OXFORD

Perspective

The Three Domains of Conservation Genetics: Case Histories from Hawaiian Waters

Brian W. Bowen

From the Hawai'i Institute of Marine Biology, PO Box 1346, Kaneohe, HI 96744.

Address correspondence to Brian W. Bowen at the address above, or e-mail: bbowen@hawaiii.edu.

Corresponding editor: C. Scott Baker

Abstract

The scientific field of conservation biology is dominated by 3 specialties: phylogenetics, ecology, and evolution. Under this triad, phylogenetics is oriented towards the *past* history of biodiversity, conserving the divergent branches in the tree of life. The ecological component is rooted in the *present*, maintaining the contemporary life support systems for biodiversity. Evolutionary conservation (as defined here) is concerned with preserving the raw materials for generating *future* biodiversity. All 3 domains can be documented with genetic case histories in the waters of the Hawaiian Archipelago, an isolated chain of volcanic islands with 2 types of biodiversity: colonists, and new species that arose from colonists. This review demonstrates that 1) phylogenetic studies have identified previously unknown branches in the tree of life that are endemic to Hawaiian waters; 2) population genetic surveys define isolated marine ecosystems as management units, and 3) phylogeographic analyses illustrate the pathways of colonization that can enhance future biodiversity. Conventional molecular markers have advanced all 3 domains in conservation biology over the last 3 decades, and recent advances in genomics are especially valuable for understanding the foundations of future evolutionary diversity.

Subject areas: Conservation genetics and biodiversity
Key words: biodiversity, ecosystem-based management, evolutionary conservation, marine conservation.

Since the inception of conservation biology, 2 scientific disciplines have claimed primacy as a conceptual foundation: ecology and phylogenetics. The first perspective maintains that the foundations of conservation are healthy ecosystems (Noss 1996). If these trophic webs are functional, then individual species can thrive without taxon-specific management programs. In the introduction to the seminal *First International Conference on Research in Conservation Biology* (September 6–9, 1978), conveners Michael Soulé and Bruce Wilcox placed an emphasis on ecology, writing "The purpose of this conference is to accelerate and facilitate the development of a rigorous new discipline called conservation biology—a multidisciplinary field drawing its insights and methodology mostly from population ecology, community ecology, sociobiology, population genetics, and reproductive biology." The validity of this perspective is beyond dispute, and it is the starting point for much of contemporary wildlife management. Protected areas are designed to encompass ecosystem functions while minimizing human perturbation. Ecosystem-based management is emerging as the predominant paradigm for wildlife management, as indicated by the 2012 establishment of the United Nations Global Centre for Ecosystem Management (http://www.unep.org/ecosystem-management/) and the IUCN Commission on Ecosystem Management (https://www.iucn.org/about/union/commissions/cem/).

An ongoing problem with this conservation approach is defining the geographic boundaries of an ecosystem. Rarely are these self-enclosed, and this problem is particularly apparent in the dispersive medium of the oceans (Kinlan et al. 2005; but see Spalding et al. 2007). However, oceanic islands such as the Hawaiian Archipelago can provide a simplified case of ecosystems that begin or end at the waterline. As illustrated below, population genetics can provide guidelines for defining isolated ecosystems.

The phylogenetic perspective is that units of conservation are unique organismal lineages (Dimmick et al. 1999; Posadas et al.

2001; Mora et al. 2003). In particular, the long branches in the tree of life hold a disproportionate reservoir of the genetic and organismal diversity in the biosphere, indicating an especially high priority for conservation (Forey et al. 1994). The echidna (family Tachyglossidae), an egg laying mammal, and the leatherback sea turtle (*Dermochelys coriacea*), a warm-blooded reptile, are both over 100 million years apart from closest extant relatives. They embody unique and irreplaceable aspects of biodiversity. The recognition that unique or unusual taxa deserve protection has deep roots in European culture; Aristotle, in *Historia Animalium* (circa 350 B.C.E.), listed unique features of dolphins, along with a plea to prevent the harvest of these marine animals that suckle their young, provide parental care, and (according to legend) occasionally assist humans adrift at sea. The recognition of unique organismal lineages as conservation priorities is the foundation for captive breeding programs, as well as the US Endangered Species Act, Canada's Species at Risk Act, China's Protection of Wildlife Law, and similar legislation around the world.

Both the ecological and phylogenetic perspectives are valid, but neither alone is sufficient for conservation. For example, ecosystem protection may foster sedentary organisms, but not the migratory ones. The loggerhead sea turtle (*Caretta caretta*) traverses entire ocean basins in the course of a lifetime (Bowen et al. 1995; Bolten et al. 1998). What ecosystem boundaries will protect them? In these cases, species-specific management plans are mandated, to protect the vulnerable bottlenecks in life history, usually the reproductive phases. Management plans that protect the sea turtle nesting beach, and preclude harvest of eggs and nesting females, have been highly successful over the last 4 decades (Dutton et al. 2005; Chaloupka et al. 2008; Mortimer et al. 2011). Notably the nesting beach is not an ecosystem, it is a substrate to incubate eggs. Based on natal homing behavior of humpback whales (*Megaptera novaeangliae*), calving areas serve the same purpose, not as an ecosystem but as a haven for reproduction (Baker et al. 2013). Taxon-specific management plans are a proven success for the sea turtles, whales, and many other marine megafauna, especially the highly mobile species.

Evolutionary Conservation

The third and most recent scientific specialty to claim primacy in conservation biology is evolution, defined here as the study of the origins and progenitors of future biodiversity. As it is accepted that all organisms face new challenges through time, then too it is indisputable that the building blocks for future biodiversity are an essential part of conservation (Lande and Shannon 1996; Fraser and Bernatchez 2001; Moritz 2002; Frankham 2005; Hendry and Waples 2008). The original textbook on conservation biology had an implicit recognition of this ecological–evolutionary partnership (Soulé and Wilcox 1980). However, this aspect of conservation biology can seem like divining the future by peering into a crystal ball. Who can predict the progenitors of future biodiversity? Until recently, the same could be said of predicting hurricanes and cyclones: A crystal ball was as useful as a meteorologist in predicting the pathway of destruction. Fortunately, careful science has brought predictive power to the study of devastating weather. The unknown does not remain unknowable. As will be illustrated below, scientists have made outstanding progress on this evolutionary enigma in recent decades, resolving genetic and ecological processes to get ever closer to solving evolution's "mystery of mysteries" (Darwin 1859). For example, Erwin (1991) suggested that recent history of

diversification is one indicator of future evolutionary potential. This would mandate conservation priorities for the highly speciose cichlid fishes (family Cichlidae) rather than the living fossils such as the coelacanth (genus *Latimeria*), a seeming conflict with the phylogenetic priority. Additional indicators of the origins of biodiversity lie in biogeographic pathways (Briggs and Bowen 2013; Bowen et al. 2016) and the genomic signatures of selection (Hohenlohe et al. 2011; Pespeni et al. 2012; Harrisson et al. 2014; Gaither et al. 2015).

