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Salinity-driven habitat use of marine-estuarine batoids on the Amazon Coast

Ana Rita Onodera Palmeira-Nunes · Ricardo de Souza Rosa · Jorge Luiz Silva Nunes · Nivaldo Magalhães Piorski · João Braullio de Luna Sales · Jamerson Aguiar Santos · Ana Paula Barbosa Martins · Rachel Ann Hauser-Davis · Getulio Rincon · Keyton Kylson Fonseca Coelho · Luís Fernando Rodrigues-Filho · Natascha Wosnick

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Abstract The behavioral plasticity of non-marine elasmobranch species allows these animals to strategically inhabit areas where salinity aligns with their physiological needs. Thus, this study aimed to investigate habitat use by rays in an Amazonian estuary, following a categorization of non-marine species based on the type of environment in which critical life history phases occur. Data on the capture of ray species in fishing weirs were acquired through a monitoring program conducted from March 2011 to April 2012. One hundred and forty-five coastal-estuarine rays, representing seven species, were sampled over 1 year in the estuary, across a salinity range from 12.9 to 41.3 ppt (26.8 ± 11.6 ppt). The dominant presence of neonates and juveniles, constituting approximately 70% of the total rays captured year-round, is noteworthy. Additionally, the presence of pregnant females with embryos at various developmental stages indicates the importance of the study area for the life cycle of various elasmobranch species. Our data suggest that *Hypanus guttatus* and *Hypanus geijskesi* fit into the estuarine generalist category, and

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A. R. O. Palmeira-Nunes (✉) · J. L. S. Nunes · N. M. Piorski
Programa de Pós-Graduação em Biodiversidade e Biotecnologia (BIONORTE), Laboratório de Organismos Aquáticos, Universidade Federal do Maranhão, São Luís, Maranhão, Brazil
e-mail: anarits@gmail.com

R. de Souza Rosa
Programa de Pós-graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Campus I, João Pessoa, Brazil

J. B. de Luna Sales
Grupo de Investigação Biológica Integrada, Centro de Estudos Avançados da Biodiversidade, Universidade Federal do Pará, Belém, Pará, Brazil

J. A. Santos
Instituto Federal do Maranhão, Barreirinhas, Maranhão, Brazil

A. P. B. Martins
Centre for Sustainable Tropical Fisheries and Aquaculture and College of Science and Engineering, James Cook University, Townsville, QLD, Australia

R. A. Hauser-Davis
Laboratório de Avaliação e Promoção da Saúde Ambiental (LAPSA), Instituto Oswaldo Cruz (Fiocruz), 21040-360 Rio de Janeiro, Rio de Janeiro, Brazil

G. Rincon
Universidade Federal do Maranhão, Campus de Pinheiro, Pinheiro, Maranhão, Brazil

K. K. F. Coelho
Laboratório de Organismos Aquáticos, Universidade Federal do Maranhão, São Luís, Brazil, Maranhão

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Gymnura aff. *micrura* fits into the non-marine transient category. We identify salinity as a key driver of ray temporal distribution within the Amazonian coast, a crucial region for elasmobranch conservation. Future studies should, therefore, aim to understand how climate change might impact elasmobranch habitat use in this region.

Keywords Estuary · Stingrays · Euryhaline · Reproduction · Parturition

Introduction

Investigations into abiotic factors influencing the habitat use of sharks and rays shed light on the complex dimensions of their interactions with the environment (Constance et al. 2023). Considering that abiotic factors can influence the movement of sharks and rays, several studies indicate that elasmobranch species may seek out or avoid specific environmental conditions to optimize their fitness, which implies maximization of advantages and minimization of costs (Heupel and Simpfendorfer 2008, 2014; Ubeda et al. 2009; Knip et al. 2011; Simpfendorfer et al. 2011; Dwyer et al. 2020). These comprehensive assessments encompass various aspects of the life cycle of these organisms, exploring the full spectrum of their biological and ecological activities, in which their behavioral responses can vary according to species, sex, developmental stage, season, and geographic location (Schaff et al. 2014).

Salinity is one of the most prominent abiotic factors that influence the distribution and habitat use of aquatic species (Khlebovic 1969; Franco and Santos 2018; Kyne and Lucifora 2022). Spatial and temporal salinity variations critically influence ecological processes, shaping the structure and functioning of aquatic ecosystems (Franco and Santos 2018). Thus, salinity acts as an ecological filter, delineating the range of species that can thrive within specific gradients (Williams et al. 1990; Callihan et al. 2015). In this sense, studies investigating the relationship between species distribution and salinity gradients may provide important insights into conservation planning and spatial management strategies (Grant et al. 2019).

These investigations are of particular significance for animals that present monitoring challenges, such as sharks and rays, as they can offer important insights into seasonal movement, reproductive behavior, and habitat selection (Ballantyne and Robinson 2010; Wosnick and Freire 2013; Dwyer et al. 2020). Some elasmobranch species can use non-marine environments during critical stages (Grant et al. 2019), such as early life stages, to access food and protect themselves from predators (Constance et al. 2023). Currently, 55 species of Chondrichthyes occur in low-salinity environments (~ 5% of all extant species), of which 45 are obligate freshwater ray species (Kyne and Lucifora 2022). Thus, few species exhibiting physiological and behavioral plasticity capable of adapting to variable salinity conditions and truly inhabiting different aquatic ecosystems remain (Ballantyne and Robinson 2010; Schlaff et al. 2014; Bangley et al. 2018). These non-marine elasmobranchs form a scientifically less well-known group compared to marine ones, and some species may be more susceptible to negative anthropogenic pressures (Grant et al. 2019). To classify them, certain criteria have been employed, such as osmoregulation capacity, rectal gland functionality, distribution of occurrence data in non-marine waters, and the type of environment in which the critical stages of life history occur (Thorson et al. 1983; Compagno and Cook 1995; Compagno 2002; Last 2002; Martin 2005; Grant et al. 2019).

The initial proposal considered the osmoregulation process, which in elasmobranchs is facilitated through specialized physiological mechanisms, including a rectal gland and kidneys used in ion and urea regulation and in water balance (Takei 1993; Piermarini and Evans 2000; Janech et al. 2008; Ballantyne and Robinson 2010; Ballantyne 2016). These adaptations enable sharks and rays to maintain both intra- and extracellular compositions within optimal ranges and allow some species to traverse from freshwater, characterized by lower salinity values, to high salinity marine ecosystems (Pillans et al. 2008; Ballantyne

L. F. Rodrigues-Filho
Programa de Pós-Graduação em Aquicultura e Recursos Aquáticos Tropicais (AqRAT), Universidade Federal Rural da Amazônia, Grupo de Estudos Marinhos e Costeiros da Amazônia (GEMCA), Capanema, Pará, Brazil

N. Wosnick
Programa de Pós-Graduação em Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

and Fraser 2012; Gleiss et al. 2015; Ballantyne 2016). Marine elasmobranch species maintain blood osmolarity close to that of the external environment through high urea and trimethylamine oxide (TMAO) concentrations, while euryhaline species reduce urea concentrations when in freshwater (Yancey 2015). Employing a different strategy, freshwater rays (potamotrygonins from South America) exhibit very low urea concentrations and produce large amounts of dilute urine to remain hyperosmotic in freshwater (Klimley 2013; Kyne and Lucifora 2022).

Even based on this important criterion regarding osmoregulatory capacity and rectal gland functionality, the proposal by Thorson et al. (1983) was not widely accepted due to a lack of detailed physiological studies on elasmobranch species (Grant et al. 2019).

In the most acceptable proposal of categorization of non-marine elasmobranch species, Compagno and Cook (1995) considered the distribution and regularity of occurrence data of species in categories. However, this criterion did not present an ecological context of life history for habitat use of the categorized species, such as reproductive data. The behavioral adaptations in elasmobranchs in response to salinity gradients are integral to the survival of this group, so many species display selective preferences for specific salinity concentrations during key life stages, such as reproductive and growth periods (Osgood et al. 2021).

Elasmobranch behavioral plasticity allows these animals to strategically inhabit areas where salinity aligns with their physiological requirements, optimizing resource utilization and reproductive success (Schlaff et al. 2014). Thus, the categorization of species that occur in non-marine waters based on the type of environment associated with critical life history stages proposed by Grant et al. (2019) allows for a greater understanding of these factors and comprises five different categories, as follows: (1) obligate freshwater species, whose entire life history occurs exclusively in freshwater (reproductive and ecological functions); (2) euryhaline generalist species, which occur in freshwater to marine environments and present the physiological capacity to withstand long periods in these environments and use freshwater and/or estuarine environments during certain life stages, such as parturition and/or nursery; (3) estuarine generalist species, which commonly occur in estuarine to marine environments and may penetrate lower salinity estuarine waters for prolonged periods but cannot withstand prolonged periods in freshwater, while also using estuarine environments during certain life stages, i.e., pregnancy and parturition, like nursery areas; (4) non-marine transient species, which may occur in non-marine environments but carry out all life history stages in marine waters and may not withstand prolonged exposure to estuarine or freshwater environments; (5) non-marine vagrant species, with no identifiable biological association with non-marine environments throughout their life history, and are not expected to occur in a non-marine environment and are not considered to be physiologically capable of prolonged exposure to estuarine or freshwater environments.

The characteristic salinity variability of the region, along with a range of physical and chemical components brought by the Amazon River freshwater plume (Silva et al. 2009), plays a key role in determining the distinct habitat preferences of elasmobranch species (Constance et al. 2023; Lofthus et al. 2024) and can act as a speciation force (Rodrigues-Filho et al. 2023). The Brazilian Amazon Coast (BAC) is a tropical region differentiated by unique attributes. Most notably, it boasts the world's second-largest expanse of mangrove ecosystems (Souza-Filho 2005) and is home to the mesophotic reefs forming the Great Amazon Reef System (GARS) (Moura et al. 2016). The region receives a substantial influx of freshwater discharge from multiple hydrographic systems (ANA 2020; Prestes et al. 2020) and exhibits specific oceanographic features, such as macrotides (Bezerra et al. 2013), high marine current speeds ($\leq$ 2 m/s), and an extensive continental shelf ($\leq$ 330 km) (Palma 1979; Geyer et al. 1991; Moura et al. 2016; de Freitas et al. 2024). Additionally, the BAC holds international recognition as a RAMSAR site (ICMBio 2018; RAMSAR 2018). The average annual Amazon River discharge can reach 16% of the global freshwater discharge to the ocean (Richey et al. 1989; Silva et al. 2009; Ward et al. 2015), creating an extensive offshore freshwater plume spanning thousands of square kilometers (Coles et al. 2013; Moura et al. 2016) and extending for over 200 km into the ocean (Silva et al. 2009). This phenomenon induces density stratification arising from the disparity in salinity levels between riverine and oceanic waters (Molinas et al. 2014). This stratification manifests as a layer

of shallower, less saline water overlaying a deeper, more saline water layer, thereby exerting a substantial influence on local hydrodynamics (Geyer et al. 1996; Molinas et al. 2014; Reverdin et al. 2021).

Given the significant influence of local salinity fluctuations, this study aimed to investigate the habitat use of ray species within an estuary along the BAC. Our inquiries center on their spatial–temporal distribution, population structure, and developmental stages, all within the context of local salinity fluctuations. Considering the categories proposed by Grant et al (2019), one empirically testable hypothesis was established, namely to verify if some ray species maintain a year-round presence in the estuary, including for mating and parturition, while others migrate towards the coastline during high-salinity periods for mating and parturition.

Material and methods

Study area

This study was carried out within the Camará River estuary (0°35′30.58″S and 47°41′12.94″W), located on the BAC, within the jurisdiction of the Marapanim Municipality in the state of Pará, northern Brazil (Fig. 1). The area is renowned for its prolific fish production resulting from small-scale weirs, a thriving practice due to the region's favorable physiographic and oceanographic conditions (Krumme et al. 2014).

