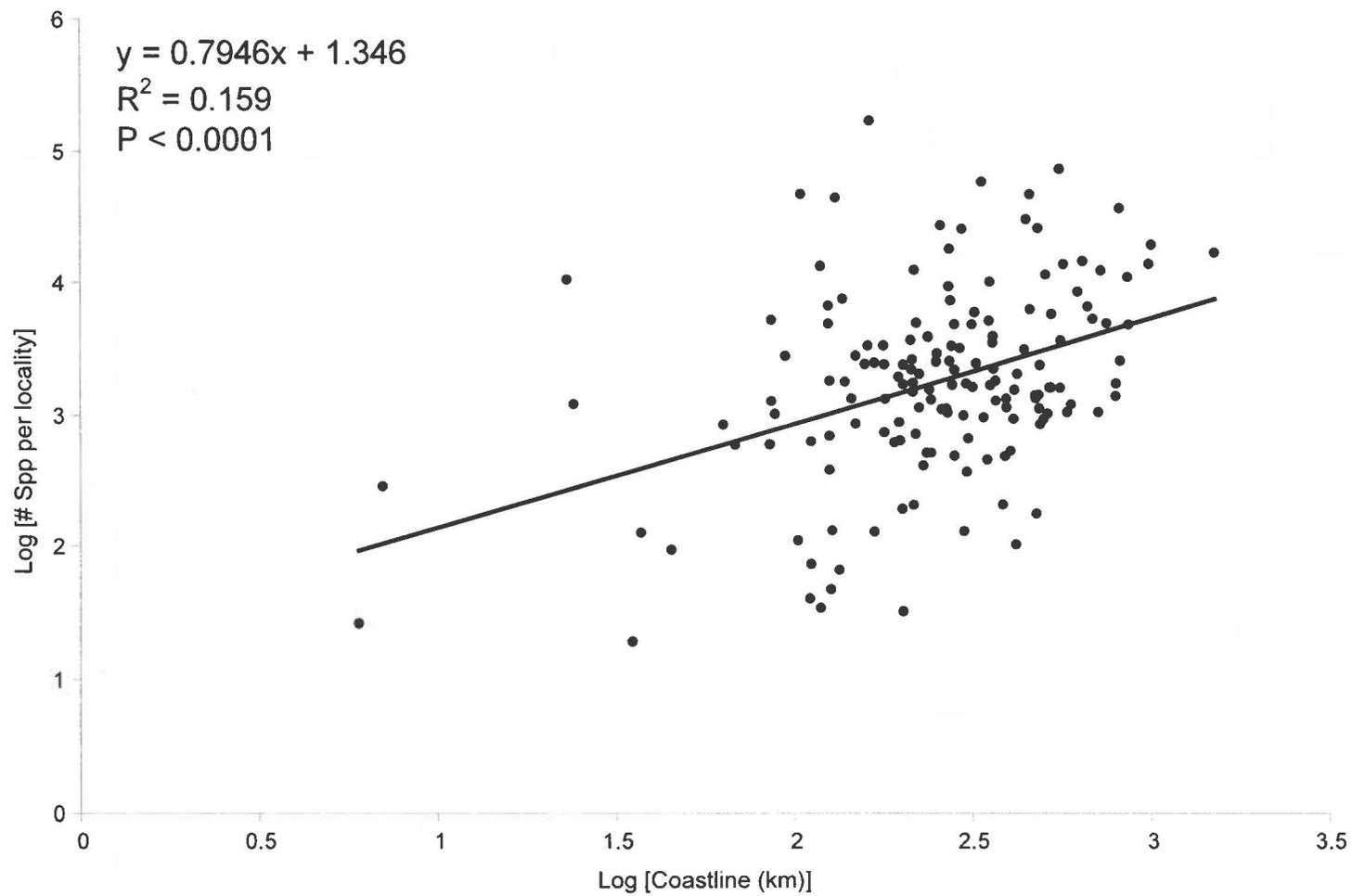


Figure 8. Range size species-area curve, with the number of species per defined locality ($N = 155$) plotted against \log_{10} of coastline length (km) per locality. A linear regression is fit to the data with the representative R^2 value and P-value shown.

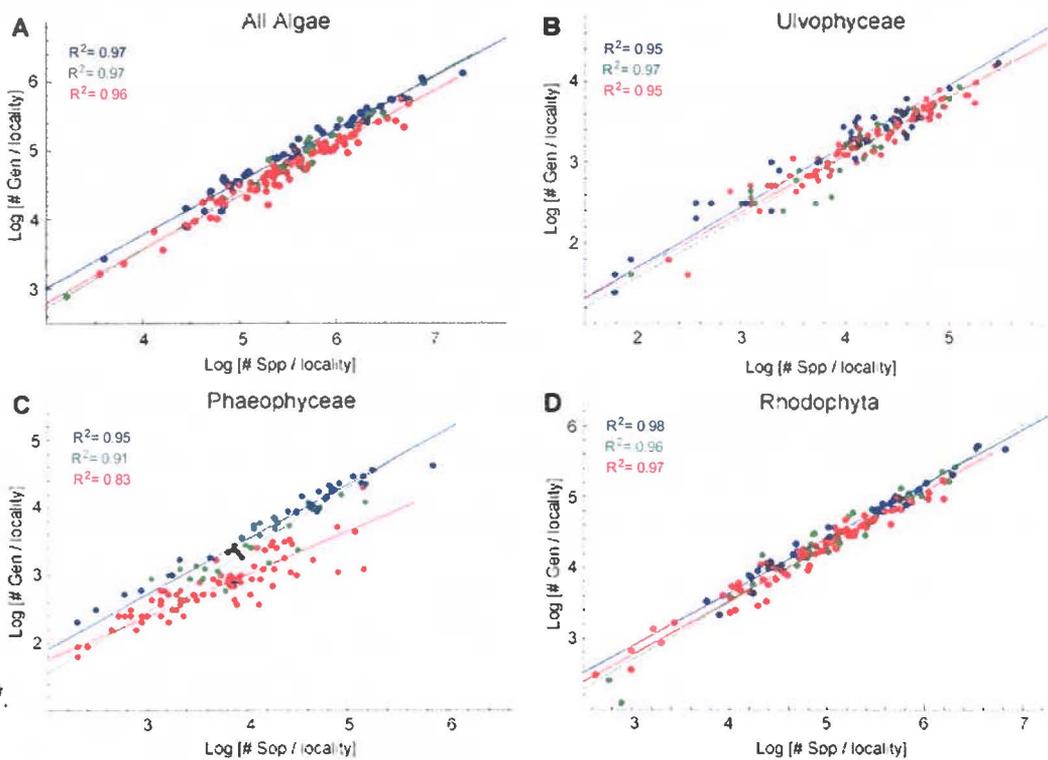


Figure 9. Species-to-genus regressions representing individual regressions of \log_{10} [Generic Richness] per locality over \log_{10} [Species Richness] per locality for three temperature zones (Temperate = Blue; Subtropical = Green; Tropical = Red). (A) represents all algal groups combined; (B - D) represent regressions by temperature for individual algal groups, noted by their titles. Each datum represents an individual locality within a given temperature region. Note that scales of axes are not constant among all four graphs because each algal group varies widely in the total number of species found per locality.

Table 1. Outcome of species-to-genus regression analyses. Results of ANOVA and ANCOVA analyses of pair-wise comparisons of regression lines accompany Figure 9 (TE = Temperate, ST = Subtropical, TR = Tropical). Tests at alpha = 0.05. Note that in ANCOVA analyses, only parallel slopes are tested for significant differences in Y-intercepts (elevation). Full statistical results in Appendices 1-4.

	ANOVA & post-hoc Tukey Significantly different pair-wise comparisons	ANCOVA Significantly different Slopes	ANCOVA Significantly different Y-intercepts (elevation)
All algae	TE x ST, ST x TR, TR x TE	TE x ST, ST x TR	TR x TE
Ulvophyceae	none	none	TE x ST, TR x TE
Phaeophyceae	none	ST x TR, TR x TE	TE x ST
Rhodophyceae	TR x TE	TE x ST, ST x TR	TR x TE

One of the more puzzling results of this study was that while the general diversity patterns for algal species and genera were remarkably similar across geographic gradients (Figures 10, 11), when the ratio of species-to-genera (SGR) in different localities were compared the tropics had more species per genus compared to temperate regions (Figure 12). Overall SGR was highest in the Philippines and India, with secondary peaks in Honshu-Hokkaido (Japan), the Caribbean, the Great Barrier Reef (Australia), and Indonesia (Figure 12). With the exception of Honshu-Hokkaido, which are the most diverse localities for algae globally, the other peak SGR regions are all tropical.

Yet, for algae temperature differences exist, whereby the relative SGR increased in the tropics but reduced in temperate waters, a finding that would not be revealed if only algal richness patterns were examined. For instance, the Philippines, while not overly diverse at the species or genus levels (Figures 10, 11), had the highest SGR globally, with SGR decreasing poleward from a 20° north peak (Figure 12). While the algal SGR intersection between latitude and longitude fell within the lower South China Sea, localities within this region were not the most diverse in terms of overall taxa. Specifically, while the Philippines (the most species- and genus-rich locality in the region) had the highest overall SGR (3.93), it ranked only 33 out of 137 (excluding Arctic and Antarctic localities) in terms of total algal genera (207) and eighth for total species (813).

Unlike what would be expected if the SGR of algae did not represent a valid metric (as suggested by Jarvinen 1982), an extremely tight relationship existed between species and genera of different algal groups and temperature regions, with most regression equations being significantly different from each other (Figure 9). This finding contrasts with Enquist *et al.*'s (2002) results, where the SGR of tree populations did not vary significantly with geography or habitat.

If only the top 10% of the range of SGR values per algal class (and for algae as a whole) are considered recent speciation hotspots (as opposed to historical speciation hotspots, which might be determined by generic richness alone or molecular techniques),

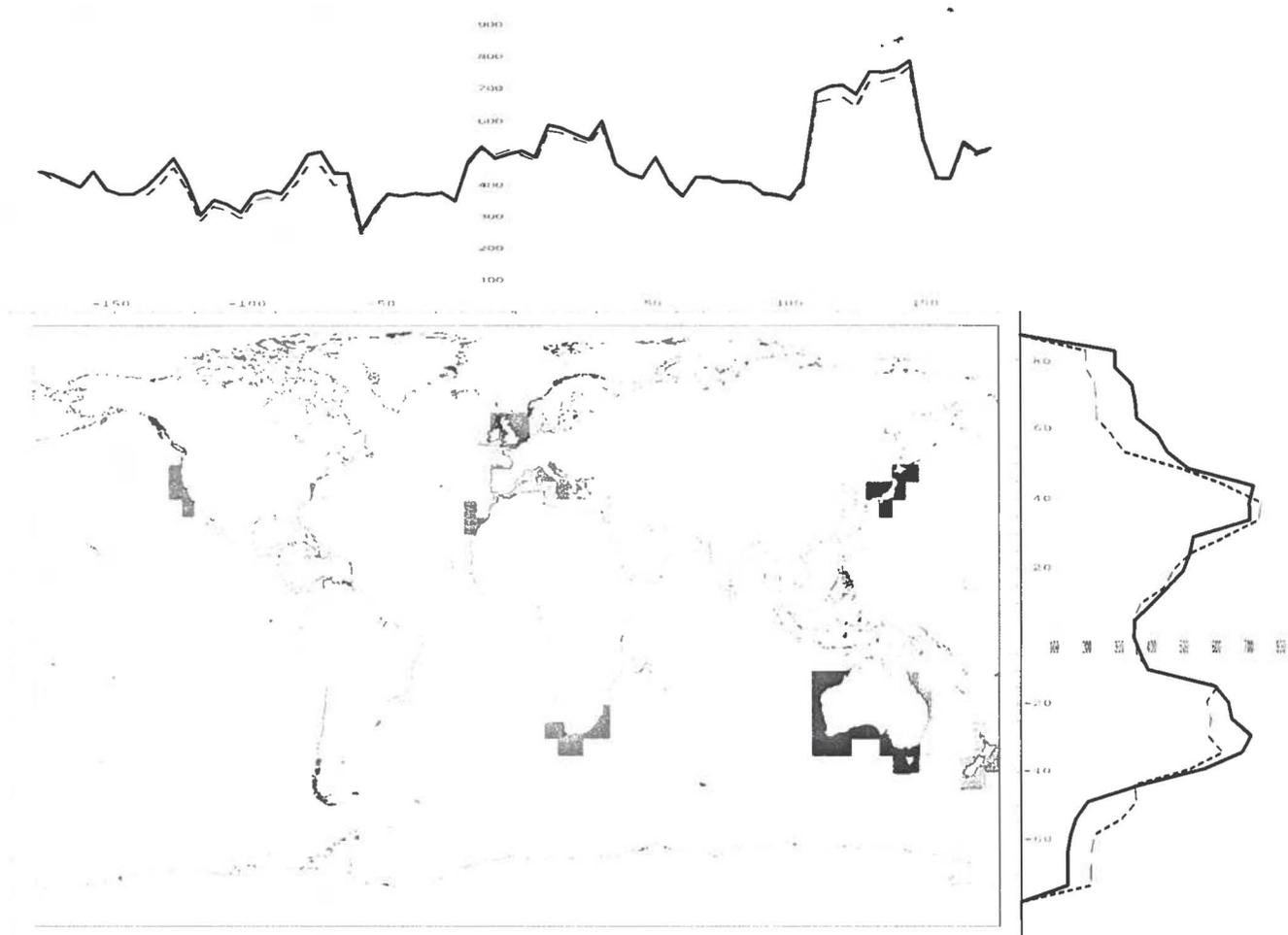


Figure 10. Global richness (genera) of marine algae represented on a continuous gradient from white (no genera present or open ocean) to black (highest number of genera, 459 in Honshu and Hokkaido, Japan). Richness curves represent total numbers of unique genera per 5° bin of latitude or longitude. Solid lines represent unfiltered data; dashed lines represent richness data after removing the residual effects of coastline distance per 5° bin of latitude or longitude. Note that scales are inappropriate in this Plate Carrée Equirectangular Cylindrical Map Projection because the globe is plotted along a 5° x 5° latitude-longitude grid with all degree lengths equal in size.

