Aquatic species listed in the CITES Appendices

Variability of life history parameters and productivity in elasmobranchs and other commercially exploited aquatic species

Background document to the technical workshop on Aquatic species listed in the CITES Appendices *(Geneva, April 2024)*

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Executive summary

Elasmobranchs (sharks, skates, and rays) are a very diverse group of fishes showing extreme variability in some of their life history traits, including maximum size and age, size and age at maturity, offspring size, number of offspring, gestation period, breeding frequency, and growth rate. This diversity of life history traits can be viewed as a continuum that is ultimately expressed as largely different productivity values, which affects the vulnerability of the different species to human-induced stressors.

Information from multiple recent studies on elasmobranch life history and productivity as well as data for commercially exploited fish species and some marine mammals was collected to compare productivity patterns among these groups. A scheme proposed by Musick (1999) was used as an example of how to group species into four productivity categories (high, medium, low, and very low) according to several life history parameters indicative of productivity (growth completion rate, age at maturity, maximum age, and fecundity) as well as a direct measure of productivity (r_{max} or the intrinsic rate of population growth).

Combined results using data from all studies explored indicated that skates are the most productive species, followed by rays, and sharks. Elasmobranchs as a group are less productive than teleosts and more productive than marine mammals, but there is overlap in productivity values between elasmobranchs (in particular skates) and teleosts and also between elasmobranchs (in particular sharks) and marine mammals. The distribution of species from the different taxa into the four productivity categories based on r_{max} revealed that batoids (skates and rays) had a very large proportion of species in the combined medium and high productivity categories, similar to teleosts, whereas sharks had large, similar proportions of species in the medium and low categories. The proportion of shark species in the combined low and very low categories and in the combined medium and high categories were similar to the proportion of marine mammal species in the very low and low categories, respectively. The four productivity categories can be associated with different population decline thresholds that would trigger a listing of vulnerable, with the very low productivity category associated with a decline threshold of 70%. Based on this classification, only 14% and 1% of the shark and batoid species, respectively, included in the analysis would fall in the very low productivity category associated with a 70% decline.

Regardless of the productivity categories and population decline thresholds ultimately chosen, results of this study show that life history parameters and the associated productivity vary extensively in elasmobranchs along a continuum (as in other taxa) and that grouping all species in a single productivity category and corresponding decline threshold is not supported by the data. This has also been recognized in the fisheries arena where other measures of productivity are used to define associated biological reference points for exploited populations.

Background on life history of cartilaginous and bony fishes

As exhaustively reported in the literature cartilaginous fishes (sharks, skates, rays, and chimaeras; class Chondrichthyes) as a group have a K-selected life history strategy generally characterized by slow individual growth, late age at maturity and first reproduction, low fecundity, long gestation period, low frequency of births, production of well-developed offspring, low natural mortality, and long lifespan. This is in contrast with bony fishes (superclass Osteichthyes) which are generally much more productive and follow an r-selected life history strategy characterized by fast growth, early age at maturity, and high fecundity leading to potentially high recruitment despite having high natural mortality.

However, there is very significant variation in life history traits of cartilaginous fishes expressed in widely different life history strategies (see Cortés (2000) for a review of sharks and Dulvy and Forrest (2010) for a review of chondrichthyans in general) that define their vulnerability to fishing and other anthropogenic stressors such as habitat destruction and climate change. The varying life history traits that underpin these alternative life history strategies ultimately result in substantially different productivity values.

Variability in life history traits of elasmobranch and other fishes

Data sources

To help illustrate the very large variability in life history traits data from multiple sources were extracted. For sharks, the analysis of life history traits by Cortés (2000) was augmented (hereafter referred to as "Cortés (2000) augmented") with information extracted from numerous studies that have become available since that study was conducted (n = 603; **supplementary material 1**). This was done by examining the life history trait values reported in the original studies obtained with searches in Google Scholar and from articles listed in the Shark References monthly newsletters (www.shark-references.com; Pollerspöck and Straube 2023). For batoids (skates and rays), data from Barrowclift et al. (2023; n = 150) were used. For bony fishes, data from Thorson et al. (2023) that had been extracted from FishBase (n = 2,401) were used. Additionally, direct estimates of productivity (expressed as the intrinsic rate of increase, r_{max}) were obtained from several sources: augmenting the study from Cortés (2016; n = 101; hereafter referred to as "Cortés (2016) augmented" for sharks; Barrowclift et al.'s (2023) study (n = 85) for batoids; Gravel et al.'s (2024) study for elasmobranchs and teleosts (n = 224); and Finucci et al.'s (2024) study for chondrichthyans and marine mammals (n = 106; using the average of three reported estimates). For all species available in each dataset it was also noted whether they were listed in a CITES Appendix or not. Listed species for different taxa were downloaded from Species+ (speciesplus.net). **Table 1** summarizes and describes all the life history traits that were explored in this study.

As an illustration of this extreme variability in life history traits of sharks, maximum size can range from 22 cm total length (TL) in the pigmy shark (*Euprotomicrus bispinatus*) to about 1900 cm TL in the whale shark (*Rhincodon typus*); maximum litter size, from 1 pup in the Gulper shark (*Centrophorus granulosus*) to 300 pups in the whale shark; gestation period, from 4-5 months in the bonnethead shark (*Sphyrna tiburo*) to perhaps 3.5 years in the frilled shark (*Chlamydoselachus anguineus*); breeding frequency from 1 year in many species to 3 years in several other species; *k* (the von Bertalanffy growth coefficient that describes how fast maximum length is reached), from 0.01 yr^{-1} in male blackbelly lanternshark (*Etmopterus lucifer*) to 1.34 yr^{-1} in male Australian sharpnose sharks (*Rhizoprionodon taylori*); age at maturity, from 1 year in the Australian sharpnose shark to 36 years in the spiny dogfish (*Squalus acanthias*); and lifespan, from 4 years in male Australian sharpnose sharks to at least 81 years in female spiny dogfish (and potentially 272 years in the Greenland shark (*Somniosus microcephalus*), although this may be an overestimate).

Data for batoids (**supplementary material 1**) show that maximum length can range from 26 cm TL in the Chilean round ray (*Urotrygon chilensis*) to 730 cm TL in the longcomb sawfish (*Pristis zijsron*); disk width, from 26 cm in the dwarf stingray *(Urotrygon nana*) to 700 cm in the giant oceanic manta ray (*Mobula birostris*), maximum litter size, from 1 offspring in the Brazilian large-eyed stingray (*Hypanus marianae*) to 167 eggs in the thornback ray (*Raja clavata*); gestation period, from 3 months in the white-edge freshwater whipray (*Fluvitrygon signifer*) to 15 months in the bottlenose skate (*Rostroraja alba*); breeding frequency, from 0.074 years in the big skate (*Beringraja binoculata*) up to 4.5 years in the reef manta ray (*Mobula alfredi*); *k* from 0.02 yr^{-1} in the graytail skate (*Bathyraja griseocauda*) to 0.54 yr^{-1} in the roughskin skate (*Dipturus trachyderma*); age at maturity, from 1 year in Roger's round ray (*Urotrygon rogersi*) to 24.7 years in the roughtail skate (*Bathyraja trachura*); and lifespan, from 3.5 years in Bleeker's whipray (*Pateobatis bleekeri*) to 50 years in the common skate (*Dipturus batis*).

Length-frequency histograms of female and male sharks and batoids (sexes combined) included in the analyses show that populations of species listed in CITES Appendices (n = 315) tend to be larger than those not listed (n = 438; **Figure 1**). In contrast, there is no clear trend for the fewer species of teleosts listed in CITES Appendices (n for listed = 31; n for non-listed = 2012; **Figure 2**).

For teleosts (**supplementary material 2**), the data show that maximum theoretical length can range from 3.1 cm TL in the Emerald clingfish (*Acyrtops beryllinus*) to 474 cm TL in the Indo-Pacific blue marlin (*Makaira Mazara*); length at maturity from 1.6 cm TL in the sinaripan (*Mistichthys luzonensis*) to 219.2 cm TL in the Indo-Pacific blue marlin; *k* from 0.03 yr^{-1} in the beluga (*Huso huso*) to 5.3 yr^{-1} in the silver-stripe round herring (*Spratelloides gracilis*); age at maturity, from 0.2 years in the cyprinid (*Cynopoecilus melanotaenia*) to 24.8 years in the beluga; and lifespan, from 0.6 years in the silver-stripe round herring to 92.5 years in the rougheye rockfish (*Sebastes aleutianus*).

Factors affecting the estimates of life history traits and parameters

Our best understanding and most widely accepted views of the life history of elasmobranchs come from a small subset of species globally, notably small and large coastal sharks and pelagic sharks that have historically received more attention. But the vast majority of species have been the subject of comparatively limited research (e.g., deep-water chondrichthyans such as many sharks and chimaeras).

There is inherent uncertainty associated with the measurement and estimation of life history traits, which affects their comparison. Numerous factors can affect this comparison, including sampling bias, measurement technique, analytical method, density-dependent responses, geographic variability and phenotypic plasticity, species distribution, and increased research efforts. Following is a brief discussion of each of these factors focusing on elasmobranchs.

Samples collected in a given study are only partially representative of the entire extent of the population, and are subject to selectivity based on the type of gear used for collection, which may select preferentially for certain sizes but not the entire range of the population. For example, Moulton et al. (1992) found that length-selective fishing mortality affected the computation and comparison of growth parameters from two separate time periods in gummy sharks (*Mustelus antacticus*). Since many species also segregate by size/age and sex their distribution in time and space differs, which can also affect sampling. Despite the best efforts to obtain a representative coverage of the population most studies only provide a snapshot of the population in time and space.

Francis (2006) emphasized the importance of standardized length measurement methods for cartilaginous fishes noting that different techniques, such as measuring total length with the tail in a natural vs. stretched position or along the body curvature vs. in a straight line affects total length and therefore comparisons among studies of growth, maturation, and size.

Analytical methods, notably in age and growth studies, can also affect estimated parameters. In general, one can consider the more recent studies more reliable from an analytical standpoint because multiple growth functions are typically fit to age-length data and the best fitting model selected based on statistical fit considerations. However, discerning growth bands at the edges of vertebrae or spines typically used to determine age in elasmobranchs is always difficult and subject to some degree of bias. This is aggravated by the fact that at least some species may stop depositing growth bands at some point in their life cycles and that band deposition may be related to factors other than age (Natanson et al. 2018).

The degree of depletion of the population, which affects the density-dependent response, is also reflected in the life history traits displayed by the species. For example, the expectation is that individuals in a (heavily) fished population will reach sexual maturity earlier and at a smaller size than before exploitation as a compensatory response expressed as an increased growth rate (e.g. Carlson and Baremore 2003).

Geographic and latitudinal variation as well as phenotypic plasticity (the ability of one genotype to produce more than one phenotype when exposed to different environments) can also affect life-history traits. For example, Lombardi-Carlson et al. (2003) found that bonnethead sharks (*Sphyrna tiburo*) in the Gulf of Mexico reached a higher size and age at maturity, larger maximum size and size of near-term embryos, and faster growth rate at the northern end of the range compared to their counterparts found at two and five degrees of latitude to the south. Cope (2006) explored intraspecific life-history patterns in sharks more generally and also found that populations in northern latitudes tended to be larger, mature later in life, have longer lifespans, and have greater fecundity compared to conspecifics in central and southern latitudes.

Increased research efforts can also lead to new findings or hypotheses about life-history traits. For example, blacknose sharks (*Carcharhinus acronotus*) believed to have only a biennial reproductive cycle (i.e., producing pups every two years; Driggers et al. 2004) were later found to display an annual cycle as well (Sulikowski et al. 2007), which led in part to the splitting of this species into two populations (Gulf of Mexico with a biennial cycle and southeastern Atlantic coast of the USA with an annual cycle). Even within the same population there is evidence of differing length of the reproductive cycle (i.e. annual and biennial), as Driggers and Hoffmayer (2009) found for finetooth shark (*Carcharhinus isodon*) in the Gulf of Mexico. This in general shows that the more data that become available, the higher the accuracy of the estimates. Diminished research effort is not exclusive to elasmobranchs; for example, Ducatez and Shine (2017) found that the number of IUCN Red List threat types assigned varied based on research attention, which may explain in part why terrestrial vertebrates have more assigned threats on average compared to marine ray-finned fishes, which are less studied (Bak et al. 2023).

Life history strategies of elasmobranchs and bony fishes

Despite these pervasive issues, there are some general rules of thumb that can be identified to describe chondrichthyan life histories at the species level (Cortés 2000; Dulvy and Forrest 2010): 1) the bigger you are, the more offspring you have; 2) the bigger you are, the larger your offspring are; 3) the more offspring you have, the smaller their relative size; 4) the faster you grow, the smaller your maximum size and the shorter your lifespan; 5) the shorter your lifespan, the earlier you must breed; and 6) the quicker you die (high natural mortality), the shorter your lifespan. **Figure 3** illustrates some correlations between life history parameters for elasmobranchs from the combined Cortés (2000) augmented study and that of Barrowclift et al. (2023). For example, it can be seen that maximum length and length at maturity ($r = 0.88$), maximum age and age at maturity ($r = 0.76$), length at maturity and offspring size (0.74), and maximum length and maximum litter size (0.69) are highly correlated. Most of these rules also apply to other taxa, such as teleosts, as can be seen in the life history parameter correlations for teleosts with data from Thorson et al. (2023) in **Figure 4**.

These life rules in turn define different life history strategies. Using Principal Component Analysis (PCA) and cluster analysis, Cortés (2000) proposed at least three distinguishable strategies that may be linked to how different species cope with neonate and juvenile mortality: 1) species characterized by large litter sizes, small offspring, intermediate to large body size, variable but generally substantial longevity, and relatively slow growth, such as the blue shark (*Prionace glauca*), which likely suffer high mortality as neonates and young; 2) large species with large but few offspring, slow growth, and high longevity, such as the dusky shark, whose young are exposed to reduced mortality owing to their large size; and 3) species with small to moderate body size, low to moderate longevity, small offspring and litter size, fast growth, and reduced lifespan, such as species in the genus *Rhizoprionodon* (e.g., Atlantic and Australian sharpnose sharks), which are exposed to high mortality as young, but compensate by being born at a high percentage of their maximum size and reach maturity very quickly.

Using phylogenetic comparative methods and "phylogenetic trait imputation" Thorson et al. (2023) identified three life-history strategies for fishes, defined as an "extreme combination of trait values that frequently occur together, such that all fishes can be characterized as some mixture of strategies", also defined as "archetypes" following the usage of Winemiller and Rose (1992). The first archetype was characterized by higher maximum age, trophic level, slow growth, and low temperatures, a suite of traits corresponding to an "equilibrium" strategy, represented by elasmobranchs and scorpaenid teleosts. A second archetype would correspond to an "opportunistic" strategy, characterized by the lowest maximum age and fecundity, and high natural mortality and probability of guarding the young, largely represented by Gobiidae (gobies). The third archetype would correspond to a "periodic" strategy typified by somewhat intermediate growth and size, typically the highest fecundity, being mainly pelagic, and having the highest probability of a non-guarding reproductive strategy, largely represented by clupeids (sardines and herrings).

Comparison of life history traits of elasmobranchs and other fishes

The life history traits and strategies ultimately define productivity. Productivity can be expressed in different forms, but it is most commonly as the intrinsic rate of population growth or r_{max} especially in conservation contexts. Previous studies have shown that there is a continuum of life history traits and therefore productivity in elasmobranchs that also influences their vulnerability to human-induced stressors.

Cortés (2002) found that there was a continuum of life history traits that defined productivity and was also linked to the importance of the different life stages (neonates, juveniles, adults) for population growth. In general terms, sharks at the "fast" end of the spectrum (characterized by early maturation, short lifespan, and large litter size) had high r_{max} values, short generation times, and similar importance of the juvenile and adult stages, whereas sharks at the "slow" end of the spectrum (exemplified by late maturation, long lifespans and small litters) had low r_{max} values, long generation times, but higher importance of the juvenile stage compared to that of the adult stage. Cortés (2016) found similar results on productivity, with r_{max} obtained with the same methodology (life tables/Leslie matrices) ranging from values close to 0 to about 0.5 yr^{-1}. Smith et al. (1998) also found a continuum of productivity values, expressed as a "rebound potential", that was strongly affected by age at maturity. Au et al. (2008) compared the rebound potential of 27 selected shark species to that of 11 teleost species (several tunas, swordfish, marlin, and sardine) finding that it was negatively related to age at maturity. While the teleost fishes had generally higher productivity, there was overlap with some of the most productive shark species (e.g. the grey smoothhound [*Mustelus californicus*], the brown smoothhound [*Mustelus henlei*], the bonnethead [*Sphyrna tiburo*], and the Atlantic sharpnose shark [*Rhizoprionodon terraenovae*]) as can be seen from the range of productivity values depicted as vertical lines in **Figure 5**. These more productive shark species were also those located at the fast end of the productivity spectrum identified by Cortés (2002), which can withstand more exploitation (see species located at bottom left of **Figure 6**).

A similar fast-slow continuum of life history traits and vital rates was proposed for batoids (skates and rays), with large body size typically associated with increased size and age at maturity, longevity, and biological vulnerability to exploitation (Frisk 2010). As for sharks, juvenile and adult survival and age at maturity appear to be the most important vital rates that influence population growth rates in batoids (Frisk et al. 2005). More recently, Gravel et al. (2024) also identified this fast-slow continuum of life history traits (and metabolic rate) noting that while teleosts are at the fast end of the spectrum and elasmobranchs are at the slow end, there is considerable overlap between the two groups (see next section).

