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Species Radiations in the Sea: What the Flock?

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Abstract

Species flocks are proliferations of closely-related species, usually after colonization of depauperate habitat. These radiations are abundant on oceanic islands and in ancient freshwater lakes, but rare in marine habitats. This contrast is well documented in the Hawaiian Archipelago, where terrestrial examples include the speciose silverswords (sunflower family Asteraceae), *Drosophila* fruit flies, and honeycreepers (passerine birds), all derived from one or a few ancestral lineages. The marine fauna of Hawai'i is also the product of rare colonization events, but these colonizations usually yield only one species. Dispersal ability is key to understanding this evolutionary inequity. While terrestrial fauna rarely colonize between oceanic islands, marine fauna with pelagic larvae can make this leap in every generation. An informative exception is the marine fauna that lack a pelagic larval stage. These low-dispersal species emulate a "terrestrial" mode of reproduction (brooding, viviparity, crawl-away larvae), yielding marine species flocks in scattered locations around the world. Elsewhere, aquatic species flocks are concentrated in specific geographic settings, including the ancient lakes of Baikal (Siberia) and Tanganyika (eastern Africa), and Antarctica. These locations host multiple species flocks across a broad taxonomic spectrum, indicating a unifying evolutionary phenomenon. Hence marine species flocks can be singular cases that arise due to restricted dispersal or other *intrinsic* features, or they can be geographically clustered, promoted by *extrinsic* ecological circumstances. Here, we review and contrast intrinsic cases of species flocks in individual taxa, and extrinsic cases of geological/ecological opportunity, to elucidate the processes of species radiations.

Key words: ancient lakes, dispersal, endemism, monophyly, oceanic islands, sympatric speciation

The first species flock recognized in scientific circles was the tanager finches native to the Galápagos Islands (Darwin 1859). Since that time, the concepts of species flocks and adaptive radiations have been intertwined in the evolutionary literature, although they are not the same thing. Ribbink (1984) defined a species flock as "an assemblage of a disproportionately high number, relative to surrounding areas, of closely related species which apparently evolved rapidly within a narrowly circumscribed area to which all the member species are endemic." The essential features of this definition are evolutionary radiation and endemism. In contrast, an adaptive radiation is defined by phenotypes that confer fitness advantages in specific habitats (Schluter 2000), and does not require endemism. The difference between a species flock and an adaptive radiation is readily apparent in Hawaiian spiders: The genus *Orsonwelles* (family Linyphiidae) has 13 Hawaiian species with little ecological differentiation, distinguished by allopatric ranges (Hormiga et al. 2003), whereas the genus *Tetragnatha* has 56+ Hawaiian species (many with overlapping ranges) distinguished by adaptations in morphology, coloration, and feeding behaviors (Gillespie 2016; Cotoras et al. 2018). The former is a nonadaptive radiation, the latter an adaptive radiation, but both are species flocks. Greenwood (1984) added the criterion of monophyly for species flocks, which is followed in most cases by subsequent authors, but may not be an absolute criterion. Based on these definitions and research on Antarctic icefishes, Eastman and McCune (2000) endorsed 5 criteria: evolutionary radiation, high endemicity, monophyly, plus morphological/ecological diversity and habitat dominance (high proportion of biomass). Lecointre et al. (2013), identified the first 3 as criteria for "core flocks," with the addition of morphological/ecological diversity and habitat dominance for "full flocks." Here, we adopt this set of standards for core and full flocks, with the understanding that the "high endemicity" of Lecointre et al. (2013) is concordant with the "narrowly circumscribed area" of Ribbink (1984).

Hawai'i provides perhaps the best documented setting to examine the evolutionary processes that transpire above and below the water line. The isolated volcanic islands of the Hawaiian Archipelago constitute a semi-continuous line that spans 30 million years and 2600 km of the North Pacific. The nearest continental habitat lies 3500 km away in Central America. Consequently, colonization by terrestrial faunas is rare and usually ancient (>10 Ma; Keeley and Funk 2011, but see Price and Clague 2002). In contrast to this extreme terrestrial isolation, the closest shallow marine 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). Despite the difference in colonization distance/age between terrestrial and marine habitats, the unifying theme is that every Hawaiian species has origins somewhere else.

Like the Galápagos Islands, Hawai'i is a showcase for adaptation, and these evolutionary radiations can be spectacular. Terrestrial examples include, for example, 28 silverswords (sunflower family Asteraceae; Wagner et al. 1990), 41 Achatinellinae tree snails (Achatinellidae, plus over 150 extinct species; Cowie et al. 2008), 800+ *Drosophila* fruitflies (Drosophilidae; e.g., Bonacum et al. 2005), 23 *Megalagrion* damselflies (Coenagrionidae; Jordon et al. 2003), 400+ *Hyposmocoma* moths (Cosmopterigidae; Haines et al. 2014), 38 *Laupala* crickets (Gryllidae; Mendelson et al. 2005), 13 *Orsonwelles* spiders (Linyphiidae; Hormiga et al. 2003), and 50+ honeycreepers (passerine birds, Fringillidae; Pratt 2005), all derived from one or a few ancestral lineages. In contrast, the endemic *Cellana* limpets (family Nacellidae) provide a rare example of a marine radiation in Hawai'i, with only 3 species (Bird et al. 2011). Hourigan and Reese (1987) and Wainwright (2015) attributed the scarcity of species radiations in the marine fauna of Hawai'i to the high dispersal potential of pelagic (oceanic) larvae.

The disparity between marine and terrestrial speciation in Hawai'i has another dimension in freshwater radiations. The most complete treatise on evolution of fish species flocks (Echelle and Kornfield 1984) has 18 chapters, all focused on Lakes Baikal and Tanganyika. In these ancient lakes, both older than 9 MY, species flocks exist across a broad taxonomic spectrum of invertebrates and vertebrates.

The purpose of this synthesis is to ask why members of marine species flocks may number in the single digits, while members of terrestrial and freshwater radiations number in the 10s–100s. We accomplish this first by examining specific organismal cases, and patterns of diversification in these marine faunas. We subsequently examine the geographic cases (both freshwater and marine) where aquatic species flocks occur. We chose this format because there are individual cases of species flocks that can be attributed to intrinsic natural history (especially reproductive mode), and there are geographic clusters of species flocks that are promoted by extrinsic ecological opportunity.

Organismal Cases

Here, we review patterns of radiations in specific taxonomic groups, determine whether species flocks (geographic clusters of closely related species) exist in these groups, and seek shared life history traits that may promote radiations.