In considering these 3 scientific foundations for conservation, Bowen and Roman (2005) described a temporal framework for the domains of phylogenetics, ecology, and evolution. Phylogenetic studies illuminate the *past*, the history of biodiversity. Ecological studies evaluate the *present*, the contemporary support systems for life. Evolutionary studies are concerned with *future* developments, and the processes for biodiversity moving forward through time. The division of conservation domains into the past, present, and future is embodied in the Orlog, a worldview from northern European mythology that serves as a metaphor for conservation biology (Box 1).

Hawaiian Case Histories

The remainder of this review provides Hawaiian examples across all 3 domains, including; 1) phylogenetic studies that have demonstrated previous unknown legacies in Hawaiian biodiversity; 2) population genetic studies that show concordant breaks across this linear archipelago, indicating the geographic limits of marine ecosystems for contemporary management, and 3) phylogeographic signals that indicate pathways into Hawai'i, an inception-point for future biodiversity and a centerpiece of evolutionary conservation. The focus here is marine, but terrestrial examples corroborate these 3 focal points for conservation genetics.

Setting: The Evolutionary Theater of Hawai'i

The Hawaiian Archipelago is formed by an ancient hot spot in the Earth's mantle. As the Pacific plate moves northwest across this hotspot, volcanic islands are thrust up, in a semi-continuous line that spans 70 million years. It is the longest, largest, and most isolated linear island chain in the world, reaching across 2600 km of the North Pacific (Figure 1).

Every Hawaiian species originated somewhere else. This simple premise provides contrasting evolutionary outcomes for marine and terrestrial faunas. The nearest continental habitat is 3500 km to the east in Central America. Colonization of terrestrial faunas is rare and usually ancient (>10 Ma; Keeley and Funk 2011); the sole native mammal above the waterline is the Hawaiian Hoary Bat (*Lasiurus cinereus semotus*). In contrast to the extreme terrestrial isolation, the nearest reef habitat is 865 km to the southwest at Johnston Atoll, and marine colonization of Hawai'i spans both ancient (>10 Ma) and ongoing events (Craig et al. 2010; Coleman et al. 2014; Hodge et al. 2014). More dispersive aquatic fauna, such as reef fishes with extended pelagic larval stages, show strong genetic affiliations with the other islands of the central Pacific, as indicated by low levels of population differentiation (F_{ST} values) in mtDNA surveys (Eble et al. 2011a; Reece et al. 2011).

Colonization of terrestrial fauna into Hawai'i, while rare, can result in spectacular adaptive radiations, with classic cases in crickets (dozens of endemic species restricted to single islands; Shaw 1995), *Drosophila* fruit flies (about 1000 native species, probably

Box 1. The Orlog metaphor for conservation

The "Orlog" is a world view in Norse culture, wherein the actions of the past and present influence future outcomes, in contrast to the concept of fate, wherein the future is predetermined (http://galdrtanz-runedance.blogspot.com/2013/02/aspects-of-beings-orlog-wyrd-and.html). In the Orlog, all biodiversity dwells in the tree of life, Yggdrasil, which is guarded by 3 sisters: Urd, Verdandi, and Skuld. The 3 sisters nurture the tree and protect it from dragons that seek to destroy the domain of life. They are personifications of the past, present, and future, or "was, being, and shall be" that correspond to the scientific disciplines of phylogenetics, ecology, and evolution. The sister Urd (past; phylogenetics) is depicted as an old woman, learning the lessons of history. The sister Verdandi (present; ecology) is depicted as a valkyrie (woman warrior), a strong vital force. The sister Skuld (future; evolution) is looking forward with apprehension, holding a scroll that has yet to be opened. All 3 scientific disciplines contribute to conservation genetics, by identifying the historical lineages that comprise extant biodiversity (phylogenetics), the spatial boundaries for ecosystem-based management (molecular ecology and population genetics), and the contemporary foundations of future biodiversity (genomics and phylogeography) (Bowen and Roman 2005). Illustration by C. Ehrenberg in Guerber (1909).

from a single founder; Hardy and Kaneshiro 1981), *Tetragnatha* spiders (similar ecomorphs arising independently on multiple islands; Gillespie 2004), honeycreeper finches (colonization from Asia ~5 Ma; Lerner et al. 2011), and island-hopping colonization in flowering plants (Funk and Wagner 1995). These terrestrial radiations within Hawaii are clearly augmented by limited dispersal and allopatric isolation. In sharp contrast, no such radiations have occurred in the dispersive and continuous aquatic medium; the native marine fauna typically have close relatives elsewhere in the central Pacific (Randall 1998). If a reef organism colonizes Hawaii, and cannot maintain contact with the parental population, it may become an endemic species. The new lineage may radiate further in Hawaiian waters, but not to the extent observed in terrestrial systems (Bird et al. 2011).

Marine species that arise in Hawai'i can disperse to island habitats elsewhere in the Pacific, a process that is rare in the terrestrial fauna (O'Grady and Desalle 2008; Harbaugh et al. 2009; Eble et al. 2011b). Hence, the evolutionary theater of Hawaii has 2 storylines with the same themes (adaptation, isolation, speciation), but different tempos and outcomes above and below the waterline.