Identifying vulnerable aquatic species

One possible framework to identify vulnerability based on productivity is that proposed by Musick (1999). This author provided some guidelines on criteria to define extinction risk in marine fishes in the context of IUCN (International Union for the Conservation of Nature) Red List assessments. He proposed a system of risk criteria modified from the IUCN Red List system whereby fish species are classified into four productivity categories (high, medium, low, very low) based on several parameters (intrinsic rate of increase, *r*; growth coefficient from the von Bertalanffy growth curve, *k*; annual fecundity; age at maturity; and lifespany).

Classification based on life-history parameters

Musick's (1999) criteria were used to classify sharks in the Cortés (2000) augmented study into the four productivity categories (high, medium, low, and very low) for four of the parameters (*k*, age at maturity, lifespan, and fecundity) for males and females separately (except for fecundity). For *k*, 38% of females and 54% of males fell in the medium and high categories (**Figure 7 top**); for age at maturity, 16% of females and 24% of males fell in the medium and high categories (**Figure 8 top**); for lifespan, 17% of females and 28% of males fell in the medium and high categories (**Figure 9 top**); and for fecundity, 0% of females fell in the medium and high categories (**Figure 10 top**).

Batoid species reported in Barrowclift et al. (2023) were also classified into the four productivity categories (for sexes combined since the data in that study were not sex specific). For *k*, 42% of species fell in the medium and high categories (**Figure 7 bottom**); for age at maturity, 18% of species fell in the medium and high categories (**Figure 8 bottom**); for lifespan, 19% of species fell in the medium and high categories (**Figure 9 bottom**); and for fecundity, 17% of females fell in the medium and high categories (**Figure 10 bottom**).

Bony fishes (mostly teleosts; Actinopterygii) used in Thorson et al. (2023) were also classified into the four productivity categories (also for combined sexes). For *k*, 89% of species fell in the medium and high categories (**Figure 11 top**); for age at maturity, 79% of species fell in the medium and high categories (**Figure 11 middle**); and for lifespan, 58% of species fell in the medium and high categories (**Figure 11 bottom**).

Table 2 shows the classification into the various productivity categories for sharks (females and males averaged), batoids, teleosts, and marine mammals. Sharks and batoids had generally similar values in each productivity category for all life history parameters compared (*k*, age at maturity, and lifespan), with the exception that batoids had substantially higher productivity based on fecundity (17% medium productivity for batoids vs. 0% medium productivity for sharks; **Table 2**). As expected, teleosts were classified as having substantially larger high and medium productivity based on the life history traits analyzed here (*k*, age at maturity, and lifespan) compared to those of the two groups of elasmobranchs. Fecundity for teleosts is obviously very high and low fecundity, especially for sharks, is the Achilles heel of this group.

However, the distributions of life history trait values from Thorson et al. (2023) (**Figures 12**, **13**, and **14;** supplementary material 2) show that there is overlap between teleosts (Actinopterygii) and elasmobranchs especially in *k* and age at maturity (**Figure 12**), lifespan and natural mortality (**Figure 13**) values as further attested by the 95% confidence intervals (computed as the 2.5th and 97.5th percentiles) (**Table 3**).

Classification based on r_{max}

Multiple sources that listed values of r_{max} were used to classify groups into the same four productivity categories (**supplementary material 3**). For sharks, using the Cortés (2016) augmented dataset, 27% of sharks fell into the medium and high categories (**Figure 15 top; Table 2**). For batoids, data from Barrowclift et al. (2023; n = 85) indicated that 88% of species fell into the medium and high categories (**Figure 15 bottom; Table 2**), whereas data from Gravel et al. (2024) for elasmobranchs (sharks, batoids; n = 94 and 1 chimaera) and teleosts (n = 129) indicated that 82% of the elasmobranchs in the dataset fell into the medium and high categories (**Figure 16 top**) compared to 93% of the teleosts included in their dataset (**Figure 16 bottom; Table 2**). Finally, data from Finucci et al. (2024) for elasmobranchs (sharks and batoids; n = 85) and marine mammals (n = 21) indicated that 59% of the elasmobranchs in the dataset (54% for sharks and 76% for batoids) fell into the medium and high categories (**Figure 17 top**) compared to 0% of the marine mammals included in their dataset (**Figure 17 bottom; Table 2**).

The distribution of productivity (r_{max}) values from the Cortés (2016) augmented study and the Barrowclift et al. (2023) studies suggests that skates are the most productive elasmobranchs, followed by rays and sharks, and that there is overlap among these taxa, particularly between skates and rays (**Figure 18**). Adding the values for elasmobranchs and teleosts reported in Gravel et al. (2024) also shows overlap among the different taxa, in particular between skates and teleosts (**Figure 19**). Finally, adding values for elasmobranchs and marine mammals from the Finucci et al. (2024) study shows some overlap between marine mammals and sharks and rays (and even some overlap for minimum values for teleosts), but especially some overlap between marine mammals and sharks (**Figure 20**).

Table 4 lists summary statistics of r_{max} for the different taxa from each of the studies. When grouping data from all studies it can be seen that batoids, in particular skates, are more productive than sharks, and that elasmobranchs as a group are less productive than teleosts and more productive than marine mammals. However, as attested by the 95% confidence intervals there is considerable overlap between elasmobranchs, in particular skates, and teleosts.

There was a large difference in r_{max} of sharks based on the Cortés (2016) augmented dataset compared to those from the Gravel et al. (2024) and Finucci et al. (2024) studies, and the values for batoids from the two latter studies and that of Barrowclift et al. (2023) for batoids seemed high (ranging from 0.161 to 0.301 on average for rays and from 0.356 to 0.448 for skates). The differences in reported r_{max} values from these multiple studies may be at least in part explained by methodological differences since the Barrowclift et al. (2013), Gravel et al. (2024), and Finucci et al. (2924) studies used an age-aggregated modified Euler-Lotka equation (Pardo et al. (2016)), whereas Cortés (2016) used an age-structured Euler-Lotka equation/life table approach, where the fertility and mortality schedules vary by age as opposed to the more simplified age-aggregated approach.

Nevertheless, the r_{max} values for batoids (in aggregate, mean = 0.336, median = 0.283, 2.5th percentile = 0.079, 97.5th percentile = 0.997, n = 137), especially those for skates, are surprisingly high and much more in line with those of teleost fishes than those for other large marine and terrestrial marine vertebrates. For example, Hutchings et al. (2012) reported a mean r_{max} of 0.43 for teleost fish (n = 47). Values reported for other marine vertebrates ranged from 0.02 to 0.18 for marine mammals (Wade 2009) and were extremely low for sea turtles (Heppell 1998); even if these values were not representative of the true r_{max}, both of these taxa are believed to have population growth rates more akin to those of some sharks. For further context and leaving potential methodological differences aside, r_{max} values for rays and skates reported in the combined Barrowclift et al. (2023), Gravel et al. (2024), and Finucci et al. (2024) studies are comparable to those of terrestrial vertebrates reported in Oli and Dobson (2003), such as the carnivores Arctic fox (*Alopex* *lagopus*; 0.372), wolf (*Canis lupus*; 0.458), cat (*Felis catus*; 0.434), and red fox (*Vulpes vulpes*; 0.388); and rodents such as Gunnison's prairie dog (*Cynomys gunnisoni*; 0.380) and Townsend's ground squirrel (*Spermophilus townsendii*; 0.274) to name a few.

The distribution of r_{max} for all aggregated sharks was also examined according to their CITES listing. While listed sharks tended to have lower productivity (**Table 5**), there was no clear pattern (**Figure 21**). Listed batoids (rays) also tended to have lower productivity (**Table 4**) but no clear pattern (**Figure 22**).

Decline thresholds

Musick (1999) subsequently suggested several distinct population segments (DPS) decline thresholds (over the longer of 10 years or 3 generations) based on the productivity categories discussed to list the species as vulnerable (**Table 2A**). Very low, low, medium, and high productivity categories would correspond to decline thresholds of 70%, 85%, 95%, and 99%, respectively. Using the average classification of the five productivity parameters (k, t_{mat}, t_{max}, fecundity, and r_{max}) from the Cortés (2000) augmented and Barrowclift et al. (2023) datasets, 32% of sharks and only 17% of batoids would fall in the *very low* productivity category corresponding to the least productive species ($r < 0.05 yr^{-1}$; $k < 0.05\ yr^{-1}$; fecundity < 10; age at maturity > 10 years; and lifespan > 30 years), with a corresponding decline threshold of 70% to be listed as vulnerable (**Table 2B**). For comparison, the average classification of three productivity parameters (k, t_{mat}, t_{max}) from the Thorson et al. (2023) dataset also results in only 2% of teleosts falling in the very low productivity category. Taking r_{max} as the most representative parameter of productivity (since it uses all the other parameters in its computation), only 23% of sharks and 2% of batoids would fall in the very low productivity category. Adding the two additional datasets that had r_{max} values (Gravel et al. (2024) and Finucci et al. (2024)) results in a more optimistic classification of productivity with only 14% and 1% of sharks and batoids, respectively falling in the very low productivity category (**Table 2B**). **Figure 23** depicts the classification of the different taxa into these four productivity categories based on r_{max}. Teleosts have the highest proportion of species in the high productivity category—as expected—followed by batoids and sharks, but batoids have a high proportion of species in the medium productivity category whereas sharks have similar proportions in the medium and low productivity categories. Unsurprisingly, the marine mammal species analyzed only fall in similar proportions in the very low and low productivity categories.

Regardless of the productivity categories and decline thresholds ultimately chosen to list species, these results show that elasmobranchs exhibit a high degree of variation in their life history and productivity and that "one size does not fit all" when trying to set these thresholds.

These results also indicate that there is only a small percentage of elasmobranch species, in particular sharks, that have very low productivity and would be subject to the most restrictive population decline threshold of 70%. This criterion coincides with the recommendation first introduced by Sainsbury (2008) that best-practice Limit Reference Points (LRPs; Clarke and Hoyle 2014) —used to set boundaries so that harvesting can be constrained within safe biological limits; sometimes referred to as conservation reference points—for elasmobranchs be set at $0.3B_0$ or, in other words, at a stock size 30% of the virgin level.

Annex 5 of Resolution Conf. 9.24 (Rev. CoP17) states that a general guideline for a marked historical extent of decline is a percentage decline to 5% to 30% of the baseline, depending on the biology and productivity of the species. Footnote 2 in Annex 5 refers to a historical extent of population decline to 15-20% to assess whether a decline is 'marked' for commercially exploited aquatic species with low productivity; a range of 5-10% being applicable for species with high productivity and 10 – 15% for species with medium productivity. In other words, the 30% decline referred to in Annex 5 seems to align with the population decline contemplated in the LRP above and the Musick (1999) criterion for listing very low productivity species as vulnerable in the IUCN scheme. In contrast, the IUCN Red List (IUCN 2012) under criterion A1 (for population reduction where the causes of the reduction are clearly reversible and understood and have ceased) classifies species with ≥ 70% population reduction as endangered (their second highest extinction risk category).

Variability in productivity, associated vulnerability, and management reference points in elasmobranchs

Additional measures of productivity and associated reference points are often used in fisheries contexts. Steepness, defined as the ratio of recruitment when stock abundance has decreased to 20% of its virgin level divided by recruitment when the stock is unexploited, is one common way of expressing vulnerability to fishing. Steepness can also be expressed in terms of SPR (spawning potential ratio), which is the ratio between spawners (or eggs) produced over a recruit's lifetime (given fishing mortality F) and spawners produced without fishing. After specifying the appropriate %SPR, the fishing mortality F that achieves that SPR ($F_{\%SPR}$) can be calculated given fishery selectivity. Both steepness and SPR measure the proportional reduction in total potential productivity that can be attributed to fishing (Brooks et al. 2010). Steepness ranges from 0.2 to 1, with values close to its lower limit indicating that less exploitation is allowable. Similarly, when specifying an appropriate fishing level ($F_{\%SPR}$) the closer %SPR is to 100% the less exploitation is allowed. Brooks et al. (2010) defined an analogous measure of SPR termed SPR_{MER} (SPR at Maximum Excess Recruitment) which also varies from 0 to 100% and is related to yet another quantity known as the maximum lifetime reproductive rate ($\hat{\propto}$), which is the number of recruits produced by a recruit over its entire lifetime in the absence of fishing. All these metrics ($\hat{\propto}$, SPR_{MER}, and steepness) can be obtained analytically if life history information is available. Brooks et al. (2010) found that values of SPR_{MER} for 11 shark populations assessed with fishery stock assessment methods ranged from 0.26 to 0.89 and Cortés and Brooks (2018) found that $\hat{\propto}$ ranged from 1 to ~19 for 33 assessed shark stocks.

The position of the inflection point of population growth curves (R) or the associated shape parameter—the fraction of the carrying capacity (K) at which the maximum production occurs—varies along a continuum across animal species (Fowler 1981a, 1988). Very productive commercial fish species reach the inflection point at a low fraction of K, whereas some large mammals are believed to reach the inflection point at population levels well above 0.5K (Fowler 1981b, 1987). In traditional fisheries surplus production models, the assumption is that the inflection point occurs at 0.5K, which defines the biomass at Maximum Sustainable Yield or B_{MSY} or, in other words, that MSY is reached at half the carrying capacity. However, for species with delayed density dependence (where negative effects of density dependence do not depress growth until near K), such as large mammals, the net change in abundance occurs near K. The inflection point (R) can be analytically derived based on the dimensionless rate of increase per generation (the product of r_{max} and generation time). Cortés (2008) in a study of eight pelagic shark species found that values of R ranged from near 0.5K for the blue shark to values close to K for some of the other species (**Figure 24**). This information was updated with data from the Cortés (2016) augmented dataset. Any species with an R value lower than 0.5 is capable of withstanding larger population declines since they reach their maximum production when their populations are decreased to less than 0.5 the virgin biomass (**Figure 25**).

Challenges of grouping all sharks and rays into a single entity for management purposes

The different metrics of productivity all show that there is a continuum of values and that the "one- size-fits-all" paradigm can be problematic because productivity is determined by the life history traits and vital rates of each species/stock. As a group, sharks and cartilaginous fishes in general are less productive and more susceptible to fisheries exploitation than teleosts and more akin to marine mammals, but given the variety of life history strategies in this group they cannot all be managed identically since the life history traits/vital rates and ensuing measures of productivity strongly determine the management reference points. This shortcoming is explicitly recognized in the definition of Decline in Annex 5 of Resolution Conf 9. 24 (Rev. CoP17) where it is stated that "the extremes of 5% and 30% will be applicable to only a relatively small number of species, but some species may even fall outside of these extremes. However, both these figures are presented only as examples, since it is not possible to give numerical values that are applicable to all taxa because of differences in their biology ([2]see footnote with respect to application of decline to commercially exploited aquatic species)”.

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Table 1. Summary and description of the life history traits/parameters included in the different datasets used in this study.

Life history trait	Abbreviation	Unit	Meaning
Growth completion rate	k	/ year	A constant that describes how quickly the maximum length is reached. Also referred to as the growth coefficient from the von Bertalanffy growth function
Age at maturity	t_{mat}	years	The age at which (50% of) individuals become mature
Maximum age	t_{max}	years	The maximum age of individuals in a population
Annual fecundity	fecundity	pups / year	The number of pups produced by a female in a year
Intrinsic rate of increase	r_{max}	/ year	The rate at which a population increases in a year. A direct measure of productivity
Natural mortality rate	M	/ year	The rate at which animals die in a year
Theoretical maximum length	L_{inf}	cm total length	The theoretical maximum mean length of a population
Length at maturity	L_{mat}	cm total length	The length at which (50% of) individuals become mature

Table 2. A) Values of productivity based on life history parameters (*k*: growth coefficient from the von Bertalanffy growth function; t_{mat}: age at maturity; t_{max}: maximum age; fecundity: annual number of pups produced; and r_{max}: intrinsic rate of population growth) suggested by Musick (1999) to categorize species into four categories (high, medium, low, and very low); B) classification of sharks, batoids, teleosts, and marine mammals into each of these four categories according to several productivity parameters with the corresponding decline threshold that would trigger a listing of *vulnerable*. Data are from several sources: sharks (Cortés (2000) augmented; Cortés (2016) augmented; Gravel et al. (2024); Finucci et al. (2024)), batoids (Barrowclift et al. (2023; Gravel et al. (2024); Finucci et al. (2024)); teleosts (Thorson et al. (2023)); marine mammals (Finucci et al. 2024).

