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Review

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Trends in elasmobranch feeding ecology studies

Hugo Bornatowski[1], Maiara A. Hayata[2], Renato H. A. Freitas[2]*

[1] Centro de Estudos do Mar - Universidade Federal do Paraná (Avenida Beira Mar, s/n - Pontal do Sul - Pontal do Paraná - Brazil).
[2] Laboratório de Biologia de Teleósteos e Elasmobrânquios (LABITEL) - Centro de Ciências Biológicas-(CCB) - Departamento de Ecologia e Zoologia (ECZ) - Universidade Federal de Santa Catarina (Trindade - Florianópolis - Santa Catarina- Brazil).

* Corresponding author: renato.freitas@ufsc.br

Abstract

Reviews can be useful to provide an overview of specific knowledge areas to facilitate research guidelines and the comparison of study results. Therefore, we aimed to detect regions, environments, and taxonomic groups of elasmobranch that lack information on their feeding ecology and consequently need further attention. Using specific keywords on diet and feeding studies, we searched for articles on the trophic and feeding ecology of elasmobranchs. We found an increase in studies over the last 24 years, with an emphasis on stomach contents and stable isotopes. The USA, Australia, Mexico, Argentina, and Brazil were the countries with the highest number of published articles. Australia, the USA, Argentina, Brazil, Mexico, South Africa, Spain, Uruguay and India were the countries with the highest number of species studied. Estuarine and freshwater environments seem to need more attention, since studies on species in these environments were scarce (~3%). The total number of shark and ray species studied showed no significant differences (164 and 186, respectively), but most of the articles reviewed concerned sharks (67.5%). The larger elasmobranch families also need more attention, especially demersal species such as Rajidae, Dasyatidae, Arhynchobatidae, and Sycliorhinidae. Feeding studies only analyze some of the data deficient (DD) species (~7%) included in the IUCN Red List, pointing to the need to obtain more information about them.

Descriptors: Chondrichthyes, Conservation, Diet, Stomach Contents, Trophic Ecology

INTRODUCTION

The class Chondrichthyes (sharks, rays, and chimeras) consists of approximately 1,220 species, with 520 species of sharks and 650 species of rays currently described (subclass Elasmobranchii) (*sensu* Last et al., 2016; Weigmann, 2017). Elasmobranchs are aquatic organisms with more than 400 million years of evolutionary success, having survived various mass extinctions (Camhi et al., 2009; Stein et al., 2018). Despite their evolutionary success, the extinction risk for Chondrichthyes is substantially higher than for most other vertebrates, especially due to overfishing and habitat degradation (Dulvy et al., 2014; Stein et al., 2018), affecting more than one-third of species (Dulvy et al., 2021).

Elasmobranchs range in size from the smallest dwarf lantern shark, *Etmopterus perryi* (Springer and Burgess, 1985), a species of up to 21 cm in total length (TL), to the largest whale shark, *Rhincodon typus* Smith, 1828, which reaches about 20 m TL (but 12 m TL is more common) (Compagno et al., 2005). Sharks and batoids are uniformly accepted as carnivores, represented from secondary to top predators (Cortés, 1999;

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Heithaus and Vaudo, 2012; Hussey et al., 2014). However, one exception has recently been better investigated: the bonnethead shark *Sphyrna tiburo* (Linnaeus, 1758) consumes significant amounts of seagrass, suggesting an omnivorous diet (Leigh et al., 2018).

In general, the diet of most shark and batoid species includes mainly teleosts, followed by crustaceans and cephalopods (Ellis et al., 1996; Navia et al., 2007; Barbini and Lucifora, 2011; Bornatowski et al., 2014a, 2014b). Teleosts are the most common sharks' prey, while crustaceans and other invertebrates seem to be more frequently consumed by benthic species (Wetherbee and Cortés 2004;; Martinho et al., 2012). Elasmobranchs are mainly found in the diet of the large sharks *Carcharhinus leucas* (Valenciennes, 1839), *Carcharhinus obscurus* (Lesueur, 1818), *Sphyrna* spp., *Galeocerdo cuvier* (Péron and. Lesueur, 1822), *Hexanchus griseus* (Bonnaterre, 1788), *Notorynchus cepedianus* (Péron, 1807), and *Carcharodon carcharias* (Linnaeus, 1758) (Strong et al., 1990; Cliff and Dudley 1991; Cliff, 1995; Lowe et al., 1996; Ebert, 2002; Bornatowski et al., 2014b), and a small proportion of them often feed on mammals, such as seals, dolphins, and dugongs (*C. carcharias*, *N. cepedianus*, *H. griseus*, *G. cuvier*) (Lowe et al., 1996; Ebert, 1994, 2002,). However, the ontogenetic change in feeding habits is a common phenomenon in elasmobranchs, in which small individuals (neonates and juveniles) eat smaller prey, such as teleosts, crustaceans, and cephalopods, while adults of large species change their diets to elasmobranchs, reptiles, and/or mammals (Lowe et al., 1996; Ebert, 2002; Bornatowski et al., 2014b).

