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review

The application of genetics to marine management and conservation: examples from the Indo-Pacific

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ABSTRACT.—Molecular tools and analyses have played pivotal roles in uncovering the processes and patterns of biodiversity in the Indian and Pacific oceans. However, integrating genetic results into management and conservation objectives has been challenging, with few examples that show practical applicability. This review aims to address some of the perceived barriers to an enhanced approach that integrates molecular data into management and conservation goals, by reviewing papers relevant to both conservation and fisheries management in the Indo-Pacific region, particularly with respect to phylogeography, connectivity, and species identification, as well as stock delineation, restoration of depleted wild stocks, mislabeled marine resources and "molecular forensics." We also highlight case studies from each of these areas that illustrate how molecular analyses are relevant to conservation and management in the Indo-Pacific, spanning a variety of vertebrate and invertebrate species. We discuss the application of genetic data to the design and evaluation of the effectiveness of marine protected area networks, stock delineation, and restoration and the usage of exclusion tests and parentage analyses for fisheries management. We conclude that there is a distinct need for increasing public awareness and ownership of genetically unique lineages and, ultimately, the increased inclusion of genetic research into management policy and conservation. Finally, we make a case for the importance of clear and effective communication for promoting public awareness, public ownership, and for achieving conservation goals within the region.

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The Indo-Pacific, which encompasses large areas of the tropical Indian and Pacific oceans, houses an incredible array of marine biodiversity, with almost 4000 described species of fishes (Allen 2007), >700 tropical reef corals (Connolly et al. 2003), an undescribed diversity of invertebrates (Bouchet et al. 2002, Appletans et al. 2012), and is thus celebrated as a prominent marine biodiversity hotspot. Covering a large geographical area, it encompasses both developed and developing countries, which face vastly different pressures from global and climate change. Many of these pressures, including increasing sea-surface temperatures, ocean acidification, pollution, legal and illegal overfishing, and destructive fishing methods, have negative impacts on biodiversity. Thus, there is a clear need for improved conservation efforts in the region, which also allow sustainable exploitation and development of all Indo-Pacific nations.

Genetic approaches are one tool that can help inform the conservation and management objectives unique to marine systems. The past 20 yrs have seen a significant increase in the use of molecular tools addressing marine species evolution, biodiversity, and distributions. There is a wide array of studies, which at the broader scale include phylogeography (including comparative phylogeography), connectivity and migration, speciation and diversification, to more fine-scale studies that examine parentage analyses, population dynamics and demographic change, barcoding initiatives, and invasive species. Despite significant numbers of papers published, many state only the necessity of using genetic data for management and conservation; largely such data are not applied to real-life situations. This is primarily because of a lack of theoretical and practical frameworks to guide the use of genetic data (Beger et al. 2014). Other discrepancies arise from the differing approach and terminology in the disparate fields of conservation genetics, spatial conservation science, and fisheries management. Further, the multitude of genetic approaches, their interpretation, and follow-on research are often difficult for non-specialists to grasp; this challenge is addressed by Bowen et al. (2014).

Genetic research in the Indo-Pacific has been carried out on a diverse array of invertebrate and vertebrate species and has spanned the limits of the oceans, from southern Africa and the east African coast to the west coast of the United States and Australia. A brief web-based literature search carried out in Web of Science using the following search terms (Indo-Pacific and gene*, Indo-Pacific and fish* man*, Indo-Pacific and marine conservation, Indo-Pacific and pop* gen*) between January 2009 and April 2012 suggests that the most common research threads are phylogeography and population genetics, followed by phylogenetics and taxonomy and the development of new molecular markers (data not shown; see also Keyse et al. 2014). There is wide taxonomic coverage, with corals and fishes being especially well represented. Some invertebrate taxa including crustaceans and echinoderms (particularly those of commercial interest) have been reasonably well studied, but in the context of conservation and management, many smaller invertebrate taxa such as molluscs, polychaete, and annelid worms and sponges are dramatically under represented.

This review aims to address some of the perceived barriers to an enhanced approach that integrates molecular data into management and conservation goals, by reviewing papers and highlighting case studies that apply a genetic approach to address issues around: (1) species identification and (2) spatial management within the Indo-Pacific region (Fig. 1). Specific case studies are selected to illustrate the

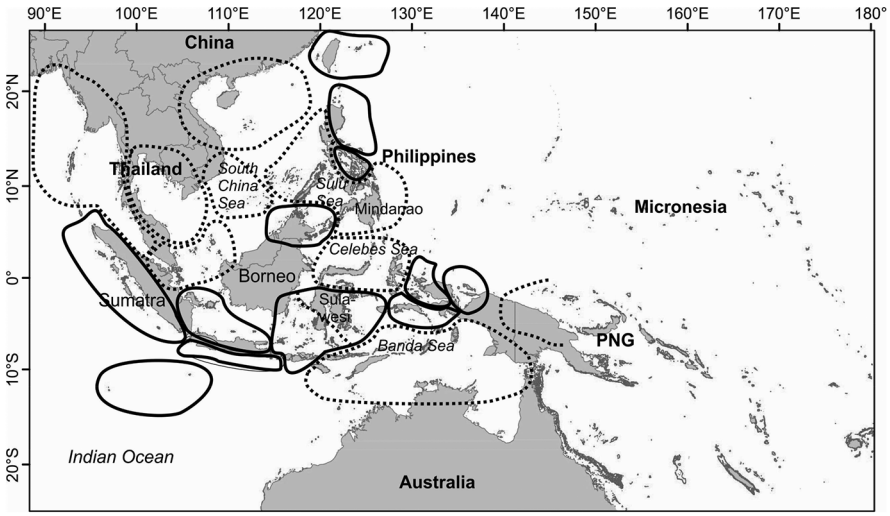


Figure 1. Example of management units derived from overlaying genetic breaks occurring in three or more species (bold line). Management units in dashed lines are formed by breaks in fewer than two species, or where sampling was either incomplete, or lacking, or not covered by the literature reviewed here. Studies which formed part of this map are listed in Online Table 1.

application of genetic tools across a variety of conservation and management issues within each of these broad themes. Future applications of molecular tools in the region are then briefly discussed.

Species Identification

Identifying Cryptic Species and Hybridization Events to Better Characterize Biodiversity of the Indo-Pacific.—Species are cryptic when two or more reproductively isolated species are classified as one recognized species, because, most commonly, phenotypic characters that distinguish them are either absent or share a large degree of overlap. Accurate species inventories that are skewed by undescribed cryptic species are important for several reasons including precise biodiversity inventories, which are crucial for understanding ecological functions. Cryptic species also may play a large role in the management of exploited species. For example, the giant clam *Tridacna squamosina* (= *T. costata* in Richter et al. 2008, see Online Appendices for species authorities) was shown to be genetically, ecologically, and morphologically distinct from *Tridacna maxima,* and *T. squamosa,* and at the same time to have been exploited for at least 125,000 yrs, with substantial overfishing reducing *T. squamosina* to <1% of stocks of giant clam in the Red Sea (Richter et al. 2008).

Tropical marine systems, such as those found in the Indo-Pacific, have been highlighted as potentially rich in cryptic species given that they are among the most species-rich habitats and as such should harbor greater numbers of cryptic and/or sibling species (Bickford et al. 2007). For example, von der Heyden (2011) suggests that most cryptic fish species in southern Africa would belong to the western Indian Ocean fish fauna rather than the cool-temperate Atlantic.

Molecular tools have been at the forefront of identifying cryptic species. Interestingly, rather than suspecting that a single species may actually be composed

of multiple species and then testing this hypothesis, most cryptic species discoveries are probably accidental. Barcoding initiatives and phylogeographic surveys especially seem to discover unknown biodiversity (Barber and Boyce 2006, Concepcion et al. 2008, Zemlak et al. 2010, DiBattista et al. 2011, Hubert et al. 2012), and such studies can afford an excellent view into the processes driving speciation in marine systems (von der Heyden et al. 2011).

