Rev Fish Biol Fisheries (2024) 34:65–89
https://doi.org/10.1007/s11160-023-09807-1

REVIEWS

A review of the life history and ecology of euryhaline and estuarine sharks and rays

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Received: 28 May 2023 / Accepted: 20 September 2023 / Published online: 23 October 2023

Abstract One-third of all elasmobranchs (sharks and rays) are threatened with extinction. Euryhaline and estuarine generalist elasmobranchs are a group of 29 species that occupy non-marine environments during particular life-stages. These species are poorly known and disproportionately threatened, with 72.4% at risk of extinction or Data Deficient. A detailed knowledge of a species' life history characteristics, movement ecology, habitat use, and population structure are required for the implementation of appropriate management and conservation measures. To date, research on euryhaline and estuarine species has lagged behind marine species. Here, a literature review and gap analysis of the euryhaline and estuarine species was conducted to identify gaps in 14 key parameters required for management. Of the 29 species, only the Bull Shark (*Carcharhinus leucas*) and the Largetooth Sawfish (*Pristis pristis*) had detailed information on a majority of parameters assessed. Nine species lack information on most parameters, while the Broadnose Wedgefish (*Rhynchobatus springeri*) lacks information on all but one of the parameters investigated. There is a high level of understanding of age- and size-at-maturity, size-at-birth, and growth for only five species, while nine species have estimates of natural mortality. Comprehensive reproductive biology data is unavailable for six species. Both short- and long-term movement ecology is well-understood for only two species, and habitat use for six species. Population structure has been studied in only eight species. Data on key life history parameters, population structure, and habitat requirements of the euryhaline and estuarine elasmobranchs are urgently required to develop appropriate management strategies and to secure populations.

Keywords Elasmobranchs · Euryhaline · Estuarine · Conservation · Management

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11160-023-09807-1.

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Introduction

Biodiversity loss resulting from anthropogenic activities is a global concern (Millennium Ecosystem Assessment, 2005; Butchart et al. 2010; Jaureguiberry et al. 2022). Ecosystems have changed rapidly over the past ~ 70 years, primarily due to overexploitation by humans, habitat loss and degradation, invasive

species, nutrient pollution, and climate change (Millennium Ecosystem Assessment 2005; Butchart et al. 2010; Jaureguiberry et al. 2022). Subsequently, species extinction rates are significantly exceeding normal background levels (Hoffmann et al. 2010; Hooper et al. 2012). Freshwater, estuarine, and marine species have been particularly affected by anthropogenic pressures and have undergone significant declines in diversity and abundance (e.g., Dudgeon et al. 2006; Selig et al. 2014; Dulvy et al. 2021). Freshwater and estuarine ecosystems and the immense species richness they support are particularly threatened due to their proximity to human populations and threatening processes (Dudgeon et al. 2006). Aside from their intrinsic value, healthy ecosystems provide several crucial services to humans, such as water, food, disease prevention, and climate regulation (Millennium Ecosystem Assessment 2005; Hooper et al. 2012). As recognition for the importance of maintaining biodiversity has grown, protection of biodiversity has become a priority for conservation scientists, resource managers, and policymakers (Selig et al. 2014).

The cartilaginous fishes (class Chondrichthyes) are one of the three major extant fish lineages. They are comprised of the elasmobranchs (sharks and rays) and the holocephalans (chimaeras) and are one of the most evolutionary distinct radiations of vertebrates on the planet (Compagno 1990; Stein et al. 2018). They are also now one of the most threatened groups on the planet. According to the International Union for the Conservation of Nature Red List of Threatened Species (hereafter 'IUCN Red List'), 32% (397 species) are currently threatened with extinction (Critically Endangered, Endangered, or Vulnerable; IUCN 2023). Chondrichthyans generally have low rates of population increase and reduced capacity to recover from anthropogenic threats such as overfishing and habitat loss and degradation (Musick 1999; Jabado et al. 2018b). Although variation among species is considerable, chondrichthyans typically have slow growth, low fecundity, long life spans, relatively late age-at-maturity, and have low natural mortality (Musick 1999; White and Kyne 2010; Jabado et al. 2018b). Overfishing is the sole threat for over two-thirds of all threatened chondrichthyans, and catch statistics are often under-reported or unreported (Dulvy et al. 2021; Jorgensen et al. 2022).

While chondrichthyans are primarily marine species, non-marine elasmobranchs comprise a relatively small number of species. Non-marine species can be freshwater obligate, euryhaline generalist, estuarine generalist, non-marine transient, or non-marine vagrant, and elasmobranchs are categorised into one of these five groups by how species interact with their environments throughout critical parts of their life histories (see Grant et al. 2019). The latter two groups (transients and vagrants) are primarily marine and do not rely on non-marine environments (Grant et al. 2019). Freshwater obligate, euryhaline generalist, and estuarine generalist elasmobranch species constitute 6.1% of the world's described elasmobranch species (74 of 1,209 species; Grant et al. 2019; Ebert et al. 2021b; Kyne and Lucifora 2022). The 29 euryhaline generalist and estuarine generalist species (hereafter 'euryhaline' and 'estuarine' species, respectively; see definitions in Methods) are disproportionately at risk of extinction or are severely unknown, with 72.4% (21 species) listed as threatened with extinction (20 species, 69.0%) or Data Deficient (one species, 3.4%) on the IUCN Red List (IUCN 2023; Table 1). This highlights an urgent need for appropriate management of their habitats and populations.

Estuaries and rivers are highly productive and support high levels of biodiversity. River systems are however, becoming increasingly degraded and the landward boundaries of river systems minimise the ability of non-marine elasmobranch species to evade threats (Nilsson et al. 2005; Knip et al. 2010; Lyon et al. 2017), making them increasingly susceptible to anthropogenic pressures. Unfavourable conditions in non-marine environments are also likely to become more frequent and severe with climate change and increased reliance on these systems by humans (Grant et al. 2019; Lennox et al. 2019). Non-marine elasmobranch species also primarily occur in tropical regions (Grant et al. 2019) where elasmobranchs face an elevated risk of extinction due to larger human population growth in these regions and resulting high rates of overfishing, habitat modification and destruction, and pollution (Compagno and Cook 1995; Knip et al. 2010; Grant et al. 2019; Dulvy et al. 2021).