Phylogenetic Studies to Resolve Hawaiian Endemic Species

In the course of recent genetic surveys of Pacific shallow-water taxa, a growing number of endemics have been identified in Hawai'i (Table 1). These are usually detected in phylogeographic studies as divergent
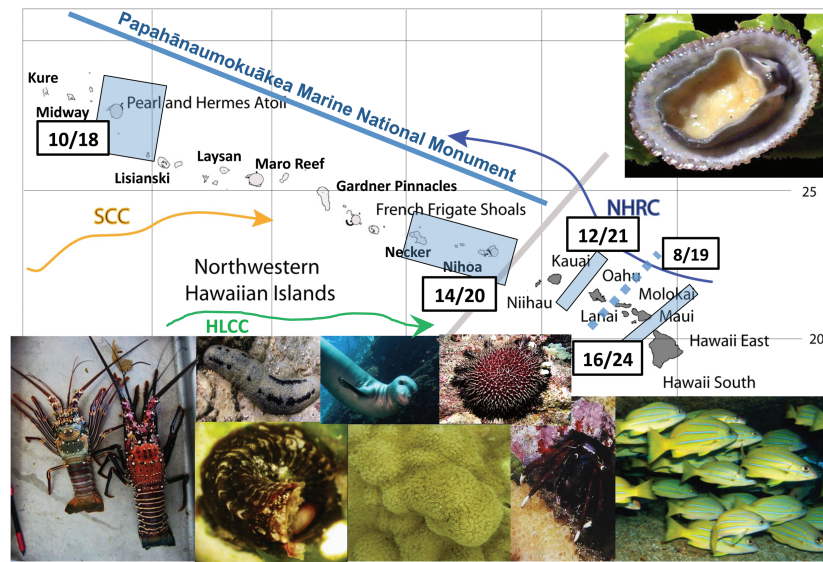
Figure 1. Population genetic partitions can indicate appropriate boundaries for ecosystem-based management and marine protected areas. In the Hawaiian Archipelago, shared genetic breaks based on mtDNA and microsatellite surveys of 27 marine taxa indicate six isolated marine ecosystems (Toonen et al. 2011). Population genetic separations are clustered in the areas indicated by blue bars along the Hawaiian Archipelago. The broad bar including Nihoa and Necker island indicates uncertainty about the exact location of the barrier. The dotted blue line between Lana'i and Oahu indicates a barrier in eight organisms that was marginally significant. Adjacent to each bar is a fraction indicating the proportion of organisms surveyed across the barrier that show population genetic separations. The two westerly partitions lie within the Papahānaumokuākea Marine National Monument, approximately 2000 km long and the largest protected area in the United States. The gray vertical bar indicates the partition between the high volcanic Main Hawaiian Islands and the calcareous (uninhabited) low islands and atolls of the Northwest Hawaiian Islands. Regional currents are indicated by wavy arrows with the following abbreviations: HLCC = Hawaiian Lee Countercurrent; NHRC = North Hawaiian Ridge Current; SCC = Subtropical Countercurrent. Photos represent the diversity of taxa in population genetic surveys (from left to right) including lobsters (*Panulirus penicillatus, Panulirus marginatus*; Iacchei et al. 2014 and unpublished data), sea cucumber (*Holothuria atra*; Skillings et al. 2011), worm snail (*Dendropoma rhyssoconcha*; Faucci 2007), seal (*Monachus schauinslandi*; Schultz et al. 2011), coral (*Porites lobata*; Polato et al. 2010), sea star (*Acanthaster planci*; Timmers et al. 2011), hermit crab (*Calcinus hazletti*; Baums et al. 2014 and unpublished data), fish (*Lutjanus kasmira*; Gaither et al. 2010), limpet (*Cellana sandwicensis*; Bird et al. 2007), with additional data from Ramon et al. (2008), Eble et al. (2009), Andrews et al. (2010), Daly-Engel et al. (2010), Eble et al. (2011), Rivera, Andrews et al. (2011), Concepcion et al. (2014), and Tenggardjaja et al. (2016). Redrawn from Toonen et al. (2011) with permission of R.J. Toonen.

mtDNA lineages (see Avise 2000). Subsequently evolutionary distinctiveness is evaluated with morphological and behavioral comparisons. A very common outcome is that a widespread marine organism is subdivided into a Hawaiian species and a widespread Pacific species (Hidaka et al. 2008; Randall et al. 2008; Randall and Rocha 2009; Randall et al. 2011). In other cases, endemic Hawaiian species are found to be species complexes (Faucci et al. 2007; Santamaria et al. 2013). The discovery of cryptic endemic species in Hawaiian waters is an ongoing process, with many more discoveries likely to occur, especially among the invertebrate fauna, and at the understudied deep (mesophotic) reefs (Luck et al. 2013; Kahng et al. 2014).

The identification of novel phylogenetic lineages is a straightforward application of genetics in the service of taxonomy and conservation. The splitting of a widespread taxon into 2 or more species is certain to realign conservation priorities, as small range endemics are regarded as more vulnerable to extinction (Harvey et al. 2011). Most of these newly discovered species occur in the Papahānaumokuākea Marine National Monument, a 2000 km stretch of atolls and islands with rigid habitat protection, no fishing, and no permanent human habitation.

Molecular Ecology: Population Genetic Studies to Define Hawaiian Marine Ecosystems

Ecosystem-based management is impeded by the fact that cohesive systems of biotic interactions can be difficult to define in a geographic context, and ecosystems can be very large in marine environs (Hixon et al. 2002; Kinlan et al. 2005). Pelagic ecosystems can

also shift swiftly in response to oceanographic conditions, prompting a call for very large protected areas (Sheppard et al. 2012; Toonen et al. 2013). Resolving population genetic separations provides one means of distinguishing isolated habitats that might warrant protection (Allendorf et al. 2013). However, even closely related taxa can have very different patterns of population connectivity (DiBattista et al. 2012; Baums et al. 2014; Selkoe et al. 2014; Ahti et al. 2016; Waldrop et al. 2016). Several recent studies have addressed this discordance by examining multiple co-distributed species to illuminate general trends in connectivity. In the Coral Triangle between the Indian and Pacific oceans, Barber et al. (2011) and Carpenter et al. (2011) found concordance among co-distributed invertebrates, indicating signatures of isolation and speciation. Notably they observed less concordance among 9 fish species. Kelly and Palumbi (2010) summarized data from 50 nearshore or intertidal invertebrates on the west coast of North America, and observed higher genetic structure in more northerly latitudes (Oregon to Alaska), relative to the coast of California. They also observed significantly more structure in high-intertidal invertebrates relative to submerged taxa. Toonen et al. (2011) documented 6 significant breaks along the 2600 km Hawaiian Archipelago based on mtDNA sequence data and microsatellite allele frequencies (Figure 1). In most cases the population genetic partitions are on the low end (mtDNA $F_{ST} < 0.10$) indicating distinct management units rather than incipient evolutionary divergence. Selkoe et al. (2014) reviewed population structure in 35 marine species across the Hawaiian Archipelago, and found that habitat specialists and endemic species provided most of the resolution for regional structuring. As with the studies in the Coral Triangle, most of the concordant

Table 1. Recent examples of cryptic evolutionary lineages and new species identified in Hawaiian waters with DNA sequence data. In most cases (except noted with [a]), a previously widespread species is split into an Indo-Pacific taxon and an endemic Hawaiian taxon. In all cases, the new species are restricted to the Hawaiian biogeographic province, which may include Johnston Atoll to the south. In some cases, Hawai'i is the type location for the original species description, and so the scientific binomial name is retained for the Hawaiian species, but designated here as *sensu stricto*. 16S = mtDNA 16S ribosomal gene; COI = mtDNA cytochrome oxidase subunit 1; CR = mtDNA control region; cytb = mtDNA cytochrome *b*; nDNA = nuclear DNA sequences.

