



Magnificent dimensions, varied forms, and brilliant colors: the molecular ecology and evolution of the Indian and Pacific oceans

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ABSTRACT.—The tropical Indian and Pacific oceans form the world's largest and most speciose marine biogeographic region: the Indo-Pacific. Due to its size and political complexity, the Indo-Pacific is rarely studied as a whole, yet comprehensive studies of the region promise to teach us much about marine ecology and evolution. Molecular methods can provide substantial initial insights into the processes that create and maintain biodiversity in the region while also providing critical spatial information to managers. This special issue presents six synthetic papers that discuss the current state of molecular work in the Indo-Pacific region as well as best practices for the future. Following these synthetic papers are 15 empirical papers that extend our knowledge of the region considerably. A comprehensive understanding of the biodiversity that we stand to lose in the Indo-Pacific is going to require increased cooperation and collaboration among laboratories that study this region, as exemplified by papers in this special issue.

Date Submitted: 19 December, 2013.
Date Accepted: 19 December, 2013.
Available Online: 7 January, 2014.

"It is excusable to grow enthusiastic over the infinite numbers of organic beings with which the sea of the tropics, so prodigal of life, teems..." — Charles Darwin, Cocos (Keeling) Islands, 1836

"...the clearness of the water afforded me one of the most astonishing and beautiful sights I have ever beheld. The bottom was absolutely hidden by a continuous series of corals, sponges, actiniae, and other marine productions, of magnificent dimensions, varied forms, and brilliant colours... It was a sight to gaze at for hours, and no description can do justice to its surpassing beauty and interest." — Alfred Russel Wallace, Pulau Ambon, Indonesia, 1859

Running from the east coast of Africa in the Indian Ocean all the way to Easter Island in the Pacific Ocean, the Indo-Pacific is, by many definitions, the largest biogeographic region in the world (Ekman 1953, Briggs 1974, Spalding et al. 2007). It is the primary heir to the evolutionary lineages of the Tethys Sea (Renema et al. 2008, Williams and Duda 2008, Cowman and Bellwood 2013) and is host to the world's highest levels of marine biodiversity, reaching an apex at its core in the "Coral Triangle" (Bellwood and Hughes 2001, Allen and Werner 2002, Carpenter and Springer 2005, Paulay and Meyer 2006, Hoeksema 2007, Veron et al. 2010). The intricate and vivid splendor of this biodiversity has drawn the attention of some of

the world's most distinguished naturalists and has inspired generations of marine biologists from around the globe.

Species ranges in the Indo-Pacific region can span tens of thousands of kilometers, and at evolutionary timescales these ranges are united into enormous genetic neighborhoods created by long-distance dispersal of propagules (Palumbi 1994, Lessios et al. 2001, Planes and Fauvelot 2002, Crandall et al. 2008a). Thus, although the fundamental evolutionary processes that govern biodiversity in the Indo-Pacific region (and the marine biome in general) are probably qualitatively similar to those that govern terrestrial biodiversity, the specific parameters of those processes are likely very different (Mayr 1953, Palumbi 1994, Paulay and Meyer 2002, Carr et al. 2003, Dawson and Hamner 2008, Grosberg et al. 2012, Bowen et al. 2013). Given the vast size of the Indo-Pacific and the logistical difficulty of making direct observations of marine species distributions and behavior, molecular methods offer us important initial insights into these processes (Palumbi 1997, Benzie 1999, Hellberg 2009). For example, what is the dominant mode of speciation in the sea? There are few obvious barriers that could limit gene flow via larval dispersal to the levels required for allopatric speciation, but the number of known species is growing as more and more cryptic lineages are sequenced (Knowlton 2000, Barber and Boyce 2000, Huelsken et al. 2013; for examples in this issue see DeBoer et al. 2014a, Szabo et al. 2014, Yasuda et al. 2014). However, trans-oceanic gene flow at evolutionary timescales can create long-term effective population sizes that reach well into the millions (Crandall et al. 2008a, 2008b). These large effective population sizes can in turn increase the influence of natural selection relative to genetic drift, which may increase the potential for ecological speciation relative to what has been estimated for terrestrial systems (Bird et al. 2012, Bowen et al. 2013). Is ecological speciation more common in the sea, and does it help to explain the “bulls-eye” gradient of biodiversity in the Indo-Pacific region? This is one of many tantalizing questions that can be answered through comprehensive study of this region using molecular methods.

