REVIEW

A review of batoid philopatry, with implications for future research and population management

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ABSTRACT: Animal movements, in particular residency or return migrations (collectively defined as 'philopatry'), can shape population structure and have implications for management. This review examines the evidence for philopatry in batoids, which are some of the least understood and most threatened vertebrates, and updates a prior review of the same in sharks. Evidence for philopatry in batoids was found in 46 studies, including 31 species that involve 11 species complexes. Batoid philopatry research has lagged behind shark philopatry research, with the annual publication rate of shark philopatry studies in the last 5 yr (17 yr^{-1}) being more than twice that of batoids (7 yr^{-1}). Philopatry research on both sharks and rays is taxonomically skewed: <50% of elasmobranch families are represented. Research is also skewed towards charismatic megafauna (white sharks, whale sharks, and manta rays), while the batoid philopatry literature is biased towards 'Near Threatened' species, even though approx. 47.5% of batoids are considered to be 'Data Deficient' by the IUCN. Limited evidence was found for residency in batoids, contrary to popular assumptions that they are sedentary, and there was limited evidence for sex-differentiated movements. Hypothesis-driven research, longer study durations, more taxon and life stage diverse studies, and consistent use of philopatry terminology are needed to advance the fields of batoid philopatry and conservation. Given strong evidence of philopatry in some species of batoids, management should proceed at the local scale until more studies are conducted.

KEY WORDS: Philopatry · Population structure · Conservation · Management · Movements · Sharks

INTRODUCTION

Many sharks and rays (subclass: Elasmobranchii; elasmobranchs) are vulnerable to extinction due to overfishing, bycatch, habitat loss, and climate change (Wearmouth & Sims 2009, Simpfendorfer et al. 2011, Ward-Paige et al. 2013, White et al. 2013, Dulvy et al. 2014). Management of these threatened species will require an understanding of their movements (Chapman et al. 2015). Although research focusing on elasmobranch movements has increased over time (Papastamatiou & Lowe 2012), a large portion of elasmobranch research and media attention has concentrated on charismatic

sharks, with limited correlation to their extinction vulnerability (Muter et al. 2013). According to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (www.iucnredlist.org; as of 2013), approximately 19.9% of known batoid (superorder: Batoidea; skate, stingray, wedgefish, guitarfish, and sawfish) species are threatened with extinction (IUCN Red List Categories 'Vulnerable', 'Endangered', and 'Critically Endangered'), and 47.5% of known batoid species are listed as 'Data Deficient', a category that requires more research in order to understand the status of these species and develop effective management strategies (Dulvy et al. 2014). Batoids are among the least understood vertebrates (Arlyza et al. 2013, Bräutigam et al. 2015), with unresolved taxonomy for many species (Naylor et al. 2012), poorly understood and restricted ranges (Dulvy et al. 2014), and have some of the most valuable elasmobranch products on the market (Ward-Paige et al. 2013, White et al. 2013, Dulvy et al. 2014). There is also limited knowledge of their role in the ecosystem (Schluessel et al. 2010, Ajemian et al. 2012, Braun et al. 2014, Newby et al. 2014). Many management and conservation actions for batoids will not only require an understanding of their ranges and ecosystem role, but also of their movements (Simpfendorfer et al. 2011).

Population dynamics are partially shaped by individual movements, in certain cases via a behavior known as 'philopatry' (Fig. 1; Chapman et al. 2015). Philopatry is defined as individuals frequently returning to or staying in their home ranges, birthplaces, or other specific localities (Mayr 1963, Hueter et al. 2005, Speed et al. 2010, Chapman et al. 2015). Evidence supporting the occurrence of philopatry can be divided into 2 broad categories.

The first category is defined by direct evidence of individual movements (i.e. residency, seasonal residency, site fidelity, and site affinity; Fig. 1) and is often determined using telemetry, conventional tagging techniques, or photographic identification (photo-ID) to track these movements (Couturier et al. 2011, Chapman et al. 2015). When individuals remain in one location for a known period of time that is at least 12 mo, it is known as 'residency' (Chapman et al. 2015). When presenting evidence of residency, associated spatial and temporal details are required (e.g. lemon sharks are residents of Bimini lagoon for at least 3 yr; Chapman et al. 2015). Individuals can exhibit 'seasonal residency' when there is evidence that they remain in an area for only several months at a time (at least 90 d) before moving elsewhere (Chapman et al. 2015). When the individual makes a long-distance movement away from a defined location and then returns to it, the behavior is defined as 'site fidelity' (Chapman et al. 2015). When the available evidence does not clearly demonstrate the difference between site fidelity and residency (i.e. it is unclear whether or not a known individual has been in an area for an extended period or has left and then returned), the term 'site affinity' should be used (Couturier et al. 2011). The second category for evidence of philopatry is based on where an individual reproduces as opposed to simply where it moves (i.e. natal philopatry and regional philopatry; Fig. 1; Chapman et al. 2015). This type of evidence also enables inferences to be made about where individuals are moving, which could be further explored by tracking their movements. 'Natal philopatry' is when an individual returns to its exact birthplace to reproduce (Chapman et al. 2015). In contrast, individuals exhibiting 'regional philopatry' return simply to the general region in which they were born to reproduce (Chapman et al. 2015).