Category (family)	Former species name	New Hawaiian species name	Basis for distinction of Hawaiian form	Reference
Shrimp[a] (Atyidae)	*Halocaridina rubra*	Undescribed	Two allopatric lineages on Hawaii Island, distinguished by 2.7–4.9% in mtDNA COI	Santos (2006)
Sea slug (Tergipedidae)	*Phestilla minor*	Undescribed	Lineages distinguished by 8.1–11.1% in COI/16S, accompanied by coral host shift	Faucci et al. (2007)
Bonefish (Albulidae)	*Albula neoguinaica*	*A. virgata*	Resurrected species based on morphological comparisons	Hidaka et al. (2008)
Sharpnose puffer (Tetradontidae)	*Canthigaster coronata*	*C. coronata* (sensu stricto)	Hawaiian form distinguished by morphology, coloration, and divergence in mtDNA CR	Randall et al. (2008)
Wrasse (Labridae)	*Halichoeres ornatissimus*	*H. ornatissimus* (sensu stricto)	Hawaiian form distinguished by morphology, coloration, and 1% divergence in mtDNA COI	Randall and Rocha (2009)
Surgeonfish (Acanthuridae)	*Acanthurus nigroris*	*Acanthurus nigroris* (sensu stricto)	Hawaiian form distinguished by morphology and 4.1% divergence in mtDNA cytb	Randall et al. (2011)
Round Herring (Clupeidae)	*Etrumeus micropus*	*Etrumeus makiawa*	Hawaiian form distinguished from Japanese species by morphology and 4.6% divergence in mtDNA cytb	Randall and Dibattista (2012)
Stony Coral[a] (Agariciidae)	*Leptoseris* spp.	Undescribed	Lineage distinguished by morphology, depth distribution, and divergence at *cox*1-1-rRNA mtDNA intron	Luck et al. (2013)
Isopod[a] (Ligiidae)	*Ligia hawaiensis*	Multiple undescribed	Multiple colonization from coastal to terrestrial habitat. Three deep mtDNA/nDNA lineages accompanied by differences in body shape	Santamaria et al. (2013)

[a]Indicates new species discovered within endemic Hawaiian species.

population structure in Hawai'i is driven by invertebrates, with fish showing little structure overall. Hence a primary lesson emerges from the Hawaiian experience: To resolve the limits of genetic connectivity for large marine ecosystems and protected areas, a focus on the invertebrates and endemics is appropriate.

These very large studies have increased our understanding of dispersal in the ocean, however the statistical methods to combine DNA data from multiple species is still rudimentary. Toonen et al. (2011) used a simple Chi-squared test for significant geographic clusters of population genetic breaks in codistributed species. Additional tests with multivariate statistics show promise for resolving general patterns in population genetic data from multiple species (Selkoe et al. 2014).

Evolutionary Studies to Resolve Origins of Hawaiian Biodiversity

Biodiversity hotspots have long been heralded as conservation priorities (Roberts et al. 2002). However, a less appreciated priority is the dispersal pathways between ecosystems or biogeographic provinces, the gateways that allow the expansion and proliferation of biodiversity. One example is the Agulhas Province in southern Africa, a warm-tropical system that can occasionally allow Indo-Pacific species to colonize the tropical Atlantic (Rocha et al. 2005; Briggs and Bowen 2013). This colonization is mediated by climate-glacial cycles, and so is not directly under the purview of human influences (yet). In Hawai'i, avenues of colonization are the foundation for all life in this isolated archipelago. Bird et al. (2011) demonstrated that the endemic limpets (genus *Cellana*) in Hawai'i are the product of a single colonization from the vicinity of Japan, about 3–7 Ma. Craig et al. (2010) showed that endemic butterflyfish (genus *Chaetodon*) in Hawai'i colonized from both the South Pacific and West Pacific.

Hodge et al. (2014) show that the reef fishes of Hawai'i arrived in 2 primary pulses, the first about 8–12 Ma and the second less than 3 Ma, coincident with changes in ocean circulation.

More directly pertinent to Hawaiian conservation is the case of Johnston Atoll, 865 km south of the Hawaiian Archipelago and the closest shallow reef habitat. Based on species composition, Johnston is assigned to the Hawaiian biogeographic province (Briggs and Bowen 2012), and this atoll has long been postulated to be a gateway into the Hawaiian Islands (Grigg 1981; Maragos and Jokiel 1986; Hourigan and Reese 1987; Kosaki et al. 1991). More recently, oceanographic data indicate larval transport from Johnston into the center of the Hawaiian Archipelago (Kobayashi 2006) (Figure 2a). Phylogeographic surveys also support this hypothesis. In studies of 4 Hawaiian bottomfishes, 3 showed elevated genetic diversity in the middle of the archipelago, a finding that authors attribute to propagule input from Johnston Atoll (Figure 2b; Rivera et al. 2011; Gaither et al. 2011; Andrews et al. 2014). Population genetic surveys based on mtDNA and microsatellites also show low or no significant F_{ST} between Johnston and the middle of the Hawaiian Archipelago for damselfish (*Dascyllus trimaculatus*; Leray et al. 2010), sea cucumber (*Holothuria atra*; Skillings et al. 2011), crown-of-thorns sea star (*Acanthaster planci*; Timmers et al. 2011), and butterflyfish (*Chaetodon lunulatus*; Waldrop et al. 2016). This gateway might be bidirectional, as Johnston is an outpost of Hawaiian endemic fauna (DiBattista et al. 2011; Skillings et al. 2011). In this case, phylogeography, oceanography, and biogeography support the hypothesis that Johnston Atoll is a gateway for Hawaiian biodiversity, making this tiny outpost a high priority in terms of evolutionary conservation.