In the understudied Indo-Pacific, numerous cryptic species have been described including fishes (Colborn et al. 2001, Messmer et al. 2005, Hubert et al. 2012), sponges (Muricy 2011), several groups of crustaceans (Barber and Boyce 2006, Poore and Andreakis 2011), molluscs (Bouchet et al. 2002, Pola et al. 2012), echinoderms (Landry et al. 2003, Hart et al. 2006, Uthicke et al. 2010), and jellyfishes (Dawson and Martin 2001, Holland et al. 2004). Uncovering cryptic species, either as sibling species or as species flocks, allows rare insights into the processes driving speciation in marine environments, especially where species co-occur without evidence of strong vicariant barriers (von der Heyden et al. 2011, Bowen et al. 2013). Such studies can have direct management consequences, such as the pending petition to list rare species of corals under the US Endangered Species Act, where the species status of many of those corals is in dispute (e.g., Forsman et al. 2010). Some of the strongest evidence for both cryptic species comes from coral reef fishes (Rocha and Bowen 2008), which display morphological variation that can be used as a baseline for genetic investigations. For example, in the genus *Centropyge*, mtDNA revealed deep geographic separation that is incongruent with species delineation, whereas nuclear analyses suggest ongoing gene flow between species (DiBattista et al. 2012). It is often difficult to pinpoint the processes involved in speciation and the maintenance of species boundaries, but assortative mating and other selective forces have been suggested (Palumbi 1994, Hellberg 1998, McMillan et al. 1999).

Hybridization is another complex process that skews our understanding of traditional species, although it may be somewhat easier to detect when parental species are morphologically distinct. Most hybrids in contact zones studied to date show at least some morphological intermediacy with both parent species, although this is not always apparent (Pyle and Randall 1994, McMillan et al. 1999, van Herwerden et al. 2006, van der Meer et al. 2012, von der Heyden and Connell 2012). Hybrids have been recorded in fishes, echinoderms, molluscs, and corals of the region (Lessios and Pearse 1996, van Herwerden et al. 2006, Yaakub et al. 2006, Richards et al. 2008, Hobbs et al. 2009, Montanari et al. 2012, Ladner and Palumbi 2012, van der Meer et al. 2012, Zigler et al. 2012).

Hybridization appears to be common between species that underwent historical allopatry, i.e., for example during sea-level changes that created vicariant barriers, followed by subsequent contact of closely related sister lineages. Hybridization studies can contribute toward our understanding of historical processes involved in speciation events; however, they can also confound population genetic analyses (and therefore potentially also fisheries or management assessments) if hybrids prove problematic to separate (e.g., Addison and Hart 2005). For example coral trout, *Plectropomus leopardus,* is the primary commercial fishery on the Great Barrier Reef, where it has hybridized historically with a closely related congener, *Plectropomus maculatus*, and mtDNA does not differentiate them, although

mtDNA distinguishes them elsewhere in their range (van Herwerden et al. 2006, also see Morgan et al. 2012).

There are several regions within the Indo-Pacific that have been highlighted for potential interest in promoting hybridization in marine species. For example, the eastern Indian Ocean at the Christmas and Cocos islands has been suggested as a marine hybrid hotspot in fishes (Hobbs et al. 2009). The Indo-Pacific barrier also influenced the divergence of marine species during glacial cycles, with subsequent overlap of sister lineages or species (Gaither et al. 2011). Other examples of processes driving hybridization between species include those where hybridization appears to be driven by unequal parent ratios, i.e., if one parent species is rare, mating with conspecific hybrids increases (Marie et al. 2007, Hobbs et al. 2009, Burford et al. 2011, Montanari et al. 2012, von der Heyden and Connell 2012). Human or ecological disturbance may also increase the rate of hybridization in fishes (van Herwerden et al. 2002, Mullen et al. 2012), although whether this also holds for invertebrate species in the Indo-Pacific region remains a large research gap (but see Uthicke et al. 2005). Further, whether rates of hybridization in marine species will increase with global change scenarios remains to be tested, but this has been suggested for at least one pair of hybridizing shark species (Morgan et al. 2012).

Detection of Invasive Species and Reconstruction of Invasion Histories.—Invasive species have played a large role in changing global marine systems, in some cases drastically altering the biological communities of invaded areas (Blum et al. 2007, Robinson et al. 2007, Banks et al. 2010), and are recognized as a pressing global concern (Sutherland et al. 2010). The Indo-Pacific is no exception, with a number of non-indigenous species (NIS) recorded throughout the region. Monitoring of invasive species is critical for understanding the biological and economic consequences of invasions, although the extent of invasive species is unknown in many developing countries that do not necessarily have the resources and capacity to track marine invasions. Molecular tools are able to provide an additional dimension in our understanding of the dynamics of marine species invasions, such as resolving the genetic relationships of invasive species with native species, monitoring potential hybridization of invasive and native species, and unraveling the geographic provenance of native populations. For example, for seaweeds in southern Africa (Bolton et al. 2011), fishes (Gaither et al. 2013), and jellyfishes in the Hawaiian Islands (Holland et al. 2004), species initially thought to be native have been exposed as being invasive, as morphological characteristics alone were not able to distinguish clearly between native and NIS.

Phylogeography has been successfully used to determine the likely founder populations or to track range expansions of marine NIS in the Indo-Pacific region. For the highly invasive green crab, *Carcinus maenas*, it was shown that South Africa experienced multiple invasions from the North Atlantic, with at least some individuals originating from northern Europe (Darling et al. 2008). For the invasive barnacle, *Balanus glandula*, which has outcompeted southern African *Chthamalus dentatus*, the invasive population could be traced back to the coast of Oregon (Simon-Blecher et al. 2008). To the contrary, four invasive species of ascidians appear to have experienced decades of anthropogenically mediated transport so that no genetic signal of potential native populations can be distinguished (Rius et al. 2013). Alternative examples also exist where invasive

species thought to be alien were shown to be native rather than introduced. A good example is the snowflake coral, *Carijoa*, which was thought to be introduced into the Hawaiian archipelago from the Caribbean, yet molecular analyses revealed that *Carioja* was native to the Indo-Pacific, rather than introduced from the Caribbean-Atlantic (Concepcion et al. 2010). This clearly highlights the need for not only genetic monitoring of invasive species, but that molecular systematics remain highly important in evaluating the status of invasive and NIS.

Molecular tools become invaluable when examining species without diagnostic morphological features. For example, endosymbiotic *Symbiodinium* dinoflagellates could potentially be dispersed to and associate with new coral hosts via natural and anthropogenic means. Stat and Gates (2008) detected an unusual *Symbiodinium* lineage A1 in *Acropora cythera* from the Northwestern Hawaiian Islands and suggested that this may have been transported into Hawaii by an NIS jellyfish vector. Even larger animals such as seahorses have proven confusing; *Hippocampus kuda* in Hawaii is thought to be an introduced species through the aquarium trade. However, molecular, as well as careful morphological analyses show that seahorses in Hawaii are genetically and morphologically distinct from *H. kuda* (Szabó et al. 2011) and that they are not introduced. Both studies highlighted above support the need for large-scale geographic sampling for putative NIS to prevent "false positives" and a potential misuse of funds for monitoring so-called NIS, which turn out to be indigenous. Such extensive sampling will of course be more demanding for smaller-sized species or those with extensive global distributions and is emphasized in a paper by Bolton and Graham (2006), which highlights the dangers of trade in live aquatic species that may disperse invasive species such as jellyfishes (that may be morphologically indistinguishable) into new environments.

