Running Title:

Non-marine elasmobranchs review

Categorising use patterns of non-marine environments by elasmobranchs and a review of their extinction risk

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Abstract

As the state of non-marine aquatic environments (freshwater and estuarine environments with salinities ≤ 30 ppt) continues to decline globally, there is increasing concern for elasmobranchs (sharks and rays) that use them at critical stages of their life history. Due to a range of impediments including unresolved taxonomy, lack of fisheries data, and poor public perception, our knowledge of elasmobranchs in non-marine environments has lagged behind marine species. Here, we refine previous categorisations of elasmobranchs that occur in non-marine environments by reviewing the timing and duration of freshwater (≤ 5ppt) and/or estuarine (>5 to ≤ 30 ppt) habitat use throughout each species' life history. We identified five categories describing elasmobranchs in non-marine environments: 1) freshwater obligates (43 spp.); 2) euryhaline generalists (10 spp.); 3) estuarine generalists (19 spp.); 4) non-marine transients; 5) non-marine vagrants. Criteria for species inclusion is provided for all categories, and species lists are presented for categories 1–3. Euryhaline and estuarine generalists had the highest number of species that are threatened with extinction on the IUCN Red List of Threatened Species (50% and 65%, respectively), and freshwater obligate species have a very high portion of Data Deficient and Not Evaluated species (77%). The refinement of non-marine elasmobranch categories will aid in our understanding of elasmobranchs that occur in non-marine environments, helping facilitate more strategic conservation and management initiatives. Research on the biology of elasmobranchs and their human interactions in non-marine environments are suggested, as this will lead to better availability of information for conservation and management.

Key words: Conservation; Elasmobranchs; Estuaries; Euryhaline; Freshwater; Management

Introduction

Elasmobranchs (sharks and rays) that use non-marine environments (salinities < 30 ppt, McLusky 1993) during critical stages of their life history are one of the most poorly understood and threatened groups of vertebrates (Compagno and Cook 1995; Dulvy et al. 2014). Elasmobranchs occurring in these environments may be obligate freshwater species or euryhaline species (Lucifora et al. 2015). Approximately 56 (~5%) of all elasmobranch species are known to regularly occur in low salinity environments (Lucifora et al. 2015). Most of these species are rays from the families Potamotrygonidae (neotropical stingrays) and Dasyatidae (stingrays) that reside exclusively in freshwater throughout their entire life history. Meanwhile, only a few elasmobranchs are euryhaline, able to transition between marine and freshwater environments for prolonged periods e.g. bull shark (*Carcharhinus leucas*) and largetooth sawfish (*Pristis pristis*). Almost all freshwater and euryhaline elasmobranchs occur across tropical latitudes with a few species also extending marginally into temperate zones such as *C. leucas* and green sawfish (*Pristis zijsron*), while the Maugean skate (*Zearaja maugeana*) occurs exclusively in temperate waters of Tasmania, Southeastern Australia (Compagno 2002; Compagno and Cook 1995).

With most elasmobranchs that use non-marine environments occurring in tropical latitudes, they have been exposed to a range of anthropogenic pressures associated with the higher levels of human population growth in tropical regions (Collen et al. 2014; Smith 2003). Fisheries pressure (mostly commercial but also artisanal and recreational) is the primary threat to elasmobranchs in freshwater and estuarine environments (Kyne and Feutry 2017; Lucifora et al. 2015; Lucifora et al. 2017). River engineering, habitat destruction, and pollution also pose considerably greater threat to elasmobranchs in non-marine environments, compared to species that use only marine environments (Compagno and Cook 1995; Dulvy et al. 2014; Lucifora et al. 2016; White and Kyne 2010). Elasmobranchs are inherently susceptible to population decline due to low productivity, which includes slow growth, late age-at-maturity, longevity, low fecundity, low natural mortality, and often protracted breeding cycles (Cortés 2000). These 'slow' life history traits are particularly unfavourable in spatially-confined freshwater and estuarine environments, where population size is inherently constrained (Ballantyne and Robinson 2010).

Temporally, freshwater and estuarine environments are much more variable in their physical parameters (e.g. temperature, salinity, turbidity, dissolved oxygen, water flow) compared to marine environments (McLusky 1993; Pinto and Marques 2015). Furthermore, it is likely that fluctuations in these physical parameters will become more frequent and severe with climate change (Lennox et al. 2019). Unlike their marine counterparts, elasmobranchs in freshwater and estuarine environments cannot always readily escape unfavourable environmental and anthropogenic pressures (Compagno and Cook 1995). Nor have they evolved strategies such as rapid growth, short life cycles or the ability to aestivate or breath air in order to outlast unfavourable environmental conditions like some teleost fishes (Compagno 2002).

In recent decades, significant concern has been raised about the status of freshwater and euryhaline elasmobranch populations (Dulvy et al. 2014; Lucifora et al. 2015). Many species have become increasingly threatened and rapid local extinctions have been observed in regions of dense human population (Dulvy et al. 2014; Dulvy et al. 2016; Moore 2017). Of the 33 freshwater species identified in Dulvy et al. (2014) (a grouping which includes obligate freshwater and euryhaline species), 12 are listed as threatened with extinction on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species ('the Red List') (IUCN 2018). The conservation status of euryhaline elasmobranchs indicates they have the highest susceptibility to negative anthropogenic pressures. This likely because they move between freshwater and marine environments during their life history, thereby increasing potential for exposure across a range of environments (Compagno and Cook 1995).

Sawfishes (Pristidae) for example, are one of the most threatened marine vertebrate families with all five species assessed as either Critically Endangered or Endangered on the IUCN Red List (Dulvy et al. 2016). Similarly, river sharks of the genus *Glyphis*, also assessed as either Critically Endangered or Endangered, have seemingly disappeared from river systems throughout Asia and are now only reliably found in northern Australia (Li et al. 2015). Both these groups of species are known to utilise non-marine environments during their life histories, and high exposure to anthropogenic pressures has been attributed to their threatened status.

Conservation and management of freshwater and euryhaline elasmobranch populations is impeded by several factors (Compagno 2002). Firstly, a lack of information on their exploitation by fisheries targeting more commercially viable crustacean and teleost species (Compagno and Cook 1995). Secondly, artisanal and subsistence fisheries dominate regions where most species occur, and collection of biological data at fish landing and market sites can be difficult as shark and ray landings are often quickly consumed, finned, and portioned for sale (Appleyard et al. 2018; Feitosa et al. 2018; Fluet-Chouinard et al. 2018). Thirdly, poor taxonomic resolution within key taxa (i.e. Dasyatidae, *Glyphis*, Potamotrygonidae, and Pristidae), has impeded collection of reliable biological data and confused species distributions (both geographically and their temporal occurrence in freshwater, estuarine, and marine environments) (Compagno and Cook 1995; Faria et al. 2013; Rosa et al. 2010; White et al. 2017). Lastly, elasmobranchs have had a poor reputation in non-marine environments as they can be dangerous to humans and cause damage to fishing gear, generally reducing interest in implementing conservation and management (Castello 1975; da Silva et al. 2015; Thorson 1987). Due to these factors, biological research on elasmobranchs in non-marine environments has generally lagged behind studies on their marine counterparts.