This conservation priority is heightened by the history of Johnston Atoll, under US jurisdiction since 1858. For over
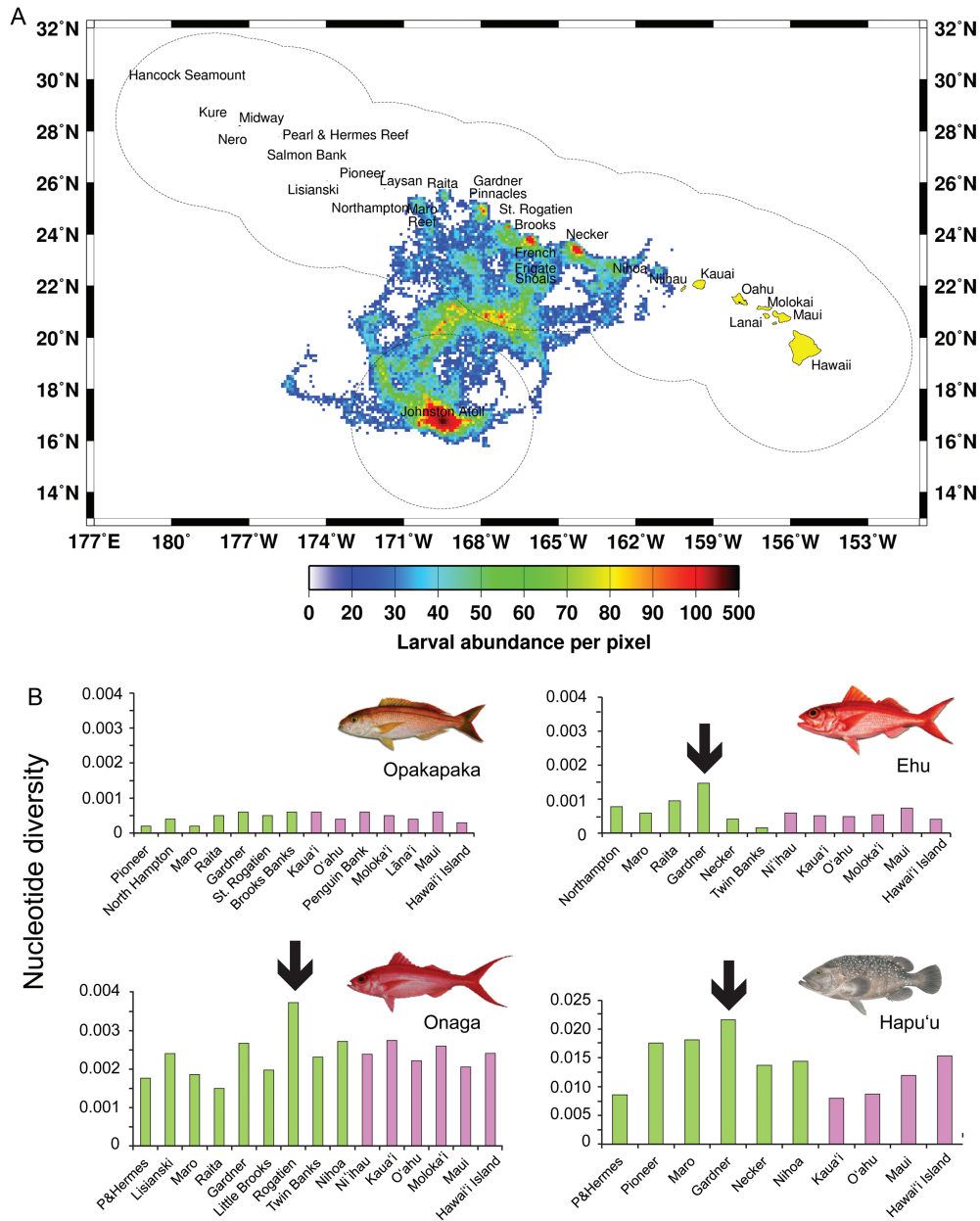
Figure 2. (**A**) Above: Pathway showing projected larval dispersal from Johnston Atoll into the middle of the Hawaiian archipelago, using a Lagrangian model and ocean current data (from Kobayashi (2006) with permission). (**B**) Below: Three of four bottomfishes show significantly elevated nucleotide diversity in the middle of the archipelago, as indicated by black arrows, consistent with larval input from Johnston Atoll. Species designations are Opakapaka (*Pristipomoides filamentosus*), Ehu (*Etelis carbunculus*), Onaga (*Etelis coruscans*), Hapu'u (*Hyporthodus quernus*). Pink bars indicate locations in the inhabited main Hawaiian Islands and green bars indicate locations in the Papahānaumokuākea Marine National Monument. Data are from Rivera, Andrews et al. (2011), Gaither et al. (2011), and Andrews et al. (2014).

70 years, it was a military installation, cumulatively housing tens of thousands of personnel. Two new islands were created by dredging the coral reefs. Johnston was a nuclear test site in the 1960s, resulting in heavy plutonium contamination that was dumped (as topsoil) into the lagoon. Subsequently this atoll was used to test biological weapons, then was a storage facility for 25 000 barrels of the defoliant 'agent orange' (used in the Vietnam War from 1961 to 1971) and nerve gas, both of which leaked into the environment (Lobel 2003). In the years 1990–2001, it was a chemical weapons disposal site for the United States, to eliminate nerve gas that had been banned by international treaty. Chemical contamination is believed to be the cause of developmental abnormalities in resident

reef fishes (Lobel 2011), and the cumulative effects are postulated to be the reason why marine mammals are rare at Johnston Atoll (Lobel 2003). The military presence at Johnston ended in 2004 and the site is now protected as a marine national monument administrated by the US Fish and Wildlife Service. However, the marine gateway into Hawai'i was subject to severe environmental insults over the last century.

Conclusion

Conservation efforts can be classified into 3 broad categories, addressing phylogenetic, ecological, or evolutionary priorities. The

isolated Hawaiian Archipelago provides a microcosm to examine these 3 priorities, in a way that may be obscured on more complex seascapes or landscapes. Genetic resolution of phylogenetic partitions, ecosystem partitions, and dispersal pathways, are all relevant to conservation. Evolutionary conservation has received the least attention, but has the inevitability of time's march, as conservation horizons extend from decades into millennia. The rapidly developing technology and methodology for genomics will advance evolutionary conservation (Funk et al. 2012; Gaither et al. 2015), but the venerable fields of taxonomy, ecology, and biogeography are the starting points for these ventures.

References

Ahti AP, Coleman RR, DiBattista JD, Berumen ML, Rocha LA, Bowen BW. 2016. Phylogeography of Indo_Pacific reef fishes: Sister wrasses *Coris gaimard* and *C. cuvieri* in the Red Sea, Indian Ocean, and Pacific Ocean. *J Biogeogr*, doi:10.1111/jbi.12712.

Allendorf FW, Aitken SN, Luikart G. 2013. *Conservation and the genetics of populations*. Hoboken (NJ): Wiley-Blackwell Publishing.

Andrews KR, Karczmarski L, Au WWL, Rickards S, Vanderlip CA, Bowen BW, Toonen RJ. 2010. Rolling stones and stable homes; Social structure, habitat diversity, and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*). *Mol Ecol*. 19:732–748.

Andrews KR, Moriwake V, Wilcox C, Kelley C, Grau EG, Bowen BW. 2014. Population genetic analyses of *Etelis coruscans* and *Etelis marshi* reveal consistent patterns of genetic structure for deepwater fishes across the Hawaiian Archipelago. *PLoS One*. 9:e91665.