The physical parameters of estuarine and freshwater environments, such as temperature, salinity, dissolved oxygen, and turbidity are highly variable compared with marine environments (e.g., Wenner et al. 2004; Mateus et al. 2008; Regnier et al. 2013). Environmental variability can influence behaviour of elasmobranchs, for example, species moving

Table 1 Euryhaline and estuarine elasmobranchs by family. Regularly used or recent synonyms were sourced from Fricke et al. (2022). The number of species in each family relative to the global total (Ebert et al. 2021b) is provided under each family name

Family	Species	Synonym(s)	Common name	IUCN Red List category
Euryhaline species				
Carcharhinidae (4/56 spp)	*Carcharhinus leucas*		Bull Shark	VU
	Glyphis gangeticus	*Glyphis fowlerae* *Glyphis siamensis*	Ganges River Shark	CR
	Glyphis garricki		Northern River Shark	VU
	Glyphis glyphis		Speartooth Shark	VU
Pristidae (1/5 spp)	*Pristis pristis*	*Pristis microdon* *Pristis perotteti*	Largetooth Sawfish	CR
Dasyatidae (5/97 spp)	*Hemitrygon bennettii*	*Dasyatis bennettii*	Bennett's Stingray	VU
	Hypanus guttatus	*Dasyatis guttata*	Longnose Stingray	NT
	Hypanus sabinus	*Dasyatis sabina*	Atlantic Stingray	LC
	Urogymnus dalyensis	*Himantura dalyensis*	Freshwater Whipray	LC
	Urogymnus polylepis	*Himantura polylepis* *Himantura chaophraya*	Giant Freshwater Whipray	EN
Estuarine species				
Dasyatidae (12/97 spp)	*Fontitrygon colarensis*	*Dasyatis colarensis*	Colares Stingray	CR
	Fontitrygon margarita	*Dasyatis margarita*	Daisy Whipray	VU
	Fontitrygon margaritella	*Dasyatis margaritella*	Pearl Whipray	NT
	Hemitrygon fluviorum	*Dasyatis fluviorum*	Estuary Stingray	NT
	Himantura australis		Australian Whipray	LC
	Himantura uarnak	*Raja uarnak* *Himantura tutul*	Coach Whipray	EN
	Hypanus say	*Dasyatis sayi* *Dasyatis say*	Bluntnose Stingray	NT
	Pastinachus ater	*Pastinachus atrus*	Broad Cowtail Ray	VU
	Pastinachus solocirostris		Roughnose Cowtail Ray	EN
	Pateobatis hortlei	*Himantura hortlei*	Hortle's Whipray	NT
	Urogymnus acanthobothrium		Mumburarr Whipray	DD
	Urogymnus lobistoma	*Himantura lobistoma*	Tubemouth Whipray	EN
Pristidae (4/5 spp)	*Anoxypristis cuspidata*		Narrow Sawfish	EN
	Pristis clavata		Dwarf Sawfish	CR
	Pristis pectinata		Smalltooth Sawfish	CR
	Pristis zijsron		Green Sawfish	CR
Rhinidae (1/10 spp)	*Rhynchobatus springeri*		Broadnose Wedgefish	CR
Rhinopteridae (1/10 spp)	*Rhinoptera bonasus*		American Cownose Ray	VU
Rajidae (1/157 spp)	*Zearaja maugeana*	*Dipturus maugeanus*	Maugean Skate	EN

IUCN Red List of Threatened Species categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient (IUCN 2023). Adapted from Grant et al. (2019)

up- or downstream in response to tidal and seasonal fluctuations in salinity (Dwyer et al. 2020; Pillans et al. 2020). Resource use and activity in euryhaline elasmobranchs may also change ontogenetically (Simpfendorfer et al. 2010). Adults of euryhaline elasmobranch species may occur in any salinity, while juveniles are likely to be found in lower salinities or freshwater and are rarely seen in marine environments

(Thorburn and Rowland 2008; Pillans et al. 2009; Morgan et al. 2011; Grant et al. 2019). Euryhaline species retain functional osmoregulatory organs that are required in both freshwater and marine environments (Pillans et al. 2005; 2006; Ballantyne and Robinson 2010). There is no indication that juveniles of euryhaline species are physiologically restricted to specific salinity environments – rather juveniles may be using nursery areas for other ecological reasons, such as to avoid large coastal predators, avoid competition from other marine species, or prefer specific upstream conditions (e.g., light, temperature) (Heupel et al. 2007; Grant et al. 2019; Pillans et al. 2020). Estuarine species are typically found in low salinity areas of estuaries as juveniles and in marine environments as adults (Grant et al. 2019). Unlike euryhaline species, estuarine elasmobranchs may not have the physiological adaptations to cope with freshwater environments, as they do not occur in freshwater environments for prolonged periods (Grant et al. 2019). Identification of estuarine species is difficult as the physiology and osmoregulatory differences of the estuarine species described by Grant et al. (2019) has not been explicitly studied.

For most non-marine elasmobranch species, fundamental life history traits, movement ecology, habitat use, and distribution of species throughout their life cycles are poorly understood (Grant et al. 2019). Understanding life history, biology, and natural mortality of a species is required to manage its population, facilitate recovery, and understand how species may respond to threats or disturbance, such as increased mortality from fishing (Simpfendorfer et al. 2008; Jorgensen et al. 2022; Villagra et al. 2022). A knowledge of the mechanisms which drive movements, habitat choice, and community structure is also critical for understanding how a species may respond to environmental changes and to implement appropriate protective measures (Margules and Pressey 2000; Schlaff et al. 2014; Dwyer et al. 2020; Pillans et al. 2022). For many species, particularly highly mobile species, it is difficult to effectively manage or conserve their entire geographic range and life history, thus habitats important for foraging, mating, parturition, and juvenile development may become critical for protection (Papastamatiou et al. 2015; Hyde et al. 2022).

The aim of this study is to conduct a review of the life history and ecology of euryhaline and estuarine elasmobranchs. This review will identify current knowledge gaps in life history, movement ecology, habitat use, and population structure research through a gap analysis approach. This gap analysis will help to identify where data is lacking on the species-level, identify broader trends in species groups, and identify potential future research areas. Although understanding human dimensions, both through understanding uses and values, and threats, is important to species conservation, particularly in the global south, this study focuses on life history, biology, and ecology. The human dimension is outside the scope of this review.

Methods

A review was conducted on the existing knowledge on important life history and ecological parameters of all 29 known euryhaline generalist (hereafter, 'euryhaline') and estuarine generalist (hereafter, 'estuarine') elasmobranch species (following Grant et al. 2019; Table 1). Euryhaline species are capable of living in and moving between salinity gradients from marine (~35 ppt) to estuarine (5–30 ppt) to freshwater (<5 ppt), are physiologically capable of prolonged exposure to a range of salinities, and typically use freshwater and/or estuarine environments for specific life stages (e.g., parturition and/or nursery areas) (Grant et al. 2019). Estuarine species commonly occur in environments ranging from estuarine to marine, are physiologically capable of occurring in lower salinity waters of estuaries for prolonged periods, however, cannot withstand prolonged exposure to freshwater, and typically use estuarine environments during early life stages (e.g., nursery areas) (Grant et al. 2019).

Parameters reviewed for each species consisted of maximum recorded size, size-at-birth, size- and age-at-maturity, maximum age (observed or age at which asymptotic growth reached), growth, generation length, natural mortality, reproductive mode and cycle, litter size, gestation length, parturition (seasonality), short- and long-term movement ecology, habitat use, depth range, and population structure, and these fell under four main topics (Tables 2, 3).

Searches were conducted online via Google Scholar and the Charles Darwin University Library search database. Searches were initially conducted using species names and regularly used or recent

synonyms (Table 1). Literature encompassing the above parameters were then selected. Additional search terms were developed by including each species' name and each of the above parameters individually, for example '*Hemitrygon fluviorum* reproduction'. Articles cited include peer-reviewed journal articles, grey literature such as reports to governments and organisations, and IUCN Red List Assessments (IUCN, 2023) where they contained unpublished or primary data.