Porifera

Sponges are the oldest metazoans (>500 Ma) found in a variety of freshwater and marine habitats, including those known to be epicenters for species flocks (Van Soest et al. 2012). Although a few species flocks in sponges have been identified (see below), proving the 5 conditions of the species flock concept defined by Lecointre et al. (2013) is hindered by several taxonomic challenges. These difficulties include poorly supported morphological characters, discordance between morphological and molecular evidence, polyphyly in some orders, and slowly-evolving genetic loci (Pöppe et al. 2010; Redmond et al. 2011; DeBiasse and Hellberg 2015). Many species lack diagnostic characters, making the application of integrative approaches invaluable for taxonomic resolution of species. In addition to these taxonomic challenges, endemism among potential species flocks is based on a limited number of expeditions and samples. While it has been difficult to confirm the criteria for species flocks among sponges, a few examples of endemic sponge species with monophyletic, apomorphic characters have been identified in the Weddell Sea (Antarctica), deep and bathyal habitats of the Galápagos Archipelago, and Lake Baikal (Itskovich et al. 2007; Vargas et al. 2017; Schuster et al. 2018).

The sponge species flock from Lake Baikal belongs to the endemic family Lubomirskiidae, which is comprised of 4 genera and 14 species. The most speciose genera are the *Baikalospongia* (7 species) and *Lubomirskia* (4 species) (Van Soest et al. 2015). Although molecular markers support a deep divergence of fresh water sponges from marine Haplosclerida, the Lubomirskiidae are polyphyletic with other Baikal sponges belonging to the family Spongillidae (Itskovich et al. 2013, 2015), which makes the monophyletic condition for species flocks difficult to prove for the radiation of individual species. In addition, morphological characters that are diagnostic for several families within Haplosclerida are absent in Lubomirskiidae, further complicating the taxonomy of this group. Integrative taxonomy approaches have recently shown the microbial communities and fatty acid composition of the Lubomirskiidae to be species specific and could potentially solve the monophyly dilemma for this family (Itskovich et al. 2017).

One of the only marine sponges that unequivocally meet all criteria of a species flocks are glass sponges (genus *Rossella*), endemic to the Weddell Sea (Antarctica). The radiation in this genus, with at least 5 recognized species, is believed to be a product of Antarctic isolation events and the ecological opportunity thereby provided, as both the origin of *Rossella* (40 ± 20 Ma) and the opening of the Drake passage (~30 Ma, a key event in isolating Antarctica) share a similar timeline (Lawver and Gahagan 2003; Dohrmann et al. 2013). One of the 5 species, *Rossella ricovitzae*, is likely a species complex with 4 lineages defined by high morphological diversity and monophyletic mtDNA lineages (Vargas et al. 2017). An additional species flock could be argued for carnivorous sponges (family Cladorhizidae) from the Weddell Sea, where 15 out of 27 species are endemic (Dressler-Allame et al. 2017). Specifically, the genus *Lycopodina* in the Antarctic includes 4 species, 3 of which are endemic to the Weddell Sea. Further phylogenetic analyses of mitochondrial and nuclear DNA, which show monophyly for other *Lycopodina* spp. (Hestetun et al. 2016) would help confirm the species flock hypothesis for this group.

Similar to the Weddell Sea, the isolated Galápagos Archipelago shows high endemism for a number of invertebrate phyla (James 2013). Approximately 50% of the sponges (37 out of 70 species) are endemic and a recent study has shown that deep-sea habitats extending to the bathyal zone could be a potential hot spot for endemism of tetractinellid sponges (Schuster et al. 2018). Among 7 new species descriptions, Schuster et al. report 3 new species belonging to the genus *Racodiscula* which are closely related to conspecifics in the Caribbean. Nevertheless, Galápagos *Racodiscula* diverge morphologically from Caribbean specimens and monophyly is well supported by mitochondrial and nuclear markers. Collectively, these characters meet all conditions for a species flock for the Galápagos *Racodiscula* spp. although other deep-sea habitats throughout the world should be explored to confirm endemism of Galápagos conspecifics.

Cnidaria

This phylum consists mostly of soft bodied organisms (e.g., jellies, hydroids, sea anemones, sea pens, and corals), that may transition between several forms during their life cycle (e.g., benthic or planktonic larvae, sessile polyps, or free-living medusae). Like the sponges, the documentation of species flocks within cnidarians is inhibited by the scarcity of informative morphological characters, and remarkable morphological flexibility in adult stages. Reproductive modes and planktonic larval duration can be highly variable in cnidarians, even within species.

Coral species relationships are challenging to resolve due to pervasive phenotypic plasticity (Todd 2008), convergent evolution, and potential hybridization between species (van Oppen et al. 2001; Vollmer and Palumbi 2002; Willis et al. 2006; Forsman et al. 2017). Cnidarians in general have slowly evolving or uninformative genetic markers (Huang et al. 2008) with limited utility for evaluating recent evolutionary radiations (Neigel et al. 2007; Shearer and Coffroth 2008). Comparisons of more ancient divergences have resulted in taxonomic upheaval (Romano and Palumbi 1996), and surprising examples of convergent evolution between families and genera of reef building corals (Fukami et al. 2004). This taxonomic uncertainty has obscured biogeographic patterns and confounded conservation strategies. Many corals have been proposed for endemic, threatened, or endangered status, yet, while they may have trade protection through CITES, only a few corals are actually listed for IUCN protected status despite rapid global decline (Brainard et al. 2011).

Informative molecular markers have been the exception rather than the rule (Flot and Tillier 2007; Forsman et al. 2013; Luck et al. 2013; Pochon et al. 2015; Johnston et al. 2018), yet despite these challenges, several studies have discovered patterns of genetic structure consistent with recent divergence across habitat gradients. Carlon and Budd (2002) discovered shallow genetic divergence in 2 ecomorphs ("tall" and "short") of Caribbean mushroom coral *Favia fragum* across a depth distribution, despite the absence of spatial barriers to gene flow (see also Carlon and Lippé 2011). Similar patterns of recent divergence across depth gradients have been observed in other reef building corals, for example, *Seriatopora hystrix* and associated algal symbionts showed more genetic structure by depth than geographic location across the Great Barrier Reef (Bongaerts et al. 2011). Genetic structure across depth gradients has also been observed in *Porites* corals in Sāmoa (Barshis et al. 2010) and Hawai‘i (Tisthammer and Richmond 2018), and in Agaricid coral species in the Caribbean and Hawai‘i (Bongaerts et al. 2013; Luck et al. 2013; Pochon et al. 2015). Although these radiations are recent and monophyletic, endemic status is uncertain due to sparse sampling across the geographic range.

In contrast to geographic isolation as a driver of adaptive radiations, there are multiple examples of host–symbiont, or host–parasite radiations within this group, for example, in myxozoa which are obligately parasitic cnidarian animals (Fiala et al. 2015), or in hydrozoa, which have highly host-specific symbiotic relationships (Puce et al. 2008). Endosymbionts of cnidarians may be driving adaptive radiations (Thornhill et al. 2014; LaJeunesse et al. 2018).