A	Productivity			
	High	Medium	Low	Very low
k	>0.30	0.16-0.30	0.05-0.15	<0.05
t_{mat}	<1 yr	2-4 yr	5-10 yr	>10 yr
t_{max}	1-3 yr	4-10 yr	11-30 yr	>30 yr
fecundity (yr^{-1})	>10000	100-1000	10-99	<10
r_{max} (yr^{-1})	>0.50	0.16-0.50	0.05-0.15	<0.05

B										
	Productivity						Productivity			
Sharks	High	Medium	Low	Very low		**Batoids**	High	Medium	Low	Very low
k	0.13	0.33	0.45	0.08		k	0.10	0.32	0.48	0.11
t_{mat}	0.01	0.19	0.49	0.31		t_{mat}	0.01	0.17	0.61	0.22
t_{max}	0.00	0.23	0.60	0.17		t_{max}	0.00	0.19	0.68	0.13
fecundity (yr^{-1})	0.00	0.00	0.20	0.80		fecundity (yr^{-1})	0.00	0.17	0.44	0.39
r_{max} (yr^{-1})	0.00	0.27	0.50	0.23		r_{max} (yr^{-1})	0.22	0.66	0.09	0.02
Mean	0.03	0.20	0.45	0.32		Mean	0.07	0.30	0.46	0.17
r_{max} (yr^{-1})*	0.04	0.45	0.37	0.14		r_{max} (yr^{-1})*	0.19	0.68	0.12	0.01
Teleosts						**Marine mammals**				
k	0.53	0.36	0.11	0.00		r_{max} ($yr^{-1)}$	0.00	0.00	0.52	0.48
t_{mat}	0.09	0.70	0.18	0.03						
t_{max}	0.06	0.52	0.39	0.04						
Mean	0.22	0.52	0.23	0.02						
r_{max} (yr^{-1})**	0.64	0.29	0.05	0.02						
Decline threshold	99%	95%	85%	70%		Decline threshold	99%	95%	85%	70%

* Adding values from Gravel et al. (2024) and Finucci et al. (2024)

** Values from Gravel et al. (2024)

Table 3. Summary statistics of life history parameters (L_{inf}: theoretical maximum length (cm); *k*: growth coefficient from the von Bertalanffy growth function (yr^{-1}); t_{max}: maximum age (years); t_{mat}: age at maturity (years); *M*: natural mortality rate (yr^{-1}); and L_m: length at maturity (cm)) from Thorson et al. (2023) for Actinopterygii (teleosts) and elasmobranchs (sharks and rays). lcl = lower 95% confidence limit; ucl = upper 95% confidence limit; n = sample size.

Teleosts	L_{inf}	k	t_{max}	t_{mat}	M	L_m
mean	47.1	0.439	11.4	3.1	0.77	24.9
median	35.9	0.316	8.7	2.4	0.57	20.2
lcl	8.2	0.091	2.2	0.6	0.12	4.8
ucl	151.6	1.401	40.1	10.0	2.76	74.7
n	2041	2041	2041	2041	2041	2041
Elasmobranchs						
mean	186.4	0.158	19.9	8.8	0.26	114.1
median	126.8	0.140	17.1	7.3	0.23	82.3
lcl	58.9	0.055	7.8	2.8	0.10	41.8
ucl	530.4	0.462	48.7	22.5	0.62	301.8
n	107	107	107	107	107	107

Table 4. Values of productivity (r_{max} (yr^{-1})) for sharks, rays, skates, batoids (skates and rays), elasmobranchs (sharks, skates and rays), teleosts, and marine mammals extracted from multiple recent studies. lcl = lower 95% confidence limit; ucl = upper 95% confidence limit; n = sample size.

Study	Cortes	Barrowclift et al. (2023)			Gravel et al. (2024)					Finucci et al. (2024)				
Taxon	Sharks	Rays	Skates	Batoids	Rays	Skates	Sharks	Elasmobranchs	Teleosts	Rays	Skates	Sharks	Elasmobranchs	Marine mammals
mean	**0.117**	**0.301**	**0.448**	**0.357**	**0.276**	**0.356**	**0.261**	**0.278**	**0.748**	**0.161**	**0.410**	**0.221**	**0.239**	**0.058**
median	0.085	0.250	0.368	0.286	0.296	0.366	0.191	0.235	0.729	0.154	0.381	0.157	0.176	0.053
lcl	0.007	0.032	0.179	0.056	0.119	0.253	0.058	0.067	0.105	0.080	0.177	0.042	0.043	0.020
ucl	0.353	0.803	1.090	1.031	0.517	0.531	0.571	0.571	2.081	0.347	0.848	0.746	0.825	0.131
n	101	53	32	85	13	15	67	95	129	12	12	61	85	21

	All datasets combined						
	Sharks	Rays	Skates	Batoids	Elasmobranchs	Teleosts	Marine mammals
mean	**0.186**	**0.274**	**0.417**	**0.336**	**0.243**	**0.748**	**0.058**
median	0.146	0.231	0.366	0.283	0.191	0.729	0.053
lcl	0.020	0.051	0.177	0.079	0.022	0.105	0.020
ucl	0.571	0.592	1.011	0.957	0.675	2.081	0.131
n	227	78	59	137	365	129	21

Table 5. Values of productivity (r_{max} (yr^{-1})) for sharks and rays extracted from multiple recent studies according to whether they are listed or not in CITES appendices. lcl = lower 95% confidence limit; ucl = upper 95% confidence limit; n = sample size.

	Sharks		Rays	
	listed	not listed	listed	not listed
mean	0.156	0.234	0.239	0.283
median	0.116	0.202	0.227	0.233
lcl	0.012	0.034	0.022	0.082
ucl	0.525	0.571	0.506	0.718
n	140	87	15	63

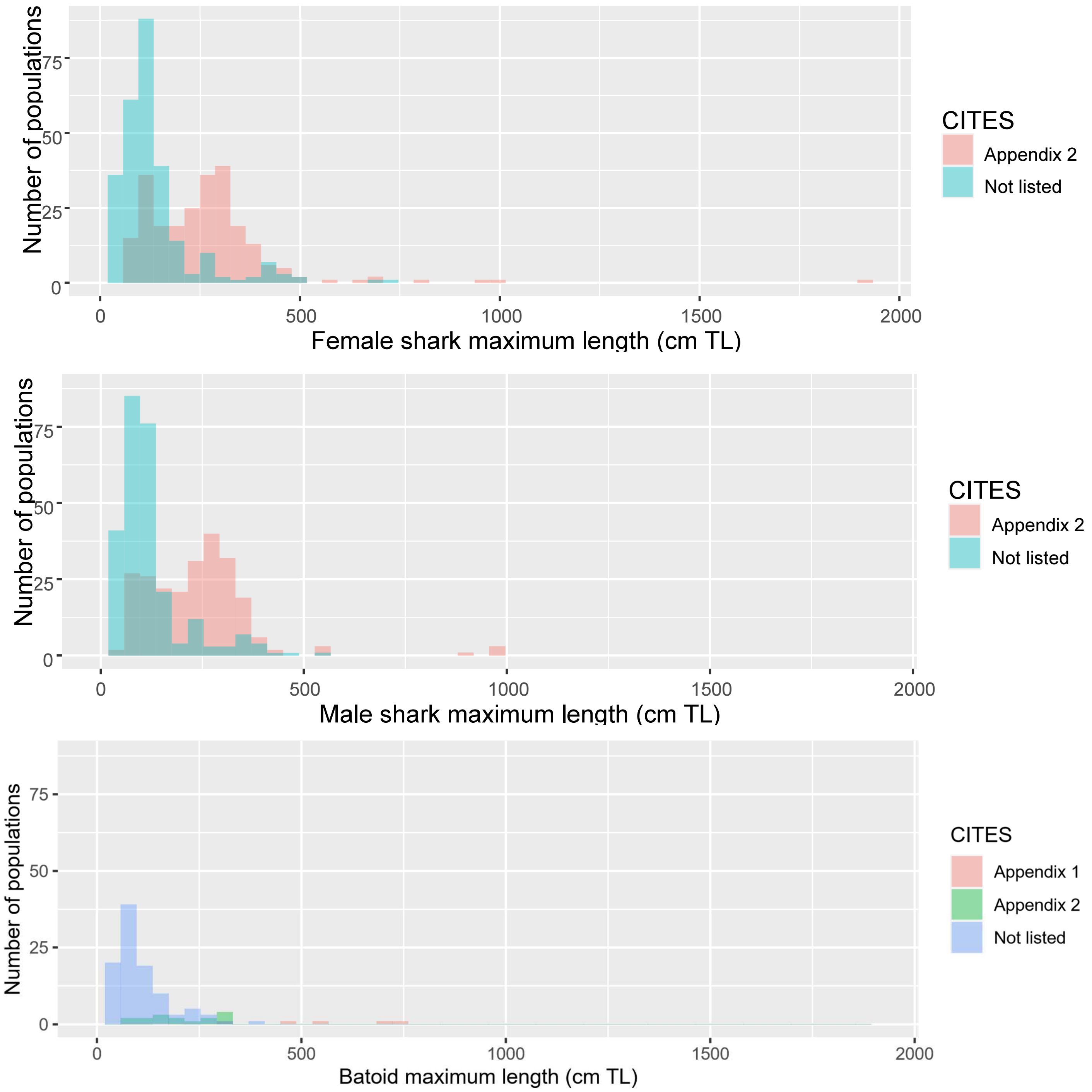


Figure 1. Length frequency distributions of female sharks (top), male sharks (middle), and batoids (bottom) for populations of listed and non-listed CITES species obtained with combined data from the Cortés (2000) augmented study and that of Barrowclift et al. (2023).

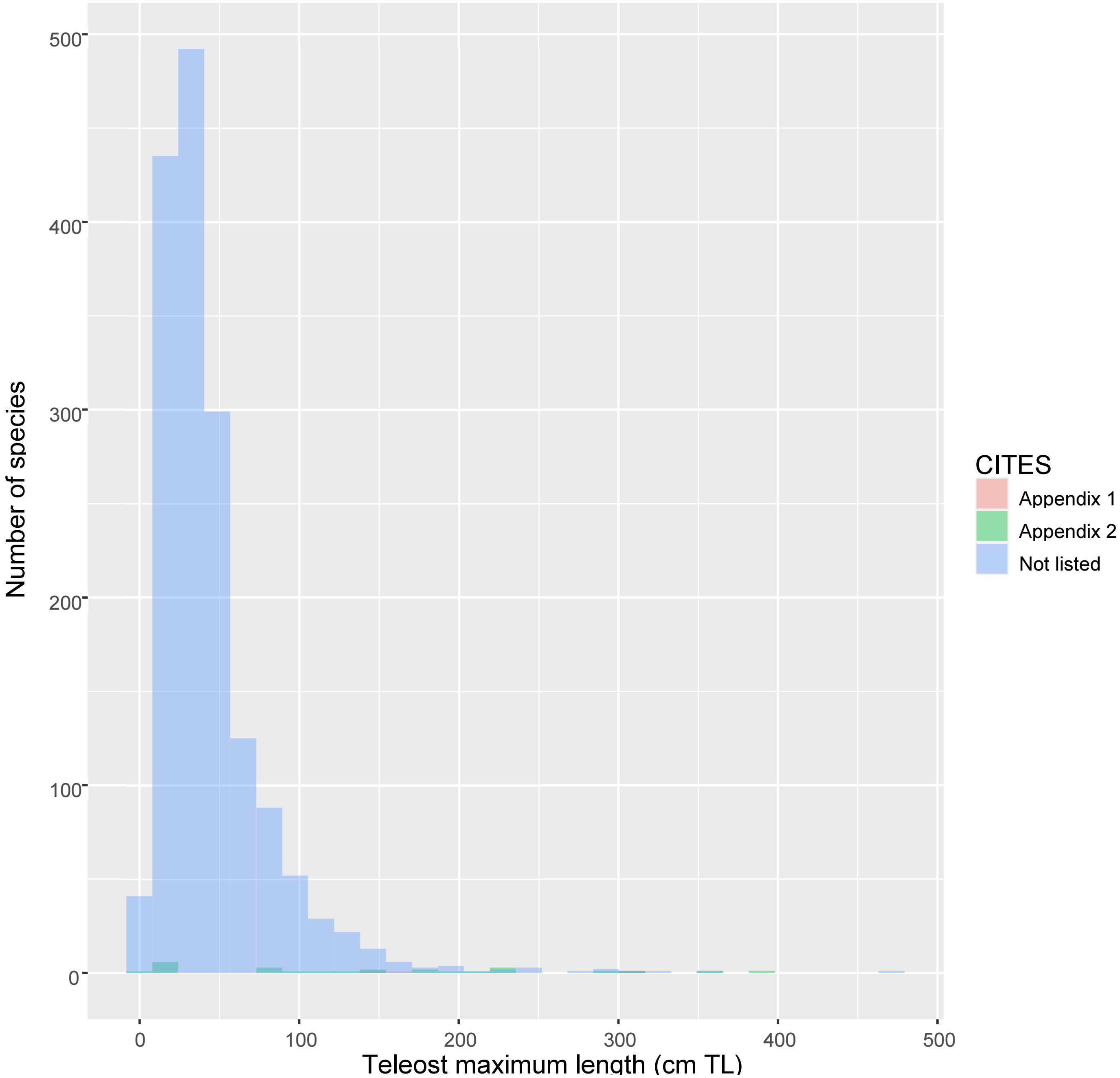


Figure 2. Length frequency distributions of teleosts for listed and non-listed CITES species obtained with data from Thorson et al. (2023).

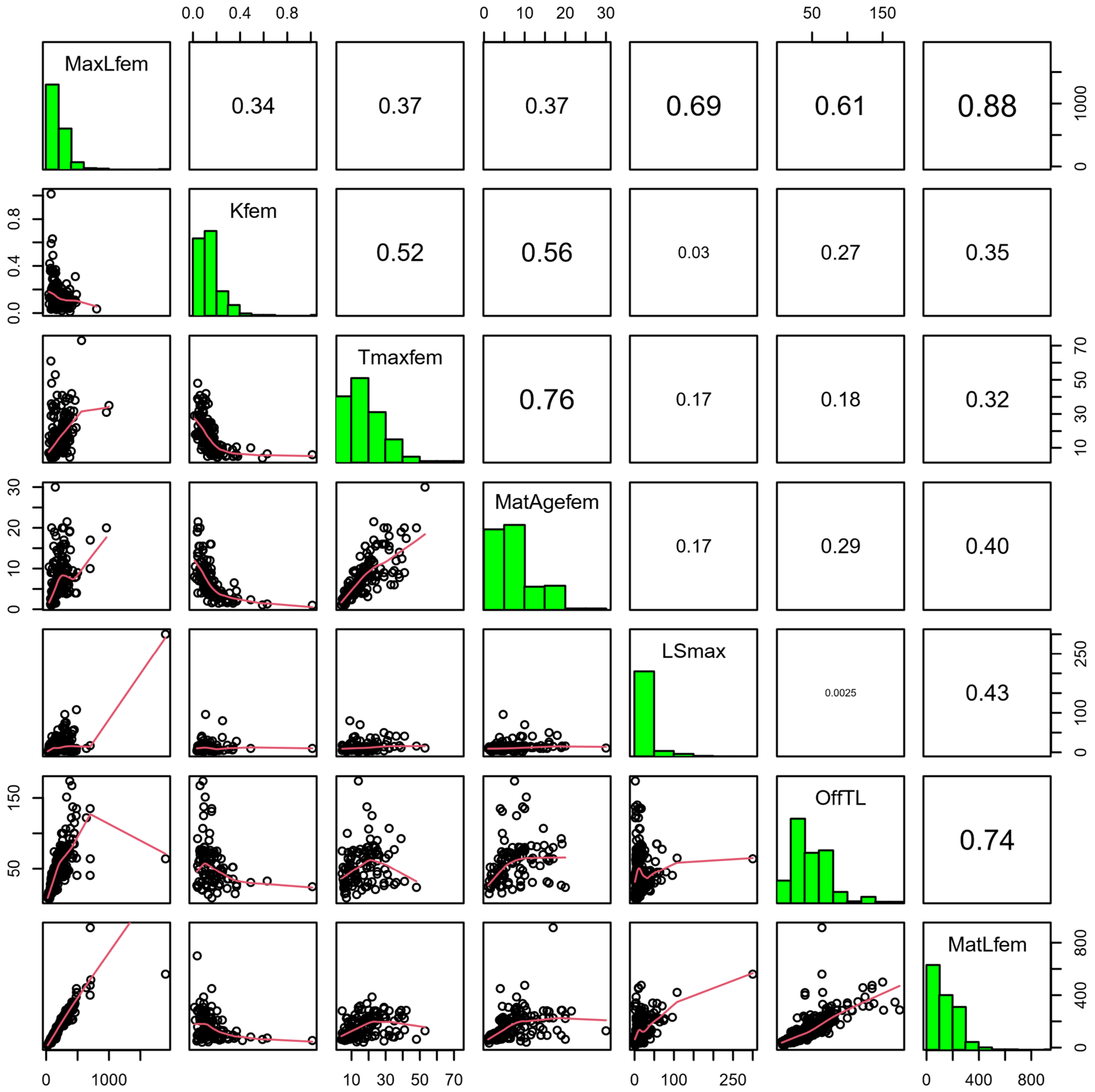


Figure 3. Scatter plot matrix of life history parameters (MaxLfem=female maximum length, Kfem=female k, Tmaxfem=female maximum age, MatAgefem=female age at maturity, LSmax=maximum litter size, OffTL=offspring size, MatLfem=female length at maturity) obtained with combined data from the Cortés (2000) augmented study and that of Barrowclift et al. (2023). Correlation coefficients are shown in the upper panels; histograms in the diagonal panels, and smoothed regressions in the lower panels.