The Camará River estuary, representative of the Amazonian region, experiences a hot and humid tropical climate with an average annual precipitation of 2800 mm, marked by distinct rainy and dry seasons (Marengo 2006). The Amazon River discharge

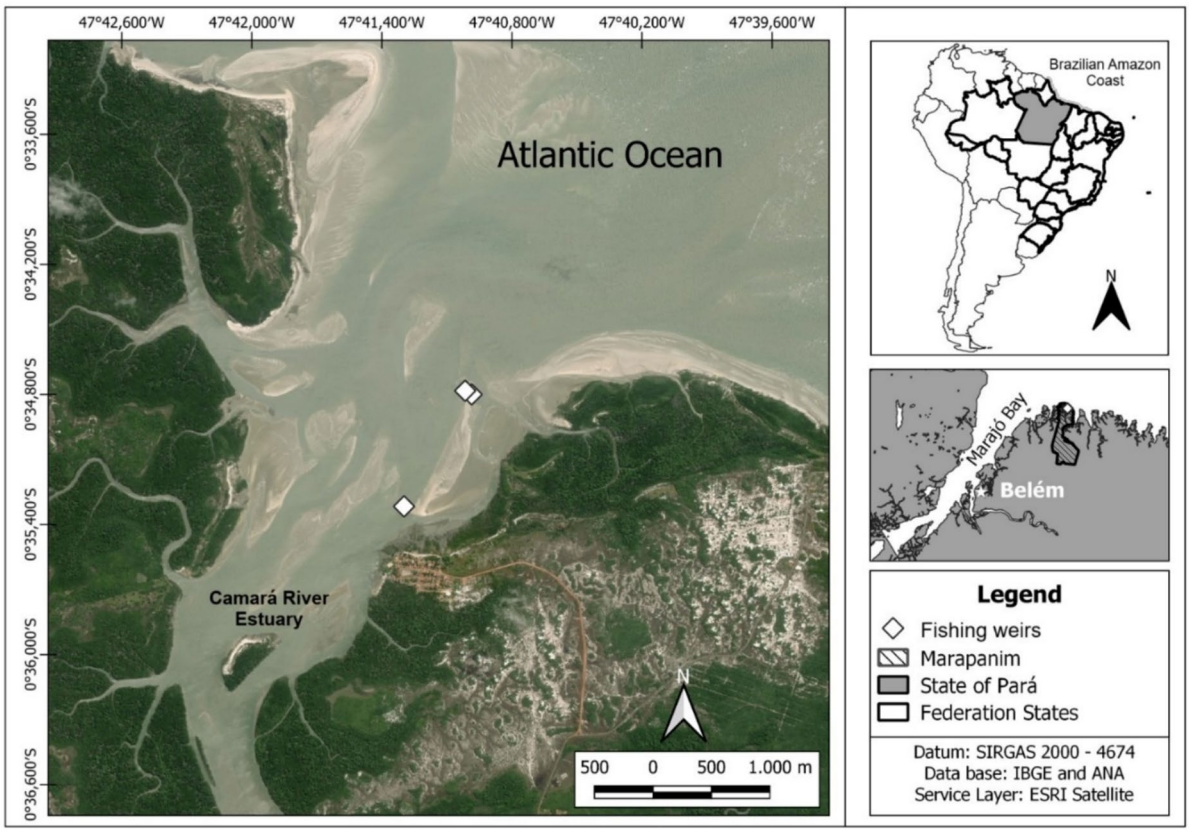

Fig. 1 Geographical position of the Camará River estuary within the Marapanim municipality, in the state of Pará, located on the Brazilian Amazon Coast. Map created using QGIS software (version 3.22.16-Białowieża) employing the SIRGAS 2000 Coordinate Reference System (EPSG: 4674). The South America and Brazilian state layers were obtained from the National Water and Basic Sanitation Agency (ANA) and the Brazilian Institute of Geography and Statistics (IBGE) database

significantly reduces coastal salinity and intensifies marine currents, particularly during the rainy season (Tavares et al. 2005). Important local oceanographic features include a macrotidal regime with semi-diurnal tidal cycles (El-Robrini et al. 2018; de Freitas et al. 2024), shaping a coastal plain composed of sedimentary materials such as sand and clay from continental drainage. This dynamic landscape supports thriving mangrove ecosystems, key environments for the early life stages of many fish species (Camargo and Isaac 2003; Souza-Filho 2005; ICMBio 2018).

Sampling

Most fishers in the studied estuary use fishing weirs, non-selective fixed traps built with mangrove wood that operate continuously throughout various phases of the tidal cycle (Piorski et al. 2009; Krumme et al. 2014). Situated on the tidal flat, which can reach depths of up to 3 m during high tide, fishing activities predominantly take place during low tide when the weirs become fully exposed (Supplementary Fig. 1). Data on the capture of ray species in fishing weirs was acquired through an extensive monitoring program conducted from March 2011 to April 2012. This initiative comprised ten monthly excursions to closely observe fishing operations within three fishing weirs. The selected weirs were uniformly constructed, with similar ray-capture dimensions and capacity. One weir was strategically located near Camará, while the remaining two were positioned about 4 km away from the beach on the estuary.

Artisanal longline fishing activities were monitored monthly in a channel of the studied estuary. Commercial fishers deployed longlines during nighttime low tide periods and retrieved them during the subsequent low tide, as a strategy to target both catfish and ray species. Sporadic gillnetting operations were also incorporated into the monitoring framework. This comprehensive approach, encompassing both longlines and gillnets, facilitated the assessment of the presence of species in adjacent areas and at depths exceeding 3 m.

Rays were identified using taxonomic references (Bigelow and Schroeder 1953; Last et al. 2016; Petean et al. 2020), with the following species recorded: *Hypanus guttatus* (Bloch and Schneider, 1801), *Gymnura* aff. *micrura* (Bloch and Schneider, 1801), *Hypanus geijskesi* (Boeseman, 1948), *Styracura schmardae* (Werner, 1904), *Aetobatus narinari* (Euphrasen, 1790), *Hypanus berthalutzae* Petean et al. 2020, and *Pseudobatos percellens* (Walbaum, 1792). Concerning *G.* aff. *micrura*, a recent study by Gales et al. (2024) indicates that the species found on the Brazilian coast is genetically different from the one in Suriname, which is the *Gymnura micrura* type locality. The specimens were subjected to standard morphometric measurements following Santos et al. (2004), employing a measuring tape (cm) and a 200-mm metal caliper.

Reproductive system assessments were performed through macroscopic analyses according to Conrath (2005), and life stages were categorized based on developmental criteria adapted from Santander-Neto et al. (2016), encompassing neonate (immature), juvenile (immature), subadult (maturing), and adult (mature) individuals. Fully developed free-swimming individuals with umbilical scars were classified as neonates. Immature individuals without an umbilical scar were considered juveniles. Subadults were defined as juveniles nearing the size of mature specimens collected locally. Testes are undeveloped in male subadults, and the uterus and ovaries are filamentous and undeveloped in female subadults. Mature males showed rigid claspers due to their calcification, and mature females were considered pregnant when eggs or embryos were present in the uterus.

Lastly, comprehensive environmental data were systematically collected once a day during the monitoring periods, to update the knowledge base on other local abiotic factors, as these may also influence elasmobranch movements, even under different conditions. Water and atmospheric temperatures were quantified during fishing activity monitoring using a Dymax© digital thermometer (Dymax©, Dimax Technology, Singapore), while salinity, pH, and dissolved oxygen levels were determined using an Alfakit© chemical titration kit (Alfakit©, Alfakit Ltda, Brazil). The kit employs argentimetric titration to measure salinity, and the indicator method applies a 4.50 to 8.00 chart to determine pH, while the Winkler method was used to measure dissolved oxygen. A manual refractometer, Biobrix© brand, model 211, was also used for salinity determination. Rainfall data were extracted from the Hydro-Meteorological Information System (https://portal.inmet.gov.br) from the Salinópolis Station in Pará, Brazil, the closest station

to the study area. Samplings were conducted with the approval of the Brazilian Ministry of Environment (IBAMA/ICMBio- SISBIO no. 26393–1).

Data analysis

Data encompassing abiotic variables, capture frequency throughout the year, sex of the sampled individuals, disc width, and developmental stages were systematically compiled. These datasets were subsequently mapped and visually represented, enabling the evaluation of habitat use patterns among ray species within the tidal flat of the Camará River estuary. Local salinity values equal to or below 22 ppt were considered low, and those above 22 ppt were considered high. To assess the expected 1:1 sex ratio between males and females, a chi-squared (χ^2) test was applied to species with larger sample sizes.

Abundance measurements were based on the absolute count of individuals recorded monthly. The effects of salinity fluctuations on the abundance and developmental stages of ray species were investigated using a permutational multivariate analysis of variance (PERMANOVA) employing a Bray–Curtis dissimilarity matrix, applying prior logarithmic transformation ($\log[x] + 1$), using the vegan package (Oksanen et al. 2022). Additionally, correlations between salinity and the number of ray specimens were explored by a Pearson correlation analysis. The normality assumption of the residuals in the linear model was assessed using the Shapiro–Wilk test, considering a significance level of alpha < 0.05. All statistical analyses were conducted using R software, R version R 4.4.3 (R Core Team 2023).

The categorization proposed by Grant et al. (2019) was considered herein, based on the type of environment in which critical life history stages take place (parturition, nursery areas and mating).

Results

The monthly mean salinity ranged from 12.90 to 41.30 ppt over the 1-year period (mean ± standard deviation; 26.80 ± 11.60 ppt). The average salinity decreased to below 22 ppt from December 2011 to May 2012, noteworthy as the least saline period during the study. Monthly average atmospheric temperatures fluctuated between 27.50 and 30.70 °C (29.04 ± 0.86 °C), while monthly average water temperatures ranged from 27.60 to 30.40 °C (29.14 ± 0.70 °C). pH values remained relatively constant during the study period, ranging from 7.40 to 7.60 (7.50 ± 0.05), while mean dissolved oxygen displayed minimal variations, ranging from 7.00 to 7.60 mL L^{-1} (7.11 ± 0.16 mL L^{-1}). The monthly average values of the analyzed abiotic factors are reported in Supplementary Table 1. Monthly average rainfall (223.23 ± 242.80 mm) conformed to the typical Amazon region pattern, with consistent year-round rainfall alternating between high (from December to May) and low (from June to November) intensity periods (see Camargo and Isaac 2003) (Supplementary Fig. 2).

All abiotic factors were positively correlated with salinity, except for rainfall, which exhibited a negative relationship (Supplementary Fig. 3). These abiotic data were collected to enhance fundamental ecological knowledge concerning the local environment, and salinity emerged as the most decisive environmental factor affecting the presence or absence of rays in the area.

A total of 145 coastal-estuarine rays representing seven species were sampled across the three weirs. *Hypanus guttatus* ($n = 81$) and *Gymnura* aff. *micrura* ($n = 36$) were the most prevalent, jointly constituting 81% of the total captures. Additionally, *Hypanus geijskesi* ($n = 14$), *Styracura schmardae* ($n = 9$), *Aetobatus narinari* ($n = 1$), *Hypanus berthalutzae* ($n = 1$), and *Pseudobatos percellens* ($n = 1$) were also sampled. Differences in species abundance were observed during the two salinity periods that occur in the Amazon estuaries. Herein, the low salinity period took place from December to May, and the high salinity period, from June to November (PERMANOVA: Pseudo-$F = 5.13$; df = 1. 10; $p = 0.009$) (Fig. 2).

Immature and maturing individuals were prevalent among all captured ray species, constituting 71% of the total recorded specimens. Peak abundances of these stages were observed in July and September (salinity values of 37.51 and 41.30 ppt); the lowest abundance was detected in January and February (17.90 and 13.00 ppt). Differences in the abundance of ray individuals across life stages were not influenced by salinity fluctuations (PERMANOVA: Pseudo-$F = 1.85$; df = 1.10; $p = 0.16$) (Fig. 3).