Avise JC. 2000. *Phylogeography. The history and formation of species*. Cambridge (MA): Harvard University Press.

Baker CS, Steel DJ, Calambokidis J, Falcone E, González-Peral U, Barlow J, Burdin AM, Clapham PJ, Ford JKB, Gabriele CM, *et al.* 2013. Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Mar Ecol Prog Ser*. 494:291–306.

Barber PH, Cheng SH, Erdmann MV, Tengardjaja K, Ambariyanto. 2011. Evolution and conservation of marine biodiversity in the Coral Triangle: insights from stomatopod Crustacea. *Crustacean Issues*. 19:129–156.

Baums IB, Godwin S, Franklin E, Carlon D, Toonen RJ. 2014. Discordant population expansions in four species of coral-associated, Pacific hermit crabs (Anomura: Diogenidae) linked to habitat availability resulting from sea level change. *J Biogeogr*. 41:339–352.

Bird CJ, Holland BS, Bowen BW, Toonen RJ. 2007. Contrasting population structure in three endemic Hawaiian limpets (*Cellana* spp.) with similar life histories. *Mol Ecol*. 16:3173–3186.

Bird CE, Holland BS, Bowen BW, Toonen RJ. 2011. Diversification of endemic sympatric limpets (*Cellana* spp.) in the Hawaiian Archipelago. *Mol Ecol*. 20:2128–2141.

Bolten AB, Bjorndal KA, Martins HR, Dellinger T, Biscoito MJ, Encalada SE, Bowen BW. 1998. Trans-Atlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analyses. *Ecol Appl*. 8:1–7.

Bowen BW, Roman J. 2005. Gaia's handmaidens: the Orlog model for conservation biology. *Cons Biol*. 19:1037–1043.

Bowen BW, Abreu-Grobois FA, Balazs GH, Kamezaki N, Limpus CJ, Ferl RJ. 1995. Trans-Pacific migrations of the loggerhead sea turtle demonstrated with mitochondrial DNA markers. *Proc Natl Acad Sci USA*. 92:3731–3734.

Bowen BW, Gaither MR, DiBattista JD, Iacchei M, Andrews KR, Grant WS, Toonen RJ, Briggs JC. 2016. Comparative phylogeography of the ocean planet. *Proc Natl Acad Sci USA*.

Briggs JC, Bowen BW. 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. *J Biogeogr*. 39:12–30.

Briggs JC, Bowen BW. 2013. Evolutionary patterns: marine shelf habitat. *J Biogeogr*. 40:1023–1035.

Carpenter KE, Barber PH, Crandall ED, Ablan-Lagman MCA, Mahardika GN, Manjaji-Matsumoto BM, Juinio-Meñez MA, Santos MD, Starger CJ, Toha AHA. 2011. Comparative phylogeography of the Coral Triangle and implications for marine management. *J Mar Biol*. Article ID 396982.

Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB, Ehrhart LM, Limpus CJ, Suganuma H, Troëng S, Yamaguchi M. 2008. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob Ecol Biogeogr*. 17:297–304.

Coleman RR, Gaither MR, Kimokeo B, Stanton FG, Bowen BW, Toonen RJ. 2014. Large-scale introduction of the Indo-Pacific damselfish *Abudefduf vaigiensis* into Hawai'i promotes genetic swamping of the endemic congener *A. abdominalis*. *Mol Ecol*. 23:5552–5565.

Concepcion GT, Baums IB, Toonen RJ. 2014. Regional population structure of *Montipora capitata* across the Hawaiian archipelago. *Bull Mar Sci*. 90:257–275.

Craig MT, Eble J, Bowen BW. 2010. Origins, ages, and populations histories: Comparative phylogeography of endemic Hawaiian butterfly fishes (genus *Chaetodon*). *J Biogeogr*. 37:2125–2136.

Daly-Engel TS, Grubbs RD, Feldheim KW, Bowen BW, Toonen RJ. 2010. Is multiple paternity beneficial or unavoidable? Low multiple paternity and genetic diversity in the shortspine spurdog shark (*Squalus mitsukurii*). *Mar Ecol Prog Ser*. 403:255–267.

Darwin CR. 1859. *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: John Murray.

DiBattista JD, Wilcox C, Craig MT, Rocha LA, Bowen BW. 2011. Phylogeography of the Pacific Blueline Surgeonfish *Acanthurus nigroris* reveals a cryptic species in the Hawaiian Archipelago. *J Mar Biol*. Article ID 839134.

DiBattista JD, Craig MT, Rocha LA, Feldheim KA, Bowen BW. 2012. Phylogeography of the Indo-Pacific butterflyfishes, *Chaetodon meyeri* and *Chaetodon ornatissimus*: Sister species reveal divergent evolutionary histories and discordant results from mtDNA and microsatellites. *J Hered*. 103:617–629.

Dimmick WW, Ghedotti MJ, Grose MJ, Maglia AM, Meinhardt DJ, Pennock DS. 1999. The importance of systematic biology in defining units of conservation. *Cons Biol*. 13:653–660.

Dutton DL, Dutton PH, Chaloupka M, Boulon RH. 2005. Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biol Cons*. 126:186–194.

Eble JA, Toonen RJ, Bowen BW. 2009. Endemism and dispersal: comparative phylogeography of three surgeonfish species across the Hawaiian Archipelago. *Mar Biol*. 156:689–698.

Eble JA, Rocha LA, Craig MT, Bowen BW. 2011a. Not all larvae stay close to home: Long-distance dispersal in Indo-Pacific reef fishes, with a focus on the Brown Surgeonfish (*Acanthurus nigrofuscus*). *J Mar Biol*. Article ID 518516.

Eble JA, Toonen RJ, Sorenson L, Basch LV, Papastamatiou YP, Bowen BW. 2011b. Escaping paradise: Larval export from Hawaii in an Indo-Pacific reef fish, the Yellow Tang (*Zebrasoma flavescens*). *Mar Ecol Prog Ser*. 428:245–258.

Erwin TL. 1991. An evolutionary basis for conservation strategies. *Science* 253:750–752.

Faucci, A. 2007. *The influence of larval dispersal potential on speciation, phylogeography, and genetic population structure in two Pacific marine snail groups*. Ph.D. thesis, University of Hawai'i, Honolulu, HI.

Faucci A, Toonen RJ, Hadfield MG. 2007. Host shift and speciation in a coral-feeding nudibranch. *Proc Roy Soc Lond B*. 274:111–119.

Forey PL, Humphries CJ, Vane-Wright RI, editors. 1994. *Systematics and Conservation Evaluation. Systematics Association special volume 50*. Oxford: Clarendon Press.

Frankham R. 2005. Genetics and extinction. *Biol Cons*. 126:131–140.