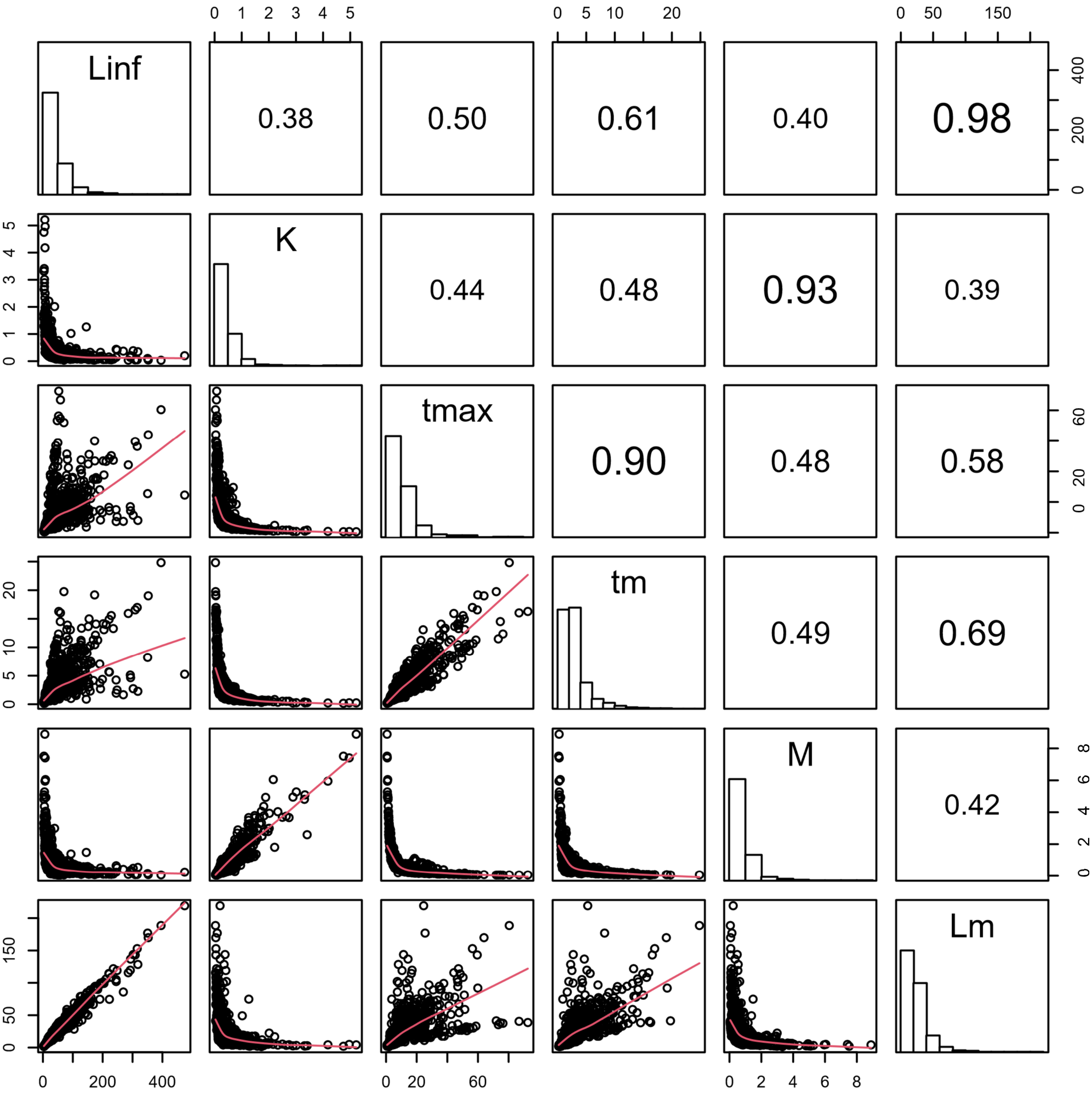


Figure 4. Scatter plot matrix of life history parameters (Linf=theoretical maximum length, *k*, tmax=maximum age, tm=age at maturity, M=natural mortality, Lm=length at maturity) obtained with data from the Thorson et al. (2023) study. Correlation coefficients are shown in the upper panels; histograms in the diagonal panels, and smoothed regressions in the lower panels.

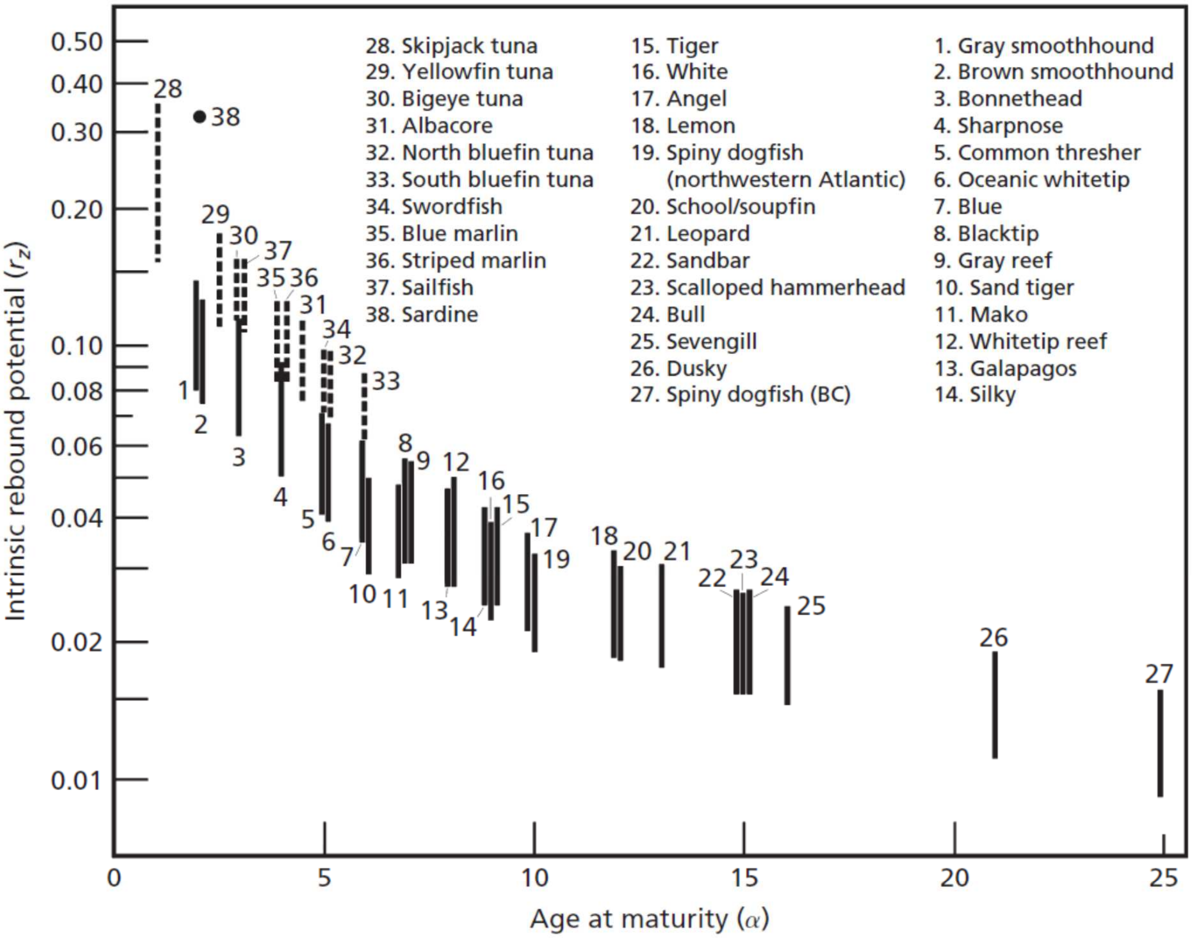


Fig. 26.2 The relationship of rebound potential r_Z to age at maturity α for selected sharks (numbered 1–27) and teleosts (numbered 28–38). The r_Z are represented as ranges delimited by r_Z calculated with b-ratio 1.25 and 1.00, respectively (with $Z = 1.5M$ for sharks and $2.0M$ for the pelagic teleosts). The estimate for sardine productivity is from Murphy (1967) (solid circle). Ten of the sharks shown are from Table 26.1; the other 17 are recalculated from Smith *et al.* (1998), using $Z = 1.5M$. Note that the y-axis is log scale.

Figure 5. Extracted from Au et al. (2008). The vertical lines depict a range of productivity values for each species (solid lines are for sharks; dashed lines are for teleosts).

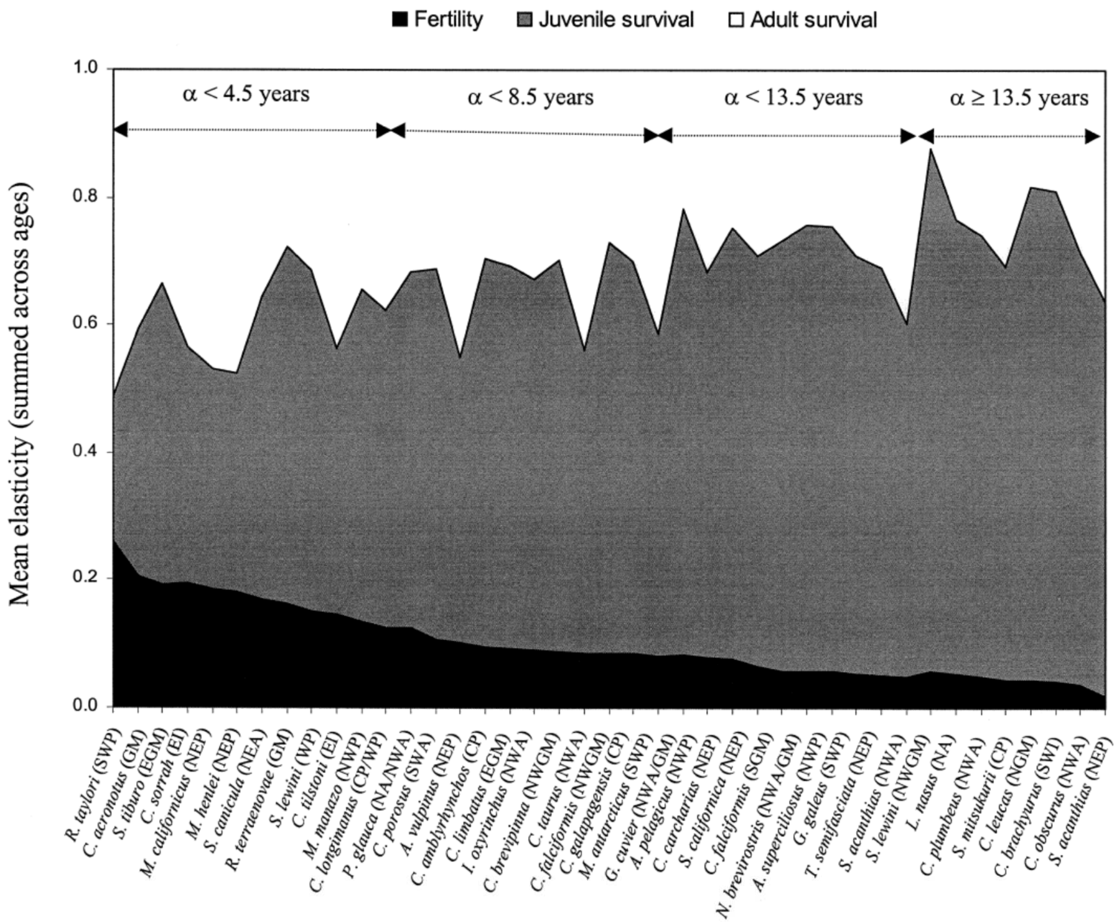


Figure 3. Mean elasticities (summed across ages) of 41 shark populations from 38 species obtained through Monte Carlo simulation. Populations are grouped by age at maturity (α) and ordered by increasing generation time. Geographical codes in parentheses after species names are as follows: GM, Gulf of Mexico; NWGM, northwestern Gulf of Mexico; SGM, southern Gulf of Mexico; EGM, eastern Gulf of Mexico; NWA, northwestern Atlantic; NA, northern Atlantic; NEA, northeastern Atlantic; SWA, southwestern Atlantic; CP, central Pacific; WP, western Pacific; NEP, northeastern Pacific; NWP, northwestern Pacific; SWP, southwestern Pacific; SWI, southwestern Indian; EI, eastern Indian.

Figure 6. Extracted from Cortés (2002). Species/populations listed in this figure are increasingly less productive (mature later and have longer generation lengths) as one moves from left to right.

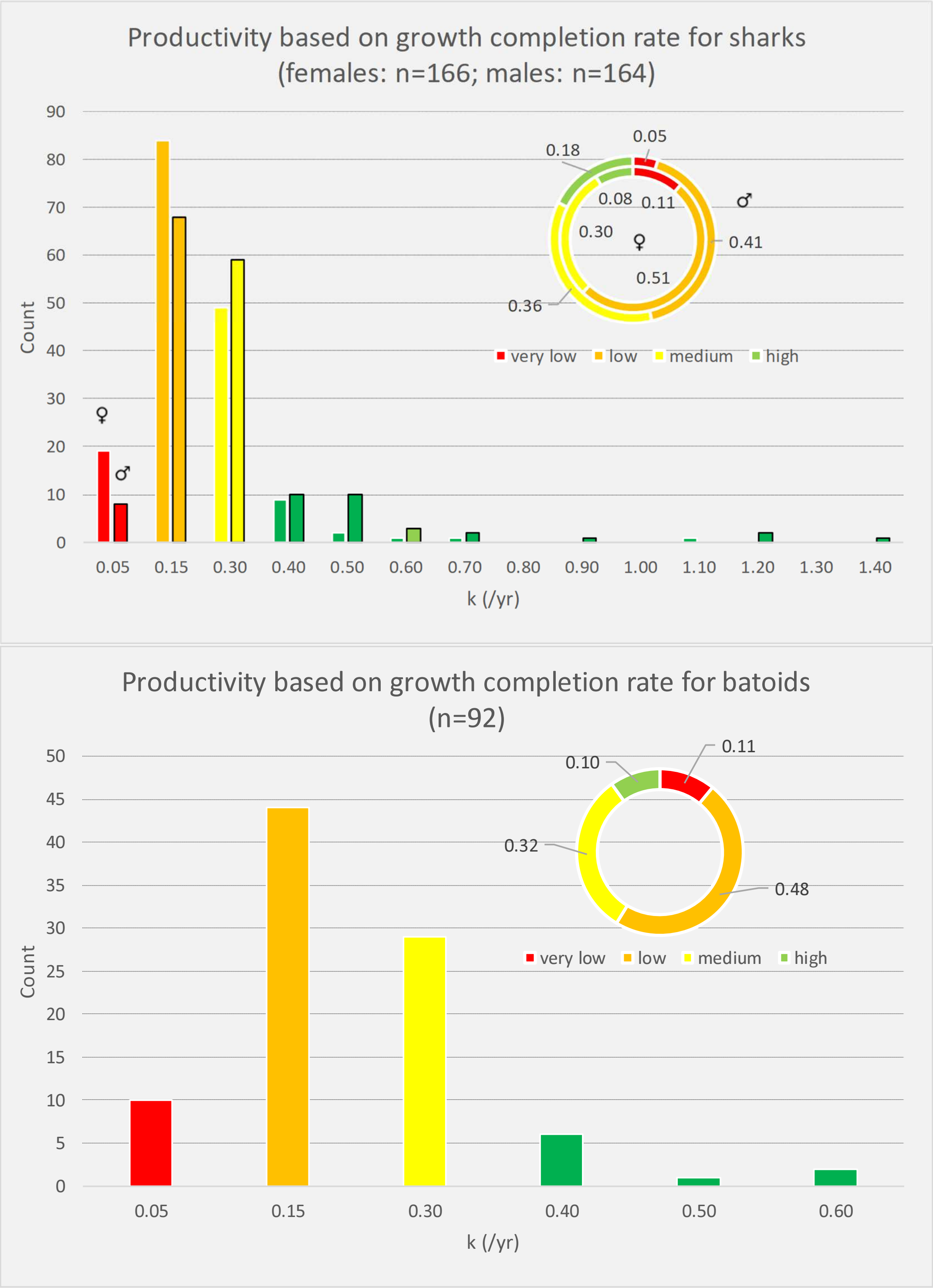
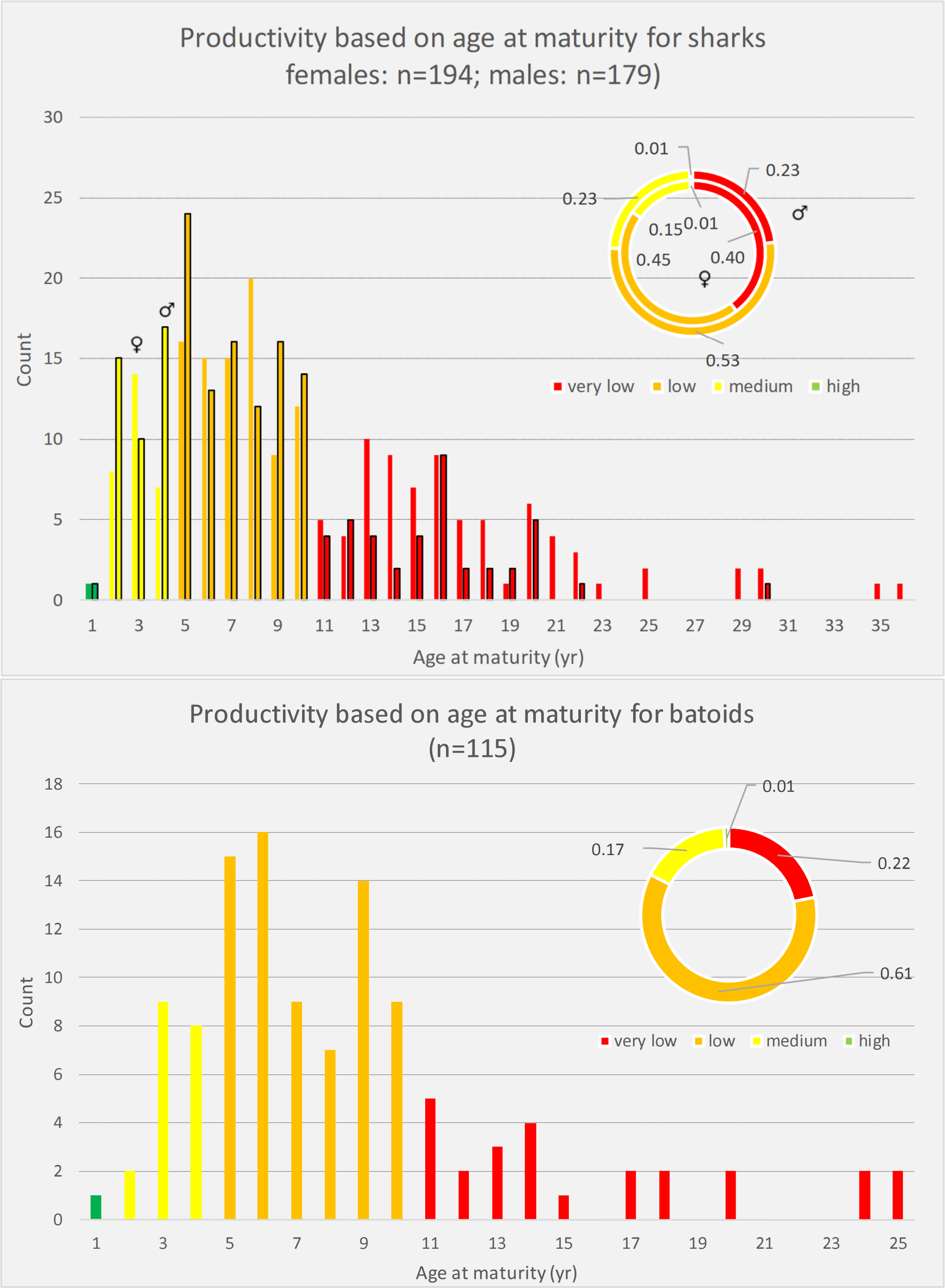


Figure 7. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for parameter ***k*** (growth completion rate from the von Bertalanffy growth curve) from Musick (1999). Top panel: sharks; bottom panel: batoids. For sharks, bars with black outline are for males and those without, for females. The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.