Feeding ecology studies based on stomach contents are a common practice in elasmobranchs and other teleost fishes (Cortés, 1997; Braga et al., 2012; Wetherbee et al., 2012; Amundsen and Sánchez-Hérnandez, 2019). However, the search for alternative methods has been extremely useful to understand the trophodynamics of species. For instance, the use of stable isotopes is an important tool to examine diet, trophic position, feeding strategy, and movements of predators over short or long periods (MacNeil et al., 2005; Hussey et al., 2010, 2012, 2015). In addition, this method can be considered nonlethal, since only small pieces of tissue from the predator and prey are needed to perform the analysis (Hussey et al., 2012). Fatty acid profiles are also used to infer integrated dietary signatures of sharks and to assess dietary preferences and trophodynamics (Belicka et al., 2012; Couturier et al., 2013; Pethybridge et al., 2014). The interest in studying fish feeding is to better understand the natural history of a species and its role in the ecosystem trophic web (Braga et al., 2012). Moreover, this information is essential to provide a basis for conservation actions (Cortés, 1999; Heithaus, 2001; Ebert and Bizzarro, 2007; Simpfendorfer et al., 2011). For example, the feeding ecology of a species can provide information for more complex studies on resource partitioning (Valls et al., 2017; Mulas et al., 2019), competition (Fallows et al., 2013; Lea et al., 2019), behavior (Shibuya et al., 2012; Freitas et al., 2019), energy transfer (Sandin et al., 2008; Mourier et al., 2016), carbon cycle (Atwood et al., 2015), macroecology (Cortés, 1999; Ebert and Bizzarro, 2007; Barbini et al., 2018), food webs (Bornatowski et al., 2014c; Navia et al., 2017), and ecotrophic models (Stevens et al., 2000; Coll et al., 2013; Bornatowski et al., 2018a). These approaches often depend on diet descriptions and are therefore affected by the lack of basic knowledge of the species' diet (Braga et al., 2012).

Reviews on elasmobranch feeding studies focus basically on macroecology and meta-analyses (Cortés, 1999; Ebert and Bizzarro 2007; Barbini et al., 2018) or on a particular area, such as physiology (Cortés et al., 2007), evolution (Wilga et al., 2007), behavior (Motta et al., 2004), and methods (Cortés, 1997). A broad review with systematic analyses showing the knowledge gaps is still unknown for elasmobranchs. Thus, we aimed to review scientific journals in order to identify and comment on the general gaps in elasmobranch feeding ecology studies. Basically, we sought to analyze: (a) trends in feeding studies (stomach, stable isotopes, fatty acids) over 20 years; (b) which countries published the most articles on elasmobranch feeding ecology; (c) which environments were more studied (e.g., coast, oceanic, estuary); (d) which groups (sharks and batoids) and species were most studied; and (e) the existence of a trend towards the study of threatened species.

METHODS

We searched for articles on the trophic and feeding ecology of elasmobranchs in the Scopus database published from 1995 to 2019. We chose this database because it is considered one of the largest abstract and citation databases of peer-reviewed articles, and also because it allows the search to be saved without loss of information. We selected the "Advanced Search" mode on www.scopus.com, following these search criteria: (TITLE-ABS-KEY(elasmo*) AND TITLE-ABS-KEY(feeding)) OR (TITLE-ABS-KEY(elasmo*) AND TITLE-ABS-KEY(diet)) OR (TITLE-ABS-KEY(shark) AND TITLE-ABS-KEY(feeding)) OR (TITLE-ABS-KEY(shark) AND TITLE-ABS-KEY(diet)) OR (TITLE-ABS-KEY(batoid*) AND TITLE-ABS-KEY(feeding)) OR (TITLE-ABS-KEY(batoid*) AND TITLE-ABS-KEY(diet)) OR (TITLE-ABS-KEY (skate*) AND TITLE-ABS-KEY (feeding)) OR (TITLE-ABS-KEY (skate*) AND TITLE-ABS-KEY (diet)) AND PUBYEAR > 1994 AND PUBYEAR < 2020. On the first attempt, results not exclusively related to feeding ecology appeared (e.g., human diet in elasmobranchs, biochemistry, biomechanics, human health, physiology, ecotoxicology, and others). Therefore, we used the title and abstract to refine the results. Moreover, review articles that were not related to the meta-analysis were not included to avoid duplication of data (e.g., counting a species twice). The information obtained from the articles included:

Type of studies: to assess the trend in the use of research methods over 24 years, we considered terms such as "Behavior," "Fatty acid," "Isotopes," and 'Stomach content," aiming to identify general patterns.

Environment and geographic information: as elasmobranch species are mostly marine, we considered the coastal, ocean, freshwater, bay, and estuarine environments, aiming to identify any information gaps (i.e., for freshwater rays). We also obtained data on the location (by country) where the study took place. Information on the number of species recorded by country was also obtained for further analysis.

Species information: taxonomic families and species were classified according to Froese and Pauly (2023). We conducted analyses on the largest categories (i.e., sharks and rays), to assess differences between groups, and the most studied species (> 5 studies). When sharks and batoids were studied in the same article, we estimated for both. We also recorded the species' status on the Red List of the International Union for the Conservation of Nature (IUCN, 2023): extinct (EX), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC) and data deficient (DD).