Species richness was positively correlated with salinity ($p = 0.006$; $r = 0.73$; $r^2 = 0.54$; $a = 0.34$ (− 1.36–2.04); $b = 0.90$ (0.03–0.15)), and the

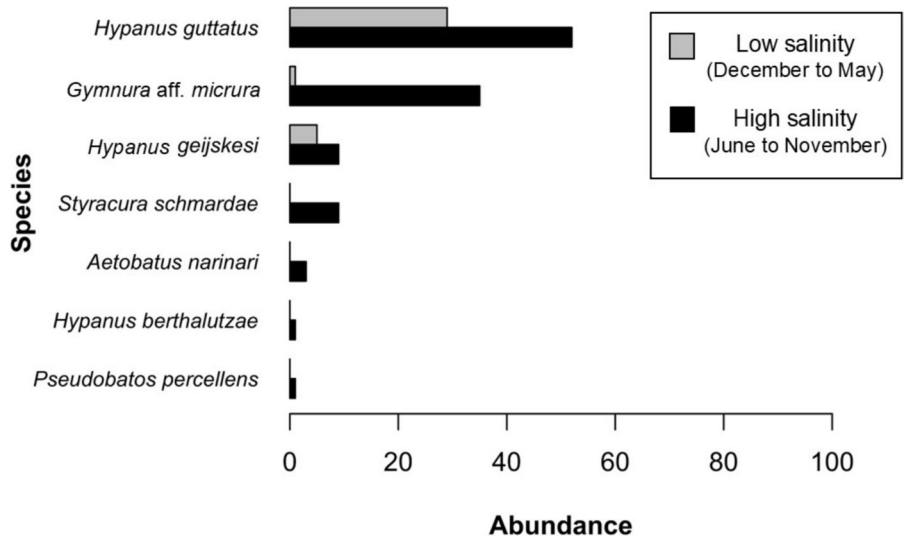

Fig. 2 Abundance of ray species in the Camará River estuary during contrasting salinity periods on the Brazilian Amazon coast. Gray bars represent low salinity levels (12.00–22.00 ppt), while black bars denote high salinity conditions (22.10–42.00 ppt). Statistics were performed by PERMANOVA, comparing the abundance of ray species between salinity levels, pseudo-$F = 5.13$; df = 1.10; $p = 0.009$

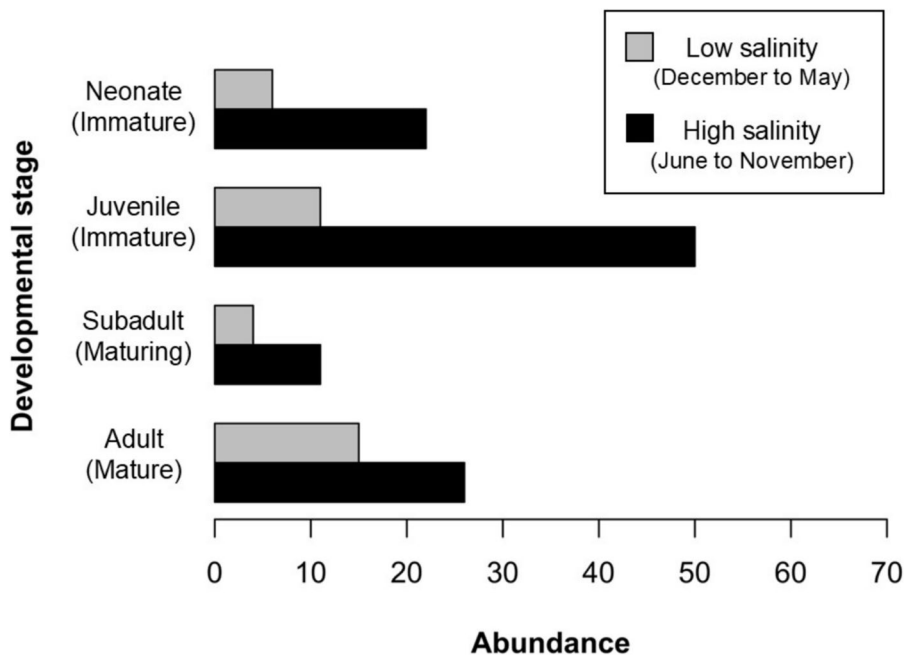

Fig. 3 Abundance of developmental ray stages in the Camará River estuary during varying salinity periods on the Brazilian Amazon coast. Gray bars represent low salinity levels (12.00–22.00 ppt), while black bars denote high salinity conditions (22.10–42.00 ppt). Statistics performed by PERMANOVA, comparing the abundance of ray individuals among life stages, pseudo-$F = 1.86$; df = 1.10; $p = 0.16$

assumption of normality of the model residuals was met (Shapiro–Wilk: $W = 0.91$, $p = 0.21$) (Fig. 4), indicating that higher salinity values result in higher species richness.

Pregnant females belonging to three species were captured with embryos in different development stages, indicating the use of the estuary during pregnancy (Table 1). However, accurate counting of pregnant females was challenging due to premature births induced by capture stress, potentially leading to neonate misclassification. Alongside the presence of neonates in the area, this may indicate the possible use of the region for parturition. Moreover, pregnant *H. guttatus* and *H. geijskesi* females were notably observed at the beginning of the dry season or high salinity period. During the period characterized by low monthly average salinity (13.70 and 18.80 ppt), only two pregnant *H. guttatus* were observed, contrasting with the remaining captures that took place in high salinity conditions ranging from 36.40 to

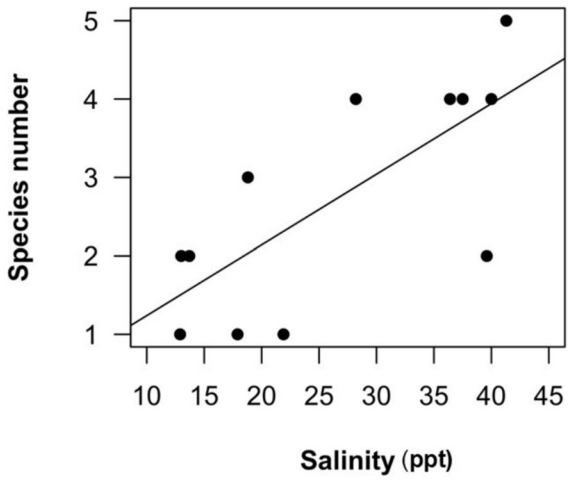

Fig. 4 Correlation between ray species richness and salinity (ppt) in the Camará River estuary. Statistics were performed by Pearson correlation, associating richness of ray species with salinity, $p = 0.006$; $r = 0.73$; $r^2 = 0.54$; $a = 0.34$ (− 1.36–2.04); $b = 0.90$ (0.03–0.15)

41.30 ppt. The size of pregnant *H. guttatus* varied between 612 to 1030 mm of disc width (DW), with recorded uterine fecundity ranging from 1 to 4 eggs or embryos in the left uterus. Generally, rays present a pair of uteruses in their reproductive system, although this can vary in some species. In the case of *H. guttatus*, only the left uterus is functional. This coincided with the presence of vitellogenic follicles exceeding 1.00 cm in diameter in the ovaries. In the case of *G.* aff. *micrura*, two pregnant females were documented during a high salinity period (37.50 and 41.30 ppt), measuring 463 and 520 mm DW and carrying both eggs and embryos in the uterus. Regarding *H. geijskesi*, a pregnant female measuring 930 mm DW was observed with an egg in the uterus at the onset of the most saline period, characterized by a monthly average salinity of 36.40 ppt.

Hypanus guttatus captures occurred year-round across varying salinity levels, ranging from 12.90 to 41.30 ppt (30.80 ± 10.87 ppt). Neonates and juvenile individuals comprised 66.7% of the total captures, with their prevalence extending through 75% of the monitoring period (Fig. 5). This prevalence was especially pronounced when average salinity values exceeded 20.00 ppt. Neonates were observed during periods marked by salinity fluctuations, ranging from 12.90 to 41.30 ppt (33.00 ± 9.19 ppt), with a noteworthy increase in their presence in high salinity conditions. Neonates exhibited disc widths spanning from 132 to 193 mm, indicating that the species birth size falls within this range. Juvenile individuals (except subadults), with disc widths ranging from 168 to 345 mm, were observed during high and low salinity periods, apparently supporting values ranging from 13.70 to 41.30 ppt (33.70 ± 10.90 ppt). Despite this, juveniles were most predominant in the most saline period. Adults were recorded during both salinity periods, displaying a broad tolerance of salinity variation. The sex ratio between males and females of *H. guttatus* specimens in the study region was 1:1.38 for all developmental stages ($\chi^2 = 0.11$; $p > 0.005$).

Gymnura aff. *micrura* individuals were observed during the high salinity period (38.90 ± 4.00 ppt; range 18.80–41.30 ppt). Neonates and juveniles constituted 75% of the total catches of this species, with

Table 1 Data on pregnant females and embryos, for individual animals, belonging to different ray species captured at the Camará River estuary. *Size data are not available

Species	Females (DW) (mm)	Embryos/ uterine eggs (*n*)	Embryos (DW) (mm)	Monthly salinity average (ppt)	Month
Hypanus guttatus	612	2	Uterine eggs	36.40	Jun
Hypanus guttatus	630	1	Uterine egg	37.50	Jul
Hypanus guttatus	755	4	115—118	36.40	Jun
Hypanus guttatus	835	2	61—67	13.70	Apr
Hypanus guttatus	860	1	70	37.50	Jul
Hypanus guttatus	903	3	Uterine eggs	39.60	Oct
Hypanus guttatus	1030	2	37—39	18.80	May
Gymnura aff. *micrura*	463	1	Uterine egg	37.50	Jul
Gymnura aff. *micrura*	520	2	Embryos*	41.30	Sep
Hypanus geijskesi	930	1	Uterine egg	36.40	Jun

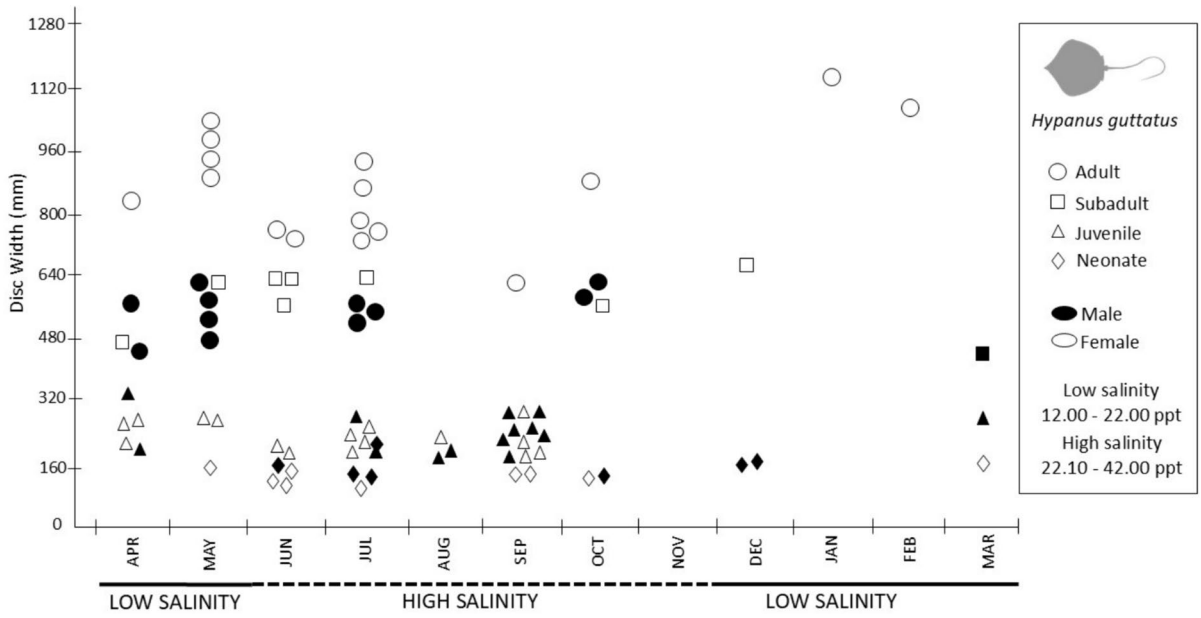

Fig. 5 Seasonal distribution of *Hypanus guttatus* at various developmental stages across salinity variations in the Camará River estuary. Diamonds represent the neonates; triangles, the juvenile individuals; squares, the subadult individuals; and circles, the adult individuals. Dark geometric figures represent male specimens, while white geometric figures represent female specimens. Below the *x*-axis, the solid line indicates the low salinity period, with this factor ranging from 12.00 to 22.00 ppt, while the dashed line denotes the high salinity period, with a range between 22.10 and 42.00 ppt

a progressive increase in immature individuals from May to September. Neonates measuring between 175 and 200 mm DW were found in waters with high and relatively stable salinity (38.50 ± 2.10 ppt; 36.40–41.30 ppt), while juveniles were observed during periods of large amplitude salinity values (38.90 ± 5.20 ppt; 18.80–41.30 ppt). One adult male was recorded at the salinity peak (41.30 ppt), whereas adult females were present during the high salinity period (38.90 ± 2.10 ppt; 36.40–41.30 ppt). The sex ratio between males and females was 1:2.03 ($\chi^2 = 0.01$; $p < 0.005$) (Fig. 6).