Productivity based on age at maturity for sharks
females: n=194; males: n=179)

Productivity based on age at maturity for batoids
(n=115)

Figure 8. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for **age at maturity** from Musick (1999). Top panel: sharks; bottom panel: batoids. For sharks, bars with black outline are for males and those without, for females. The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

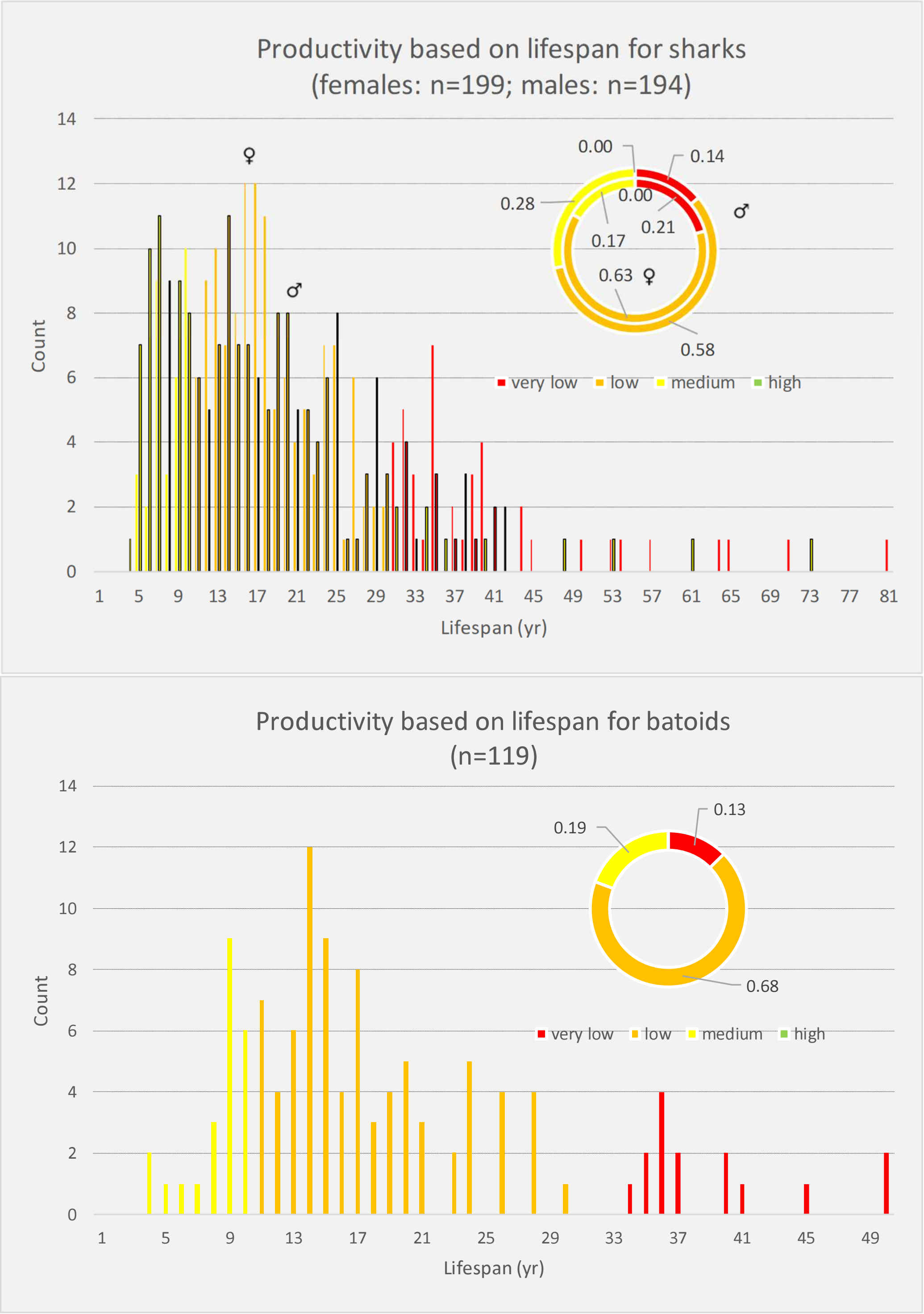


Figure 9. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for **lifespan** from Musick (1999). Top panel: sharks; bottom panel: batoids. For sharks, bars with black outline are for males and those without, for females. The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

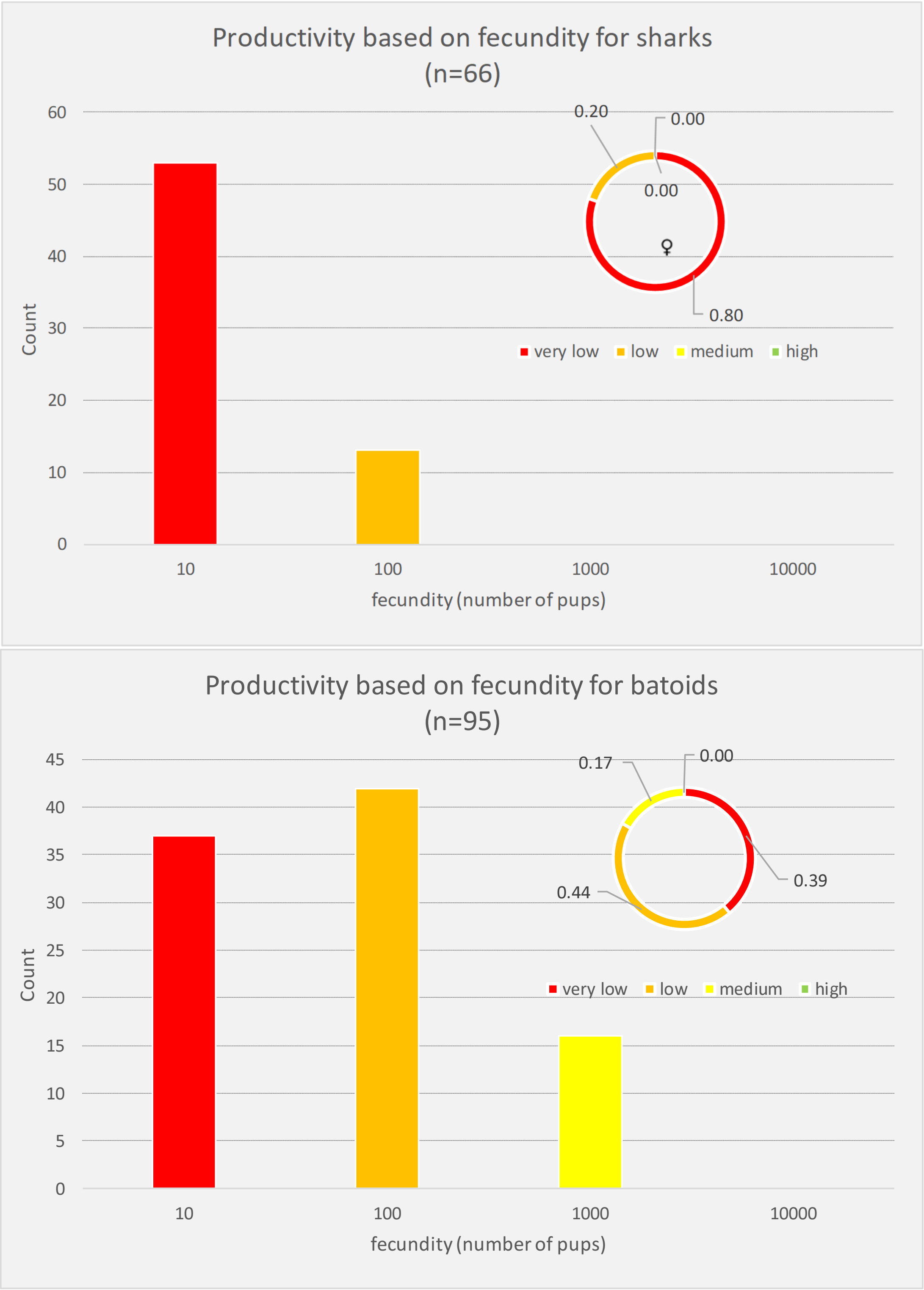


Figure 10. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for **fecundity** from Musick (1999). Top panel: sharks; bottom panel: batoids. The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

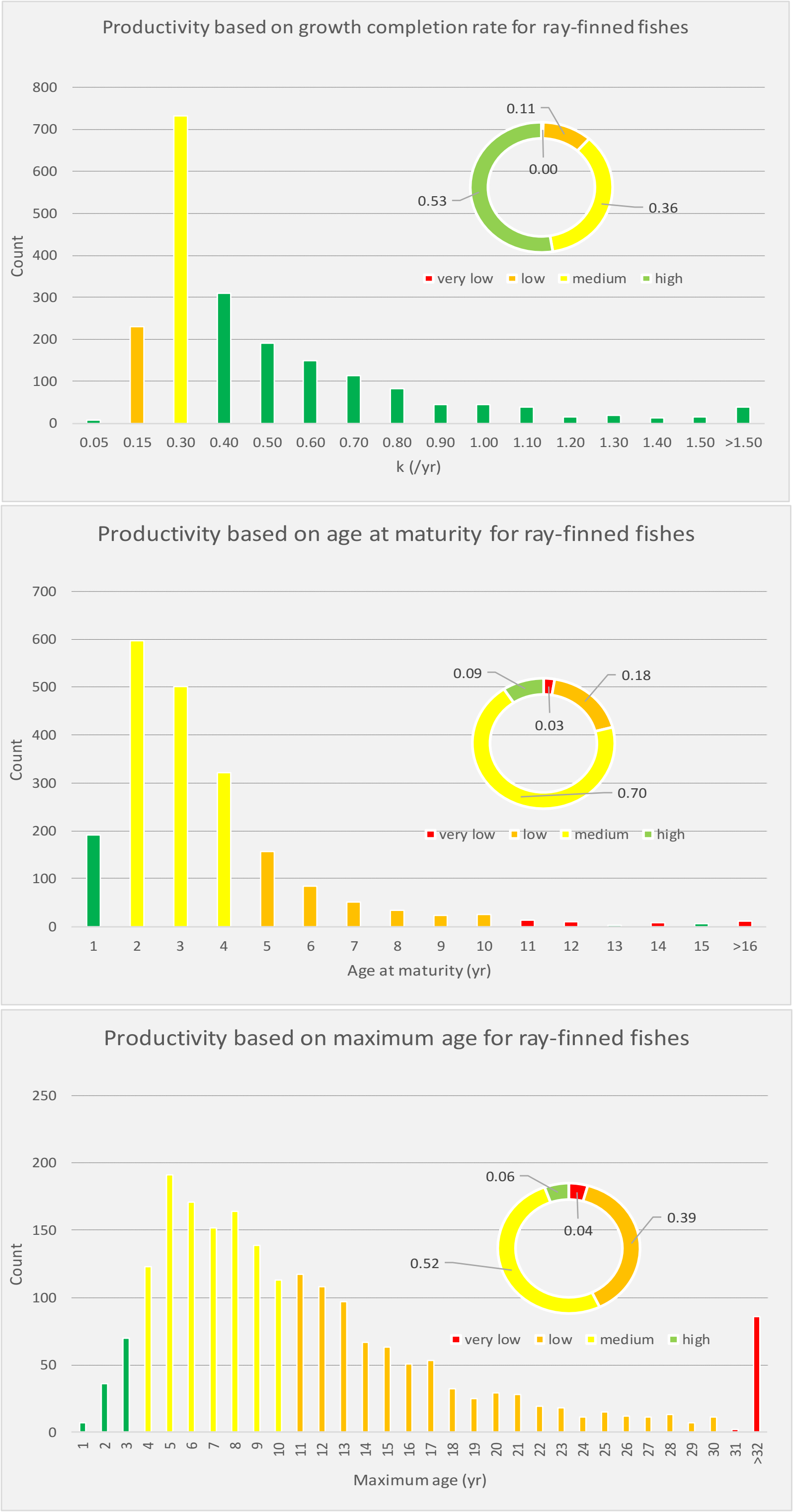


Figure 11. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for ***k*** (top), **age at maturity** (middle), and **maximum age** (bottom) from Musick (1999) for teleosts (n=2,041). The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

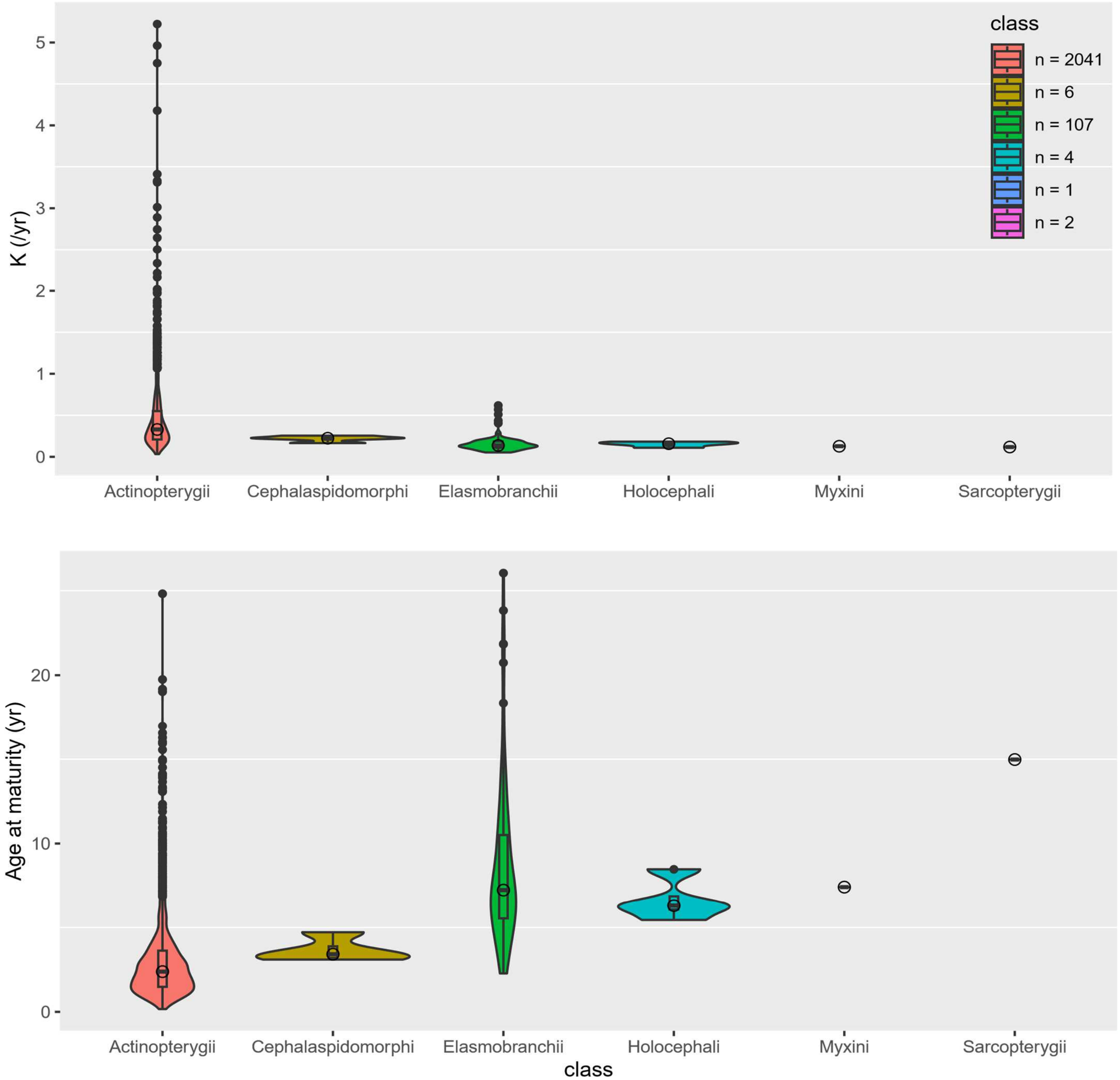


Figure 12. Violin/box plots of the distribution of *k* (top) and age at maturity (bottom) for classes of fishes included in data from Thorson et al. (2023) extracted from FishBase. The violin plot indicates density of points; inside the violin are the median (dash), mean (circle), interquantile range (25th to 75th percentile; box), 1.5 x IQR (whiskers), and outliers (dots).