Evidence for species flocks remains scarce for corals and other cnidarians, but it is not yet clear if this is due to lack of adequate study. As genomic resources become more common and widely available (Wang et al. 2009; Shinzato et al. 2011; Shumaker et al. 2019), and high throughput assays continue to be developed (e.g., Quattrini et al. 2018), biogeographic patterns will be more thoroughly resolved. As with other marine invertebrates, biodiversity is poorly studied relative to terrestrial taxa. However, species flocks appear less common than diversification associated with symbiont/parasite/host relationships, or across habitat gradients.

Gastropoda

Vermetid gastropods are known as tube snails or worm snails, because their tubular shells are cemented to rock or other hard surface. Three marine species in the Hawaiian Archipelago (*Dendropoma gregarium*, *Dendropoma platypus*, *Dendropoma rhyssoconchum*) are characterized by multiple cryptic evolutionary lineages, with monophyletic clades that appear to be isolated by historical lava flows (Faucci 2007). The highly structured phylogeographic patterns within and among islands are more similar to that of terrestrial animals, than to marine species studied to date. Notably, these species mostly lack planktonic stages, with larvae that crawl away on the substrate before cementing themselves into a permanent home. Mediterranean populations of the vermetid gastropod *Dendropoma petraeum* are divided into at least 4 distinct geographic areas according to concordant genetic divergences in COI and ITS sequence data (Calvo et al. 2009). Differences in life histories among the distinct geographic areas of this species with crawl away larvae led Calvo et al. (2009) to postulate that *D. petraeum* is a cryptic species complex.

This pattern of highly divergent populations (or cryptic species) has been observed in other marine gastropods. The turbinid gastropod *Astralium rhodostomum* was originally described as widespread on oceanic islands of the Indo-Pacific, but is actually a species complex comprising at least 30 monophyletic lineages, each corresponding to a single or a few neighboring islands. Meyer et al. (2005) found endemic lineages on islands separated by as little as 180 km, in a pattern they likened to terrestrial fauna of oceanic islands.

Cone snails (family Conidae, genus *Conus*) are a remarkable group of venomous snails with a worldwide distribution and more than 700 species. They are characterized by a suite of specialized venoms that allow exploitation of prey that would otherwise be unavailable, including fishes (Olivera et al. 2014). Most *Conus* species are widely distributed with planktonic larvae, but Cape Verde hosts 47 endemic species that are direct developers. Most of these endemic species are restricted to single islands or to particular bays within islands. Low levels of gene flow and patchy distributions of suitable habitat resulted in one of the few cases of marine species flocks occurring in a narrowly circumscribed geographic area (Duda and Rolán 2005). It is possible that species flocks occur elsewhere in the global range of this speciose group (e.g., Kohn 2015).

Crustacea

Crustaceans are unusual among marine animals in that sperm are nonmotile, and thus fertilization is internal (Subramoniam 2017). Internally fertilized eggs are brooded by females until they hatch and are released as larvae. Crustaceans are also known for their complex, biphasic, life histories in which they pass through multiple larval phases (planktonic or lecithotrophic). These larval forms are often radically different from the adult form and thus are exposed to selective forces apart from the adult phase (Charmantier 1998). However, some crustaceans (e.g., isopods, amphipods, and branchiopods) lack a larval stage completely, and pass directly from embryo to juveniles (manca stage), which typically results in reduced dispersal (Martin et al. 2014).

Crustacean species flocks have been well documented from ancient lakes and inland seas for mysids (Väinölä 1995), ostracods (Martens 1997; Wouters and Martens 2001; Schön and Martens 2012), and amphipods (Naumenko et al. 2017), but are rare in marine environments. The primary exceptions to this rarity are the amphipoda and isopoda of the Southern Ocean, particularly Antarctica, which lack a pelagic larval stage. Two genera of amphipods, *Eusirus* (>50 species) and *Epimeria* (>80 species), include large species with oxygen requirements that are most likely only attainable in the cold waters of the Southern Ocean (Lecointre et al. 2013). Both genera are distributed outside of the Southern Ocean, but their Antarctic representatives are monophyletic (Loerz et al. 2009; Baird et al. 2011; Verheye et al. 2017). The Antarctic *Eusirus* is estimated to have evolved between 4 and 14 Ma (Verheye 2011) and the *Epimeria* were estimated to have split from their last common ancestor about 15.7 Ma, with their closest extant relatives found in New Zealand (Lörz and Held 2004; Loerz et al. 2009). The rapid speciation and ecological diversification in the *Epimeria* may have resulted from the close link between the diversity of feeding modes and various modes of mobility observed in this group (Dauby et al. 2002). Among Antarctic isopods, the family *Serolidae* is the only group that clearly satisfies all of the requirements of a full species flock, despite the speciosity and endemicity of several other Antarctic isopod lineages (Lecointre et al. 2013). These are benthic animals on soft-bottom habitats that brood their young and lack a free-swimming stage (Held 2000). The Antarctic *Serolidae* (>30 species) are estimated to have evolved after the establishment of the Drake Passage, ~30 Ma (Wägele 1994), and their closest ancestors are found on the continental shelves of South America (Held 2000).

Commensal amphipods in the Caribbean show high endemism on islands, but no population structure along the Florida coast, indicating that limited dispersal potential and fragmented habitat have prompted the higher diversity among islands (Richards et al. 2012). Along the west coast of North America, the intertidal copepod *Tigriopus californicus* is characterized by high intraspecific COI divergences (up to 23%) with F_2 hybrid breakdown, indicating true evolutionary partitions (Burton and Lee 1994; Edmands 2001). Divergences may be propelled by small effective population sizes because of frequent bottlenecks in this fluctuating environment (Edmands 2001; Burton et al. 2006). In Mediterranean marine caves, endemic direct-developing mysids show 5 deep divergent clades originating in the early Miocene (~15 Ma; Rastorgueff et al. 2014). In sum, the crustaceans may provide the clearest example of different evolutionary trajectories in direct developers versus pelagic species, with the former including almost all examples of species flocks in this subphylum.

Marine Teleosts (Bony Fishes)

Most marine teleost fishes exhibit high fecundity and a widely dispersive pelagic larval stage. This life history strategy is thought to be effective in maintaining gene flow across vast distances thereby reducing opportunities for isolation and allopatric speciation (Eble et al. 2015). One family that may form species flocks is the Triplefins (family Tripterygiidae), diminutive reef dwellers in tropical and temperate waters. These species dominate the New Zealand continental shelf, consisting of 24 endemic species with sympatric distributions, at least 18 of which are close relatives (Hickey and Clements 2005). This group appears to have evolved via a local radiation that includes both ecological and geographic components (Hickey et al. 2009). The rockfishes (*Sebastes*) consist of approximately 110 species, of which 96 are found in the northern Pacific Ocean, 62 being restricted to the northeastern Pacific and 28 restricted to the northwest Pacific Ocean (Ingram and Kai 2014). A key feature of this group is viviparity (bearing live young), bypassing the dispersive pelagic stage. Many species within this genus are indistinguishable morphologically but differ in coloration. For instance, the gopher rockfish, *Sebastes carnatus*, and the black-and-yellow rockfish, *S. chrysomelas*, are identical in meristic counts but differ in coloration and habitat preference, with the former inhabiting deeper water. They differ by an average sequence divergence $d = 0.038$ in control region comparisons, but they are not monophyletic (Johns and Avise 1998; Alesandrini and Bernardi 1999; Burford and Bernardi 2008).