Unfortunately, regions of high biodiversity in the Indo-Pacific tend to coincide with high levels of human impact on the marine environment (Roberts et al. 2002, Nañola et al. 2011). Molecular tools are a principal method by which marine population structure and connectivity can be examined (Palumbi 2003, Hedgecock et al. 2007, Selkoe et al. 2008, Riginos and Liggins 2013). As these and other methods reveal shortened mean larval dispersal distances and the importance of intermediate habitat (Kinlan and Gaines 2003, Pinsky et al. 2010, Saenz-Agudelo et al. 2011, Crandall et al. 2012, Almany et al. 2013), they are bringing us closer to the possibility of systematic conservation planning and true science-based spatial management in the Indo-Pacific region (Margules and Pressey 2000, Fernandes et al. 2005, Levin and Lubchenco 2008, Gaines et al. 2010, Toonen et al. 2011, Carpenter et al. 2011; see von der Heyden et al. 2014, Beger et al. 2014 in this issue).

INTRODUCTION TO THE SPECIAL ISSUE

Given its preeminent size and biological richness it would seem obvious that the Indo-Pacific region should be the focus of international scientific efforts to study both the origins and maintenance of marine biodiversity and how it can be protected. However, the same geographical size and biological scope that make the region so fascinating also create significant challenges to studying it in a comprehensive

manner. First, much of the tremendous species diversity is undescribed and much of it is cryptic (Barber and Boyce 2006). Second, below the species level, large effective population sizes lead to high levels of genetic diversity, which depress the maximum value of various estimators of F_{ST} (Hedrick 2005, Bird et al. 2011). These characteristics make delineating population structure quite difficult, let alone inferring evolutionary history or local adaptation, when using traditional population genetic methods (Waples 1998, Hellberg 2009). Finally, from a practical point of view there are numerous technical, logistical, and political challenges created by the sheer size of the region and the fact that it encompasses islands and coastlines of over 50 nations (see Barber et al. 2014, Bowen et al. 2014, Keyse et al. 2014 in this issue for detailed discussion of these issues).

In March 2012, the National Evolutionary Synthesis Center (NESCent) hosted 35 scientists from 10 countries including both university academics and conservation practitioners unified by their appreciation of the Indian and Pacific oceans. We identified many structural impediments to comprehensive studies of this region and the application of science to management in the region. This special issue of the *Bulletin of Marine Science* includes six papers, presented as synthetic perspectives and reviews. These papers were conceived at the NESCent meeting to address the issues discussed above. In addition, an abundance of new empirical work from the research groups and colleagues of many participants is described (15 empirical papers), providing one of the most extensive collections of phylogeographic studies on the Indo-Pacific region in a single journal issue to date.

The state and prospects of phylogeography, population genetics, and population genomics for the Indo-Pacific region are addressed in three synthetic papers. First, Bowen et al. (2014) re-affirm the strength of comparative approaches, wherein genetic data from multiple species are used to make inferences about spatial and biological phenomena. Although there is much enthusiasm today for population genomics, an overemphasis on single species genomic studies hinders advances that rely on the comparisons among species. While the need and desire for genomic breadth is well understood (Felsenstein 2006), ecosystem-based science and management require taxonomic breadth as well, especially in the hyper-diverse Indo-Pacific region. Bowen et al. (2014) discuss how a sequential sampling scheme could be most productive: use comparative surveys of multiple species based on mtDNA or a few nuclear loci to identify questions, locations and species of interest and then follow up with targeted population genomics of those interesting places and species.

