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REVIEW

Batoid nurseries: definition, use and importance

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ABSTRACT: Nursery areas are crucial for many elasmobranch species, providing benefits that increase fitness and survival. Shark nurseries are well studied and our knowledge of their function and importance has expanded over the past few decades. However, little attention has been given to batoid nurseries, with studies covering less than 6% of the 663 currently described species. Threats of extinction faced by batoids reinforce the importance of defining these critical habitats. This review synthesises current knowledge of batoid nursery areas to provide a better understanding of their ecological roles and importance. Historically, different criteria have been used to define viviparous and oviparous batoid nurseries, causing confusion that could lead to failure of conservation and management strategies by under- or overestimating the importance of areas and delaying effective action. We suggest the criteria used to identify shark nurseries be applied to juvenile batoids, standardizing this nursery definition for all elasmobranchs, but we also advocate for a second set of criteria that identifies egg case nurseries. Batoids are thought to play 3 main ecological roles in nursery areas: energetic links, bioturbators and mesopredators. Biotic and abiotic features affect abundance and distribution of batoids within nurseries and likely play a key role in their habitat use. However, analysis of batoid ecological roles in nursery areas is limited by the lack of research on their early life history stages. Thus, identification of areas that support sensitive life stages and an improved understanding of early life history are crucial for the efficient management and conservation of batoid species and their nurseries.

KEY WORDS: Sawfish · Skate · Stingray · Guitarfish · Habitat use · Ecological role

INTRODUCTION

Nursery areas are crucial for the health of many elasmobranch populations (Heupel et al. 2007). These areas provide biotic and abiotic features that benefit the development and survival of juveniles (Castro 1993, Heupel & Simpfendorfer 2011). In the past 30 yr, studies of shark nursery areas have significantly progressed our understanding of their function and importance (e.g. Simpfendorfer & Milward 1993, Stevens & West 1997, Heupel & Simpfendorfer 2005, 2011, Keeney et al. 2005, Grubbs & Musick 2007, McCandless et al. 2007). However, the use of nurseries by batoid species remains poorly understood.

Batoids are the most diverse group of cartilaginous fishes (Aschliman et al. 2012), consisting of 23 families, 663 species and at least 50 more yet to be described (Last et al. 2016). However, batoids are the most endangered group of elasmobranchs, with 19.9% of species listed in a Threatened category by the IUCN Red List (Dulvy et al. 2014, Last et al. 2016). Batoids are increasingly taken by artisanal and industrial fisheries around the world, which has contributed to population declines (Stevens et al. 2000,

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Cavanagh et al. 2003, Cailliet et al. 2005, Stevens et al. 2005, White et al. 2006, Dulvy et al. 2003, 2014). Habitat loss (Stevens et al. 2005) and changes in climate (Rahmstorf 2007, Chin et al. 2010) also represent increasing threats to many species. Due to their relatively unproductive life history characteristics (e.g. slow growth, large body size, late sexual maturity, low fecundity and high longevity), batoid populations can rapidly be depleted when exposed to one or more of these anthropogenic pressures (Stevens et al. 2000, Fowler et al. 2005). Collapses of populations of the common skate *Dipturus batis* (Brander 1981, Dulvy & Reynolds 2002), the purple eagle ray *Myliobatis hamlyni* (White & Kyne 2010) and all sawfish species (Pristidae) (Dulvy et al. 2016), for example, have all been reported as a result of intense human pressures. Furthermore, stock size and recruitment are closely related in batoids, resulting in long recovery periods after over-exploitation (Holden 1974, Stevens et al. 2000). Therefore, intensive management and conservation effort is required to sustainably fish these populations or aid their recovery (Simpfendorfer & Dulvy 2017).

The ability to effectively manage and conserve batoid populations is affected by a lack of knowledge on their biology and ecology (Cerutti-Pereyra et al. 2014, Last et al. 2016). The ecology and life history of batoids are poorly understood (256 Data Deficient species in the IUCN Red List) and long-term species-specific data are scarce, such as the scale and timing of movements (Bonfil 1999), level of philopatry (Vaudo & Lowe 2006) and location or presence of foraging, mating and nursery areas (Le Port et al. 2012).

The identification of elasmobranch nurseries is complicated by their different reproductive modes. Many batoids exhibit aplacental viviparous reproduction, but skates (4 families: Rajidae, Arhynchobatidae, Gurgesiellidae, Anacanthobatidae; 38 genera; at least 288 described species) are a strictly oviparous group (Conrath & Musick 2012). Historically, elasmobranch nursery theories have largely been developed based on viviparous species models (e.g. Heupel et al. 2007). Hoff (2016) did consider nursery areas for oviparous skates, but there is a need to develop a unified definition of nursery areas that are suitable for all elasmobranch reproductive modes. Hence, the aim of this review was to provide a synthesis of the current knowledge on oviparous and viviparous batoid nursery areas. In addition, we aimed to contribute to a better understanding of ecological roles of batoids within these areas, which is crucial for developing effective management strategies for batoids and their nursery habitats worldwide.