The adaptation, distribution, duration, and timing of use of freshwater, estuarine, and marine environments throughout the life history of most species remain poorly understood. Apart from the obligate freshwater potamotrygonid rays, there is generally a poor understanding on which species remain in a freshwater environment throughout their life history and those that are euryhaline, only occurring in freshwater during particular stages of their life history. Similarly, for estuarine environments, a number of species are commonly observed in lower salinity waters of estuaries but are also often observed in marine environments. There is presently a lack of distinction between species that routinely use estuarine environments for critical parts of their life history (e.g. nursery areas) and predominantly marine species that may only be transient and are otherwise intolerant of prolonged exposure to non-marine salinities (Compagno and Cook 1995; Last 2002). Due to the heightened susceptibility of elasmobranchs to adverse anthropogenic and environmental pressures in non-marine environments, it is important to understand how different species are temporally distributed in these environments throughout their life history. Identifying species, or groups of species, that may be more susceptible to anthropogenic threats based on their frequency of occurrence and reliance on particular non-marine environments will lead to more integrated and strategic conservation and management regimes (Compagno and Cook 1995; Simpfendorfer et al. 2011a).

Here, we aim to review elasmobranchs that are known to occur in non-marine environments and identify those species that require a non-marine environment within their life history from those that do not. Previous categorisations of elasmobranchs that occur in non-marine environments (i.e. Compagno and Cook 1995; Last 2002; Martin 2005; Thorson et al. 1983) are refined with updated categories and species lists compiled. The present IUCN Red List category of species that require a non-marine environment within their life history are also compiled and future research directions are discussed.

Previous categorisations of elasmobranchs found in non-marine environments

There have been limited attempts to systematically categorise the elasmobranch species known from non-marine environments (i.e. Compagno and Cook 1995; Last 2002; Martin 2005; Thorson et al. 1983). The first attempt was proposed by Thorson et al. (1983) who presented two sets of criteria; the first criterion ranked species into eight categories based on their osmoregulatory ability to alter urea concentrations within their blood in response to the ambient environment. The second criterion related to the functionality of the rectal gland. In the absence of detailed studies of many species' physiology, only a small number of species could be accurately assigned to a category, and most of these were Atlantic species based on Thorson's earlier works (e.g. Gerst and Thorson 1977; Thorson 1976; Thorson 1983; Thorson et al. 1973; Thorson et al. 1978). Furthermore, these two categorisation systems were exceptionally convoluted in describing euryhaline elasmobranchs, with the 'urea' criteria suggesting six, and the 'rectal gland' criteria three, different categories to which the osmoregulatory physiology of euryhaline elasmobranchs may be placed. These systems also lacked a life history context to the habitat use and reproductive requirements of species within each category, rather only stating their physiological osmoregulatory tolerance to lower salinities. This restricted their use and application to conservation and management as these categorisations did not explain the importance that particular non-marine environments may have to the life history of the elasmobranchs that occur in them.

The most widely accepted categorisation of freshwater and euryhaline elasmobranchs, was proposed by Compagno and Cook (1995). They divided the known and 'thought to be' freshwater and euryhaline species at the time, into four categories:

1. obligate freshwater: *species confined to freshwater;*
2. euryhaline: *species that readily penetrate far into freshwater but also regularly occur in inshore marine waters;*
3. brackish-marginal: *species confined to brackish water only; and,*

4. marginal: *coastal shelf species that penetrate freshwater in estuaries or river mouths but were not found far from the sea*.

Assignment of species into these categories was based on distribution and regularity of occurrence data rather than physiological ability specific to certain osmoregulatory features as used by Thorson et al. (1983). This provided a vastly improved system for categorising freshwater and euryhaline elasmobranchs as species with little biological study could be categorised based on their occurrence within particular salinity ranges alone. Compagno and Cook (1995) listed 29 obligate freshwater species, 14 euryhaline species, and 1 brackish marginal species, and stated there were "*at least 26 marginal and possibly marginal species, with considerable uncertainty to which category some species belong to*" (p.66).

With the paucity of life history information and unresolved taxonomic issues at the time, clear distinctions between categories, their criteria, and the species that fit them could not be made. Like Thorson et al. (1983) these categorisations lacked a life history context to the habitat use and reproductive requirements of species within each category. For example, the criteria given for the '*Euryhaline*' category does not infer a reproductive or ecological context to a particular non-marine environment within their life history, rather it only implies that populations of these species are distributed across marine and freshwater environments. Meanwhile, the criteria given for the '*Marginal*' category might imply these species are also euryhaline but do not venture as far up rivers as the '*Euryhaline*' species do. Within the species listed in these two categories by Compagno and Cook (1995) and later by Compagno (2002), Last (2002), and (Martin 2005), there was no clarity provided between species that use a freshwater and/or brackish (estuarine) environment during their life history and those which may only transiently occur in lower salinity waters. Furthermore, Compagno and Cook (1995) did not define the salinity ranges for freshwater, brackish, and marine environments.

The resulting confusion was demonstrated by Martin (2005), whose refinements largely corresponded with those originally proposed by Compagno and Cook (1995). The attempt by Martin (2005) to modify the definition of '*Brackish marginal*' to "*…common in brackish to freshwater habitats…*" (p.1052) suggests that species in this group could also be classified as '*Euryhaline*' as most species listed in this category are predominately marine. The categorisations presented by Martin (2005) resulted in three categories with criteria implying that species could be found in freshwater to marine environments with still limited ecological or reproductive context provided to distinguish between species in each category. Aside from species that exclusively reside in freshwater, there is currently no clear distinction between how different groups of species use non-marine environments during their life history. This makes consistent and accurate allocation of species to categories difficult.

Since the publication of the above-mentioned categorisation schemes, there have been notable studies on the occurrence, physiology, taxonomy, reproductive biology, and ecology for elasmobranch species that occur in non-marine environments. Some of these studies have provided life history (e.g. Charvet-Almeida et al. 2005; Charvet et al. 2018; Morgan et al. 2011), population structure and distribution (e.g. Faria et al. 2013; Lucifora et al. 2016; White et al. 2015), movement (e.g. Almeida et al. 2009; Collins et al. 2008; Heupel et al. 2010), and osmoregulatory physiology (e.g. Pillans et al. 2005; Tam et al. 2003) information for many of the species originally listed in each category by Compagno and Cook (1995). Given this improvement in the availability of relevant data, better differentiations between how some elasmobranchs use non-marine environments throughout critical parts of the life history can now be made. The categories originally proposed by Compagno and Cook (1995) can be refined to improve the accuracy, precision and consistency between categories and their criteria. A revised, more informed, categorisation would aid in our understanding of elasmobranchs that occur in non-marine environments and will help facilitate more strategic conservation and management initiatives.