A comparative approach requires coordinated sampling of taxa across their ranges. In the second paper, Keyse et al. (2014) analyze published genetic surveys from 116 species that have been conducted to date in the Indo-Pacific region, looking for opportunities to combine results across studies and for short-falls that would benefit from new empirical investigations. Analysis of co-sampled locations reveals a very real challenge for regional geographic surveys: multiple studies focus on relatively similar regions, but do not integrate across species ranges. For example, studies within the Coral Triangle tend not to include other regions, and conversely geographically extensive studies tend not to include locations within the Coral Triangle. Both Keyse et al. (2014) and Bowen et al. (2014) stress the importance of research coordination and collaboration among laboratories to the advancement of Indo-Pacific marine science.

Willette et al. (2014a) complete this first trio of syntheses by looking forward to the application of massively parallel sequencing technologies to science and resource management in the Indo-Pacific region. They identify two major categories of questions that benefit from greater sequencing breadth across both individuals and genomes: population genomics and studies of local adaptation. While there are a few groundbreaking examples of Indo-Pacific projects utilizing “second generation” methods (Barshis et al. 2013, Toonen et al. 2013), these technologies lie in the future for most molecular practitioners working in the Indo-Pacific region. Willette et al. (2014a) accordingly provide advice for those who would like to add massively parallel sequencing to their toolkit, including textboxes outlining the basics for six specific methodologies ranging from RAD-seq to metagenomics. Finally, they align themselves with Bowen et al. (2014) by stressing that the scientific question should guide the use of sequencing technology, rather than vice versa.

A second trio of papers in this special issue takes tangible steps toward improving communication among science and conservation professionals in the region. Not surprisingly, most well-studied and well-managed biogeographic regions can be found in proximity to developed nations (Beheregaray 2008, Fisher et al. 2010, McCreless et al. 2013). Despite general goodwill among scientists and conservation planners in the Indo-Pacific region, our meeting revealed polarities in vision between empirical geneticists and conservation planners, as well as between scientists from developed and developing countries. The difficulty in cross-communicating ideas, results, and outcomes was a major topic of discussion and subsequent thought.

Although numerous nations throughout the Indo-Pacific region have recently made political commitments to set aside marine reserves for the health of regional fisheries, recommendations from genetic inferences are just starting to be developed for this region. In the first of the conservation and management focused reviews and perspectives, von der Heyden et al. (2014) outline case-studies in which existing genetic data could contribute (or already are contributing) to conservation and fisheries management decisions in the Indo-Pacific region. Identification of species, including cryptic species, hybrids, invasives, and forensic identification of fisheries products and the usage of genetics for spatial planning and restoration are major topics of emphasis, followed by specific examples of management decisions in the Indo-Pacific region that were informed by genetic information.

Beger et al. (2014) then address the theory and practicality of using population genetic data in a formal spatial conservation prioritization framework. By way of translation among fields they develop a set of decision rules for managers and conservation biologists based on measurable genetic attributes. The various possible approaches are illustrated with an empirical data set from the giant clams, *Tridacna crocea* Lamarck, 1819 (with these data described in detail by DeBoer et al. 2014b, also in this issue). The cross-consideration of genetic information and habitat type yielded substantially different conservation priorities than when habitat data were considered alone, illustrating the additional information that genetic data could contribute to conservation planning.

Although much of the molecular research discussed in the special issue has been carried out in laboratories in developed countries, the long-term future of ecological and evolutionary biology in the Indo-Pacific region as well as marine conservation will depend on leadership from scientists and laboratories throughout the region. Barber et al. (2014) examine the current political and logistical challenges

to biodiversity research in Southeast Asia, including misapplication of laws derived from the Convention on Biological Diversity and the practice of “parachute science” whereby scientists from developed countries conduct field research in developing countries without meaningful engagement with local scientists. They call on Indo-Pacific nations to cultivate local biodiversity research and to take care to distinguish in their permitting between biodiversity researchers who happen to use genetic tools and bioprospectors who seek direct profit from genetic data through development of biopharmaceuticals. Equally they call on universities and funding agencies in developed nations to encourage collaborative research in developing countries. Finally, they highlight a number of case studies where governments and researchers from developing and developed nations have taken the first tentative steps toward fully collaborative science.

