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Habilitationsschrift

Life-History Strategies of Recent Fishes: a Meta-Analysis

vorgelegt von

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Abstract

This study explores life-history strategies of recent fishes based on a data set that is two orders of magnitude larger than those used in previous studies. Trophic level, size and productivity were taken as key traits and proxies for many other closely related traits. Size was strongly correlated with most life-history traits of fishes and also with morphological characters, behaviour, and preferred environmental conditions. Size was also a good predictor of placement on the r-K continuum. Productivity was derived from growth, age at maturity, maximum age, and fecundity data. It was positively correlated with metabolism and level of activity and was also an indicator for placement of species on the r-K continuum. It was strongly correlated with most life-history traits of fishes and also with morphological characters, behaviour, and preferred environmental conditions. It was negatively correlated with status of threat. The position of species in the food web was shown to restrict life-history options. The addition of trophic level as an orthogonal axis on the r-K continuum revealed unoccupied regions such as the combination of small size and high productivity with either herbivory or top-predatory, and the combination of very large size and very low productivity with herbivory.

Discrete classes of size, trophic level and productivity were used to define 80 life history strategies. Only 50 of these strategies were used by recent species, with an exponential decline in species' numbers from the most to the least used strategies. This decline is interpreted as an exponential increase in constraints associated with less-used strategies. Analysis of trade-off or constraint curves in life-history space revealed unoccupied areas as well as local maxima, i.e., areas occupied by more species than the surrounding space. Such a local optimum was occupied by very large top predators with very low productivity. Low-level predators of small to medium size and medium to high productivity were the three strategies used by altogether 60% of the species. Strategies used in extreme environments such as the deep and polar seas or high-altitude lakes were not 'specialist strategies' but rather among the 10 most-used strategies, suggesting that constraints imposed by extreme environments excluded strategies that had a high degree of inherent constraints. The number of strategies used by phylogenetic, environmental, morphological or behavioural groupings of fishes was highly predictable from the number of species in the respective groups.

A preliminary chronology of life-history strategies showed that over 2/3 of recent strategies were invented only 200-150 million years ago during several radiations of the Actinopterygii, including small size, very large size (invented in parallel by Elasmobranchii), high productivity, and true herbivory. Phylogeny restricted the life-history options available to species with respect to size, place in the food web and productivity. There was evidence for a non-overlap of preferred life-history strategies between the two largest recent Classes, with Elasmobranchii tending towards large size and low to very low productivity, and Actinopterygii tending towards medium size with medium to high productivity.

Nine selection theories were tested as to their ability to correctly predict adaptation of life-history traits in response to environmental conditions such as salinity, climate, zoogeographic realm, ocean basin, and habitat type. Predictions were 88 – 100% correct when cases where different theories predicted different adaptations were excluded. In conflicting cases, predictions by temperature theory usually prevailed over those by r-K and succession theories.

Life-history strategies were examined with respect to their correlations with body shape, brain size, reproductive guild, migratory behaviour and status of threat. Productivity increased with

body shape from eel-like to short and/or deep, with brain size from very small to normal and large, and with migratory behaviour from catadromous to amphidromous and non-migratory. Size decreased with migratory behaviour from catadromous to non-migratory, and with parental care from nonguarders to bearers (in Actinopterygii). Trophic level decreased with increase in brain size. Several life-history strategies were only used by migratory species. Non-threatened fishes had significantly higher productivity than threatened fishes. Life history-strategies that combined large size and low productivity contained proportionally more threatened species than other strategies.

Independent estimates of abundance and distributional range of species were used as indicators of success of life-history strategies. Species showed preferences for strategies that were associated with high abundance or small to medium ranges. When abundance and range were combined into a single measure of success (Impact), most strategies were associated with impacts that were not significantly different from the overall mean. Only medium-sized low-level predators and omnivores with high productivity had significantly higher impact; these two strategies were used by 39% of the species.

Introduction

Fishes are the most numerous and diverse group of vertebrates dominating the waters of the world. The diversity of fish far exceeds that shown by terrestrial vertebrates and is a result of their long evolutionary history (Volff 2004). It has been suggested that there are so many kinds of fishes, occupying such diverse habitats, evolving in such complex ways, and with such complicated ecological traits, that a total synthesis of 'understanding fishes' will always elude ichthyologists and ecologists (Matthews 1998). In this study I try to advance our understanding of fishes by exploring the evolutionary response of life history traits to different environmental conditions using the largest available data sets.

Recent fish species have evolved from basal ancestors to survive, feed, reproduce and die in a given ecological niche within a given aquatic ecosystem. Phylogeny and niche thus provide the framework, i.e., the options and limitations for the evolution of life-history strategies (Stearns 1977). For example, a cyprinid feeding on epiphytes in the shallow water zone of freshwater lakes cannot have the size of a whale shark. Conversely, a species crossing the oceans to feed on coral reef spawning blooms cannot have the size of a stickleback. Less obviously, it has been suggested (Monty Priede, University of Aberdeen, pers. comm., 2001) that you cannot be a shark if your niche is the deep ocean below 3,500 m. And finally, you cannot enter freshwater, grow 2 meters in length, or lay 1,000 eggs if your ancestor was a hagfish.

The life-history strategy of a species is a complex of evolved traits that are related to the allocation of energy; along with morphology, physiology, and behaviour, it defines the species (Moyle and Cech 2004). Only those fishes whose hydrodynamic, trophic, and reproductive traits all fit the available microhabitats will reside in a given location; life-stage or seasonal migrations among sites may reflect different traits at different life stages or seasonal changes of the environment (Matthews 1998). Also, life-history traits that are advantageous in one kind of environment, such as seasonally fluctuating rivers may also be advantageous in new habitats such as man-made reservoirs (Cambray and Bruton 1984).

There are two schools of thought as to how the species composition found in a given ecosystem has evolved (Hubbell 2001). The main-stream perspective is that species compete for limited resources and their respective success in this and other biotic interactions determines which species are present or absent from the community; species coexist in interactive equilibrium. The other perspective asserts that "communities are open, nonequilibrium assemblages of species largely thrown together by chance, history and random dispersal […] and stochastic local extinction. […] the number of cases in which local extinction can be definitively attributed to competitive exclusion is vanishingly small. […] the evidence is strong that communities undergo profound compositional changes, sometimes gradual, sometimes episodic, on timescales of centuries to millennia and longer" (Hubbell 2001). In this study I focus on the diversity and evolution of life-history strategies, without emphasis on the particular species that use a given strategy in a given environment. In other words, I expect fish communities in similar ecosystems to have similar patterns of life-history strategies, but I do not expect them to host the same species, Genera or Families.

In recent years the term 'life-history' has taken on a more narrow perspective, focusing mostly on reproductive characteristics. Life-history strategies as understood here follow the original, broader meaning encompassing all of the 'natural history' of a given fish species, including what it eats, how fast it grows and how old and large it gets, when it matures and how successfully it reproduces, and other aspects of its biology (Matthews 1998). Most of these traits are directly or indirectly correlated. For example, if maximum size is beyond 1 m length then maturity will not be reached within one year and longevity will be beyond three years (compare Table 6).

Evolution optimizes life-history strategies in response to a given niche by balancing the trade-offs of key traits (Stearns 1976, Roff 1984, Wootton 1992). In this study I look at the correlations between selected traits in order to better understand the life-history strategies that recent fishes have evolved in response to constraints set by niche and ancestry. In particular I search for patterns in response to environmental parameters such as salinity, climate zone, and depth; in response to large ecosystems such as oceans, zoogeographic realms, and habitat types; in response to migratory behaviour and distributional range; and in response to functional morphology such as body shape and relative brain size. I also evaluate how good the various life-history strategies can handle new threats caused by humans, such as rapid environmental degradation and overfishing. Finally, I try to establish and explore a measure of success of life history strategies.

There are quite a number of studies that have explored life history strategies of fishes, however most have focused on growth, mortality and reproduction, and rarely included trophic ecology. Most studies have been local (e.g. Matthews et al. 1994) or regional (e.g. Winemeyer and Rose 1992). Also, as Wootton (1992) stressed, progress in the development of a more comprehensive life history theory for fishes has been hampered by the paucity of good-quality data and most studies were based on less than a few hundred species. Here I address these issues by taking a global perspective, including trophic level, and employing the largest data sets available for fishes with typically two orders of magnitude more records than have previously been investigated.

Most studies of life history strategies have placed a lot of weight on reproductive traits such as fecundity, egg size, number of spawning events, age and size at maturity, reproductive life span, extent of spawning season and parental care. In this study I look at the combined outcome of all these traits, i.e., the maximum intrinsic rate of population increase, here expressed as productivity (see discussion of Table 6).