Market-based Surveys, Mislabeling of Marine Resources, and Molecular Forensics.—Globally, fisheries resources are under pressure, with the majority of fish stocks fully exploited, overexploited, or depleted (Anticamara et al. 2011), including some of those in the Indo-Pacific (Pauly et al. 1998). Seafood fraud, whether through the intentional mislabeling of species or accidentally misidentifying or misnaming catches, is under-reported globally, with most examples from North America (Marko et al. 2004, Wong and Hanner 2008, Hanner et al. 2011, Cline 2012) and Europe (Miller and Mariani 2010, Garcia-Vasquez et al. 2011). Fraud in the seafood market most commonly takes place when low-value or more readily available species are substituted for expensive species or those that are rare and in high-demand, including protected species such as whales (Baker et al. 1996, Jacquet and Pauly 2008, Marko et al. 2011, Cline 2012). This especially is prevalent in processed products, where diagnostic characters are removed. Molecular tools, primarily barcoding approaches, are therefore most commonly used to identify mislabeled seafood products in the market place (Ogden 2008, Rasmussen and Morrissey 2008). Within the Indo-Pacific, however, levels of seafood mislabeling and fraud remain almost unknown as only a few studies have been carried out in the region.

In Japan, developments of a reliable PCR-RFLP method has allowed for the discrimination of locally caught chub mackerel, *Scomber japonicas,* and imported Atlantic mackerel, *Scomber scombrus* (Aranishi 2005), although no market-related validation was carried out. Likewise, whale meat being sold or served in Korea and

Japan was "spot-checked" using mtDNA sequences and shown to represent at least six species of whale and some dolphin species (Baker et al. 1996). In South Africa, >50% of fish fillets tested (comprising four different species) were mislabeled, with kob, *Argyrosomus* spp., having a substitution rate of >80% (von der Heyden et al. 2010). Further, over half of the fishes that were found to be substitutes were not recorded from southern African waters, suggesting large-scale import and renaming of marine species from elsewhere, including Australia (von der Heyden et al. 2010). Protocols also exist to identify shark fins and assign them to species (Shivji et al. 2002) and the largest shark fin market in the world, Hong Kong, has been monitored using genetic tools to identify the most heavily traded species (Clarke et al. 2006). This application of genetics is vital to conservation and fisheries management, because the largely unregulated trade in shark fins is one of the most serious threats to shark populations worldwide. Magnussen et al. (2007) also developed a species-specific genetic assay to monitor trade in basking shark (*Cetorhinus maximus*) products, as this Appendix II CITES listed species is particularly sensitive to exploitation due to premium prices achieved for its products.

Barcoding initiatives (Lemer et al. 2007, Wörheide and Erpenbeck 2007, Plaisance et al. 2009, Uthicke et al. 2010, Hubert et al. 2012) within the Indo-Pacific region should therefore be expanded to not only assess species substitutions, but also provenance of marine species. For example, fish marketed as "South African" kingklip, *Genypterus capensis*, was found to be substituted by pink ling, *Genypterus blacodes,* caught in New Zealand waters (von der Heyden et al. 2010). Further, the use of barcoding to discriminate between populations of swordfish, *Xiphias gladius*, suggests that the COI gene is sensitive enough to separate fishes caught in the Atlantic and Indian oceans, as well as the Mediterranean (Pappalardo et al. 2011), although the study did not reveal any substitution with fishes caught in the Indian Ocean. Barcoding has also been successfully applied in monitoring the shark fishery in Madagascar (Doukakis et al. 2011) determining the most commonly marketed species.

For molecular methods to be useful in determining levels of seafood fraud and mislabeling in the Indo-Pacific, overall monitoring of fishing activities and reporting of catches (at local and regional scales) needs to be drastically improved. Further, resolving cryptic species and describing unknown biodiversity will also greatly aid in molecular techniques being applied to tracing products within the seafood chain and combating mislabeling. Ultimately, an approach that allows individuals to be assigned to populations [using for example Single Nucleotide Polymorphisms (SNPs) such as used by the FishPopTrace Consortium (2012)], rather than simply species, will ensure more effective policing of Indo-Pacific marine resources, although this has to date not been applied widely and remains a challenge globally.

Spatial Planning and Restoration

Spatial Management of Wild Marine Species within the Indo-Pacific.—Knowledge of the scale and direction of connectivity among sites is pertinent to effective marine conservation (Almany et al. 2009, McCook et al. 2009, Beger et al. 2010, Kininmonth et al. 2011, Olds et al. 2012) and fisheries

management (e.g., Leis et al. 2011). Particularly when combining genetic information with biophysical models (Kininmonth et al. 2010, White et al. 2010, Kool et al. 2011, Foster et al. 2012, Treml and Halpin 2012), genetic data can underpin the delineation of management areas by identifying consistently located breaks (Carpenter et al. 2011, Toonen et al. 2011; Fig. 1). For conservation or fisheries target species, genetic tools can assist with identifying and protecting genetically isolated populations (Palsbøll et al. 2007) or cryptic species (Griffiths et al. 2010b) from overfishing and other threats. In the context of fisheries management, the identification of subpopulations from seemingly uniform stocks is also important, affecting spatial structuring of management (Table 1). For example, although deep-water snapper, *Pristipomoides filamentosus*, stocks are highly connected across the Indo-Pacific, the Hawaiian Archipelago supports an isolated subpopulation requiring separate fisheries management (Gaither et al. 2011). Similarly, a northern Australian cryptic species of the blue swimmer crab, *Portunus pelagicus,* discovered in an allozyme study highlighted the need for differential management measures (Bryars and Adams 1999). Genetic structure relevant to fisheries management can sometimes be observed at inter-regional and larger spatial scales, but not within regions or locally such as in coral trout, *Plectropomus leopardus* (Table 1). Where highly structured populations relate to localized circulation patterns, such as for fisheries species in the South Californian Bight, genetic analysis can identify source sites to protect for maintaining sustainable fisheries (Table 1; Selkoe et al. 2007, White et al. 2010). Similarly, the identification and incorporation of such population source-sink dynamics is among the last remaining frontiers in marine spatial planning (Crowder et al. 2000, Bode et al. 2006, López-Duarte et al. 2012).

In the context of marine spatial planning for biodiversity conservation, the delineation of genetically differentiated subpopulations that are treated as management units aids the spatial structuring of conservation measures that aim to represent all facets of biodiversity. Several examples utilize a variety of genetic approaches to allocate organisms to management units, such as basing the grouping of sites for management on a measure of connectivity among sites (Kininmonth et al. 2010, Toonen et al. 2011), evolutionary significant units (Barber et al. 2006), phylogeography (Reece et al. 2011), and evolutionary processes (Crandall et al. 2011). To include measures of connectivity in spatial planning, genetically differentiated units, akin to management units, were determined in a model that combined F_{ST} values between pairs of sites with connectivity values derived from a biophysical model and biogeographic measures (Kininmonth et al. 2010). Comparative phylogeography across several taxa in the Philippines (Carpenter et al. 2011) and Hawaii (Toonen et al. 2011) was used to highlight potential management units for spatial planning aiming to preserve core evolutionary processes and histories. Marine phylogeography is also informative for identifying management units, evolutionary significant units, cryptic species, and endemism (Rocha et al. 2007). Isolated evolutionary significant areas are defined when spatially and genetically differentiated patterns in local populations of multiple species are repeatedly identified at specific locations; for example, various coral reef fish species at the eastern edge of the west Pacific—Hawaii, Marquesas, and French Polynesia [e.g., the parrotfishes *Chlorurus sordidus* (Bay et al. 2004) and *Scarus psittacus,* (Winters et al. 2010); the snappers *Lutjanus fulvus*

Table 1. Example of molecular studies and species in the Indo-Pacific which resolve either population genetic structure or low/no structure. Studies such as these give critical insight into population connectivity over large geographical distances.