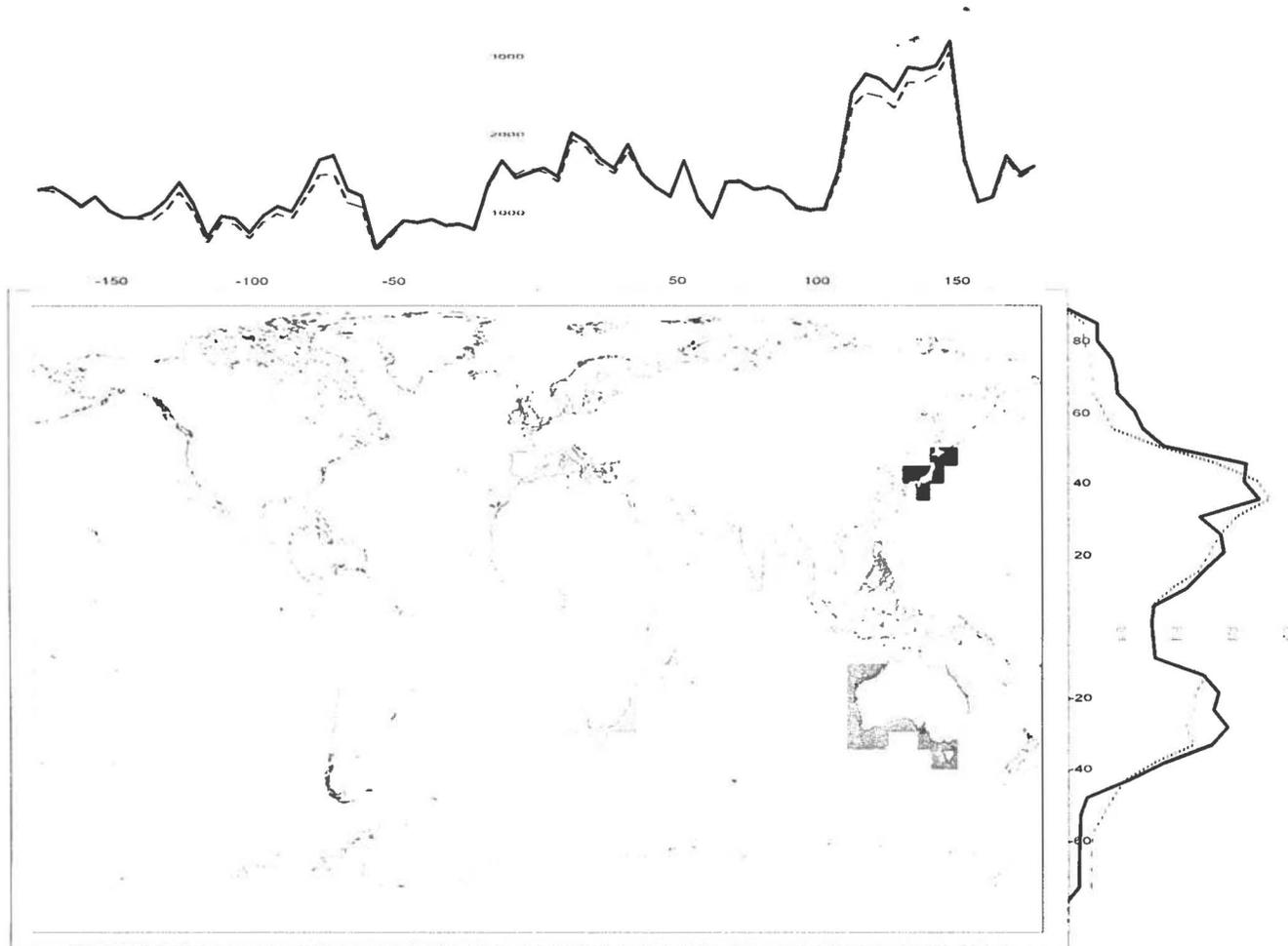


Figure 11. Global richness (species) of marine algae represented on a continuous gradient from white (no species present or open ocean) to black (highest number of species, 1504 in Honshu and Hokkaido, Japan). Richness curves represent total numbers of unique species per 5° bin of latitude or longitude. Solid lines represent unfiltered data; dashed lines represent richness data after removing the residual effects of coastline distance per 5° bin of latitude or longitude. Note that scales are inappropriate in this Plate Carrée Equirectangular Cylindrical Map Projection because the globe is plotted along a 5° x 5° latitude-longitude grid with all degree lengths equal in size.

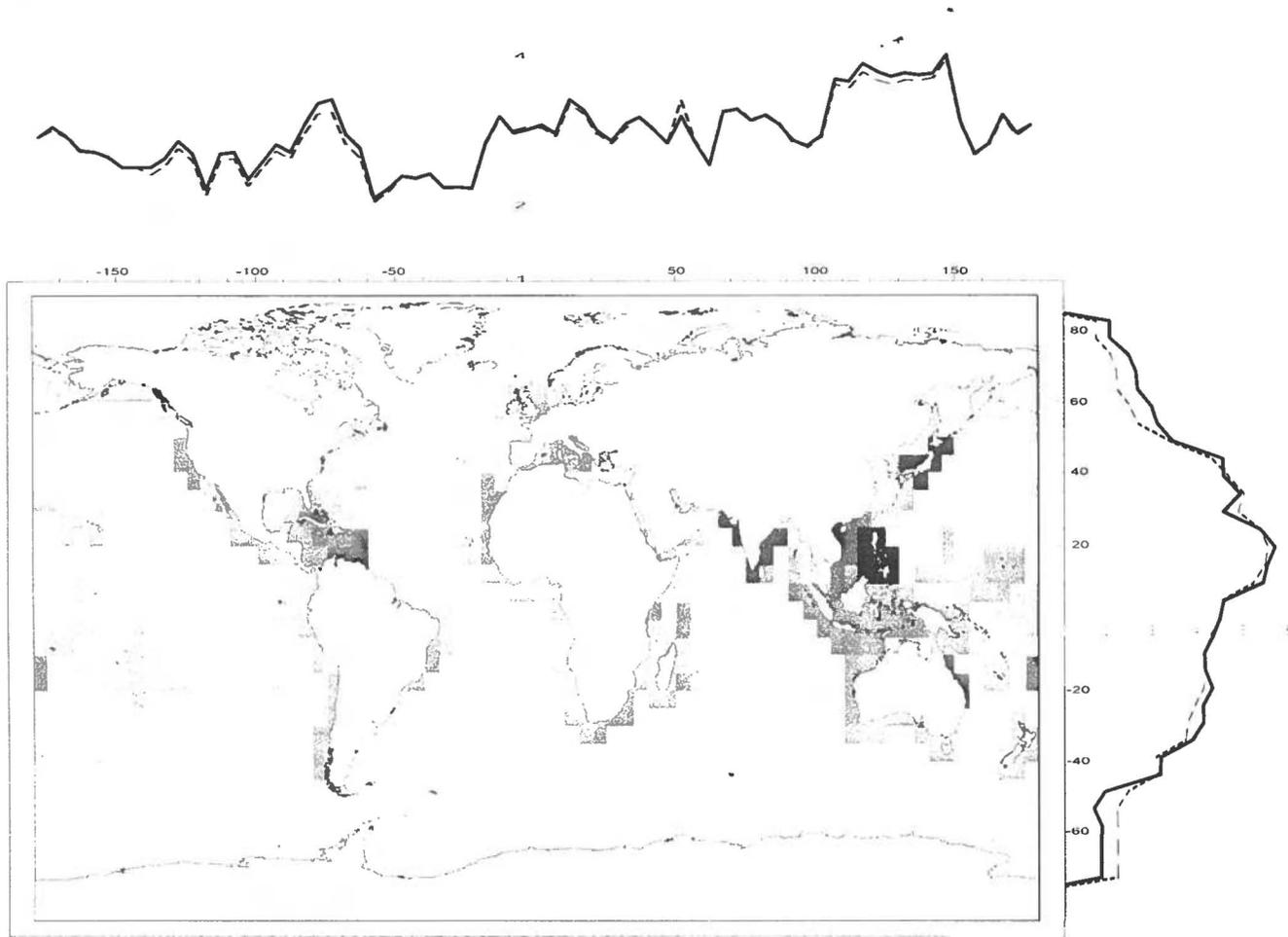


Figure 12. Global richness (species-to-genus ratio, SGR) of marine algae represented using the SGR on a continuous gradient from white (no algae present or open ocean) to black (highest SGR, 3.93 in the Philippines). The lowest SGR possible is 1.0. Richness curves represent the SGR of total unique species per 5° bin of latitude or longitude divided by the total unique genera per bin. Solid lines represent unfiltered data; dashed lines represent richness data after removing the residual effects of coastline distance per 5° bin of latitude or longitude. Note that scales are inappropriate in this Plate Carrée Equirectangular Cylindrical Map Projection because the globe is plotted along a 5° x 5° latitude-longitude grid with all degree lengths equal in size.

very few localities qualify. Algae as a whole and the Ulvophyceae have only the Philippines as a hotspot by this definition, while the Phaeophyceae hotspot is southern China only, and the Rhodophyta hotspots are the Philippines, and Honshu-Hokkaido.

The mean SGR values for the top 10% most diverse localities in each category (Table 2) are 3.0 (\pm 0.7) for all algae, 2.7 (\pm 0.5) for the Rhodophyta, 3.7 (\pm 0.5) for the Ulvophyceae, and 4.4 (\pm 2.3) for the Phaeophyceae. The mean SGR for the middle 80% of each category (eliminating outliers) is 2.1 (\pm 0.5) for all algae, 2.0 (\pm 0.5) for the Rhodophyta, 2.1 (\pm 0.9) for the Phaeophyceae, and 2.6 (\pm 0.8) for the Ulvophyceae. Interestingly, while the highest overall SGR values occur within the Phaeophyceae (but with the greatest range of values), the highest mean SGR occurs within the Ulvophyceae.

All Algae

ANOVA of algae within different temperature zones (Appendix 1) revealed that there was a very significant difference among the regressions of data for all three temperatures. Post-hoc Tukey tests revealed that all temperature zones were significantly different from each other. Additional ANCOVA tests to ascertain differences between regression equations for each temperature region revealed that the slopes of all temperature zones were significantly different from each other (*i.e.*, not parallel). Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6) revealed that only the regression lines of the temperate (TE) and tropical (TR) algae were parallel (Table 1). Multiple comparisons among elevations using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7) revealed that the parallel slopes of the temperate and tropics had significantly different Y-intercepts.

When all algal classes were grouped (Figure 9A), ANOVA and ANCOVA revealed that significant differences existed among algae in each temperature region. These could be explained by the different slopes (or species-to-genus ratios, SGRs) found between pair-wise comparisons of TE x ST and ST x TR (Table 1). Algae within the subtropics have a closer

Table 2. Hotspots of algal species-to-genus ratio (SGR) diversity for all algae combined and separately by algal systematic group. Hotspots are defined as the top 10% SGR values for localities globally (excluding the Antarctic and Arctic). Localities are listed by rank, with peak SGR per category at the top and lowest SGR hotspot at the bottom of the table. SGR values are noted in parentheses below each locality. *Southern China is defined as Guangdong province, Hong Kong, Macao, and the Xisha Islands. †Southern Indonesia is defined as Sumatra (and offshore islands), Java, and the Lesser Sunda Islands, and also includes Timor-Leste and Christmas Island (Indian Ocean); Northern Indonesia includes all other Indonesian Islands and the entire island of Borneo, but not the Papua New Guinea side of the island of New Guinea. ‡Greater Eritrea includes the countries of Eritrea and Djibouti. ††Eastern Adriatic excludes Italy and extends to the border between Albania and Greece. †Greater Canary Islands includes the Canary, Madeira, and Salvage Islands. ∩Sea of Cortez extends to the border between Sinaloa and Nayarit states in Mexico; Pacific Southern Mexico includes the Pacific coast of Mexico south of the border between Sinaloa and Nayarit. °Greater Mauritania includes Western Sahara, Mauritania, Senegal, The Gambia, Guinea-Bissau, and Guinea.