Fraser DJ, Bernatchez L. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol Ecol*. 10:2741–2752.

Funk VA, Wagner WL. 1995. Biogeography of seven ancient Hawaiian plant lineages. In: Wagner WL, Funk VA, editors. *Hawaiian biogeography; evolution on a hotspot Archipelago*. Washington (DC): Smithsonian Institution Press.

Funk WC, McKay JK, Hohenlohe PA, Allendorf FW. 2012. Harnessing genomics for delineating conservation units. *Trends Ecol Evol*. 27:489–496.

Gaither MR, Bowen BW, Toonen RJ, Planes S, Messmer V, Earle J, Ross Robertson D. 2010. Genetic consequences of introducing allopatric lineages of Bluestriped Snapper (*Lutjanus kasmira*) to Hawaii. *Mol Ecol*. 19:1107–1121.

Gaither MR, Jones SA, Kelley C, Newman SJ, Sorenson L, Bowen BW. 2011. High connectivity in the deepwater snapper *Pristipomoides filamentosus* (Lutjanidae) across the Indo-Pacific with isolation of the Hawaiian Archipelago. *PLoS One*. 6:e28913.

Gaither MR, Bernal MA, Coleman RR, Bowen BW, Jones SA, Simison WB, Rocha LA. 2015. Genomic signatures of geographic isolation and natural selection in coral reef fishes. *Mol Ecol*. 24:1543–1557.

Gillespie R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science*. 303:356–359.

Grigg RW. 1981. *Acropora* in Hawai'i. Part 2. Zoogeography. *Pac Sci*. 35:15–24.

Guerber HA. 1909. *Mythos of the Norsemen: from the eddas and the sagas*. London: G.G. Harrap.

Harbaugh DT, Wagner WL, Allan GJ, Zimmer EA. (2009). The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: an example from the plant genus *Melicope* (Rutaceae) *J. Biogeogr*. 36:230–241.

Hardy DE, Kaneshiro KY. 1981. Drosophilidae of the Pacific Oceania. In: Ashburner M, Carson HL, Thompson JJN, editors. *The genetics and biology of Drosophila*. New York: Academic Press.

Harrisson KA, Pavlova A, Telonis-Scott M, Sunnucks P. 2014. Using genomics to characterize evolutionary potential for conservation of wild populations. *Evol Appl*. 7:1008–1025.

Harvey MS, Rix MG, Framenau VW, Hamilton ZR, Johnson MS, Teale RJ, Humphreys G, Humphreys WF. 2011. Protecting the innocent: studying short-range endemic taxa enhances conservation outcomes. *Invert Systemat*. 25:1–10.

Hendry AP, Waples R. editors. 2008. Evolutionary perspectives on salmonid conservation and management. *Evol Appl*. 1:183–423.

Hidaka K, Iwatsuki Y, Randall JE. 2008. A review of the Indo-Pacific bonefishes of the *Albula argentea* complex, with a description of a new species. *Ichthy Res*. 55:53–64.

Hixon MA, Pacala SW, Sandin SA. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*. 83:1490–1508.

Hodge JR, van Herwerden L, Bellwood DR. 2014. Temporal evolution of coral reef fishes: global patterns and disparity in isolated locations. *J Biogeogr*. 41:2115–2127.

Hohenlohe PA, Bassham S, Etter PD, Stiffler N, Johnson EA, Cresko WA. 2010. Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genet*. 6:e1000862.

Hourigan TF, Reese ES. 1987. Mid-ocean isolation and the evolution of Hawaiian reef fishes. *Trends Ecol Evol*. 2:187–191.

Iacchei M, O'Malley JM, Toonen RJ. 2014. After the gold rush: population structure of spiny lobsters in Hawai'i following a fishery closure and the implications for contemporary spatial management. *Bull Mar Sci*. 90:331–357.

Kahng SE, Copus JM, Wagner D. 2014. Recent advances in the ecology of mesophotic coral reef ecosystems (MCEs). *Curr Opin Environ Sustain*. 7:72–81.

Keeley SC, Funk VA. 2011. Origin and evolution of Hawaiian endemics: new patterns revealed by molecular phylogenetic studies. In Bramwell D, Caujapé-Castells J, editors. *The biology of island floras*. Cambridge: Cambridge University Press. p. 57–88

Kelly RP, Palumbi SR. 2010. Genetic structure among 50 species of the northeastern Pacific rocky intertidal community. *PLoS One*. 5:e8594.

Kinlan BP, Gaines SD, Lester SE. 2005. Propagule dispersal and the scales of marine community process. *Divers Distrib*. 11:139–148.

Kobayashi DR. 2006. Colonization of the Hawaiian Archipelago via Johnston Atoll: a characterization of oceanographic transport corridors for pelagic larvae using computer simulations. *Coral Reefs*. 25:407–417.

Kosaki RK, Pyle RL, Randall JE, Irons DK. 1991. New records of fishes from Johnston Atoll with notes on biogeography. *Pac Sci*. 45:186–203.

Lande R, Shannon S. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*. 50:434–437.

Leray M, Beldade R, Holbrook SJ, Schmitt RJ, Planes S, Bernardi G. 2010. Allopatric divergence and speciation in coral reef fish: the three-spot dascyllus, *Dascyllus trimaculatus*, species complex. *Evolution*. 64:1218–1230.

Lerner HR, Meyer M, James HF, Hofreiter M, Fleischer RC. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Curr Biol*. 21:1838–1844.

Lobel LK. 2011. Toxic caviar: using fish embryos to monitor contaminant impacts. In:Pollock NW editors. *Diving for Science 2011. Proceedings of the American Academy of Underwater Sciences 30th Symposium*. Dauphin Island (AL): American Academy of Underwater Sciences.

Lobel PS. 2003. *Marine life of Johnston Atoll, Central Pacific Ocean*. Honolulu (HI): Natural World Press.

Luck DG, Forsman ZH, Toonen RJ, Leicht SJ, Kahng SE. 2013. Polyphyly and hidden species among Hawai'i's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agariciidae) *PeerJ*. 1:e132.

Maragos JE, Jokiel PL. 1986. Reef corals of Johnston Atoll: one of the world's most isolated reefs. *Coral Reefs*. 4:141–150.

Mora C, Chittaro PM, Sale PF, Kritzer JP, Ludsin SA. 2003. Patterns and processes in reef fish diversity. *Nature*. 421:933–936.

Moritz C. 2002. Strategies to protect biological diversity and the processes that sustain it. *Systemat Biol*. 51:238–254.

Mortimer JA, von Brandis RG, Liljevik A, Chapman R, Collie J. 2011. Fall and rise of nesting green turtles (*Chelonia mydas*) at Aldabra Atoll, Seychelles: positive response to four decades of protection (1968–2008). *Chelonian Cons Biol*. 10:165–176.