Data analysis

A Spearman correlation test was used to investigate the relationship between the number of species by country found in our search and their number of described species. We also investigated the relationship between the number of species by family found in our search and the total number of species by family according to Froese and Pauly (2023). Finally, we correlated the total number of species according to the Red List status (IUCN, 2023) found in this review with the criteria for the total number of species worldwide (Dulvy et al., 2021). Previously, a Shapiro-Wilk test was conducted to test the normality of the data. All statistical analyses, maps, and graphs were performed and designed in the R software (R Core Team, 2022).

RESULTS

A total of 1,832 articles matching our keywords were listed in the database. Of these, 599 fit the criteria (i.e., elasmobranch feeding studies) and were therefore reviewed (see all articles in Supplementary Material, Data S1). The total number of feeding studies grew over the 24 years, particularly regarding stomach content analysis, followed by stable isotopes and behavioral studies (Figure 1). Other methods, such as DNA-based prey identification and gastric lavage, were less representative (see Data S1).

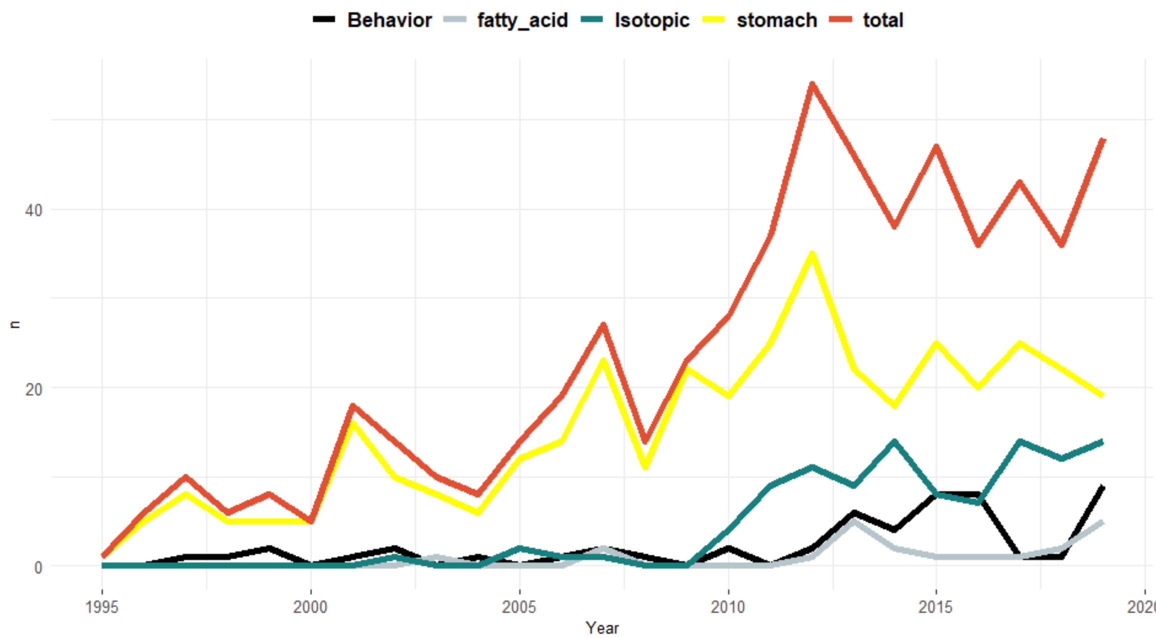

Figure 1. Trend of studies in 24 years represented by the main methods found.

We found that 65.8% of studies were conducted in coastal habitats, followed by 16.6% in ocean areas. Reef studies represented 4.2% and aquarium studies 2.7%. Freshwater and estuarine habitats represented ~3% of studies.

Most studies took place in the USA (17.0%), followed by Australia (13.4%), Mexico (8.5%), Argentina (7.0%), Brazil (5.5%), and South Africa (3.8%) (Figure 2). According to the 15 countries with the highest number of species studied, the Spearman correlation test showed a significant correlation between the number of species described by country and the number of species studied in each (Figure 3). However, almost all the countries are represented by less than 25% of the total number of species described (Figure 3).