Surfperches (family Embiotocidae) are another viviparous marine fish endemic to the temperate North Pacific. Over the last 13–18 Ma they have radiated into 13 genera and 25 species occupying a variety of habitats including sand bottom, seagrass, kelp forests, estuaries, and even freshwater (Longo and Bernardi 2015). The combination of restricted gene flow (no pelagic larval stage) and an intrinsic ability to invade novel ecosystems, allowed a surfperch radiation similar to the cichlids of Lake Tanganyika (see below).

Seven-spined gobies (family Gobiidae) are endemic to the New World with more than 130 species in 24 genera (Rüber et al. 2003). These gobies underwent rapid radiation, first by diverging into major habitat zones such as coastal-estuarine (including freshwater, brackish, and saltwater), rocky intertidal, and coral reef, and even the deep-sea. Subsequent diversification was driven by behavioral and niche specializations, including close ecological associations such as commensal living with snapping shrimp, sea urchins, sponges, or even obligate cleaning behavior.

Few teleosts have the viviparous reproductive mode of rockfishes and surfperches, analogous to brooding or direct development in the invertebrates. One well-studied example is the brooding damselfish *Acanthochromis polyacanthus* (Pomacentridae), which is distributed across the Indo-Australian Archipelago and one of the only coral reef fish species that has direct development from egg to fully developed juvenile (Kavanagh 2000). The lack of a pelagic phase in the species has led to high levels of population structure and apparent adaptation to local environments. Color variants are observed throughout the species range but typically are consistent within populations (van Herwerden and Doherty 2005).

While examples of species flocks exist in groups with very large radiations at small geographic scales, there are other potential cases that require more taxonomic and molecular work. The sand gobies (genus *Pomatoschistus* and their relatives) of the eastern Atlantic-Mediterranean include 14 species in a monophyletic group that appears to have radiated following the Messinian salinity crisis and to a lesser extent during the Pleistocene epoch (Huyse et al. 2004). The intertidal gobies (genus *Luciogobius*) consist of 16 recognized species but as many as 20 more undescribed species likely exist (Yamada et al. 2009; Kanagawa et al. 2011). Finally, the hamlets (genus *Hypoplectrus*) of the Caribbean and Western Atlantic consist of 10 recognized species which have similar morphologies and overlap in habitat and diet but vary considerably in coloration pattern (McCartney et al. 2003).

It is possible that in teleost fishes and other dispersive marine taxa, the perceived absence of species flocks is an artifact of geographic scale. Indo-Pacific reef fishes have an average range size of 9 357 000 km^2, an area roughly the size of China (Allen 2008). Due to the high dispersal potential of pelagic larvae, vast ranges in most cases, and a dearth of geographic barriers to dispersal, the geographic scale of species flocks could simply be much larger in marine systems. This theme is reinforced by the scale of Indo-Pacific sister species distributions; many reef fishes are divided into Pacific and Indian Ocean forms that are divergent across a range from population structure to full species (Bowen et al. 2016). The Coral Triangle (between the Philippines, Indonesia, and New Guinea) is the premier biodiversity hotspot in the Indo-Pacific, hosting many closely-related species. Cowman and Bellwood (2013) estimate that 60% of the Indo-Pacific reef biodiversity has origins here, so this region fulfills at least some of the criteria for species flocks.

Elasmobranchs (Cartilaginous Fishes)

The Chondrichthyes—the class of fishes that are characterized by cartilaginous skeletons—are an ancient group dating back to the Devonian (360–420 Ma), with species occupying marine and freshwater habitats around the globe. The subclass Elasmobranchii, which contains the sharks, skates, and rays, is particularly diverse, with more than 1100 described species (Fowler and Cavanagh 2005). In addition to their species diversity, elasmobranchs display a remarkable level of ecological diversity, having adapted to both marine and freshwater habitats, and having developed an array of feeding strategies ranging from benthic durophagy (rays in the family Myliobatidae and sharks in the order Heterodontiformes) to epipelagic filter-feeding (whale shark *Rhincodon typus* and the rays of the genus *Manta*).

After the K-T extinction event approximately ~65 Ma, these groups underwent a major radiation (Kriwet et al. 2009; Aschliman 2011). For the batoids (skates and rays), the 2 largest centers of radiation were the Indo-West Pacific and the New World; even today, the Indo-West Pacific contains both the greatest species diversity and the highest rates of endemism among the batoids (Aschliman 2011).

Despite extensive morphological and ecological radiations, species flocks are not well-documented within the elasmobranchs. The ancient origins of the major clades, coupled with a high level of vagility observed in many groups, may at least partially explain this paucity. However, it's possible that even groups with lower dispersal capability were able to greatly expand their overall distribution due to continental drift. This is especially true for benthic species occupying shallow, near-shore habitats (Musick et al. 2004), such as the bullhead sharks (order Heterodontiformes), and some carpet sharks (order Orectolobiformes), many of which demonstrate exceptionally limited vagility and small range sizes. Thus, the best candidates for species flocks within the Elasmobranchii are clades that are both 1) the result of relatively recent radiations, and 2) exhibit highly limited range sizes and/or vagility.

Following these criteria, we identify at least 2 potential candidates for elasmobranch species flocks. The first are the carpet sharks (genus *Hemiscyllium*) including 9 small, benthic species, all of which are restricted to New Guinea, northern Australia, and the nearby Indonesian island of Halmahera (Compagno 2001; Allen et al. 2016). The extremely limited distribution of this genus indicates a species flock. However, to date there has been no thorough phylogenetic treatment of this group, and while there is fossil evidence to suggest a late-Cretaceous, Tethyan origin of the genus (Kriwet et al. 2007), there is no recorded fossil evidence of the group within the Indo-Pacific. Therefore, more work is needed to determine the nature and timing of their origins in this region.