SGR rank (all algae)	SGR rank (Ulvophyceae)	SGR rank (Phaeophyceae)	SGR rank (Rhodophyta)
Philippines (3.928)	Philippines (3.928)	Southern China* (7.909)	Philippines (3.389)
India (3.285)	Lesser Antilles (3.870)	Philippines (6.429)	Honshu-Hokkaido (3.174)
Honshu-Hokkaido (3.277)	India (3.783)	Singapore (4.692)	India (2.882)
Southern China* (3.182)	Tanzania (3.722)	Southern Indonesia† (4.450)	Italy (2.831)
Vietnam (3.048)	Namibia (3.692)	India (4.211)	Vietnam (2.812)
Singapore (2.985)	Pakistan (3.667)	Greater Eritrea‡ (4.118)	Lesser Antilles (2.682)
Queensland, Australia (2.925)	Kenya (3.618)	Vietnam (4.077)	Queensland, Australia (2.674)
Lesser Antilles (2.906)	Fiji (3.550)	Sri Lanka (4.000)	Eastern Adriatic†† (2.620)
Greater Antilles (2.768)	Greater Antilles (3.537)	Northern Indonesia† (3.769)	Pacific USA (2.618)
Italy (2.763)	Chile (3.536)	Andaman & Nicobar Isl. (3.733)	Greater Canary Islands † (2.561)
Southern Indonesia† (2.747)	Greater Mauritania° (3.500)	Seychelles (3.733)	Sea of Cortez∩ (2.547)
Fiji (2.639)	Indian Ocean S. Africa (3.500)	Honshu-Hokkaido (3.461)	Greater Antilles (2.543)
Sri Lanka (2.624)	Southern Indonesia† (3.486)	Peninsular Malaysia (3.357)	Pacific S. Mexico∩ (2.540)
Tanzania (2.617)	Honshu-Hokkaido (3.435)	Kenya (3.263)	Chile (2.496)

relationship to algae within the tropics for low-diversity localities and algae within the temperate region for higher-diversity localities (Figure 9A). Only TR x TE had significantly different Y-intercepts.

Ulvophyceae

An ANOVA of the Ulvophyceae (green algae) distributions in different temperature zones revealed no significant difference among all three temperatures (Appendix 2). Post-hoc Tukey tests revealed that no slopes were significantly different among all temperature pair-wise comparisons. Multiple comparisons among elevations using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7) indicated that while there were no significant differences between slopes, there was a very significant difference with elevation (Y-intercept) between TE x ST and TE x TR pair-wise comparisons of algae within different temperature zones (Appendix 2). The ST x TR comparison was not significantly different for both slope and elevation.

No significant differences were found between temperature zones for the Ulvophyceae (Table 1). ANCOVA indicated no significant slope differences among algae in each temperature region, but differences were found between temperatures when elevations were analyzed.

Phaeophyceae

As with the Ulvophyceae, the ANOVA of the Phaeophyceae (brown algae) distributions for different temperature zones revealed no significant difference among all three temperature zones (Table 1; Appendix 3). Post-hoc Tukey tests of the ANOVA revealed that no slopes were significantly different among all temperature pair-wise comparisons. ANCOVA revealed that slopes were significantly different for temperature regression equations among the Phaeophyceae (Appendix 3), so a multiple comparison among slopes test was performed to determine among which temperature regimes the

significant difference laid. The significant difference in slopes was due to the tropics, which was different from both subtropical and temperate regions. Only the TE and ST regression equations had parallel slopes, and thus an ANCOVA could be performed only on that pair of distributions. An ANCOVA-adapted Tukey test for multiple comparisons of elevations (following Zar 1999 Section 18.7) revealed that the temperate and subtropical regions had significantly different Y-intercepts, with temperate algae having a higher Y-intercept than subtropical algae (Figure 9C).

The Phaeophyceae had the most variation in SGR among evaluated algal classes, as evidenced by slightly lower R^2 values (although the relationship between genera and species was still remarkably tight for all temperature regions, Figure 9C). The tropics have the most variability and an SGR slope different from other algal groups (Figure 9). The shallower slope for the tropics suggests that more phaeophyte species occur per genus in the tropics (*e.g.*, *Sargassum* spp. are particularly diverse in the South China Sea and the Philippines). It is possible that the particular richness of the Rhodophyta in the southern hemisphere displaces the Phaeophyceae, as the latter is generally more diverse in the northern hemisphere and its peak in diversity is also in Honshu-Hokkaido (about 350 species), so competition may not be the only reason driving phaeophyte diversity in the northern hemisphere.

Rhodophyta

The initial ANOVA of the Rhodophyta (red algae) distributions in different temperature zones (Appendix 4) revealed a significant difference in regression equations with regards to temperature, with post-hoc Tukey tests showing that this difference is between the tropics and temperate regions only (Table 1). Further ANCOVA analyses revealed that only the regression slopes between temperate and tropical algae were parallel, but their Y-intercepts were significantly different (Appendix 4).

ANCOVA of the Rhodophyta data revealed significant slope differences between the algae of the subtropics and all other temperature zones, but not between the temperate and tropical zones with each other (Table 1). A significant difference was found between the latter regions when elevations were analyzed. These results follow the Phaeophyceae, in that significant differences existed among all regions, but the subtropics appeared to be more unique among the Rhodophyta.

The Rhodophyta, while having the lowest overall SGR ratio, still have more genera overall than the Phaeophyceae and Ulvophyceae combined. This reflects the older geologic age of the Rhodophyta compared to other algae, or the difference in taxonomic classification among algal classes. SGR peaks in the tropics, where many members of the Ulvophyceae have their highest richness (*e.g.*, the Bryopsidales; Kerswell 2006). The high overall SGR among the Ulvophyceae might reflect relatively recent adaptation of that group to tropical habitats (especially within the Caribbean Sea, where they have their highest diversity) or might represent a genuinely higher SGR compared to other algal groups for unknown life history reasons.

BIOGEOGRAPHIC PATTERNS

Algal diversity was measured with three metrics: species richness, generic richness, and the ratio of species to genera (SGR). To test whether the greater surface area along the equator played a role in shaping algal richness patterns, species and generic richness findings had been scaled with respect to coastline length per bin. With some differences in total species per locality, Bolton's (1994) results were generally repeated in this study (Figure 11).

Both generic richness patterns (Figure 10) and species richness patterns (Figure 11) had clear bimodal richness curves (whether scaled with area or unscaled), with peaks between 30-40° in both northern and southern hemispheres. When all taxa are summed over broad temperature classifications, the tropics of the northern hemisphere had the

greatest overall diversity. This is possible only because of the small species range sizes of algae in the tropics (Figure 13B). The area uniformization of data resulted in a southern shift in richness peaks (Figures 10, 11), with a key peak among the bin encompassing subantarctic islands. Lowest diversity for both taxonomic levels occurred at the poles and in the tropics, with troughs at the equator. The prediction that algal diversity would be comparatively higher in the Atlantic than diversity of corals and shore fishes proved true, especially in the Caribbean and Mediterranean seas.

Similar overall patterns of diversity existed for all three metrics longitudinally, but a pronounced latitudinal difference existed for SGR compared to the richness metrics (Figure 12). The area uniformization transformation revealed that when sampling area was standardized, little variation of richness or SGR results occurred from non-standardized patterns. As such, the patterns seen in this study are assumed to be valid, although more analyses are needed to ascertain the mechanisms contributing to such patterns (Figures 10, 11, 12).

In algae, when the diversity of genera is considered, three localities stand out as the most diverse: Honshu and Hokkaido (459 genera), southern Australia (424), and western Australia (395). However, localities that were very diverse generically were not necessarily as diverse at the species level (and vice versa) when relative richness was compared to all locations globally. This algal pattern is different from corals and fishes, in which localities retain the same relative level of richness across taxonomic levels (Figure 1).

While Kerswell (2006) found that Bryopsidales species (Figure 2B) have their highest diversity in the tropics, when all algal species are considered, a similar pattern to generic diversity occurs (Figure 11). The tropics, centered on the Philippines, had the highest SGR overall (Figure 12), with SGR decreasing pole-ward away from the 20° north maximum. As the results of ANCOVA linear regression analyses reveals, not only does SGR vary with temperature, it also varies by algal class (Figure 9).

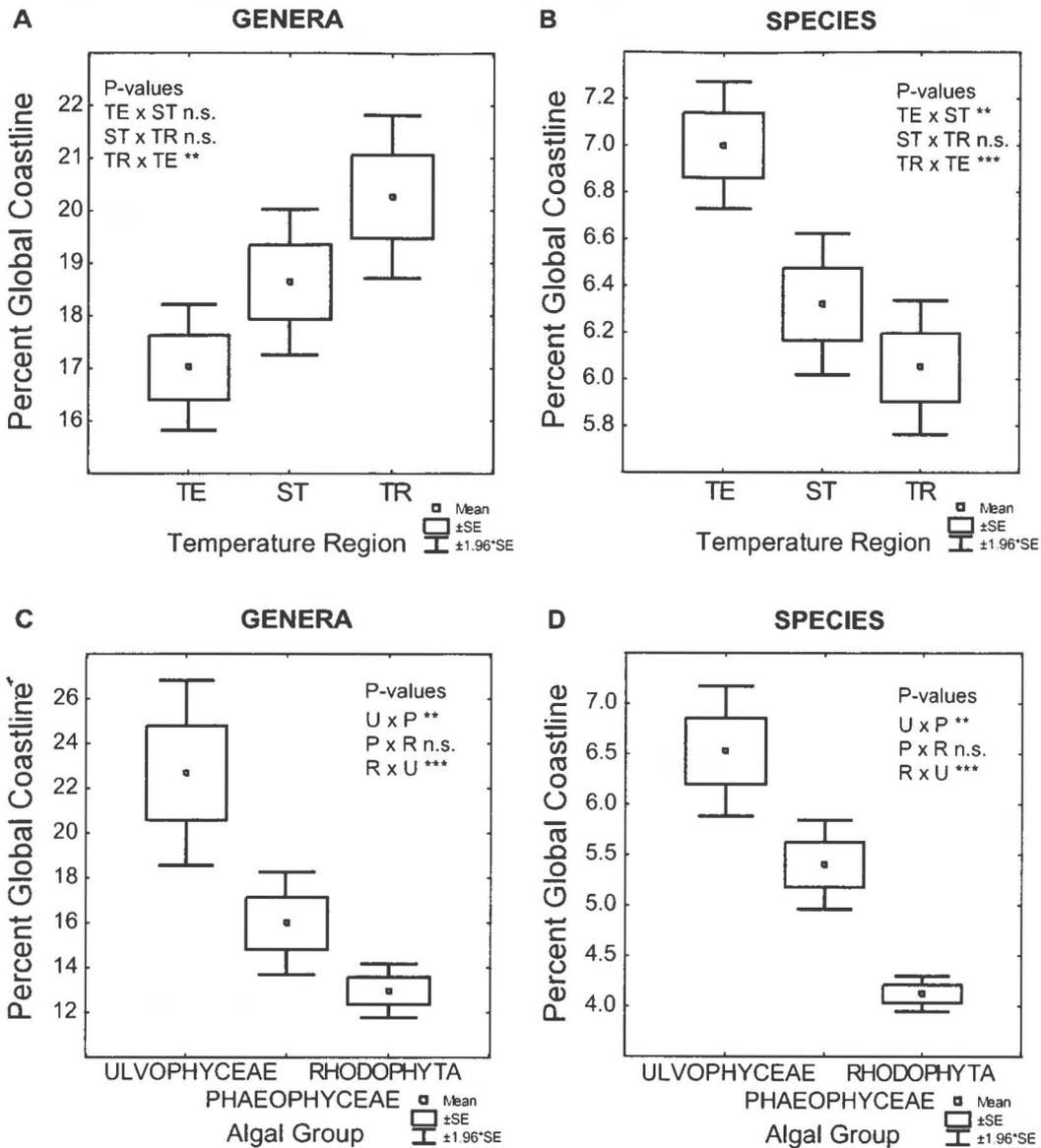


Figure 13. Range distributions of genera and species by temperature and algal group. All ranges are represented by Whisker-Box plots as percent of global coastline in KM (excluding Arctic and Antarctic localities from measurements). Boxes are delimited by ± 1 SE from the mean, while whiskers bound $\pm 1.96^*SE$ from the mean of each category. (A) represents generic range of the algal populations of localities within individual temperature regions (TE = Temperate, ST = Subtropical, TR = Tropical). (B) represents species range by temperature. (C) represents the generic range extents globally of all localities by algal group (U = Ulvophyceae, P = Phaeophyceae, R = Rhodophyta). (D) represents the species range extents of algal groups. Results of ANOVA and post-hoc Tukey tests are in Appendix 5. Note that scale varies in each graph. P-values are significant at α : * = 0.05, ** = 0.01, *** = 0.001.

The three metrics showed no clear trends longitudinally, but the primary peak in richness for all metrics occurred between 100° and 150° east. This peak, however, was largely the result of high richness in Japan and Australia, rather than richness in the Indo-West Pacific triangle (IWP), where highest diversity of corals and fishes occurs. The IWP play an important role in SGR richness, however, with Southeast Asia, which was relatively depauperate in species and generic richness compared to Japan and Australia, having comparatively high SGRs. All three metrics showed the next highest richness in the longitudinal range spanning South Africa, the Mediterranean, and Atlantic Europe.

A third peak in richness was found around the Caribbean, but the peak is stronger for the SGR metric compared to species or genus richness and is a result of the particularly high number of species of Ulvophyceae within the Caribbean region. When algae are grouped regardless of temperature, the Indian and Pacific Oceans are very similar in their response to increasing distance between localities (Figure 14), but respond quite differently than each other when temperature is accounted for (Figure 15; Table 3). The results of the temperature analyses show that temperature (even crudely defined) has an effect on how floras turnover as distance increases (Figure 15) and that information is lost when localities are lumped into larger geographic regions like oceanic basins (Figure 14).

Evaluation of temperature only revealed that Atlantic tropical algae have a unique response to distance between localities compared to tropical algae in other oceans, and are much more unique in their distance decay response than temperate or subtropical floras (Figure 15). Additionally, the affinities of subtropical algae are closer to temperate algae, except in the Indian Ocean, where there are only a handful of temperate localities.