ELASMOBRANCH NURSERY AREA CONCEPTS

Historically, nursery areas were defined as places where mature females give birth and juveniles reside until they reach maturity (Meek 1916, Springer 1967, Bass 1978, Castro 1993). According to Springer (1967), Bass (1978) and Branstetter (1990), these places should offer abundant food resources and lower predation risk for neonates. Thus, most estuarine and shallow marine ecosystems were automatically identified as nurseries based on the presence of juveniles and assumptions of high productivity and protection against predation (Beck et al. 2001). This concept was widely accepted and applied, although a clear definition of what constituted a nursery was not developed. Lack of a clear definition of nursery habitats inhibited conservation efforts because the identification of vast areas as nurseries meant that protection was expensive and difficult to implement (Heupel et al. 2007). Thus, the need for a refined definition of nursery areas increased over time, with the first step to resolve the definition proposed by Beck et al. (2001).

Beck et al. (2001) specifically noted that nursery areas for marine animals were not just places where juveniles occur, but regions where juveniles occur at higher densities, avoid predation more successfully and grow at a faster rate than the average for that species. Beck et al. (2001) also stated that nurseries contribute more individuals per unit area to adult stocks than other habitats where juveniles occur. Consequently, not all areas where juveniles are found are nurseries. This approach to defining nursery areas was more precise and reduced part of the risk of diluting management and conservation efforts.

However, the definition outlined by Beck et al. (2001) had gaps, especially regarding inter-annual variability in nursery use and recognition of the difficulty in defining the contribution of a single area to an adult population. While Beck et al. (2001) suggested that some habitats are more likely to be nursery areas than others, testable approaches to identify these areas were not proposed. To provide practical means to identify nursery areas for elasmobranchs, Heupel et al. (2007) proposed a set of criteria specific for the group based on Beck et al.'s (2001) concept, but incorporating aspects such as higher than average abundance and philopatry as metrics. Using this approach, an elasmobranch nursery area should be defined based on 3 criteria where newborn or young-of-the-year individuals (1) are more commonly encountered in the area than in other areas, (2) have a tendency to remain or return for extended periods and (3) repeatedly use the area or habitat across years.

This definition allowed researchers to test the existence of nursery areas for sharks in a straightforward manner. Moreover, Heupel et al. (2007) proposed new terms to the literature to define areas used by juvenile elasmobranchs that are not nurseries, such as pupping, birthing and egg-laying or hatching grounds. Heupel et al.'s (2007) criteria have been successfully applied by elasmobranch researchers (e.g. Hussey et al. 2009, Froeschke et al. 2010, Henderson et al. 2010, Espinoza et al. 2011, Francis 2013), but in general have been limited to viviparous species.

Identifying nursery areas for skates and other oviparous species has proven more challenging because of their reproductive mode. Until recently, authors commonly identified skate nursery areas as those where high densities of eggs occur (egg density criterion), with little consideration of the abundance of neonates and juveniles (e.g. Hoff 2008, Hunt et al. 2011, Treude et al. 2011, Amsler et al. 2015). Hoff (2016) emphasized the difficulty in defining nurseries for oviparous batoids and developed a set of criteria to identify their nursery areas. He suggested separating the areas used for eggs and juveniles, with the addition of 2 terms to the literature: 'egg case nursery' and 'juvenile nursery'. To be defined as an egg case nursery, an area should have high densities of eggs and egg cases in contact with the benthos or permanent structures. In addition, the area must be used as an egg-laying area over multiple years, and newborns should leave the area promptly after hatching. The egg case nursery definition uses criteria similar to those of Heupel et al. (2007), making it easily testable. Hoff's (2016) juvenile nursery was defined as an area that should have a high abundance of neonate and juvenile skates, be distinct from the egg case nursery and strongly contribute to population recruitment. This definition is also similar to that of Heupel et al. (2007) for shark nursery areas, and is functionally equivalent.

However, some confusing points in the nomenclature and concepts of oviparous batoids have been observed, especially regarding the definition of egg-laying and hatching sites as nurseries. According to Heupel et al. (2007), egg-laying and hatching sites could be nurseries, but only if the post-hatching young remain in the same area, a criterion which contradicts Hoff's (2016) description. Generally, elasmobranch nursery areas are defined as those where many of the young live after birth (Springer 1967, Bass 1978, Branstetter 1990, Beck et al. 2001), but eggs are a developmental stage that contain unborn individuals. The requirements for optimal development of eggs and juveniles may also differ. In other words, optimal conditions for egg development are not always advantageous for juvenile growth. Hoff (2008, 2010), Love et al. (2008) and Hunt et al. (2011), for example, observed no or very few neonates and juvenile skates in areas identified using the egg density criteria, reinforcing that newborn skates are likely to leave these areas soon after hatching. Thus, the egg case nursery as defined by Hoff (2016) is different than an egg-laying ground since not all areas where eggs are found would meet the egg case nursery criteria. Under such usage, almost all of the areas previously identified as skate nursery areas are in fact egg case nursery areas and not juvenile nurseries. This is not to say that these species do not have juvenile nurseries, just that the areas identified to date are egg case nurseries and juvenile nursery areas remain to be determined.