The second, and perhaps most compelling, candidate for a species flock within the Elasmobranchii is the stingrays of the family Potamotrygonidae. With the exception of the recently described genus *Styracura* (Carvalho et al. 2016), the family comprises at least 24 species, all of which are obligate freshwater stringrays endemic to tropical and subtropical rivers and wetlands of South America, east of the Andes (Rosa et al. 2010; Garcia et al. 2016). This freshwater radiation appears to be the result of a single invasion event by a marine ancestor about 25 Ma (Rosa et al. 2010; Lucifora et al. 2015; Bloom and Lovejoy 2017). Hence the expansion into freshwater habitat lies at the base of this species flock.

Conclusions about Organismal Cases

This review cannot be comprehensive, so we have focused on taxonomic groups with sufficient information to resolve species flocks (Table 1). It is important to note that most marine radiations do not qualify as species flocks. At least 7 families of hydrothermal vent fauna underwent an adaptive radiation in middle Eocene to early Oligocene (~40 Ma; Lorion et al. 2013; Vrijenhoek 2013). However, these do not meet the species flock criterion of geographic proximity, being globe-spanning in distribution.

One of the difficulties in assessing marine species flocks is underestimated invertebrate diversity, as evidenced by the many cryptic species discovered through molecular techniques. Even groups with large and conspicuous individuals, such as sea cucumbers, are still underestimated. Michonneau et al. (2013) show that the diversity curve of

Table 1. Examples of marine species flocks

	Taxon	Species/lineages	Dispersal	Region of endemism	Flock type	Citation
Porifera	*Rossella* spp.	5+	Low	Antarctica	Full	Vargas et al. (2017)
	Lycopodina spp.	4	Low	Antarctica	Core	Dressler-Allame et al. (2017)
	Racodiscula spp.	3	Low	Galapagos	Core	Schuster et al. (2018)
Gastropoda	*Dendropoma gregarium*	17 lineages[a]	DD[b]	Hawaii	Core	Faucci (2007)
	Dendropoma platypus	11 lineages	DD	Hawaii	Core	Faucci (2007)
	Dendropoma rhyssoconchum	15 lineages	DD	Hawaii	Core	Faucci (2007)
	Dendropoma petraeum	4 lineages	DD	Mediterranean	Core	Calvo et al. (2009)
	Astralium rhodostomum	30+ lineages	Low	Indo-Pacific	Core	Meyer et al. (2005)
	Conus spp.	50	DD	Cape Verde	Full	Duda and Rolán (2005)
	Doris kerguenenensis	29 lineages	DD	Antarctica	Full?	Wilson et al. (2009b)
	Cellana spp.	3	Pelagic	Hawaii	Core	Bird et al. 2011
Crustacea	*Eusirus* spp.	>50	DD	Antarctica	Full	Lecointre et al. (2013)
	Epimeria spp.	>80	DD	Antarctica	Full	Lecointre et al. (2013)
	Serolidae spp.	>30	DD	Antarctica	Full	Lecointre et al. (2013)
	Hemimysis margalefi	5	DD	Mediterranean	Core	Rastorgueff et al. (2014)
Teleostei	Tripterygiidae	26	Limited	New Zealand	Full?	Hickey et al. (2009)
	Sebastes spp.	62	DD	Northeast Pacific	Full?	Ingram and Kai (2014)
	Sebastes spp.	28	DD	Northwest Pacific	Core?	Ingram and Kai (2014)
	Embiotocidae	25	DD	Northeast Pacific	Full	Longo and Bernardi (2015)
	Notothenioids w/ AFGPs[c]	>50	Pelagic	Antarctica	Full	Lecointre et al. (2013)
	Hypoplectrus spp.	10	Pelagic	Caribbean	Core	McCartney et al. (2003)
Echinoidea	Schizasteridae	27	DD	Antarctica	Core	Chenuil et al. (2018)
	Ctenocidarinae	21+	DD	Antarctica	Core	Chenuil et al. (2018)
Chondrichthyes	*Hemiscyllium* spp.	9	DD	Indo-Australian Archipelago	Core?	Compagno (2001)

[a] "Lineages" denotes a group of possibly undescribed or cryptic species.
[b] "DD" denotes known direct development.
[c] AFGP = Antifreeze glycoproteins.

littoral sea cucumbers on the island of Guam still does not asymptote despite many survey efforts by specialists throughout almost 200 years. Marine vertebrates are better documented, but many uncertainties remain. Among the migratory marine megafauna, including sea turtles, cetaceans, and tunas, species boundaries seem to arise between ocean basins, with little evidence of radiations in geographic proximity (Gaither et al. 2016). We conclude that when individual taxa develop species flocks in the sea, a key feature is limited dispersal of propagules, a primarily terrestrial mode of reproduction. In the next section, we document the geographic circumstances that promote species flocks, not in individual taxa, but in a broad range of biota.

Geographic Cases

Lakes as Islands: What Can Freshwater Cases Tell Us?

Several researchers have noted the similarity of lakes and oceanic islands as evolutionary incubators (Eastman and McCune 2000; Dawson et al. 2016; Naumenko et al. 2017). Most lake cases involve depauperate habitats colonized by one or a few ancestors that subsequently radiated into dozens or hundreds of species. This pattern is remarkably concordant with the cases of terrestrial fauna on oceanic islands: one or a few ancestors, a rare colonization event, followed by proliferation of species in a multitude of niches. Another parallel between lakes and islands is the concept of ecological opportunity: early arriving lineages seem to have greater opportunities to radiate relative to later arrivals, supporting the concept of niche preemption on islands and lakes (Silvertown et al. 2005; Fraser et al. 2015).

Ancient Freshwater Lakes

Most lakes have a relatively short life span, and only a few span more than 100 000 years (Gorthner 1994). The exceptions are about a dozen ancient lakes, including the 2 largest and oldest: Lake Tanganyika in eastern Africa, and Lake Baikal in southern Siberia. These lakes are 3 orders of magnitude older than most other lakes (>9 MY) and are recognized as evolutionary incubators due to their high levels of faunal diversity and endemism (Martens 1997; Salzburger et al. 2005).

The Haplochromine cichlid fishes (family Cichilidae) in the African Great Lakes (including Tanganyika) provide one of the most compelling examples of species flocks in aquatic environments. This is the largest vertebrate radiation, with more than 1000 species (Turner et al. 2001). African cichlids occupy a variety of ecological niches, exhibit a wide range of morphologies and feeding strategies, with many examples of convergent evolution.

Several hypotheses have been proposed to explain the high levels of speciation within African Great Lake cichlids (Galis and Metz 1998), including sexual selection and mate choice. Hybridization has also been implicated (Seehausen 2004); Meier et al. (2017) utilized nearly 13 000 SNPs to demonstrate a role for hybridization in the origin of more than 500 cichlid species in Lake Victoria, despite being less than 15 000 years old. Due to the highly varied feeding strategies and available habitats, niche partitioning is also a likely avenue for rapid diversification.