There are a number of theories predicting the evolution of specific sets of life history traits in response to environmental conditions (Stearns 1976). The most widely accepted theory is the r-K continuum (MacArtur and Wilson 1967, Pianka 1970), where r is the Malthusian parameter of intrinsic rate of population increase and K the equilibrium density, i.e., the number of individuals when the population size is close to theoretical saturation of the environment (Stearns 1976). r-K theory predicts that highly fluctuating environments will select for rapid development and early maturity, semelparity, larger reproductive effort, more young and short life (r-selection). In contrast, stable environments will select for slow development and late maturity, iteroparity, smaller reproductive effort, fewer young, and longer life (K-selection). In fishes which have indefinite growth, maximum life span may be taken as the age corresponding to 95% of the asymptotic size of the von Bertalanffy growth function (Taylor 1958). As a result short life corresponds to small size and long life—with few exceptions—corresponds to large size. Speed of development corresponds to the von Bertalanffy growth parameter K (Adams 1980, Roff 1984), which expresses the rate at which asymptotic size is approached. Age at first maturity, maximum age and fecundity are known for many fishes and co-vary with productivity. Number of young is linked to and limits population growth in fishes with very few eggs or pups such as in live-bearing sharks but has no relation with reproductive success (Froese and Luna 2004) or recruitment and population growth (Myers and Barrowman 1996) in highly fecund bony fish; thus in this study fecundity was only used as a constraint on productivity and not as a factor increasing productivity beyond what was suggested by other factors (see discussion of Table 6). Semelparity occurs in annual fishes such as killifish and a few longer-lived species such as eels, lampreys and some salmons, but no comprehensive data were available for use in this study. Reproductive effort is defined as "the proportion of resources diverted to reproduction, summed over the time in question" (Stearns 1976). Other than in homeotherms the weight of ovaries is highly correlated with body weight in fishes (Roff 1984) but no global data were available to compare, e.g., gonado-somatic indices in relation to different environments. However, parental care is also an energy consuming activity that diverts resources to reproduction and such data are available. Thus, in this study I tested predictions of r-K theory against size, productivity, and parental care.

Pauly (1979, 2000c) presents a theory of gill size and temperature as governing factors in fish growth. This theory predicts that within a taxonomically well-defined group there is selection for smaller size with increasing temperature (Longhurst and Pauly 1987). Maximum size and the rate at which it is approached are highly interlinked in fishes with the result that most small fishes have fast growth, early maturation and short lives (r-selection traits), and most large fishes have slow growth, late maturation and long lives (K-selection traits). In this study I test the predictions of temperature theory against size and productivity.

Pauly (2000b) suggests that herbivory is a low-latitude phenomenon because of "the difficulties most fish have in establishing and maintaining, throughout and subsequent to a feeding bout, the low pH levels required for digestion of plant material, especially at low temperatures." This theory thus predicts an overall low percentage of herbivorous species and an increase in herbivorous and omnivorous species with an increase in environmental temperature. Although not mentioned explicitly by Pauly (2000b), it also predicts relatively more herbivores and thus lower trophic levels in freshwater which tend to have lower pH values—and thus a lower gradient to overcome—than in the marine environment. I refer to this as herbivory theory and test its predictions against the observed distributions of trophic levels.

Kostas (2000) suggests that oligotrophic environments such as the eastern Mediterranean or the open oceans will select for smaller size, shorter life, earlier maturity, and higher natural mortality. He presents support for this hypothesis by comparing von Bertalanffy growth parameters in Greek waters with global estimates in FishBase. I refer to this as the trophy theory and test it against the observed distributions of size and productivity.

Odum (1969) presents ecosystem attributes as a function of early versus mature stages in ecosystem development. For mature ecosystems he predicts, among other, large size, low productivity, long life cycles and K-selection of organisms, increased variety of species and complex 'web-like' food chains with narrow niche specialization. Conversely, for less mature ecosystems he predicts small species with high productivity, short life cycles and r-selection, less variety of species and linear (plant-herbivore-carnivore) food chains with broad niche specialization as a consequence of low diversity. Odum (1969) does not explicitly predict impact of ecosystem successional stages on trophic levels, but from his description we can infer that web-like food chains with narrow niche specialization will use more trophic levels and display a higher 'trophic diversity', whereas early development stages with linear food chains and broad niche specialization will use fewer trophic levels and display a lower 'trophic diversity'. Also, we can infer that increased variety of species with narrow niche specialization results in a higher number of life-history strategies in mature systems whereas less variety of species with broad niche specialization results in a lower number of life-history strategies. Odum's (1969) concept of mature or 'stabilized' ecosystems is very similar to the 'stable environments' of r-K theory. Ecosystems in early stages of development are more difficult to grasp on a global scale; these can be perceived as 'young' ecosystems in evolutionary time that did not yet have enough time to evolve species for all niches, such as some lakes or areas affected by recent ice ages. Also, these can be systems that are periodically disturbed by the physical environment such as estuaries or boreal regions and are thus hindered in evolving the diversity characteristic of mature systems; thus, these systems are similar to the 'highly variable environments' of r-K theory. I refer to this as succession theory and test its predictions for distribution of size, productivity, trophic diversity and number of species and life-history strategies.

There are several factors bearing on the number of species by geographic or environmental category (see e.g. Huston 1994, Rosenzweig 1995, Waide et al. 1999, Chown and Gaston 2000, Gaston 2000): everything else being equal, the number of species is expected to increase

1) with suitable area;
2) with temperature;
3) with structural heterogeneity of habitats;
4) with isolation of ecosystems from gene flow of neighbouring ecosystems; and
5) with closeness to the respective center of biodiversity.

In addition, there are factors such as geological history and the time that was available for colonizing an area. Also primary production is known to be related with species numbers, i.e., very low and very high primary production is typically tolerated by fewer species than intermediate production; however, the type of relationship may change depending on the size of the ecosystem, with a unimodal relationship at local scales and a positive relationship at regional or global scales (see review in Waide et al. 1999). The exact mechanisms determining species numbers are still debated, see discussions in Matthews (1999), Gaston (2000) or Chown and Gaston (2000). Here I will examine the factors listed above with respect to their ability to explain the observed patterns in species richness, keeping in mind that no single mechanism is likely to adequately explain a given pattern, that observed patterns may vary with spatial scale, that processes at global scales influence patterns observed at regional ones, and that no pattern is without variations and exceptions (Gaston 2000).

A summary of the selection pressures predicted by the theories presented above is given in Table 1. I test the predictions of these theories using the large datasets that have been compiled in FishBase (Froese and Pauly 2000) under my supervision and with inputs from world experts during the past 14 years. In addition I create an extended data set to overcome the bias towards large and temperate species which have been studied more intensively than, e.g., small tropical fishes. I look more closely at cases where the data do not support predictions. Particularly, I look at cases where different theories predict parallel or opposing selection pressures. In the latter case we would expect intermediate results or cases where stronger selection forces prevail. The strongest patterns can be expected when all the different mechanisms pull in the same direction (Gaston 2000).

Also, I explore hypotheses about life-history strategies of fishes, especially those presented in recent ichthyology text books such as Berra 2001, Boyle and Cech 2004, Helfman et al. 1997 and Matthews 1998. I compare my findings with the largest previous studies of life history patterns in fishes, that of Winemiller and Rose (1992) who studied 216 North American fish and Vila-Gispert et al. (2002) who studied 301 fish species from Europe and the Americas.

Table 1. Selection pressures on species richness, size, productivity and trophic diversity as predicted by various selection theories.

Theory	Environment	Species / Strategies	Size	Productivity	Trophic diversity
r-K	variable		small	high	
	stable		large	low	
Succession	less mature	low	small	high	low
	mature	high	large	low	high
Temperature	high temp.	high	small	high	
	low temp.	low	large	low	
Herbivory	high temp. / low pH				high
	low temp. / high pH				low
Trophy	oligotrophic		small		
Area	large	high			
	small	low			
Heterogeneity	high	high			
	low	low			
Isolation	high	high			
	low	low			
Closeness to Center	near	high			
	far	low			

Although this Habilitationsschrift is not a cumulative publication, it builds on much of my previous work such as the FishBase book (Froese and Pauly 2000) and FishBase information system (www.fishbase.org), and other publications dealing with issues of taxonomy in relation to large databases (Froese 1996, Froese 1997, Froese et al. 1999, Froese et al. 2000, Froese and Bisby 2000, 2002, Froese and Reyes 2003, Froese et al. 2003), body shapes (Froese 1991), availability of data (Froese et al. 1996, Froese 1998, Capuli and Froese 1999, Froese and Garilao 2002, Froese and Binohlan 2003, Froese et al. 2004), exploring relationships between traits (Klingenberg and Froese 1992, Froese and Pauly 1994, Albert et al. 1999, Froese and Binohlan 2000, Froese and Luna 2003), analysing and comparing ecosystems (Froese et al. 2001, Froese and Sampang 2004, Froese at al. 2004), analysing fisheries (Pauly et al. 1998, Froese and Pauly 2003, Watson et al. 2003, Froese 2004a,b), analysing threats to fishes (Froese and Torres 1999), and studying extraordinary fishes (Froese and Friess 1992, Froese and Rechlin 1992, Weber and Froese 1993, Froese and Palomares 2000).

Material and Methods

Data sources are described at the beginning of the respective chapters dealing with length, trophic level, productivity, phylogeny, environment parameters, behaviour, functional morphology, and human uses of fishes.

Standard plots of frequency distribution are shown for most parameters. Most parameters were approximately log-normal distributed but statistical tests often rejected normality, which is to be expected with large datasets (Hintze 2001). I therefore used the median and its 95% confidence limits to detect significant differences between groups of data. For this and other statistics such as linear, robust, non-linear and multiple regressions I used the NCSS 2004 statistic software (Hintze 2001).