The patterns at the genus and species levels were similar for the Indian and Pacific Oceans, with the same shift higher in elevation (Y-intercepts) for genera as noted above. The Indian Ocean is the smallest ocean basin and has unique ocean current patterns that are driven by seasonal monsoons. It may be for these reasons (allowing greater potential

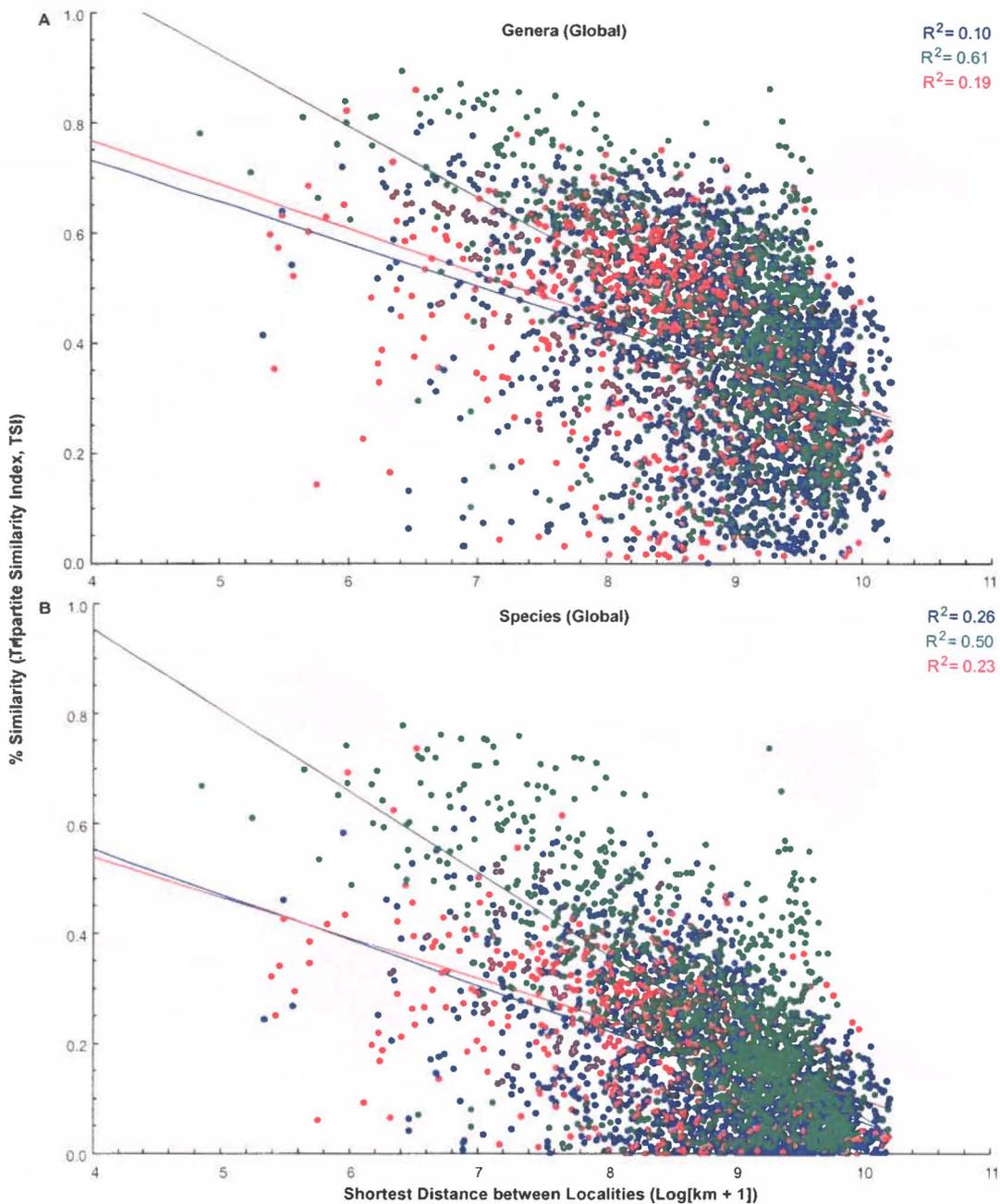


Figure 14. Similarity versus distance between localities of three oceanic basins (Global). X-axis values represent minimum distances between pairwise locality comparisons in Ln [km + 1] and are calculated using Dijkstra's algorithm for shortest paths according to the Materials and Methods. Y-axes represent percent similarity between locality pairs within a temperature region, and are calculated according to the Tripartite Similarity Index as noted in the Materials and Methods. Pacific Ocean = Blue; Atlantic Ocean = Green; Indian Ocean = Red. (A) represents genus-level regression patterns of percent similarity across distance and (B) represents species-level patterns. Full statistical results and regression equations in Appendices 6-7.

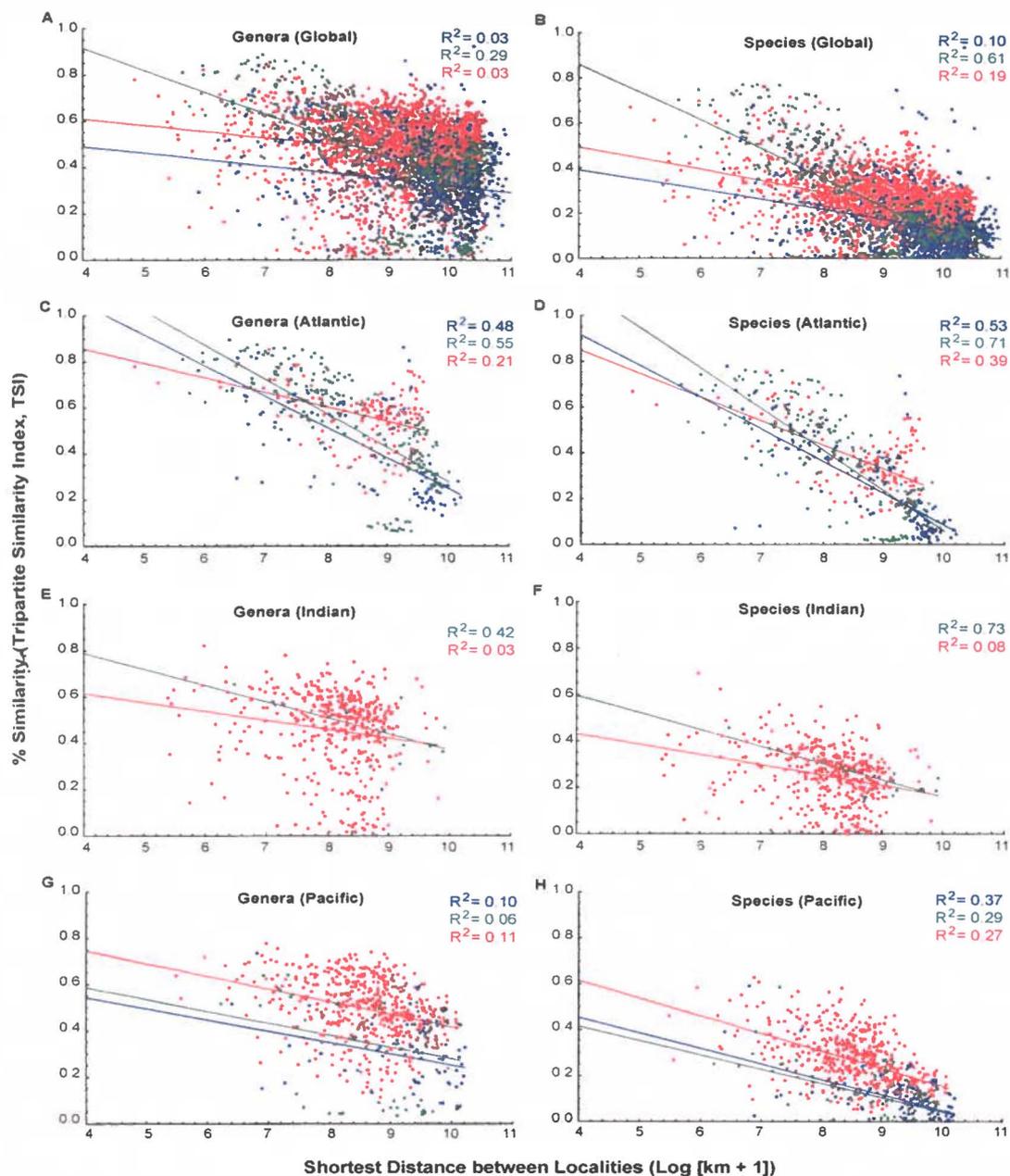


Figure 15. Similarity of genera versus distance between localities of three temperature regions. Temperature definitions follow Materials and Methods. Scales of axes are kept constant across all figures. X-axes values represent minimum distances between pairwise locality comparisons in $\text{Ln}[\text{km} + 1]$ and are calculated using Dijkstra's algorithm for shortest paths according to the Materials and Methods. Y-axes represent percent similarity between locality pairs within a temperature region, calculated according to the Tripartite Similarity Index as noted in the Materials and Methods. Temperate localities = Blue; Subtropical Localities = Green; Tropical Localities = Red. Generic regression patterns are shown in lefthand figures, with species-level patterns shown in righthand figures. (A-B) represent all localities globally, while (C-H) represent individual data for localities within each oceanic basin. Note that for Indian Ocean graphs, no regression line exists for temperate localities because there are only 2 temperate localities in the Indian Ocean according to definitions in the *Materials and Methods*, resulting in only a single pairwise comparison. Full statistical results and regression equations in Appendices 8-15.

Table 3. Outcome of species-genera Tripartite Similarity Index regression analyses. Results of ANCOVA analyses of pair-wise comparisons of regression lines accompany Figures 14-15 (A = Atlantic Ocean, I = Indian Ocean, P = Pacific Ocean; TE = Temperate, ST = Subtropical, TR = Tropical). Tests at alpha = 0.05. Full statistical results in the Appendix. ANCOVA analyses could not be performed for species in temperature regions of the Atlantic Ocean because no slopes were parallel. *Note that for the Indian Ocean temperature comparisons, regression lines could only be calculated for the Subtropics and Tropics because only two Temperate localities occur in the Indian Ocean (see *Materials and Methods* for definitions). Full statistical results in Appendices 6-15.

	ANOVA & post-hoc Tukey Significantly different slopes	ANCOVA Parallel Slopes	ANCOVA Significantly different Y-intercepts (elevation)
Genera (Oceans)	P x A, A x I	I x P	I x P
Genera (Global)	TE x ST, ST x TR	TR x TE	TR x TE
Genera (Atlantic)	ST x TR, TR x TE	TE x ST	TE x ST
Genera (Indian)*	none	ST x TR	ST x TR
Genera (Pacific)	none	TE x ST, ST x TR, TR x TE	ST x TR, TR x TE
Species (Oceans)	P x A, A x I	I x P	I x P
Species (Global)	TE x ST, ST x TR	TR x TE	TR x TE
Species (Atlantic)	TE x ST, ST x TR, TR x TE	n/a	n/a
Species (Indian)*	none	ST x TR	ST x TR
Species (Pacific)	none	TE x ST, ST x TR, TR x TE	ST x TR, TR x TE

connectivity between localities) that in the Indian Ocean, subtropical localities showed higher similarities as distance increased compared to tropical localities, while the opposite pattern was seen in the Pacific Ocean (Figure 15). There were comparatively fewer subtropical locality pairs in the Indian Ocean compared to the Pacific Ocean, so finer-scale temperature analyses may reveal different gradients of taxonomic turnover.

The patterns at the genus and species levels varied more for the Atlantic Ocean and globally (when localities were only sorted by temperature region, irrespective of ocean basin; Figure 15). In the Atlantic Ocean, similarities between tropical localities sharply decreased with distance (especially for species), with the temperate and subtropical localities showing similar patterns (regression slopes) compared to tropical localities. This pattern can be attributed to most tropical localities in the Atlantic occurring in the Caribbean, and thus, similarities are much higher for longer distances in the tropics compared to other regions because of regional affinities of the flora.

Surprisingly, when oceanic basins were ignored and localities were grouped only with respect to temperature, tropical and temperate localities responded more similarly, while individual oceanic basin analyses revealed that the subtropical and temperate localities behaved more similarly. Globally, the subtropics revealed a distinct pattern compared to other temperature regions (Figure 15, Table 3), with very high similarities among geographically close localities and sharply decreasing similarities with distance.

The Rhodophyta contributes disproportionately to overall richness within higher-diversity localities because the Rhodophyta have more total genera (752) and species (5251) than the other algal groups combined. It is likely that the affinity of the Rhodophyta lies closer to temperate regions, skewing the subtropical regression towards the temperate region as total composition of the Rhodophyta increases (Figure 9A). ANCOVA of the slopes indicated that they were the same for the tropics compared to the temperate region, but the Y-intercepts were significantly different (Table 1). This difference between the tropics and the temperate region manifests as a significantly higher SGR for the tropics

compared to the temperate region. While Honshu-Hokkaido was the locality with the highest overall rhodophyte richness (just over 900 species), the Rhodophyta is generally richer in the southern hemisphere.

With the Ulvophyceae however, slopes and elevations were the same for the tropics compared to the subtropics (Figure 9B). The SGR of the Ulvophyceae in the temperate region is the lowest, suggesting that the Ulvophyceae are generally more tropical as a taxon. The Ulvophyceae do not generally have a clear unimodal peak in richness in the tropics, but it is the only algal group without a strong bimodal amphitropical richness curve. The latitudes with the highest average Ulvophyceae species richness are -20° and 40° , largely as a result of subtropical localities (e.g., Honshu-Hokkaido, western Australia, and South Africa), although this group is also extremely diverse in the Caribbean and the Philippines. Evaluation of its SGR suggests that the Ulvophyceae has a large tropical affinity, but given its low overall diversity compared to the Rhodophyta, its deviation from Rhodophyte patterns is masked when algae are grouped.