Genetic structure			Low/no genetic structure		
Species	Region	Reference	Species	Region	Reference
Round scad mackerel, *Decapterus macrosoma*	Indo-Malay Archipelago	Borsa 2003	Kawakawa, *Euthynnus affinis*, along the,	Indian coast	Kumar et al. 2012
Bigeye tuna, *Thunnus obesus*	Indian Ocean	Appleyard et al. 2002	Barramundi, *Lates calcarifer*	Northern Australia	Salini and Shaklee 1988, Chenoweth et al. 1998)
Coral trout, *Plectropomus leopardus*	Indo–West Pacific	van Herwerden et al. 2009	Coral trout, *Plectropomus leopardus*	Great Barrier Reef	van Herwerden et al. 2009
California sheephead, *Semicossyphus pulcher*	South Californian Bight	Selkoe et al. 2007	Two threadfin salmon, *Eleutheronema tetradactylus* and *Polydactylus macrochir*	Great Barrier Reef	Horne et al. 2011, 2012
Kelp bass, *Paralabrax clathratus*	South Californian Bight	Selkoe et al. 2007	Blue shark, *Prionace glauca*	Australia, Indonesia	Ovenden et al. 2009
Tiger shrimp, *Penaeus monodon*	Western Indian Ocean	You et al. 2008, Mkare et al. unpubl data)	Blacktip shark, *Carcharinus limbatus*	Australia, Indonesia	Ovenden et al. 2010
Mud crab, *Scylla serrata*	Indo–West Pacific	(Gopurenko et al. 1999	Lemon shark, *Negaprion acutidens*	Schultz et al. 2008	
Zebra shark, *Stegosoma fasciatum*	Northern Australia/ Southeast Asia/	Dudgeon et al. 2009			
Spot-tail shark, *Carcharinus* sorrah; milk shark, *Rhizoprionodon acutus*	Australia, Indonesia	Ovenden et al. 2009			
Pigeye shark, *Carcharhinus amboinensis*	East and northwest Australia	Tillett et al. 2012			

and *Lutjanus kasmira* (Gaither et al. 2010), the boring clam, *Tridacna crocea*, (DeBoer et al. 2008; Fig. 1)]. Populations at such isolated locations should be managed independently to preserve genetic diversity.

Genetic approaches are also highly relevant to benchmark protected area and management success. For example, DNA genetic fingerprinting allowed the monitoring of stock recovery for overfished holothurians on the Great Barrier Reef in combination with repeated large scale surveys to identify stock status (Uthicke et al. 2004). On smaller spatial and time scales, parentage analysis has been used to establish patterns of self-recruitment in anemone fishes, *Amphiprion polymnus* (Jones et al. 2005), gobies, *Elacatinus evelynae* (Taylor and Hellberg 2003), butterfly fishes, *Chaetodon vagabundus* (Almany et al. 2007), yellow tang, *Zebrasoma flavescens*, damselfish, *Stegastes partitus* (Christie et al. 2010a,b) and striped snappers, *Lutjanus carponotatus* (Harrison et al. 2012), helping to quantify recruitment patterns in and out of reserves. Similarly, the rates of dispersal from a parent site to other suitable habitats in the region were identified for an anemone fish and a butterfly fish in Kimbe Bay, Papua New Guinea, with parentage analysis as the most robust tool for quantifying connectivity under high gene flow scenarios (Saenz-Agudelo et al. 2009).

Genotype assignments in conjunction with mtDNA sequence analyses have also been used successfully to identify insular, self-seeding local populations of inshore fishes displaying low gene flow in tropical northern Australia, e.g., the polynemid fishes *Eleutheronema tetradactylum* (Horne et al. 2011) and *Polydactylus macrochir* (Horne et al. 2012). Regardless of the method, estimates of connectivity and dispersal distances determined with genetic tools are important for choosing the most effective size of marine reserves to protect recruitment processes, which has been applied to corals (van Oppen et al. 2008, Underwood et al. 2009) and fishes (Almany et al. 2007, Buston et al. 2011, Harrison et al. 2012). A number of caveats remain when calculating dispersal distances from genetic data (Palumbi 2003, Hellberg 2009). These include inferring a lack of dispersal as the cause of differentiation (Hart and Marko 2010, Marko and Hart 2011), the influence of pelagic larval duration (PLD) on dispersal ability (Weersing and Toonen 2009, Selkoe and Toonen 2011, Riginos et al. 2011, Faurby and Barber 2012) and realized dispersal on population genetic structure and gene flow.

Further, other issues that are often not addressed pertain to: (1) differences in stock structure and genetic connectivity when measured using markers assumed to be either neutral (due to genetic drift alone) or under selection (adaptive; but see Bowen et al. 2014); conservation genomics has set the stage to address this, so we expect to see such studies emerging in the coming years. (2) Differences in genetic structure may be detected due to rarely examined temporal variation, but where it has been examined, it is unclear how this affects larger-scale structure. This may also depend on the biological characteristics of the study species (e.g., Bjorndal and Bolton 2008).

Genetic Studies of Stock Enhancement and Restoration in the Indo-Pacific.—Release of cultured juveniles has been undertaken to rebuild or enhance wild stocks (e.g., Bell et al. 2005). Aside from animal health considerations, there are concerns about negative impacts on the wild gene pool due to the relocation of individuals and/or the release of hatchery-produced individuals into the natural

environment (Blankenship and Leber 1995, Tringali and Bert 1998). In theory, the loss of genetic diversity through introgression and interbreeding of cultured and wild stocks may result in decreased fecundity, slowed growth, and high mortality (Uthicke and Purcell 2004); these effects can occur within a single generation (Christie et al. 2012). Coupled with environmental stress, a decrease in the fitness of a species may eventually result in extinction. It has also been suggested that maintaining high genetic diversity is important in strengthening the resilience of the wild population to changes in environmental conditions (Gamfeldt et al. 2005). In relation to these potential genetic effects, genetic characteristics of the natural populations should be considered before any stock restoration and stock enhancement initiative (Blankenship and Leber 1995). As a precautionary measure, it is recommended that a large number of broodstock should be taken directly from the population to be enhanced and in cases where broodstock are no longer available from the area to be enhanced, the most genetically-similar populations should be used (Ward 2006). However, this would only be tenable if baseline population genetic information is available.

Few stock enhancement or restocking efforts in the Indo-Pacific have taken genetics into consideration. In Thailand, genetic differences of the giant clam, *Tridacna squamosa,* and the abalone, *Haliotis asinina,* from the Andaman Sea and Thailand Gulf have been investigated. Both species are cultured and commercially important and have potential for restocking. Isozyme analysis of the giant clam *T. squamosa* revealed significant differences in genotypic and allelic frequencies between populations from the two regions (Kittiwattanawong et al. 2001). Further, Random Amplification of Polymorphic DNA (RAPD) and microsatellite markers revealed high population genetic differences in founder populations of cultured *Haliotis asinina* (Tang et al. 2005). Both studies suggested that stocks from these sites should be managed separately to maintain the unique genetic characteristics of the regions for fishery conservation and sustainable aquaculture. Restocking without considering wild population structure can have potentially disastrous effects on local populations. For example, the intentional stocking of the Japanese shortneck clam from China and the Korean peninsula to enhance depleted Japanese populations backfired when it turned out to be a cryptic species that is now rapidly hybridizing with the native population such that the hybrid proportion now exceeds 50% (Kitada et al. 2013).

Commercial culture of sandfish, *Holothuria scabra,* has spurred interest in sea ranching and other culture-based initiatives in the Indo–West Pacific (Eriksson et al. 2012, Purcell 2012). Sandfish is among the most expensive tropical sea cucumber species and has thus been heavily exploited across the region (e.g., Heinen 2001, Hasan 2005, Ahmed and Lawrence 2007). Genetic surveys using allozymes on *H. scabra* populations from Indonesia, Torres Strait, in northeast Australia, Solomon Islands, and New Caledonia detected significant genetic structure among many populations, which indicate restricted gene flow despite the high dispersal potential of the larvae (Uthicke and Benzie 2001, Uthicke and Purcell 2004). Based on these results, it was recommended that management of *H. scabra* should be implemented at local scales and establishment of local marine reserves is also necessary (Uthicke and Benzie 2001). Both studies also emphasized the importance of using locally-sourced spawners for hatchery production in relation to stock enhancement interventions. In this case, it is imperative to apply

precautionary approaches to conserving genetic diversity in scaling-up culture-based management efforts over the entire range of this species.