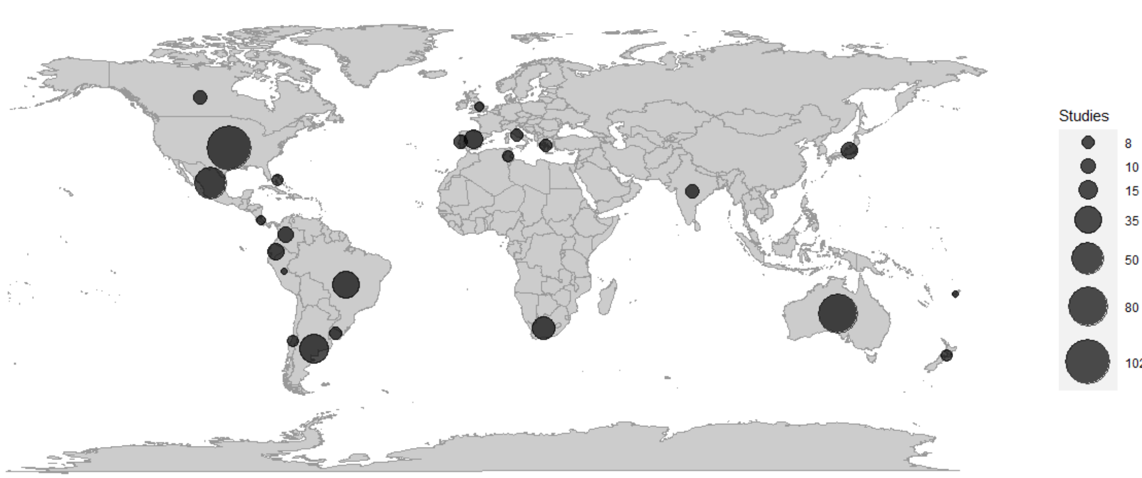

Figure 2. World map showing the number of studies found in each of the 23 most represented countries.

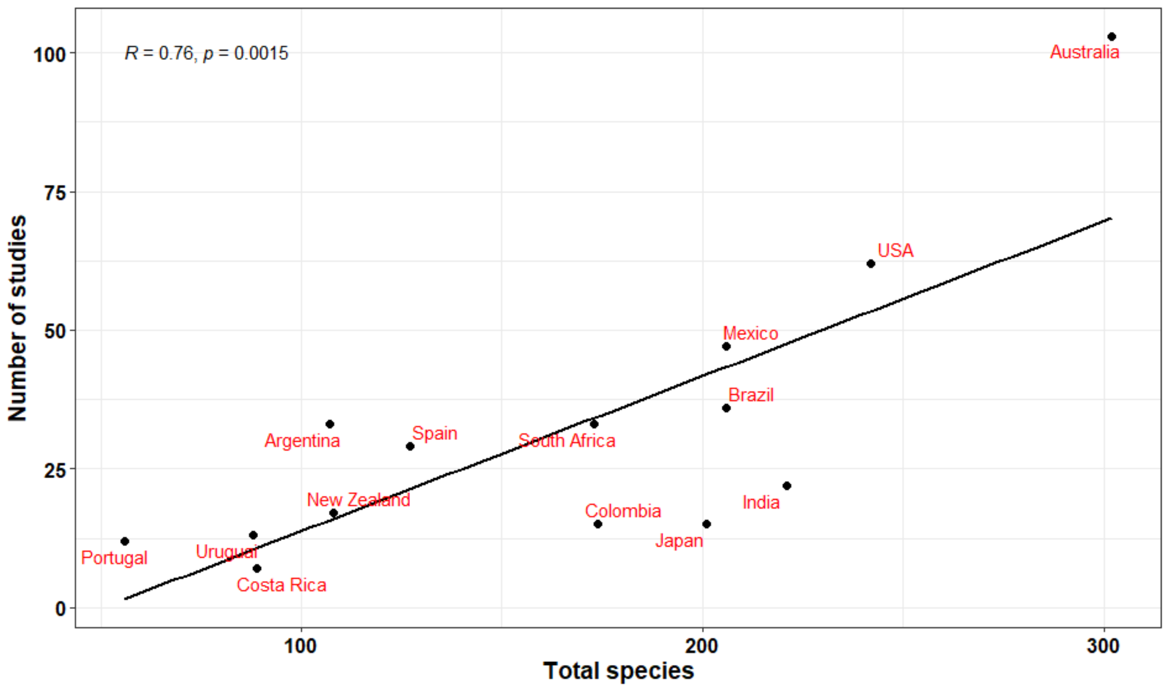

Figure 3. Correlation between the number of species from the most represented countries found in our search and the total number of species described by country. The countries below the line represent a low number compared with the total number found by country.