Refinement of categories

Here we refine the categorisation of elasmobranchs that occur in non-marine environments proposed by Compagno and Cook (1995) by considering how different groups of elasmobranch species interact with non-marine environments throughout critical parts of their life history. Previous listings of elasmobranchs in non-marine environments (Compagno 2002; Compagno and Cook 1995; Last 2002; Martin 2005), taxonomic guides (e.g. Ebert et al. 2013; Last et al. 2016a; Last et al. 2016b), and primary literature were used to identify species that are known or suspected to use non-marine environments. Following this, primary literature and IUCN Red List assessments (IUCN, 2018) were reviewed to determine their non-marine habitat use (or not). Species were then grouped into categories based on the type of environment (i.e. freshwater, estuarine, or marine, Table 1) that critical life history stages including parturition, nursery areas, and mating were identified to occur in. The distribution of each species were then grouped into eight continental regions including North and Central America, South America, West Africa, East Africa, The Arabian/Persian Gulf (hereafter referred to as 'The Gulf'), South Asia, Southeast Asia, and Oceania (regions are defined in Fig. 1). The IUCN Red List category of each species was also collated to assess trends in extinction risk for each non-marine environment use category and continental region.

Five categories describing elasmobranchs in non-marine environments are proposed: 1) freshwater obligates; 2) euryhaline generalists; 3) estuarine generalists; 4) non-marine transients; and, 5) non-marine vagrants (Table 2).

Freshwater obligates

Freshwater obligate species complete their entire life history in freshwater. Potamotrygonid rays of South America (36 spp.) are the dominant family, while seven species of dasyatid rays inhabiting the tropical rivers of Southeast Asia and West Africa are also included (Table 3). These dasyatids spend their entire life history in freshwater, but unlike potamotrygonids maintain low levels of urea as an osmolyte within their blood chemistry (Ballantyne and Robinson 2010; Ip et al. 2005; Otake et al. 2005; Tam et al. 2003). The loss of the ability to synthesise and retain urea in potamotrygonids is presumably due to their prolonged historic isolation within South American river basins (Thorson et al. 1983). Some of the dasyatids listed here may make irregular excursions outside of freshwater although there is little evidence they persist or carry out part of their life history in higher salinity waters. For example, white-edge whipray (*Fluvitrygon signifer*) has been demonstrated to survive in brackish water (20 ppt) for at least two weeks in the laboratory, though has not been observed outside of freshwater environments in the wild (Tam et al. 2003; Wong et al. 2013). Furthermore, some potamotrygonid species including the ocellate river stingray (*Potamotrygon motoro*), smooth-back stingray (*Potamotrygon orbignyi*), and the whitespotted freshwater stingray (*Potamotrygon scobina*) are reported occasionally in estuarine water at the mouth of the Amazon River (Almeida et al. 2009). These movements are presently only considered to be transient and there is limited evidence that populations of these species use environments other than freshwater at all critical stages of their life history hence, they are here categorised as obligate to freshwater systems.

Euryhaline generalists

There are 10 species of elasmobranchs that fit the criteria of euryhaline generalist. Four are carcharhinid sharks including *C. leucas* and all extant members of the genus *Glyphis*, and six are rays including *P. pristis*, Bennett's stingray (*Hemitrygon bennettii*), two *Hypanus* spp. and two *Urogymnus* spp. (Table 4). Generally, adults of these species may be encountered in any salinity environment, although juveniles are typically found in very low salinities or freshwater (Morgan et al. 2011; Pillans et al. 2009; Thorburn et al. 2003; Thorburn and Rowland 2008). Populations of *P. pristis* and *C. leucas* in the Río San Juan region of Central America may occupy the freshwater lacustrine environment of Lake Nicaragua for long periods of time throughout their life history (Thorson 1971; Thorson 1982). Similarly, a population of Atlantic stingray (*Hypanus sabinus*) occurs exclusively in the freshwater environments of Lake Jesup, Florida, USA (Piermarini and Evans 1998), while other populations of this species use marine environments of the Northwest Atlantic, frequenting freshwater rivers on a seasonal (Schwartz 1995), or may persist year-round in estuaries and marine environments (Ramsden et al. 2017), depending on latitude. *Hemitrygon bennettii* has not been observed in freshwater in South Asia (Muktha et al. 2019), although this species is reported in the freshwaters of the Pearl River in China (Zhang et al. 2010). All 10 species occur in tropical and subtropical waters with the exception of *C. leucas*, which also extends into temperate regions. Juveniles of euryhaline generalists are rarely observed in marine environments, as they tend to move upstream into freshwater or lower salinity environments following birth (Pillans et al. 2005; Pillans et al. 2009; Thorson 1982; Thorson et al. 1973). This may be a facultative behaviour related to predator avoidance away from large coastal sharks, decreased ecological competition from other marine species, or possible preference of physical environmental conditions such as light, temperature, and salinity (Simpfendorfer et al. 2005; Whitty et al. 2008; Whitty et al. 2017; Whitty et al. 2009). Inversely, juveniles of the longnose stingray (*Hypanus guttatus*) occur in higher salinity estuarine and coastal marine environments, while only adults occur in both freshwater and marine environments (Barrios-Garrido et al. 2017; Thorson 1983; Yokota and Lessa 2007). There is no indication that juveniles of euryhaline generalists are physiologically restricted to particular salinity environments. Studies on *C. leucas* in the Brisbane River, eastern Australia, indicated that juveniles tolerate a significantly higher osmotic pressure gradient in freshwater compared to marine, despite their preferential use of lower salinity environments as nursery areas (Pillans and Franklin 2004; Pillans et al. 2005). In the Caloosahatchee River, Florida, USA, acoustic tracking of *C. leucas* indicated that juveniles migrate up and down stream presumably to reside within particular salinity ranges, although this may have unidentified ecological benefits (Heupel and Simpfendorfer 2008; Heupel et al. 2010; Simpfendorfer et al. 2005). However, *C. leucas* is noted to occupy lower salinity areas of the

Caloosahatchee River compared to other elasmobranchs that frequent higher salinity areas closer to the river mouth e.g. smalltooth sawfish (*Pristis pectinata*) and the bonnethead shark (*Syphrna tiburo*) (Heupel et al. 2006; Simpfendorfer et al. 2011b). Therefore, unlike other elasmobranchs that may frequently occur in estuarine areas, species listed here as euryhaline generalists are those that additionally occur in low salinity areas of estuaries and freshwater at some point during their life history.

Estuarine generalists

Estuarine generalists consist of 19 ray species from five families (Table 5). These species are generally found in low salinity areas of estuaries as juveniles, while adults more typically occur in marine environments. Unlike species of the euryhaline generalist category, estuarine generalist species do not occur in freshwater environments for prolonged periods. This suggests they are unable to physiologically cope with freshwater environments. An example of an estuarine generalist is the mumburarr whipray (*Urogymnus acanthobothrium*). Juveniles of this species have only been recorded in brackish (estuarine) water of rivers in Northern Australia, while large mature individuals have been observed in coastal marine environments around Northern Australia and Papua New Guinea (Last et al. 2016c). Similarly, both the daisy stingray (*Fontitrygon margarita*) and the pearl stingray (*Fontitrygon margaritella*) occur in estuarine and shallow inshore environments in heavily fished areas of West Africa, but are not reported in freshwater catches (Compagno and Roberts 1984; Séret 1990). Other estuarine generalists such as the tubemouth whipray (*Urogymnus lobistoma*) and *Z. maugeana* may spend their whole life cycle in estuaries, never penetrating into freshwater or marine environments (Manjaji-Matsumoto and Last 2006; Treloar et al. 2017). All pristid species, except *P. pristis*, are estuarine generalists as juveniles are consistently recorded in estuarine nursery areas although adults are generally more frequently observed in marine environments (Morgan et al. 2011; Poulakis et al. 2011; Simpfendorfer et al. 2011b; Taniuchi 2002; Thorburn et al. 2008; White et al. 2017). The physiology of species regarded here as estuarine generalist has not been specifically studied and no data exist to explicitly describe the osmoregulatory differences between estuarine generalists and other euryhaline or steno-marine elasmobranchs. Identification of estuarine generalists is potentially clouded by the extensive array of elasmobranchs that may occur in estuarine systems transiently. However, unlike transient species, estuarine generalists are dependent on estuaries for part, or all, of their life history stages.