Table 2 Summary of the parameters included in the literature review on availability of data for euryhaline and estuarine elasmobranch species. Parameters with * indicate those that were excluded from the gap analysis

Topic	Parameter
Growth, age-at-maturity, and natural mortality	Maximum recorded size*
	Size-at-birth
	Size-at-maturity
	Age-at-maturity
	Maximum age
	Growth coefficient (k)
	Generation length
	Natural mortality
Reproductive biology	Reproductive mode*
	Reproductive cycle
	Litter size and fecundity
	Gestation length
	Parturition (seasonality)*
Movement ecology and habitat use	Short-term movement ecology
	Long-term movement ecology
	Habitat use
	Depth range*
Population structure	Genetic population structure
	Philopatry*

Where there were a range of values for a particular parameter, a range encompassing the lowest and highest values was given in the results. Variation in parameters may result from a parameter being estimated in multiple studies or from regional variation.

Generation length (GL) can be defined as the average age of parents in the current cohort and there are several methods available for calculating this (Cooke et al. 2018). Where data were available, a simple measure of GL was calculated using only female age-at-maturity and maximum age to account for data scarcity among these species following Kyne et al. (2021c), where:

$$\mathrm{GL} = \left[(\text{maximum age-age-at-maturity})/2\right] + \text{age-at-maturity}$$

Fecundity was calculated as the number of pups per year if reproductive periodicity was known.

Once information was gathered, a gap analysis was conducted to identify priority research areas. Most parameters from Table 2 were included in the gap analysis, excluding maximum recorded size, reproductive mode and seasonality, depth range, and philopatry. Maximum recorded size and depth range are basic data which are available for all species and therefore excluded from the gap analysis. Reproductive mode is known or presumed to be viviparous

Table 3 Definitions of some key parameters reviewed for each species

	Definition
Natural mortality	Natural (e.g., predation, disease, old age) rate of loss of a population (Villagra et al. 2022)
Movement ecology	The study of individuals in a population and their behaviours within their (local) environments with a focus on environmental and biological causes and consequences of movement (Jeltsch et al. 2013)
Habitat use	The proportion of time that an animal spends in a particular habitat, that is, an environmental space which is made up of environmental variables that may be biotic or abiotic, dynamic or static (Johnson 1980; Beyer et al. 2010)
Nursery area	A location where newborns or young-of-the-year are more commonly encountered than other areas, where juveniles remain or return for extended periods (weeks or months), and which is repeatedly used across years (Heupel et al. 2007)
Population structure	The identification of subpopulations with genetic differentiation (Frisk et al. 2014)
Philopatry	The tendency for individuals to return to their natal sites (often for breeding – reproductive philopatry) which can be indicative of complex migrations/movement (Chapman et al. 2015)

for all species, except for *Zearaja maugeana* which is oviparous (Grant et al. 2019; Awruch et al. 2021), and philopatry is included within population structure for the purposes of the gap analysis. The exclusion of these parameters results in 14 gap analysis parameters. A level of understanding for the remaining parameters was assessed and categorised as high, medium, and low (no data). These categories were assessed for each species and each gap analysis parameter based on the outcomes of the review. For example, (a) for age-at-maturity, if age-at-maturity for a species was approximately estimated with no information on difference between age-at-maturity between sexes, the species was categorised as having a medium level understanding of this parameter; if no estimate of age-at-maturity has been made, the species was categorised as having a low level of understanding for that parameter; (b) if litter size was known for a number of individuals of a species, the species was categorised as having a high level of understanding for that parameter; if a species had a litter size from only one individual, that species was categorised as having a medium level of understanding; and if there were no records of litter size, the species was categorised as having a low level of understanding.

Results

Available information on the growth, age- and-size-at-maturity, and natural mortality, reproductive biology, movement ecology and habitat use, and population structure (Table 2) of the 29 euryhaline and estuarine species (Table 1) are presented in the Supplementary Information (Online Resources 1–4). A gap analysis follows summarising the level of understanding for all species across each parameter (Table 4).

Of 14 parameters included in the gap analysis (Table 4), only two species (6.9%) had a high level of understanding of at least 80% of these parameters (euryhaline species; *Carcharhinus leucas* and *Pristis pristis*). Seven species (24.1%) had a high level of understanding of 40–79% of parameters (two euryhaline species [20.0%]: *Hypanus guttatus*, *H. sabinus*; five estuarine species [26.3%]: *Fontitrygon margaritella*, *Hypanus say, Anoxypristis cuspidata*, *Pristis pectinata*, *Rhinoptera bonasus*). Most species (69.0%) had a high level of understanding of less than 40% of parameters. Nine species had a low level of information for at least 80% of the gap analysis parameters (31.0%; two euryhaline species [20.0%]: *Glyphis gangeticus*, *Hemitrygon bennettii*; seven estuarine species [36.8%]: *F. colarensis*, *F. margarita*, *Himantura uarnak*, *Pastinachus solocirostris*, *Pateobatis hortlei*, *Urogymnus lobistoma*, *Rhynchobatus springeri*). *Rhynchobatus springeri* was lacking information on all but one of the gap analysis parameters.

Growth, age-at-maturity, and natural mortality

Only five species (17.2%; three euryhaline [30.0%]: *C. leucas*, *P. pristis*, *H. guttatus*; two estuarine [10.5%]: *F. margaritella*, *R. bonasus*) have a high level of information of age- and size-at-maturity, size-at-birth, and a growth coefficient estimate (k). Considerable variation exists in growth and age-at-maturity in euryhaline and estuarine species (Online Resource 1). *Pristis zijsron* attains the largest body size at 730 cm total length (TL; Compagno et al. 1989), followed by *P. pristis* at 705 cm TL (Devadoss et al. 1989), and *F. margaritella* is the smallest-bodied species, attaining 34 cm disc width (DW; Moore et al. 2019) (Online Resource 1).

Anoxypristis cuspidata is estimated to be the fastest growing species (k 0.31 year^{-1}; Peverell, 2009), followed by *R. bonasus* (0.262 year^{-1}; Fisher et al. 2013). The slowest growth estimates are for *C. leucas* (0.035 year^{-1}; Thorburn and Rowland 2008) and *P. pristis* (0.045 year^{-1}; Simpfendorfer 2000). *Carcharhinus leucas* is estimated to be the longest-lived species, with a maximum observed age of 48.9 years (Wintner et al. 2002). *Anoxypristis cuspidata* is the shortest-lived species, reaching 9 years (Peverell 2009). Of the eleven species aged, mean maximum age is 24.8 years.