I used notched box plots to illustrate and compare three main features of variables: their center, their spread, and their outliers. The horizontal line near the middle of a box is the median; the top and the bottom of the box are the 75th and 25th percentile, thus marking the interquartile range (IQR), i.e., the box includes 50% of the data. The notched part of the box marks the 95% level of confidence for the median. Thus, if the notched parts of two variables do not overlap then their medians are significantly different. The lines extending above and below the boxes represent 'adjacent values', where the upper adjacent value is the largest observation that is less than or equal to the 75th percentile plus 1.5 times IQR, and the lower adjacent value is the lowest value that is more than or equal to the 25th percentile minus 1.5 times IQR. Values outside the upper or lower adjacent values are considered outliers. Those that fall within 3 IQRs from the 75th or 25th percentile are considered 'mild' outliers and are not unusual; they are represented by an open dot. Values that fall outside 3 IQRs are considered severe outliers and are rare; they are represented by a black dot (Hintze 2001).

I also present cross-tabulations of life-history strategies versus various other discrete parameters, such as salinity, climate zone, habitat or migratory behaviour. These tables are mostly based on the extended data set and I looked for the following:

- Strategies that were used by most species within a given category of a respective parameter, e.g., the Low-Medium-High' strategy used by 3,024 species within the 'freshwater' category of the 'salinity' parameter (Table 28);
- Strategies that were used by more species in a given category then suggested by the overall percentage obtained by that category; for example, of 28,786 species with salinity assignments, 42.6% fall into the 'freshwater' category (Table 23); within the 'freshwater' column of Table 28, more than twice as many species (94.7%) that use the 'Herb-Medium-Low' strategy are freshwater species, suggesting that freshwater fishes have a preference for this strategy;
- Groups of strategies that were preferred or avoided within a certain category, often in an attempt to confirm with the extended data set used in the cross-tabulations the trends discovered when exploring, e.g., box plots of observed data; for example, in the 'diadromous' category of Table 28, eight of ten top predators strategies have higher species numbers than suggested by the overall percentage of diadromous species, indicating that among diadromous species there are relatively more top predators;
- Combinations of strategies and categories that were used by only one or two species may be highly interesting, because these species might explore a very rare niche; however, after exploring a couple of these cases, I found that most often these were 'data or modelling outliers' rather than 'natural outliers', in the sense that if the respective species were better known, at least one of the parameters leading to the current placement was likely to change; since this study was more interested in

> patterns than in outliers I refrained from researching all the potential cases; however, in the discussion of the respective tables I use the number of observed strategies in comparison to the number of predicted strategies as an indicator for the likelihood of these 'little-used' strategies to be confirmed or disproved if more data became available.

In order to compare observed productivity between different environments, habitats and behaviours I calculated the approximate mean intrinsic rate of population increase (r'_{max}) and its 95% confidence limits. For this purpose I assigned the following r_{max} values to the productivity categories used in this study: High = 0.75, Medium = 0.23, Low = 0. 1 and Very low = 0.025, based on values given by Musick (1999) (see also Table 6).

The Shannon-Wiener diversity index (Equation 1) was used as a measure of trophic diversity or food web complexity.

$$H' = - \Sigma (p_i) (\log_2 p_i)$$

Equation 1. Shannon-Wiener index applied to trophic diversity, where H' is the diversity index for i = 1 to S, S = number of trophic levels with 0.1 class width and p_i = proportion of total number of species using that trophic level.

Shannon-Wiener evenness (J') was calculated by Equation 2.

$$J' = H' / (\log_2 * S).$$

Equation 2. Shannon-Wiener evenness index for trophic diversity, where J' is the evenness index and H' and S are as defined above.

Throughout the text I capitalized Class, Order, Family, and Genus when referring to the respective taxonomic groups.

Results and Discussion

Key Components of Life-history Strategies

Evolution favours the traits of those individuals that, under given circumstances, produce the highest number of reproductively successful individuals. In order to produce successful offspring individuals have to survive, feed and grow to reach maturity, mate with best matching partners, and maximize chances of survival for their offspring, including dying at a rate that reduces competition with their offspring for space, food, or mates. Life-history strategies thus have to balance various traits related to predator avoidance, position in the food web, mating success, number of offspring, parental care, and longevity. Individuals inherit a specific life-history strategy depending on the place of their species in the phylogenetic hierarchy of fishes. Winemiller and Rose (1992) compare results of principal component analysis involving five live history variables with all available fish species and with only one species per Genus to test for influence of phylogeny at the Genus level; they found nearly identical results and concluded that evolutionary divergences play a more important role among higher taxa such as Orders. In this study I will focus on phylogeny at the Class level and on species as the evolutionary unit and bearer of life history strategies. The number of conceivable life-history patterns is essentially infinite, if we judge by the possible combinations of the many traits that have been observed (Cole 1954). Here I focused on three traits that impact on the above themes and which are highly correlated with many other traits and thus can serve as proxies. As a practical consideration these traits had to be available for a high number of species across all Classes of fishes. The traits I selected and discuss below are size, trophic level and productivity.

Phylogeny

I used the taxonomic hierarchy contained in FishBase 11/2004 which follows Eschmeyer's (1998) Catalog of Fishes database, version of January 2004. Numbers of Orders, Families, Genera and Species for six Classes of fishes are shown in Table 2, together with an indication of when each class shared a common ancestor with the Classes below it based on Preikshot et al. (2000).

Note that FishBase 11/2004 contained 500 (1.8%) subspecies which, for the purpose of this study, were treated as species and were included in the respective numbers given for species.

Table 2. Classes of fishes with indication of common ancestry and number of Orders (6), Families (528), Genera (4,812) and Species (28,786 including Subspecies), respectively.

Classes	Common ancestor (million y)	Orders (n)	Families (n)	Genera (n)	Species (n, %)	
Myxini (hagfishes)	600	1	1	6	69	0.2
Cephalaspidomorphi (lampreys)	450	1	2	9	42	0.2
Holocephali (chimaeras)	420	1	3	6	37	0.1
Elasmobranchii (sharks and rays)	420	11	44	175	965	3.4
Sarcopterygii (lobe-finned fishes)	420	3	4	4	11	0.04
Actinopterygii (ray-finned fishes)	400	45	474	4,612	27,662	96.1

The number of species in a taxon (here: Class) is a function of the evolutionary time since the appearance of the common ancestor and the respective speciation and extinction rates and can be expressed by Equation 3 (Bokma 2003):

$$n_t = e^{(\lambda-\mu)t}$$

Equation 3. Number of species per taxon, where n_t is the number of species at time t, λ is the speciation rate and μ is the extinction rate.

From the numbers in the 'Common ancestor' and 'Species' columns in Table 2 it becomes clear that net speciation rates (λ-μ) of Actinopterygii have far exceeded those of the other Classes, despite those being older by 20 to 200 million years. Such uneven distribution of species richness by higher taxa is well known from other taxonomic groups (Owens et al. 1999, Purvis and Hector 2000). One classic hypothesis links high species richness with small body size and short generation time (Hutchinson and MacArthur 1959) or high reproductive rate (Purvis and Hector 2000), which I test below.

Size

Size is correlated with almost all other life-history traits, most notably mortality (e.g. Pauly 1980), metabolism (e.g. Winberg 1960, 1971, Blueweiss et al. 1978), growth (von Bertalanffy 1938, 1951), trophic level (Pauly and Christensen 2000), total egg volume (Wootton 1992), maturity (Rochet 2000) and fecundity (Bagenal, 1978, Moyle and Cech 2004), but also with intrinsic rate of population increase and 'environmental resistance' (Pianka 1970). With respect to size, fish cover a wider range than any other group of recent organisms on earth, ranging from about 1 cm and 0.2 g in some minute gobies such as *Pandaka pygmea* Herre, 1927, to about 20 m and 34 tons in the Whale shark *Rhincodon typus* Smith, 1828. The smallest fish may represent the minimum size achievable by the vertebrate grade of organisation (Wootton 1992), with significantly lower reproductive potential and high metabolic rates (Harrison 1996). The largest fishes may be constrained by the low concentration of oxygen in water and volume-area allometry between body volume and gill surface (Pauly 1981). In fish, length is often used as a proxy for weight because it is easy to measure, less variable than weight and available for most species.

I used maximum total length estimates of 23,685 fishes as compiled in FishBase version 11/2004. Lengths were used as reported in the literature if they were given in total length; otherwise they were transformed to total length using conversion parameters available in FishBase. If no conversion parameters were available for a given species, the mean conversion factor of 1.1 was used to transfer fork length and 1.2 to transfer standard length to total length. Although FishBase contains preliminary estimates of length (based on lengths of closest relatives) for fishes without length information, these estimates were not used in this study.