Non-marine transients

Non-marine transients do not directly or consistently use a non-marine environment during their life history. Non-marine transients generally occupy inshore coastal habitats and are often observed in the sheltered marine waters of bays, lagoons, and lower reaches of river systems (Harasti et al. 2017; Salini et al. 1990). Short excursions into lower salinity environments may allow these species to exploit these resources but avoid the osmoregulatory stress induced by prolonged exposure to lower salinities. Non-marine transients include numerous species, mostly from the shark families Carcharhinidae (whaler sharks), Orectolobidae (wobbegongs), Sphyrnidae (hammerhead sharks), Squatinidae (angel sharks), and Triakidae (hound sharks); and the ray families Aetobatidae (pelagic eagle rays), Arhynchobatidae (softnose skates) Dasyatidae, Glaucostegidae (giant guitarfishes), Myliobatidae (eagle rays), Narcinidae (numbfishes), Rhinobatidae (guitarfishes), and Torpedinidae (torpedo rays). For example, juvenile pigeye sharks (*Carcharhinus amboinensis*) are common within and around river and creek outflows throughout tropical Australia and East Africa, although they display avoidance of freshwater during periods of high freshwater-flow and resulting low salinity plumes associated with rainfall (Knip et al. 2011a; Knip et al. 2011b). Although individuals of this species are suspected to enter non-marine environments, data indicate *C. amboinensis* populations do not complete significant periods of their life cycle in non-marine environments as a range of size classes are commonly captured in inshore coastal marine areas (Bass et al. 1973; Cliff and Dudley 1991; Stevens and McLoughlin 1991). Similar habitat use patterns around estuaries have been observed for numerous elasmobranchs including the angular angel shark (*Squatina guggenheim*) (Colonello et al. 2006), lemon shark (*Negaprion brevirostris*) (Yeiser et al. 2008), scalloped hammerhead (*Sphyrna lewini*) (Brown et al. 2016), *S. tiburo* (Heupel et al. 2006), shovelnose guitarfish (*Pseudobatos productus*) (Márquez-Farías 2007), and to a lesser extent, the white shark (*Carcharodon carcharias*) (Harasti et al. 2017). Movement studies on these species indicate that coastal marine habitats adjacent to river outflows are important for particular life stages of non-marine transients as they may provide nursery areas (Harasti et al. 2017; Heupel et al. 2007; Heupel et al. 2006; Martins et al. 2018; Wiley and Simpfendorfer 2007). However, there is presently no evidence that they penetrate lower salinity waters of estuaries for prolonged periods, nor at consistent parts of their life history. Thus, they are considered transient in non-marine environments.

Non-marine vagrants

All other marine species that have reported occurrences in non-marine environments and do not fit the criteria of non-marine transient are considered non-marine vagrants. Accounts of vagrancy in elasmobranchs are rarely reported, and furthermore the term ‘vagrant’ has not previously been properly defined within elasmobranch literature. Last (2002) proposed a list of 41 species that were categorised as “*Marine species – vagrant in brackish/freshwater*” in Australia, whereby vagrant species were defined in the context of his categorisations as “*marine species that are known from but which are rarely recorded from estuaries*” (p. 185–187). However, this definition of vagrant is only applicable to vagrancy in estuaries by marine species, and therefore is not suitable for use in other scenarios of vagrancy. Furthermore, this definition of vagrant by Last (2002) did not capture the key concept of vagrancy, i.e. an individual is found outside the known distribution of its species (Lees and Gilroy 2014; Norton 1998). For example Duffy et al. (2017) reported what was likely a single individual whitetip reef shark (*Triaenodon obesus*) observed four times over a 12 month period at reefs in temperate New Zealand, despite the closest known population’s distribution being 598 km away in tropical waters of southern Fiji. Under the definition provided by Last (2002) this account would not fit the term vagrant, although under traditional definitions of the term (i.e. those of other taxa), this is clearly an example of vagrancy. Therefore, in order to avoid present and future confusion around the term within elasmobranch literature, we define vagrant to better encompass all scenarios of vagrancy, and also to provide a definition more comparable with other taxa e.g. birds (Lees and Gilroy 2014), plants (Norton 1998), marine mammals (de Bruyn et al. 2006). Here, we define vagrant as:

An individual found outside of the known distribution of its species, with no apparent biological context.

Under this definition, a non-marine vagrant is an individual of a coastal, shelf, or pelagic species that has no identifiable biological association with non-marine environments throughout its life history. The distributions of populations of these species are not considered to extend into, nor be adjacent to non-marine environments, though individuals of these species may very occasionally have anomalous sightings in lower salinities. This contrasts to non-marine transient species, where a) there is an ecological context to their occurrence in non-marine environments; and, b) their distribution is adjacent, or encroaches into, non-marine environments. Factors leading to vagrancy have not been studied specifically for elasmobranchs but likely causes include abnormal weather and ocean current conditions driving species out of their 'normal' marine distribution. Under our present understanding of non-marine vagrant species, the conservation of non-marine environments likely has little importance to their populations.

Discussion of categories

This review has identified three categories of elasmobranchs, each of which require a non-marine environment as part of their life history: freshwater obligates, euryhaline generalists, and estuarine generalists. Additionally, two categories of marine species occurring in non-marine environments are defined; non-marine transients and non-marine vagrants. This refinement builds on the categories originally proposed by Compagno and Cook (1995) to provide clearer distinctions between groups of species that require non-marine environments throughout their life histories. Primarily, clarity has been provided in how species in each category interact with non-marine environments throughout their life history, and the range of their non-marine environment use. The new categorisation also quantifies salinity profiles of each habitat type, allowing species to be more accurately categorised. This categorisation system thus provides an applicable and informative framework for applying conservation and management strategies to elasmobranchs that occur in non-marine environments. For most species however, further information is still required on fundamental aspects of their life history traits, movement and habitat use patterns, and demographic attributes in order to better understand the conservation and management requirements of their populations. Due to the lack of information for some species, or groups of species, these proposed categorisations are intended to provide a 'testable baseline' from which our understanding of how elasmobranchs interact with non-marine environments throughout their life histories can improve.