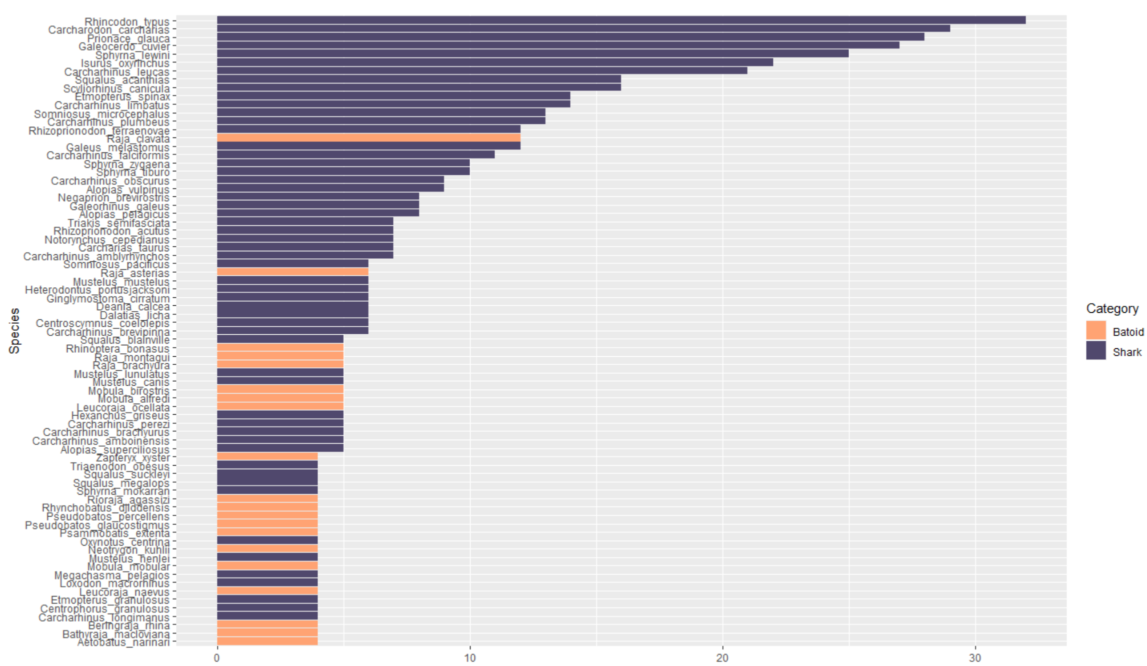

Figure 4. Total number of studies found in our review by species with n > 4 studies.

A total of 1,036 species (not separated by species/specific) were found in our review. Although batoids were the most studied group (n = 186) against 164 shark species, most articles reviewed (total number) concerned sharks (67.5%) rather than rays (32.5%) (Figure 4). Regarding all species (n = 729), sharks were the main group studied in all countries, but batoids were well studied in Australia, USA, Mexico, Argentina, Uruguay, Brazil, and Spain (Figure 5).

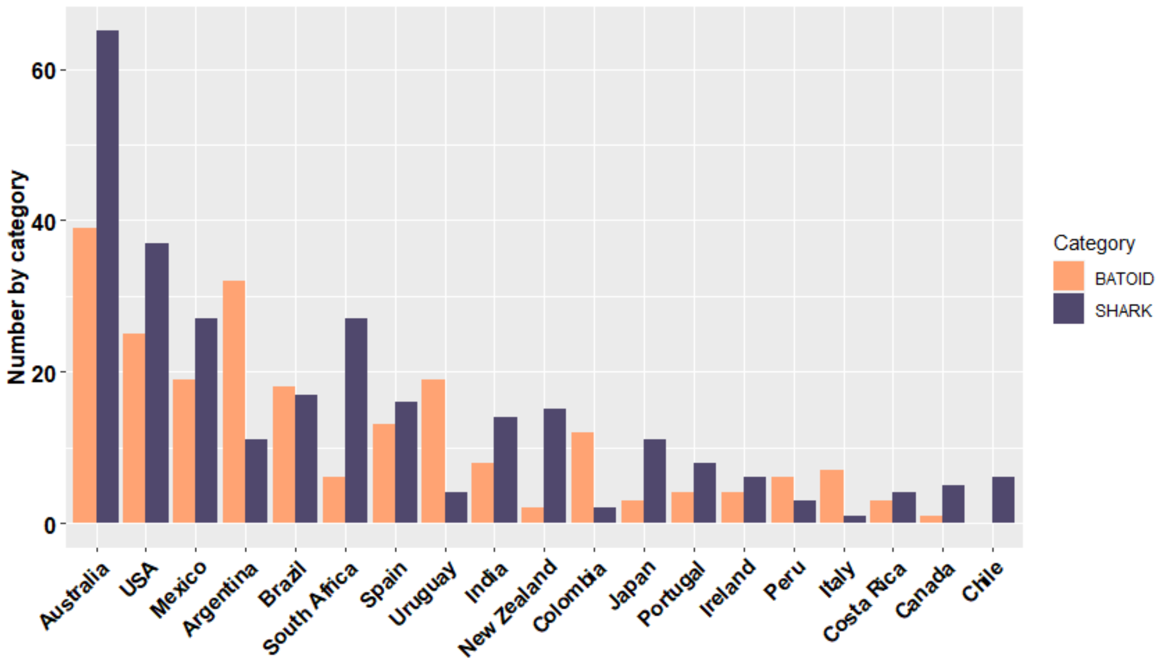

Figure 5. Total number of species studied by category (i.e., shark and batoid) divided by the most representative countries.

Regarding the species, *Rhincodon typus*, *Carcharodon carcharias*, *Prionace glauca*, *Galeocerdo cuvier*, (Linnaeus, 1758), *Sphyrna lewini* (Griffith a nd S mith, 1 834), *Isurus oxyrinchus* (Rafinesque, 1810), *Carcharhinus leucas* (Müller and Henle, 1839), *Scyliorhinus canicula* (Linnaeus, 1758), *Squalus acanthias* Linnaeus, 1758, were the most studied (more than 15 studies) (Figure 4). *Raja clavata* (Linnaeus, 1758), *R. asterias* (Delaroche, 1809), *Leucoraja ocellata, Rhinoptera bonasus* (Mitchill, 1815), *Mobula alfredi* (Krefft, 1868), *Mobula birostris* (Walbaum, 1792), *Raja brachyura* (Lafont, 1871), and *R. montagui* (Fowler, 1910), were the only species with significant numbers among the batoids (more than five studies).