Fine-scale Patterns of Local Recruitment within the Indo-Pacific.—Understanding recruitment dynamics of marine organisms is a key factor both at the theoretical level—as it links demographic, resilience, and succession issues—and at applied levels, since it informs managers about the effectiveness of the placement and distance between fragmented marine reserves. Parentage analyses are able to provide fine-scale resolution on recruitment dynamics in marine systems. Similar to forensic methods of paternity analyses, parentage analyses require a reasonable proportion of the adult population and many offspring to be genotyped using a large panel of microsatellite markers and SNPs (single nucleotide polymorphisms). Assignment tests are then carried out to link offspring and potential parents based on a likelihood estimate. The likelihood estimate of parentage association depends on the number of loci, their allelic diversity, and the distribution of alleles in the adult population. To use the parentage assignment method, one needs to find a species amenable to this type of analysis, where the species is not very abundant, and both adults and recruits are easy to find and sample. In a study carried out in Kimbe Bay, Papua New Guinea, anemonefish, *Amphiprion polymnus,* presented the perfect model system (Jones et al. 2005) since they live exclusively in easy to find anemones that have low abundance, thus ensuring that most parents in a surveyed area are sampled. Results showed extreme local patterns of recruitment dynamics, and confirmed the early, coarser estimates of self-recruitment, based on tagged otoliths of the recruits (Almany et al. 2007, Jones et al. 2005, Saenz-Agudelo et al. 2009, 2011). Interestingly, it was possible to directly compare the relative power of the genetic and otolith microchemistry approaches since specific individuals were both genotyped and used for otolith analyses. While otolith microchemistry provides a unique understanding of the type of chemical environment (water mass) larvae encounter each day before recruitment, genetic approaches were found to be more powerful in identifying the fraction of self-recruitment in the population (Berumen et al. 2012), although some studies suggest otherwise (Lopez-Duarte et al. 2012). Besides simple recruitment assessment, precise patterns could be identified, such as the relative contribution of females of different sizes, where larger females were shown to disproportionally contribute to the self-recruiting population (Beldade et al. 2012).

For parentage analysis studies to be broadly relevant, more species needed to be examined. The study of anemonefish was therefore expanded to one species of butterflyfish, *Chaetodon vagabundus*, in Kimbe Bay, Papua New Guinea (Berumen et al. 2012), as well as yellow tangs and Caribbean damsels (Christie et al. 2010a,b). While these species present considerable challenges compared to the simpler anemonefish system, each was able to assign offspring to specific parents, proving that the general method of parentage analysis could be expanded to other reef fish species with more typical pelagic larvae. More importantly, some showed a direct application of parentage analysis approaches to conservation by linking their results to the efficiency and design of marine reserves (Berumen et al. 2012). Most parentage studies have used fishes, although an expansion of using parentage and kinship relationships comes from a recent study on California spiny

lobsters, *Panulirus interruptus*, which require 240–330 d of pelagic development prior to settlement. Despite high gene flow and extensive mixing, Iacchei et al. (2013) showed specific populations, associated with upwelling fronts, contained significantly more kin than expected and were thus significantly differentiated from other sites throughout the species range.

The design of marine protected areas (MPAs) has generally been based on a number of considerations, often not relevant to the biology of the species that they are supposed to protect (Sala et al. 2012). The application of parentage and kinship analyses to our understanding of connectivity among reefs is still in its infancy, yet it has yielded some very promising results that are likely to inform managers as to the proper design of future MPAs. New studies have now used parentage or kinship analyses to understand connectivity between reefs using species that are commercially important and highly relevant to fisheries managers. Specifically, bar-cheeked coral trout, *Plectropomus maculatus*, and Spanish flag snapper, *Lutjanus carponotatus,* from the Keppel Islands on the Great Barrier Reef, Australia, were used to identify the levels of connectivity between MPAs within the area, the levels of self-recruitment within MPAs and the levels of recruit spillover from MPAs into surrounding reefs open to fishing (Harrison et al. 2012). This indicated how a network of MPAs may effectively sustain itself and areas open to fishing. Such studies have fueled a paradigm shift over the past decade, from the general idea of open populations to the discovery that self-recruitment may be far more prevalent than once imagined. We are still clearly at the beginning of applying the method. Indeed, microsatellites have inherent technical limitations and a comparison of the effectiveness of microsatellite and SNPs in parentage analysis favored the latter (Hauser et al. 2011). It is likely that next generation sequencing (NGS) approaches that rapidly identify and concurrently screen large numbers of SNPs across many individuals will be the method of choice for parentage analyses in non-model organisms in the near future (Allendorf et al. 2010).

Management Cognizant of Changing Sex, Stock Structuring, and Group Spawning.—One difficulty in generalized management decisions stems from the unique life histories of species targeted for harvest in the Indo-Pacific, including sequential hermaphroditism and group spawning. Approximately 900 species of fish form the primary targets of artisanal and commercial fisheries in the Indo-Pacific. Targeted families with species which are sequential hermaphrodites include wrasses (Labridae), parrotfishes (Scaridae), emperors (Lethrinidae), and to some extent groupers (Serranidae) (Nelson 2006). When using genetic tools to assess populations, one needs to take into consideration this fundamental life history trait, as it may result in confusing genetic signatures that could be misinterpreted otherwise. For example, a classic interpretation of differences in the genetic results for male and female individuals is a difference in dispersal between genders, where one gender shows site fidelity and the other does not. For sequential hermaphrodites, such a trait, which is essential to proper management, would be masked in a genetic study where life history is not taken into account. Iconic species such as the humphead wrasse, *Cheilinus undulatus,* and the bumphead parrotfish, *Bolbometopon muricatum*, have been driven locally extinct in many places (Bellwood et al. 2003, Sadovy et al. 2003, Dulvy and Polunin 2004). In the past, management has generally recommended smaller size limit to

catches, although it is now moving toward slot approaches where both size and quantities are taken into account. In the case of sequential hermaphrodites, where individuals change sex over the course of their lifetime, with younger individuals being one gender (female for protogynous hermaphrodites, male for protandrous hermaphrodites) and older individuals being the other gender, removing larger individuals results in a number of substantial population consequences. The natural disappearance of the largest individual triggers the sex change of the next largest individual (Warner and Swearer 1991). By removing large individuals via harvest, individuals change sex at an unnaturally small size. The consequences are many-fold. First the production of one type of gametes, for example, sperm in protogynous hermaphrodites, such as humphead wrasse and bumphead parrotfish, is lowered, since individuals assume the male role at a smaller size than natural, resulting in reduced fertilization success. Second, such smaller terminal phase males are less able to guard harems of females because they cannot fend off other males from taking over the harems (Warner and Swearer 1991). Likewise, larger females produce exponentially more, and often bigger, eggs that develop up to three times faster and survive starvation for more than twice as long as larvae produced by smaller females (Berkeley et al. 2004, Birkeland and Dayton 2005). Thus, beyond the mere negative impacts of overfishing large individuals, in the case of sequential hermaphrodites, the removal of large individuals is in fact a selective removal of a key life history stage of the species that results in far reaching consequences (Armsworth 2001, Birkeland and Dayton 2005). Importantly, while we discuss here only such impacts as a modification of fundamental life history traits, there are additional consequences at the level of the entire ecosystem, such as the overall health of coral reefs (Mumby et al. 2006, Hughes et al. 2007), which directly impacts coral reef resilience (Adam et al. 2011).