The first objective of this review was to describe documented cases of philopatric behavior in batoids by assembling data from peer-reviewed published literature. The second objective was to compare these data with an updated review of philopatry in sharks (Hueter et al. 2005, Speed et al. 2010, Chapman et al. 2015). The final objective was to outline goals for future movement research and the main implications of batoid philopatry for population management.

Category I: evidence of individual movements

Residency

Seasonal residency

Site fidelity

Site affinity

Category II: evidence of reproduction in birthplace or birth region
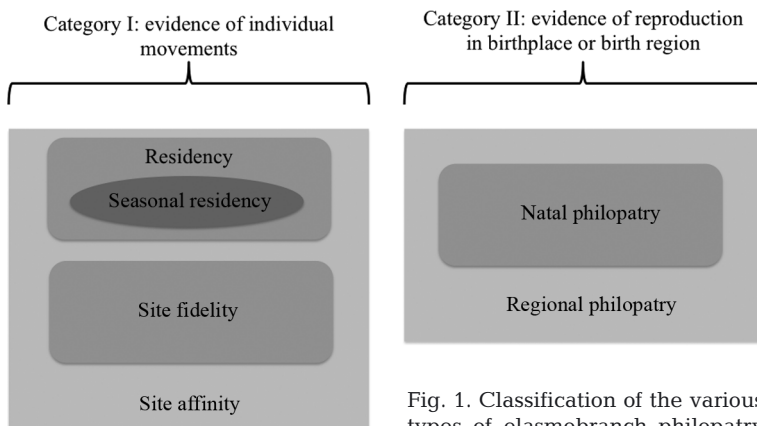
Natal philopatry

Regional philopatry

Fig. 1. Classification of the various types of elasmobranch philopatry

METHODS

Peer-reviewed published batoid movement literature available up to 7 December 2015 was reviewed, following the definitions of philopatry outlined previously. Taxonomic queries for 'batoid', 'stingray', 'sawfish', 'manta ray', 'eagle ray', 'cownose ray', 'skate', 'guitarfish', 'wedgefish', 'electric ray', 'myliobatiformes', 'rajiformes', 'pristiformes', and 'torpediniformes' were individually coupled with 'philopatry', 'site fidelity', and 'residency' in a Google Scholar (https://scholar.google.ca) search. To expand the search, 'batoid', 'stingray', and 'sawfish' were each coupled with methodological terminology 'telemetry', 'tag', 'photographic identification', 'population genetics', and 'phylogeography'. The remaining taxonomic terms were not coupled with methodological terms because at 'sawfish' no new papers were discovered. Since 'site affinity' was commonly used in manta ray publications (Couturier et al. 2011), 'batoid', 'stingray', and 'manta ray' were coupled with the term 'site affinity' in a final search. The references from all discovered batoid philopatry studies were then reviewed in an attempt to find any remaining published literature on the topic. Because of widespread taxonomic uncertainty in batoids, the IUCN Red List taxonomic definitions were used (Dulvy et al. 2014). One exception was made for the flapper skate *Dipturus* cf. *intermedia*, as it was assessed in 2006 on the IUCN Red List as the common skate *Dipturis batis* (Dulvy et al. 2006), but more recent taxonomic work has clarified it is a distinct species (Iglésias et al. 2010, Neat et al. 2015). However, *D. batis* was still used for the common skate. IUCN Red List Categories and Criteria were also used to classify extinction risk for each species included in this review.

Techniques for tracking horizontal movements of individuals include conventional tagging (dart tags, Peterson discs, passive integrated transponder tags), photo-ID, acoustic telemetry (active and/or passive), satellite tracking (pop-off satellite archival transmitters, satellite transmitters), DNA profiling (parentage analysis), and population genetic approaches (Chapman et al. 2015). Studies were only included in this review that met several additional methodological criteria. Conventional tagging, photo-ID, and active acoustic monitoring studies needed to have repeated effort to recapture or track individuals over time in a defined area (Marshall & Pierce 2012, Chapman et al. 2015). Passive acoustic monitoring studies were required to have an array of receivers placed in the study area for at least one season (i.e. ≥90 d) of a cal-

endar year, which would minimally allow individuals to be categorized as seasonal residents. Similarly, satellite tags needed to be deployed on an individual batoid for at least 90 consecutive days of a calendar year. In comparison to the methodology in Chapman et al. (2015), where shark telemetry studies were only included if they lasted for at least one calendar year, the methodology used in this review was more inclusive for batoid studies in order to increase sample size. Population genetic studies were included as evidence of regional philopatry when they tested for structure along a continuous distribution that was not impeded by physical barriers to movement, such as open ocean or upwelling zones (Chapman et al. 2015). Following the methodology of Chapman et al. (2015), the shark philopatry literature available up to 7 December 2015 was reviewed in order to provide an updated comparison to the batoid philopatry literature.