Rajidae, Carcharhinidae, Arhynchobatidae, Dasyatidae, Triakidae, Rhinobatidae, Myliobatidae, Scyliorhinidae, Etmopteridae, and Somniosidae were the most studied families (Figure 6). The proportion of studies found for each family and the proportion of total species described were strongly correlated (r = 0.89; $p < 0.05$; Figure 6). However, rich families such as Dasyatidae, Rajidae, Arynchobatidae, and Scyliorhinidae were poorly represented when considering their total number of species.

Of the species studied, 57.2% were not threatened according to the IUCN Red List, 3.2% were DD, 16.8 NT, and 37.2 LC. Vulnerable (20.6%), endangered (14.7%), and critically endangered (7.4%) were the threat categories represented. We found no significant correlation between the number of species studied within each category and the total number of species included in each of them (Figure 7). In a general comparison, only 7.1% of the total DD species were studied according to Dulvy et al. (2021).

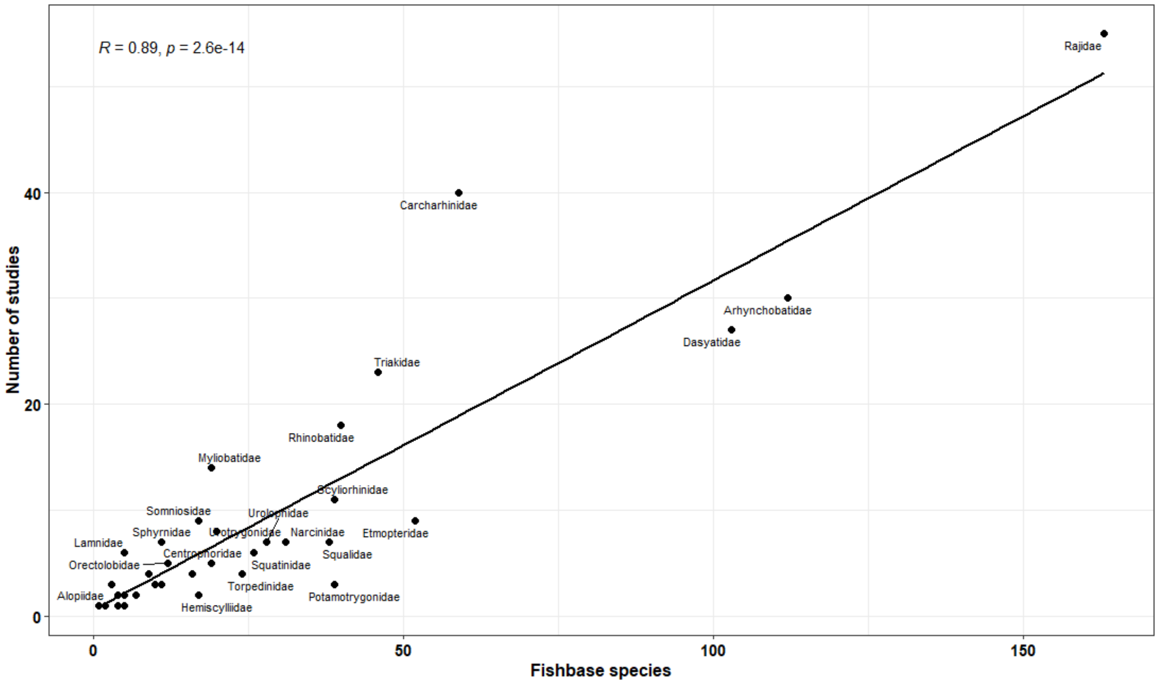

Figure 6. Correlation between the families studied and the species actually described for each family according to FishBase (2023). The families below the line represent a low number compared with the total number of the family.