The earliest age-at-maturity among the euryhaline and estuarine species is two years in male *F. margaritella* and *A. cuspidata* (Peverell 2009; Clements et al. 2022). *Carcharhinus leucas* has the latest age-at-maturity, with males maturing at up to 25 years old in the Indo-Pacific (Wintner et al. 2002). Among species with larger distributions, regional variation in growth, size, and maturity have been recorded (e.g., *C. leucas* [e.g., Wintner et al. 2002; Tillett et al. 2011], *P. pristis* [Thorson 1976; Peverell 2009], *H. guttatus* [Yokota and Lessa 2007], *R. bonasus* [Neer

Table 4 Gap analysis of availability of information on growth and age-at-maturity, reproductive biology, movement ecology, habitat use, and population structure of the euryhaline and estuarine elasmobranchs. Cells shaded green represent a high level of understanding, yellow represents a medium level, and red represents a low level (see Methods)

Species	Sbir	Smat	Amat	Amax	k	GL	M	RC	LS	GesL	STM	LTM	Hab	PopS
Euryhaline species														
Carcharhinus leucas														
Glyphis gangeticus														
Glyphis garricki														
Glyphis glyphis														
Pristis pristis														
Hemitrygon bennettii														
Hypanus guttatus														
Hypanus sabinus														
Urogymnus dalyensis														
Urogymnus polylepis														
Estuarine species														
Fontitrygon colarensis														
Fontitrygon margarita														
Fontitrygon margaritella														
Hemitrygon fluviorum														
Himantura australis														
Himantura uarnak														
Hypanus say														
Pastinachus ater														
Pastinachus solocirostris														
Pateobatis hortlei														
Urogymnus acanthobothrium														
Urogymnus lobistoma														
Anoxypristis cuspidata														
Pristis clavata														
Pristis pectinata														
Pristis zijsron														
Rhynchobatus springeri														
Rhinoptera bonasus														
Zearaja maugeana														

Sbir, size-at-birth; Smat, size-at-maturity; Amat, age-at-maturity; Amax, maximum age; k, growth coefficient; GL, generation length; M, natural mortality; RC, reproductive cycle; LS, litter size; GesL, gestation length; STM, short-term movement ecology; LTM, long-term movement ecology; Hab, habitat use; PopS, population structure.

and Thompson 2005; Fisher et al. 2013]). *Carcharhinus leucas* has the longest generation length (up to 35 years; this study) and *A. cuspidata* has the shortest generation length of 6 years (this study).

Natural mortality has been estimated for nine species (31.0%; three euryhaline species [30.0%]; six estuarine species [31.6%]) (Online Resource 1). All five sawfish species have estimates of natural mortality, forming the majority of natural mortality information among euryhaline and estuarine species combined. Among euryhaline species, natural mortality ranges from 0.08 year^{-1} (*C. leucas*, life-history and telemetry data; Heupel and Simpfendorfer 2011) to 0.866 year^{-1} (*P. pristis*, telemetry data; Buckley et al. 2020). *Rhinoptera bonasus* has the lowest natural mortality of estuarine species (0.076 year^{-1}, age-dependent; Myers et al. 2007), and *A. cuspidata* has the highest (0.631 year^{-1}, age-dependent; Moreno Iturria, 2012).

Reproductive mode and biology

All euryhaline and estuarine species are viviparous or presumed viviparous, except for *Z. maugeana* which is oviparous (Grant et al. 2019; Awruch et al. 2021). All euryhaline sharks are viviparous with placentotrophy (Pillans et al. 2009; White et al. 2015; Pirog et al. 2019; Bester-van der Merwe et al. 2022). The sawfishes and *R. springeri* are lecithotrophic viviparous (e.g., Thorson 1976; White et al. 2017; Kyne et al. 2020), and the dasyatid rays are histotrophic viviparous (e.g., Last et al. 2006; White et al. 2006; White et al. 2017).

Litter sizes range from 1–20 pups, although there is considerable variation between species. The majority of euryhaline and estuarine species produce litters of up to five pups (15 species; 51.7%) (Online Resource 2). Larger litter sizes are observed in the carcharhinid sharks, the sawfishes, and *Z. maugeana*

is also predicted to produce up to 20 eggs per batch, possibly multiple times per year (Bell et al. 2016; Awruch et al. 2021). The smallest litter sizes are among the dasyatid rays, with eight species (27.6%) producing three pups or less per reproductive cycle (Online Resource 2).

There is no information on reproductive biology for *G. gangeticus*, *H. bennettii*, *U. dalyensis*, *P. hortlei*, *P. clavata*, or *R. springeri*. Reproductive cycle is unknown for 18 species (62.1%) and presumed in a further five species (17.2%; three euryhaline [30.0%]: *C. leucas* [Brunnschweiler and Baensch 2011; Pirog et al. 2019], *G. garricki* [Pillans et al. 2009], *H. guttatus* [Yokota and Lessa 2007]; two estuarine [10.5%]: *H. fluviorum* [Pierce and Bennett 2010a], *A. cuspidata* [Peverell 2009]) (Table 4). Potential regional differences in reproductive cycle have been noted in *P. pristis*, with a suspected biennial cycle in Lake Nicaragua (Thorson 1976) and a suspected annual cycle in northern Australia (Peverell 2009).

Movement ecology and habitat use

There is a high level of understanding of both short- and long-term movement for two species (6.9%; *C. leucas*, *P. pristis*). A further seven species (24.1%) have at least a medium level of understanding of both short- and long-term movement ecology (three euryhaline [30.0%]: *G. glyphis* [juveniles only], *H. sabinus*, *U. dalyensis*; four estuarine [21.1%]: *P. clavata*, *P. pectinata*, *P. zijsron*, *R. bonasus*) (Table 4, Online Resource 3).

Short-term movement ecology is thought to follow tidal cycle and direction for eight species (27.6%; five euryhaline [50.0%], three estuarine [15.8%]: *C. leucas* [Pillans 2006; Ortega et al. 2009; Pillans et al. 2020], *G. glyphis* [Pillans et al. 2008; Pillans et al. 2009], *P. pristis* [Whitty et al. 2009; Buckley et al. 2020], *U. dalyensis* [Campbell et al. 2012], *H. sabinus* [Brinton and Curran 2017], *P. ater* [Martins et al. 2020], *P. clavata* [Stevens et al. 2008], *P. zijsron* [Morgan et al. 2017]). Ten species undergo seasonal migrations in response to environmental factors such as salinity and temperature (34.4%; five euryhaline [50.0%], five estuarine [17.2%]: *C. leucas* [Thorburn and Rowland 2008; Espinoza et al. 2021], *G. glyphis* [Lyon et al. 2017; Dwyer et al. 2019; Pillans et al. 2022], *P. pristis* [Peverell 2009], *H sabinus* [Ramsden et al. 2017; Brinton and Curran 2017], *U. dalyensis* [Campbell et al. 2012], *F. colarensis* [Last et al. 2016a], *P. clavata* [Morgan et al. 2021], *P. pectinata* [Simpfendorfer et al. 2011], *P. zijsron* [Morgan et al. 2017], *R. bonasus* [Collins et al. 2008; Fisher et al. 2013]) (Online Resource 3).

Euryhaline and estuarine species are benthic, demersal, and pelagic in marine waters, estuaries, rivers, floodplains, and lakes (Online Resource 3). Seven species (24.1%; two euryhaline [20.0%]: *G. gangeticus*, *U. polylepis*; five estuarine [26.3%]: *H. uarnak*, *H. say*, *P. solocirostris*, *U. lobistoma*, *R. springeri*) have no habitat use information aside from knowledge of habitat based on presence/absence or capture locations. Habitat use is understood at a high level in six species (20.7%; four euryhaline [40.0%]: *C. leucas*, *G. glyphis* (juveniles only), *P. pristis*, *H. sabinus*; two estuarine [10.5%]: *Z. maugeana*, *P. pectinata*) (Table 4).