Concerning *H. geijskesi*, neonates were recorded exclusively during low salinity periods (13.40 ± 0.50 ppt; 13.00–13.70 ppt), averaging 215 mm in DW. Juveniles were observed in both salinity periods throughout the year, indicating their putative tolerance to salinity variations (25.20 ± 11.60 ppt; 13.00–40.00 ppt). Subadults were captured during the high salinity period (41.30 ppt). Adults of both sexes, including a pregnant female, were most abundant during the early high salinity period (33.90 ± 6.70 ppt; 18.80–36.40 ppt) (Table 1). One subadult female measured 657 mm DW, while the smallest adult female measured 820 mm DW, indicating a sexual maturation size within this DW range. Male subadults were not captured, and the smallest adult male measured 550 mm DW (Fig. 7). The sex ratio between males and females for this species was 1.33:1 ($\chi^2 = 0.16$; $p > 0.005$) for all developmental stages.

Styracura schmardae was recorded at various developmental stages, ranging from neonates to subadults. A 168 mm DW neonate was observed during a high salinity period (40.00 ppt), while all juveniles were sampled during the end of this period (28.20 ppt; all caught on the same day). Subadults were captured during the early high salinity period (37.20 ± 0.60 ppt; 36.40–41.30 ppt), with the largest individual comprising a subadult male measuring 934 mm DW (Fig. 8).

Immature *A. narinari*, *H. berthalutzae*, and *P. percellens* specimens were recorded during the high salinity period (35.30 ± 9.70 ppt; 28.20–41.30 ppt) (Fig. 9).

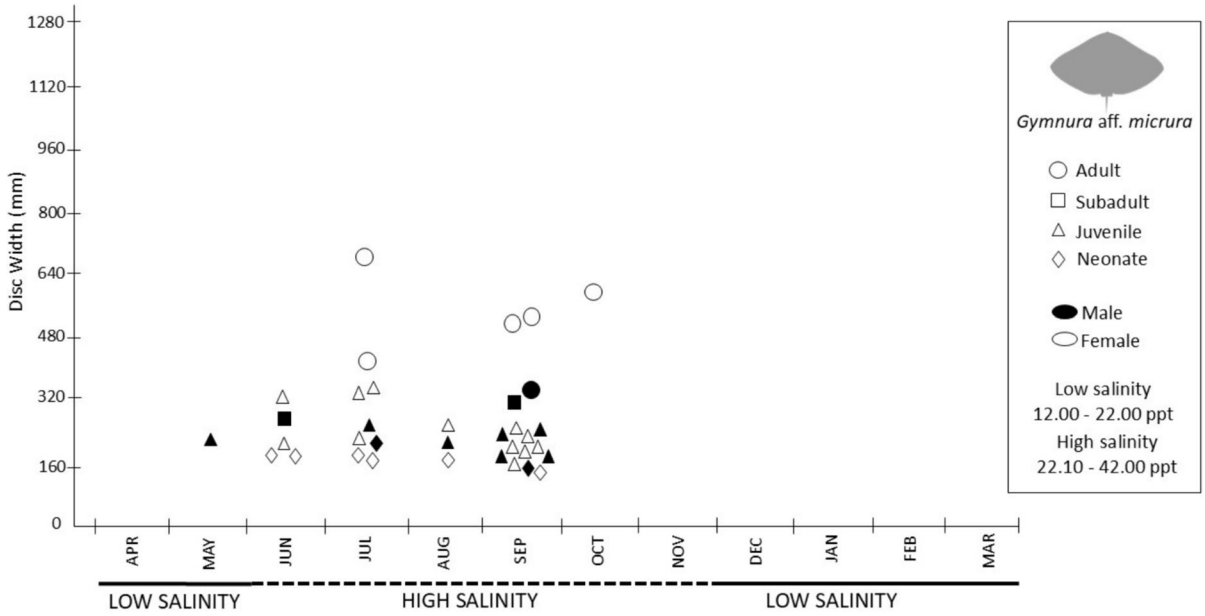

Fig. 6 Seasonal distribution of *Gymnura* aff. *micrura* at various developmental stages across salinity variations in the Camará River estuary. Diamonds represent the neonates; triangles, the juvenile individuals; squares, the subadult individuals; and circles, the adult individuals. Dark geometric figures represent male specimens, while white geometric figures represent female specimens. Below the *x*-axis, the solid line indicates the low salinity period, with this factor ranging from 12.00 to 22.00 ppt, while the dashed line denotes the high salinity period, with a range between 22.10 and 42.00 ppt

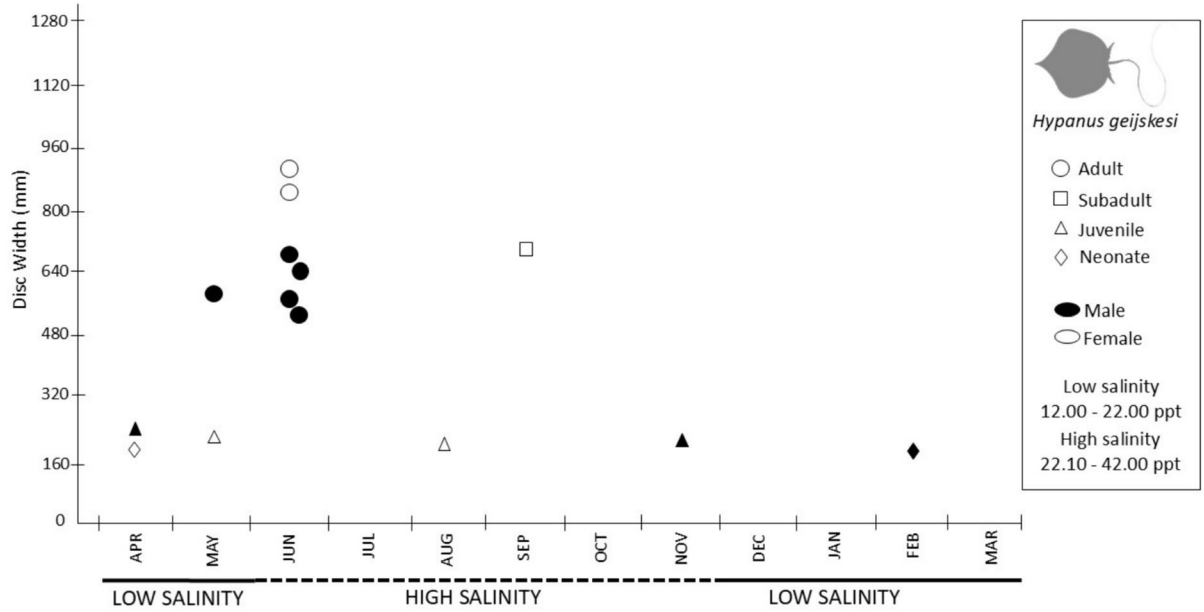

Fig. 7 Seasonal distribution of *Hypanus geijskesi* at various developmental stages across salinity variations in the Camará River estuary. Diamonds represent the neonates; triangles, the juvenile individuals; squares, the subadult individuals; and circles, the adult individuals. Dark geometric figures represent male specimens, while white geometric figures represent female specimens. Below the x-axis, the solid line indicates the low salinity period, with this factor ranging from 12.00 to 22.00 ppt, while the dashed line denotes the high salinity period, with a range between 22.10 and 42.00 ppt

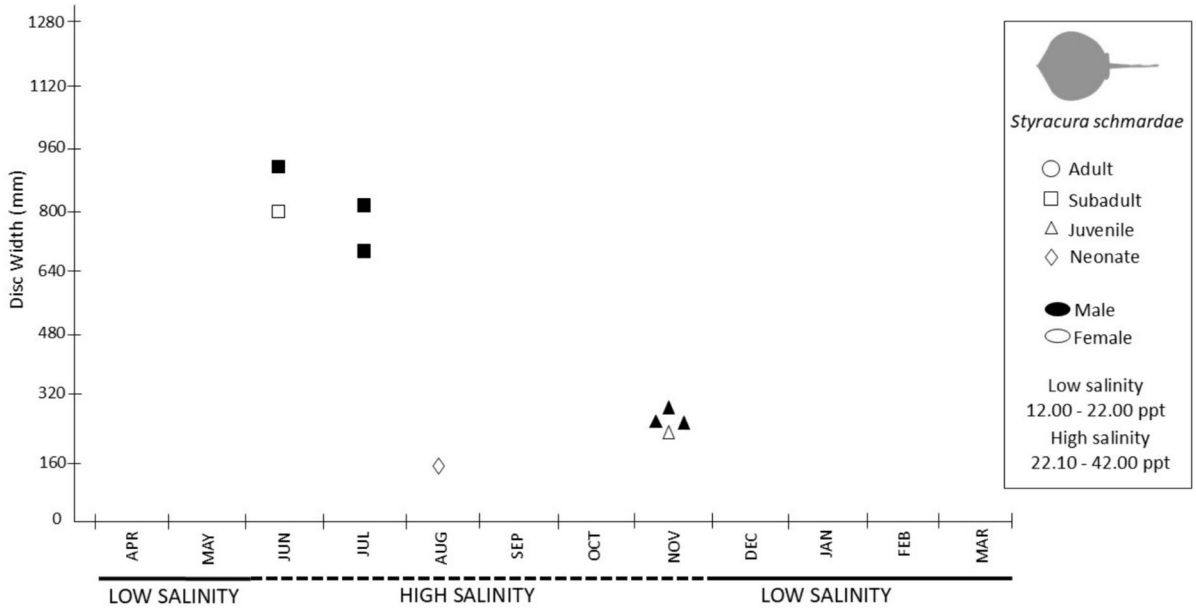

Fig. 8 Seasonal distribution of *Styracura schmardae* at various developmental stages across salinity variations in the Camará River estuary. Diamonds represent the neonates; triangles, the juvenile individuals; and squares, the subadult individuals. Dark geometric figures represent male specimens, while white geometric figures represent female specimens. Below the *x*-axis, the solid line indicates the low salinity period, with this factor ranging from 12.00 to 22.00 ppt, while the dashed line denotes the high salinity period, with a range between 22.10 and 42.00 ppt