NEW EMPIRICAL GENETIC STUDIES FROM THE INDO-PACIFIC REGION

Also included in this special issue are 15 new empirical studies covering a magnificent set of geographic dimensions. The sampling locations span 242 degrees of longitude and 57 degrees of latitude and include points as far west as the Red Sea (Giles et al. 2014), east to Panama (Bernardi et al. 2014), north to Japan's Satsunan Islands (Yasuda et al. 2014), and south to the Kermadec Islands (Liggins et al. 2014). Several studies make important contributions in consolidating genetic information from the Coral Triangle or Hawaii with other Indo-Pacific locations (Coral Triangle: Crandall et al. 2014, Giles et al. 2014; Hawaii: Szabo et al. 2014).

The taxonomic forms in the issue are quite varied. These include corals (Concepcion et al. 2014, Marti-Puig et al. 2014, Yasuda et al. 2014), giant clams (DeBoer et al. 2014a,b), lobsters (Iacchei et al. 2014), and a number of echinoderms (Crandall et al. 2014, Liggins et al. 2014, Skillings et al. 2014). Vertebrates are represented by sharks (Giles et al. 2014), and a wide spectrum of bony fishes including sardinella (Willette et al. 2014b), tuna and mackerel (Jackson et al. 2014), and a veritable school of reef fishes (Bernardi et al. 2014, Raynal et al. 2014, Szabo et al. 2014). Underscoring the importance of genetics for revealing cryptic species (see von der Heyden et al. 2014) a number of distinct cryptic lineages are described here from corals (Yasuda et al. 2014), giant clams (DeBoer et al. 2014a), and goatfish (Szabó et al. 2014), as well promising approaches for using corallite morphology to identify genetic lineages in corals (Marti-Puig et al. 2014).

Several papers undertake a comparative approach as advocated by Bowen et al. (2014), identifying concordant genetic structure across multiple species (Bernardi et al. 2014, DeBoer et al. 2014a, Iacchei et al. 2014, Jackson et al. 2014, Liggins et al. 2014, Skillings et al. 2014) or across different classes of genetic markers (Concepcion 2014, DeBoer et al. 2014b). Two studies are notable for finding surprisingly high levels of genetic structure in putatively high dispersal taxa: a coral with long-lived larvae (Concepcion et al. 2014) and five species of pelagic fishes (Jackson et al. 2014). Together, these studies represent a substantive contribution to our understanding of ecology and evolution in the Indo-Pacific region.

LOOKING TO THE FUTURE

The brilliant colors and prodigious bounty of the tropical Indo-Pacific region are still remarkable even 150 yrs after the Industrial Revolution. Then, they were notable to two naturalists who lacked even a mask and snorkel to see below the surface. Now, they continue to awe snorkelers and scuba divers, some of whom choose to become marine biologists based on what they have seen. The fact that the colors are fading and giving way to coral bleaching, overfishing, and algal blooms among other forms of anthropogenic degradation is detailed extensively here and elsewhere (Hughes et al. 2003, Carpenter et al. 2008, Iacchei et al. 2014, von der Heyden et al. 2014). Rigorous and comprehensive science to underpin conservation and management in the Indo-Pacific region is going to require open-minded international collaboration among researchers. Where scientists lead, international collaborative conservation efforts will surely follow.

ACKNOWLEDGMENTS

This material is based upon work supported by the National Science Foundation through the National Evolutionary Synthesis Center (NESCent) under grant number NSF #EF-0905606. We thank all the participants of the 2012 Catalysis meeting and the staff at NESCent for their ongoing support. We also thank S Sponaugle, JE Serafy, G Shideler, and RJ Araújo at the *Bulletin of Marine Science* in all their assistance and guidance in putting together this special issue and PH Barber for helpful editorial comments on this manuscript.

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