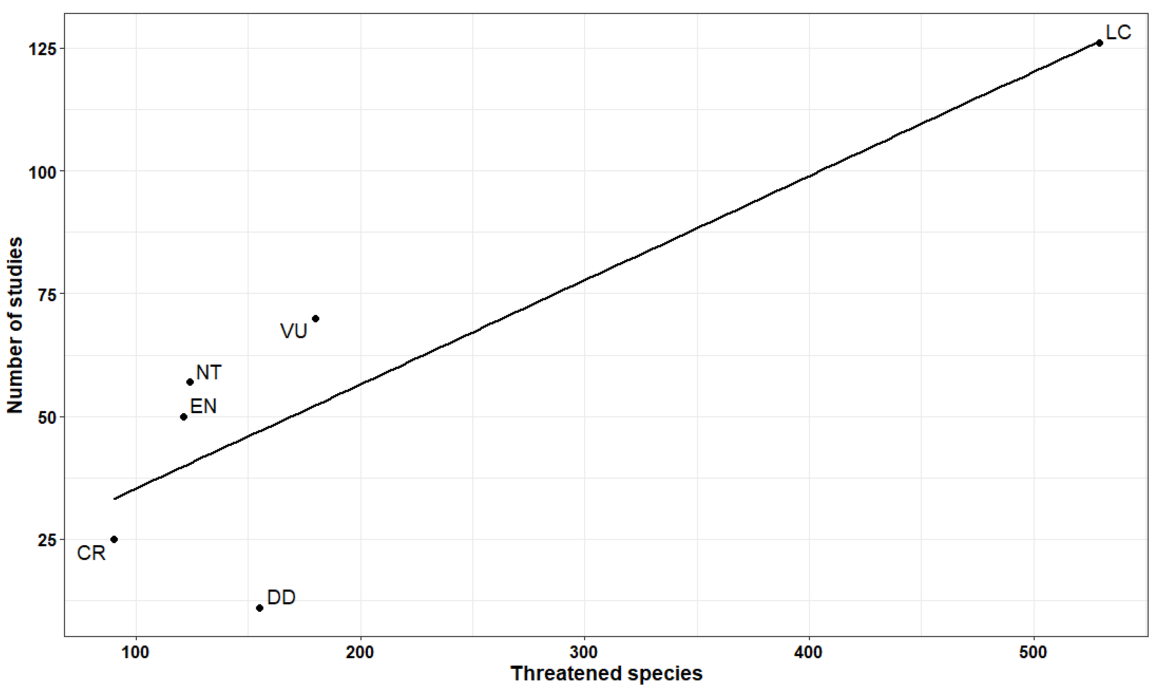

Figure 7. Correlation between the number of species studied divided by threatened categories and the total number of species found in the IUCN Red List categories (2023). The categories below the line represent a low number compared with the total number of threatened species.

DISCUSSION

This study clearly showed an increase in studies on elasmobranch feeding ecology over time. However, some gaps were found in the number of studies by country, the number of species and families studied, and we found that estuarine and freshwater ecosystems are poorly studied.

Dietary studies have been growing since 1995, especially stomach analysis research. However, in the last years of our study, an increase in studies on stable isotopes, behavior, and fatty acids became apparent. According to our review, the digestion process and feeding behavior have been successfully analyzed in captive studies (Shibuya et al., 2012; Meyer and Holland, 2012; Guallart et al., 2015). Another method, still poorly explored, is the DNA-based prey identification (Rosel and Kocher, 2002). This new tool can be strongly useful to identify morphologically unidentifiable prey in stomachs, guts, and fecal contents (Jarman and Wilson, 2004; Riccioni et al., 2018). It is important to highlight that most of the animals used on feeding studies based on stomach content analysis were often obtained opportunistically from fishing landings, without the sacrifice of animals only for this purpose (Navia et al., 2007; Consalvo et al., 2010; Martinho et al., 2012; Bornatowski et al., 2014b). Finally, diet and feeding ecology studies need to be more complete and detailed, enabling the construction of more complex research on topics such as macroecology, food webs, and prediction models (Cortés, 1999; Bornatowski et al., 2014c; Barbini et al., 2018).

The countries with the highest number of species studied were Australia (104), the USA (62), Argentina (43), Brazil (35), Mexico (46), South Africa (33), Spain (29), Uruguay (23), and India (22). Although these numbers are far lower than the total number of species described for each country, the proportion of studies is correlated. There are 302 species described for Australia (Last and Stevens, 2009; Last and White, 2011), i.e., the species studied represents only less than 34% of the total. This is repeated for other countries: only 26% of species from the USA were studied (242 species – Ebert and Stehmann, 2013; Ebert et al., 2017), 10% from India (221 species – Akhilesh et al., 2015; Ebert et al., 2013), 23% from Mexico (206 species – Del Moral-Flores et al., 2015), 17% from Brazil (206 species – Rosa and Gadig, 2014; Lasso et al., 2014), 19% from South Africa (181 species – Compagno, 2013; Ebert and van Hees, 2015), and 31% from Argentina (108 species – Menni and Lucifora, 2007). Moreover, the lack of feeding data in countries with high biodiversity, such as Indonesia (Fahmi, 2010; Last and White, 2011), Japan (Ebert et al., 2017), Taiwan (Ebert et al., 2013), and Southeast Asia (Wanchana et al., 2016) is evident. One hypothesis is that articles on the feeding ecology of these species from developing countries with high biodiversity were published in non-indexed journals or lack research incentives (Braga et al., 2012).

Freshwater and estuarine habitats represented ~3% of the studies reviewed. Although most elasmobranchs are marine throughout their lives, a small portion (5%) are euryhaline, tolerating low-salinity environments (e.g., *C. leucas* and some Dasyatidae species), while only 3% to 4% are exclusive to freshwater environments (e.g., Potamotrygonidae stingrays) (Martin, 2005; Ballantyne and Robinson, 2010). For instance, the bull shark *C. leucas* commonly enters estuaries and/or freshwater systems and interacts with species in these habitats (Werry et al., 2011). There are 31 freshwater stingrays currently described (Lasso et al., 2016) and their feeding ecology remains poorly understood. Moreover, two species of Potamotrygonidae stingrays, *Potamotrygon amandae* Loboda and Carvalho, 2013 and *Potamotrygon falkneri* (Castex and Maciel, 1963), are considered invasive species of the upper Paraná River, Southern Brazil (see Vitule et al., 2012, and Santos et al., 2019, for details), threatening ecosystem services in this region (Garrone-Neto et al., 2014; Santos et al., 2019). Thus, the expansion of the feeding ecology and behavior of freshwater and/or transient species is strongly recommended.