RESULTS AND DISCUSSION

General patterns in the literature

A total of 46 studies provided evidence of philopatry in batoids (Table 1), while a total of 128 studies showed the same in sharks (Table S1 in the Supplement at www.int-res.com/articles/suppl/m562p251 supp.pdf). Although elasmobranch movement research has steadily increased over time (Papastamatiou & Lowe 2012), the publication rate for shark philopatry is much higher than that of batoids (Fig. 2). In the last 5 years (2011–2015), the median number of shark philopatry publications was 17 yr^{-1}, while the median number of batoid philopatry publications was 7 yr^{-1}. However, the methodology used in this review was more inclusive for batoids; therefore, if the methodological bias was removed, this pattern would be stronger. The annual publication rate for shark philopatry studies has been growing continuously, but has been unsteady for batoid philopatry studies.

Research on elasmobranch philopatry is taxonomically skewed, where only 10 of 23 batoid families were represented (43.5%; Fig. 3) and 16 of 34 shark families were represented (47.1%; Fig. S1 in the Supplement). In general, the number of batoid and shark species studied per family is low (Fig. 3, Fig. S1). A total of 31 batoid species were represented in the literature (5.8% of all known batoid species, N = 539, Dulvy et al. 2014), where the median number of publications per species was 1. In contrast, 44 shark spe-

Table 1. Evidence for philopatry in batoids reviewed through 7 December 2015. R: residency; SR: seasonal residency; SA: site affinity; SF: site fidelity; RP: regional philopatry; NP: natal philopatry

Species	Type	Reference(s)
Aetobatus narinari	SA	Ajemian et al. (2012), Bassos-Hull et al. (2014)
	RP	Sellas et al. (2015)
Dasyatis akajei	RP	Li et al. (2013, 2015)
Dasyatis americana	R	Corcoran et al. (2013)
Dasyatis brevicaudata	SR	Le Port et al. (2008)
	RP	Le Port & Lavery (2012)
Dipturus batis	SA	Wearmouth & Sims (2009)
Dipturus cf. *intermedia*	SR	Neat et al. (2015)
Glaucostegus typus	SA	Vaudo & Heithaus (2012)
	SF	White et al. (2014)
	SR	Cerutti-Pereyra et al. (2014), White et al. (2014)
	R	Cerutti-Pereyra et al. (2014), White et al. (2014)
Himantura dalyensis	SF	Campbell et al. (2012)
	SR	Campbell et al. (2012)
	R	Campbell et al. (2012)
Himantura fai	SA	Vaudo & Heithaus (2012)
	SR	Gaspar et al. (2008)
Himantura granulata	SR	Davy et al. (2015)
Himantura uarnak	SA	Vaudo & Heithaus (2012)
	SR	Cerutti-Pereyra et al. (2014)
Malacoraja clavata	SA	Ellis et al. (2011)
	SF	Hunter et al. (2006)
	SR	Hunter et al. (2006)
	RP	Chevolot et al. (2006)
Manta alfredi	SA	Deakos et al. (2011), Marshall et al. (2011), Kitchen-Wheeler et al. (2012), Couturier et al. (2014), Germanov & Marshall (2014)
	SF	Germanov & Marshall (2014), Jaine et al. (2014), Braun et al. (2015)
	SR	McCauley et al. (2014), Braun et al. (2015)
Manta birostris	SF	Dewar et al. (2008)
	SR	Dewar et al. (2008)
Myliobatis californicus	SA	Matern et al. (2000)
Neotrygon kuhlii	SA	Pierce et al. (2009)
	RP	Borsa et al. (2012), Arlyza et al. (2013)
Paratrygon ajereba	RP	Frederico et al. (2012
Pastinachus atrus	SA	Vaudo & Heithaus (2012)
	SR	Cerutti-Pereyra et al. (2014)
	R	Cerutti-Pereyra et al. (2014)
Pristis clavata	RP	Phillips et al. (2011)

Table 1. (continued)