Noss RF. 1996. Ecosystems as conservation targets. *Trends Ecol Evol*. 11:351.

O'Grady P, Desalle R. 2008. Out of Hawaii: the origin and biogeography of the genus *Scaptomyza* (Diptera: Drosophilidae). *Biol Lett*. 4:195–199.

Pespeni MH, Garfield DA, Manier MK, Palumbi SR. 2012. Genome-wide polymorphisms show unexpected targets of natural selection. *Proc Roy Soc Lond B*. 279:1412–1420.

Polato NR, Concepcion GT, Toonen RJ, Baums IB. 2010. Isolation by distance across the Hawaiian Archipelago in the reef-building coral *Porites lobata*. *Mol Ecol*. 19:4661–4677.

Posadas P, Miranda Esquivel DR, Crisci JV. 2001. Using phylogenetic diversity measures to set priorities in conservation: an example from southern South America. *Cons Biol*. 15:1325–1334.

Ramon M, Nelson P, DeMartini E, Walsh W, Bernardi G. 2008. Phylogeography, historical demography, and the role of post-settlement ecology in two Hawaiian damselfish species. *Mar Biol*. 153:1207–1217.

Randall JE. 1998. Zoogeography of shore fishes of the Indo-Pacific region. *Zool Studies* 37:227–268.

Randall JE, Rocha LA. 2009. *Halichoeres claudia*, a new Indo-Pacific wrasse (Perciformes: Labridae), the fourth species of the *H. ornatissimus* complex. *Zool Studies* 48:709–718.

Randall JE, DiBattista JD. 2012. *Etrumeus makiawa*, a new species of Round Herring (Clupeidae: Dussumierinae) from the Hawaiian Islands. *Pac Sci*. 66:97–110.

Randall JE, Williams JT, Rocha LA. 2008. The Indo-Pacific tetradontid fish *Canthigaster coronata*, a complex of three species. *Smithiana* 9:3–13.

Randall JE, DiBattista JD, Wilcox C. 2011. *Acanthurus nigros* Gunther, a valid species of surgeonfish, distinct from the Hawaiian *A. nigroris* Valenciennes. *Pac Sci*. 65:265–275.

Reece JS, Bowen BW, Larson A. 2011. Long larval duration in moray eels (Muraenidae) ensures ocean-wide connectivity despite differences in adult niche breadth. *Mar Ecol Progr Ser*. 437:269–277.

Rivera M, Andrews K, Kobayashi D, Wren J, Kelley C, Roderick G, Toonen RJ. 2011. Genetic analyses and simulations of larval dispersal reveal distinct populations and directional connectivity across the range of the Hawaiian Grouper (*Epinephelus quernus*). *J Mar Biol*. Article ID 765353.

Roberts CM, McClean CJ, Veron JE, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, *et al*. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*. 295:1280–1284.

Rocha LA, Robertson DR, Rocha CR, Van Tassell JL, Craig MT, Bowen BW. 2005. Recent invasion of the tropical Atlantic by an Indo-Pacific coral reef fish. *Mol Ecol*. 14:3921–3928.

Santamaria CA, Mateos M, Taiti S, DeWitt TJ, Hurtado LA. 2013. A complex evolutionary history in a remote archipelago: Phylogeography and morphometrics of the Hawaiian endemic *Ligia* isopods. *PLoS One*. 8:e85199.

Santos SR. 2006. Patterns of genetic connectivity among anchialine habitats: a case study of the endemic Hawaiian shrimp *Halocaridina rubra* on the island of Hawaii. *Mol Ecol*. 15:2699–2718.

Schultz JK, Baker JD, Toonen RJ, Harting AL, Bowen BW. 2011. Range-wide genetic connectivity of the Hawaiian monk seal and implications for transplantation. *Cons Biol*. 25:124–132.

Selkoe KA, Gaggiotti OE, Bowen BW, Toonen RJ; ToBo Laboratory. 2014. Emergent patterns of population genetic structure for a coral reef community. *Mol Ecol*. 23:3064–3079.

Shaw KL. 1995. Biogeographic patterns of two independent Hawaiian cricket radiations (*Laupala* and *Prognathogryllus*). In: Wagner WL, Funk VA, editors. *Hawaiian Biogeography; Evolution on a Hotspot Archipelago*. Washington (DC): Smithsonian Institution Press.

Sheppard C, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Eble J, FitzSimmons N, *et al*. 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: Why it is the world's largest no-take marine protected area. *Aquatic Cons: Mar Freshw Ecosyst*. 22:232–261.

Skillings DJ, Bird CE, Toonen RJ. 2011. Gateway to Hawai'i: Genetic population structure of the tropical sea cucumber *Holothuria atra*. *J Mar Biol*. Article ID 783030.

Soulé ME, Wilcox, editors. 1980. *Conservation biology: an evolutionary-ecological perspective*. Sunderland (MA): Sinauer Associates.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdana ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, *et al*. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*. 57:573–583.

Tenggardjaja KA, Bowen BW, Bernardi G. 2016. Reef fish dispersal in the Hawaiian Archipelago: comparative phylogeography of three endemic damselfishes. *J Mar Biol*. In press.

Timmers MA, Andrews K, Bird CE, deMaintenon MJ, Brainard RE, Toonen RJ. 2011. Widespread dispersal of the crown-of-thorns sea star, Acanthaster planci, across the Hawaiian Archipelago and Johnston Atoll. *J Mar Biol*. Article ID 934269.

Toonen RJ, Andrews KR, Baums IB, Bird CE, Concepcion CT, Daly-Engel TS, Eble JA, Faucci A, Gaither MR, Iacchei M, *et al*. 2011. Defining boundaries for applying ecosystem-based management: A multispecies case study of marine connectivity across the Hawaiian Archipelago. *J Mar Biol*. Article ID 460173.

Toonen RJ, Wilhelm TA, Maxwell SM, Wagner D, Bowen BW, Sheppard C, Taei SM, Teroroko T, Moffitt R, Gaymer CF, *et al*. 2013. One size does not fit all: The emerging frontier in large-scale marine conservation. *Mar Poll Bull*. 77:7–10.

Waldrop E, Hobbs JP, Randall JE, DiBattista JD, Rocha LA, Kosaki RK, Berumen ML, Bowen BW. 2016. Phylogeography, population structure, and evolution of coral-feeding butterflyfishes (Family Chaetodontidae, genus *Chaetodon*, subgenus *Corallochaetodon*). *J Biogeogr*. Advance Access published January 11, 2016, doi:10.1111/jbi.12680