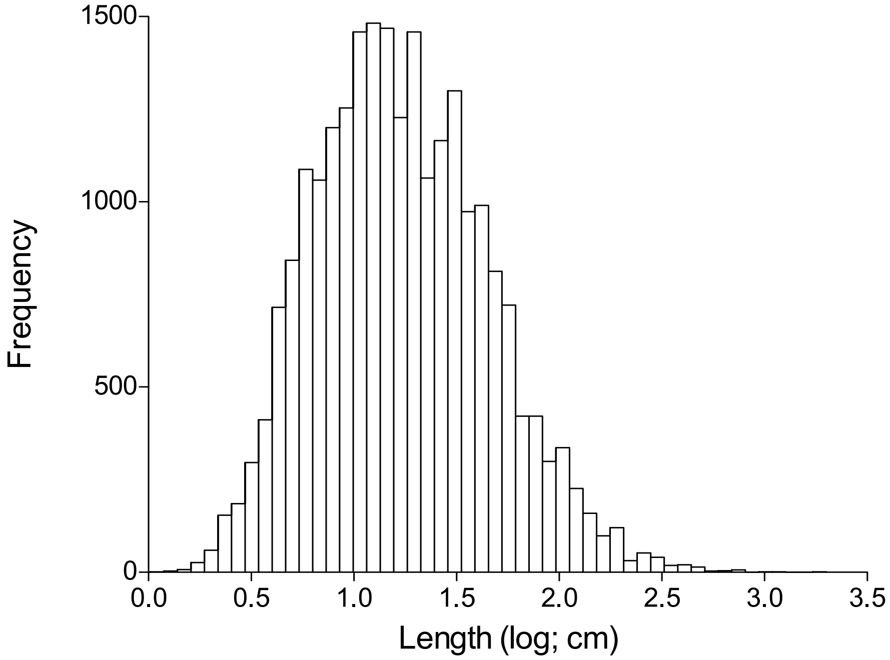


Figure 1. Frequency distribution of maximum lengths in 23,685 species of fishes. Median = 15.9 cm, 95% CL = 15.6-16.0 cm.

Figure 1 shows the frequency distribution of maximum total lengths of 23,603 species of fishes. Maximum length appears roughly log-normal distributed, but is actually right-skewed towards large fishes. Fifty percent of fishes have maximum lengths between 9 and 33 cm, and ninety percent between 4 and 96 cm. Given the high number of species contributing to Figure 1, I intentionally chose a high number of bars (50) to explore the claim of Cumming and Havlicek (2002) that the null hypothesis for the distribution of body size across a range of related species should be one of multimodality, i.e., there will be a preference for certain sizes. As can be seen, because of the high number of peaks especially on the right side of the frequency distribution, this claim can not be refuted; Cumming and Havlicek (2002) formally tested a subset of the data shown in Figure 1 and found statistical evidence for multimodality. A frequency graph of maximum length of 705 North American freshwater fishes in Knouft and Page (2003; their Figure 1) is also right-skewed and apparently multimodal. Note, however, that maximum length of fishes as reported in the literature is often a 'rounded best guess' of the respective expert, which results in artificial accumulation of species in length classes containing 5 (log=0.7), 10 (log=1.0), 20 (log=1.3), 30 (log=1.5), 50 (log=1.7), 100 (log=2.0) and 200 (log=2.3) cm total length; these log numbers are suspiciously close to the peaks shown in Figure 1 and might also explain the multi-modal pattern.

For the purpose of forming discrete life-history strategies I needed to create length groups. There are no a-priori criteria for grouping fish into length classes from 'Small' to 'Very large.' I tried two approaches:

1) I divided the known maximum length of 20 m into four classes of equal width (Wilson 1964) of 0.825 on a logarithmic scale, resulting in the length group ranges shown in Table 3.
2) I assumed log normality for length distribution with a mean = 1.240 and a standard deviation SD = 0.423. Then 'Small' fishes can be defined as those from Mean – 3 SD to Mean – SD; 'Medium-sized' fishes as those within Mean +/- SD; 'Large' fishes as

those between Mean + SD to Mean + 3 SD; and ‘Very large’ fishes as quasi outliers above Mean + 3 SD; there were no fishes smaller than Mean – 3 SD = 0.003 = 1 cm. This approach resulted in the ranges shown in Table 4.

The results of these two approaches were surprisingly similar. For the purpose of this study I selected the second, less arbitrary approach with length ranges shown in Table 4.

Table 3. Resulting length ranges when maximum known length of 20 m is divided into 4 groups of equal width on a log scale, with percentage of species falling into each group, for 23,685 species with available length data.

Length group	**Length range** (cm; log)	**Length range** (cm)	**Species** (%)
Small	< 0.825	< 6.7	17.4
Medium	0.825 – 1.65	6.7 – 44.7	66.1
Large	> 1.65 – 2.475	> 44.7 – 302	16.2
Very large	> 2.475	> 302	0.3

Table 4. Ranges of length groups used in this study.

Length group	**Length range** (cm; log)	**Length range** (cm)	**Species** (%)
Small	< 0.817	< 6.6	17.3
Medium	0.817 - 1.663	6.6 – 46.0	67.1
Large	> 1.663 – 2.509	> 46.0 - 323	15.3
Very large	> 2.509	> 323	0.29

Trophic Level

The feeding niche determines a large proportion of the environmental variance experienced by an organism (Winemiller and Rose 1992; Hubbell 2001) and thus the constraints acting on various life history traits. FishBase 11/2004 contained estimates of trophic level for 7,500 species derived either from published diet compositions or from known food items using a Monte Carlo routine (Pauly and Christensen 2000, Pauly and Sa-a 2000). Figure 2 shows the multimodal frequency distribution of trophic level for fish with available data. For the purpose of forming discrete life-history strategies I had to create trophic groups. Palomares (2000) suggests defining herbivores as those with trophic levels from 2.0 – 2.2, corresponding to at least 80% plant matter in their diet; for omnivores she suggests trophic levels between 2.2 and 2.8, corresponding to a maximum of 80% animals of trophic level 2 in their diet; she makes no suggestions for distinguishing secondary and tertiary consumers and top predators. If we follow her 80% scheme then tertiary consumers can be defined as those with at least 80% of secondary consumers and at most 20% of herbivores in their diet, resulting in a lower trophic level range of 3.8. Top predators can be defined as those with at least 80% tertiary consumers and 20% fourth level consumers in their diet, resulting in a lower trophic level range of 4.2. Table 3 shows the resulting classification into trophic groups with percentage of species. Note that the ranges of this classification include the peaks of the respective groups in the frequency distribution of Figure 2 (see also Stergiou and Karpouzi 2002).

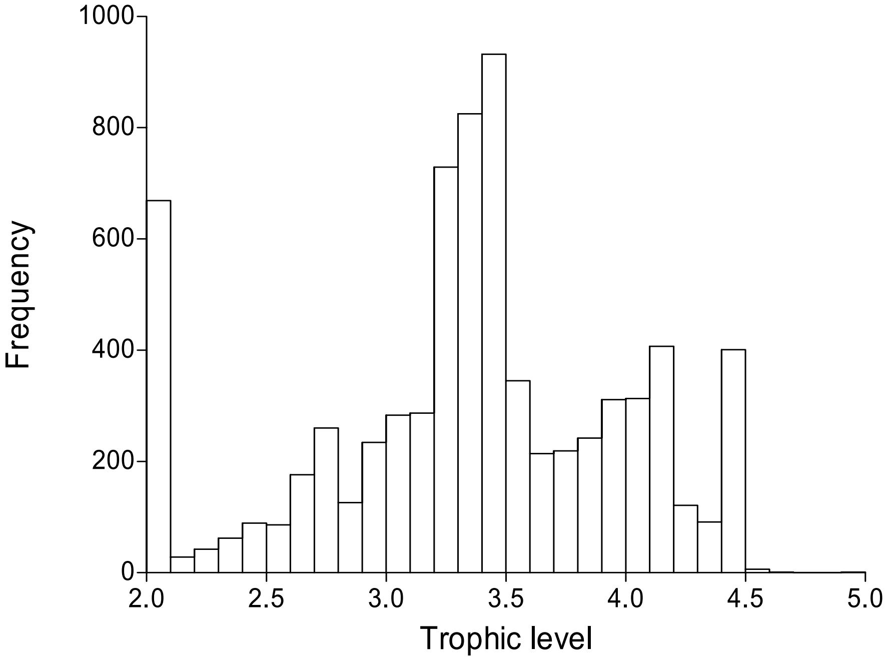


Figure 2. Frequency distribution of trophic level for 7,500 species of fishes: median 3.40, 95% CL 3.40-3.40, IQR 3.1-3.8.

Table 5. Trophic groups as defined for the purpose of this study, with number and percentage of species, for 7,491 species with available data.

Trophic group	Trophic level	Species (n, %)	
Herbivores	2.0 - 2.2	700	9.3
Omnivores	>2.2 – 2.8	712	9.5
Low-level predators	>2.8 – 3.8	4,194	55.9
Mid-level predators	> 3.8 -4.2	1,273	17.0
Top predators	>4.2	612	8.3

The trophic groups in Table 5 correspond to those used by Winemiller and Rose (1992) as follows: detritivore/herbivore = herbivores; omnivorous = omnivores; invertebrate-feeder = low-level predators; piscivore = mid-level or top predators. Note that the percentage of herbivores in Table 5 is probably too high because there has been more emphasis on this group than on the others. Pauly (2000b) expects the overall contribution of herbivorous fish species to be less than 2%.

Productivity

In the context of this study I used the term productivity to describe the ability of a population or species to recover from drastic reductions in population size caused either by environmental conditions or anthropogenic activities such as overfishing, i.e., as a proxy for the maximum intrinsic rate of population increase (Musick 1999). I used productivity values as contained in FishBase 11/2004. These values were assigned by FishBase staff according to Table 6 which is based on Musick (1999), who uses this assignment to determine the vulnerability of fishes to extinction. The first row of Table 6 gives the maximum intrinsic rate of population increase (r_{max}), which is difficult to estimate and thus rarely available in fishes (see Myers et al. 1999 and Smith et al. 1998 for reviews and few available data), and which here indicates the respective range of the productivity categories rather than being an input parameter. It is related to all other parameters of Table 6 but most sensitive to changes in age at first reproduction (Stearns 1976). The minimum time (t_d) it takes a population at low density to double in numbers is calculated as t_d (years) = ln(2) / r_{max} and the more familiar concept of the interest rate (I) earned if the stock were capital in the bank is calculated as I (%) = 100 * ($e^{r_{max}}$ -1) (Froese et al. 2000). Data for the parameters in the rows below interest rate were available from studies compiled in FishBase; the assignment of species to a productivity category was to the lowest category matched by available data. For example, a species with age at maturity between 2 and 4 years was assigned 'Very low' productivity if fecundity was less than 10 offspring per year.