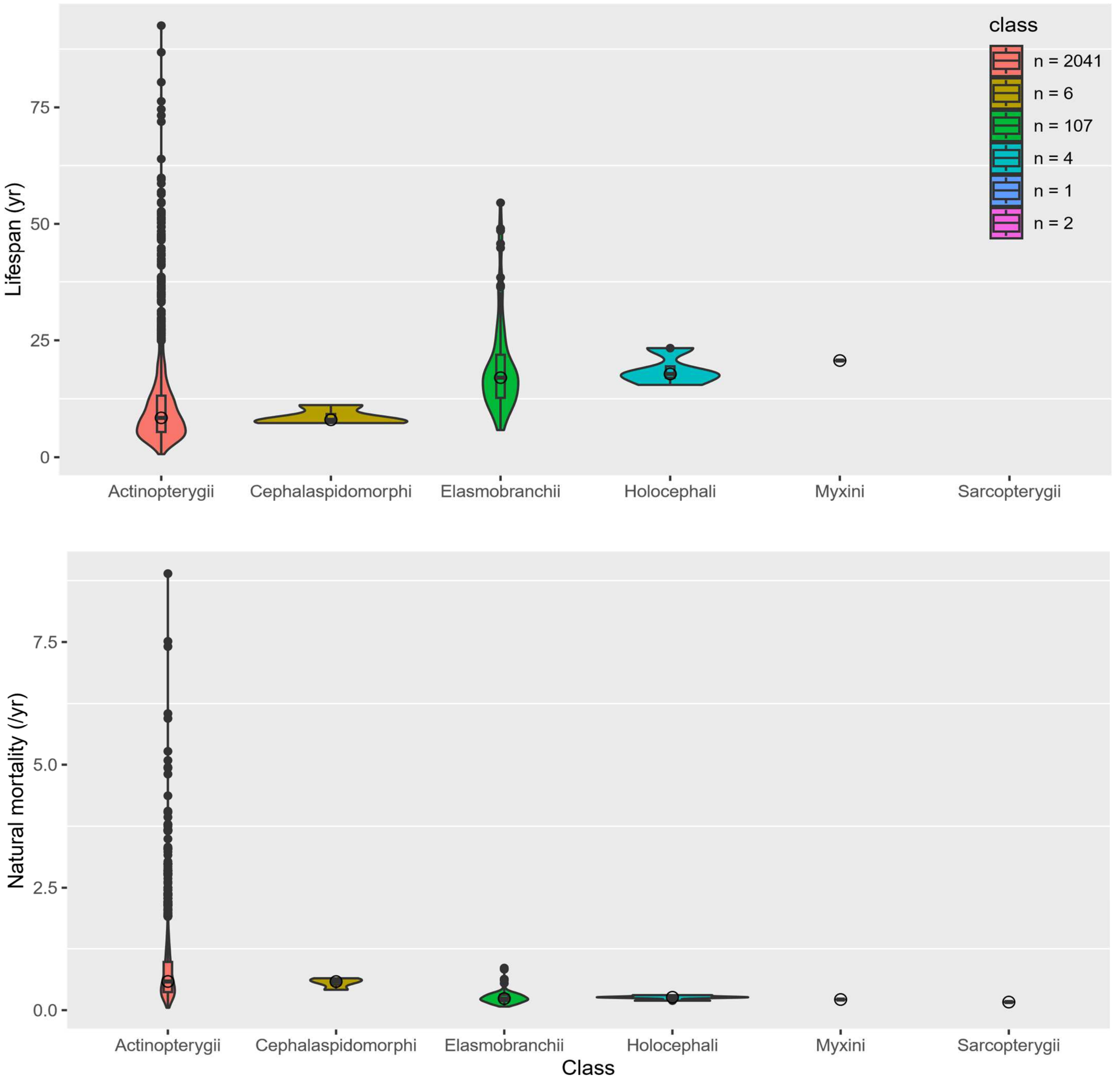


Figure 13. Violin/box plots of the distribution of lifespan (top) and natural mortality (bottom) for classes of fishes included in data from Thorson et al. (2023) extracted from FishBase. The violin plot indicates density of points; inside the violin are the median (dash), mean (circle), interquantile range (25th to 75th percentile; box), 1.5 x IQR (whiskers), and outliers (dots).

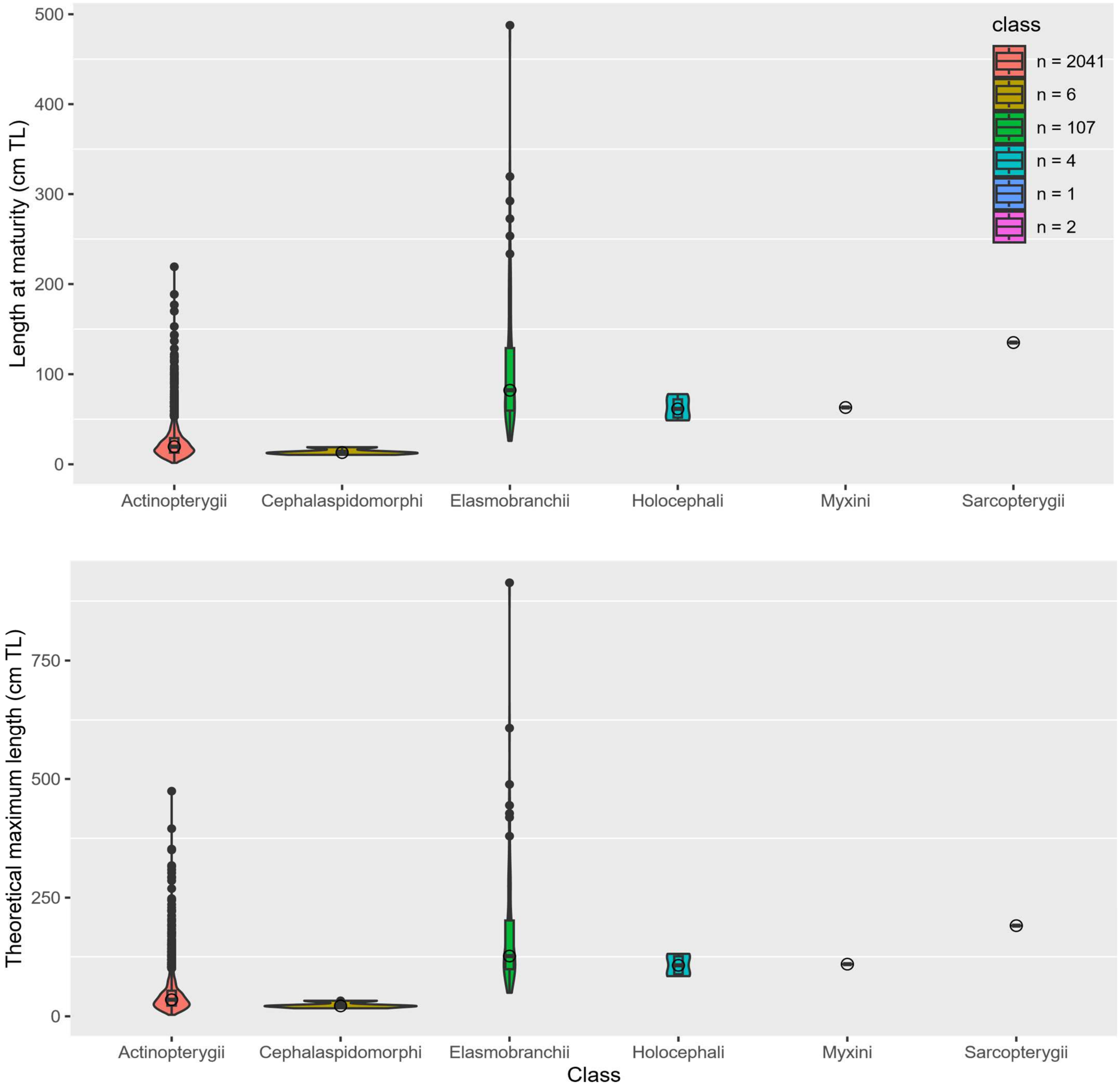


Figure 14. Violin/box plots of the distribution of length at maturity (top) and theoretical maximum length (bottom) for classes of fishes included in data from Thorson et al. (2023) extracted from FishBase. The violin plot indicates density of points; inside the violin are the median (dash), mean (circle), interquantile range (25th to 75th percentile; box), 1.5 x IQR (whiskers), and outliers (dots).

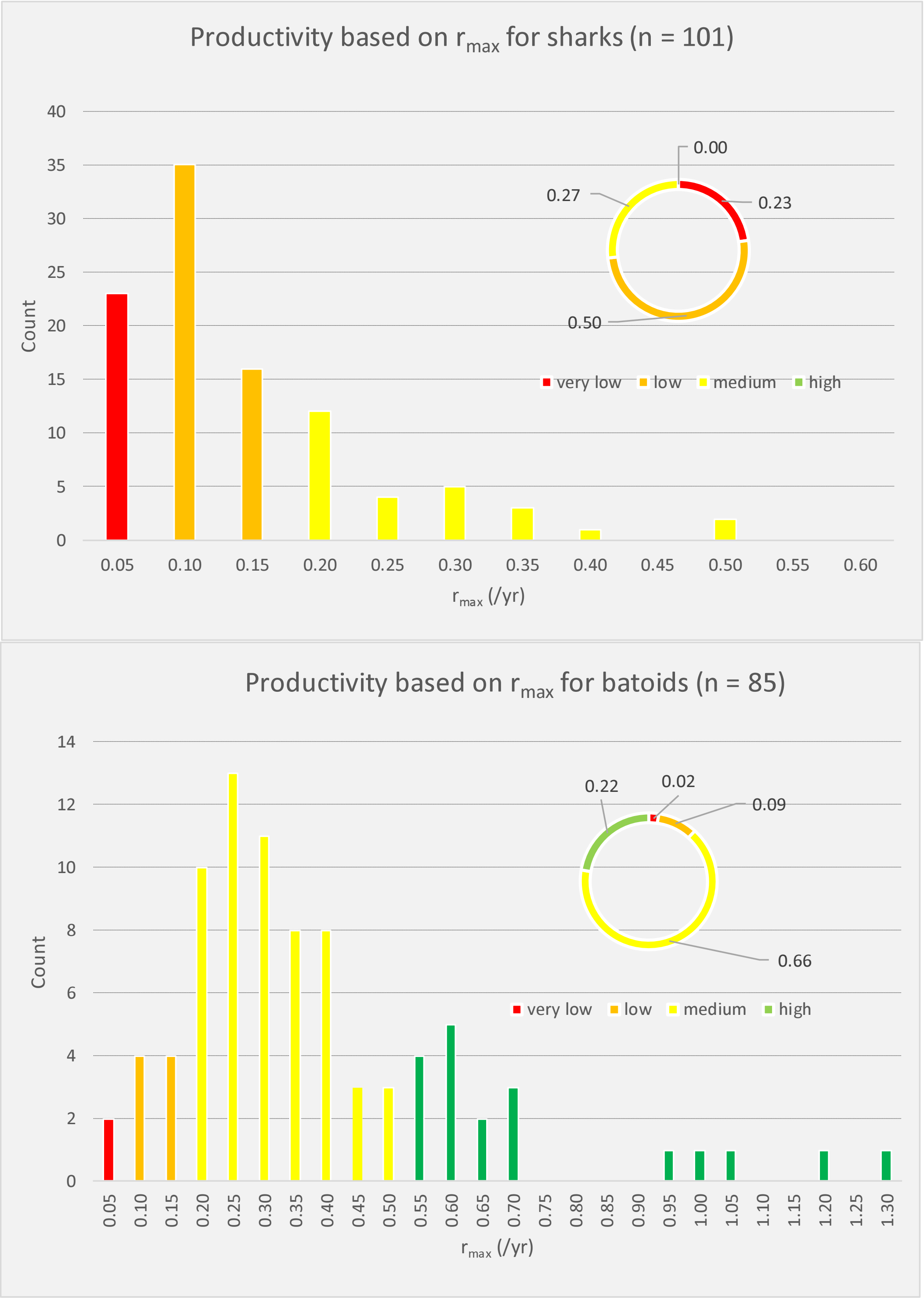


Figure 15. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for r_{max} from Musick (1999). Top panel: sharks (data from Cortés (2016) augmented); bottom panel: batoids (data from Barrowclift et al. (2023)). The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

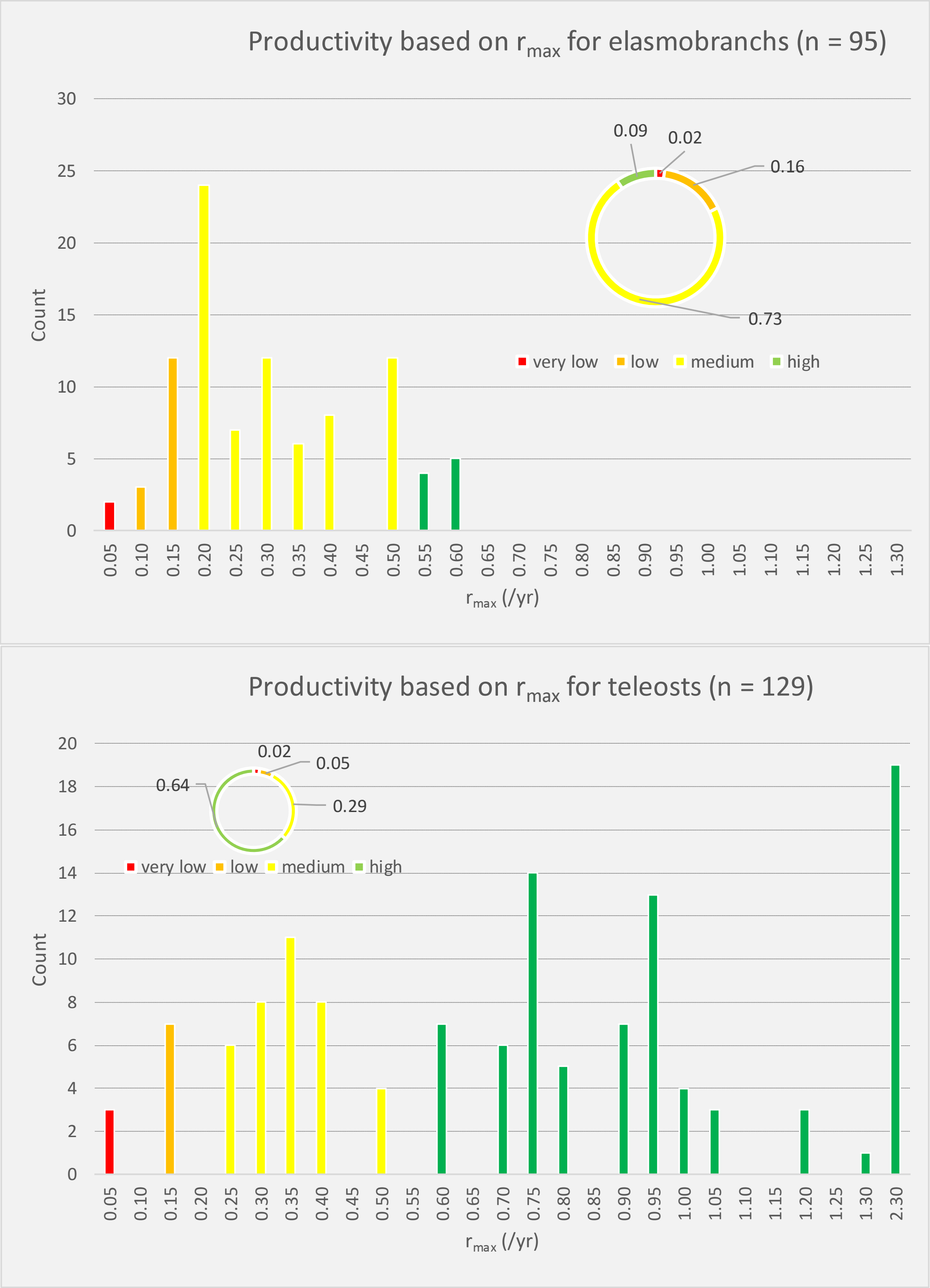


Figure 16. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for r_{max} from Musick (1999). Top panel: elasmobranchs; bottom panel: teleosts (all data from Gravel et al. (2024)). The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