Many commercial fishermen have traditionally targeted spawning aggregations. A number of fish families targeted by fishermen in the Indo-Pacific display spawning aggregations, groupers (Serranidae) and snappers (Lutjanidae) being the most studied, although other families, for example surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae) also exhibit group spawning, but are less targeted (Sadovy and Colin 2012). Spawning aggregations are remarkable because they involve species that are usually found singly or in small groups, and are therefore not easy to catch in great numbers. During specific times of the year (usually related to moon phases), large numbers of individuals (thousands, sometimes tens of thousands) migrate to a single locale to spawn (Meyer et al. 2007, Erisman et al. 2012). These locales remain the same over the years, allowing fishermen to predict and target the time and place of spawning. As mentioned above, fishing spawning aggregations is not a new activity; however, the advent of localization devices such as GPS has allowed the precise pinpointing of spawning grounds, something that traditionally prevented the extirpation of localized populations, in areas where spawning aggregations are not protected by artisanal fishermen (Jokiel et al. 2011). Removing large numbers of mature individuals at such a crucial period of the life cycle has obvious devastating effects. For example, the Caribbean Nassau grouper, *Epinephelus striatus*, which used to form aggregations of tens of thousands of individuals, are now considered endangered and most spawning aggregations

have either disappeared entirely or have greatly diminished in numbers to the point where hundreds to a few thousand individuals may be seen (Sala et al. 2001).

Case Studies for Applied Management and Conservation Integrating a Genetic Approach

Stock Delineation in the Context of Restoration: a Case Study from the Philippines.—Sea urchin fisheries are among the most lucrative shell fishery in some parts of the world, with *Tripneustes gratilla* being the most commercially important shell fishery in the tropical Indo-Pacific. The high market demand for export and unregulated harvesting of this species led to the collapse of the fishery in Bolinao, Pangasinan, NW Luzon, Philippines. Population genetic studies were undertaken to guide efforts to rebuild depleted spawning populations through release of hatchery produced juveniles (Juinio-Meñez al. 1998, 2008). Allozyme analysis detected no significant genetic structuring in the region (Malay et al. 2000). The population genetic structure of this species was re-investigated after the recovery of the fishery using mitochondrial and microsatellite markers (Casilagan 2011). Neither marker detected significant genetic differentiation among populations in the northwest Luzon, nor among populations in regions where there has been no restocking and grow-out culture of hatchery produced sea urchins. Results of genetic studies concur with larval dispersal modeling studies, which indicated that *T. gratilla* populations in northwest Luzon were highly connected by larval transport due to the reversing monsoons (Juinio-Meñez and Villanoy 1995). Given the lack of dispersal barriers among localities and the spatio-temporal variability in recruitment due to hydro-meteorological factors, establishment of a regional network of marine protected areas and grow-out culture are strategic in conserving *T. gratilla* in the region (Juinio-Meñez et al. 2008). The high genetic diversity of the species despite recent recovery from depletion indicates the resilience of this species when populations are reestablished and sustainably managed.

Genetic Tools That Identify Both Sides of the Dispersal—Retention Coin in Australian Reef Fishes.— Management actions need to include both the dispersal and retention elements of connectivity to ensure replenishment and ecological persistence in demographic timeframes, while also securing that genetic diversity can be maintained. Genetic diversity is important for several reasons, including the avoidance of inbreeding depression, the maintenance of healthy immune systems, and the maintenance of raw material for selection to act on different populations during times of environmental change (Bowen and Roman 2005). Here, we highlight two case studies of tropical Australian marine fishes that illustrate the important difference in dispersal over ecological and evolutionary time scales and the need to understand both in making management recommendations. Each case study is relevant to either conservation (the former) or fisheries (the latter) management. Each study, funded by a relevant industry stakeholder, will be incorporated into management strategies.

Connectivity and retention of the endemic anemonefish, *Amphiprion mccullochi*, living at the edge of south east Australian coral reef systems, was examined using mtDNA partial control region (D-loop) sequences and seventeen microsatellite

DNA loci (van der Meer et al. 2012). Extensive sharing of mtDNA haplotypes among sampling sites separated by up to 160 km indicates a lack of significant dispersal barriers over evolutionary time scales. In contrast, contemporary migration estimated using a Bayesian assignment technique indicated high levels of self-replenishment, with 68% to 84% of recruitment coming from within the same population (van der Meer et al. 2012). The low proportion of dispersal among sites (1%–16%) indicates that populations are predominantly maintained by self-replenishment and should be managed separately, despite the lack of obvious barriers to dispersal through time seen in the mtDNA haplotype data. By understanding the interplay of self-recruitment and dispersal at various temporal and spatial scales, managers can seek to maintain self-seeding populations and high genetic diversity in this low abundance endemic species with a small geographic range and ecological specialization that make it more vulnerable to extinction.

In a counter example, the tropical Indo–West Pacific shorefish, *Eleutheronema tetradactylus*, from northern Australia was examined using partial mtDNA COI sequences and five microsatellite loci (Horne et al. 2011). Both microsatellite and mtDNA data indicated strong genetic structure existed among sites throughout northern Australia, suggesting that local populations are largely independent and insular, regardless of time scales. This inference was further substantiated for demographic timescales by non-genetic measures of connectivity in the same post-juvenile individuals, including: stable isotope profiles from sagittal otoliths (Newman et al. 2011), parasite composition (Moore et al. 2011), and life history characteristics (Ballagh et al. 2011). Together, these studies formed the basis for recommendations to establish regional management within each jurisdiction, cognizant of the resident nature of the populations.

Marine Protected Areas and Connectivity in South Africa.—South Africa is the meeting place of the Indian and Atlantic ocean and is bounded by two great ocean currents, the cold Benguela and the warmer Agulhas Current; with three distinct biogeographic regions in the area (Griffiths et al. 2010a). MPAs have been used globally to limit the impact of human activities on the marine environment, especially in the context of recreational and commercial exploitation (Roberts et al. 2001, Halpern and Warner 2002, Fernandes et al. 2005). However, to be effective, it is recognized that networks of MPAs must be connected, either via adult or juvenile migration (Botsford et al. 2009). Measuring connectivity using biological data is extremely difficult, but can involve tagging of migratory species or the use of otolith chemistry, trace-elemental fingerprinting, or trans-generational marking (see Levin 1990, 2006, Thorrold et al. 2006, Cowen and Sponaugle 2009, Carson et al. 2011).

In South Africa, around 21% of the coastline is formally protected by MPAs, although only 9% are protected as "no-take" zones, in which all forms of exploitation are prohibited. Whether this network is effectively connected, especially across biogeographic boundaries remains unclear. Therefore a preliminary phylogeographic approach that compared multiple species, with different life-histories, across the same geographic range was used to determine connectivity between South African MPAs. Congruent genetic breaks across multiple species arise regardless of life history characteristics when there is a shared break or barrier to gene flow (Avise 1992, Kuo and Avise 2005). Therefore, a study that included twenty species

(fishes, crustaceans, corals, echinoderms and molluscs) with different life history characteristics (broadcast spawning, brooding and live-bearing; see von der Heyden 2009) compared their population genetic patterns across this region. Most species analyzed showed at least one clear phylogeographic break across the range sampled, yet not all species showed the same breaks (Teske et al. 2011). A similar finding comes from a comparison of 27 species in Hawaii, where strong congruent patterns of genetic differentiation emerged, but no single species in the comparative analysis showed the emergent multispecies pattern (Toonen et al. 2011). Interestingly, dispersal estimates (calculated using isolation-by-distance approaches) of <10 km for brooding and live-bearing species are common (Wright et al. unpubl data).