Table 6. Ranges of key traits of fishes used to assign species to productivity categories, where r_{max} is the maximum intrinsic rate of population increase, t_d is the minimum population doubling time in numbers corresponding to r_{max}; interest rate is the maximum annual interest gained if the population was capital; K is the von Bertalanffy growth parameter; t_m is age at first maturity, and t_{max} is maximum age.

Parameter	High	Medium	Low	Very low
r_{max} (1/year)	> 0.5	0.16 – 0.50	0.05 – 0.15	< 0.05
t_d (years)	<1.4	1.4 - 4.4	4.5 - 14	> 14
Interest rate (%)	> 65	17 – 65	5 - 16	< 5
K (1/year)	> 0.3	0.16 – 0.30	0.05 – 0.15	< 0.05
Fecundity (1/year)	> 10,000	100 – 1000	10 – 100	< 10
t_m (years)	< 1	2 – 4	5 – 10	> 10
t_{max} (years)	1 – 3	4 – 10	11 – 30	> 30

In some cases, productivity categories were assigned to species on the basis of reasonable assumptions. For example, for members of shark families where known annual fecundities never exceeded 100 offspring, species without data were assigned to the 'Low' category with remark 'Assuming fecundity < 100.'

Table 7. Numbers and percentages of fishes by productivity group for 2,932 species for which data were available.

Productivity	Species (n, %)	
High	410	14.0
Medium	1066	36.4
Low	1167	39.8
Very low	289	9.9

Estimates of productivity were available for 2,932 species in FishBase 11/2004 (Table 7). Approximate mean r'_{max} was 0.23 (n = 2,932, 95% CL = 0.223 – 0.239). Note that behind these aggregated estimates stand large standardized compilations of studies on growth (6,695 records), maximum age (1,176 records), maturity (1,843 records), and fecundity (1,149 records).

Productivity is also related to metabolism (e.g. Winberg 1960, Winberg et al. 1971), for which FishBase contained 6,857 records albeit for only 306 species (Torres and Froese 2000). Accepting only records with standard or routine metabolism and no specified experimental stress resulted in 2,918 records for 175 species.

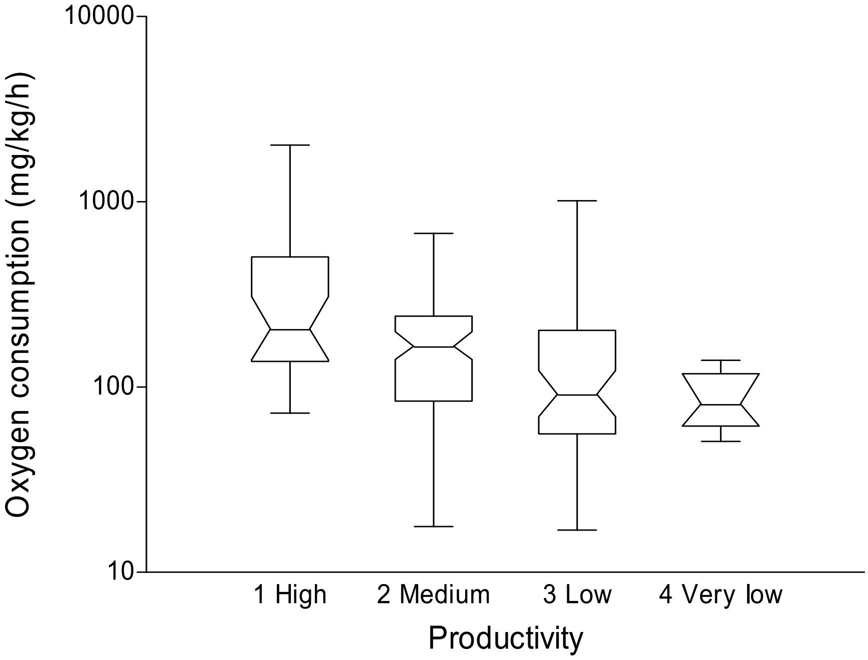


Figure 3. Mean oxygen consumption in mg/kg/h at standard or routine metabolism by productivity group, for 175 species with available data: High productivity with n = 27, median = 207, 95% CL = 148 – 432; Medium productivity with n = 92, median = 167, 95% CL = 126 – 195; Low productivity with n = 50, median = 92.4, 95% CL = 75.8 – 155; and Very low productivity with n = 6, median = 81.6 , 95% CL = 50.8 – 139.

Figure 3 shows the distribution of mean relative oxygen consumption of 175 species by productivity group. Median relative oxygen consumption decrease continuously from high to very low productivity. Relative oxygen consumption is significantly higher in the high and medium productivity groups than in the low and very low productivity groups. This confirms the correlation between productivity as derived and used in this study and metabolism as determined by relative oxygen consumption.

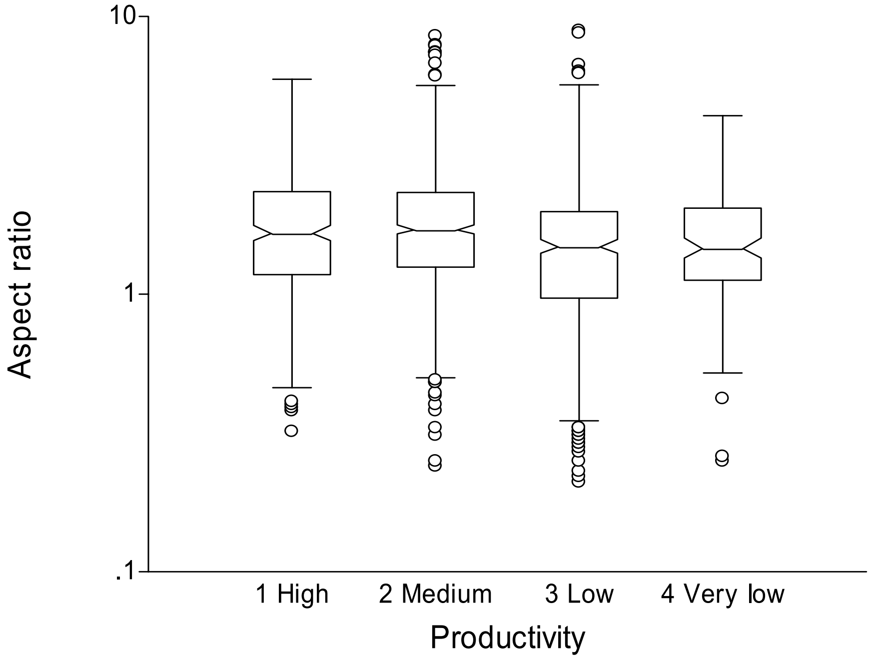


Figure 4. Aspect ratios of caudal fin by productivity group for 1,496 species with available data: High productivity with n = 297, median = 1.66, 95% CL = 1.58 – 1.82; Medium with n = 685, median = 1.71, 95% CL = 1.62 – 1.8; Low with n = 386, median = 1.49, 95% CL = 1.39 – 1.57; and Very low with n = 128, median = 1.47, 95% CL = 1.35 – 1.64.

Pauly (1989) suggests that the aspect ratio of the caudal fin of fishes provides a simple index for their metabolic level and their average level of activity. Figure 4 shows the distribution of aspect ratios by productivity group for 1,496 species with available data. Despite the high variance median aspect ratio in the low productivity group is significantly lower than those in the high and medium productivity groups; median aspect ratio in the very low productivity group is lowest, but the 95% confidence limits overlap with those of the other groups. In summary, the correlations of productivity with metabolism (Figure 3) and with average level of activity (Figure 4) confirm the validity of productivity as used in this study. Another confirmation is given by the significant correlation between productivity categories and abundance of species (Figure 68).

The parameters used in Table 6 match those proposed by Pianka (1970) for positioning an animal on the r – K continuum of MacArthur and Wilson (1967), where ‘r’ refers to the maximum intrinsic rate of population increase (r_{max}), and ‘K’ refers to the carrying capacity. Thus, in this study high productivity represents the r-end and very low productivity represents the K-end of the r-K continuum. The ranges in Table 6 confirm the observation of Pianka (1970) that “fish, in particular, span the range of the r-K continuum.” Paine (1990) and Bart and Page (1992) suggest that body size and/or phylogeny explain much of the tendency for life history traits to co-vary along the r-K continuum. This is discussed below.

The Lotka-Volterra equations normally used to determine the intrinsic rate of population increase and the corresponding placement on the r – K continuum have been developed mainly with data for terrestrial animals; among other parameters, they require knowledge of the number of offspring and their survival to a certain age, something that is difficult to estimate in fishes. Also, the use of fecundity in various simplified versions of these equations assumes a correlation between fecundity and reproductive success. While such relationship exists in many terrestrial animals and in fishes with few offspring such as most sharks (e.g.