The categories presented here share some similarities with the guild approach (see Elliott et al. 2007; Potter et al. 2015) used to classify teleost fishes interactions with estuaries. However, teleost fishes are vastly more specious than elasmobranchs and they have numerous different life history strategies and trophic roles, each with complex and various arrays of associated habitat use behaviours not observed within elasmobranchs (e.g. planktonic larval phases and semelparity). Furthermore, the physiology of teleost fishes allows them to more easily adapt to non-marine environments throughout various stages of their life history (Ballantyne and Robinson 2010). Collectively, this necessitates a more intricately structured categorisation system to encapsulate all the different ways that teleost fish interact with non-marine environments (Elliott et al. 2007). By contrast, elasmobranchs that occur in non-marine environments are relatively uniform in their life history strategy. They are all live bearing (except for *Z. maugeana*), all produce small litter sizes of well-developed young, reproductive seasonality often spans of several months, they generally have well defined nursery areas, and they occupy similar ecological trophic roles. Therefore, a simpler approach can be taken to categorise their habitat use patterns. While it is true that some elasmobranchs listed in this review could be allocated into existing categories of teleost fishes (e.g. *C. leucas* may be amphidromous using the guild approach of Elliott et al. (2007)), the simpler structure of our categorisation are more compatible with the limited information available for most elasmobranchs that occur in non-marine environments.

There are still some discrepancies within our present categorisations, and it is likely that a better understanding of these species will result in future alterations and/or subsequent categories. Within the euryhaline generalist category for example, some species have populations that persist in freshwater environments for longer portions of their life history than others. Thorson (1976) noted a range of *P. pristis* size classes, including reproducing females in Lake Nicaragua and considered this freshwater system may support the ecological and reproductive necessities of this species. Similarly, Lake Jesup, Florida, USA, contains a closed freshwater population of *H. sabinus* (Piermarini and Evans 1998). The only factor separating these *P. pristis* and *H. sabinus* populations from dasyatids in the freshwater obligate category is that these species also have conspecifics that use and persist in estuarine and marine environments at particular life history stages (Schwartz 1995; Whitty et al. 2017). On the other end of the spectrum in the euryhaline category, *H. guttatus* may require higher salinities in juvenile age classes while only adults seem able to persist in freshwater. Hence, it is plausible that a category of elasmobranchs is included that sits between the potamotrygonid rays that are physiologically obligate to freshwater and euryhaline species that require access to marine environments. Such a category might include species that can complete their whole life history within freshwater, though are still capable of osmoregulation in higher salinities (i.e. non-obligate freshwater species). This category would include the freshwater dasyatids (and possibly some potamotrygonids e.g. *P. motoro*) and euryhaline species that have a population(s) that complete their life cycle exclusively within freshwater (i.e. *H. sabinus*). However, considering the information currently available on the environmental distribution and osmoregulatory physiology of these species throughout their life histories, their conservation requirements do not diverge from those of the present freshwater obligate or euryhaline generalist category. Therefore, the dasyatid rays that reside exclusively in freshwater are categorised with the potamotrygonid rays as their conservation and management concerns only freshwater environments. Similarly, euryhaline species with sub-populations that may be able to reside exclusively in freshwater are categorised with other species that occur from freshwater to marine environments as conservation and management of all of the populations of these species concerns environments ranging from freshwater to marine.

Knowledge gaps in the distribution of species throughout their respective life histories are a common theme in historic and present understanding of elasmobranchs in non-marine environments. The estuarine generalist category for example is a group of rays that have been overlooked in all previous categorisation attempts (Compagno and Cook 1995; Martin 2005; Thorson et al. 1983). These species were regarded as either 'euryhaline' or 'marginal' by Compagno and Cook (1995), although almost no life history and movement information existed on these species at the time. It is only with recent studies that they have been separated here on the basis that populations of these species are noted to consistently use lower salinity waters of estuaries (generally as nurseries) within their life histories e.g. *P. clavata* was previously listed as 'Marginal' by Compagno and Cook (1995) although, presently it is categorised as an estuarine generalist as juveniles are considered to use low salinity estuarine areas as nurseries (Morgan et al. 2011; Peverell 2005). Therefore, the conservation and management of these species concerns estuarine and marine environments. It is likely that the species listing of this category will be subject to changes over time as there is generally a lack of information on the life history and movement patterns of estuarine generalist species (and possible estuarine generalist species not included here e.g. Atlantic chupare (*Styracura schmardae*) and the daggernose shark (*Isogomphodon oxyrhynchus*)) and furthermore, no studies on their osmoregulatory physiology are presently available.

Constraints to elasmobranchs in non-marine environments

From this review, only 72 (5.8%) of total chondrichthyan species (~1250) were identified to use a non-marine environment within their life history. This provides an update on the number of species previously considered to use non-marine environments (freshwater and euryhaline species) by Lucifora et al. (2015) (56 spp.). In comparison, 47–53% of teleost species (~15,000) occur in freshwater either fulltime or at critical parts of their life history (Reid et al. 2013). The potamotrygonid rays of South America are the most specious family to occur in non-marine environments. They adapted to freshwater by vicariant processes, following marine incursions on the South American continent, and have subsequently speciated throughout many of South America's northern and central river systems (Kirchhoff et al. 2017). However, it is less clear what factors have led a small number of dasyatid rays to colonise freshwater on differing continents and why so few chondrichthyan species have adapted to use non-marine environments in general.

The higher incidence of teleost species adapting to non-marine environments is likely due to differences in osmoregulatory physiology between chondrichthyans and teleosts that originate from their marine origins (Ballantyne and Robinson 2010). Unlike teleosts, chondricthyans in marine environments regulate their osmotic balance through the retention of nitrogenous compounds (urea and tri-methyl amine oxide [TMAO]). This increases their blood osmolarity to that of salt water reducing their requirement to actively intake water (Thorson et al. 1973). While this strategy of osmo-conformation through retention of nitrogenous compounds is well suited to marine environments, it results in a significantly higher net metabolic offset in maintaining homeostasis in lower salinities (Pillans and Franklin 2004; Pillans et al. 2005; Thorson et al. 1973). Despite this offset, euryhaline generalist and estuarine generalist species (and possibly freshwater obligate dasyatid rays) still use non-marine environments at critical parts of their life history.

A pattern that has emerged from the present review is that most euryhaline and estuarine generalist species tend to occur at their lowest salinity environment as juveniles. Nursery areas are important for most elasmobranch species (Heupel et al. 2007; Martins et al. 2018). They generally increase survivorship and fitness of juvenile age classes through decreased predation and offer beneficial abiotic and biotic conditions and features (Heupel et al. 2007). Typical elasmobranch nursery habitats include shallow coastal inshore areas, embayments, river mouths, seagrass and algae beds, coastal lagoons and rocky/coral reefs (Martins et al. 2018). However, many elasmobranch species may co-occur within these habitats (Castro 1993; Simpfendorfer and Milward 1993) and interspecific competition may be high (Heupel et al. 2019; Kinney et al. 2011). Thus, species that can access nursery environments further up rivers eliminate interspecific competition for resources and may lower predation risk, thereby resulting in higher survivorship than if they persisted around river mouths or coastal inshore areas. This may have been a driving factor in the historic colonisation of freshwater and estuarine environments by elasmobranchs.