Importantly, for a single species, egg case nursery and juvenile nursery areas could overlap and therefore result in a single nursery area serving both functions. Although there are no known examples, overlaps in egg case and juvenile nursery grounds might occur in batoid species with small home ranges or restricted distributions. Nevertheless, if egg and juvenile nurseries overlap in a delineated area, but are not mostly segregated from the adult population, this area cannot be a nursery (Knip et al. 2010). This area might provide benefits for a population (e.g. food abundance, optimal temperature) but does not provide specific advantages for egg development or juvenile growth and survival separate from the needs of adults. Difficulty in distinguishing egg case and juvenile nurseries is also an issue for oviparous sharks. For example, Cau et al. (2013, 2017) identified a nursery area for the small spotted catshark *Scyliorhinus canicula* in the central-western Mediterranean Sea using the egg density criteria, although several specimens of *S. canicula* of different life stages were also observed in the same area.

In fact, both egg case nursery and juvenile nursery areas are essential fish habitats (EFH), and their importance to populations must be recognized. For this reason, these definitions should not be aggregated, as has been common in the literature. Confusion and inconsistency in the literature highlights the need for understanding and defining these essential habitats for early life stage batoids. However, the use of multiple and sometimes confusing terms could impede conservation and management efforts by under- or overestimating the importance of specific areas, diluting resources and delaying effective protection. We suggest that Hoff's (2016) second term, 'juvenile nursery area', be simplified to 'nursery', since it is consistent with Heupel et al. (2007), which defines nursery areas as associated with the presence and occurrence of juveniles. Thus, we recommend the use of the Heupel et al. (2007) criteria for nursery areas and the Hoff (2016) criteria for egg case nursery as they provide clear, simple, testable and widely applied methods to standardize the definitions for all elasmobranchs.

Therefore, for the purposes of viviparous and oviparous elasmobranch populations, the criteria for an area to be considered a nursery would be (1) newborn or young-of-the-year individuals are more commonly encountered there than in other areas, (2) newborn or young-of-the-year individuals have a tendency to remain or return for extended periods and (3) newborn or young-of-the-year individuals repeatedly use the area or habitat across years. For oviparous species, an egg nursery area can be identified using the following criteria: (1) high densities of eggs and egg cases in contact with benthic or stationary materials, (2) adults use the area or habitat to lay eggs repeatedly over multiple years and (3) newborn or young-of-the-year individuals leave the area promptly after hatching.

PREVALENCE OF ELASMOBRANCH NURSERY AREA USE

Many elasmobranch species use nursery areas (e.g. Castro 1993, Yokota & Lessa 2006, Heupel et al. 2007, DeAngelis et al. 2008, Freitas et al. 2009, Speed et al. 2010, Cerutti-Pereyra et al. 2014). These areas can be critical to early life stages of large-bodied species with low fecundity and slow growth (Yokota & Lessa 2006, Hussey et al. 2017). These species generally have relatively small litters and longer periods between reproductive events. Hence, survival during early life is crucial for population persistence (Heupel et al. 2007, Cerutti-Pereyra et al. 2014). For this reason, slow-growing and low-fecundity species are more likely to benefit from delineated nursery areas that increase survival rates of the young-of-the-year age class (Heupel & Simpfendorfer 2011).

Nevertheless, exceptions may occur. As emphasized by Springer (1967), McElroy et al. (2006) and Heupel et al. (2007), some elasmobranch species do not use distinct nursery grounds. Small elasmobranch species with productive life history characteristics and fast reproductive cycles often lack nurseries (Knip et al. 2010). For those species, the absence of a nursery, which could result in high mortality rates, is overcome by their relatively rapid growth, early sexual maturity and high reproduction. Knip et al. (2010) also hypothesised that the level of protection against predation in a nursery could be small or even irrelevant for small-bodied elasmobranch species since some small-bodied sharks are likely to be preyed upon throughout their life, even in nursery areas, as juveniles of co-occurring larger species could be potential predators. Thus, the use of nurseries is determined by the life history components of each species and as such may be traded off for other advantages (Branstetter 1990).

BATOID USE OF NURSERY AREAS

Nursery areas have been reported in a range of batoids, including sawfishes, stingrays, skates, guitarfishes and numbfishes (Table 1). Here, we examine some of the studies that have described batoid nursery areas in a variety of habitats and consider application of nursery theory to these species.

Identification of batoid nursery areas has historically used differing criteria (Table 1). Few studies occurred prior to 2007, but those that did used the occurrence of neonates and pregnant females as indicators (e.g. Yokota & Lessa 2006). Since 2007, most studies on viviparous batoids have used the Heupel et al. (2007) criteria (11 studies), while the egg density criterion has been used for the majority of studies on oviparous batoids (8 studies).

Whether all batoid species rely on nursery areas is unclear due to the limited number of studies on these species. Existing studies cover less than 6% of the currently described species — only 38 of 663 species and 12 of 26 living families. In addition, the existing studies are restricted to a few families — mainly Arhynchobatidae (soft nose skates), Dasyatidae (whiptail stingrays) and Pristidae (sawfishes). Sawfishes in particular have been increasingly studied due to their imminent threat of extinction (Dulvy et al. 2014, 2016). The concentration of research effort to a select few families shows a strong bias in batoid nursery research. As a consequence, knowledge about nurseries of several ecologically and economically important batoid species, and/or threatened families remain scarce or nonexistent.