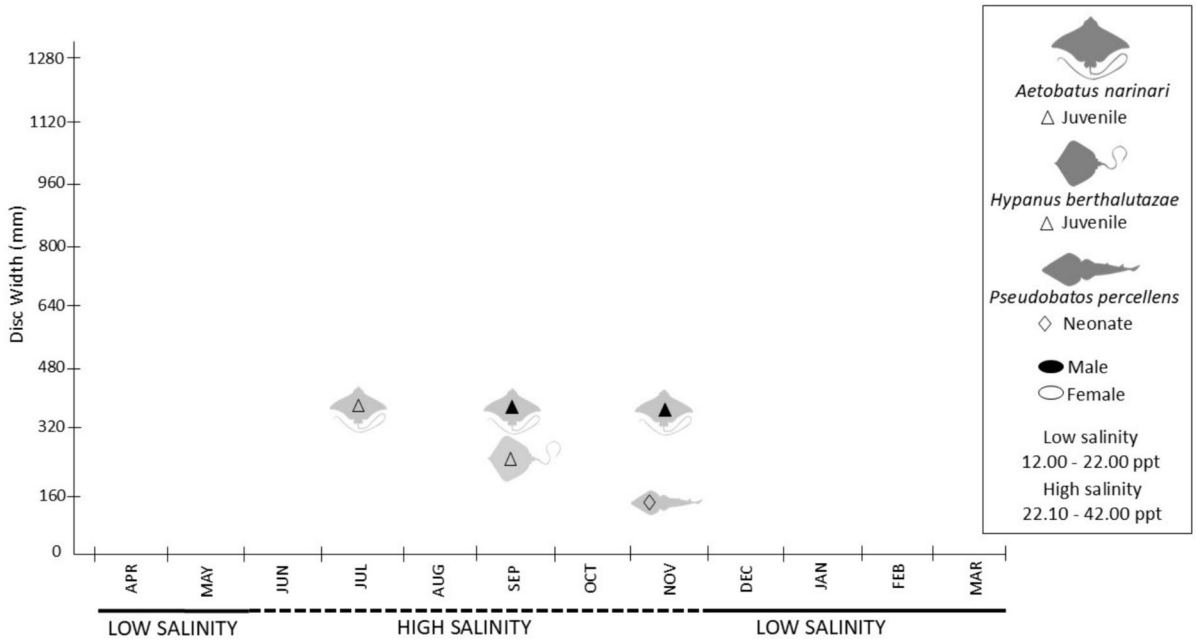

Fig. 9 Seasonal distribution of *Aetobatus narinari*, *Hypanus berthalutzae*, and *Pseudobatos percellens* at various developmental stages across salinity variations in the Camará River estuary. Diamonds represent the neonates, and triangles represent the juvenile individuals. Dark geometric figures represent male specimens, while white geometric figures represent female specimens. Below the *x*-axis, the solid line indicates the low salinity period, with this factor ranging from 12.00 to 22.00 ppt, while the dashed line denotes the high salinity period, with a range between 22.10 and 42.00 ppt

Discussion

Estuaries along the BAC stand out from other Neotropical Atlantic estuaries, primarily due to their substantial discharge volume (Filizola et al. 2025). This creates a complex environment characterized by high productivity and seasonal variability, requiring that local species develop strategies and adaptations to cope with the imposed physiological stress (De Almeida-Val et al. 2005; Val and Wood 2022). Previous research in the BAC region has linked salinity variations to the speciation and endemicity of several marine taxa, including elasmobranchs (Tourinho et al. 2012; Sales et al. 2017; Wosnick et al. 2019a; Rodrigues-Filho et al. 2023; Gales et al. 2024). Within this context, this study investigated the habitat use of ray species in a typical BAC estuary, exploring the influence of salinity variation. According to Grant et al. (2019), our findings suggest that *H. guttatus* is not an euryhaline generalist species, as suggested in the review by Kyne and Lucifora (2022). Instead, this species seems to be an estuarine generalist species, similar to its congener *H. geijskesi*. On the other hand, *G.* aff. *micrura* seems to be a non-marine transient species and only approaches the coast during the high saline periods, potentially to give birth. *Styracura schmardae*, *P. percellens*, *A. narinari*, and *H. berthalutzae* also approach the coast during high saline periods.

A prominent factor for biological processes

The salinity variations across the two Amazon seasons (rainy and dry seasons) seem to play an important role in the movements of the studied species, providing a broad view on their specific preferred times for each developmental stage. While acknowledging the multidimensional factors influencing the distribution and abundance of elasmobranchs in each region, especially in the diverse and resource-rich BAC environment, it is well known that seasonal temperature variability in tropical settings is minimal (Sousa et al. 2013; De Freitas et al. 2020). This highlights salinity as an important driving force of temporal habitat use in the study region, due to the substantial freshwater discharge from various river basins and high rainfall indices (Camargo and Isaac2003; Sousa et al. 2013).

As a result, the Camará River estuary salinity levels undergo a significant decrease during the rainy season, while other factors such as temperature, dissolved oxygen, and pH exhibit minimal variations, following the pattern from the BAC region to the surface waters of the Amazon plume (Sousa et al. 2013). In response to seasonal salinity and freshwater flow variations, some previously studied estuarine elasmobranchs (e.g., *Glyphis glyphis* (Müller & Henle, 1839) and *Carcharhinus leucas* (Valenciennes in Müller & Henle, 1839)) have displayed movements, such as migrations, apparently in search of saline gradients that would reduce their energetic costs (Lyon et al. 2017; Constance et al. 2023). This reinforces the hypothesis that these animals use the behavior of seeking optimal environments to reduce the metabolic demands associated with physiological processes such as osmoregulation. In this way, the animals may direct this energy towards their growth, reducing their times in size classes in which mortality rates are higher (Froeschke et al. 2010). Thus, osmoregulation capacity emerges as a critical determinant for the presence of rays in the BAC.

A key region for reproduction

The dominant presence of neonates and juveniles, constituting approximately 70% of the total rays recorded captures year-round, is particularly noteworthy. This aligns with previous propositions for the BAC as a nursery for sharks and rays (Almeida et al. 2000; Feitosa et al. 2020, 2021). Additionally, the presence of mature and gravid females with embryos at various developmental stages indicates the importance of the study area for the life cycle of various elasmobranch species. It is possible that the number of pregnant females is underestimated, as the count may have been impaired due to premature births induced by capture stress (Adams et al. 2018; Wosnick et al. 2019b), identifying them as possible neonates given that they were at term. While definitive determination of the area as a pupping or nursery ground remains challenging due to the lack of long-term monitoring data and resources, the prevalence of neonates and juveniles, as well as the presence of pregnant females, is evidence of the importance of the Camará River estuary for the reproduction of coastal rays. This holds scientific significance, as key regions for critical biological processes such as reproduction emerge as focal points for strategic conservation planning (Chin et al., 2023). In this sense, the

data derived from the present study contribute further empirical support to position the BAC region as integral for the global conservation initiatives targeting the ray species recorded here.

Habitat use of the species recorded in the BAC

The rays species recorded at the Camará River estuary exhibited different habitat uses throughout the year, correlating to seasonal salinity variations in the region, revealing the ability of some species to use this estuarine environment even during the low salinity period. Among the identified species in the estuary, *H. guttatus* and *H. geijskesi* exhibit a noteworthy adaptability to a broad range of salinities during different seasons but do not seem to use freshwater rivers during part of their life cycles (usually as nurseries). Thus, both appear to fit into the estuarine generalist species category according to Grant et al. (2019).

Hypanus guttatus exhibits a strong association with estuarine areas (Feitosa et al. 2021; Queiroz et al. 2024), which may explain its local abundance (Camargo and Isaac 2003; Rodrigues-Filho et al. 2020), as the Camará River estuary is located within the second largest extension of mangrove ecosystems in the world (Souza-Filho 2005). These environments are strongly influenced by tides, leading to continuous changes in abiotic conditions, including salinity regimes (Camargo and Isaac 2003). Therefore, to capitalize on the advantages of more sheltered areas, species must cope with highly variable environmental conditions. Previously, *H. guttatus* was categorized as a euryhaline generalist (Grant et al. 2019), with some uncertainty, as it has never been recorded in a strictly freshwater habitat (Kyne and Lucifora 2022). However, the evidence presented herein indicates that neonate and young *H. guttatus* individuals occur mainly in high salinity, not in freshwater.

In Northeastern Brazil, trace element concentrations in vertebrae also indicate that pups use high-salinity environments during their first year of life (Feitosa et al. 2021), later moving to low-salinity estuarine areas (Queiroz et al. 2023; Queiroz et al. 2024). As a result, this species plays an important role in the energy flow between these areas in the Southwest Atlantic Ocean with hypoxic zones, such as mangroves in this case (Queiroz et al. 2024). Therefore, *H. guttatus* appears to fit the criteria of estuarine generalist species, as it inhabits both estuarine and marine environments, does not withstand prolonged exposure to freshwater, and uses estuarine environments for certain life stages, such as parturition and/or as nursery areas (Grant et al. 2019).

Catch composition records for offshore shrimp trawls on the northern Brazilian coast indicate that *H. guttatus* comprised 90% of the catches and *H. geijskesi*, 10%, constituting the main species recorded in research cruises (Holanda et al. 2008). Although the endemic *H. geijskesi* is a rarer species in the region's fisheries, they inhabit the same type of environment, and a similar tolerance pattern to low salinity was noted for *H. guttatus*, indicating that this species may also benefit from coastal and sheltered areas within the BAC, even under more extreme saline regimes. However, *H. geijskesi* neonates occurred at low salinity in the Camará River estuary, indicating a tolerance of this life stage to less saline waters. In contrast, the presence of mature individuals of both sexes recorded mainly during the beginning of the dry season may be an indication of this species approaching the coast, in shallow high salinity waters, for mating. Due to the species' physiological capacity to penetrate the lower salinity waters of the Camará River estuary for prolonged periods, *H. geijskesi* can be considered an estuarine generalist species.

Gymnura aff. *micrura*, although prominently abundant in the studied estuary, was limited to the high salinity period. This pattern observed in BAC suggests that the species operates within a narrow window of physiological tolerance compared to the aforementioned species. It is also plausible that *G.* aff. *micrura* employs behavioral strategies, such as swimming to other locations with preferred environmental conditions during low salinity periods to evade the physiological challenges posed by low salinity stress (Schlaff et al. 2014). This strategy was not, however, observed for the species in Northeastern Brazil, where *G.* aff. *micrura* was captured throughout the year, and noted as employing the coast of Caiçara do Norte for reproduction (Yokota and Lessa 2006; Yokota et al. 2012). Salinity variations are very small near the shelf break in this region, between 36.00 and 37.00 ppt (Castro and Miranda 1998), and rays do not need to move to other locations in search of optimal environments. This reinforces the role of salinity as a driver for the movement of populations of species that inhabit the BAC and appears to place *G.* aff.

micrura in the non-marine transient category. In contrast to the observed sex ratios in the other analyzed species, *G.* aff. *micrura* exhibited a significantly different sex ratio of two females for each male. A possible explanation would be that females approach the coast to give birth while males remain in greater depth areas and, thus, are not captured by fishing pens located in the shallow waters of the tidal flat of the Camará River estuary. However, in Caiçara do Norte (Northeastern Brazil), *G.* aff. *micrura* catches reveal a greater number of adult males in the beach trawl fishery, indicating that males can indeed approach the coast (Yokota et al. 2012). Thus, it is plausible that the observed sex ratio for the species results from a complex interaction of multiple factors, including the influence of salinity on male physiology and metabolism. Further investigations are, therefore, required to determine the mechanisms contributing to the sex ratio dynamics of *G.* aff. *micrura* in the studied region and the potential diverse influences shaping its demographic composition.