The richest families according to FishBase (2023) are Rajidae (n = 163), Arhynchobatidae (n = 112), Dasyatidae (n = 103), Carcharhinidae (n = 59), Etmopteridae (n = 52), and Triakidae (n = 46). However, even though there is a correlation between the total number of species per family and the number of species reviewed per family, many large groups remain poorly studies: only 34% of Rajidae, 27% of Arynchobatidae, 26% of Dasyatidae, and 17% of Etmopteridae. The families most found in articles reviewed were Carcharhinidae (68%), Somniosidae (53%), and Triakidae (50%). Moreover, families with fewer species, such as Lamnidae, Alopiidae, Cetorhinidae, Megachasmidae, Rhincodontidae, and Pseudocarchariidae, were better studied. Therefore, we can conclude that the correlation was influenced by less rich families.

Although the number of studied species per group is not different (164 for sharks, 186 for rays), sharks appeared 697 times in the articles reviewed while batoids only appeared 335 times. These findings show the disparity between the amount of attention paid to each group. Of the 52 species with more than five studies, only eight species were batoids. This may be due to the fact that the main shark species studied are coastal or oceanic, and are globally caught by fishing (Baum et al., 2003; Molina and Cooke, 2012; Barreto et al., 2016; Roff et al., 2018; Queiroz et al., 2019), which could explain the easy access to biological data. Another hypothesis is that studies have focused on more iconic species such as whale, white, and tiger sharks. In any case, considering the high levels of batoid catches (e.g., Indonesia, India, Mexico, and Brazil) (Davidson et al., 2015; Last et al., 2016; Bornatowski et al., 2018b), the degree of endemicity (Dulvy et al., 2014; Stein et al., 2018), and that five of the seven most threatened elasmobranch families are within rays (Dulvy et al., 2014), further research on the auto-ecology of these species is urgently needed. This also extends to other poorly studied shark groups, such as Scyliorhinidae, Squalidae, Etmopteridae, Triakidae, and more.

Of the total species studied, less than 50% are considered threatened (42.8%) (Dulvy et al. 2021). However, the proportion found was slightly higher than 33% of the threatened species recorded worldwide (Dulvy et al., 2021). Thus, considering the decline in elasmobranch populations worldwide, noninvasive and/or nonlethal methods are highly required (Heupel and Simpfendorfer 2010). Moreover, the methods need to respect best practices and animal ethics (Metcalf and Craig, 2011). The number of data deficient species according to the IUCN Red List is particularly high compared with that found in feeding studies. It is important to emphasize that a taxon in this category may be well studied and its biology well known, but appropriate data on abundance and/or distribution are lacking (IUCN Standards and Petitions Committee, 2019). Therefore, it is not possible to certify how threatened the taxon is. There are demands for global conservation and management plans for elasmobranchs, especially due to the data deficiency of many species (Stevens et al., 2000; Dulvy et al., 2008). This motivates the expansion of autoecology studies for all species, especially those categorized as data deficient.

CONCLUSIONS

Feeding ecology studies provide information on the natural history of species, hence their importance. Furthermore, feeding studies accompanied by basic information (frequency of occurrence of prey, prey weight, and relative importance index; Cortés, 1997; Amundsen et al., 2019) provide a basis to support food webs (Bornatowski et al., 2014c; Navia et al., 2017) and macroecology studies (Cortés, 1999; Barbini et al., 2018), as well as for ecotrophic models with Ecopath and Ecosim software (Coll et al., 2013; Bornatowski et al., 2018a). Ecopath models make it possible to understand ecosystem structure, functioning, and changes, besides examining fisheries management options at the ecosystem level (Coll et al., 2015). These more complex approaches often depend on diet descriptions and thus are affected by the lack of basic knowledge of the diet of fish species (Braga et al., 2012). For this reason, based on the gaps found here, there is an increasing need to expand feeding studies worldwide, especially in highly rich countries such as Southeast Asia, Taiwan, China, and Indonesia. Feeding studies need to be accompanied by basic and accurate information, such as good taxonomic identification and basic metrics (Cortés, 1997; Amundsen et al., 2019). The larger elasmobranch families need more attention, especially demersal species. Estuarine and freshwater environments also need further research. Considering the number of sharks and rays caught worldwide, often landed in specific ports, biological information on these animals must be collected. Moreover, we encourage the use of alternative techniques to assess information on the feeding of species, such as DNA-based prey identification, stable isotopes, and behavior.

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AUTHOR CONTRIBUTIONS

H.B.: Conceptualization; Investigation; Methodology; Writing – original draft; Analysis; Writing – review & editing.

M.A.H.: Investigation; Methodology; Writing – original draft; Analysis; Writing – review & editing.

R.H.A.F.: Supervision; Writing – review & editing.

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