Smith et al. 1998, Frisk et al. 2001), it does not exist in highly fecund bony fishes as has been explicitly demonstrated by Froese and Luna (2004). Once more than e.g. 1000 eggs are produced per female per year then the fecundity constraint is overcome and the addition of more eggs does not increase reproductive success (compare fecundity ranges as used in Table 6). Interestingly, Cole (1954) makes a similar point regarding tapeworms and redwood trees when he writes: “With so large a litter size one wonders if iteroparity in this case may not represent something other than an adaptation for increasing biotic potential.” He concludes that in highly fecund species without parental care survival of offspring may be increased by distributing eggs more widely in time and space. Williams (1964) already states that “In order that the number of individuals in a species should remain stable the death rate before maturity must balance the birth rate. So the fecundity of a species is an indication of the dangers of its early life.” Beverton (cited in the discussion of Partridge and Sibly 1991) states: “Clearly, fecundity and pre-mature mortality rate must vary inversely for the population to be balanced [..].” Similarly, Froese and Luna (2004) stress that high fecundity of bony fish has to be always viewed in connection with larval and juvenile mortality, such as integrated by the annual reproductive rate which gives the mean number of replacement spawners produced per spawner (Myers et al. 1999).

The uncritical use of fecundity of highly fecund bony fish as important trait in life history studies (e.g. in Winemiller and Rose 1992, Wootton 1992, Jennings et al. 1998, Rochet 2000, and Vila-Gispert et al. 2002) has lead to some confusion about the proper placement of fishes such as the Atlantic cod *Gadus morhua*, Linnaeus 1758 on the r-K continuum: its growth (e.g. K = 0.15) and maximum age (e.g. 25 years) put it on the K-side, whereas its very high fecundity (2 - 9 million eggs) put it on the r-side. Applying the rules associated with Table 6 the assignment here was to the lowest productivity category supported by data, i.e., the high fecundity was ignored and low productivity was assigned based on growth and maximum age. This result is supported by Myers et al. (1999) who find a low to medium annual reproductive rate for cod, if compared with other bony fish, and Smith (1954) who estimates r_{max} for cod as less than 0.05, which places it into the ‘very low’ category of Table 6. Similarly, Winemiller and Rose (1992) find lake sturgeon *Acipenser fulvescens* Rafinesque, 1817 and paddlefish *Polyodon spathula* (Walbaum, 1792) to be extreme outliers in principle component analysis of five life history variables of North American freshwater fishes, because age and size at maturation are large (supposedly K-selected) but eggs are numerous and small in relation to body size (supposedly r-selected). In this study lake sturgeon had very low (t_m = 16 - 26; t_{max} = 97; K = 0.04) and paddle fish had low productivity (t_m = 6 - 9; t_{max} = 30) putting both near the K-end of the r-K continuum (see Table 6 for using t_m, t_{max} and K for assigning productivity).

Relationships between Size, Trophic Level and Productivity

Ideally for a statistical analysis we would like the traits used for describing life history strategies to be independent of each other. However, in biology a given character evolves in concert with all other characters of an individual and thus especially key characters are expected to be correlated. The question then is whether the correlation is so strong that one character can be expressed and replaced by another. In this chapter I explore the correlations between the selected key traits as well as the remaining variance. I also compare the results with the findings of other authors.

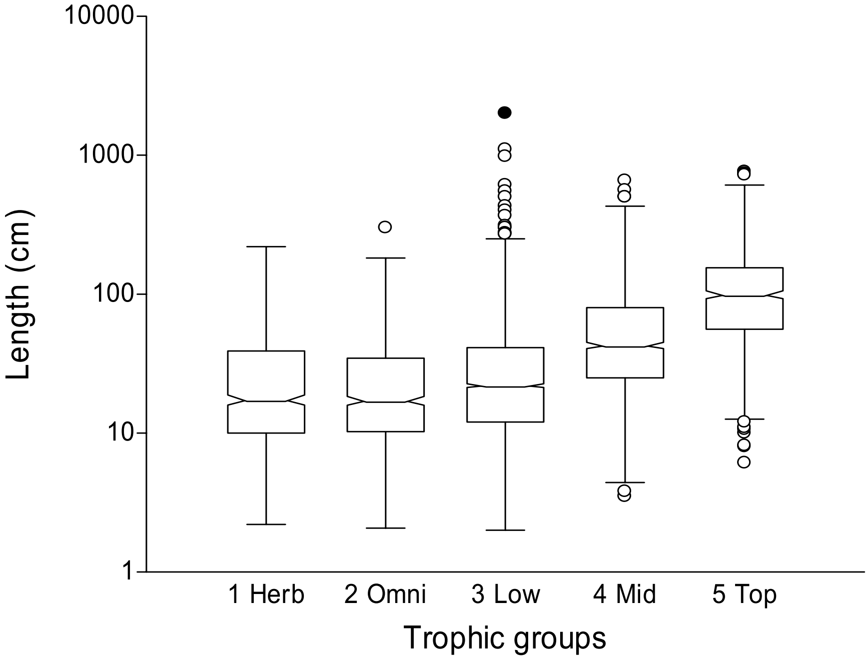


Figure 5. Length distribution by trophic group for 7,289 species: 1 Herbivores with n = 673, median = 17.3, 95% = CL 15.9-19.5; 2 Omnivores with n = 696, median = 17.1, 95% CL = 15.9-18.5; 3 Low-level predators with n = 4,080, median = 22.0 cm, 95% CL = 20.1-22.5; 4 Mid-level predators with n = 1,227, median = 42.7, 95% CL = 40.0-46.0 cm; and 5 Top predators with n = 613, median = 99.0, 95% = CL 88.8-100.0; all lengths are maximum total length in cm.

Figure 5 gives the length distribution by trophic group for 7,289 species with available data. The null hypothesis of similar median length across trophic groups is rejected with only the confidence limits of herbivores and omnivores overlapping. Median lengths increase from omnivores to top predators, as expected because in fish predators are usually larger than their prey (Welcomme 1999, Pauly 2000a). The smallest fishes are herbivores, omnivores or low-level predators. The extreme outlier in the 'Low-level predator' group is the Whale shark which feeds on zooplankton. Fishes between 10 and 200 cm maximum length occur in all trophic groups and thus the correlation is not strong enough to replace one key trait with the other. The trends in Figure 5 confirm the finding of Winemiller and Rose (1992) of a positive relationship between maximum length and trophic status.

Figure 6 shows the length distribution by productivity group for 2,621 species with available data, with a clear and significant increase in length with decreasing productivity. The greater productivity of small fish has long been established (Welcomme 1999), even within one species (Matthews 1971). Productivity as used in this study is also a proxy for metabolism (see Figure 3); relative metabolism (e.g. oxygen consumption per body weight) is known to decrease with increase in body size (Winberg 1960, Blueweiss 1978, Damuth 1987, Harrison

1996, Torres and Froese 2000). Frisk et al. (2001) demonstrate significant relationships between Elasmobranch total length and vital rates (von Bertalanffy K, maximum age, age at maturity, and fecundity, i.e., the parameters used in Table 6 to determine productivity). Baltz (1984) shows a positive correlation between size and age at maturity and maximum age for surfperches (Embiotocidae). Jennings et al. (1999) suggest "that maximum size may be a useful surrogate for a species' life history" and showed an inverse relationship between maximum size and resilience to fishing pressure. Summarizing previous evidence Pianka (1970) suggests a strong inverse correlation of r_{max} – for which productivity is a proxy—with body size.

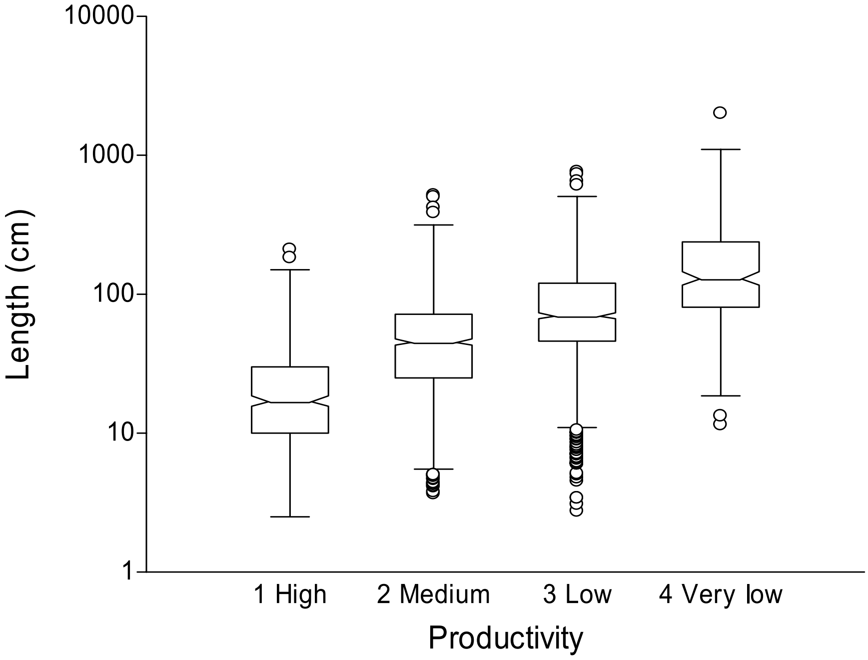


Figure 6. Length distribution by productivity group for 2,621 species with available data: 1 High productivity with n = 403, median = 17.0, 95% CL = 15.3-19.5; 2 Medium productivity with n = 1,048, median = 45.3, 95% CL = 43.0-48.8; 3 Low productivity with n = 937, median = 70.0, 95% CL = 68.0-75.0; and 4 Very low productivity with n = 233, median = 130, 95% CL = 110-150; all lengths are maximum total length in cm.