Research bias is also evident when habitat types for batoid nursery areas are evaluated (Table 1). The majority of Dasyatidae and Pristidae species inhabit shallow, sheltered coastal and tropical waters. On the other hand, Arhynchobatidae species tend to be

Table 1. Identified batoid nursery areas to date

Family	Species	Location	Habitat	Criteria	References
Aetobatidae	*Aetobatus narinari*	Northeastern Brazil rocky reef	Coastal sandbanks and juveniles and pregnant females	Occurrence of neonates, small	Yokota & Lessa (2006)
Arhynchobatidae	*Bathyraja aleutica*	Eastern Bering Sea	Flat sandy mud	Egg density and distribution	Hoff (2008)
	Bathyraja interrupta	Eastern Bering Sea	Flat sandy mud	Egg density and distribution	Hoff (2008)
	Bathyraja parmifera	Eastern Bering Sea	Flat sandy mud	Egg density and distribution	Hoff (2008)
	Raja rhina	Southern California Bight	Rocky outcrop sitting on the edge of a submarine canyon	Egg density and distribution	Love et al. (2008)
	Bathyraja parmifera	Eastern Bering Sea	–	Egg density and distribution	Hoff (2009)
	Bathyraja aleutica	Eastern Bering Sea	Flat sandy to muddy bottom	Egg density and distribution	Hoff (2010)
	Bathyraja interrupta	Eastern Bering Sea	Flat sandy to muddy bottom	Egg density and distribution	Hoff (2010)
	Bathyraja parmifera	Eastern Bering Sea	Flat sandy to muddy bottom	Egg density and distribution	Hoff (2010)
	Bathyraja smirnovi	Shiribeshi Seamount Sea of Japan	Rocky area	Egg density and distribution	Hunt et al. (2011)
	Bathyraja spp.	Eastern Mediterranean Sea	Cold-seep carbonates	Egg density and distribution	Treude et al. (2011)
	Bathyraja spp.	Western Antarctic Peninsula	Sandy and rock seabed	Egg density and distribution	Amsler et al. (2015)
	Bathyraja aleutica	Eastern Bering Sea	Flat sandy to muddy bottom	Hoff (2016)	Hoff (2016)
	Bathyraja parmifera	Eastern Bering Sea	Flat sandy to muddy bottom	Hoff (2016)	Hoff (2016)
	Bathyraja brachyurops	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
	Bathyraja macloviana	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
	Bathyraja sp.	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
	Bathyraja albomaculata	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
	Psammobatis lentiginosa	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
	Psammobatis normani	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
Dasyatidae	*Hypanus americanus*	Northeastern Brazil	Coastal sandbanks and rocky reef	Occurrence of neonates, small juveniles and pregnant females	Yokota & Lessa (2006)
	Hypanus guttatus	Northeastern Brazil	Coastal sandbanks and rocky reef	Occurrence of neonates, small juveniles and pregnant females	Yokota & Lessa (2006)
	Hypanus marianae	Northeastern Brazil	Coastal sandbanks and rocky reef	Occurrence of neonates, small juveniles and pregnant females	Yokota & Lessa (2006)
	Hypanus americanus	United States Virgin Islands	Shallow seagrass flat	Heupel et al. (2007)	DeAngelis et al. (2008)
	Bathytoshia lata	Kane'ohe Bay, Hawaii, USA	Mud habitats	Heupel et al. (2007)	Dale et al. (2011)
	Himantura uarnak	Ningaloo Reef, Western Australia	Reef lagoon	Heupel et al. (2007)	Cerutti-Pereyra et al. (2014)
	Pastinachus ater	Ningaloo Reef, Western Australia	Reef lagoon	Heupel et al. (2007)	Cerutti-Pereyra et al. (2014)
	Urogymnus asperrimus	Ningaloo Reef, Western Australia	Reef lagoon	Heupel et al. (2007)	Cerutti-Pereyra et al. (2014)
	Urogymnus granulatus	Orpheus Island, Australia	Reef flat and mangroves	Heupel et al. (2007)	Davy et al. (2015)
Glaucostegidae	*Glaucostegus cemiculus*	The Gulf of Gabes, southeastern Tunisian, central Mediterranean Sea	Sandy bottoms	Occurrence of females with encapsulated eggs, neonates and juveniles	Bradai et al. (2006)

Table continues on next page

Table 1 (continued)