Range Distributions

ANOVAs (Figure 13) indicated that the ranges of genera in the temperate zone were significantly smaller than those of the tropics, but the ranges of genera in the tropics were not significantly different from those of the subtropics. The ranges of genera in the subtropics were intermediate between the temperate and tropical zones. The opposite pattern was seen for ranges of species. Significantly longer ranges were found in the temperate zone than both the subtropics and tropics (Figure 13).

Comparisons of ranges by algal class revealed that the genera of the Ulvophyceae had significantly longer ranges (as percent coastline) than the Phaeophyceae and the Rhodophyta (Figure 13). While the Phaeophyceae had a longer mean generic range than the Rhodophyta, the overall ranges of each were not significantly different (Figure 13). When species ranges were examined, all three algal groups were significantly different from

each other, with the Ulvophyceae having the longest ranges, followed by the Phaeophyceae and Rhodophyta.

Generic ranges were remarkably similar for temperature regions and for algal groups, with mean ranges between 13-23% of global coastline kilometers (Figure 13). Species ranges were also similar between temperature regions and algal groups, with mean ranges between 4-7% of global coastline (Figure 13).

Tripartite Similarity Index

Algal genera and species had similar regression patterns at the oceanic basin level when locality data were grouped regardless of temperature region (Figure 14), except that TSI values were generally shifted higher for genera than species. This is to be expected because genera are more widespread than species and distant localities, on average, share more genera in common than species. Distinct differences were seen for similarities across distances of algal genera and species with respect to temperature gradients and between oceanic basins (Table 3). When the similarity of genera and species across localities within each oceanic basin was analyzed with ANCOVA (Figure 14) at both taxonomic levels, the results revealed that the Indian Ocean and Pacific Ocean floras did not significantly differ in similarity response according to distance between localities, but that the Atlantic Ocean was significantly different from both the Indian and Pacific Oceans (Table 3).

When the similarity of algal genera across distance was compared for each oceanic basin across temperature regions, differences were seen between all oceans (Table 3, Figure 15). When species-level patterns were analyzed, all ocean basins showed similar regressions across distance compared to genera (Table 3), but Y-intercepts were higher for generic regression lines compared to species regressions. The Indian and Pacific Oceans showed similar patterns at the species-level compared to genera for the same basins (Table 3), but comparisons of regression lines showed a general shift of higher overall similarity at

the generic level compared to species-level patterns, even though the overall slopes were very similar.

Endemism

At the oceanic scale, the Pacific has the highest diversity with just under 75% of all global genera occurring there. The Antarctic is the least diverse with only 17.5% of all global genera (and while many species are restricted to the Antarctic, Figure 16B, few genera are), followed by the Arctic Ocean. Of 1137 unique genera, 388 (34.1%) are specific to a single ocean, while only 91 genera (8%) occur in all oceans. Oceanic endemism is highest in the Pacific Ocean (19.7% of all Pacific genera are only found in the Pacific).

Of 8091 total algal species analyzed, 2726 (over one-third) were found in only a single locality. While Honshu-Hokkaido had the greatest overall numbers of total species and single-locality endemics (362 out of 1504 total species), species richness was not a linear predictor of high endemism values. Localities with high species richness (Figure 11) do not uniformly have high endemism richness (Figure 16), although as total numbers of species increase, some increase in the proportion of range-restricted species is expected. Given the high number of species only found in Honshu-Hokkaido, it is possible that the Japanese flora is singularly large and isolated. Honshu-Hokkaido had the highest species richness of any locality, with nearly one-quarter of all species found being restricted there.

In a variation of Linder's (2001) original weighted endemism approach, locality size was ignored. The same endemism hotspots found with the original Linder (2001) methodology were found again with the modified methodology (Figure 16B) but many localities missed previously by the first methodology proved to have a much higher proportion of range-restricted species, especially towards the poles. Given current data limitations (occurrence data for geographic entities as opposed to uniform cells), the second method is more applicable for algae. Towards the poles, endemism is elevated (Figure 16B), which might suggest that increased speciation rates coupled with low dispersal

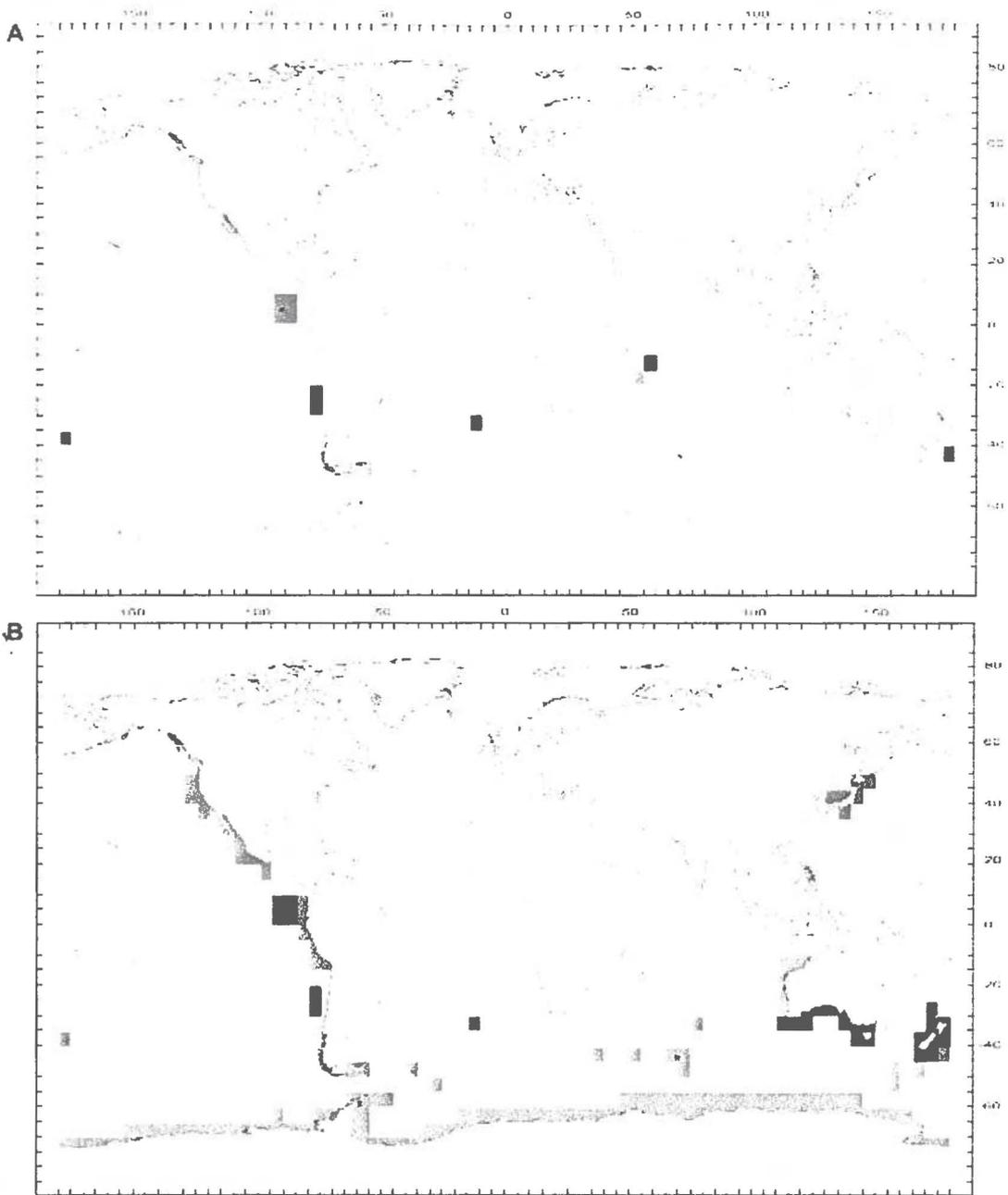


Figure 16. Biogeographic patterns of richness by a corrected-weighted measurement of endemism. In both graphs, the world is plotted on an equal-area grid with cells of 5° latitude by 5° longitude. Algal diversity is represented using endemism measured as the proportion of range-restricted species within each grid cell (A) or locality (B) on a continuous gradient from white (no algae present or open ocean) to black (highest proportion of range-restricted species in a given cell: 0.3339 for A, 0.4937 for B). Note that scales are inappropriate in this *Plate Carrée* Equiarectangular Cylindrical Map Projection because the globe is plotted along a 5° x 5° latitude-longitude grid with all degree lengths equal in size.

capacities for algae lead to a young, unique flora that will slowly radiate and invade toward the equator. The poles are the areas of the lowest richness (Figures 10, 11), showing that richness and endemism are not concordant in marine polar algae. The entire western coast of the Americas (including tropical regions) had high endemism (Figure 16B).

In both variations of Linder's (2001) weighted endemism approach, several isolated islands and archipelagoes had the highest proportion of range-restricted species: the Galapagos, San Juan and Felix islands in the eastern Pacific, the Chatham, Bounty, and Antipodes islands in the southwestern Pacific, the Cargados Carajos Shoals and Saya de Malha Banks in the Indian Ocean, and Tristan da Cunha in the Atlantic (Figure 16). When locality size was ignored, amphitropical localities had a much higher proportion of range-restricted species, as did the entire western coast of the Americas (Figure 16B).

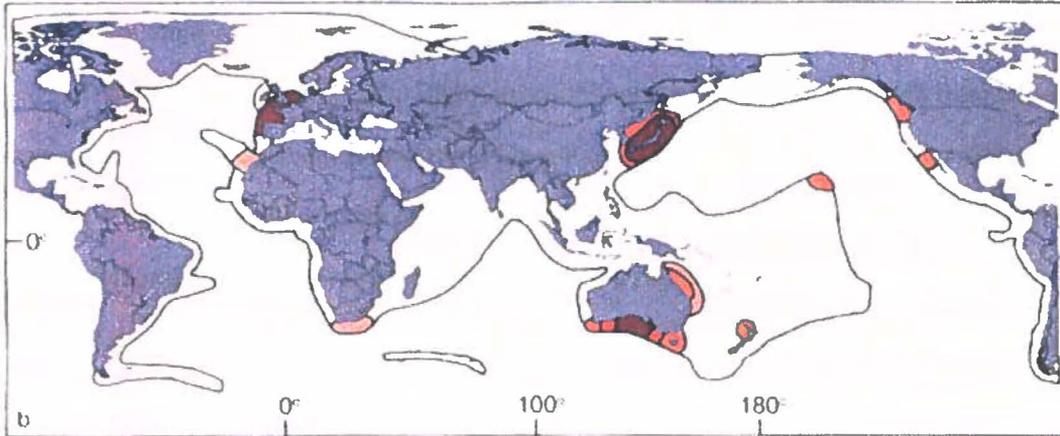
Localities with high endemism values for algae (Figure 16) were not necessarily concordant with areas of high generic or species richness for algae (Figures 10, 11). Several localities (India, the Japanese islands of Honshu and Hokkaido, the main Hawaiian islands, New Zealand, South Africa, and Southern Australia) had high diversity along all three metrics. The majority of locations showed no concordance, partially because many localities with a high proportion of range-restricted species were not particularly diverse in genera or species.

Kerswell's (2006) approach (Figure 17) uncovered some of the key areas of endemism found in this study using a range-restriction approach (Figure 16B). Kerswell's (2006) method inflates the occupied area of algae by creating a range area based on connecting all points of a taxa's range. Given the patchy nature of algae, this approach extends algal ranges over open water artificially.

Many, but not all, upwelling regions had a high proportion of range-restricted species (Figure 16B). The only localities where corals, fishes, and algae all have high endemism are Easter Island, the main Hawaiian Islands, the Mascarene Islands (especially Mauritius), the Sea of Cortez, Sri Lanka, South Africa, and Western Australia (Figure 16B). In the tropics,

A

No. endemic genera 0 2 4 8 12 13+

**B**

No. endemic Bryopsidales species 0 1 2 4 6 7+

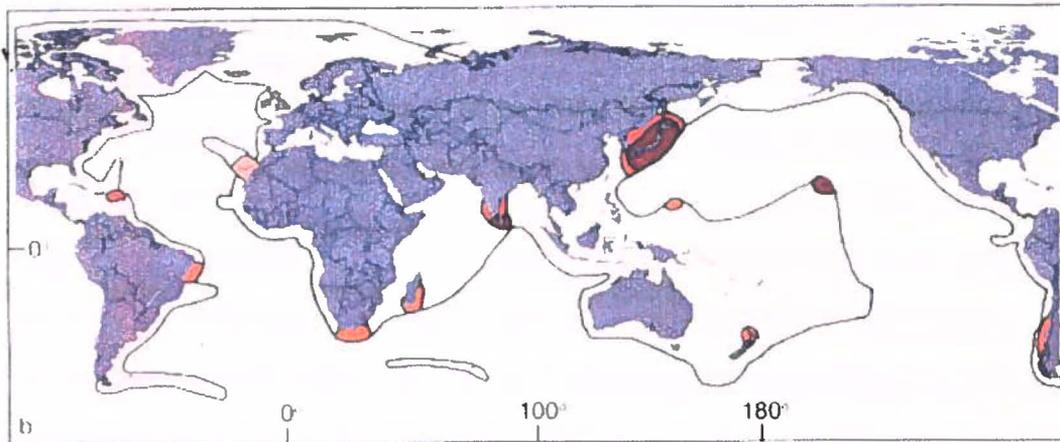


Figure 17. Global algal endemic richness (from Kerswell 2006). Graph (A) represents total numbers of endemic genera per area; Graph (B) represents total numbers of endemic species among the Bryopsidales (Ulvophyceae). Endemics, as defined by Kerswell, are taxa found in only a single location or with a geographic range size $< 1 \times 10^6 \text{ km}^2$ for genera and $< 0.5 \times 10^6 \text{ km}^2$ for species.

endemism was generally low (Figure 16B). Yet, the SGR of algae is highest in the tropics.