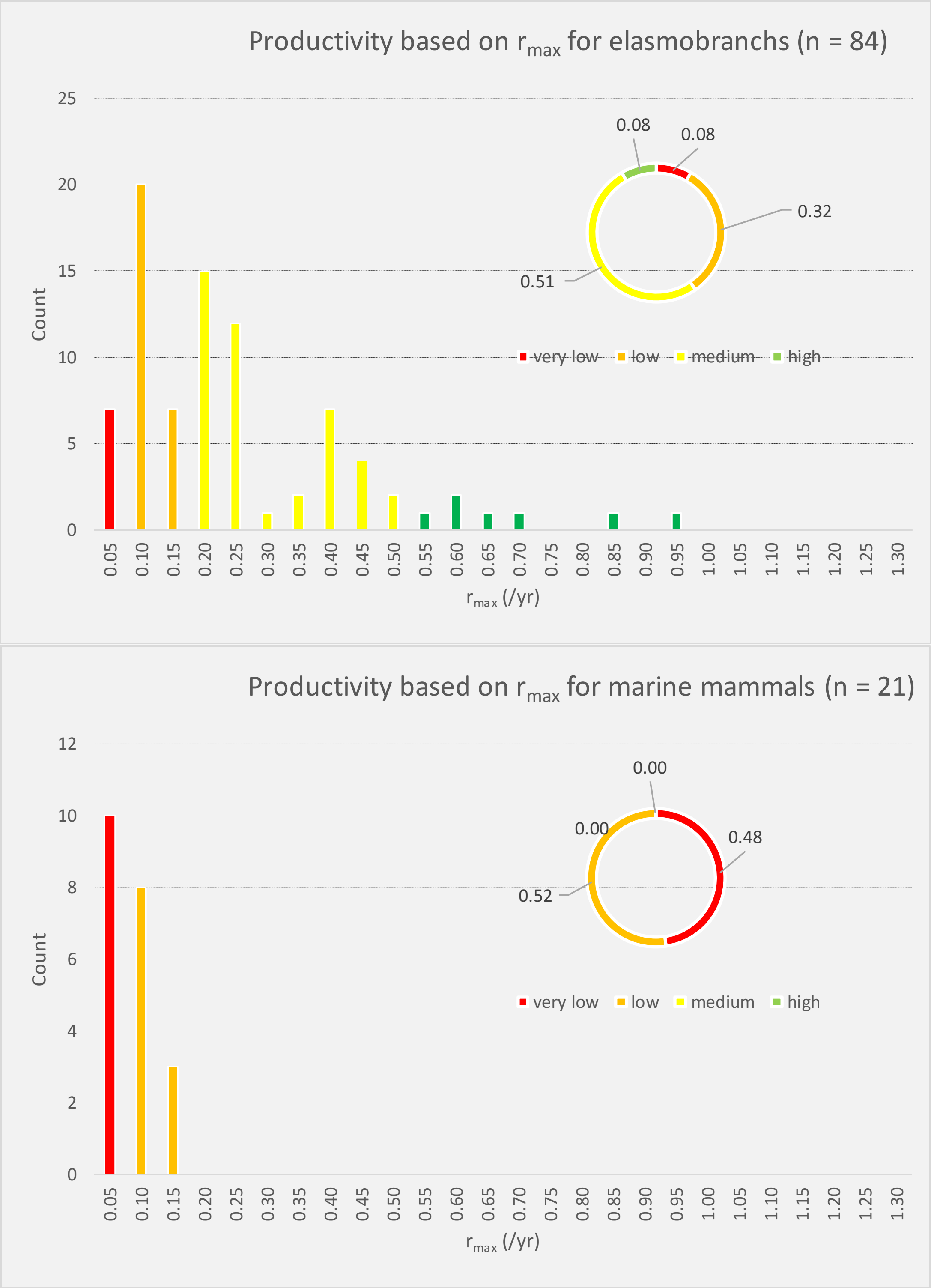


Figure 17. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for r_{max} from Musick (1999). Top panel: elasmobranchs; bottom panel: marine mammals (all data from Finucci et al. (2024)). The inset pie charts show the percentage contribution of the species analyzed to each of the four productivity categories.

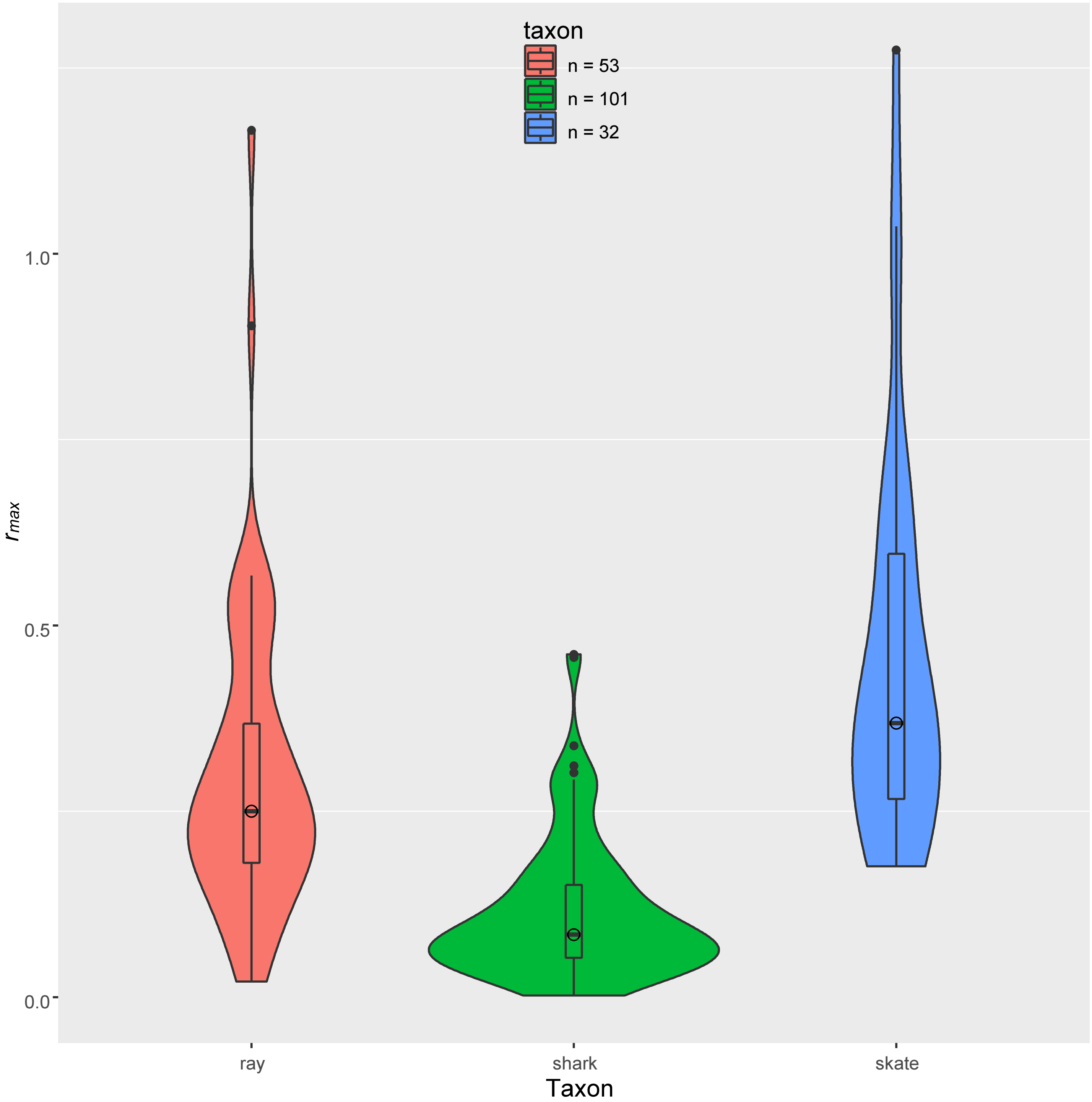


Figure 18. Productivity (expressed as r_{max} (yr^{-1}) for batoids (skates and rays) and sharks based on values from the Cortés (2016) augmented and Barrowclift et al. (2023) studies. The violin plot indicates density of points; inside the violin are the median (dash), mean (circle), interquantile range (25th to 75th percentile; box), 1.5 x IQR (whiskers), and outliers (dots).

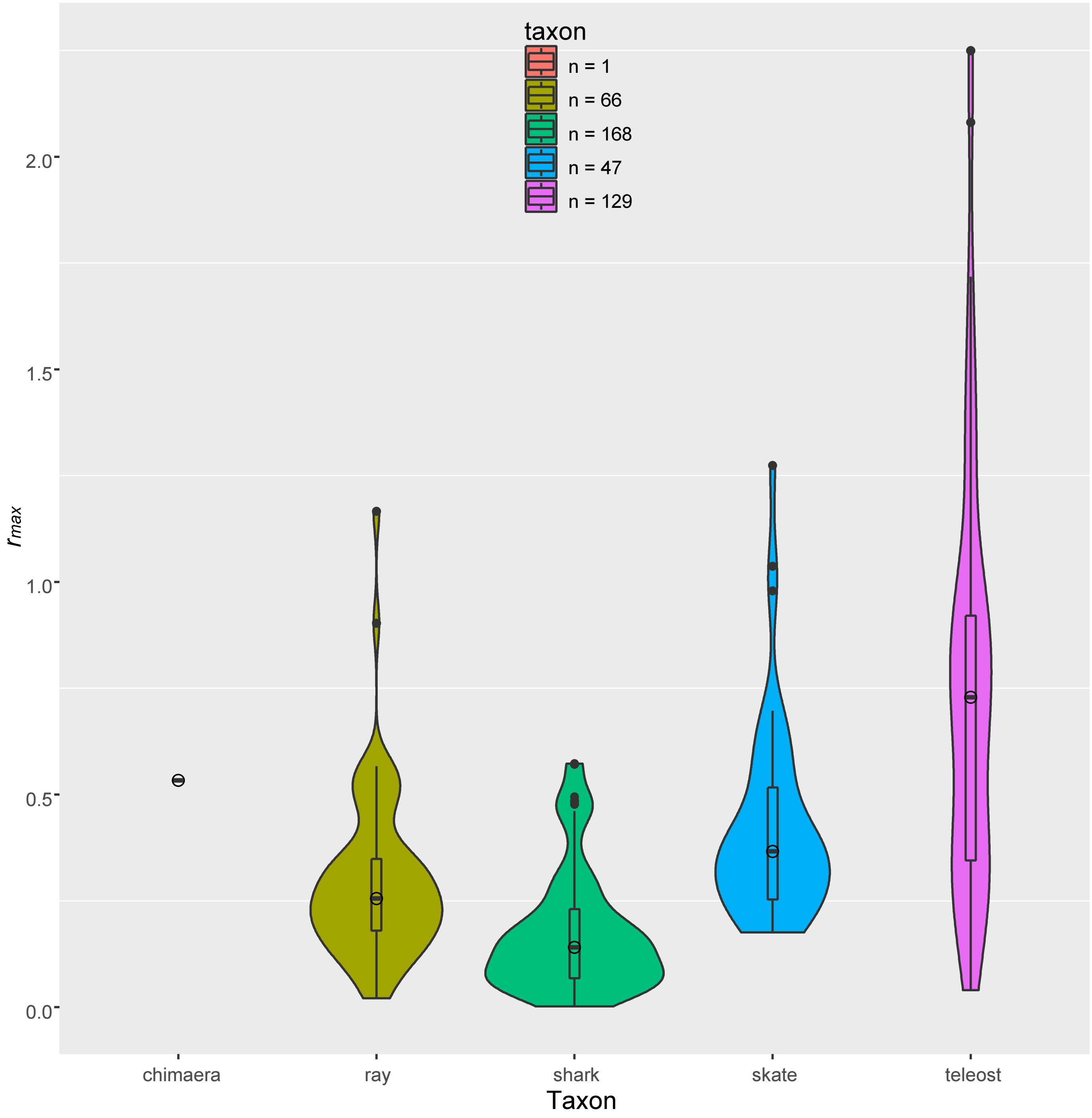


Figure 19. Productivity (expressed as r_{max} (yr^{-1}) for batoids (skates and rays), sharks, and teleosts based on values from the Cortés (2016) augmented, Barrowclift et al. (2023), and Gravel et al. (2024) studies. The violin plot indicates density of points; inside the violin are the median (dash), mean (circle), interquantile range (25th to 75th percentile; box), 1.5 x IQR (whiskers), and outliers (dots).

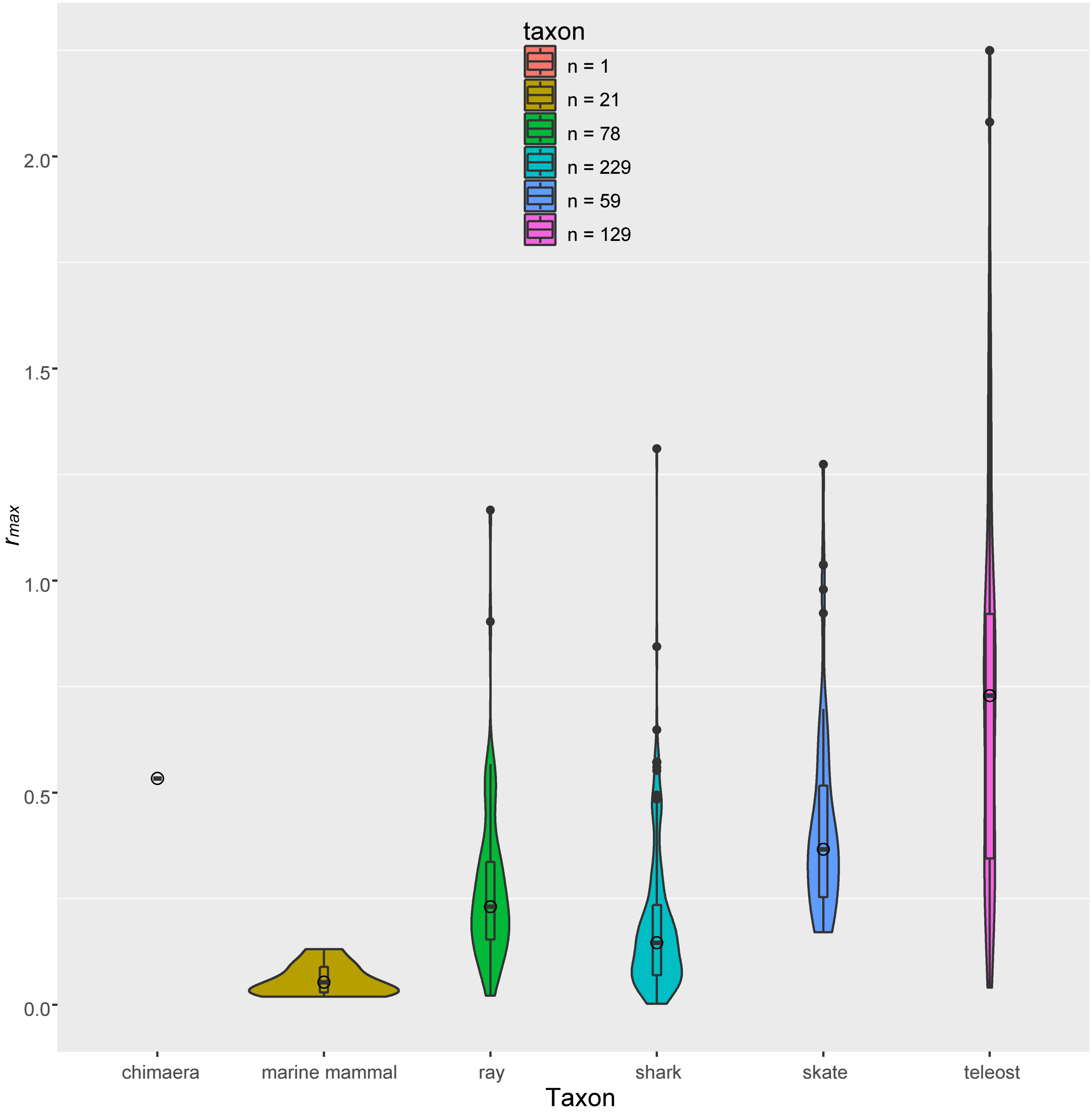


Figure 20. Productivity (expressed as r_{max} (yr^{-1}) for batoids (skates and rays), sharks, teleosts, and marine mammals based on values from the Cortés (2016) augmented, Barrowclift et al. (2023), Gravel et al. (2024), and Finucci et al. (2024) studies. The violin plot indicates density of points; inside the violin are the median (dash), mean (circle), interquantile range (25th to 75th percentile; box), 1.5 x IQR (whiskers), and outliers (dots).