Family	Species	Location	Habitat	Criteria	References
	Glaucostegus typus	Ningaloo Reef, Western Australia	Reef lagoon	Heupel et al. (2007)	Cerutti-Pereyra et al. (2014)
	Glaucostegus cemiculus	The Gulf of Gabes, southeastern Tunisian, central Mediterranean Sea	Sandy−muddy bottoms	Occurrence of gravid females, neonates with visible umbilical scars and the permanence of juveniles	Enajjar et al. (2015)
Narcinidae	*Narcine brasiliensis*	Northeastern Brazil	Coastal sandbanks and rocky reef	Occurrence of neonates, small juveniles and pregnant females	Yokota & Lessa (2006)
	Narcine brasiliensis	Paraná, Brazil	Mangrove shorelines and sandy−muddy bottoms	Heupel et al. (2007)	Martins et al. (2009)
Pristidae	*Pristis pectinata*	South Florida, USA	Shallow, sheltered and mangrove shorelines	Heupel et al. (2007)	Simpfendorfer et al. (2010)
	Pristis pectinata	Southwestern Florida, USA	Shoreline habitats with overhanging vegetation	Heupel et al. (2007)	Poulakis et al. (2011)
	Pristis pectinata	Florida, USA	Mangrove shorelines and shallow euryhaline habitats	Heupel et al. (2007)	Norton et al. (2012)
	Pristis zijsron	Western Australia	Tidal mangrove creeks	Heupel et al. (2007)	Morgan et al. (2011)
Rajidae	*Raja asterias*	South Ligurian and north Tyrrhenian Sea	Muddy bottoms	High abundance of juveniles	Serena & Relini (2006)
	Raja. clavata	Ionian Sea	–	High abundance of juveniles	Serena & Relini (2006)
	Raja spp.	Outer Thames estuary, Isle of Wight, Bristol Channel and Lleyn Peninsula	–	High abundance of juveniles	Ellis et al. (2005)
	Raja brachyura	Portugal Coast	Sandy and rock seabed	Occurrence of juveniles and adults	Serra-Pereira et al. (2014)
	Raja clavata	Portugal Coast	Sandy and rock seabed	Occurrence of juveniles and adults	Serra-Pereira et al. (2014)
	Raja montagui	Portugal Coast	Sandy and rock seabed	Occurrence of juveniles and adults	Serra-Pereira et al. (2014)
	Amblyraja doellojuradoi	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
	Zearaja chilensis	Southwest Atlantic Ocean, northern part of the Argentine Continental Shelf	Sands, shells, gravels, muds, consolidated sediments and rocks	Egg density and distribution	Vazquez et al. (2016)
Myliobatidae	*Myliobatis goodei*	Southern Brazil	Flat sandy mud	Heupel et al. (2007)	Araújo et al. (2016)
	Myliobatis ridens	Southern Brazil	Flat sandy mud	Heupel et al. (2007)	Araújo et al. (2016)
Gymnuridae	*Gymnura micrura*	Northeastern Brazil	Coastal sandbanks and rocky reef	Occurrence of neonates, small juveniles and pregnant females	Yokota & Lessa (2006)
Gurgesiellidae	*Fenestraja plutonia*	Cape Lookout	Coral banks	Occurrence of females with encapsulated eggs and neonates	Quattrini et al. (2009)
Rhinobatidae	*Pseudobatos percellens*	Northeastern Brazil rocky reef	Coastal sandbanks and small juveniles and pregnant females	Occurrence of neonates,	Yokota & Lessa (2006)
	Pseudobatos productus	Southern California, USA	Estuary	Heupel et al. (2007)	Farrugia et al. (2011)
	Rhinobatos rhinobatos	The Gulf of Gabes, southeastern Tunisian, central Mediterranean Sea	Sandy−muddy bottoms	Occurrence of gravid females, neonates with visible umbilical scars and the permanence of juveniles	Enajjar et al. (2015)
Rhinopteridae	*Rhinoptera bonasus*	Northeastern Brazil	Coastal sandbanks and rocky reef	Occurrence of neonates, small juveniles and pregnant females	Yokota & Lessa (2006)

found in cold and deep waters, such as the eastern Bering Sea and western Antarctic Peninsula. This tendency shows that very little attention has been given to pelagic batoids inhabiting open water/offshore systems. The reason for focusing on particular batoid families and habitats is not clear, but might reflect the limited number of researchers dedicating time to better understand batoids and current limitations faced by these researchers to meet funding requirements to access remote locations.

KEY FACTORS AFFECTING BATOID USE OF NURSERIES

Batoids that demonstrably use nurseries are attracted to these locations for a combination of biotic and abiotic features. Differences in these features can directly affect abundance and distribution (Sguotti et al. 2016). Even small variations can lead to spatial and temporal variability (Felley & Felley 1986, Heupel & Hueter 2002). Shallow coastal ecosystems, for example, are some of the most variable in the marine world. Given the common (but not exclusive) use of coastal habitats as nurseries by batoids and their variable nature, juveniles that rely on these habitats must be able to cope with significant environmental changes over relatively short time periods (e.g. Knip et al. 2010, Schlaff et al. 2014). Thus, the features determining batoid abundance, residency and fidelity in nursery areas will depend on the species and its geographical location. A better understanding of these features will be crucial to long-term assessments of batoid spatial ecology and development of site-specific management. Here, we discuss some common features affecting batoid use of nurseries.

Energy partitioning into food acquisition

Obviously, food is an essential nursery feature. If there is not enough food, survival will be too low. However, energy requirements and resulting behaviour may differ greatly between species. In theory, abundant food enhances juvenile development and survival. However, in practice, this is not always true. Davy et al. (2015) observed that food was not a major driver of mangrove whipray *Urogymnus granulatus* movements within a nursery area. Thus, while the availability of food resources is an important feature, it is not the only essential nursery feature for some batoids.