Ballantyne and Robinson (2010) suggested three stages of freshwater colonisation from marine environments by elasmobranchs: i) estuarine species transiently enter freshwater; ii) species remain in freshwater for prolonged periods (or their whole life) though still maintain functional osmoregulatory organs; and, iii) species reside in freshwater exclusively and lose the ability to osmoregulate in higher salinities. These stages of evolutionary colonisation match well with the categories formulated in this review. Estuarine generalist species fit well with stage i and the potamotrygonid rays represent stage iii, while species fitting the definition of stage ii include the euryhaline generalist species and also dasyatid rays from the freshwater obligate category. The observation that estuarine and euryhaline species tend to occur in lower salinity areas as juveniles, supports the model of gradual colonisation of freshwater proposed by Ballantyne and Robinson (2010). It is reasonable that over time juveniles may adapt to persisting in these lower salinities for longer periods if immediate ecological needs are met. However, high variability in physical parameters of non-marine environments create challenges for elasmobranchs with their prolonged life histories (Compagno and Cook 1995; Frisk et al. 2001). Slow growth, late ages of sexual maturation, and small litters of live young (only a single elasmobranch with life history stages in non-marine environments, *Z. maugeana*, is oviparous (Treloar et al. 2017)) make elasmobranchs susceptible to density-independent environmental factors such as periods of drought and flooding, or adverse changes in water quality associated with sporadic flow regimes (Lozano et al. 2019; Mills and Mann 1985). Only 29 species appear to occur in estuarine environments for prolonged periods within their life history. Furthermore, *U. lobistoma* and *Z. maugeana* are the only species that reside solely within estuaries for the duration of their life histories. The small number of elasmobranchs identified in this review that persist in estuaries for a life history stage supports the suggestion of Kirchhoff et al. (2017) that estuarine waters are an evolutionary bottleneck in elasmobranch adaptation to freshwater from marine environments. Once they have colonised freshwater environments, Kirchhoff et al. (2017) suggest these species actually have speciation rates equal to their marine counterparts.

Conservation status and distribution

Elasmobranch populations have declined globally due to adverse anthropogenic influence and exploitation of aquatic and marine environments (Davidson et al. 2016; Dulvy et al. 2014). Freshwater and estuarine environments have been subject to an increased intensity of adverse anthropogenic influences due to their accessibility to humans for resource exploitation (Collen et al. 2014; Compagno and Cook 1995; Darwall et al. 2011), and may also be at most risk from climate change impacts (Chin et al. 2010). Consequently, elasmobranchs that use or require access to these environments within their life history have increased susceptibility to population decline.

Over half (51%) of elasmobranch species within the freshwater obligate, euryhaline, and estuarine generalist categories identified in this review are either assessed as Data Deficient or are Not Evaluated against the IUCN Red List Categories and Criteria (Table 6). Of those with sufficient data available for assessment, 25 (74%) are classified as threatened with extinction (IUCN Red List categories CR, EN, VU). Of the 10 freshwater obligate species that have been assessed, seven are threatened with extinction, raising serious concern for the threatened status of the Data Deficient (16 spp.) and Not Evaluated (17 spp.) species within this category. Estuarine generalist species have the highest proportion of species that are threatened with extinction (65%), while euryhaline generalists contain the most species with an elevated extinction risk with 50% classified as either CR (3 spp.) or EN (2 spp.) (Table 6). Furthermore, an undescribed *Glyphis* species known from Borneo and Bangladesh has only four documented observations (Li et al. 2015) and is also likely to be threatened with extinction due to its occurrence in areas of very high human population density and consequential inshore and riverine fishing pressure.

The distribution pattern of species that require a non-marine environment within their life history raises concern, as there is a high level of endemism to regions (regions specified in Fig. 1). These high rates of endemism reflect the dependency of non-marine environments during the life history of these species as it likely restricts their movement between neighbouring river systems and furthermore, ocean basins to other regions. Overall, 81% (58/72 spp.) are endemic to a region with just 14 species found in two or more regions, and only *C. leucas* and *P. pristis* are found throughout all regions (Fig. 1). Rates of endemism in each category are: 100% (43/43) for freshwater obligates; 40% (4/10) for euryhaline generalists; and, 58% (11/19) for estuarine generalists. It should be noted that *P. motoro* has been introduced into a reservoir in the upper Seletar River in Singapore (Ng et al. 2010), while *P. motoro*, *Potamotrygon leopoldi*, and *P. orbignyi* have been reported from freshwater systems in China (Xiong et al. 2015), presumably due to released 'pets' from the ornamental industry. These 'distributions' have not been included in the present review as the validity of their establishment in these regions is complex (see Ng et al. 1993) and further verification of the viability of their populations is needed (Xiong et al. 2015).

More than half of all freshwater, euryhaline, and estuarine species occur in South America, although this is mainly comprised of freshwater obligates with 36 (84%) of the world's 43 freshwater species found in the region (Fig. 1). This is largely consistent with global diversity patterns of other freshwater vertebrate taxa (Collen et al. 2014). Other regions of high species density include Southeast Asia (18 spp.) and Oceania (14 spp.). In Southeast Asia and Oceania, 44% and 57% of species are endemic, respectively. Although no obligate freshwater species occur in the Oceania region, it is a centre of diversity for euryhaline and estuarine elasmobranchs. Five of the ten euryhaline generalist species listed are found in the region, three of which are endemic. Additionally, nine estuarine generalist species are found here also, with five of these endemic (Fig. 1). West Africa also represents a smaller pocket of freshwater and estuarine elasmobranch diversity, with four of its seven (57%) species endemic, although *P. pristis* is possibly extinct in the region (Dulvy et al. 2016). No species are endemic to East Africa, The Gulf, or South Asia.

The region with the highest imperative for future research is South America. Of the 37 species endemic to the region, 32 remain Data Deficient (15 spp.) or Not Evaluated (17 spp.), and only four potamotrygonid rays have been assessed in a data-sufficient category on the IUCN Red List. However, formal taxonomic descriptions have only been given to some potamotrygonid species in recent years. Oceania, South Asia, and Southeast Asia have the highest concentrations of CR species that occur in non-marine environments. However, the occurrence of *P. pristis* and *P. zijsron* is now irregular in both South Asia (Bineesh et al. 2014) and Southeast Asia (Kyne and Simpfendorfer 2014), and the Ganges river shark (*Glyphis* *gangeticus*) is rarely seen in these regions on a year-to-year basis (Li et al. 2015). Due to dense human population and conjunctly high fisheries pressure, it is likely that only small populations persist in these regions. Oceania supports the highest population densities of CR species that occur in non-marine environments (Morgan et al. 2011; Thorburn et al. 2003; White et al. 2017). The tropical coastline of Australia has very low human population density and an extensive array of protected areas. Healthy populations of many euryhaline species that have otherwise been subject to significant range contractions throughout the Indo-Pacific indicate that it is one of the last multi-species elasmobranch conservation strongholds in the world (White and Kyne 2010).