Diversity Hotspots

The prediction that equally high peaks in diversity would occur in both hemispheres proved true at both the species and genus levels (Figures 10, 11). As a result, determining hotspots of algal diversity is more difficult than the same task with corals and shore fishes.

Hotspots can be defined as localities with the highest numbers of species (Lomolino *et al.* 2006). If the top 10% most diverse regions are calculated in this manner and considered hotspots, then by rank, the hotspots for algae are the Japanese islands of Honshu and Hokkaido (1504 species), western Australia (999), southern Australia (983), Italy (862), the Queensland coast of Australia (857) not including the northern Australian component (*i.e.*, Cape York Peninsula), the Pacific coast of the USA (816), the Philippines (813), the Indian Ocean side of South Africa (795), the Greater Canary Islands (792), India (749), Britain (722), the Atlantic coast of South Africa (709), the Lesser Antilles (683), and the eastern coast of the Adriatic Sea (660). New Zealand (641) and the Greater Antilles (620), while not in the top 10% of localities, have sufficient diversity to be included as well.

Only four localities have species richness peaks both latitudinally and longitudinally: Honshu-Hokkaido, southern Australia, the Atlantic coast of South Africa, and the two adjacent localities of Italy and the eastern coast of the Adriatic Sea (Figure 11). These four localities of latitude and longitude intersections might be considered regional centers of algal diversity. Localities of highest algal diversity are usually widespread (though several adjacent localities have very high diversity; Figures 10, 11).

When individual algal classes are considered, hotspots vary for each algal group compared to hotspots for overall algal diversity. Only three localities globally are within the top 10% most diverse localities (SGR peaks) for all algae and for individual algal groups: the Philippines, India, and Honshu-Hokkaido (Table 2). These three localities are not always the top three most diverse localities for each algal systematic group, however (Table 2).

DISCUSSION

ALGAL BIODIVERSITY PATTERNS AND A COMPARISON TO PAST FINDINGS

This examination of algal richness patterns on a global scale verified some past results while revealing many new discoveries. The species-area curve relationship for algae (Figure 9) contrasts with most terrestrial systems, where a tight linear (log-log) relationship exists between area and numbers of species (Rosenzweig 1995). Algal biodiversity patterns differ depending upon which method is considered or which taxonomic group is examined.

According to analyses of the Algal Records Database, temperate waters have higher numbers of uniquely temperate genera than the tropics, but the majority of genera are found throughout all temperature regions. The distinct subtropical pattern (Figure 15, Table 3) suggests that this temperature region is not merely a buffer or transition zone between the tropics and temperate regions (Adey & Steneck 2001), but rather, behaves distinctly. In fact, the localities and regions of the highest diversity occur in the subtropics (Japan, the Mediterranean, South Africa). Finer-scale temperature and locality analyses may reveal distinct patterns compared to those seen here.

Relying on the intersection of latitude and longitude peaks to designate hotspots (as done for other marine groups; see Mora *et al.* 2003) is not the best method for algae because many localities with very high total numbers of species are excluded if similarly rich localities are not found within a given latitude or longitude bin (*e.g.*, the Philippines). This is because such measures rely on the summed values of multiple localities. Corals and fishes don't have these considerations because both have unimodal richness peaks latitudinally and longitudinally. It is unlikely that a single locality is a singular hotspot for the algae of all other localities, as with the Indo-West Pacific for corals and shore fishes (Figure 1).

Algae have patchy richness, such that some localities within a latitudinal band are very diverse, while others have a poor richness (Figure 11). While the general richness patterns of algal genera (Figure 10) and species (Figure 11) are similar on a global scale,

much local variability exists such that a locality that is rich for one taxon is not necessarily so at another taxonomic level (Figures 10, 11). The patchiness of algae can be explained by the small distribution ranges of algae compared to other marine groups (Figure 3; Kinlan & Gaines 2003). As such, a range extension approach for demarcating algal distribution boundaries (Kerswell 2006), where maximal range extents are plotted and algae are assumed to occur in all places between maxima, is inappropriate.

Generic richness is used sometimes as a proxy for species richness (Figures 1, 2A; Kerswell 2006). For organisms that show the same richness pattern across taxonomic levels (Figure 1), this approach avoids the taxonomic problem associated with solely examining species richness (*i.e.*, genera are more monophyletically robust to phylogenetic studies than species). In algae, when the diversity of genera is considered, three localities stand out as the most diverse: Honshu and Hokkaido (459 genera), southern Australia (424), and western Australia (395). Kerswell (2006) found also that Honshu-Hokkaido and southern Australia were the most diverse generically (Figure 2A). Even though the algal richness pattern differs from corals and reef fishes, a similar qualitative pattern exists across taxonomic levels (as seen in Figure 1 for the latter groups). This pattern is in contrast to certain groups of algae, such as the Bryopsidales (Figure 2B), which Kerswell (2006) found to have their highest diversity in the tropics. When all algal species are considered, however, a similar pattern to generic diversity occurs (Figure 11).

If the world is merely divided into three broad temperature zones, the temperate region has highest overall algal diversity at both the species and genus level. Algal diversity is highest at latitudinal midpoints (30°S and 40°N), but only when total taxa (richness) are considered. Generic diversity increases as latitude increases (up to the Arctic and Antarctic border regions, where diversity decreases). Since speciation to the generic level takes longer than speciation at the species or lower levels, more genera in temperate regions may be the result of greater evolutionary ages for temperate algae compared to tropical algae. Considering that temperate algae are more than twice as diverse than tropical algae (Figures

10, 11), and that relatively few genera have high species diversity in the tropics, most algal genera likely evolved in temperate regions.

Algal richness peaks are the result of less overlap in species composition within given latitudes and longitudes compounded as coastline increases per 5° bin. While it is desirable to have high resolution geographic information for all algal data so that biogeographic relationships can be fine-tuned, the use of quasi-political entities in this study does not negate the validity of the results. Overall algal richness peaks at 130°E like corals and shore fishes (Hughes *et al.* 2002; Mora *et al.* 2003), but much more variability occurs elsewhere and richness plots for algae are not unimodal (Figures 10, 11) as they are for corals and fishes (Mora *et al.* 2003). No locality is a single hotspot of algal richness, unlike corals and shore fishes, which have a single hotspot of richness in the Indo-West Pacific (IWP) triangle (Figure 1). Reef fish richness increases with increasing coral reef area (Ormond & Roberts 1997), with reef fish richness peaking where coral habitat peaks in the IWP (Ormond & Roberts 1997). Because algae have such small range sizes (Figure 3; Kinlan & Gaines 2003), similarly rich regions (*e.g.*, Honshu-Hokkaido, and southern and western Australia) have very different floras. These findings support the assertion that regions can be both hotspots and coldspots of diversity depending upon which metric is used (Price 2002), complicating previous biogeographic findings for algae.

While most algae are restricted to one or several localities, the vast majority of corals are widespread (Veron 1995; Veron & Stafford-Smith 2000). The high contribution of extremely range-restricted algae to overall diversity explains why most algae have very small ranges (Figure 13). This pattern is unique compared to those of corals and fishes. Depending on methodologies, endemics have been considered important or insignificant to coral diversity (*e.g.*, compare Hughes *et al.* 2002 and Mora *et al.* 2003).

Kerswell (2006) found that endemic algae made a minor contribution to the flora of localities (particularly at the genus level), although she defined endemic algae as taxa found only in one location or having a geographic range smaller than 0.5% of the largest

geographic range of genera or species (Figure 17). In a range-restricted approach, Western Australia and the eastern Pacific are shown to have much higher weighted endemism (Figure 16B) than Kerswell (2006) found (Figure 17). Also, while Kerswell noted moderately high endemism for the Canary Islands (at the species level for Bryopsidales) and Atlantic western Europe (Figure 17), endemics are proportionally less in these localities when the range extents of all species are considered (Figure 16B). Most of the localities highlighted as endemic rich for corals, fishes, marine snails, and lobsters (Roberts *et al.* 2002) do not have particularly high endemism values for marine algae, partly because the former groups have peaks in diversity within the tropics while algae do not.

The small ranges overall of algae (Figure 13) results in a high accumulation of range-restricted species, even if the majority are found in more than one location. More than one-fourth of all algal species analyzed were only found in a single locality and nearly 80% were found in the shortest 20% of range distributions. As a result, algae with medium-sized ranges may contribute most to overall global diversity. Isolation by distance has traditionally been proposed as the main factor influencing endemism in this way (MacArthur & Wilson 1967). Indeed, for algae, many isolated islands and archipelagoes (especially in the temperate southern hemisphere) have numerous endemics.

High endemism on isolated islands also supports general distance decay findings for a wide range of organisms (Soininen *et al.* 2007). Given the generally low dispersal capacity of algae (Kinlan & Gaines 2003), one might expect a high degree of patchiness between localities. This is exactly what occurs, with overall binned biodiversity patterns for 5° latitudinal or longitudinal bands not uniformly replicated among individual cells of localities within each band. Plotting ranges as the maximum contour around furthest range extents of algae (assuming algae occur at all localities between sites with positive occurrence data; *e.g.*, Kerswell 2006) is inappropriate for algae. This approach makes sense for corals where many taxa are widespread, but not so for algae, which have ranges up to two orders of magnitude smaller than corals and fishes (Figure 3; Kinlan & Gaines 2003). This approach

ignores the fact that benthic habitats take up a very small percentage of open ocean ranges, and therefore, a total coastline approach is more appropriate for benthic organisms with habitats separated by large regions of open water.

While some regions with high endemism values also had high overall species diversity, many regions with high overall diversity had low numbers of endemics and vice versa (compare Figures 10 and 15). This pattern has also been seen in reef fishes (Mora *et al.* 2003). Unlike with fishes however, the Indo-West Pacific did not have singularly high endemic diversity among marine algae. Localities with high algal endemism did not usually correspond with localities of high reef fish endemism (Hughes *et al.* 2002; Mora *et al.* 2003), even if only tropical localities were examined. Algae are consistent with the proposition that patterns of endemism are not generally concordant across marine taxa (Hughes *et al.* 2002). Some regions may be species rich and have a high proportion of range-restricted species (Roberts *et al.* 2002).

Surprisingly, the entire west coast of the Americas had high weighted endemism (Figure 16). Kerswell (2006; Figure 17) largely missed this region using a methodology for defining endemism similar to that used for corals (*i.e.*, Hughes *et al.* 2002). This region has low coral endemism because relict coral populations from the closure of the Isthmus of Panama died off and the eastern Pacific was reinvaded by wide-ranging western Pacific species (Veron 1995).

Jablonski *et al.* (2006) found that endemism decreased away from regions of high diversity (and in their view, origination). While Jablonski *et al.* (2006) evaluated coral reefs, where diversity is highest in tropical latitudes, algae have bimodal diversity peaks at temperate mid-latitudes. Tropical regions had a much lower proportion of range-restricted species than temperate regions (Figure 16B). However, localities of particularly high algal species richness were not necessarily localities with high endemism (despite broad geographic patterns remaining similar), so it is unclear how general Jablonski *et al.*'s (2006) findings are for algae.

THE SPECIES-TO-GENUS RATIO REVISITED IN CONSIDERATION OF JARVINEN

While the general biodiversity patterns of genus (Figure 10) and species richness (Figure 11) are both bimodal, the SGR is unimodal. Statistically different diversity patterns are seen with respect to endemism (Figure 16), or among each temperature region (Figures 13, 15), algal class (Figures 9, 13), and ocean basin (Figures 14, 15).

Despite differences in richness patterns between algae and other marine groups, the SGR diversity pattern for algae (Figure 12) mimics closely the latitudinal richness patterns of corals, shore fishes, snails, and lobsters (Roberts *et al.* 2002). While the metrics are different, it may be possible that an unknown mechanism responsible for increased richness of many marine groups in the tropics may also be affecting algal diversity. It is unlikely that a single set of mechanisms apply to all groups, because algae have temperate peaks in diversity compared to corals and fishes.

Differences in SGR do not appear to be merely the result of sampling effort or correlated with geographic area, as suggested by Jarvinen (1982). Jarvinen (1982) reviewed the use of SGR in biogeography and outlined strong evidence that patterns in the SGR are a statistical artifact. In Jarvinen's (1982) argument, SGR increased as species richness increased, which in turn increased directly with increasing area. Interestingly, the SGR diversity pattern for algae (Figure 12) is distinct from the species richness pattern (Figure 11) only latitudinally, but mimics closely the genus and species richness patterns longitudinally (Figures 10, 11). If SGR was a mathematical artifact, then the same transformation in diversity pattern would be seen latitudinally and longitudinally.

One might be tempted to note that surface area varies latitudinally, but not longitudinally, in an attempt to support Jarvinen's (1982) claim that SGR is an artifact of area. However, while SGR peaks in the tropics (Figure 12), where global area is greatest, effective area (the area where algae can grow) is limited to coastline length, which instead peaks in the northern hemisphere (Figure 4). However, Jarvinen's (1982) position that more species occur per genus (higher SGR) in larger areas compared to smaller areas does not hold true

uniformly for algae. Regions of high species richness are not uniformly regions of high SGR (Figures 10, 11, 12).