Euryhaline and estuarine species occur at a range of depths, from 0 to 164 m (Online Resource 3). The majority occur in shallow waters with depths of up to 50 m (16 species, 55.2%; *G. gangeticus*, *G. garricki*, *G. glyphis*, *P. pristis*, *H. bennettii*, *H. sabinus*, *U. dalyensis*, *F. colarensis*, *H. fluviorum*, *H. australis*, *H. uarnak*, *P. hortlei*, *U. lobistoma*, *A. cuspidata*, *P. clavata*, *R. springeri*). Habitat partitioning between juveniles and adults occurs or is presumed based on depths or ontogenetic diet changes in eleven species (37.9%; four euryhaline [40.0%]: *C. leucas* [Thorburn and Rowland 2008], *G. glyphis* [Feutry et al. 2017], *P. pristis* [Whitty et al. 2009], *H. guttatus* [Yokota and Lessa 2007; Gianeti et al. 2019]; eight estuarine [42.1%]: *H. australis* [Cerutti-Pereyra et al. 2014], *P. ater* [Cerutti-Pereyra et al. 2014; Martins et al. 2020], *U. acanthobothrium* [Last et al. 2016b], *A. cuspidata* [Peverell 2005], *P. clavata* [Morgan et al. 2021], *P. pectinata* [Poulakis et al. 2011], *P. zijsron* [Morgan et al. 2017]). Depth partitioning where neonates and juveniles usually occur in shallow water and adults move into deeper waters is common in species with high levels of information on habitat use (as above, excluding *G. glyphis*).

Use of nursery areas by juveniles has been documented in five species (17.2%; 3 euryhaline [30.0%]: *C. leucas* [e.g., Heupel and Simpfendorfer 2008], *G. glyphis* [Feutry et al. 2017; Lyon et al. 2017], *P. pristis* [e.g., Morgan et al. 2004]; two estuarine [10.5%]: *A. cuspidata* [Peverell 2005], *P. pectinata*

[Simpfendorfer et al. 2011]). The period of time spent by these species varies, but can be several years (e.g., up to 5 years for *C. leucas* [Pillans et al. 2020] and at the onset of maturation for *P. pristis* [Thorburn et al. 2007; Whitty et al. 2008]) and depends on characteristics of the estuary or species-specific life history.

Population structure

Population genetic data exists for ten species (34.5%; five euryhaline species [50.0%]; five estuarine species [26.3%]) (Online Resource 4). The five species of sawfishes are responsible for most data, followed by all four euryhaline carcharhinid sharks. *Carcharhinus leucas* and *P. pristis* are the only species for which global population structure has been studied, where *C. leucas* has genetic connectivity along continuous continental coastlines and four global genetic clusters (Eastern Pacific, Western Atlantic, Eastern Atlantic, and Indo-West Pacific), with isolated populations in Fiji and Japan (Glaus et al. 2020; Devloo-Delva et al. 2023). *Pristis pristis* has different haplotypes from Atlantic, Indo-West Pacific, and Eastern Pacific regions (Faria et al. 2013). *Glyphis gangeticus* and *Z. maugeana* have only one genetic study each. *Glyphis gangeticus* was found to have recent molecular gene flow between populations throughout Asia, suggesting marine dispersal (Li et al. 2015). *Zearaja maugeana* lacked evidence of population structure at a fine scale within the one estuary it is known to persist in (Weltz et al. 2018).

Of the eight species for which there is population structure information, female reproductive philopatry has been documented in six species (*C. leucas*, *G. garricki*, *G. glyphis*, *P. pristis*, *A. cuspidata*, *P. pectinata*), and male-biased dispersal in five (*C. leucas*, *G. garricki*, *G. glyphis*, *P. pristis*, *A. cuspidata*) (Karl et al. 2011; Phillips et al. 2011; Tillett et al. 2012; Feldheim et al. 2017; Feutry et al. 2017; Green et al. 2018; Feutry et al. 2020; Feutry et al. 2021; Patterson et al. 2022). Reproductive dispersal is limited in *G. garricki*, *G. glyphis*, *P. clavata*, and *P. zijsron* (Phillips et al. 2017; Feutry et al. 2017; 2020; Kyne et al. 2021a; Patterson et al. 2022). Multiple paternity occurs in *C. leucas* (Pirog et al. 2019) and some polyandrous mating occurs in *P. pectinata* (Feldheim et al. 2017).

Discussion

Significant gaps exist in the knowledge required for appropriate management of elasmobranchs. Basic knowledge including species life histories is widely unavailable (Jorgensen et al. 2022). To date, studies have primarily involved charismatic or commercially important species, and research is generally hindered by the availability of funding and logistical problems such as accessing habitats (Jorgensen et al. 2022). Knowledge gaps have implications for effective management and conservation. For example, life history parameters are widely used in demographic modelling for fisheries management and species conservation (e.g., Musick 1999; Cailliet 2015). This review has identified where research is needed on euryhaline and estuarine elasmobranch life history and ecology in order to improve the baseline of understanding and therefore assist management. Comprehensive gap analyses are lacking for other elasmobranch groups, but this approach could also be applied to groups such as pelagic sharks and rays which also face high extinction risk (Pacoureau et al. 2021).

Batoids represent the bulk of euryhaline and estuarine elasmobranchs. A large proportion of elasmobranch research has focused on sharks, while research on batoids has lagged significantly behind (Flowers et al. 2016). Despite a decrease in Data Deficient ray species over the last decade from 47.5% in 2013 to 14.4% in 2022 (Flowers et al. 2016; IUCN 2022), many of the euryhaline and estuarine rays remain virtually unknown (e.g., *Urogymnus polylepis*, *Fontitrygon margarita*, *Pateobatis hortlei*, *Pastinachus solocirostris*, *U. acanthobothrium, Rhynchobatus springeri*; this study). Rays, including the euryhaline and estuarine rays, form a large proportion of commercial and artisanal catch and bycatch (e.g., Compagno and Last 2010; Dulvy et al. 2021), and a higher proportion (36%) of rays are threatened with extinction compared with 31% of sharks (Dulvy et al. 2021). Increased focus on rays in research is required to reflect their extinction risk and high levels of exploitation. Taxonomic resolution has also hindered research, with many euryhaline and estuarine species only being recently taxonomically resolved (e.g., *R. springeri* [Compagno and Last 2010], *Glyphis* spp. [Li et al. 2015], *Pristis* spp. [Faria et al. 2013]), or being placed in provisional genera (e.g., *F. colarensis*; Last et al. 2016a). Slow species delineation and

unresolved nomenclature for many non-marine species has made identification, monitoring, and management more difficult (Last et al. 2016a; Grant et al. 2019; Kyne and Lucifora 2022).

Like elasmobranchs more broadly, significant knowledge gaps exist for euryhaline and estuarine species. Of the 29 known euryhaline and estuarine species, a high level of understanding of species-specific life-history (including natural mortality), movement ecology, habitat use, and population structure is available for only two euryhaline species – *Carcharhinus leucas* and *Pristis pristis* (e.g., Thorson 1976; Peverell 2009; Heupel and Simpfendorfer 2011; Espinoza et al. 2021; see Kyne and Lucifora 2022 for review) (Table 4). Although *C. leucas* and *P. pristis* have wide global distributions throughout tropical and warm-temperate waters (in the latter case for *C. leucas*), the majority of data for the two species comes from only three regions (Australia, USA, and Nicaragua). This regionally-specific information may mask regional differences in biological parameters, for example, reproductive periodicity, growth, and mortality (e.g., Thorson 1976; Simpfendorfer 2000; Peverell 2005; Peverell 2009; Moreno Iturria 2012). Even for these species, available data may not be representative of wider populations due to its collection from isolated populations (e.g., Lake Nicaragua *P. pristis*; Thorson 1976) or due to small sample sizes (Kyne et al. 2021c). Effective management strategies cannot be implemented where a representative cross-section of the species is not tracked throughout its entire geographical range (Jorgensen et al. 2022).