Future research directions

The high incidence of increased conservation concern within freshwater, euryhaline, and estuarine species is unsurprising in the face of historic and present anthropogenic and environmental pressures on their populations. However, many of the elasmobranchs listed in the present review remain data deficient with respect to their conservation biology. This impedes the early detection of deteriorating populations and the application of effective management strategies. This can ultimately lead to abrupt local extinctions such as those observed globally for pristids (Dulvy et al. 2016).

With a trend towards a generally ‘positive’ public perception of elasmobranchs (Whatmough et al. 2011) there is an increased awareness and imperative to conserve and protect their populations (Simpfendorfer et al. 2011a). Future research needs to focus on key biological and human interaction aspects that will lead to better availability of information for the conservation and management of elasmobranchs in non-marine environments (Simpfendorfer et al. 2011a). Firstly, continued taxonomic resolution and description of new species (e.g. Potamotrygonidae, Dasyatidae, and *Glyphis*) is essential to a fundamental understanding on i) how many species are of conservation and management interest in non-marine environments; and, ii) how these species can be identified (Hutchings 2017). Taxonomic resolution facilitates collection of data on the distribution and relative abundance (e.g. catch-per-unit-effort) of species, in turn informing conservation and management as it allows increases or decreases in population distribution and size to be tracked over time (Moore 2017). Due to an absence of historical fisheries data and difficulties in documenting artisanal and subsistence fisheries catch, further information is needed on the distribution and relative abundance of many freshwater, euryhaline, and estuarine species populations (Fluet-Chouinard et al. 2018).

There are a great number of data gaps on elasmobranchs that occur in non-marine environments; data on life history (growth rate, longevity, age/length at sexual maturation, fecundity, size-at-birth, maximum size, gestation period, reproductive periodicity, and natural mortality), population structure and connectivity (i.e. population genetics), spatial ecology (long- and short-term movement patterns), and osmoregulatory physiology is needed for many species. Life history data is essential to demographic models that can be used to inform population growth, susceptibility to threats such as fishing mortality or environmental disasters, and population recovery potential (Cortés 1998). This information is vital to understanding the necessity for protection and effective management measures to be put in place. Studies on population structure inform the spatial boundaries of their populations while spatial ecology informs their temporal distribution within and between non-marine environments, from which the application of protection and management measures can most effectively be placed (Heupel et al. 2007; Heupel et al. 2015; Kinney and Simpfendorfer 2009). Information on the osmoregulatory physiological preferences of species throughout their life history will help to indirectly identify important environmental areas of particular non-marine systems, providing broadly applicable data for regions and river systems, or cryptic/elusive species that are logistically difficult to biologically survey. It is unrealistic that information in these fields will become readily available for all the species listed in this review, however a concerted research effort is needed on species facing higher levels of extinction risk and those assessed as Data Deficient.

There is also a need for information on the importance of non-marine elasmobranchs to human communities, the roles they play in livelihoods and food security, and the attitudes of human interactions to these species. For example, in developing nations with primarily artisanal and subsistence fisheries, non-marine environments may play an increased role in food security as they are more easily accessible than inshore coastal waters (including access during periods when offshore weather is poor) (Compagno and Cook 1995). Furthermore, large-bodied elasmobranchs within them may be cost effective to fish, providing both a large food source and body parts for subsequent sale (e.g. fins). Conversely, in some areas of South America, potamotrygonid rays are viewed as an impediment to tourism and human safety, as they aggregate in shallow waters that otherwise have intrinsic value for swimming and fishing activities (Araújo et al. 2004). In other regions of South America, potamotrygonid rays are targeted for their high value in ornamental markets (Moreau and Coomes 2007). Thus, key questions for the effective application of conservation and management might include: i) is there a reliance on elasmobranchs as a food or economic resource?; ii) what is the economic value of elasmobranchs?; iii) what other food or economic resources may be available?; iv) how are elasmobranchs perceived by local communities?; and, v) are there any cultural or spiritual beliefs surrounding elasmobranchs?. This type of information will indicate how supportive the public may be to conservation and management, their willingness to adopt alternative livelihoods, and the potential for communities to participate in the management and where necessary, the rebuilding of their populations. For species with restricted distributions such as the freshwater obligates, and euryhaline or estuarine species with populations confined to particular river systems, gauging local perception is vital to sustained conservation and management (Hueter et al. 2004). Other concerns and considerations may include the value of elasmobranchs in 'ecotourism' and whether they have value as a 'non-extractive' resource.

Conclusion

The present review has refined earlier categorisations of elasmobranchs known to occur in non-marine environments. The categorisations presented here are useful to conservation and management, as species and the environments they require throughout their life history can be more easily understood. However, the conservation status of freshwater obligates, euryhaline generalist, and estuarine generalist species raises concern. Euryhaline generalist and estuarine generalist species have the highest extinction risk, presumably because movement between environments throughout their life histories raises their susceptibility to anthropogenic pressures. Meanwhile, for many freshwater obligate species there is insufficient data available to assess extinction risk, and a concerted research effort on these species is needed. As human populations continue to increase, greater pressure is being placed on elasmobranchs that require use of non-marine environments. In order to develop strategic conservation and management strategies, further information is required primarily on life history traits, population structure, spatial ecology, and human interactions for these species.

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Figure captions

Fig. 1 Distribution of freshwater obligates (FW), euryhaline generalists (EU), and estuarine generalists (ES) in each continental region. The total number of species in each category is shown and the number of those that are endemic to the region is shown in parentheses.

Table 1 The salinity range of freshwater, estuarine, and marine environments. Adapted from McLusky (1993).

Environment type	**Salinity range (ppt)**
Freshwater	0 – ≤5
Estuarine	>5 – ≤30
Marine	>30

Table 2 Categories describing elasmobranch occurrence in non-marine environments and their criteria

Category	Criteria	Environment type(s) that life history stages occur in
Freshwater obligate	Complete the entirety of their life history in freshwater and carryout all of their reproductive and ecological functions in freshwater exclusively.	Freshwater
Euryhaline generalist	Encountered throughout a range of salinities (freshwater to marine); are physiologically capable of prolonged exposure to environments ranging from freshwater to marine; characteristically use freshwater and/or estuarine environments for a life stage, typically for parturition and/or nursery areas.	Freshwater, estuarine, and marine
Estuarine generalist	Commonly occur in environments ranging from estuarine to marine; are physiologically capable of penetrating into lower salinity waters of estuaries for prolonged periods, though cannot withstand prolonged exposure in freshwater; characteristically use estuarine environments for a life stage, typically as nursery areas.	Estuarine and marine
Non-marine transients	May occur in non-marine environments intermittently, though carry out all aspects of their life history in marine waters; not considered to be physiologically capable of prolonged exposure to estuarine or freshwater environments.	Marine
Non- marine vagrants	Have no identifiable biological association with non-marine environments throughout their life history; not expected to occur in a non-marine environment; not considered to be physiologically capable of prolonged exposure to estuarine or freshwater environments.	Marine

Table 3 List of freshwater obligate species, their IUCN Red List of Threatened Species category and distribution (continental regions defined in Figure 1). EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated (no species are listed as CR, Critically Endangered).