The African Great Lake phenomenon is not confined to cichlid fishes. Gastropods and *Synodontis* catfishes have also radiated in these lakes (Wilson et al. 2004; Day and Wilkinson 2006). The gastropod diversification began prior to the formation of the lakes and subsequently slowed, whereas *Synodontis* catfishes shows relatively recent divergence. Regardless of the mechanism, the environment of the lake has proven to be an evolutionary incubator for diverse taxa.

Lake Baikal, the largest, deepest, and oldest freshwater lake in the world, provides a comparable region to investigate species flocks in freshwater environments. The age of the lake (>20 Ma) and the sheer volume of available habitat space likely played a role in extensive diversification. Lake Tanganyika has a relatively thin layer of surface water that is oxygenated, leaving depths >300m uninhabitable. Conversely, the entire depth of Lake Baikal is oxygenated and habitable. It is estimated that 54% of the faunal species are endemic to the lake (Martens 1997) with diversification based on dietary strategy and habitat availability. Several of these animal groups have evolved into vast endemic species flocks including dinoflagellates, sponges, turbellarians, gastropods, ostracods, and most notably the cottids (sculpins) and gammarid amphipods (Fryer 1991; Annenkova et al. 2015).

Sculpins, the most speciose vertebrate group in Lake Baikal, have diversified into an endemic flock of 33 species, including 2 endemic families. Derived from a marine ancestor, this group extended their benthic, shallow-water habitat to include depths below 1500 m and pelagic habitat with planktivory (Sherbakov 1999; Kontula et al. 2003). Despite the great age of this lake, the rapid radiation of the Baikal sculpins occurred much later, with Pliocene or early Pleistocene origins (<5Ma).

Gammarid amphipods have perhaps the most remarkable Baikal radiation in terms of sheer numbers of species. About a third of all gammarid amphipods, including marine and freshwater, occur in Lake Baikal with nearly 350 endemic species and subspecies (Kamaltynov 1999). They have penetrated nearly every available habitat including shallow benthic, pelagic, and abyssal depths. Feeding strategies range from herbivorous to parasitic. Naumenko et al. (2017) resolved a rapid radiation of the Baikalian amphipods based on 2 invasions, with several instances of convergence in morphological features including body armor and reduction in sensory organs and appendages.

Additional examples of freshwater species flocks include Lake Ohrid, Europe's oldest lake at 2–3 Ma, hosting 8 endemic and monophyletic amphipods (genus *Gammarus*; Wysocka et al. 2013). These ancient lakes show high rates of diversification in a broad spectrum of faunal groups, with seemingly parallel ecological and phenotypic adaptations. Baikalian sculpins and African cichlids have both differentiated by habitat and trophic niches, among other mechanisms.

Young Freshwater Lakes

The phenomenon of species flocks in freshwater is not confined to ancient lakes. Boreal lakes, the product of retreating glaciers in the last 20 000 years, are also rich arenas for speciation. In the North American Great Lakes, phylogenetic reconstruction of ciscoes (*Coregonus* spp.) suggest they have undergone a recent adaptive radiation consistent with postglacial (10 000–15 000 years ago) divergences and ecological speciation (Turgeon et al. 1999). In Icelandic lakes, the radiation of arctic char (*Salveinus alpinus*) is attributed to phenotypic segregation, reproductive isolation, and trophic adaptation (Gíslason et al. 1999; Jonsson and Jonsson 2001).

Boreal lakes tend to be large and transient, but species flocks can also occur in lakes that occupy a much smaller area. Cyprinodont pupfishes show monophyletic radiations in a variety of regions including lakes in San Salvador Island (Bahamas) and Lake Titicaca (South America). In the case of San Salvador Island, a colonization within the last 6000 years produced 3 species including a scale-eating specialist and a hard-shelled prey specialist (Martin and Wainwright 2013). Lake Titicaca in the high Andean Plateau has a flock of 24 pupfishes (genus *Orestias*) and a radiation of at least 13 endemic amphipods (genus *Hyalella*). In Northern Australia, Wilson et al. (2009a) documented a species flock of isopods (genus *Eophreatoicus*) in isolated aquifers (springs) that are subjected to wet/dry cycles. Despite connections though streams during the wet season, colonization between aquifers in this region remains a rare event. The most tragic example of such species flocks is Lake Lanao in the Philippines, which formerly hosted an endemic species flock of 18 cyprinid fishes (genus *Puntius*), before human disturbance, overexploitation, and exotic introductions decimated the lake's fish fauna, with only 2 species remaining (Ismail et al. 2014).

Many of the key factors promoting adaptive radiations are ubiquitous in lake systems: ecological opportunity, evolutionary innovation, behavioral isolation, and competitive release. Although the radiations that have occurred in lakes are unparalleled in any other aquatic environment, it is clear that there is not one unifying mechanism that facilitates rapid diversification. The geographic setting, rather than any single organismal trait, promotes species flocks across a broad taxonomic spectrum.

Antarctic: The Epicenter of Marine Species Flocks

The Antarctic continental shelf and Southern Ocean are a hotbed for species flocks in the sea. Eastman and McCune (2000) identified conditions conducive to the formation of species flocks that are similar between the Antarctic seas and ancient lakes, such as Baikal and Tanganyika, including isolation, age, diversity, endemicity, and ecological opportunity. Lake fish communities are isolated by virtue of the natural discontinuity of lakes; likewise, the Antarctic shelf is isolated from other southern hemisphere shelf habitat by distance, bathymetry, ocean currents, and subfreezing temperatures. In particular, the Antarctic Circumpolar Current (ACC) and the Antarctic Polar Front (APF) serve as both dispersal barriers and biogeographic boundaries in the Southern Ocean (Clarke et al. 2005; Orsi and Whitworth 2005). The Antarctic continent has been glaciated for ca. 40 Ma and has existed under current polar conditions for 10–14 Ma (Barker et al. 2007). Since the initial onset of glaciation, ice sheets have periodically advanced and retreated across the continental shelf. Isolated and/or fragmented shelf populations displaced by grounded ice likely survived within glacial refugia. These vicariant events created circumstances within which genetic drift and natural selection could lead to speciation, a mechanism that has been named the Antarctic biodiversity pump (Clarke and Crame 1992).