How do genetics shed light on connectivity of MPAs in the region? First, the presence of at least four phylogeographic breaks that are shared between species suggests shared evolutionary processes, as has been found consistently in Indo-Pacific biogeographic studies as well (e.g., Lessios et al. 1996, Gaither et al. 2010, 2011). It therefore seems prudent to establish MPAs within each section of the coast between these phylogeographic breaks. Second, isolation-by-distance (IBD) analyses and population structuring indicate that successful dispersal might be far more limited than suggested by previous studies (Brouwer et al. 2003, Roberts and van den Berg 2005). This strongly suggests that the current MPA network is ineffective at protecting genetic diversity (and adaptive potential). Therefore, evaluating genetic findings in combination with other parameters for establishing MPAs, such as abundance and diversity data, oceanographical and current patterns, and socio-economic data (see also Beger et al. 2014) will go some way in creating a more effective network in the region. Unfortunately, current scientific, funding, and political will are lacking in engaging with a genetic approach to management in the region. However, better science will inform stronger management—if genetics are increasingly used in marine conservation and management internationally, then South Africa will be placed in a strong position to build on existing genetic data.

Incorporating Genetics into Management Policy: Conservation in Hawaii.—Hawaii provides some of the better examples of genetic studies being incorporated directly into resource management policy. For example, population genetic studies of the endemic Hawaiian limpet, known locally as ʻopihi (*Cellana* spp.), revealed that there was no detectable population differentiation within islands, but differentiation among islands (Bird et al. 2007). Together with community involvement to survey and quantify population density differences among islands in the Hawaiian archipelago, this finding corroborated native Hawaiian practices to manage the stocks locally and has led to the introduction of several bills to change fisheries regulations for this species. Likewise, Christie et al. (2010a) tracked individual larval yellow tang, *Zebrasoma flavescens*, that were transported out of fisheries replenishment areas into adjacent regions open to collection along the Kona coast of the Big Island of Hawaii, documenting fisheries spillover from marine protected areas in Hawaii for the first time. This work revealed not only that spawning of abundant stocks in the replenishment area had benefits in the adjacent open areas, but also that long-lived pelagic larvae of these fishes recruit along the same coastline on which they were produced (Christie et al. 2010a). The recruitment of locally produced juveniles along the same coast was surprising to many, and has played a prominent role in the on-going debate about local

management and the marine ornamental trade in Hawaii. Finally, a multispecies survey of population structure across the Hawaiian Archipelago revealed that the majority of 27 coral reef species surveyed showed genetic breaks between each of the adjacent Main Hawaiian Islands, despite the fact that they are geographically less separated than the more isolated Northwestern Hawaiian Islands (Toonen et al. 2011). Together, these studies have reformed the way that resource managers view populations of marine species in the Hawaiian Archipelago, resulting in a move away from archipelago-wide management strategies and a push for increased local management of marine resources. Efforts to communicate these findings widely are changing the type of policy being introduced by lawmakers as a result.

Increasing Public Ownership through Genetic Uniqueness in Fiji.—A population genetic survey revealed that Fijian regional color morphs of five putatively widespread fishes from the Indo–West Pacific (Amphiprion melanopus, Chrysiptera talboti, Pomacentrus moluccensis, Cirrhilabrus punctatus, and Labroides dimidiatus) were genetically differentiated from other locations with the typical color morph (Drew et al. 2008). This information was something that excited local villagers and inspired a sense of nationalistic pride in the unique resources of the region. A public awareness and education campaign was launched, aimed at communicating that the people of Fiji are the stewards of their resources and that they are responsible for the health and survival of the world's entire population of these endemic fishes. The result has been an emerging realization of responsibility along with nationalistic pride, leading to the local phrase "Na ika kai viti," the "Fijian Fish" that has produced a widespread desire for conservation of these natural resources (J Drew, Columbia University, pers comm). With this sense of ownership and realized responsibility, environmental campaigns aimed at reducing anthropogenic impacts leading to coral reef decline, such as a campaign to control marine debris from the Fijian capital of Suva on the surrounding reefs, have become more prominent and well received.

Stock Structure and Cryptic Speciation in New Caledonian Mackerel (*Scomberomorus* spp.).—Improving knowledge of New Caledonian marine resources to increase sustainability is the global objective of the multi-disciplinary program called ZoNéCo (Programme d'évaluation des resources marines de la zone économique de Nouvelle-Calédonie). Designed and launched >15 yrs ago by the Governments of France and New Caledonia and its three Provinces, together with locally-based research institutions, ZoNéCo acts as an interface linking science and policy, with the aim to support the implementation of research projects and to facilitate the uptake of research results by policy makers, the private sector, and civil society. Since its creation, the results produced and disseminated by the ZoNéCo program have led to a tremendous improvement in the knowledge of the marine ecosystems of New Caledonia.

Spanish mackerel, *Scomberomorus commerson*, is one of the most important commercially exploited and valuable fishes in New Caledonian waters and became the target of a major research program aimed at: (1) gathering knowledge on the ecology and exploitation of the species in the Indo-Pacific and New Caledonia, (2) monitoring biological parameters from populations throughout New Caledonia, and (3) determining management units within the archipelago. With this perspective, the genetic composition of *S. commerson* was investigated using mtDNA sequences (control-region and cytochrome-*b* gene fragments), and

microsatellite allele frequencies at various spatial scales, from the local (Bélep in the North Province of New Caledonia) to the larger Indo-Pacific.

At the broadest scale, high levels of genetic divergence (>11%) were observed using mitochondrial sequences between Indo-Malay-Papua archipelago (IMPA) and both the southwestern Pacific, and the Persian Gulf and Oman Sea, suggesting the occurrence of two sister-species (Fauvelot and Borsa 2011). Further phylogeographic partitioning was evident between the western IMPA and the regions sampled east and south of it, i.e., northern Australia, West Papua, and the Coral Sea. Strong allele-frequency differences were found between local populations in the southwestern Pacific, both at the mtDNA (Φ_{ST} = 0.306–0.586) and microsatellite loci (West Papua vs New Caledonia: F_{ST} = 0.202–0.311), indicating geographic isolation of *S. commerson* populations at this spatial scale (Fauvelot and Borsa 2011).

Within the New Caledonia lagoon, nuclear data analyses revealed genetically distinct populations (F_{ST} = 0.008–0.015; $P < 0.01$), one grouping samples from the East coast of New Caledonia and northern Bélep Islands, and another grouping samples from the west and south coasts of the main island (including Poya, Nouméa and Mont-Dore samples). The investigation of the temporal genetic composition of *S. commerson* captured in Bélep at the beginning of the year and at the end of the year were also genetically different (F_{ST} = 0.008; $P < 0.01$). Although this genetic differentiation is low, it is significant and suggests that the Bélep Islands may host distinct reproductive stocks. The molecular data, which provides strong evidence for genetic structuring across a wide variety of spatial scales, is currently being discussed with policy makers to manage distinct stocks, and thus ensure long-term sustainable exploitation of this important resource.

Genetic Structure of Philippine Populations of *Siganus fuscescens:* Implications for Fisheries Management.—Rabbitfishes (Family Siganidae) are a commercially valuable fishery and aquaculture species in the Philippines. Of the estimated 15 rabbitfish species which occur across the Philippine archipelago, the mottled spinefoot, *Siganus fuscescens,* is considered the most exploited, with evidence of overfishing (Jumawan-Nanual and Metillo 2008, Soliman et al. 2009). Widely-distributed in reef flats and seagrass meadows, the species is harvested throughout most of its life cycle: presettlement juveniles are collected as they arrive in dense schools to settle on the reef flat, and juvenile and adult stages are fished year round (Campos et al. 1994). Relatively much is known about the biology and ecology of the mottled spinefoot (e.g., Alcala et al. 1979, de la Paz and Aragones 1990, Woodland 1990), although some confusion still exists in distinguishing the species from its morphologically similar sibling species, *Siganus canaliculatus*. Several studies of mottled spinefoot populations in the Philippines have focused on population structure, dynamics, and exploitation status toward rationalizing and proposing management schemes for catch regulation (Soliman and Yamaoka 2010) or establishment of marine reserves (Bellefleur 1997, Jumawan-Nanual and Metillo 2008).