Styracura schmardae occurs from the Gulf of Campeche, Mexico, to the state of Ceará in Brazil, and in the Greater and the Lesser Antilles and the Bahamas (Dulvy et al. 2021). It, however, stands out as one of the rarest species east of the Amazon River mouth, with isolated records off northeastern Brazil (Nunes and Nunes 2020; Sales et al. 2020). This species with benthic habits appears to have occupied very specific niches in the region's estuaries, where it is found on sandy or muddy bottoms (Nunes and Nunes 2020; Dulvy et al. 2021). Moreover, the capture of a free-swimming individual with an umbilical scar suggests that *S. schmardae* may use the region for parturition, at least during the high salinity period. This individual, the smallest specimen ever recorded for the species, is cataloged in the ichthyological collection of the Federal University of Paraíba (UFPB 7548, 168 mm DW). Although the size at maturity for this species has been estimated at 850 mm DW based on specimens from the Bahamas (O'Shea et al. 2021), field analyses at Camará River estuary recorded an immature male specimen over 900 mm DW. Thus, the species needs to be monitored at the BAC to better understand its life history. Kyne and Lucifora (2022) state that rays of the subfamily Styracurinae, which include *S. schmardae* and *Styracura pacifica* (Beebe & Tee-Van, 1941), are neither obligatory freshwater nor euryhaline generalist species. Despite being considered a marine species (Kyne and Lucifora 2022) and given its presence in such specific BAC habitats (Nunes and Nunes 2020), we strongly suggest that monitoring during the low salinity period be continued to verify the possibility of *S. schmardae* fitting into the estuarine generalist category.

Regarding the other evaluated species, the data indicate that they are less tolerant to low salinity than the aforementioned species, as juvenile *A. narinari*, *H. berthalutzae* individuals, and a single neonate *P. percellens* were all captured at high salinity.

Conservation and the climate change challenges

Research efforts should also aim to inform evidence-based management strategies that are paramount in ensuring the conservation of ray populations within the BAC. Firstly, given the similarity in temporal habitat use across all life stages for *H. guttatus* and *H. geijskesi*, it is plausible to infer that conservation measures beneficial to one will likely extend their positive impacts to the other. Considering the high level of endemism and the risk of extinction faced by *H. geijskesi*, currently categorized as Critically Endangered by the International Union for Nature Conservation (IUCN Red List) (Pollom et al. 2020a), conservation strategies focused on preserving the study area and its unique environmental characteristics can yield benefits not only for this species but also for *H. guttatus*, categorized as Near Threatened (Carlson et al. 2020). Even within this category, *H. guttatus* is experiencing intense fishing pressure in the region (Marceniuk et al. 2019), requiring additional management measures. On the other hand, conservation measures based on spatial planning, beneficial for the previously mentioned species, may not necessarily apply to *G.* aff. *micrura*, as this species presents a different behavioral strategy apparently caused by lower tolerance to the local low salinity.

This adaptive plasticity of some species across fluctuating salinity gradients also holds conservation implications (Martin 2005; Constance et al. 2023). In the face of ongoing climate changes, understanding both climate-induced shifts in salinity patterns and adaptive elasmobranch strategies to cope with these shifts becomes paramount, especially for freshwater/estuarine and coastal/inshore sharks and rays (Chin et al. 2010). As an example, some of the predicted climate alterations will influence saltwater circulation

patterns and transport within coastal environments, modifying the hydrodynamics of estuaries and the recruitment of fish species dependent on these areas (Kennedy et al. 2002). In addition, changes in precipitation and runoff can alter coastal and estuarine salinity gradients and, consequently, long-term salinity patterns (Wiseman 1986; Röthig et al. 2023). Thus, ecological communities will need to adapt to new high or low salinity conditions (Kennedy et al. 2002). Such insights contribute to the predictive modeling of elasmobranch responses to changing environmental conditions and allow for conservation measures focused on preserving these species in an ever-dynamic aquatic landscape. In this sense, ecological models can demonstrate how important salinity is for characterizing sites with suitable environmental conditions for elasmobranchs' critical life history stages (Santana et al. 2025).

Amidst the evolving environmental scenarios, including the impacts of climate change and anomalous regimes of both El Niño and La Niña, the salinity dynamics at the BAC faces direct consequences from intense drought periods in northern Brazil (Kay et al. 2022). Conspicuously, in another BAC estuary, years marked by exceptionally low discharge from the Pindaré River resulting from reduced precipitation rates led to the intrusion of the saline plume reaching approximately 95 km upstream towards smaller basins (Yauri and Barbieri 2022). Subsequently, an unprecedented event occurred in Lake Viana, 110 km above the mouth of the Pindaré River, during the dry season, in which a *Carcharhinus oxyrhynchus* (Valenciennes, 1839) shark individual, an endemic and critically endangered species (Pollom et al. 2020b), was recorded in a freshwater system, deviating from what is considered its natural habitat (Feitosa et al. 2019). This unique event raises the possibility that other estuarine species may sporadically venture into areas with lower salinity waters during the dry season and under tidal influence. While the life cycle of euryhaline generalist species includes phases in brackish or even freshwater areas (e.g., *Carcharhinus leucas* (Valenciennes, 1839)) (Heupel and Simpfendorfer 2008; Feitosa et al. 2016; Grant et al. 2019), the presence of the *C. oxyrhynchus* in obligatory freshwater systems is uncommon (Feitosa et al. 2019). This species appears to be an estuarine generalist species that inhabits shallow and turbid estuarine waters (Lessa et al. 1999; Feitosa et al. 2019) though it cannot withstand prolonged exposure in freshwater (Grant et al. 2019). Thus, monitoring the presence of near-estuarine species in the region, particularly during severe El Niño periods and events linked to climate change, is paramount given the substantial impact these occurrences have on the Amazon region and its biodiversity conservation (Kay et al. 2022; Lian et al. 2023).

Conclusion

The comprehensive analysis of seven ray species in this study indicates the importance of the Camará River estuary for neonates, juveniles, and mature and pregnant females. These findings provide compelling evidence that the area serves as an important habitat during the early stages of their life cycles. None of the species fits into the euryhaline generalist category, as none presented the capability of prolonged exposure to freshwater environments. Based on the obtained data, *H. guttatus* and *H. geijskesi* were categorized as estuarine generalists, while *Gymnura* aff. *micrura* fits into the non-marine transient species category. Concerning *S. schmardae*, *A. narinari*, *H. berthalutzae*, and *P. percellens*, more data are required to confirm their respective categories.

This study also highlights the importance of ongoing ecological and fisheries monitoring initiatives targeting elasmobranch species within the BAC. These investigations play an important role in systematically monitoring temporal habitat use among ray populations, particularly considering the susceptibility of less tolerant species to environmental fluctuations and anthropogenic influences. The identification of salinity as a key driver influencing the dynamics of the temporal distribution of ray species within the studied region emphasizes the need for future studies to delve deeper into understanding how climate change and human development might adversely impact the presence of elasmobranchs and the temporal use of this critical region for elasmobranch conservation on a global scale. Furthermore, the insufficiently understood biological characteristics of the species investigated in the present study further emphasize the urgency for future studies investigating other biological features that may better explain species tolerance or susceptibility to the local dynamic environmental features.

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Author contribution All authors contributed to the study conception and design and intellectual following revisions. Material and data collection and their initial analysis were performed by Ana Rita Onodera Palmeira-Nunes. The first draft of the manuscript was written by Ana Rita Onodera Palmeira-Nunes and Jorge Luiz Silva Nunes. Data analysis and confection of the figures and tables were conducted and prepared by Ana Rita Onodera Palmeira-Nunes, Jorge Luiz Silva Nunes, and Jamerson Aguiar Santos. The initial translation of the manuscript and later adjustments were made by Natascha Wosnick. The English revision was performed by Rachel Ann Hauser Davis and Ricardo de Souza Rosa. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability The following information is supplied regarding data availability: The data are available in the figures and tables of the manuscript and supplementary information.

Declarations

Animal ethics Not applicable. All sampled animals were already dead at the time of sampling and were donated by fishers. According to the Brazilian National Council for the Control of Animal Experimentation, an Animal Use Ethics Committee authorization is not required in this case.

Conflict of interest Dr. Ricardo Rosa is on the Editorial Board of Environmental Biology of Fishes and is a Guest Editor of this special issue, but he was not involved in the peer review of this article and had no access to information regarding its peer review.

References

Adams KR, Fetterplace LC, Davis AR, Taylor MD, Knott NA (2018) Sharks, rays and abortion: the prevalence of capture-induced parturition in elasmobranchs. Biol Conserv 217:11–27. https://doi.org/10.1016/j.biocon.2017.10.010

Almeida ZS, Nunes JS, Costa CL (2000) Presencia de *Urotrygon microphthalmum* (Elasmobranchii: Urolophidae) en aguas bajas de Maranhão (Brasil) y notas sobre su biologia. Bol Investig Mar Costeras 29:67–72

ANA Agência Nacional de Águas (2020) Rio Tocantins. https://www.ana.gov.br/sala-de-situacao/tocantins/saiba-mais-tocantins/rio-doce-saiba-mais. Accessed 28 March 2020

Ballantyne JS (2016) Some of the most interesting things we know, and don't know, about the biochemistry and physiology of elasmobranch fishes (sharks, skates and rays). Comp Biochem Physiol b: Biochem Mol Biol 199:21–28. https://doi.org/10.1016/j.cbpb.2016.03.005

Ballantyne JS, Robinson JW (2010) Freshwater elasmobranchs: a review of their physiology and biochemistry. J Comp Physiol B 180(4):475–493. https://doi.org/10.1007/s00360-010-0447-0

Ballantyne JS, Fraser DI (2012) Euryhaline elasmobranchs. Fish Physiol Biochem 32:125–198. https://doi.org/10.1016/B978-0-12-396951-4.00004-9

Bangley C, Paramore L, Shiffman D, Rulifson R (2018) Increased abundance and nursery habitat use of the bull shark (*Carcharhinus leucas*) in response to a changing environment in a warm-temperate estuary. Sci Rep 8:6018. https://doi.org/10.1038/s41598-018-24510-z

Bezerra MOM, Freitas PP, Baltazar LRS, Rollnic M (2013) Estuarine processes in macro-tides of Amazon estuaries: a study of hydrodynamics and hydrometeorology in the Marajó Bay (Pará-Brazil). J Coast Res 65:1176–1181

Bigelow HB, Schroeder WC (1953) Fishes of the Western North Atlantic. Sawfishes, guitarfishes, skates and rays. Sears Foundation for Marine Research 1(2):1–558

Callihan J, Cowan J, Harbison M (2015) Sex-specific movement response of an estuarine sciaenid (*Cynoscion nebulosus*) to freshets. Estuar Coast 38:1492–1504. https://doi.org/10.1007/s12237-014-9889-z

Camargo M, Isaac VJ (2003) Ictiofauna estuarina. In: Fernandes MEB (ed) Os manguezais da Costa Norte Brasileira. Fundação Rio Bacanga, São Luís, pp 105–142

Carlson J, Charvet P, Blanco-Parra MP, Briones Bell-lloch A, Cardenosa D, Derrick D, Espinoza E, Marcante F, Morales-Saldaña JM, Naranjo-Elizondo B, Schneider EVC, Simpson NJ (2020). *Hypanus guttatus*. The IUCN Red List of Threatened Species 2020: e.T44592A104125629. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T44592A104125629.en. Accessed on 07 February 2025

Castro BM, Miranda LB (1998) Physical oceanography of the Western Atlantic continental shelf located between 4 N and 34 S. In: Robinson RA, Brink KH (eds) The sea. John Wiley & Sons, New York, pp 209–251

Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great

Barrier Reef. Glob Change Biol 16(7):1936–1953. https://doi.org/10.1111/j.1365-2486.2009.02128.x

Chin A, Molloy FJ, Cameron D, Day JC, Cramp J, Gerhardt KL et al (2023) Conceptual frameworks and key questions for assessing the contribution of marine protected areas to shark and ray conservation. Conserv Biol 37(1):e13917. https://doi.org/10.1111/cobi.13917

Coles VJ, Brooks MT, Hopkins J, Stukel MR, Yager PL, Hood RR (2013) The pathways and properties of the Amazon River plume in the tropical North Atlantic Ocean. J Geophys Res: Oceans 118(12):6894–6913 https://doi.org/10.1002/2013JC008981

Compagno LJV, Cook SF (1995) The exploitation and conservation of freshwater elasmobranchs: status of taxa and prospects for the future. J Aquac Aquat Sci 7:62–90