Predator avoidance

Several authors have hypothesised that, even by delaying maturity and recruitment, the permanence of juvenile batoids in an area protected from large predators would be an important strategy for population health — a trade-off between survival and maturity (Branstetter 1990, Dale et al. 2011, 2013, Dale & Holland 2012). However, nursery areas are not always predator-free. Heupel et al. (2007) highlighted that nurseries can have high levels of predators, but individuals may employ behavioural strategies to avoid them. According to Costa et al. (2015), juvenile Brazilian large-eyed stingrays *Hypanus marianae* spend more time in turbid, shallow waters with low prey abundance to minimize predation risk. Hoff (2007) hypothesised that neonate *Bathyraja parmifera* move out of egg case nurseries shortly after emergence to avoid large predators. Davy et al. (2015) also cited predator avoidance as a major driver of habitat use patterns of juvenile mangrove whiprays *U. granulatus* that stayed in shallow areas and in mangrove root habitats of the nursery to avoid encounters with large blacktip reef *Carcharhinus melanopterus* and lemon *Negaprion acutidens* sharks. Even larger batoids could present risks to juveniles. Branco-Nunes et al. (2016) reported the first evidence of predation between dasyatid species — remains of *H. marianae* were found in the stomach contents of larger *H. americanus*. Thus, given the small size and limited swimming ability of many juvenile batoids (Blake 2004, Dale et al. 2011), it is likely that predation rates can be high even inside nursery grounds.

The potential for cannibalism or intra-specific predation might be the major difference between shark and batoid nurseries. Cannibalism is common among shark groups (Compagno 2001) and thus can be an important factor in the need for nursery areas where the juveniles of a species are separated from the adults. Morrissey & Gruber (1993) and Guttridge et al. (2012), for example, reported intra-specific predator–prey interactions between juvenile, large juvenile and adult lemon sharks *Negaprion brevirostris*. On the other hand, the occurrence of cannibalism within batoid taxa has never been reported, and thus there are no known effects relative to nursery use.

Temperature

Temperature is a factor that affects the distribution and movement of a large number of species including elasmobranchs (e.g. Schlaff et al. 2014). Variations in water temperature have been shown to influence the biology and ecology of batoids (e.g. Fangue & Bennett 2003, Hopkins and Cech 2003, Cerutti-Pereyra et al. 2014). For example, Amsler et al. (2015) reported that temperature played an important role in the embryonic development and hatching of skate eggs off the western Antarctic Peninsula. Le Port et al. (2012) reported temperature was a major factor in short-tail stingray *Bathytoshia brevicaudata* movement patterns, while Dabruzzi et al. (2013) observed that ribbontail rays *Taeniura lymma* could identify optimal zones along a thermal gradient with a high level of accuracy. The ability to remain in a desired thermal range is important because juvenile ribbontail rays are often exposed to rapid and extreme temperature fluctuations in shallow coastal waters. Still, according to Dabruzzi et al. (2013), juvenile ribbontail rays must remodel biochemical pathways to improve physiological functions before recruitment and migration to the cooler, more stable habitats occupied by adults.

Batoids may also exploit variations in temperature to enhance oxygen consumption and digestive efficiency (Sims et al. 2006, Di Santo & Bennett 2011a,b). Matern et al. (2000) and Wallman & Bennett (2006) observed batoids foraging at high temperatures and moving to cooler areas after foraging to optimize digestive processes. In contrast, Tenzing (2014), through physiological tests, observed no significant variation between feeding and resting temperatures of *U. granulatus* at Orpheus Island, Australia. According to Tenzing (2014), the use of high temperature habitats might provide an ecological advantage for the species, accelerating digestive rates and, in the long term, juvenile development. Thus, higher temperatures might increase growth rates of juveniles (Wearmouth & Sims 2008, Jirik & Lowe 2012), increase reproductive success, improve feeding efficiency and increase survival through predator avoidance (Wallman & Bennett 2006). Therefore, the benefits of using nurseries with high temperatures may outweigh the potential physiological costs.

Salinity

Batoid movements and habitat use can also be influenced by salinity variations (Simpfendorfer et al. 2011, Poulakis et al. 2013). Juvenile sawfish seek out specific salinity levels to optimize their development or survival (Simpfendorfer et al. 2011, Norton et al. 2012). Similarly, Collins et al. (2008) and Heupel & Simpfendorfer (2008) suggested that some elasmobranch species actively move to remain within a specific salinity range, minimizing energetic costs of osmoregulation and freeing up energy for other processes (e.g. growth, sexual maturation). On the other hand, Poulakis et al. (2011) reported that smalltooth sawfish *Pristis pectinata* can remain in a nursery area under a wide range of salinities and continue to grow rapidly, suggesting that osmoregulation may have little influence on habitat selection for this species. Effects of environmental parameters such as salinity need to be explored in more detail to more fully define any relationships with batoid habitat use and selection, and how they influence nursery area use.

Oxygen levels

Dabruzzi & Bennett (2014) observed that the Atlantic stingray *Hypanus sabinus* commonly used shallow waters with reduced levels of dissolved oxygen. They hypothesised that by spending time in hypoxic areas, *H. sabinus* excludes direct competition with less hypoxia-tolerant organisms (Di Santo & Bennett 2011a) and reduces their vulnerability to predators. Thus, the ability to tolerate low oxygen concentrations might be an important advantage to some species of juvenile batoids and is likely a determining factor for use of some nurseries in shallow coastal areas.