Recent genetic studies of Philippine populations of *S. fuscescens* have provided additional information which, coupled with earlier studies can be used to further inform management efforts. For example, phylogenetic studies have revealed the presence of cryptic diversity within the Philippines (Ravago-Gotanco and

Juinio-Meñez 2010). While it remains unclear whether ecological partitions exist between the two distinct lineages, which occur in sympatry, these genetically distinct evolutionary units may be considered as potential management units (e.g., Bickford et al. 2007, Rocha et al. 2007). Likewise, significant population genetic structure along the eastern Philippine seaboard (Magsino and Juinio-Meñez 2008), and among three major marine basin regions, i.e., South China Sea, northeast Philippine Sea, and southeast Philippine Sea-Sulu-Celebes Seas, indicate these should be considered as distinct regional management units (Ravago-Gotanco and Juinio-Meñez 2010). Across smaller spatial scales, analyses of mtDNA sequences and microsatellite data detect significant genetic structure across the western Luzon coast, relevant in particular for *S. fuscescens* populations in Bolinao, a significant fishery characterized by high levels of exploitation over many decades (Campos et al. 1994). Assignment-based analyses of multilocus genotypes indicate asymmetric patterns of gene flow; populations in the Lingayen Gulf are self-recruiting, and serve as the source population for reefs located farther south along the western Luzon coast (Ravago-Gotanco 2010). Moreover, genetic estimates of gene flow are consistent with larval disperal estimates drawn from numerical modelling (Altemerano and Villanoy 2002). While early maturity, high fecundity, short generation time, and the relative abundance of the species throughout the extensive seagrass habitats in the Bolinao-Anda reef system confer some degree of resilience, genetic studies suggest that local management and protection of Bolinao populations of *S. fuscescens* would benefit the entire western Luzon coast.

Summary

The present study highlights some of the ways in which molecular tools could be used to address conservation and management issues among marine taxa in the Indo-Pacific using examples of how such approaches have already been successfully applied. Molecular techniques and analyses allow us to examine not only the patterns of marine biodiversity within the region, but also test hypotheses regarding the processes that have shaped these patterns. Molecular tools provide invaluable insights to biological and evolutionary processes, but have been relatively slow to be incorporated into management. Failure to integrate genetic information risks losing the processes which maintain and generate biodiversity and potentially the populations and species of the future (Bowen and Roman 2005, Rocha et al. 2007). Most of the papers reviewed above have been based on mtDNA, but instead of single species, have often relied on multi-species approaches to look for congruent genetic breaks and patterns. Such an approach becomes even stronger when it includes species with different life history characteristics (see for example von der Heyden 2009, Toonen et al. 2011). Multispecies approaches give far better resolution when elucidating the processes and patterns of marine biodiversity and can support integrative management and conservation goals. A major gap yet to be addressed is an integrated spatial planning approach which combines biological, oceanographic and socio-economic data with genetic data and evaluates spatial planning with and without taking evolutionary processes into account (see Beger et al. 2014). An innovative and integrative approach is required to prioritize regions for conservation that can also incorporate uncertainty and take future change into account.

Table 2. Summary of genetic tools used for management applications, together with a brief on the strengths and weaknesses of each. This is presented in two sections—evolutionary and ecological approaches. The footnote defines the terms used here and relevant references associated with the definitions given.

Study question	Genetic tools used	Management applications	
		Strengths	Weaknesses
Evolutionary approaches			
Phylogeography	Sequence data from mtDNA and nuclear markers e.g., introns. Phylogenetic and population genetic analyses used (F_{ST}).	Detect evolutionary partitions and define ESUs and/or MUs, F_{ST} is universally comparable across studies.	Neutral markers are popularly used, but adaptive markers may produce different genetic structures for better management outcomes. Many studies rely on single markers.
Biogeographic barriers	Phylogeographic tools, but sampling design explicitly incorporates known biogeographic barriers and tests hypotheses about genetic structure.	Capacity to identify genetic breaks across many taxa for spatial management of ecosystems and/or target spp.	As above and barriers are porous so vary over evolutionary time (e.g., sea level change creates or removes landbridges).
Cryptic species	Sequence data from mtDNA and nuclear markers, e.g. introns, as well as microsatellites. Typically discovered during phylogeographic studies and across biogeographic barriers, where morphological differences may not be evident.	Allows conservation management that incorporates true biodiversity knowledge, which may identify additional ESUs or MUS.	Shallow divergence indicates recent common ancestry, which may be difficult to unravel. Examination of biological characteristics, such as behaviour and close morphological scrutiny can further aid in species identification.
Ecological approaches			
Parentage analysis	Microsatellites (msats) and Single Nucleotide Polymorphisms (SNPs) are highly variable and allow parent-off-spring relationships to be identified.	Can be used to measure connectivity at contemporary timescales for better management than otherwise when using evolutionary tools.	Need large numbers of adult samples and/or recruits. Normally at small spatial scales, at single sampling time, so will not detect stochastic changes in space and time. Costs can be high for marker development.
Assignment/exclusion tests	Same tools as for parentage analyses, but can be done on adult populations without requiring recruits.	Is feasible with smaller adult samples than parentage, at greater spatial scales and at several times.	May underestimate connectivity and self-recruitment among subpopulations with high gene flow.

Footnote: Definitions of terms—Connectivity, measures the amount of exchange between sub-populations; introns are non-coding parts of the nuclear genome; F_{ST}, is a population genetic measure of genetic differentiation between a subpopulation and the total population that it belongs to; ESU, Evolutionary Significant Unit, provides a rational basis for identifying genetically dicrete taxa that warrant priority treatment by conservation managers; MU, Management Unit, identifies the fundamental Unit for short-term management of populations with divergent allelle frequencies; Phylogeography, a bridge between macro- and micro evolution, which identifies coinciding geographic and genetic partitions across a species range; Parentage analysis, Genetic analysis that uses allelles present in offspring to assign them to their parent(s) in a sampled population. This most often uses microsatellite markers, but can also be performed on AFLP (Amplified Fragment Length Polymorphism) and SNP data; Assignment and exclusion tests: Genetic assignment methods permit estimates of contemporary dispersal by drawing inferences about where individuals were (or were not = exclusion) born based on their observed genotype likelihoods.

Although most population genetic approaches resolve some structure, there are numerous examples where genetic approaches are unable to resolve population level differentiation (Table 1). In such cases, it is often unclear whether the lack of resolution is a result of power, methodological limitations, or a true lack of any population differentiation (Ryman et al. 2006, Lowe and Allendorf 2010, Marko and Hart 2011; Table 2). The emerging field of high-throughput next-generation sequencing shows extreme promise in facilitating broader phylogeographic studies (e.g., Puritz et al. 2012), the evolution of mating systems (e.g., Hart 2012), adaptation (e.g., Stapley et al. 2010), and has been shown to resolve very recent divergence between marine and freshwater fish populations following an initial colonization event <150 yrs ago (Czesny et al. 2012). In the Indo-Pacific region, next-generation sequencing has had a number of interesting applications and an exciting future; this is reviewed in more detail by Willette et al. (2014).

Finally, scientists need to communicate their work clearly to the general public as well as to the rest of the scientific and management community (Olsen 2009, Wilcox 2011). Well-communicated science can influence conservation, policy, and ethical behavior, and bring excitement into school learning. Having a well-informed public could ultimately support future research when decisions are made on political leadership, who in turn decide to allocate funding to research, management, and conservation. We each have a novel and exciting story to tell about the beautiful marine environment we work in, which is probably one of the best ways of increasing global ownership and helping to conserve our amazing oceans.

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