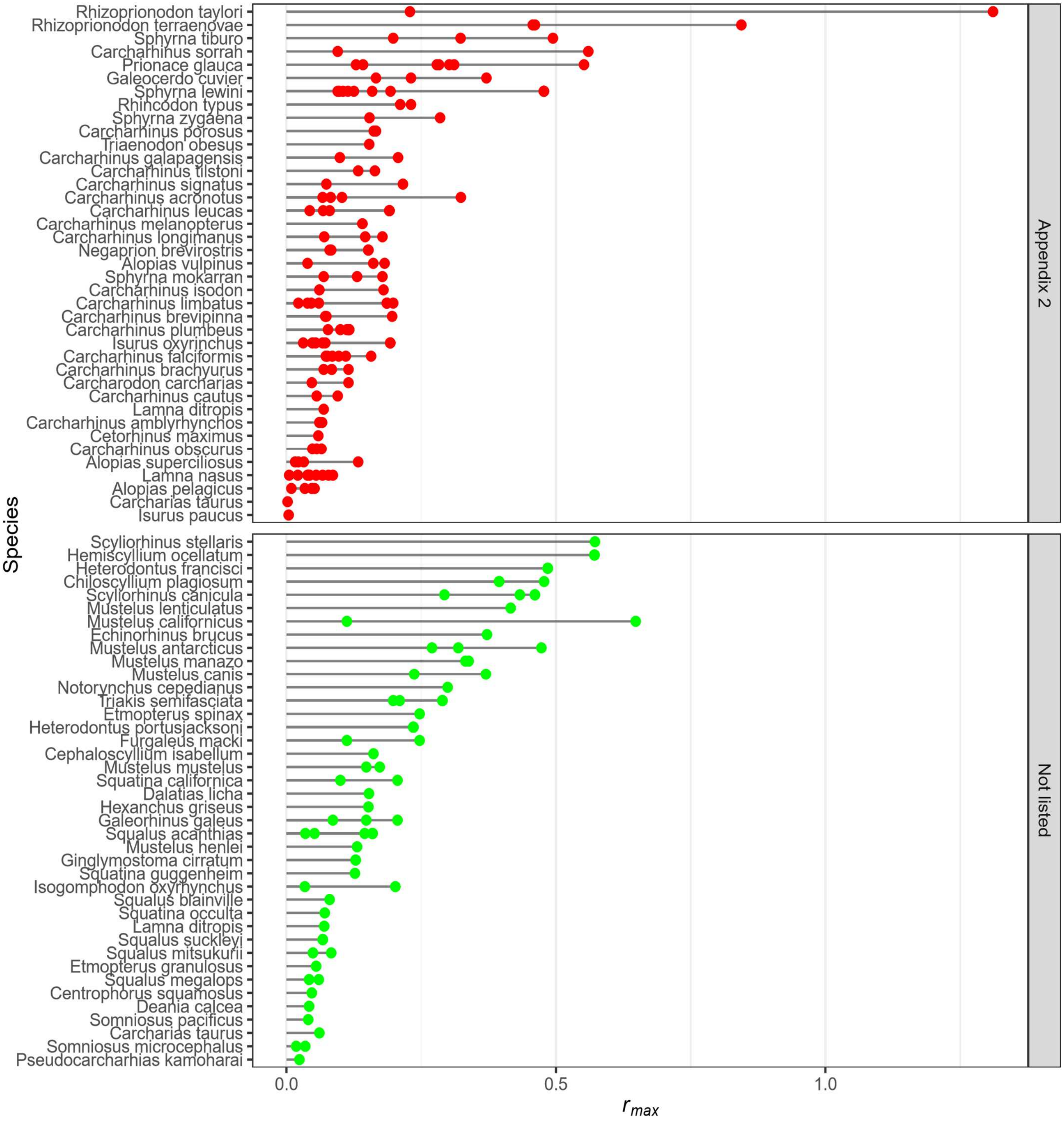


Figure 21. Productivity (r_{max} (yr^{-1})) extracted from multiple studies for sharks (n = 227) according to CITES listing. More than one point for a given species indicates multiple populations or studies.

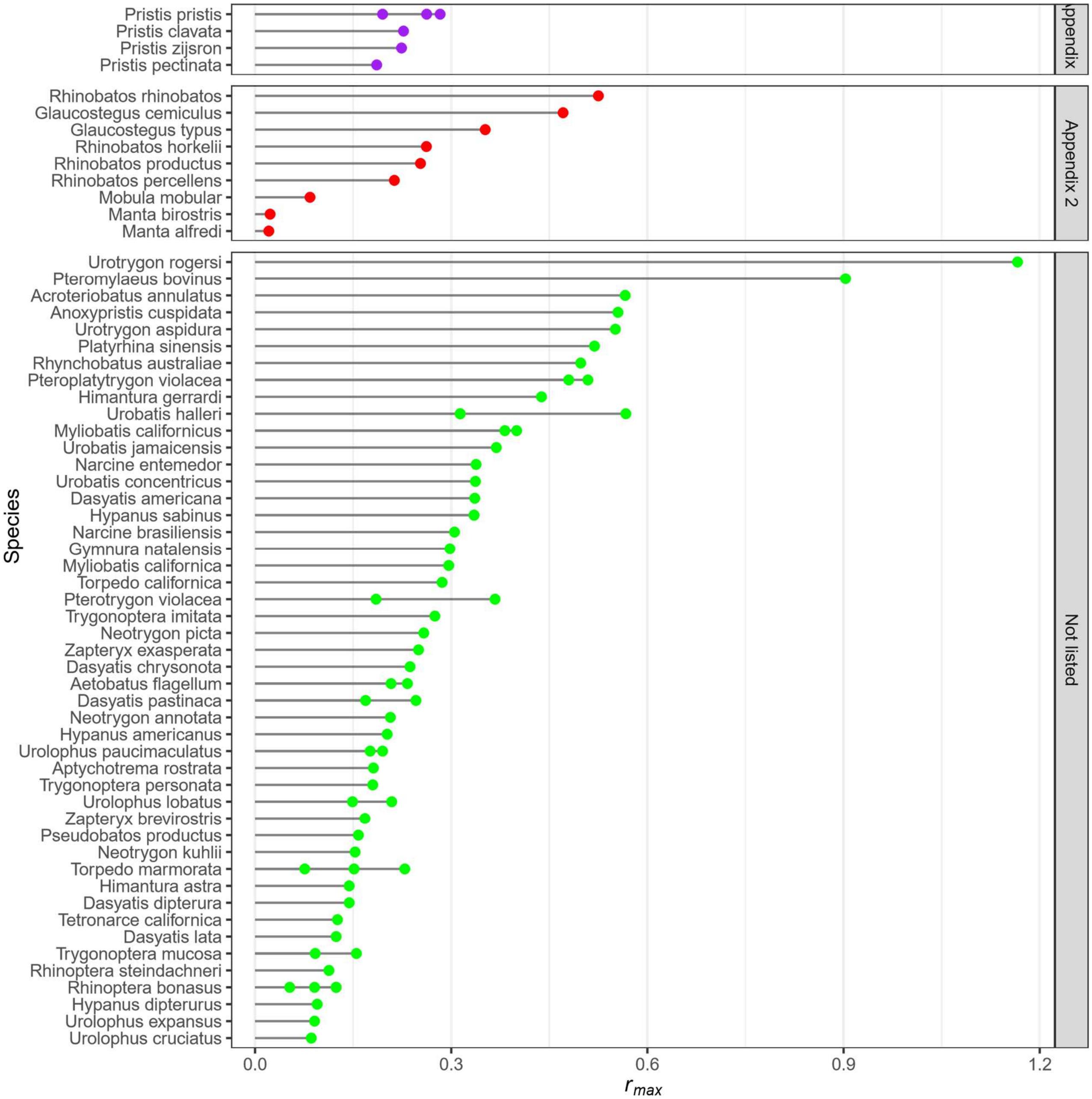


Figure 22. Productivity (r_{max} (yr^{-1})) extracted from multiple studies for rays (n = 78) according to CITES listing. More than one point for a given species indicates multiple populations or studies.

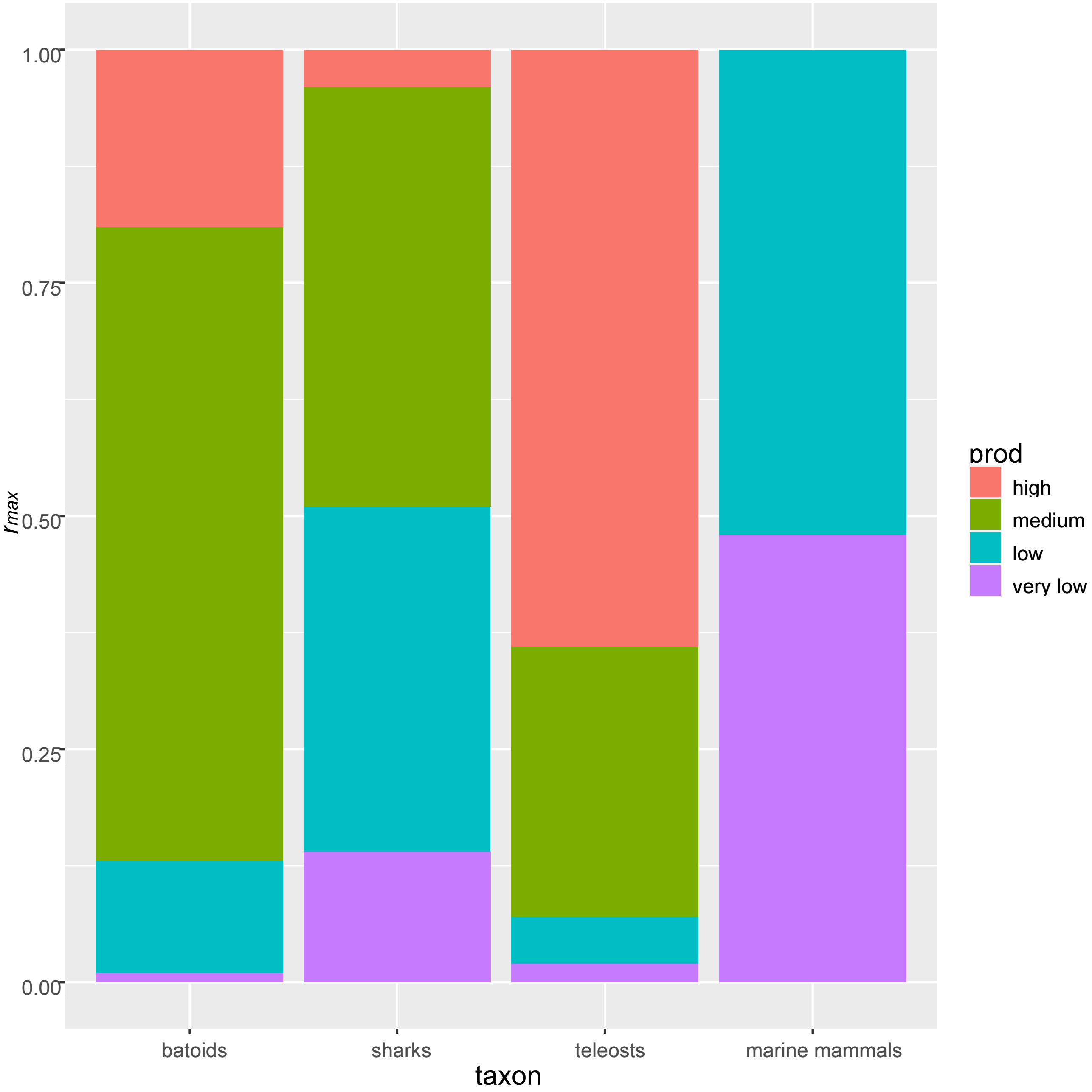


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Figure 23. Classification of productivity into four categories (high, medium, low, and very low) according to the criteria for r_{max} from Musick (1999) for several taxa. Data for batoids (skates and rays), sharks, teleosts, and marine mammals based on values from the Cortés (2016) augmented, Barrowclift et al. (2023), Gravel et al. (2024), and Finucci et al. (2024) studies.

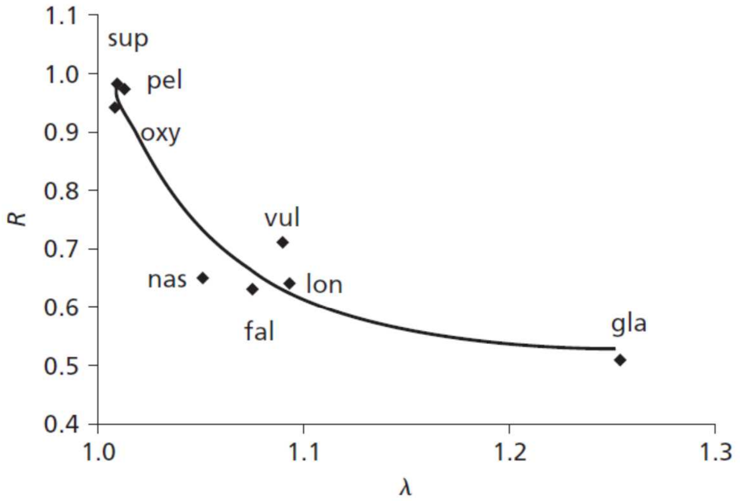

Fig. 27.2 Position of the inflection point of population growth curves (*R*) in relation to the mean population growth rate (λ) obtained through Monte Carlo simulation for eight pelagic shark species (see Fig. 27.1 for species codes). The line illustrates a nonlinear regression fitted to the data.

Figure 24. Extracted from Cortés (2008). Species with a higher value of R (position of the inflection point of population growth curves; Y axis) and a lower value of l (finite rate of population increase; X axis) would be able to withstand less exploitation. sup = *Alopias superciliosus*; pel = *Alopias pelagicus*; oxy = *Isurus oxyrinchus*; nas = *Lamna nasus*; vul = *Alopias vulpinus*; fal = *Carcharhinus falciformis*; lon = *Carcharhinus longimanus*; gla = *Prionace glauca*.

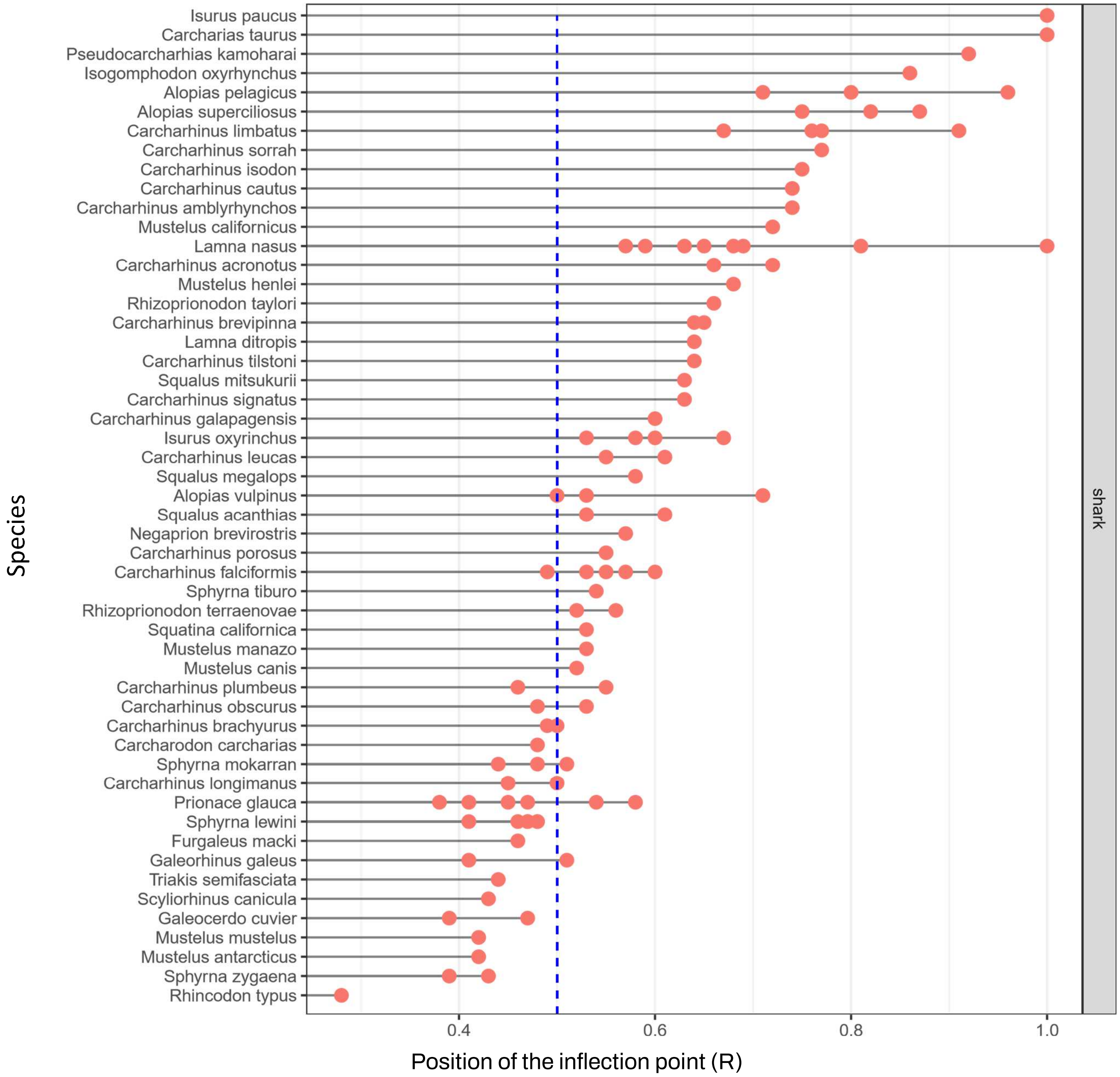

Figure 25. Position of the inflection point of population growth curves (R) for sharks (data from Cortés (2016) augmented, n = 101). The vertical blue dashed line indicates when the MSY (maximum sustainable yield) is reached at half the carrying capacity (0.5K). All species with R values to the left of this line would have a higher capacity to withstand population declines. More than one point for a given species indicates multiple populations or studies.