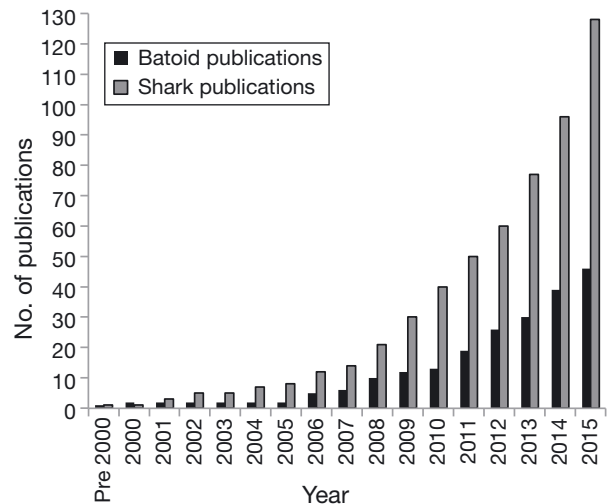| Species	Type	Reference(s)
Pristis pectinata	SA	Papastamatiou et al. (2015)
	SR	Simpfendorfer et al. (2010, 2011), Poulakis et al. (2013), Carlson et al. (2014), Papastamatiou et al. (2015)
Pristis pristis	SA	Thorson (1982), Thorburn et al. (2007)
	RP	Phillips et al. (2011)
	NP	Feutry et al. (2015)
Pristis zijsron	RP	Phillips et al. (2011)
Raja brachyura	SA	Ellis et al. (2011)
Raja microocellata	SA	Ellis et al. (2011)
Raja undulata	SA	Ellis et al. (2011)
Rhinobatos productus	SR	Farrugia et al. (2011)
Rhinoptera bonasus	SR	Collins et al. (2008)
Rhynchobatus spp.	SF	White et al. (2014)
	SR	White et al. (2014)
	R	White et al. (2014
Urobatis halleri	SF	Vaudo & Lowe (2006)
	SR	Vaudo & Lowe (2006)
Urogymnus asperrimus	SR	Cerutti-Pereyra et al. (2014)
	R	Cerutti-Pereyra et al. (2014)
Zapteryx exasperata	RP	Castillo-Páez et al. (2014)

Fig. 2. Cumulative number of publications on philopatry in sharks and batoids to 7 December 2015

cies were represented (9.5% of all known shark species, N = 465, Dulvy et al. 2014), where the median number of publications per species was 2. Flagship species, or charismatic megafauna, which we de-

fine as white sharks *Carcharodon carcharias*, whale sharks *Rhincodon typus*, and manta rays *Manta alfredi* and *M. birostris* account for 16.5% of the shark philopatry research and 15.5% of the batoid philopatry literature. This suggests the high profile of these species in the public realm may be driving funding for philopatry research. However, hypothesis-driven research on a broader range of species is required to advance the field rather than repeating effort on a handful of species. For example, 5 studies (Table 1) show reef mantas to be demonstrating site affinity. In order to progress our understanding of philopatry in manta rays, research using long-term acoustic or satellite tracking is required to distinguish between residency and site fidelity across various locations.

The batoid philopatry literature is concentrated on 'Near Threatened' species under IUCN Red List criteria (25.8%), while only 11.5% of batoid species are in this category (Dulvy et al. 2014) (Fig. 4). This could be considered a proactive way to prevent species from becoming threatened in the future, assuming that the literature contributes to management of these species. It could also mean that the current research focus is on the most accessible species. Arguing against the accessibility bias, there is some research emphasis on 'Critically Endangered' batoids (12.9% of studies; Fig. 4), with 2.6% of batoid species listed in this category. Although approximately 47.5% of batoids are considered to be 'Data Deficient' (Dulvy et al. 2014), only 12.9% of the philopatry literature focused on species in this category (Fig. 4). The lack of research attention on 'Data

Fig. 4. Overall proportion of batoid species in the philopatry literature listed by their IUCN Red List Category compared to the proportion of batoid species within each IUCN Red List Category. Note that the total number of 'Not Assessed' species is not known (Dulvy et al. 2014)

Deficient' and 'Not Assessed' batoids suggests that some of those species may become threatened with extinction before their level of philopatry and conservation status are known (Bräutigam et al. 2015). Likewise, approximately 11 out of 31 batoid species represented in the philopatry literature are considered to be complexes. Resolving taxonomic uncertainties will be fundamental to understanding which species are actually exhibiting philopatry. Batoid philopatry research should strategically focus on species based on their IUCN Red List classifications.