Nine euryhaline and estuarine species remain virtually unknown, with a low level of understanding on the majority of parameters reviewed (2 euryhaline species: *G. gangeticus*, *Hemitrygon bennettii*; 7 estuarine species: *F. colarensis*, *F. margarita*, *Himantura uarnak*, *P. solocirostris*, *P. hortlei*, *U. lobistoma*, *R. springeri*). *Rhynchobatus springeri* in particular is lacking information on all but one of the 14 parameters included in the gap analysis, with only an estimate of size-at-maturity for males (Table 4). Despite the family Dasyatidae making up the majority of euryhaline and estuarine species (17 of 29 species, 58.6%), the five sawfishes comprising the family Pristidae have the most overall directed research on life history, movement ecology, habitat use, and population structure. The lack of research for many of these species is likely due to some euryhaline and estuarine species only recently being described or delineated as well as being difficult to identify (e.g., *R. springeri* [Compagno & Last 2010], *U. acanthobothrium* [Last et al. 2016b]). Similar species may also be lumped together in catch statistics (e.g., *F. margarita* and *F. margaritella* recorded as *Fontitrygon* spp. in western Ghana [Seidu et al. 2022]). Euryhaline and estuarine elasmobranchs are also often not targeted by commercial fisheries although are regularly caught and retained as bycatch (e.g., *G. gangeticus* [Jabado et al. 2018a], *G. garricki* and *G. glyphis* [Grant et al. 2021], *F. margaritella* [Moore et al. 2019; Seidu et al. 2022], *P. zisjron* [Elhassan 2018]). The lack of data demonstrated here is not representative of a lack of conservation need. Many of these species are facing a very high risk of extinction, with thirteen (44.8%) euryhaline and estuarine species listed as Critically Endangered or Endangered (IUCN 2023). A concerted effort must be made to fill knowledge gaps and manage the conservation of these species and their habitats.

Growth, age-at-maturity, and natural mortality

Life history characteristics are crucial for understanding population dynamics and can be used as a measure of a species' sensitivity to exploitation (Cailliet 2015; Jorgensen et al. 2022). A lack of a basic understanding of a species' life history hinders its conservation and appropriate management (Jorgensen et al. 2022). Age, growth, and natural mortality estimates are essential to the management of elasmobranchs (Pauly 1980; Natanson et al. 2018). Elasmobranchs generally (although considerable variation exists) are large-bodied, have slow growth, and mature at a late age, making them particularly vulnerable to overexploitation (Musick 1999). The euryhaline and estuarine elasmobranchs exhibit a range of conservative life-history characteristics, with considerable variation in growth and age-at-maturity (Online Resource 1). Species with an estimated growth coefficient, k, below 0.1 are considered to be particularly susceptible to overexploitation (Musick 1999), and eight of the 14 euryhaline and estuarine species with estimates of growth fall within this category. The remaining 15 species (51.7%) have no estimate of k, despite its importance in management of species. Among the reviewed species, the slowest growth rate estimates are for *C. leucas* (0.035 year^{-1}; Thorburn and

Rowland 2008) and *P. pristis* (0.045 year^{-1}; Simpfendorfer 2000). The von Bertalanffy growth coefficient is considered to be an important population parameter and is often used in stock assessments, thus sampling of a population should consider variables which could affect individual growth and sample sizes should be as large as possible to be accurate and representative of the species (Kimura 2008).

Maximum age and age- and size-at-maturity estimates are a useful proxy for assessing productivity and recovery potential (Awruch et al. 2021; Villagra et al. 2022). Despite this, only nine species (31.0%) have estimates of both maximum age and age-at-maturity (Online Resource 1). Estimations of growth and age in elasmobranchs rely on lethal techniques due to the removal and analysis of vertebral sections (Awruch et al. 2021; Villagra et al. 2022). It is therefore difficult to obtain a sufficient sample size that is representative of the species, particularly for rare or threatened species (Villagra et al. 2022). Aging is also difficult to validate, often inaccurate, and is an evolving discipline, therefore many older studies using these techniques may be inaccurate (Natanson et al. 2018; Villagra et al. 2022). As improved aging techniques emerge (e.g., Rigby et al. 2016; Mayne et al. 2019), they should be applied to the euryhaline and estuarine elasmobranchs to address vital gaps in knowledge.

Natural mortality plays a key role in shaping populations and is fundamental for species-appropriate management (Heupel and Simpfendorfer 2011; Zhou et al. 2021). Of the 29 euryhaline and estuarine species, only 9 species (31.0%) have estimates of natural mortality (Online Resource 1). The majority of these estimates are for the sawfishes, with data on all five species (Simpfendorfer 2000; Moreno Iturria 2012; Buckley et al. 2020). Direct methods such as acoustic telemetry are considered the most accurate assessment of natural mortality (Liu et al. 2020). *Carcharhinus leucas* and *P. pristis* are the only species for which an estimate of natural mortality has been calculated using acoustic telemetry data (Heupel and Simpfendorfer 2011; Buckley et al. 2020). The remaining eight species use life-history methods to estimate natural mortality. Based on *C. leucas* and *P. pristis*, mortality generally declines as the animal ages and becomes larger-bodied (Simpfendorfer 2000; Heupel and Simpfendorfer 2011; Moreno Iturria, 2012; Buckley et al. 2020). *Rhinoptera bonasus* has the lowest estimated natural mortality of all euryhaline and estuarine species, at 0.076 year^{-1} (age-dependent) using the Euler-Lotka equation (Myers et al. 2007), however this estimate has been debated as too low (Grubbs et al. 2016). The Euler-Lotka equation has also been used incorrectly in many studies (Cortés, 2016; Zhou et al. 2021) and the age-independent estimates of 0.26–0.33 year^{-1} (Myers et al. 2007) are more likely. *Anoxypristis cuspidata* has the highest estimated natural mortality (0.631 year^{-1}, age-dependent; Moreno Iturria 2012), however Moreno Iturria (2012) argued that this may have been biologically unlikely and considered more conservative estimates (0.424–0.544 year^{-1}) more plausible. Information on natural mortality is lacking overall for the euryhaline and estuarine species, and direct estimates of natural mortality are required for the majority of species.