For example, even though the largest Japanese islands are outliers for total diversity, they are not singularly unique when the SGR is considered and are not the locality of highest SGR. The range of SGR values among all genera of a region might act as a metric for community complexity, but such claims cannot be made from the current Algal Records dataset because only occurrence data are used. Taxonomic distinctness might provide a viable measurement of community complexity and taxonomic similarity may provide a better index than TSI. Furthermore, once potential taxonomic problems with SGR are addressed, it may prove to be a metric similar to the Cheney ratio (Cheney 1977) if SGR thresholds for different temperature regimes can be established.

Interestingly, the SGR pattern (Figure 12) is similar in many regards to Kerswell's (2006) Bryopsidales species richness patterns (Figure 2B). Possibly, groups like the Bryopsidales, with tropical peaks in diversity, are raising the overall SGR of a region. Kerswell (2006) found that the Philippines had the highest Bryopsidalean diversity (Figure 2B), which is also the region with the highest overall SGR (Figure 12) and particularly diverse for *Sargassum* species. Further analyses of individual algal groups would help ascertain which algal groups are most diverse in the tropics and responsible for increasing SGR since their effects are too limited to affect the overall species-level richness patterns (Figure 11).

The SGR diversity pattern helps explain patterns seen in other algal data. For instance, the tropical peak in SGR can be explained after examining both the ranges of algae (Figure 13) and the endemism pattern of algae (Figure 16). Through such an evaluation, it becomes clear that only a few widespread and speciose genera in the tropics are responsible for peak SGR especially when considering that overall species and generic richness are low in the tropics (Figures 10, 11).

If SGR is a valid diversity metric (at least for algae), something is resulting in a difference in speciation rates between tropical and temperate habitats, as evidenced by

varying SGR slopes among temperature regions (Figure 9), with more species per genus occurring in the tropics but more genera overall occurring in temperate regions. The high SGR of algae in the tropics might be considered a comparatively more recent event than speciation in temperate regions, which has progressed from the evolution of separate species into multiple genera. It is hypothesized that the tropics have a higher overall SGR compared to other regions as a result of relatively few genera invading the tropics from cooler waters, where algae likely originated (noted by lower generic diversity in the tropics compared to other temperature regions of similar species richness; Figure 9), but speciating to a higher degree than the floras of cooler waters. Each taxonomic group has evolved differently (Figure 9), thus suggesting that different algal groups have different capacities for speciation in different temperature regimes. Broad examination of individual algal classes suggests contributions to SGR on a global scale.

Interestingly, when all three algal groups are compared, the SGR of the Ulvophyceae deviates from the Phaeophyceae and Rhodophyta pattern in the temperate region. The Phaeophyceae SGR pattern deviates from other algal classes in the tropics and the Rhodophyta SGR pattern is different from other algal groups in the subtropics (Figure 9). Richness of the tropics is relatively low, and the distribution range of the Ulvophyceae and Phaeophyceae is wider at both the genus and species levels compared to the Rhodophyta (Figure 13). The composition of the Ulvophyceae and Phaeophyceae is proportionally higher in the tropics and subtropics than the temperate region. The comparatively higher SGR for both groups compared to the Rhodophyta helps to explain why the tropics has the highest SGR of any other temperature region despite the lowest overall richness.

EVOLUTIONARY PROCESSES AND AN "INTO THE TROPICS" SPECIATION MODEL

In determining why algae, a clearly temperate group with highest richness in mid-latitudes (Figures 10, 11), show the highest species-to-genus ratio (SGR) in the tropics (Figure 12), speciation rates need to be considered. Diversity has been correlated with large

scale areas terrestrially (Begon *et al.* 1990). Begon *et al.* (1990) suggested that regions become “saturated” with species relatively recently, though Rohde (1992) emphasized that rates of speciation were tied closely to temperature. The different regression slopes between algal classes (Figure 9) suggest that different processes might govern speciation in each algal group and that these might reflect the separate evolutionary histories of the green, brown, and red algae.

The singularly high number of single-locality endemics in Honshu-Hokkaido reflects Santelices and Marquet's (1998) findings, where range size decreased in areas of high species richness. Santelices and Marquet (1998) found that the range sizes of algae decreased towards regions of highest diversity regardless of temperature. Algae have amphitropical richness peaks (Figures 10, 11). Santelices and Marquet's (1998) findings further corroborate the view that tropical algae are wide spread, thus explaining why few tropical localities have high algal endemism values (Figure 16). Few species are range-restricted in the tropics compared to temperate localities (Figure 16B). Tropical genera and species showed the highest similarity over long distances compared to other temperature regions, but while similarities were fairly constant among genera, a reduction in similarity occurred among species as distance increased. Tropical algae have the smallest mean species range, but the longest generic range of all temperature populations (Figure 13). If relatively few genera invaded the tropics from colder temperature regions and then speciated at a high rate, this would result in a comparatively constant but high similarity at the generic level. Because of the short dispersal capacity of algae (Kinlan & Gaines 2003; Figures 3, 12), however, species were not able to spread widely.

The SGR values for algae are highest in the tropics, while generic diversity is highest in the temperate zone. As a result, the proposition that number of species merely increases with generic age (Jokiel & Martinelli 1992) might not hold true for algae. In the Weir and Schluter (2007) model, the higher algal richness of temperate regions would not be the result of increased speciation, but rather from an accumulation of species and genera as a result of

lessened extinction pressure. Multiple parameters affect algal diversity (e.g., which algal systematic group and temperature regime is examined), and because different oceanic basins show different richness patterns (Figure 14) it is likely that different rates of speciation occur in different regions.

In contrast to the Jablonski *et al.* (2006) "Out of the Tropics" (OTT) model, an alternative might apply for algae, tentatively referred to as the "Into the Tropics" (ITT) model. In the ITT model, it is proposed that algae originated in temperate regions and not only invaded into the tropics, but taxa were retained in temperate regions because of lower extinction rates there (Weir & Schluter 2007). Molecular phylogenetic analyses to determine whether tropical algal taxa were derived from temperate taxa could be used to evaluate such a model. Additionally, the determination of extinction rates for algae based on extant taxa compared to fossilized taxa could also be used to evaluate the ITT model. Jablonski *et al.* (2006) found that taxa limited to the tropics had different extinction rates from both temperate and cosmopolitan taxa. The current range distributions of algae (Figure 13) can also be explained by an ITT model, as can the disparity of high tropical SGR as a result of relatively few speciose genera in the tropics.

FUTURE WORK

Future effort should be directed toward creating a geographically uniform dataset for algae so that grid cells can be used to calculate endemism values (Figure 16A) without the present limitations that necessitate locality-based measurements (Figure 16B). The SGR by itself is not a reliable predictor of overall taxonomic diversity, but can possibly suggest temperature or geographic affinities of individual floras, as Cheney attempted in the Atlantic Ocean (Cheney 1977) if further work showed that specific genera or algal classes had predictable SGRs in different oceanic basins or temperature regions. Ideally, the linking of sea-surface temperature values with finer-scale geographic diversity data could test this hypothesis. Additionally, performing Linder's (2001) weighted endemism approach with

corals and shore fishes at the same spatial resolution as algae will ultimately allow for direct comparisons of range restriction among all three groups.

Future work to analyze algal similarity data between localities is necessary before it can be determined if the high diversity in individual regions is the result of high overlap between adjacent regions (as suggested by Hughes *et al.* 2002) or because of unique environmental conditions. High diversity in Japan might have resulted from the persistence of relic populations that have been supplemented over recent geologic time through the creation of the Kurushio and Soya currents after the last glacial maximum, and which are known to transport warm water organisms from the south (Adey & Steneck 2001).

Finer-scale temperature analyses should be performed, with all grids of 5° x 5° assigned specific temperature profiles, especially because recent work has revealed that localized and seasonal upwelling patterns play important roles in diversity and distribution patterns along the Arabian seashores for algae (Schils 2006) and corals (Coles 2001). Integration of results with sea surface temperature (SST) data for uniform coastal blocks would help generalize to all algal taxa the thermogeographic boundaries defined recently by an analysis of widespread coralline algae (Adey & Steneck 2001). Preliminary work at generating accurate SST values for individual 5° x 5° grid cells has revealed that endemism (Figure 16) is correlated with upwelling regions (T. Schils, pers. comm. 2007).

The next step is to generate accurate coastline measurements per cell and then standardizing locality size, especially for large and speciose localities (e.g., India or Southern Australia). Once accurate coastline measurements for individual landforms are known, it will be a fairly straightforward task to analyze island occurrence data and to model connectivity networks throughout Oceania to provide rigorous tests of principles stated in island biogeography theory (MacArthur & Wilson 1967). Algal data for individual islands can be compared to coral and reef fish data and subjected to uniform transformations so that accurate comparisons of each taxonomic group can occur.

The creation of separate palaeoceanographic dispersal route networks for various geologic ages (as for Figure 7) would alter locality-pair distances as calculated by the Dijkstra's (Dijkstra 1959) shortest path algorithm, especially for presently isolated regions linked previously (e.g., the Mediterranean Sea and the Red Sea; the Caribbean Sea and the eastern Pacific Ocean). The current dispersal route network could be refined greatly as locality size decreased and as temperature and current data are integrated over various geologic ages.

Koleff *et al.* (2003) point out that "most if not all species distributions are spatially autocorrelated." Various biogeographic measurements have been developed to account for spatial autocorrelation, with the most common being Moran's I (a weighted product-moment correlation coefficient, with values reflecting geographic proximity; Moran 1950) and variations of this index (*i.e.*, Oden 1995). Moran's I and other spatial autocorrelation measures rely upon pair-wise distances between localities, thus allowing for the incorporation of connectivity networks in the marine realm for the same purposes as for similarity analyses. This study did not analyze spatial autocorrelation of similarity index values. Thus, it is possible that some results of this study appear more significant than they actually are.

The results of this study provide many building blocks for future work. Many of its methodologies are generally applicable for all marine environments, such that similar approaches to coral and reef fish data can be taken thus creating a uniform approach to studying coastal marine communities. To date, many studies have compared shore fish diversity with coral diversity, but few have added algal diversity to the equation. By comparing corals and algae uniformly in the same manner as the present study, new insights into coral reef dynamics are likely to be revealed.

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APPENDIX 1: FIGURE 9A SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S1.1. ANOVA tables for All Algae. Accompanies Figure 9A. TE = temperate; ST = subtropical; TR = tropical. Post-hoc Tukey tests performed after ANOVA. Where abbreviated, "Reg" = regression.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	0.050	0.025	15.672	< 0.0001
Error	152	0.240	0.002		
Total	154	0.290			

Post-hoc Tukey Test: {{TE x ST}, {ST x TR}, {TR x TE}}

Table S1.2. ANCOVA tables for All Algae. Accompanies Figure 9A. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	22.495	17.199	13.511	0.361	33
ST	37.377	31.401	27.184	0.804	36
TR	47.998	36.802	29.314	1.096	80
Pooled Reg				2.261	149
Common Reg	107.869	85.402	70.009	2.395	151
Total Reg	108.608	86.765	72.702	3.387	153
F regression	4.415				
One-Sided P-Value	0.014				

Table S1.3. ANCOVA tables for All Algae. Accompanies Figure 9A. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	3.081	69	~2.820
ST x TR	3.716	116	~2.800
TR x TE	0.106	113	~2.800

Table S1.4. ANCOVA tables for All Algae. Accompanies Figure 9A. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: < 0.0001

	Tukey test q	DF	Critical q [0.05]
TR x TE	10.891	113	~2.800

APPENDIX 2: FIGURE 9B SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S2.1. ANOVA tables for the Ulvophyceae. Accompanies Figure 9B. TE = temperate; ST = subtropical; TR = tropical. Post-hoc Tukey tests performed after ANOVA. Where abbreviated, "Reg" = regression.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	1.063×10^8	5.313×10^7	1.730	0.181
Error	152	4.667×10^9	3.071×10^7		
Total	154	4.774×10^9			

Post-hoc Tukey Test: { n/a }

Table S2.2. ANCOVA tables for the Ulvophyceae. Accompanies Figure 9B. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	53.361	40.319	32.016	1.551	33
ST	47.265	35.371	27.300	0.830	36
TR	50.273	35.958	27.119	1.400	80
Pooled Reg				3.780	149
Common Reg	150.899	111.648	86.434	3.827	151
Total Reg	159.163	116.544	89.503	4.167	153
F regression	0.927				
One-Sided P-Value	0.398				

Table S2.3. ANCOVA tables for the Ulvophyceae. Accompanies Figure 9B. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: 0.0016

	Tukey test q	DF	Critical q [0.05]
TE x ST	4.810	69	~2.820
ST x TR	1.101	116	~2.800
TR x TE	4.373	113	~2.800

APPENDIX 3: FIGURE 9C SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S3.1. ANOVA tables for the Phaeophyceae. Accompanies Figure 9C. TE = temperate; ST = subtropical; TR = tropical. Post-hoc Tukey tests performed after ANOVA. Where abbreviated, "Reg" = regression.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	3.938×10^8	1.969×10^8	1.579	0.209
Error	152	1.870×10^{10}	1.247×10^8		
Total	154	1.909×10^{10}			

Post-hoc Tukey Test: { n/a }

Table S3.2. ANCOVA tables for the Phaeophyceae. Accompanies Figure 9C. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	32.646	26.587	22.821	1.167	33
ST	29.594	26.976	27.112	2.522	35
TR	48.781	30.814	23.522	4.057	79
Pooled Reg				7.746	147
Common Reg	111.021	84.378	73.455	9.326	149
Total Reg	117.143	95.060	92.113	14.973	151
F regression	14.987				
One-Sided P-Value	< 0.0001				