Evidence for specific types of philopatry in batoids

Site affinity

Studies showing site affinity consist of results that could either be evidence of residency or site fidelity (Couturier et al. 2011). In this sense, site affinity is generally described in conventional tagging (e.g. Ellis et al. 2011) and photo-ID studies (e.g. Deakos et al. 2011) where it
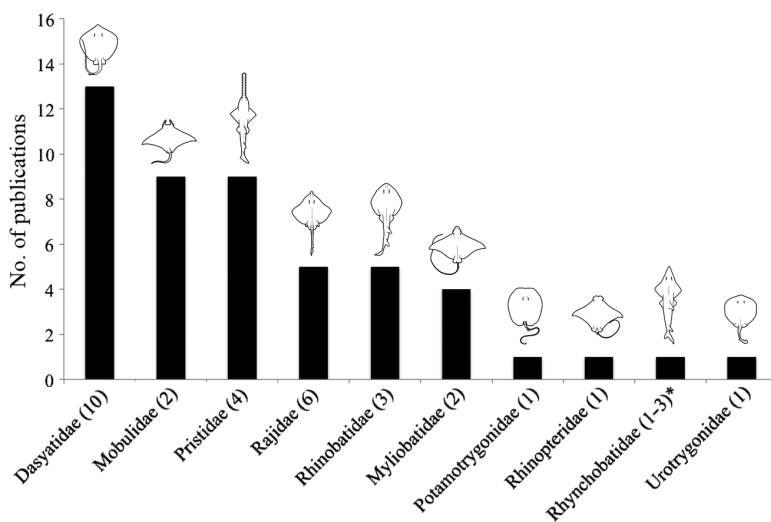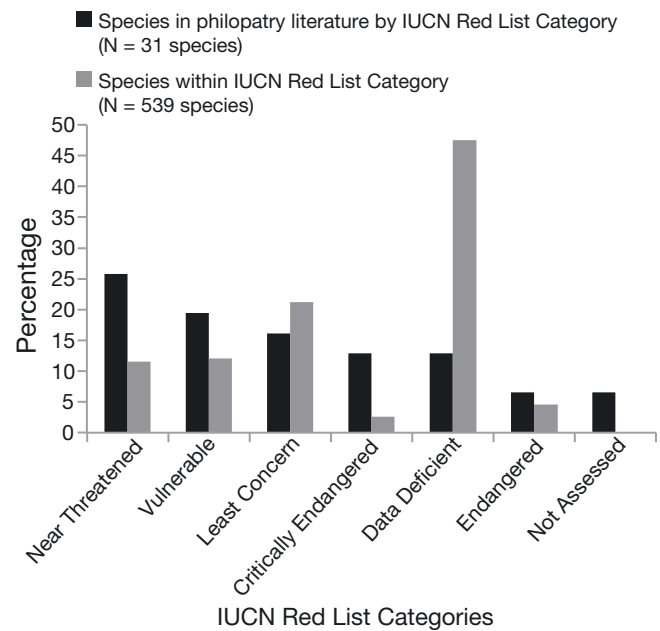

Fig. 3. Number of philopatry publications per batoid family (10 of 23 families represented). Number of species represented in the literature from each family is given in parentheses. *Number of species in the *Rhynchobatus* spp. complex

is unclear whether individuals were continuously present in an area or have left and then returned. As such, it is one of the broadest forms of philopatry and requires further research to definitively guide conservation efforts. However, acoustic telemetry using active tracking (e.g. Matern et al. 2000) or passive monitoring with a short study duration, poor receiver range, and/or a low sample size can lead to results that only indicate site affinity (e.g. Vaudo & Heithaus 2012). Evidence of site affinity was found in 15 studies, representing 15 species from 6 families including stingrays (Dasyatidae), manta rays (Mobulidae), eagle rays (Myliobatidae), sawfishes (Pristidae), skates (Rajidae), and guitarfish (Rhinobatidae) (Table 1). The majority of evidence for site affinity came from reef manta ray (*M. alfredi*) studies (n = 5), which used photo-ID as a method to recapture individuals over time (Deakos et al. 2011, Marshall et al. 2011, Kitchen-Wheeler et al. 2012, Couturier et al. 2014, Germanov & Marshall 2014). Manta rays are known to travel 100s of km and aggregate at certain sites (Couturier et al. 2014), so it is likely that individuals are exhibiting site fidelity rather than residency. However, demonstrating site fidelity using photo-ID or conventional tagging methods is difficult, as it is sometimes unclear what the animals were doing outside of the sampling period. In addition, tag retention time, long-term reliability of distinctive markings, and sampling effort can have a large effect on the catchability of an individual (Marshall & Pierce 2012). The Critically Endangered and Endangered skates (the common skate *Dipturis batis* and the undulate skate *Raja undulata*, respectively) of the United Kingdom showed evidence of site affinity using temperature depth recorders and tag-recapture, respectively (Wearmouth & Sims 2009, Ellis et al. 2011). Distinguishing between site fidelity and residency will be crucial to advancing conservation for these species. In order to determine the true type of philopatric behavior (site fidelity or residency), passive acoustic monitoring and/or satellite tracking lasting at least 12 mo should be executed (Chapman et al. 2015). Studies demonstrating evidence of site affinity should be used as the foundation of future research. Regardless, populations exhibiting site affinity should, at a minimum, be protected on a local scale as they are using a particular area for at least part of the year, if not for longer periods. Repeated use of these areas suggests they are potentially important for the life history of a species. Concentrated fisheries or other anthropogenic stressors in these areas could have a disproportionate effect on the overall population.