Reproductive mode and biology

Maternal investment has evolved to maximise offspring survival while minimising the energetic cost to the mother (Williams 1966). As a result, a range of reproductive modes are employed by the species reviewed here (Online Resource 2). Each reproductive strategy represents a differing level of maternal investment (Musick and Ellis 2005; Bester-van der Merwe et al. 2022). All non-marine elasmobranchs are viviparous (live bearing), except for *Zearaja maugeana* which is oviparous (egg laying) (Grant et al. 2019; Awruch et al. 2021). Fecundity is generally higher in oviparous species than viviparous species (Bester-van der Merwe et al. 2022), however reproductive output of *Z. maugeana* is likely reduced by its discontinuous reproductive cycle (Awruch et al. 2021). The dasyatid rays which make up the majority of euryhaline and estuarine elasmobranchs are histotrophic viviparous, whereby the walls of the uterus produce uterine milk (Bester-van der Merwe et al. 2022). Placental viviparity is unique to carcharhinid sharks, while the sawfishes and *R. springeri* are lecithotrophic (receiving nutrition only from a yolk-sac; Thorson 1976; White et al. 2017; Kyne et al. 2020; Bester-van der Merwe et al. 2022). Litter sizes are variable, but the majority of species for which litter size is known produce small litters of up to 5 pups. The number of pups in a litter is likely to be dependent on the size of the female, thus a lack

of large mature females in a population can limit a species' ability to recover (e.g., Peverell 2009; Farrell et al. 2010; Miller et al. 2022). Gestation length is known for only five of the euryhaline and estuarine species, and reproductive cycle is well understood for only three species. While the incubation length of *Z. maugeana* is estimated at around 7 months based on one individual, incubation period of skates can be highly variable depending on environmental conditions (Hoff 2008; Moreno et al. 2020). Without basic information on reproductive biology, reproductive output of a species is unknown, affecting management. For example, a longer reproductive cycle (e.g., biennial rather than annual) implies a lower fecundity (average number of pups or eggs per year), which affects recovery potential and maximum sustainable yield (Zhou et al. 2021; Villagra et al. 2022).

Closely related species and sub-populations of the same species can have significantly different life history traits in different geographic locations due to adaptations to different environmental gradients or due to different levels of anthropogenic pressures (Villagra et al. 2022). This highlights a need for geographically broad research with large sample sizes. Regional variation in growth, size, and age- and size-at-maturity have been recorded in euryhaline and estuarine species with larger distributions, likely due to regional differences in environmental variables (e.g., *C. leucas* [e.g., Wintner et al. 2002; Tillett et al. 2011], *P. pristis* [Thorson 1976; Peverell, 2009], *H. guttatus* [Yokota and Lessa 2007; Da Silva et al. 2018], *R. bonasus* [Neer and Thompson 2005; Fisher et al. 2013]). Potential regional differences in reproductive periodicity have also been observed, with biennial and annual reproductive cycles observed in *P. pristis* (Thorson 1976; Peverell 2009). Patterson et al. (2022) demonstrated evidence for both annual and biennial reproduction in *G. glyphis* within the same population through close-kin mark-recapture data. Reproductive periodicity, and therefore fecundity, may therefore be driven by regional adaptations and variability (Miller et al. 2022), and region-specific research is required for the appropriate management of species with large distributions. Despite the importance of life history data, the majority of the euryhaline and estuarine species have data based on a single or a few individuals in very few locations, and therefore at a restricted regional scale.

Movement ecology and habitat use

Management of elasmobranchs requires an understanding of their movements and distribution throughout their life histories (Chapman et al. 2015; Grant et al. 2019; Pillans et al. 2022). A detailed understanding of both short- and long-term movement ecology is understood however, for only two species (*C. leucas*, *P. pristis*) (Table 4). For the majority of euryhaline and estuarine species there is little to no data on movement ecology. In species where adults are known to move offshore (e.g., *C. leucas*, *P. pectinata*, *A. cuspidata*, presumably *G. glyphis*) the bulk of research is directed toward juveniles and nursery areas, as these shallow habitats are often more accessible and less costly for research than deeper marine waters (Peverell, 2009), despite the importance of appropriate management of adult populations for species recruitment (Prince 2005; Kinney and Simpfendorfer 2009). The movement ecology and habitat use of elasmobranchs can be driven by a range of both abiotic factors (e.g., salinity, temperature, dissolved oxygen, photoperiod) and biotic factors (e.g., prey density, activity, and availability, predator avoidance) which also need to be understood to manage and protect critical habitats (Schlaff et al. 2014). Policies for the management of elasmobranchs must consider that many sharks and rays exhibit site fidelity, (seasonal) residency, philopatry, and complex movement patterns on finer geographic scales than their dispersal ability might suggest (Chapman et al. 2015). Overfishing in areas where elasmobranchs exhibit site fidelity or residency could have a disproportionate effect on the overall species population and reduce its ability to recover (Chapman et al. 2015; Flowers et al. 2016; Pillans et al. 2022). Fragmentation of rivers resulting from dam construction also affects species migration and dispersal throughout systems, as well as altering habitat and water quality, driving declines in non-marine species (Grill et al. 2015; 2019). Parturition sites and nursery areas are also essential areas for species conservation and recovery, and exploitation in these areas could also have wider impacts on the population (Poulakis et al. 2011).

Of the movement ecology data available, seasonal migrations appear to be common among euryhaline and estuarine species (Online Resource 3). Euryhaline species tend to follow predictable downstream and upstream movements in response to seasonal

flow, salinity, dissolved oxygen, and temperature (e.g., *C. leucas*, *G. glyphis* [Dwyer et al. 2020; Pillans et al. 2020]). There is also evidence of migrations in response to environmental factors in estuarine species (e.g., *P. clavata* [Morgan et al. 2021], *P. pectinata* [Simpfendorfer et al. 2011], *P. zijsron* [Morgan et al. 2017], *R. bonasus* [Collins et al. 2007; 2008]), suggesting that euryhaline and estuarine species use behaviour to reduce metabolic demands (e.g., osmoregulation, thermoregulation; Lyon et al. 2017). Many euryhaline and estuarine elasmobranchs also use the physical characteristics of their environment, such as the strong tidal flows of tropical river systems to reduce the energy expenditure of movement by moving with tidal cycles (e.g., *G. glyphis* [Lyon et al. 2017], *U. dalyensis* [Campbell et al. 2012]; *H. sabinus* [Brinton and Curran 2017]). The movements of *P. pristis* also follow tidal flow to preserve energy during feeding rather than resisting tidal movement, which may increase growth rates, particularly in younger individuals (Whitty et al. 2009; Buckley et al. 2020).

Seven of the euryhaline and estuarine species (24.1%; Table 4) have no available habitat use information aside from knowledge of habitat based on presence/absence or capture locations, and habitat use is well understood in only six species. From the available information, habitat partitioning between juveniles and adults is relatively common among the euryhaline and estuarine species and is known or presumed based on depths or ontogenetic changes in diet in eleven species (37.9%; Online Resource 3). Juveniles tend to occur in shallower depths (e.g., Peverell 2005; Yokota and Lessa 2007; Poulakis et al. 2011), and sometimes use habitats close to mangroves for protection from predators and for foraging (e.g., Stevens et al. 2008; Cerutti-Pereyra et al. 2014; Martins et al. 2020). Use of nursery areas (Heupel et al. 2007) has been recorded for five of the euryhaline and estuarine species, with juveniles remaining in nurseries for varying periods of time depending on estuary characteristics, although this can be several years in longer-lived species such as *C. leucas* (e.g., Heupel and Simpfendorfer 2008; Pillans et al. 2020). For euryhaline species, downstream migration can also be costly for neonates and juveniles, due to an elevated predation risk and increased competition with large marine species (Dwyer et al. 2020). Euryhaline species therefore tend to spend minimal time in downstream environments as juveniles, except for during wet season months where upstream salinity is reduced due to high water flows (Dwyer et al. 2020). The period of time spent by *C. leucas* juveniles in rivers varies among river systems, likely due to differing food resources, risk of predation, and access to suitable environmental conditions (Pillans et al. 2020).