Based on the criteria defined above (monophyly, endemism, species richness, habitat dominance, and ecological/morphological diversity), Lecointre et al. (2013) identified 17 Antarctic taxa of bony fishes, echinoderms, arthropods, and molluscs that meet the first 3 criteria ("core flocks") and of those, 9 that meet all 5 ("full flocks"). Among the most studied of Antarctica's putative species flocks are the icefishes of the suborder Notothenioidei. Fossil- and time-calibrated estimations of divergence reveal diversification in the Paleocene/Eocene (57–64 Ma), with the strictly Antarctic group diverging in the early Miocene (10–20 Ma) (Near 2004) and additional radiations in the last 10 My (Near et al. 2012; Colombo et al. 2015). Species of this group, which include the plunderfishes and cod icefishes, lack a swim bladder and are mostly benthic, although several species achieved neutral buoyancy through lipid deposits and reduced bone density, and have adopted a pelagic habit (Balushkin 2000; Eastman 2013). This group comprises ~85% of benthic fish species on the Antarctic shelf (satisfying the condition for habitat dominance) and 87% of its members are endemic to waters south of the APF. This suborder of fishes contains several possible species flocks at varying degrees of nestedness, depending on how phylogeny and criteria are interpreted. At the taxonomic suborder level, notothenioids may not be truly endemic, since several species are distributed north of the APF. Conversely, the primarily Antarctic family Nototheniidae, which has been considered a species flock by some authors (e.g., Eastman and McCune 2000) is unlikely to be monophyletic (Dettai et al. 2012). However, as Lecointre et al. (2013) observe, we can include the group of fishes with antifreeze glycoproteins (AFGP), one of the key adaptations that may have allowed this flock to gain dominance in the Antarctic (Near et al. 2012). This endemic and monophyletic group includes the nototheniids along with 4 additional notothenioid families, and comprises >50 species. All species within the group are endemic at the scale of the Southern Ocean (though most are Antarctic or have an Antarctic origin; Cheng et al. 2003), exhibit habitat dominance within their range, and show a range of ecological and morphological diversification (Eastman 2005). In contrast to many other groups that have radiated as species flocks, notothenioids in general tend to have an extended larval stage, with pelagic durations averaging 2–6 months (North 2001; Matschiner et al. 2009). Despite this high dispersal potential, population genetic studies have found structure on regional spatial scales around the Antarctic shelf (Volckaert et al. 2012), although this is not consistent across the group. Adult fishes, barring the few species that have recolonized the pelagic, tend to be sedentary with small home ranges, and indeed the pelagic species have less population structure than the benthic species (Van de Putte et al. 2012).

Full species flocks *sensu* Lecointre et al. (2013) have formed within several groups of Antarctic amphipods. *Epimeria* is cosmopolitan, comprising >80 described species in several subgenera worldwide, of which >30 are currently described from Antarctica and the Southern Ocean (D'Udekem d'Acoz and Verheye 2017). While globally the genus is not monophyletic, the Antarctic lineages of *Epimeria* constitute a speciose clade with high morphological and ecological diversity (Verheye et al. 2017). Additionally, more species may exist than are currently known (Loerz et al. 2009; Verheye et al. 2016). Antarctic *Epimeria* diversified while the Antarctic was cooling, indicating that adaptation to colder waters, exploitation of niches vacated by taxa that failed to adapt, and the fragmentation/recolonization driven by the Antarctic biodiversity pump, led to the present high morphological and trophic diversity (Verheye et al. 2017). The brooding *Eusirus* amphipods mentioned above have been remarkably successful, with >50 species colonizing all available marine habitat in the Southern Ocean. As a result, they exhibit very high ecological and morphological diversity (Baird et al. 2011). Both groups of peracarid crustaceans identified as species flocks develop directly (as brooders), which limits their dispersal capability (D'Udekem d'Acoz and Verheye 2017), although *Eusirus*, despite its large body size, is known to have a strong swimming ability which may expand its dispersal capability as an adult.

The Antarctic nudibranch *Doris kerguelenensis* is a direct-developing sea slug exhibiting limited adult movement and long generation times. Its distribution is circumantarctic and extends into the southern Atlantic and Pacific. Based on its broad distribution and sedentary/nondispersive life history, Wilson et al. (2009b) hypothesized that this taxonomically complicated group might comprise multiple cryptic species. Their phylogeographic investigation of *D. kerguelenensis* uncovered 29 distinct (3–5% divergent) mitochondrial lineages independent of sampling location, as expected under the Antarctic biodiversity pump hypothesis. Wilson et al. (2013) demonstrated ecological diversity among the cryptic lineages with *D. kerguelenensis*, which potentially elevates the group beyond core species flock. However, habitat dominance will still need to be shown to accord full flock status.

In addition to the fishes, crustaceans, and molluscs mentioned above, the sea urchin families Schizasteridae and Ctenocidarinae are both endemic and speciose, yet they do not have particularly high ecological/morphological diversity or habitat dominance. None of the crinoid groups surveyed by Lecointre et al. (2013) were determined to constitute species flocks. However, Chenuil et al. (2018) reexamined crinoid genera *Isometra, Notocrinus,* and the *Promachocrinus kerguelensis*/*Florometra mawsoni* clade in light of newer mtDNA data, and suggested that each constituted multiple cryptic lineages. While these groups were shown to be more speciose than previously thought, they fall short of full species flock status based on endemicity, habitat dominance, or ecological diversity.

The primary shared characteristic among species flocks in the Antarctic appears to be limited dispersal. However, the icefishes (with pelagic dispersal on the order of weeks to months) are a noted exception. Most Antarctic taxa inhabit or originate from continental shelf habitat, which in Antarctica may be subject to continual advance and retreat of grounded ice. Thus, the biodiversity pump driven by isolated glacial refugia may be a process unique to Antarctica, promoting the formation of species flocks in groups which might otherwise be less prone to diversification. In addition, the formation of the Antarctic notothenioid species flock was concordant with a key evolutionary innovation: the development of antifreeze glycoproteins enabling the colonization of otherwise inhospitable polar habitat.

Deep Fauna

The soft sediments of the deep sea host a very large, homogeneous habitat, with a highly endemic invertebrate fauna (Raupach et al. 2007). A survey of deep Weddell Sea sponge (Porifera) fauna revealed 76 species in 30 taxonomic families (Janussen and Tendal 2007). The same region hosts at least 96 species of gastropods in 36 taxonomic families (Schwabe et al. 2007). Given the limited knowledge of these abyssal and bathyal zones, it's uncertain how much of this diversity would qualify as species flocks. However, Raupach et al. (2007) report that the widespread isopod *Betamorpha fusiformis* comprised multiple cryptic species, and postulated that this could be the case for many of the understudied deep benthic morphospecies.

The underexplored meiofauna (living in sediments both shallow and deep) account for a large fraction of the biomass and biodiversity of marine communities, and barcoding studies indicate that this community holds much cryptic diversity (Fonseca et al. 2017; Brannock et al. 2018). Many meiofauna have limited dispersal potential, and so extensive potential exists for cryptic species flocks.