ECOLOGICAL AND TROPHIC ROLE OF BATOIDS IN NURSERY HABITATS

The existing information on batoid ecological roles is based on limited research on a small number of species and locations, restricting our understanding largely to shallow water areas (e.g. Jacobsen & Bennett 2013). However, due to their high diversity and abundance, batoids are thought to play a number of key ecological roles that are integral to the functioning of several ecosystems, including nursery habitats (Costa et al. 2015). Here, we discuss 3 of these roles.

Energetic links

The limited data available indicate that juvenile batoids often remain within a restricted area over the short and medium term (weeks to months) (Vaudo & Lowe 2006, Davy et al. 2015), but some species have the capacity to move longer distances between habitats (Collins et al. 2007, 2008). These movements may have a variety of ecological effects, such as linking trophic webs and enhancing or redirecting nutrient and energy flows (Sheaves 2009). Thus, batoid movements can connect separated ecosystems at short time scales (Silliman & Gruber 1999, Matern et al. 2000, Cartamil et al. 2003, Davy et al. 2015) or over long time periods if they undertake ontogenetic or long-range migrations (Ebert & Cowley 2003, Aguiar et al. 2009, Ajemian & Powers 2014). These movements also enhance nursery area ecological roles by transporting energy and nutrients through biologically mediated pathways (Sheaves 2009). Based on current knowledge (Table 1), these connections would mostly be from very shallow coastal and estuarine habitats to deeper habitats. Further studies on deep-water species are needed to understand their role in linking energy between habitats.

Bioturbation

Many batoid species feed on infauna and meiofauna within soft sediments. To access these prey resources, batoids employ a number of behaviours (e.g. beating pectoral fins and jetting water) that suspend soft sediments and often form feeding pits — excavated depressions in the sediment (Myrick & Flessa 1996, O'Shea et al. 2012, Takeuchi & Tamaki 2014). This process, known as bioturbation, is very common in shallow coastal and estuarine nurseries with soft substrates and has a significant impact on the physical and biological habitat properties of intertidal and subtidal areas (O'Shea et al. 2012), such as density and distribution of benthic fauna (Dabruzzi et al. 2013). At a fine scale, the formation of feeding pits facilitates oxygen penetration into sediments, extending the zone of oxygenation (Gilbert et al. 1995) and affecting the nitrogen cycle (Kogure & Wada 2005). Bioturbation may also enable other species to benefit from prey items that are disturbed or excavated during foraging activities (VanBlaricom 1982, Heithaus et al. 2010). Kiszka et al. (2015) detected the association of southern stingrays *Hypanus americanus* and bar jacks *Caranx ruber*, where stingray bioturbation allowed *C. ruber* to access resources otherwise unavailable. Similarly, Kajiura et al. (2009) observed double-crested cormorants *Phalacrocorax auritus floridanus* taking advantage of *H. americanus* bioturbation to feed on teleosts. Thus, batoid bioturbation may fulfil a number of roles in soft sediment habitats within and beyond nursery grounds.

Trophic roles

Batoids can consume a wide range of prey items and have different feeding mechanisms and behaviours. They have highly variable dentition and jaw morphology among species, sex and/or life stage (Dean et al. 2007, Pardo et al. 2015). Batoid diets can also be influenced by aspects such as location, or predator and prey distribution (Ebert & Cowley 2003). Feeding strategy is another important indicator of batoid trophic relationships. Their approaches can be categorized as continuous feeders, ambush predators or filter feeders (Wetherbee & Cortés 2004).

On average, batoid trophic levels vary between 3.4 and 3.9, but can reach higher levels, such as a 4.2 for *Rostroraja velezi* (Navia et al. 2017). Navarro et al. (2013), for example, observed Mediterranean starry rays *Raja asterias* sharing trophic position with sea birds, and large demersal and pelagic fish. Batoids also play a role as food sources for larger predators in the food web (Visser 1999, Chapman & Gruber 2002, Dean et al. 2017). Therefore, most batoids function as mesopredators, providing the connection between top predators and lower trophic level organisms (Vaudo & Heithaus 2011). Navia et al. (2017) emphasized that, as a highly diverse group of mesopredators, batoids influence the stability and robustness of ecosystems (Dunne et al. 2004). Therefore, batoids likely play numerous and crucial roles in the structure and functioning of food webs. Unfortunately, due to the lack of knowledge of batoid ontogenetic changes and life cycles, the specific roles played by juvenile batoids in nursery habitats is poorly known.

ONTOGENETIC SHIFTS AND PARTITIONING OF RESOURCES IN NURSERIES

Ontogenetic shifts can be a major driver of changes in batoid diet composition (Gray et al. 1997, Colloca et al. 2010, Jacobsen & Bennett 2012). These shifts could be linked to morphological, behavioural and physiological features (Scharf et al. 2000). Dale et al. (2011), for example, observed that diet composition of brown stingrays *Bathytoshia lata* was closely related to body size. Juvenile brown stingrays tended to prey on small and abundant items due to their limited mouth gape, swimming speed and foraging abilities. On the other hand, larger brown stingrays tended to ingest less abundant but more energetically valuable items due to their greater foraging capabilities. Heithaus (2007) also emphasized the possible difficulty of larger juveniles in capturing small-sized prey. Thus, at some point, large juveniles need to switch habitats, moving away from nurseries to attain their specific dietary needs and meet their higher energetic demands. This strategy could drastically reduce time and energy used during foraging activities (Scharf et al. 2000) and competition for food resources with smaller conspecifics, producing a recognized evolutionary benefit (Dale et al. 2011, Carrier et al. 2012).