Table S3.3. ANCOVA tables for the Phaeophyceae. Accompanies Figure 9C. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	2.323	69	~2.820
ST x TR	7.071	116	~2.800
TR x TE	5.292	113	~2.800

Table S3.4. ANCOVA tables for the Phaeophyceae. Accompanies Figure 9C. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: < 0.0001

	Tukey test q	DF	Critical q [0.05]
ST x TR	4.085	69	~2.800

APPENDIX 4: FIGURE 9D SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S4.1. ANOVA tables for the Rhodophyceae. Accompanies Figure 9D. TE = temperate; ST = subtropical; TR = tropical. Post-hoc Tukey tests performed after ANOVA. Where abbreviated, "Reg" = regression.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	0.015	0.007	3.413	0.035
Error	152	0.324	0.002		
Total	154	0.339			

Post-hoc Tukey Test: {TR x TE}

Table S4.2. ANCOVA tables for the Rhodophyceae. Accompanies Figure 9D. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	29.340	22.460	17.456	0.263	33
ST	35.420	29.502	25.465	0.892	36
TR	57.000	44.156	35.377	1.171	80
Pooled Reg				2.327	149
Common Reg	121.761	96.118	78.298	2.423	151
Total Reg	124.248	98.583	80.878	2.659	153
F regression	3.082				
One-Sided P-Value	0.049				

Table S4.3. ANCOVA tables for the Rhodophyceae. Accompanies Figure 9D. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	2.956	69	~2.820
ST x TR	2.887	116	~2.800
TR x TE	0.506	113	~2.800

Table S4.4. ANCOVA tables for the Rhodophyceae. Accompanies Figure 9D. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: 0.0009

	Tukey test q	DF	Critical q [0.05]
TR x TE	5.353	113	~2.800

APPENDIX 5: FIGURE 13 SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S5.1. ANOVA tables for Generic Range Extent of All algae. Accompanies Figure 13A. TE = temperate; ST = subtropical; TR = tropical. Post-hoc Tukey tests performed after ANOVA.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	4232.627	2116.313	5.416	0.0045
Error	2438	952699.3	390.771		
Total	2440	956931.92			

Post-hoc Tukey Test: {{TE x TR}}

Table S5.2. ANOVA tables for Species Range Extent of All algae. Accompanies Figure 13B. TE = temperate; ST = subtropical; TR = tropical. Post-hoc Tukey tests performed after ANOVA.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	2164.023	1082.011	11.706	< 0.0001
Error	12939	1195992	92.433		
Total	12941	1198156.023			

Post-hoc Tukey Test: {{TE x ST}, {TE x TR}}

Table S5.3. ANOVA tables for Generic Range Extent of Algal Groups. Accompanies Figure 13C. U = Ulvophyceae; P = Phaeophyceae; R = Rhodophyceae. Post-hoc Tukey tests performed after ANOVA.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	10910.28	5455.139	16.593	< 0.0001
Error	1134	372824.7	328.770		
Total	1136	383734.98			

Post-hoc Tukey Test: {{U x P}, {U x R}}

Table S5.4. ANOVA tables for Species Range Extent of Algal Groups. Accompanies Figure 13D. U = Ulvophyceae; P = Phaeophyceae; R = Rhodophyceae. Post-hoc Tukey tests performed after ANOVA.

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	2	6573.449	3286.725	52.492	< 0.0001
Error	8025	502480.4	62.614		
Total	8027	509053.84			

Post-hoc Tukey Test: {{U x P}, {U x R}, {P x R}}

APPENDIX 6: FIGURE 14A SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S6.1. ANCOVA tables of ocean basins for All Algae (Genera). Accompanies Figure 14A. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
Pacific Ocean	976.527	-74.438	48.763	43.089	1594
Atlantic Ocean	921.245	-119.136	46.808	31.401	1346
Indian Ocean	487.268	-39.378	21.093	17.911	664
Pooled Reg				92.401	3604
Common Reg	2385.04	-232.952	116.664	93.911	3606
Total Reg	2564.12	-245.908	254411	254387	3608
F regression	29.454				
One-Sided P-Value	<< 0.0001				

Table S6.2. ANCOVA tables of ocean basins for All Algae (Genera). Accompanies Figure 14A. P = Pacific; A = Atlantic; I = Indian. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
P x A	10.271	>300	~2.772
P x I	0.711	>300	~2.772
A x I	7.819	>300	~2.772

Table S6.3. ANCOVA tables of ocean basins for All Algae (Genera). Accompanies Figure 14A. P = Pacific; A = Atlantic; I = Indian. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
P x I	21.774	>300	~2.772

APPENDIX 7: FIGURE 14B SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S7.1. ANCOVA tables of ocean basins for All Algae (Species). Accompanies Figure 14B. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
Pacific Ocean	487.268	-35.868	11.359	8.719	664
Atlantic Ocean	976.527	-80.471	25.842	19.211	1594
Indian Ocean	921.245	-135.767	39.925	19.916	1346
Pooled Reg				47.846	3604
Common Reg	2385.04	-252.107	77.126	50.477	3606
Total Reg	2564.12	-266.514	266603	266576	3608
F regression	99.111				
One-Sided P-Value	<< 0.0001				

Table S7.2. ANCOVA tables of ocean basins for All Algae (Species). Accompanies Figure 14B. P = Pacific; A = Atlantic; I = Indian. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
P x A	17.340	>300	~2.772
P x I	2.016	>300	~2.772
A x I	15.602	>300	~2.772

Table S7.3. ANCOVA tables of ocean basins for All Algae (Species). Accompanies Figure 14B. P = Pacific; A = Atlantic; I = Indian. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
P x I	33.662	>300	~2.772

APPENDIX 8: FIGURE 15A SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S8.1. ANCOVA tables of ocean basins for All Algae (Genera). Accompanies Figure 15A. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	390.262	-11.065	9.423	9.109	349
ST	800.465	-76.868	25.314	17.933	701
TR	2871.17	-78.863	69.124	66.958	3319
Pooled Reg				94.000	4369
Common Reg	4061.9	-166.796	103.861	97.012	4371
Total Reg	4112.48	-186.944	347308	347299	4373
F regression	70.001				
One-Sided P-Value	<< 0.0001				

Table S8.2. ANCOVA tables of ocean basins for All Algae (Genera). Accompanies Figure 15A. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	9.660	>300	~2.772
ST x TR	16.694	>300	~2.772
TR x TE	0.161	>300	~2.772

Table S8.3. ANCOVA tables of ocean basins for All Algae (Genera). Accompanies Figure 15A. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
TR x TE	20.268	>300	~2.772

APPENDIX 9: FIGURE 15B SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S9.1. ANCOVA tables of ocean basins for All Algae (Species). Accompanies Figure 15B. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	Σx^2	Σxy	Σy^2	Res SS	Res DF
TE	390.262	-17.132	7.910	7.158	349
ST	800.465	-101.31	21.162	8.339	701
TR	2871.17	-145.017	39.449	32.124	3319
Pooled Reg				47.621	4369
Common Reg	4061.9	-263.458	68.52	51.432	4371
Total Reg	4112.48	-276.588	365635	365616	4373
F regression	174.801				
One-Sided P-Value	<< 0.0001				

Table S9.2. ANCOVA tables of ocean basins for All Algae (Species). Accompanies Figure 15B. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	15.587	>300	~2.772
ST x TR	26.823	>300	~2.772
TR x TE	1.674	>300	~2.772

Table S9.3. ANCOVA tables of ocean basins for All Algae (Species). Accompanies Figure 15B. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
TR x TE	13.703	>300	~2.772

APPENDIX 10: FIGURE 15C SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S10.1. ANCOVA tables of Atlantic Ocean for All Algae (Genera). Accompanies Figure 15C. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	115.234	-15.391	4.293	2.238	89
ST	228.925	-33.986	9.186	4.141	188
TR	131.876	-8.294	2.527	2.005	169
Pooled Reg				8.384	446
Common Reg	476.035	-57.671	16.007	9.020	448
Total Reg	485.885	-59.345	29023.7	29016.5	450
F regression	16.92				
One-Sided P-Value	<< 0.0001				

Table S10.2. ANCOVA tables of Atlantic Ocean for All Algae (Genera). Accompanies Figure 15C. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	1.215	>300	~2.772
ST x TR	8.436	>300	~2.772
TR x TE	6.112	>300	~2.772

Table S10.3. ANCOVA tables of Atlantic Ocean for All Algae (Genera). Accompanies Figure 15C. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
TE x ST	11.667	>300	~2.772

APPENDIX 11: FIGURE 15D SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S11.1. ANCOVA tables of Atlantic Ocean for All Algae (Species). Accompanies Figure 15D. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	115.234	-15.918	4.154	1.955	89
ST	228.925	-40.367	9.999	2.881	188
TR	131.876	-13.644	3.588	2.176	169
Pooled Reg				7.012	446
Common Reg	476.035	-69.929	17.741	7.468	448
Total Reg	485.885	-71.475	30334.8	30324.3	450
F regression	14.504				
One-Sided P-Value	<< 0.0001				

Table S11.2. ANCOVA tables of Atlantic Ocean for All Algae (Species). Accompanies Figure 15D. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6).

	Tukey test q	DF	Critical q [0.05]
TE x ST	3.579	>300	~2.772
ST x TR	3.039	>300	~2.772
TR x TE	7.921	>300	~2.772

APPENDIX 12: FIGURE 15E SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S12.1. ANCOVA tables of Indian Ocean for All Algae (Genera). Accompanies Figure 15E. ST = subtropical; TR = tropical. ANCOVA testing for difference among two regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
ST	12.079	-0.842	0.140	0.081	8
TR	253.744	-9.761	12.878	12.502	433
Pooled Reg				12.583	441
Common Reg	265.824	-10.603	13.017	12.594	442
Total Reg	270.182	-10.614	26200.5	26200.1	444
Student's T (b1-b2) / (S _{b1-b2})	0.628				
One-Sided P-Value	0.265				

Table S12.2. ANCOVA tables of Indian Ocean for All Algae (Genera). Accompanies Figure 15E. ST = subtropical; TR = tropical. Multiple comparisons among two elevations on parallel slopes using an ANCOVA-modified Student's T test analysis (after Zar 1999 Section 18.2).

One-Sided P-Value: 0.076

	Student's test T	DF	Critical T [0.05]
ST x TR	1.434	>300	~ 1.960

APPENDIX 13: FIGURE 15F SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S13.1. ANCOVA tables of Indian Ocean for All Algae (Species). Accompanies Figure 15F. ST = subtropical; TR = tropical. ANCOVA testing for difference among two regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
ST	12.079	-0.882	0.088	0.024	8
TR	253.744	-11.289	6.462	5.959	433
Pooled Reg				5.983	441
Common Reg	265.824	-12.170	6.550	5.992	442
Total Reg	270.182	-12.180	27636.5	27636	444
Student's T (b1-b2) / (S _{b1-b2})	0.831				
One-Sided P-Value	0.203				

Table S13.2. ANCOVA tables of Indian Ocean for All Algae (Species). Accompanies Figure 15F. ST = subtropical; TR = tropical. Multiple comparisons among two elevations on parallel slopes using an ANCOVA-modified Student's T test analysis (after Zar 1999 Section 18.2).

One-Sided P-Value: 0.008

	Student's test T	DF	Critical T [0.05]
ST x TR	2.423	>300	~ 1.960

APPENDIX 14: FIGURE 15G SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S14.1. ANCOVA tables of Pacific Ocean for All Algae (Genera). Accompanies Figure 15G. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	51.732	-2.512	1.175	1.053	53
ST	56.544	-2.906	2.583	2.434	76
TR	319.79	-17.463	9.042	8.088	526
Pooled Reg				11.575	655
Common Reg	428.066	-22.881	12.800	11.577	657
Total Reg	457.853	-33.141	44885.5	44883.1	659
F regression	0.054				
One-Sided P-Value	0.052				

Table S14.2. ANCOVA tables of Pacific Ocean for All Algae (Genera). Accompanies Figure 15G. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
TE x ST	1.611	>300	~2.772
ST x TR	16.385	>300	~2.772
TR x TE	17.448	>300	~2.772

APPENDIX 15: FIGURE 15H SUPPLEMENTARY STATISTICAL CALCULATIONS

Table S15.1. ANCOVA tables of Pacific Ocean for All Algae (Species). Accompanies Figure 15H. TE = temperate; ST = subtropical; TR = tropical. ANCOVA testing for difference among three regression functions after Zar (1999). Where abbreviated, "Reg" = regression.

	$\sum x^2$	$\sum xy$	$\sum y^2$	Res SS	Res DF
TE	51.732	-3.500	0.634	0.397	53
ST	56.544	-3.523	0.771	0.551	76
TR	319.79	-24.583	7.095	5.205	526
Pooled Reg				6.153	655
Common Reg	428.066	-31.605	8.500	6.166	657
Total Reg	457.853	-40.464	47407.2	47403.6	659
F regression	0.662				
One-Sided P-Value	0.484				

Table S15.2. ANCOVA tables of Pacific Ocean for All Algae (Species). Accompanies Figure 15H. TE = temperate; ST = subtropical; TR = tropical. Multiple comparisons among elevations on parallel slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7).

One-Sided P-Value: << 0.0001

	Tukey test q	DF	Critical q [0.05]
TE x ST	1.432	>300	~2.772
ST x TR	22.711	>300	~2.772
TR x TE	20.997	>300	~2.772