Compagno L (2002) Freshwater and estuarine elasmobranch surveys in the Indo-Pacific region: threats, distribution and speciation. In: Fowler S, Reed T, Dipper F (eds) Elasmobranch Biodiversity, conservation and management: proceedings of the international seminar and workshop, Sabah, Malaysia, July, 1997. Information Press, Oxford, UK, pp 168–180

Conrath C (2005) Reproductive biology. In: Musick J, Bonfil R (eds) Management techniques for elasmobranch fisheries. FAO, Fisheries Technical Paper 474, pp 1–251

Constance JM, Garcia EA, Pillans RD et al (2023) A review of the life history and ecology of euryhaline and estuarine sharks and rays. Rev Fish Biol Fish 34:65–89. https://doi.org/10.1007/s11160-023-09807-1

de Almeida-Val VMF, Chippari-Gomes AR, Lopes NP (2005) Metabolic and physiological adjustments to low oxygen and high temperature in fishes of the Amazon. Fish Physiol 21:443–500. https://doi.org/10.1016/S1546-5098(05)21010-5

de Freitas Assad LP, Toste R, Böck CS, Nehme DM, Sancho L, Soares AE, Landau L (2020) Ocean climatology at Brazilian Equatorial Margin: a numerical approach. J Comput Sci 101159. https://doi.org/10.1016/j.jocs.2020.101159

de Freitas PP, Cirano M, Teixeira CEP et al (2024) Pathways of surface oceanic water intrusion into the Amazon continental shelf. Ocean Dyn 74:321–334. https://doi.org/10.1007/s10236-024-01606-x

Dulvy NK, Charvet P, Pollom R, Avalos C, Blanco-Parra MP, Briones Bell-lloch, A, Cardenosa D, Derrick D, Espinoza E, Mejía-Falla PA, Morales-Saldaña JM, Naranjo-Elizondo B, Navia AF, Simpson NJ, Schneider EVC (2021) *Styracura schmardae*. The IUCN Red List of Threatened Species 2021: e.T60161A3090840. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T60161A3090840.en. Accessed on 10 February 2025

Dwyer R, Campbell H, Cramp R, Burke C, Micheli-Campbell M, Pillans R, Lyon B, Franklin C (2020) Niche partitioning between river shark species is driven by seasonal fluctuations in environmental salinity. Funct Ecol 34:2170–2185. https://doi.org/10.1111/1365-2435.13626

El-Robrini M, Ranieiri LA, Silva PVM, Guerreiro JS, Alves MAM, El-Robrini MHS, Fenzl N (2018) Pará. In: Mueher D (org) Programa da erosão costeira no Brasil (recurso eletrônico). Ministério do Meio Ambiente, Secretaria de Recursos Hídricos e Qualidade Ambiental, Departamento de Gestão Ambiental Territorial, Brasília

Feitosa LM, Martins APB, Nunes JLS (2016) New record of *Carcharhinus leucas* (Valenciennes, 1839) in an equatorial river system. Mar Biodivers Rec 9:1–4. https://doi.org/10.1186/s41200-016-0094-6

Feitosa LM, Martins APB, Lessa RPT, Barbieri R, Nunes JLS (2019) Daggernose shark: an elusive species from Northern South America. Fisheries 1:4. https://doi.org/10.1002/fsh.10205

Feitosa LM, Dressler V, Lessa RP (2020) Habitat use patterns and identification of essential habitat for an endangered coastal shark with vertebrae microchemistry: The case study of *Carcharhinus porosus*. Front Mar Sci 7:501217. https://doi.org/10.3389/fmars.2020.00125

Feitosa LM, Queiroz APN, Labonne M, Dressler VL, Lessa RP (2021) Habitat use and nursery evaluation for the longnose stingray *Hypanus guttatus* (Bloch and Schneider, 1801) using vertebral microchemistry. J Fish Biol https://doi.org/10.1111/jfb.14858

Filizola N, Marinho R, Freitas C, Ribas C, Zuanon J, Fearnside P, Moreira-Turcq P (2025) Amazonas. In: Graça MAS, Callisto M, de Mello FT, Rodríguez-Olarte D. Rivers of South America. Elsevier, pp 213–237. https://doi.org/10.1016/B978-0-12-823429-7.00004-5

Franco A, Santos L (2018) Habitat-dependent responses of tropical fish assemblages to environmental variables in a marine-estuarine transitional system. Estuar Coast Shelf Sci 211:110–117. https://doi.org/10.1016/J.ECSS.2018.02.003

Froeschke JT, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279–292. https://doi.org/10.3354/meps08546

Gales SM, Parsons KT, Biesack EE, Ready J, Siccha-Ramirez R, Rosa LC, Rosa R, Rotundo MM, Bills R, Rodrigues AES, Rodrigues-Filho LFS, McDowell J, Sales JBL (2024) Almost half of the *Gymnura* van Hasselt, 1823 species are unknown: phylogeographic inference as scissors for cutting the hidden Gordian knot and clarify their conservation status. J Syst Evol 62(4):715–738. https://doi.org/10.1111/jse.13027

Geyer R, Beardsley R, Candela J, Castro B, Legekis R, Lentz S et al. (1991) The physical oceanography of the Amazon outflow. Oceanography 4(1):8–14. https://www.jstor.org/stable/43924556

Geyer WR, Beardsley RC, Lentz SJ, Candela J, Limeburner R, Johns WE, Castro BM, Soares ID (1996) Physical oceanography of the Amazon shelf. Cont Shelf Res 16(5–6):575–616. https://doi.org/10.1016/0278-4343(95)00051-8

Gleiss A, Potvin J, Keleher J, Whitty J, Morgan D, Goldbogen J (2015) Mechanical challenges to freshwater residency in sharks and rays. J Exp Biol 218(7):1099–1110. https://doi.org/10.1242/jeb.114868

Grant MI, Kyne PM, Simpfendorfer CA, White WT, Chin A (2019) Categorising use patterns of non-marine environments by elasmobranchs and a review of their extinction risk. Rev Fish Biol Fish 29:689–710. https://doi.org/10.1007/s11160-019-09576-w

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277–289. https://doi.org/10.3354/ab00030

Heupel M, Simpfendorfer C (2014) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. Mar Ecol Prog Ser 496:47–57. https://doi.org/10.3354/meps10529

Holanda FCAF, Santos FJS, Asano-Filho M (2008) Analysis of distribution and abundance of the stingrays *Dasyatis geijskesi* and *Dasyatis guttata*, caught with fish trawlnets in experimental fisheries off northern Brazil. Arq Ciên Mar 41(2):95–100

ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade) (2018) Atlas dos manguezais do Brasil. Instituto Chico Mendes de Conservação da Biodiversidade, Brasília

Janech M, Gefroh H, Cwengros E, Sulikowski J, Ploth D, Fitzgibbon W (2008) Cloning of urea transporters from the kidneys of two batoid elasmobranchs: evidence for a common elasmobranch urea transporter isoform. Mar Biol 153:1173–1179. https://doi.org/10.1007/s00227-007-0889-4

Kay G, Dunstone NJ, Smith DM, Betts RA, Cunningham C, Scaife AA (2022) Assessing the chance of unprecedented dry conditions over North Brazil during El Niño events. Environ Res Lett 17(6):064016. https://doi.org/10.1088/1748-9326/ac6df9

Kennedy VS, Twilley RR, Kleypas JA, Cowan Jr JH, Hare SR (2002) Coastal and marine ecosystems & global climate change. Pew Center on Global Climate Change

Khlebovich V (1969) Aspects of animal evolution related to critical salinity and internal state. Mar Biol 2:338–345. https://doi.org/10.1007/BF00355713

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Mar Ecol Prog Ser 425:233–246. https://doi.org/10.3354/meps09006

Krumme U, Giarrizzo T, Pereira R, Jesus AJS, Schaub C, Saint-Paul U (2014) Airborne synthetic-aperture radar (SAR) imaging to help assess impacts of stationary fishing gear on the north Brazilian mangrove coast. ICES J Mar Sci 72(3):939–951. https://doi.org/10.1093/icesjms/fsu188

Klimley AP (2013) The biology of sharks and rays. The University of Chicago Press, Chicago

Kyne PM, Lucifora LO (2022) Freshwater and euryhaline elasmobranchs. In Carrier JC, Simpfendorfer CA, Heithaus MR, Yopak KE (eds) Biology of sharks and their relatives. CRC Press, pp 567–602. https://doi.org/10.1201/9781003262190

Last P (2002) Freshwater and estuarine elasmobranchs of Australia. In: Fowler S, Reed T, Dipper F (eds) Elasmobranch biodiversity, conservation and management: proceedings of the international seminar and workshop. Sabah, Malaysia, July, 1997. Information Press, Oxford, UK, pp 185–193

Last P, White W, Carvalho M, Séret B, Stehmann M, Naylor G (2016) Rays of the world. CSIRO, Australia

Lessa R, Batista V, Almeida Z (1999) Occurrence and biology of the daggernose shark *Isogomphodon oxyrhynchus* (Chondrichthyes: Carcharhinidae) off the Maranhão coast (Brazil). Bull Mar Sci 64(1):115–128

Lian T, Wang J, Chen D, Liu T, Wang D (2023) A strong 2023/24 El Niño is staged by Tropical Pacific Ocean heat content buildup. Ocean-Land-Atmos Res 2:0011. https://spj.science.org/doi/full/https://doi.org/10.34133/olar.0011

Lofthus AJ, Beach-Mehrotra M, Fisher MR, Wozniak JR, Matich P (2024) Factors influencing the nursery dynamics of bull sharks *Carcharhinus leucas* in two estuaries along the Texas coast. Mar Ecol Prog Ser 728:43–58. https://doi.org/10.3354/meps14495

Lyon BJ, Dwyer RG, Pillans RD, Campbell HA, Franklin CE (2017) Distribution, seasonal movements and habitat utilization of an endangered shark, *Glyphis glyphis*, from northern Australia. Mar Ecol Prog Ser 573:203–213. https://doi.org/10.3354/meps12200

Marceniuk AP, Barthem RB, Wosiacki WB, de Macedo Klautau AGC, Junior TV, Rotundo MM et al. (2019) Sharks and batoids (Subclass Elasmobranchii) caught in the industrial fisheries off the Brazilian North coast. Rev Nordestina Biol 27(1) https://orcid.org/0000-0003-4286-0482

Marengo JA (2006) On the hydrological cycle of the Amazon Basin: a historical review and current state-of-the-art. Rev Bras Meteorol 21(3):1–19

Martin RA (2005) Conservation of freshwater and euryhaline elasmobranchs: a review. J Mar Biol Assoc UK 85(5):049–1074. https://doi.org/10.1017/S0025315405012105

Molinas E, Vinzon SB, Vilela CPX, Gallo MN (2014) Structure and position of the bottom salinity front in the Amazon estuary. Ocean Dyn 64:1583–1599. https://doi.org/10.1007/s10236-014-0763-0

Moura RL, Amado-Filho GM, Moraes FC, Brasileiro PS et al (2016) An extensive reef system at the Amazon River mouth. Sci Adv 2(4):e1501252. https://doi.org/10.1126/sciadv.1501252

Nunes AROP, Nunes JLS (2020) The mystery of *Styracura schmardae* stingrays from the Brazilian Amazon coast. Examines Mar Biol Oceanogr 3(2). https://crimsonpublishers.com/eimbo/pdf/EIMBO.000564.pdf

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) Vegan: community ecology package. R package version 2.6–4. https://CRAN.R-project.org/package=vegan

O'Shea OR, Van Leeuwen TE, Brien DO, Arrowsmith L, McCalman R, Griffiths M, Exton DA (2021) Evidence and description of a nursery habitat for the recently reclassified stingray *Styracura schmardae* from The Bahamas. Mar Ecol Prog Ser 660:141–151. https://doi.org/10.3354/meps13589

Osgood G, White E, Baum J (2021) Effects of climate-change driven gradual and acute temperature changes on shark and ray species. J Anim Ecol 90(11):2547–2559. https://doi.org/10.1111/1365-2656.13560