Globally Distributed Marine Vertebrates: The Antithesis of Species Flocks

Gaither et al. (2016) reviewed the globally distributed fishes, making a pertinent observation about speciation in the highly migratory species in the upper water column. This group included many morphologically unique species that are sole members of a genus or taxonomic family. Examples include Wahoo (genus *Acanthocybium*), Cobia (*Rachycentron canadum*, family Rachycentridae), Whale shark (*Rhincodon typus*, family Rhincodontidae), and Basking shark (*Cetorhinus maximus*, family Cetorhinidae). Gaither et al. postulated that connectivity on a global scale allowed these species to progress far along a unique morphological and evolutionary trajectory (anagenesis) without opportunity for isolation and allopatric speciation (cladogenesis). At the same time, ecological partitions do not seem to drive speciation in the somewhat ubiquitous oceanic habitat. This evolutionary consequence is dubbed the "lonely genus," comprising ancient and unique lineages with little opportunity for adaptive radiations. The leatherback sea turtle (*Dermochelys coriacea*) also fits this model, with a highly derived morphology, many unique adaptations (the only partially homeothermic reptile), a lineage tracing back more than 100 million years, and a single species with very shallow mtDNA coalescence (Dutton et al. 1999). Among the marine organisms with high connectivity on a global scale, we observe the opposite of species flocks: ancient, monotypic lineages.

Discussion

In the previous sections, we reviewed cases of individual taxa, and ecological settings, that promote species flocks. Here, we review the circumstances that augment or retard the formation of species in the sea, based on 3 cases. The first case illustrates the difficulty in completing the speciation process in broadcast spawners. The second case examines host switching as a more efficient means of speciation, and the third case seeks insights from the broadcast spawners of the terrestrial realm, the pollen-dispersing plants.

Flickers of Speciation

There are few known cases of species flocks in broadcast-spawning organisms, presumably because to radiate in a particular geographic setting, they need to diverge in sympatry. Sympatric speciation is still controversial, however there are numerous examples with no satisfactory alternative explanations (see Bird et al. 2012 for a review). Here, we consider an informative case of contrasting outcomes in 2 broadcast spawners, with sympatric speciation in limpets ('opihi, *Cellana* spp.), and incomplete speciation in sympatric color morphs of the arceye hawkfish (*Paracirrhites arcatus*). In the case of the 'opihi, 3 species diversified from a single colonizer as they became adapted to different elevations on wave-exposed rocky shores (Bird et al. 2011). Wave action at the intertidal zone initiates gamete release, such that high, middle, and low intertidal spawners may release eggs and sperm at different intervals. Habitat partitioning by tidal exposure, combined with differences in spawning timing, may have provided premating isolation and restricted gene flow sufficient for the 'opihi to differentiate into multiple species. In the case of the hawkfish, distinct color morphs segregate into light and dark habitats on the same reefs, indicating strong niche partitioning (Whitney et al. 2018a), and these color morphs coexist across a broad swath of the Indo-Pacific Ocean. Field and captive studies both show assortative mating, with females more than 5 times more likely to pair with like-colored males (Whitney 2016). Based on a microsatellite survey, Whitney et al. (2018b) observed greater genetic divergence between color morphs on the same reefs than that between the same morphs in different locations. Ecology, behavior, and genetics indicate the right ingredients for sympatric speciation, but the process has not gone to completion.

So why then did the 'opihi speciate completely but hawkfish color morphs remain only partially isolated? Although hawkfish color morphs are adapted to contrasting microhabitats and mate assortatively (like the 'opihi), they still overlap spatially and temporally (with only partial reproductive isolation) and therefore lack the stronger premating isolation in the 'opihi. Hawkfish morphs are missing a crucial ingredient to complete the process of speciation, which in this case could be stronger mating barriers, more intense selection, or some level of geographic isolation.

Diversification along ecological gradients helps promote reproductive isolation in sympatry, but some degree of geographic isolation appears to be a primary prerequisite for radiations to occur. The pattern of phylogenetic partitioning within or between adjacent islands is well documented in terrestrial Hawaiian radiations (Funk and Wagner 1995), but is absent from dispersive marine taxa in the same archipelago. Marine organisms with highly dispersive larvae lack the potential for geographic isolation that affords terrestrial colonizers the ability to diverge among isolated regions within islands.

Host Switching and Sympatric Speciation

Host choice seems to play a fundamental role in the differentiation and speciation of many small marine invertebrates (Sotka 2005), such as herbivorous amphipods (Sotka et al. 2003), sponge-dwelling alpheid shrimps (*Synalpheus* spp.; Duffy and Hultgren 2011), coral-inhabiting barnacles (*Savignium milleporum*; Mokady and Brickner 2001), and herbivorous saccoglossan sea slugs (Trowbridge and Todd 2001). Opisthobranch molluscs have undergone major evolutionary radiations in connection with habitat and diet (Jensen 1997). In sympatric nudibranchs (*Phestilla* spp.), Faucci et al. (2007) show a host switch from the coral genus *Porites* to *Goniopora* and *Tubastrea*. Host shift seems to be the primary mechanism underlying speciation in this nudibranch genus. Furthermore, *Phestilla minor* appears to comprise a cryptic species complex associated with different species of corals within a localized area in Palau (Faucci et al. 2007). The brief or nonexistent planktonic period of these species, combined with specific habitat choice, can lead to local adaptation and sympatric speciation (Kawecki and Ebert 2004; Bowen et al. 2013).

Lessons from Terrestrial Plants

Previous researchers have noted the shared evolutionary features of species flocks above and below the waterline. In particular, wind-dispersing plants on continents, and pelagic-dispersing invertebrates in the sea, share 3 general features: 1) sedentary or sessile adult stages, 2) high-dispersal propagules, and 3) very large ranges. These commonalities prompt us to suggest a fourth trait that may be shared: a rarity of species flocks.

Kinlan and Gaines (2003) estimated that marine dispersal was 1–2 orders of magnitude higher than terrestrial counterparts, but the parallels between these 2 evolutionary arenas are striking. Wind-driven seed dispersers seldom have sympatric radiations, similar to the dispersive marine fauna. In contrast, plant species pollinated by insects may have a greater propensity for sympatric speciation through specialization to specific pollinators (Hodges and Arnold 1994), similar to the diversification for host-dependent marine invertebrates.

Simpson (1953) suggested that modes of speciation can include both extrinsic opportunity and intrinsic innovation. In our view, the extrinsic opportunity applies to geographic clusters of species flocks, typically in depauperate settings that are rich in ecological opportunities. The intrinsic opportunity applies to the singular flocks that result primarily from restricted dispersal. The principle of extrinsic opportunities applies to species flocks in alpine plants, ancient lakes, and the terrestrial side of oceanic islands. In the oceans, perhaps only Antarctica qualifies as an extrinsic opportunity.

Adaptation and speciation are operating on different scales in land and sea, largely due to the high dispersal potential of most marine organisms. Nowhere is this more apparent than in the distribution of species flocks, abundant above the waterline on oceanic islands, and effectively absent below. The mechanics of evolution seem to be the same in both realms, including selection, migration, mutation, and drift, yet the tempo and outcomes are markedly different.

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