Site fidelity

Evidence for site fidelity was found across 8 studies, 6 families (Dasyatidae, Mobulidae, Rajidae, Rhinobatidae, Rhynchobatidae, and Urotrygonidae), and 6 species as well as the *Rynchobatus* species (spp.) complex (Table 1). Manta rays (*M. alfredi* and *M. birostris*) were the dominant species exhibiting this behavior (n = 4; Dewar et al. 2008, Germanov & Marshall 2014, Jaine et al. 2014, Braun et al. 2015). Reef manta rays tracked using pop-off satellite-linked archival transmitting (PSAT) tags off eastern Australia displayed site fidelity to the Capricorn Eddy region near Lady Elliot Island (Jaine et al. 2014). Several individuals made long-distance movements north or south of the eddy (100s of km) before returning near their initial tagging spot and the eddy, likely using this area as a feeding ground (Jaine et al. 2014). As mentioned above, evidence for site fidelity is more difficult to establish from photo-ID studies; however, one female manta ray was sighted at a location 450 km away from the initial sighting location, and this individual was then resighted 157 d later at the original site (Germanov & Marshall 2014), which provides evidence of site fidelity. At a minimum, protection of threatened batoid populations that are exhibiting site fidelity should be granted in the country or the particular area where the species is returning. Additionally, knowledge of where the individuals are migrating is required; however, managing populations that traverse international boundaries is generally more difficult than managing populations of resident individuals. If protection of a site-fidelic population is granted only in the area it is returning to, exploitation of the population could occur outside of this area and potentially undermine local management efforts.

Seasonal residency

Nineteen studies met the criteria required to demonstrate seasonal residency in batoids (Table 1). These studies included a total of 8 families (Dasyatidae, Mobulidae, Pristidae, Rajidae, Rhinobatidae, Rhinopteridae, Rhynchobatidae, and Urotrygonidae) as well as 15 species and both the wedgefish *Rynchobatus* spp. and flapper skate *Dipturus* cf. *intermedia* complexes. In some cases, evidence for residency may have been found if the acoustic receivers had remained in the water longer (i.e. extended study period), as was the case for one study of mangrove whiprays *Himantura granulata* (Davy et al.

2015). The pink whipray *H. fai* exhibited seasonal residency within a small marine reserve in Mo'orea, French Polynesia (Gaspar et al. 2008). The study was conducted over a small spatial scale of 1.92 km² and included areas where the rays are provisioned (Gaspar et al. 2008). Although evidence suggests seasonal residency (Gaspar et al. 2008), more research would need to be conducted on rays outside of the feeding area to determine normal movement behavior that is not driven by feeding. Cownose rays *Rhinoptera bonasus* in the Caloosahatchee River estuary of Southwest Florida, USA, also exhibited seasonal residency (Collins et al. 2008). The majority of evidence for seasonal residency was from smalltooth sawfish *Pristis pectinata* studies (n = 5; Simpfendorfer et al. 2010, 2011, Poulakis et al. 2013, Carlson et al. 2014, Papastamatiou et al. 2015). Understanding the movements and philopatric behaviors of this Critically Endangered batoid and other members of its family is vital to conserving their populations. Conservation for species living seasonally in a particular area could entail using seasonal fisheries management or time/ area closures. Critical habitat and food sources for these species will also need to be protected year-round in order to ensure these areas continue to support individuals returning on an annual basis.

Residency

Residency was found in 4 studies, 3 families (Dasyatidae, Rhinobatidae, and Rhynchobatidae), and 5 species as well as in the wedgefish complex (*Rhynchobatus* spp.) (Table 1). The limited evidence of residency in batoids could be due to the extensive research effort that is needed to show that individuals are resident. Many studies that show site affinity or seasonal residency might actually show residency with more research effort. All evidence of residency was determined using passive acoustic monitoring (Campbell et al. 2012, Corcoran et al. 2013, Cerutti-Pereyra et al. 2014, White et al. 2014). Due to low sample sizes, capture of only juveniles, and only some individuals exhibiting residency (Campbell et al. 2012, Cerutti-Pereyra et al. 2014, White et al. 2014), the best example of residency in a batoid comes from a provisioning site for southern stingrays *Dasyatis americana* (Corcoran et al. 2013). Although sample size was also low (n = 5), all individuals remained at Stingray City Sandbar at Grand Cayman Island in the Caribbean for 18 mo (Corcoran et al. 2013). Feeding ecotourism operations affected normal movement behavior in stingrays (Corcoran et al.