Partitioning of resources also allows the coexistence of competing or closely related marine predators (McPeek 2014). Several examples of partitioning of food resources between batoid species have been reported (Platell et al. 1998, Mabragaña & Giberto 2007, Treloar et al. 2007, Bornatowski et al. 2014, Bizzarro et al. 2017, Kemper et al. 2017). Pardo et al. (2015), for example, detected localised dietary partitioning between sympatric batoids in Australia, where several species foraged at the same spatiotemporal scale, but each species exhibited different prey preferences. Partitioning may also reduce competition for food resources among newborn batoids, decreasing mortality rates during early life stages. The existence of partitioning suggests that batoids may also use communal nurseries as this is a common feature in these areas (Kinney et al. 2011). The use of communal nurseries is known to provide benefits in reducing predation for sharks (Simpfendorfer & Milward 1993) and may have had great importance in their life histories. However, limited data have been presented suggesting this for batoids. Davy et al. (2015) briefly discussed the coexistence of 2 stingray species in the same bay at Orpheus Island, Australia, and there is evidence that communal groupings of batoids provide increased predator protection (Semeniuk & Dill 2006). Vazquez et al. (2016) also indicated the presence of communal egg case nurseries for several skate species in the Argentine shelf-break front. However, much more research is needed to clarify the use of communal nurseries and their benefits for batoids.

CONSERVATION OF BATOID NURSERY AREAS

The low fecundity and slow growth rates of some batoids suggest that juvenile survivorship is one of the most crucial features for sustaining stocks (Cortés 2002, Frisk 2010, Goldman et al. 2012). Unfortunately, nursery areas, especially those in shallow coastal areas, are susceptible to the influence of anthropogenic pressures (Lotze et al. 2006, Dale et al. 2013). For example, coastal nurseries can be directly affected by nutrient and sediment pollution due to their close proximity to human communities. Furthermore, coastal nursery areas support not only batoids, but often other fishery resources of major economic significance. As such, juvenile batoids in these areas may be threatened through bycatch in coastal fisheries (Heithaus 2007). The high level of philopatry seen in many of the batoid species studied (Hunter et al. 2006, White et al. 2014, Braun et al. 2015, Flowers et al. 2016) means that they may not respond well when exposed to high anthropogenic pressures. According to Heupel et al. (2007), some elasmobranch species tend to remain in their habitats, even when highly altered by human activities. This situation can lead to a catastrophic scenario for batoids, resulting in high rates of juvenile mortality and low rates of recruitment.

Thus, understanding the dynamics of batoid populations in nursery areas is crucial to improving conservation outcomes for some species (Fowler et al. 2005, Camhi et al. 2009, Dulvy et al. 2014). However, designating wide swaths of the coastline as protected nursery areas is probably not an efficient use of resources, or even politically possible. Obtaining better data to specifically target manageable areas for protection is much more likely to be successful. Thus, precise identification of areas that support important life stages (Yokota & Lessa 2006, Le Port et al. 2012), and improved understanding of batoid life histories are crucial to assessing their ecosystem function and connectivity (Espinoza et al. 2015, Munroe et al. 2015), their vulnerability to anthropogenic threats and environmental changes (Schlaff et al. 2014) and the development of efficient management and conservation strategies (Knip et al. 2012) — not only to manage batoid species as a fishery resource, but also to manage habitats (Tilley & Strindberg 2013).

CONCLUSIONS

Knowledge of batoid nursery areas is limited compared to that of sharks, although both groups appear to use nurseries in very similar ways. We recommend the use of the Heupel et al. (2007) criteria for identifying nurseries as a simple and effective way to define a nursery area for juvenile sharks and batoids. We also support the specific concept of egg case nurseries as proposed by Hoff (2016) that separates areas important for egg development in oviparous species from those important for juvenile and adult life stages. Adopting these definitions will promote the use of standardized criteria and terminology, which will assist conservation and management efforts while reducing under- or overestimations of nursery importance, dividing resources for conservation purposes and hindering effective protection.

At least in the coastal nurseries that have been studied to date, juvenile batoids play important ecological roles in nursery areas, functioning as mesopredators, vectors for energy transfer and bioturbators. However, little data are available to enable a full evaluation of batoid ecological roles in nursery areas. In addition, the concentration of identified nurseries in coastal areas highlights a research bias. A broader approach is required to better evaluate the presence of batoid nurseries in deeper and offshore ecosystems. Batoid species are at risk of extinction due to increasing anthropogenic threats and environmental changes; identification of nursery areas and a better understanding of batoid ecology are important for improving management of batoid stocks and sensitive areas, such as nurseries. By compiling what is known about the use of nursery areas by batoid species, this review provides a foundation to move towards broader and practical approaches to identify and conserve batoid populations.

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