Palma JJC (1979) Geomorfologia da plataforma continental norte Brasileira. Projeto REMAC. Geomorfologia da margem continental Brasileira e das áreas oceânicas adjacentes. PETROBRAS/CEPES/DINTEP, Rio de Janeiro, pp 25–51

Petean FF, Naylor GJ, Lima SM (2020) Integrative taxonomy identifies a new stingray species of the genus *Hypanus* Rafinesque, 1818 (Dasyatidae, Myliobatiformes), from the Tropical Southwestern Atlantic. J Fish Biol 97(4):1120–1142. https://doi.org/10.1111/jfb.14483

Piermarini P, Evans D (2000) Effects of environmental salinity on Na(+)/K(+)-ATPase in the gills and rectal gland of a euryhaline elasmobranch (*Dasyatis sabina*). J Exp Biol 203:2957–2966. https://doi.org/10.1242/jeb.203.19.2957

Pillans R, Good J, Anderson W, Hazon N, Franklin C (2008) Rectal gland morphology of freshwater and seawater acclimated bull sharks *Carcharhinus leucas*. J Fish Biol 72:1559–1571. https://doi.org/10.1111/J.1095-8649.2008.01765.X

Piorski NM, Silva S, Nunes JLS (2009) Análise comparativa da pesca de curral na ilha de São Luís, estado do Maranhão, Brasil. Arq Ciên Mar 42(1):65–71

Pollom R, Charvet P, Faria V, Herman K, Lasso-Alcalá O, Marcante F, Nunes J, Rincon G (2020a) *Fontitrygon geijskesi*. The IUCN red list of threatened species 2020: e.T60153A104172152. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T60153A104172152.en. Accessed 6 September 2023

Pollom R, Charvet P, Faria V, Herman K, Lasso-Alcalá O, Marcante F, Nunes J, Rincon G, Kyne PM (2020b) *Isogomphodon oxyrhynchus*. The IUCN red list of threatened species 2020: e.T60218A3094144. https://doi.org/10.2305/IUCN.UK.20203.RLTS.T60218A3094144.en. Accessed 20 September 2023

Prestes YO, Borba TAC, Silva AC, Rollnic M (2020) A discharge stationary model for the Pará-Amazon estuarine system. J Hydrol: Reg Stud 28:100668. https://doi.org/10.1016/j.ejrh.2020.100668

Queiroz APN, Araújo MLG, HusseyNE, Lessa RPT (2023) Trophic ecology of three stingrays (Myliobatoidei: Dasyatidae) off the Brazilian north-eastern coast: habitat use and resource partitioning. J Fish Biol 1–17. https://doi.org/10.1111/jfb.15226

Queiroz APN, Feitosa LM, Santana FM, Lessa RPT (2024) Stable isotopes and vertebrae microchemistry reveal crucial habitats for three heavily fished coastal stingrays in the Western Atlantic Ocean. Estuar Coast Shelf Sci 309:108961. https://doi.org/10.1016/j.ecss.2024.108961

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna. URL https://www.R-project.org/. 2023

RAMSAR (2018) RAMSAR Sites. https://www.ramsar.org/wetland/brazil. Accessed 18 July 2019

Reverdin G, Olivier L, Foltz GR, Speich S, Karstensen J, Horstmann J et al (2021) Formation and evolution of a freshwater plume in the northwestern tropical Atlantic in February 2020. J Geophys Res: Oceans 126:e2020JC016981. https://doi.org/10.1029/2020JC016981

Richey JE, Nobre C, Deser C (1989) Amazon river discharge and climate variability: 1903 to 1985. Science 246(4926):101–103. https://www.science.org/doi/abs/https://doi.org/10.1126/science.246.4926.101

Rodrigues-Filho LFS, Feitosa LM, Nunes Jorge LS, Palmeira ARO, Martins APB, Giarrizzo T, Carvalho-Costa LF, Monteiro I, Gemaque R, Gomes F, Souza RFC, Sampaio I, Sales JBL (2020) Molecular identification of ray species traded along the Brazilian Amazon coast. Fish Res 223:105407. https://doi.org/10.1016/j.fishres.2019.105407

Rodrigues-Filho LF, Nogueira PC, Sodré D, Leal JRS, Nunes JLS, Rincon G et al (2023) (2023) Evolutionary history and taxonomic reclassification of the critically endangered daggernose shark, a species endemic to the Western Atlantic. J Zool Syst Evol Res 1:4798805. https://doi.org/10.1155/2023/4798805

Röthig T, Trevathan-Tackett SM, Voolstra CR, Ross C, Chaffron S, Durack PJ et al (2023) Human-induced salinity changes impact marine organisms and ecosystems. Glob Change Biol 29(17):4731–4749. https://doi.org/10.1111/gcb.16859

Sales JBL, Rodrigues-Filho LFS, Ferreira YS, Carneiro J, Asp NE, Shaw PW et al (2017) Divergence of cryptic species of *Doryteuthis plei* Blainville, 1823 (Loliginidae, Cephalopoda) in the Western Atlantic Ocean is associated with the formation of the Caribbean Sea. Mol Phylogenet Evol 106:44–54. https://doi.org/10.1016/j.ympev.2016.09.014

Sales MAN, Freitas JEPD, Cavalcante CC, Santander-Neto J, Charvet P, Faria VV (2020) The southernmost record and an update of the geographical range of the Atlantic chupare, *Styracura schmardae* (Chondrichthyes: Myliobatiformes). J Fish Biol 97(1):302–308. https://doi.org/10.1111/jfb.14361

Santana PE, Nori J, Rojas-Soto O, Cortés F, Colonello JH, Elisio M (2025) Climate change threatens pupping sites of the critically endangered *Mustelus schmitti*: Insights from ecological niche models for ocean conservation. Estuar Coast Shelf Sci 314:109132. https://doi.org/10.1016/j.ecss.2025.109132

Santander-Neto J, Araújo MLG, Lessa RP (2016) Reproductive biology of *Urotrygon microphthalmum* (Batoidea: Urotrygonidae) from north-eastern Brazil, tropical west Atlantic Ocean. J Fish Biol 89(1):1026–1042. https://doi.org/10.1111/jfb.12951

Santos MLS, Medeiros C, Muniz K, Feitosa FAN, Schwamborn R, Macêdo SJ (2008) Influence of the Amazon and Pará rivers on water composition and phytoplankton biomass on the adjacent shelf. J Coast Res 24(3):585–593. https://doi.org/10.2112/05-0538.1

Santos HRS, Gomes UL, Charvet-Almeida P (2004) A new species of whiptail stingray of the genus *Dasyatis* Rafinesque, 1810 from the southwestern Atlantic Ocean (Chondrichthyes: Myliobatiformes: Dasyatidae). Zootaxa 492:1–12. https://doi.org/10.11646/zootaxa.492.1.1

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish

Biol Fish 24(4):1089–1103. https://doi.org/10.1007/s11160-014-9364-8

Silva AC, Santos MLS, Araujo MC, Bourlès B (2009) Observações hidrológicas e resultados de modelagem no espalhamento sazonal e espacial da pluma de água amazônica. Acta Amazon 39(2):361–369. https://doi.org/10.1590/S0044-59672009000200014

Simpfendorfer CA, Yeiser BG, Wiley TR, Poulakis GR, Stevens PW, Heupel MR (2011) Environmental influences on the spatial ecology of juvenile smalltooth sawfish (*Pristis pectinata*): results from acoustic monitoring. PLoS ONE 6:e16918. https://doi.org/10.1371/journal.pone.0016918

Sousa JA, Cunha KN, Nunes ZMP (2013) Influence of seasonal factors on the quality of the water of a tidal creek on the Amazon coast of Brazil. J Coast Res 65:129–134. https://doi.org/10.2112/SI65-023.1

Souza-Filho PWM (2005) Costa de manguezais de macromaré da Amazônia: cenários morfológicos, mapeamento e quantificação de áreas usando dados de sensores remotos. Rev Bras Geofis 23(4):427–435. https://doi.org/10.1590/S0102-261X2005000400006

Takei Y (1993) Role of peptide hormones in fish osmoregulation. In: Rankin JC, Jensen FB (eds) Fish Ecophysiology. Springer, Netherlands, pp 136–160. https://doi.org/10.1007/978-94-011-2304-4_5

Tavares MCS, Furtado-Júnior I, Souza RAL, Brito CSF (2005) A pesca de curral no estado do Pará. In: Tropical Journal of Fisheries and Aquatic Sciences. Bol Tec-Cien CEPNOR115–139

Thorson T, Brooks D, Mayes M (1983) The evolution of freshwater adaptation in stingrays. Nat Geogr Res 15:663–694

Tourinho JL, Solé-Cava AM, Lazoski C (2012) Cryptic species within the commercially most important lobster in the tropical Atlantic, the spiny lobster *Panulirus argus*. Mar Biol 159:1897–1906. https://doi.org/10.1007/s00227-012-1977-7

Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads, *Sphyrna tiburo,* as a response to salinity change in a Florida estuary. Environ Biol Fish 84:293–303. https://doi.org/10.1007/s10641-008-9436-5

Val AL, Wood CM (2022) Global change and physiological challenges for fish of the Amazon today and in the near future. J Exp Biol 225(10):jeb216440. https://doi.org/10.1242/jeb.216440

Ward ND, Krusche AV, Sawakuchi HO, Brito DC, Cunha AC, Moura JMS, Silva R, Yager PL, Keil RG, Richey JE (2015) The compositional evolution of dissolved and particulate organic matter along the lower Amazon River—Óbidos to the ocean. Mar Chem 177:244–256. https://doi.org/10.1016/j.marchem.2015.06.013

Williams W, Boulton A, Taaffe R (1990) Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia 197:257–266. https://doi.org/10.1007/BF00026955

Wiseman Jr WJ (1986) Estuarine-shelf interactions. Dynamics of shelf regimes. In: Mooers CNK (ed) Baroclinic processes on continental shelves, 3, pp. 109–115. https://doi.org/10.1029/CO003p0109

Wosnick N, Freire CA (2013) Some euryhalinity may be more common than expected in marine elasmobranchs: the example of the South American skate *Zapteryx brevirostris* (Elasmobranchii, Rajiformes, Rhinobatidae). Comp Biochem Physiol a: Mol Integr Physiol 166(1):36–43. https://doi.org/10.1016/j.cbpa.2013.05.002

Wosnick N, Palmeira ARO, Nunes JLS (2019a) E-Letter: Pinocchioland: the role of the Brazilian Amazonian coast in elasmobranch conservation. Science 334:1–1. https://www.science.org/doi/abs/https://doi.org/10.1126/science.1246752

Wosnick N, Awruch CA, Adams KR, Gutierre SMM, Bornatowski H, Prado AC, Freire CA (2019b) Impacts of fisheries on elasmobranch reproduction: high rates of abortion and subsequent maternal mortality in the shortnose guitarfish. Anim Conserv 22(2):198–206. https://doi.org/10.1111/acv.12458

Yancey PH (2015) Organic osmolytes in elasmobranchs. In: Shadwick RE, Farrell A, Brauner C (eds) Physiology of elasmobranch fishes: internal processes. Academy Press, pp 221–277. https://doi.org/10.1016/b978-0-12-801286-4.00004-6

Yauri WLM, Barbieri R (2022) Intrusão salina em um sistema rio–planície de inundação tropical influenciado por macromarés–Rio Pindaré (MA). Oecol Aust 26(2):271–285. https://doi.org/10.4257/oeco.2022.2602.14

Yokota L, Lessa RP (2006) A nursery area for sharks and rays in northeastern Brazil. Environ Biol Fish 75(3):349–360. https://doi.org/10.1007/s10641-006-0038-9

Yokota L, Goitein R, Gianeti MD, Lessa RTP (2012) Reproductive biology of the smooth butterfly ray *Gymnura micrura*. J Fish Biol 81(4):1315–1326. https://doi.org/10.1111/j.1095-8649.2012.03413.x