2013); therefore, it is necessary to evaluate the costs and benefits of batoid ecotourism. Resident populations of batoids need to be managed on an appropriate geographical scale in order to protect them from local extirpation. Local protection is typically easier than protecting an organism that traverses many jurisdictions, which is why it is crucial to define the geographic scale of movements within a study. Given the importance of protecting threatened batoid species, it is key that research efforts are broadened to investigate residency in these populations. This will require substantial resources to support long-term studies using acoustic telemetry via internal insertion of tags or long-term satellite tracking.

Regional philopatry

Evidence of regional philopatry was found in 10 population genetic studies. These involved 10 species of batoids, including stingrays (Dasyatidae), sawfishes (Pristidae) and guitarfish (Rhinobatidae). These studies frequently revealed structure over spatial scales of a few 100 km. Genetic studies of the red stingray *Dasyatis akajei* off the coast of China and Japan revealed population structure between samples collected from 160 to 720 km apart (Li et al. 2013, 2015). There were no physical barriers to prevent gene flow between these populations and structure was detected in both bi-parentally and maternally inherited genetic markers (Li et al. 2013, 2015). These findings demonstrate that individuals of both sexes tend to reproduce within their natal region (Li et al. 2013, 2015). This could result from residential behavior or through return-migrations by reproducing adults of both sexes to their natal region or even their exact natal site (see next section). Robust sampling across relatively small geographic scales (<100 km) and increasing use of genomic approaches to maximize power to detect subtle population genetic differentiation is recommended. Populations exhibiting regional philopatry should be managed at the spatial scale at which the structure is observed. Population-genetic studies of exploited batoids are urgently needed to delineate stocks for assessment and management, which are fundamental for sustaining fisheries.

Natal philopatry

Natal philopatry was found in 1 batoid study. It is difficult to directly demonstrate natal philopatry in

marine species because it requires tracking individuals from their birthplace back to the same area when they reproduce (Chapman et al. 2015). The first direct evidence of natal philopatry in the chondrichthyans was demonstrated by showing that female lemon sharks *Negaprion brevirostris* born in Bimini, Bahamas, between 1995 and 1999 returned from 2008 to 2012 to give birth (Feldheim et al. 2014). None of the batoids have been subjects of this type of long-term sampling so there is currently no parallel evidence of natal philopatry in this group. However, it is also possible to demonstrate natal philopatry by showing strong genetic structure between adjacent parturition areas that can only be explained by individuals selectively using their birthplace for parturition, as opposed to individuals using adjacent parturition sites randomly. Whole mitogenome sequencing was used to show that juvenile largetooth sawfish *Pristis pristis* sampled in adjacent riverine nursery areas in Australia comprised genetically distinct groups (Feutry et al. 2015). In this study, it was concluded that adult females return to their natal river to give birth because there were no physical barriers that would otherwise prevent these females from randomly using rivers for parturition (Feutry et al. 2015). Investments in studies that can sample adjacent parturition areas and then use whole mitogenome sequencing or other genomic approaches to test for structure will elucidate how common natal philopatry is in batoids and under what circumstances it occurs. Long-term tagging and genetic pedigree studies similar in design to the lemon shark study in Bimini, Bahamas (Feldheim et al. 2014), could also provide direct evidence of natal philopatry in batoids, as could chemical tracer analysis between individuals collected at adjacent parturition areas (Hussey et al. 2011).

Sex-biased dispersal

Few batoid studies provided strong evidence for differences in philopatric behavior between the sexes. Despite the fact that sample size was low, juvenile freshwater whipray *H. dalyensis* males (n = 2) displayed a seasonal migration into brackish water before returning upriver near their initial tagging site, while juvenile females (n = 2) remained in the same area for the duration of the study (Campbell et al. 2012). Acoustically tagged wedgefish *Rhynchobatus* spp. and giant shovelnose rays *Glaucostegus typus* showed evidence of site fidelity, residency, and seasonal residency over multiple years, while move-

ments varied across sexes and individuals (White et al. 2014). Wedgefish could simply be demonstrating species-differentiated movements given the *Rhynchobatus* spp. complex (White et al. 2014). Population genetic studies of sharks frequently reveal structure in maternally inherited markers but homogeneity in bi-parentally inherited markers, which provides evidence for female philopatry and male dispersal. To date there is no evidence of this phenomenon in batoids, which suggests that both sexes may exhibit similar levels of philopatry. Future studies will need to focus on higher sample sizes of all life stages that include a similar number of males and females. Managing populations that are exhibiting sex-biased dispersal is context-dependent, but should include elements of local management combined with regulations that protect movement patterns of both sexes and all life stages.