Species	Common name	IUCN Red List category	Distribution
Potamotrygonidae (36)	**Neotropical stingrays**		
Heliotrygon gomesi	Gomes' round ray	NE	South America
Heliotrygon rosai	Rosa's round ray	NE	South America
Paratrygon aiereba	Discus stingray	DD	South America
Plesiotrygon iwamae	Antenna ray	DD	South America
Plesiotrygon nana	Dwarf antenna ray	NE	South America
Potamotrygon adamastor	Adamastor's freshwater stingray	NE	South America
Potamotrygon albimaculata	Tapajós freshwater stingray	NE	South America
Potamotrygon amandae	Amanda's freshwater stingray	NE	South America
Potamotrygon amazona	Amazons freshwater stingray	NE	South America
Potamotrygon boesemani	Suriname freshwater stingray	NE	South America
Potamotrygon brachyura	Giant freshwater stingray	DD	South America
Potamotrygon constellata	Rough freshwater stingray	DD	South America
Potamotrygon falkneri	Paraná freshwater stingray	DD	South America
Potamotrygon garmani	Garman's freshwater stingray	NE	South America
Potamotrygon henlei	Henle's freshwater stingray	LC	South America
Potamotrygon histrix	Porcupine freshwater stingray	DD	South America
Potamotrygon humerosa	False reticulate freshwater stingray	NE	South America
Potamotrygon jabuti	Pearl freshwater stingray	NE	South America
Potamotrygon leopoldi	Xingu freshwater stingray	DD	South America
Potamotrygon limai	Madeira freshwater stingray	NE	South America
Potamotrygon magdalenae	Magdalena freshwater stingray	NT	South America
Potamotrygon marinae	French Guiana freshwater stingray	DD	South America
Potamotrygon marquesi	Marques's freshwater stingray	NE	South America
Potamotrygon motoro	Ocellate freshwater stingray	DD	South America
Potamotrygon ocellata	Marajó freshwater stingray	DD	South America
Potamotrygon orbignyi	Reticulate freshwater stingray	LC	South America
Potamotrygon pantanensis	Pantanal freshwater stingray	NE	South America
Potamotrygon rex	Great freshwater stingray	NE	South America
Potamotrygon schroederi	Schroeder's freshwater stingray	DD	South America
Potamotrygon schuhmacheri	Rosette freshwater stingray	DD	South America
Potamotrygon scobina	Whitespotted freshwater stingray	DD	South America
Potamotrygon signata	Parnaíba freshwater stingray	DD	South America
Potamotrygon tatianae	Tatiana's freshwater stingray	NE	South America
Potamotrygon tigrina	Tiger freshwater stingray	NE	South America
Potamotrygon wallacei	Wallace's freshwater stingray	NE	South America
Potamotrygon yepezi	Maracaibo freshwater stingray	DD	South America
Dasyatidae (7)	**Stingrays**		
Fluvitrygon kittipongi	Roughback whipray	EN	Southeast Asia
Fluvitrygon oxyrhynchus	Marbled whipray	EN	Southeast Asia
Fluvitrygon signifer	White-edge whipray	EN	Southeast Asia
Fontitrygon garouaensis	Smooth whipray	VU	West Africa

Fontitrygon ukpam	Thorny whipray	EN	West Africa
Hemitrygon laosensis	Mekong stingray	EN	Southeast Asia
Makararaja chindwinensis	Chindwin cowtail ray	DD	Southeast Asia

Table 4 List of euryhaline generalist species, their IUCN Red List of Threatened Species category and distribution (continental regions defined in Figure 1). CR, Critically Endangered; EN, Endangered; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated (no species are listed as VU, Vulnerable; or NE, Not Evaluated).

Species	Common name	IUCN Red List category	Distribution
Carcharhinidae (4)	**Whaler sharks**		
Carcharhinus leucas	Bull shark	NT	Global
Glyphis gangeticus	Ganges river shark	CR	South Asia, Southeast Asia
Glyphis garricki	Northern river shark	CR	Oceania
Glyphis glyphis	Speartooth shark	EN	Oceania
Pristidae (1)	**Sawfishes**		
Pristis pristis	Largetooth sawfish	CR	Global
Dasyatidae (5)	**Stingrays**		
Hemitrygon bennettii	Bennett's stingray	DD	South Asia, Southeast Asia
Hypanus guttatus	Longnose stingray	DD	North and Central America, South America
Hypanus sabinus	Atlantic stingray	LC	North and Central America
Urogymnus dalyensis	Freshwater whipray	LC	Oceania
Urogymnus polylepis	Giant freshwater whipray	EN	South Asia, Southeast Asia

Table 5 List of estuarine generalist species, their IUCN Red List of Threatened Species category and distribution (continental regions defined in Figure 1). CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated.

Species	Common name	IUCN Red List category	Distribution
Dasyatidae (12)	**Stingrays**		
Fontitrygon colarensis	Colares stingray	VU	South America
Fontitrygon margarita	Daisy whipray	EN	West Africa
Fontitrygon margaritella	Pearl whipray	DD	West Africa
Hemitrygon fluviorum	Estuary stingray	VU	Oceania
Himantura australis	Australian whipray	NE	Oceania
Himantura uarnak	Coach whipray	VU	East Africa, The Gulf, South Asia, Southeast Asia
Hypanus say	Bluntnose stingray	LC	North and Central America, South America
Pastinachus ater	Broad cowtail ray	LC	East Africa, The Gulf, Oceania, South Asia, Southeast Asia
Pastinachus solocirostris	Roughnose cowtail ray	EN	Southeast Asia
Pateobatis hortlei	Hortle's whipray	VU	Oceania
Urogymnus acanthobothrium	Mumburarr whipray	NE	Oceania
Urogymnus lobistoma	Tubemouth whipray	VU	Southeast Asia
Pristidae (4)	**Sawfishes**		
Anoxypristis cuspidata	Narrow sawfish	EN	The Gulf, Oceania, South Asia, Southeast Asia
Pristis clavata	Dwarf sawfish	EN	Oceania, South Asia, Southeast Asia
Pristis pectinata	Smalltooth sawfish	CR	North and Central America, South America, West Africa
Pristis zijsron	Green sawfish	CR	East Africa, The Gulf,

			Oceania, South Asia, Southeast Asia
Rajidae (1)	**Hardnose skates**		
Zearaja maugeana	Maugean skate	EN	Oceania
Rhinidae (1)	**Wedgefishes**		
Rhynchobatus springeri	Broadnose wedgefish	VU	Southeast Asia
Rhinopteridae (1)	**Cownose rays**		
Rhinoptera bonasus	Cownose ray	NT	North and Central America, South America

Table 6 Number of species in each IUCN Red List of Threatened Species category (IUCN 2018). CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated. Threatened comprises CR, EN, and VU.

Category	Species	CR	EN	VU	NT	LC	DD	NE	Threatened
Freshwater Obligate	43	0	6	1	0	3	16	17	7 (16%)
Euryhaline Generalist	10	3	2	0	1	2	2	0	5 (50%)
Estuarine Generalist	19	2	5	6	1	2	1	2	13 (65%)
Total	**72**	**5**	**13**	**7**	**2**	**7**	**19**	**19**	**25 (35%)**