Median lengths in Figure 6 are significantly different among groups and increase from high to very low productivity. Interquartile ranges and adjacent values follow the same trend. This confirms above findings by other authors and the results of Adams (1980) who finds a negative correlation between productivity (represented by t_m, t_{max}, and K) and size. It is also a consequence of productivity being a proxy for metabolism (Figure 3), length being a proxy for body weight, and metabolism being inversely related with body weight. However, species between 10 and 200 cm length are found in all productivity groups and thus the correlation is not strong enough to replace one key trait with the other.

There is also good agreement of the size-productivity groupings with the strategies proposed by Winemiller and Rose (1992): The small size - high productivity group corresponds to their 'opportunistic strategists', which they describe as "small, rapidly maturing, short lived fishes" (see Table 6 for translating age at maturity and life span into productivity); the large size - low and very low productivity group corresponds to their 'periodic strategists', which they describe as "larger, highly fecund fishes with longer life spans"; and the medium size - medium productivity group corresponds to their 'equilibrium strategists', which they define as "fishes of intermediate size that often exhibit parental care and produce fewer but larger offspring," where parental care reduces juvenile mortality and thus leads to medium productivity.

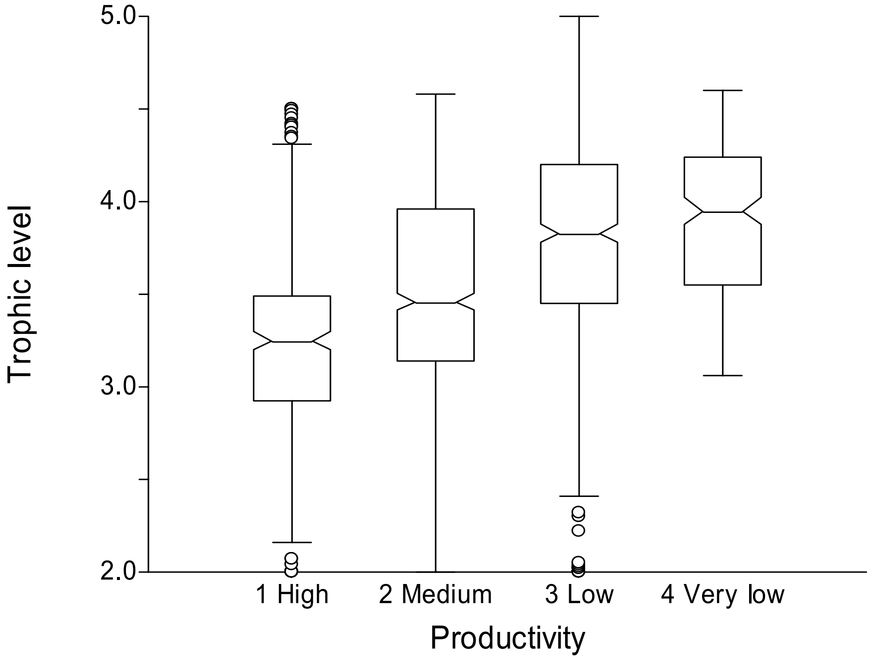


Figure 7. Trophic level distribution by productivity groups for 1,948 species: 1 High productivity with n = 325, median = 3.25, 95% CL = 3.20-3.28; 2 Medium productivity with n = 828, median = 3.46, 95% CL = 3.40-3.50; 3 Low productivity with n = 575, median = 3.83, 95% CL = 3.73-3.89; and 4 Very low productivity with n = 221, median = 3.95, 95% CL = 3.83-4.13.

Figure 7 shows the distribution of trophic levels by productivity groups for 1,948 species with available data. The null hypothesis of no difference in median trophic level between productivity groups is rejected with median trophic levels in the High and Medium productivity groups being significantly different from each other as well as from the Low and Very low groups, which have overlapping confidence limits. Overall there is a clear trend of asymptotic increase in trophic level with decrease in productivity. This confirms Winemiller and Rose (1992) who find a positive correlation of "adult growth rate with trophic status;" note that their adult growth rate is measured as mean length increment per year and thus is roughly the inverse of the von Bertalanffy growth parameter K used here for assigning productivity (see Table 6); in other words, they find a negative relationship between productivity and trophic level, as shown in Figure 7.

There were no herbivorous or omnivorous species with very low productivity; with that exception, herbivorous to top predator fishes can be found in all other productivity groups, i.e., the correlation is not strong enough to replace one trait with the other.

I am not aware of a hypothesis directly linking trophic level and productivity in carnivores (troph >= 3); rather, the observed correlation is likely to result from both parameters being correlated with body size. However, the absence of herbivorous and omnivorous species in the very low productivity group may reflect the higher energy cost associated with creating and maintaining the low pH levels required for digestion of plant material (Pauly 2000b).

In summary, while the key traits selected in this study to represent life-history strategies are not independent of each other, their variance is wide (Winemiller and Rose 1992) and leaves scope for specific combinations of traits. For example, fishes of low to high productivity can have small, medium or large size and can be herbivores, omnivores or predators.

Available Combinations of Traits: Life-History Strategies

The combination of five trophic, four productivity and four length groups allows for a maximum of 80 discrete life-history strategies. The 1,880 species for which data in all categories were available used only 45 combinations (Table 8). FishBase 11/2004 listed altogether 28,786 species and subspecies of fishes known to science, i.e., strategies were available for only 6.5% of the species and thus the analysis below is preliminary. I will return to this problem.

There are many options for grouping and sorting life history strategies in a table. The one chosen here uses the trophic groups as the basic classifier sorted from herbivores to top-predators, then size sorted from small to large, and then productivity sorted from high to very low. This inverse sorting of productivity was meant to create an r-K sorting within length groups, and since length is correlated with r_{max} (Pianka 1970) also an r-K sorting within trophic groups. Grouping species into trophically similar classes was also chosen by Hubbell (2001), who suggests that "this is perhaps the most logical, natural, and tractable way to address questions of species diversity."

The 98 herbivorous species with available data used 7 (44%) of 16 possible life-history strategies with most (60%) species having medium productivity and medium to large size. Very low productivity and very large species were absent and there were no combinations of small species with low or medium productivity.

The 114 omnivorous species with available data used 6 (38%) of 16 possible life-history strategies with 65 (57%) species having medium size and medium or high productivity and 29 (25%) having large size and medium productivity. Very large species and very low productivity were absent and there were no combinations of small species with low or medium productivity and of large species with high productivity.

The 956 low-level predators used 12 (75%) of 16 possible life-history strategies with four preferred strategies: 420 (44%) species were of medium size with medium or high productivity and 382 (40%) species were of large size and low or medium productivity. All size groups and productivity groups were present, but there were no small low-level predators with very low productivity and no very large ones with low, medium or high productivity.

The 394 mid-level predators used 10 (63%) of 16 possible life-history strategies with 236 (60%) large species of low to medium productivity. No small species were present and there were no very large mid-level predators with medium or high productivity.

The 326 top predators realized 10 (63%) of 16 life-history strategies with 259 (80%) large species of very low to medium productivity. There were no small top predators and no combinations of medium size with very low productivity and very large size with high productivity.

Herbivorous and omnivorous strategies were used by relatively few species, as predicted by Pauly (2000b) and these species used less than half (38 – 44 %) of the theoretically available strategies. In contrast, carnivore strategies were used by 3 – 9 times more species, and these species made use of 63 – 75% of the available strategies.

Table 8. Life-history strategies as combinations of key traits in 1,880 species for which data were available, with indication of number and percent of species per combination.

Trophic group	Length Group	Productivity	Species (n, %)	
Herbivores	Small	High	2	0.11
	Medium	High	16	0.85
		Medium	31	1.65
		Low	3	0.16
	Large	High	4	0.21
		Medium	28	1.49
		Low	14	0.74
Omnivores	Small	High	3	0.16
	Medium	High	39	2.07
		Medium	26	1.38
		Low	3	0.16
	Large	Medium	29	1.54
		Low	14	0.74
Low-level	Small	High	22	1.17
predators		Medium	10	0.53
		Low	3	0.16
	Medium	High	184	9.79
		Medium	236	12.55
		Low	38	2.02
		Very low	4	0.21
	Large	High	14	0.74
		Medium	198	10.53
		Low	184	9.79
		Very low	55	2.93
	Very large	Very low	8	0.43
Mid-level	Medium	High	16	0.85
predators		Medium	50	2.66
		Low	11	0.59
		Very low	5	0.27
	Large	High	8	0.43
		Medium	108	5.74
		Low	128	6.81
		Very low	49	2.61
	Very large	Low	4	0.21
		Very low	7	0.37
Top	Medium	High	6	0.32
predators		Medium	10	0.53
		Low	8	0.43
	Large	High	10	0.53
		Medium	93	4.95
		Low	113	6.01
		Very low	53	2.82
	Very large	Medium	4	0.21
		Low	15	0.80
		Very low	14	0.74

Across trophic groups there appeared to be a preference for large size with low to medium productivity (48%) and medium size with medium to high productivity (33%). These preferences were clearly biased by the available data: Table 8 contains 1.5% small, 37% medium-sized and 58% large fishes whereas the overall distribution of species by size group as shown in Table 4 has 17% small, 67% medium-sized and 16% large fishes. In other words, the above analysis of life-history strategies was biased by under-representation of small and medium-sized fishes.