Morphological constraints and long-distance movements

In contrast to sharks, which use their caudal fin, most batoids use their pectoral fins for propulsion (Schaefer & Summers 2005) with the exception of electric rays, guitarfish, wedgefish, and sawfish. Batoids that use their pectoral fins for propulsion generally exhibit one of 2 types of locomotion:oscillatory or undulatory, while morphological differences amongst genera and species can be indicative of locomotive strategy (Schaefer & Summers 2005). Rigid pectoral fins generally represent oscillatory movement exhibited by the more pelagic batoids (i.e. Myliobatidae, Mobulidae, Rhinopteridae, and Gymnuridae), while reduced calcification in the pectoral fin cartilage generally represents undulatory movement found in benthic batoids (Schaefer & Summers 2005). It is plausible to hypothesize that these differences mean that benthic batoids are limited to slower swimming speeds, which constrains them to exhibit residency to restricted areas. In contrast, pelagic rays are potentially faster, more efficient swimmers, and therefore more likely to be dispersive or undertake return migrations than be resident. This review provides evidence of residency in only 6 species of batoids, 4 of which are benthic undulatory swimmers (*Dasyatis americana*, *Himantura dalyensis*, *Pastinachus atrus*, and *Urogymnus asperrimus*; Table 1) and the remainder being benthic species that use their caudal fins for propulsion (*Glaucostegus typus* and *Rhynchobatus* spp.; Table 1). Two species of pelagic batoids (*M. alfredi* and *M. birostris*) exhibit seasonal residency (De-

war et al. 2008, McCauley et al. 2014, Braun et al. 2015), while it is presumed that another (the spotted eagle ray *Aetobatus narinari* in Bermuda) is resident even though the results can only conclusively be defined as site affinity (Ajemian et al. 2012, Ajemian & Powers 2014). Similarly, pelagic cownose rays exhibit small home ranges in the Caloosahatchee River (1 to 22.3 km; Collins et al. 2008) even though it has been hypothesized that they make large-scale migrations in response to increasing temperatures (Smith & Merriner 1987). Cownose rays are capable of moving long distances (>100 km) in the Gulf of Mexico (Ajemian & Powers 2014), but these movements are limited in comparison to earlier speculation (Smith & Merriner 1987). The round stingray *Urobatis halleri*, although a benthic undulatory swimmer, is known to move >30 km from an initial tagging site at Seal Beach, California (Vaudo & Lowe 2006). Gene flow along the California coast, USA, and Baja California, Mexico, in this species also suggests dispersal over a large area (Plank et al. 2010). Overall, although data are very limited, there are examples of pelagic batoids exhibiting residency to relatively limited areas and benthic batoids making long-range migrations, which collectively challenge the hypothesis that there is a strong link between morphology and philopatry in batoids. Further investigations should aim to resolve philopatric behavior in both groups of batoids in order to make a more robust comparison between benthic and pelagic species.

CONCLUSIONS

Philopatry occurs in a wide variety of batoids and can structure their populations over fine geographical scales. As such, conservation and management have the potential to be effective at a local scale for the recovery of threatened species and protection of vulnerable species. Local threats to residential or returning individuals will have a much greater effect than these threats would have on individuals exhibiting large-scale movements. Spatially concentrated fisheries may rapidly extirpate philopatric batoids, especially when there is limited recruitment from neighboring populations. Likewise, local conservation actions, such as protected areas or habitat restoration, have the potential to benefit philopatric batoids. There is a need to revolutionize the field of batoid movements through the use of telemetry and studies that parallel the consistency and duration of existing shark movement studies. With the exception of skates, conventional tagging efforts for batoids

have been minimal when compared with sharks. Many logistical issues such as array maintenance and cost, spatial complications (i.e. arrays not large enough to discern true movements of individuals), and external tag retention time have contributed to the lag in batoid movement studies (Ajemian & Powers 2014, Hussey et al. 2015). Another major impediment has been the lack of development of tagging techniques for batoids. The development of new telemetry technologies with small tags that have a longer battery life promises a brighter future for batoid ecology research (Ajemian & Powers 2014, Hussey et al. 2015). Future batoid research should include a variety of life stages, employ higher sample sizes, use consistent philopatry terminology, and distinguish between residency and site fidelity as almost half of the studies had evidence of site affinity only. An improved understanding of philopatry in a broader range of batoids will help match the scale of their population dynamics to the necessary scale of management.

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