Population structure

Population structure is inherently linked to movement ecology, as the movements of adult elasmobranchs primarily determines population structure while juveniles generally remain where they were pupped for a significant amount of time (Frisk et al. 2014; Chapman et al. 2015). Genetic research has been carried out on only ten of the euryhaline and estuarine species (34.5%), and there is population structure data for only eight of these. Of these, most species exhibit male-biased dispersal and female philopatry (Online Resource 4). The disproportionate energetic investment into reproduction between males and females indicates that male-biased dispersal and female philopatry should be common in elasmobranchs (Phillips et al. 2021). Female reproductive philopatry benefits females by providing a suitable parturition site after long, energetically demanding gestation periods (Phillips et al. 2021), however can make species vulnerable to significant population decline where parturition sites are overfished (Chapman et al. 2015; Phillips et al. 2021). Female reproductive philopatry is known to occur in six species (see Online Resource 4) and is also likely in *P. clavata*, *P. zijsron* (matrilineal structuring; Phillips et al. 2011), and *G. gangeticus* (based on the population structures of *G. garricki* and *G. glyphis*). Female philopatry is also possible in the oviparous *Z. maugeana*, as philopatry has been recorded in oviparous sharks (Day et al. 2019) and there are many advantages for natal philopatry in oviparous species (Refsnider and Janzen 2010). Male-biased dispersal has been identified in five species (see Online Resource 4).

The global population structure of *C. leucas* has been well-studied (Glaus et al. 2020; Devloo-Delva et al. 2023), while a basic understanding of the global population structures of the sawfishes is based on the *NADH-2* gene (Faria et al. 2013). *Glyphis garricki* demonstrates fine-scale population structuring in Australia and Papua New Guinea (Feutry et al. 2020),

while *G. glyphis* likely has two distinct populations in Australia and demonstrates haplotype differentiation and low connectivity between rivers (Feutry et al. 2017; Kyne et al. 2021a; Patterson et al. 2022). *Zearaja maugeana* is restricted to one population in Macquarie Harbour, Tasmania, Australia, and has likely undergone a recent bottleneck or founder event (Treloar et al. 2017; Weltz et al. 2018). The freshwater population of *H. bennettii* in Zuojiang River, China, is isolated from coastal waters by dams, and although breeding is occurring the isolated population is declining (Zhang et al. 2010). A thorough understanding of gene flow, dispersal, and any barriers to dispersal is critically important to assess the global conservation status of a species and manage its conservation (Phillips et al. 2021; Devloo-Delva et al. 2023). Given that reproductive dispersal is known to be limited in *G. garricki*, *G. glyphis*, *P. clavata*, and *P. zijsron* (Phillips et al. 2017; Feutry et al. 2017; 2020; Kyne et al. 2021a), and there are clear or unknown barriers to dispersal (e.g., dams for *H. bennettii*) for other euryhaline and estuarine species, a research focus on population structure and reproductive dispersal is also required for these species.

Future research directions

This gap analysis and literature review identifies several key future research priorities. Some rays in particular are lacking basic life history data. For example, the biology and ecology of *R. springeri*, which is endemic to Southeast Asia where it is heavily fished for its fins and meat (Moore et al. 2017; Jabado 2018; Kyne et al. 2020), is virtually unknown. For euryhaline and estuarine species with large geographical distributions, regional variation in parameters such as growth, size, age- and size-at-maturity, and reproductive biology (e.g., gestation length and reproductive cycle) have been identified (e.g., Wintner et al. 2002; Tillett et al. 2011; Thorson 1976; Peverell, 2009). Effort therefore needs to be made to research representative samples of a species' global population to understand these regional variations and how they affect regional management of a species. As improved non-lethal aging techniques emerge such as infrared spectroscopy (Rigby et al. 2016) and genomic aging (Mayne et al. 2019), they should be applied to the euryhaline and estuarine elasmobranchs to increase the accuracy of life history estimations while reducing the negative effect of lethal techniques on small populations.

Direct methods for calculating natural mortality are considered more accurate than indirect methods (Liu et al. 2020), however only *C. leucas* and *P. pristis* have estimates using direct methods (Heupel and Simpfendorfer 2011; Buckley et al. 2020). To better understand the resilience of euryhaline and estuarine species, direct methods should be applied to future research. Information on the short- and long-term movement ecology, the environmental drivers of movement ecology, and habitat use and preferences for the euryhaline and estuarine species is largely lacking and needs to be prioritised. Most research has occurred on juveniles in shallow habitats (Peverell 2009), despite the importance of movement ecology and habitat use throughout a species' life cycle for appropriate management (Schlaff et al. 2014; Chapman et al. 2015). A detailed understanding of how each species moves and utilises habitat is critical for understanding how modifications to habitats, such the construction of dams, may affect them. A broader understanding of genetic population structure and barriers to geneflow also needs to be developed among the euryhaline and estuarine species to understand the viability of each species and manage accordingly (Patterson et al. 2022; Devloo-Delva et al. 2023). Finally, a detailed understanding of human interactions and utilisation of these species is required to implement successful conservation measures in places where these species are an important resource for livelihoods and food security. Filling knowledge gaps will require international collaborations, knowledge sharing, adequate resourcing, and capacity building across the global tropics where most euryhaline and estuarine elasmobranchs occur.

Conclusion

Euryhaline and estuarine elasmobranchs represent a diverse and unique group of sharks and rays which are disproportionately at risk of extinction (IUCN 2023). Understanding the life history traits, movement ecology, habitat use, and population structure of these species is vitally important for the implementation of species-appropriate management and conservation measures (Pauly 1980; Schlaff et al. 2014; Cailliet 2015; Chapman et al. 2015; Phillips

et al. 2021; Jorgensen et al. 2022; Devloo-Delva et al. 2023). To date, the majority of research on elasmobranchs has focused on charismatic and commercially important marine species (Jorgensen et al. 2022), and research on non-marine elasmobranchs has lagged behind (Grant et al. 2019). Although many (if not all) of the euryhaline and estuarine species interact with fisheries (e.g., Peverell 2005; Jabado et al. 2018a; Moore et al. 2019) and also face other threatening processes, they have received little research attention. As a result, there is a detailed understanding of the life history, movement ecology, habitat use, and population structure of only 2 of 29 species – the Bull Shark *C. leucas* and the Largetooth Sawfish *P. pristis* – while 11 species remain virtually unknown. This gap analysis identifies priority species and research areas where key information for species management is lacking. Given the rarity of many of these species and the costs and logistics associated with accessing remote habitats, obtaining data for a representative sample of a population is difficult. As climate change escalates and human populations continue to grow, increasing water extraction and modification of river systems and estuaries will disrupt flows and reduce the availability of suitable habitats for non-marine elasmobranchs (Simpfendorfer et al. 2011; Lear et al. 2021). It is essential to address the knowledge gaps identified in this study to ensure the persistence of the ecologically unique and highly threatened euryhaline and estuarine elasmobranchs.

Acknowledgements The authors wish to thank Grant Johnson for his ongoing support.

Author contributions This review was conducted as a part of Julia Constance's PhD thesis. Julia Constance performed the literature review and gap analysis and drafted the article. Peter Kyne came up with the idea of the article and conducted critical revisions. Erica Garcia, Vinay Udyawer and Richard Pillans conducted critical reviews of the completed draft.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. Julia Constance was supported by an Australian Government Research Training Program Scholarship.

Declarations

Conflict of interest The authors have no competing interests to declare.

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