Cole (1954) suggests that “if it is to survive, every species must possess reproductive capacities sufficient to replace the existing species population by the time this population has disappeared.” Wootton (1992) explores constraints that limit which positions in a multivariate life history space can be occupied by fishes. He assumes that all positions that can be occupied will be occupied by recent species. He presents a hierarchy of constraints restricting life history options: physico-chemical constraints as the outer bounds; organismic constraints such as the basic traits required by a functioning animal, e.g. respiratory and digestive organs of appropriate size and functionality; allometric constraints such as the volume-area allometry in body volume interacting through gill and gut surface areas for gas and nutrient exchange, respectively; physiological constraints such that resources and metabolic power available for one activity may not be available for other activities; demographic constraints such that combinations of traits have to result in a replacement rate high enough for a population to persist; and genetic constraints such that evolution of certain traits may be hampered by the evolutionary history (or Phylogeny) of a species.

Roff (1984) states that the prediction of ‘empty’ regions of the parameter space from first principles remains a challenge for future development of life history theory. Here I present data against which such theories can be tested. The life history strategies that were not used by fishes based on available data are listed in Table 9.

Independent of trophic group the following combinations of size and productivity were not used, probably because of organismic, allometric and demographic constraints: small size (< 6.6 cm) with very low productivity and very large size (> 323 cm) with high productivity.

Within the trophic groups, surprisingly, there were no very large herbivores and omnivores. This is in contrast to terrestrial animals where the largest species are herbivores, but consistent with marine mammals where the largest species are also low-level predators (Pauly et al. 1998); this may be due to organismic constraints: phytoplankton is tiny and difficult to accumulate by large animals; the effort and morphological adaptations may not be worthwhile when instead fishes can feast on the next trophic level of zooplankton, which effectively accumulates phytoplankton; large herbivorous fishes tend to occur in freshwater, feeding on higher plants similar to large terrestrial herbivores. Hairston and Hairston (1993, 1997) suggest that aquatic food chains have more, namely four, functional trophic levels, i.e., same as was found in this study, whereas terrestric food chains consist mainly of predators controlling herbivores and allowing higher plants to flourish.

At the other end of the trophic spectrum, there were no small mid-level and top predators. This reflects the general rule that fishes swallowing their prey in one piece will on average be larger than their prey (Pauly 2000a). However, with more data becoming available we can expect small parasitic fishes to show up in the mid-level and top-predator group.

Table 9. Thirty-five life-history strategies that are not used based on analysis of 1,880 species with available data and indication of constraints that are likely to prevent usage.

Trophic group	Length group	Productivity	Constraints
Herbivores	Small	Medium	organismic, allometric
		Low	organismic, demographic
		Very low	organismic, demographic
	Medium	Very low	physiological
	Large	Very low	[occupied in extended data set]
	Very large	High	allometric, demographic
		Medium	organismic
		Low	organismic
		Very low	organismic
Omnivores	Small	Medium	[occupied in extended data set]
		Low	demographic
		Very low	demographic
	Medium	Very low	physiological
	Large	High	[occupied in extended data set]
		Very low	[occupied in extended data set]
	Very large	High	allometric, demographic
		Medium	organismic
		Low	organismic
		Very low	organismic
Low-level	Small	Very low	demographic
predators	Very large	High	allometric, demographic
		Medium	allometric, demographic
		Low	?
Mid-level	Small	High	[occupied in extended data set]
predators		Medium	organismic
		Low	demographic
		Very low	demographic
	Very large	High	allometric, demographic
		Medium	allometric, demographic
Top	Small	High	organismic
predators		Medium	organismic
		Low	demographic
		Very low	demographic
	Medium	Very low	?
	Very large	High	allometric, demographic

Partridge and Sibly (1991) also stress that of several life-history traits that increase fitness, only certain combinations can be realized in practice, because of constraints that an increase in one trait imposes on other traits. Organisms are therefore forced to reach some kind of compromise between conflicting traits, and such compromise is known as a trade-off. If one plots a set of orthogonal axes each representing one trait, then only a restricted region of this life-history space contains combinations of traits which the organisms are capable of achieving in their natural environment. While such analyses are preferably applied to traits of individuals from a given population of a certain species to avoid phylogenetic bias (see next chapter), comparisons across species are also possible if this bias is addressed. Partridge and Sibly (1991) complain that we know almost nothing about the shapes of the boundaries of viable combinations, also known as trade-off curves or constraint-curves (McCann and Shuter 1997). Partridge and Sibyl (1991) present three hypothetical shapes of such curves for the survival versus fecundity relationship, two convex and one concave, whereas McCann and Shuter (1997) identify a ‘pinched rectangular continuum’ for the relationship between peak annual ovary weight versus female body weight for about 50 fish species. In the previous chapter I explored the relationships between size, trophic level and productivity based on observed data, with the aim of understanding the extent of their cross-correlations. If we look at the respective box plots again with respect to occupied and non-occupied life-history space, then the median lines can be seen as the ridge of a mountain chain, the inter-quartile ranges determine the slope, and the adjacent values and outliers are the foothills. For length versus trophic groups (Figure 5), the ridge is curved, with length increasing exponentially from herbivores and omnivores to top predators; the upper left and the lower right corners of the graph show empty life-history space; within each trophic group, the length-frequency distribution of species is roughly log-normal; if we assume an inverse correlation between the constraints associated with a certain combination and the number of species using that combination, then there is an increase of constraints from the median line towards the adjacent values and outliers; connecting e.g. the adjacent values would represent the shape of the respective trade-off curve, albeit in log-scale space.

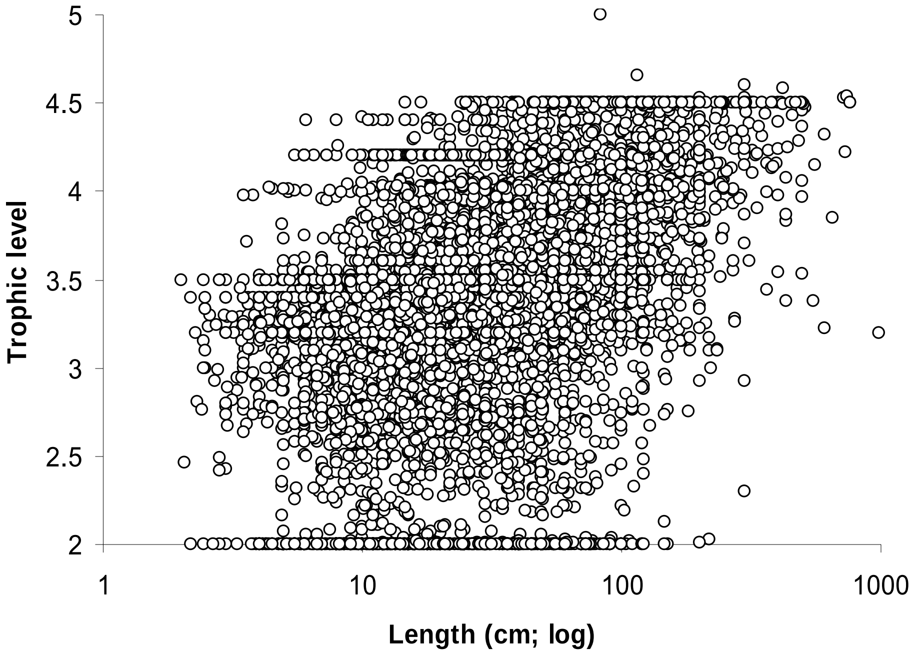


Figure 8. Trophic level versus maximum length for 7,289 species with available data. Note that the sharp upper border of the cloud of dots is an artefact of the method used to assign trophic levels.

Figure 8 shows a scatter plot of trophic levels versus length for 7,289 species with available data. The outline of the cloud of dots represents the border between used and thus obviously viable and non-used and thus presumably non-viable combinations, i.e., the trade-off curve in the sense of Partridge and Sibly (1991), albeit with a more complicated shape then the convex or concave shapes hypothesized by them. The length-axis is roughly equivalent to the r-K continuum from small r-selected to large K-selected species; the sharp lower boundary of the trade-off curve is caused by the definition of trophic levels, which in animals cannot be smaller than 2.0; the upper sharp boundary at level 4.5 results from the method of assigning trophic levels in FishBase. Note, however, that the upper limit of the trade-off curve between 4.5 and 5 is realistic and is about one trophic level higher than in terrestrial vertebrates (Hairston and Hairston 1993, 1997); this may be caused by the tiny size of phytoplankton, which is too small to be easily accumulated by large fishes and which instead is the food source of herbivorous zooplankton, which forms the main prey at the bottom of the trophic pyramid of fishes; piscivorous fishes thus feed on low-level predators rather than on herbivores. In contrast, terrestrial herbivores feed on higher plants, are often large and are a main food source for terrestrial apex predators. The grazing by zooplankton is highly efficient and consumes 2-3 times more of the net primary production than terrestrial herbivores (Hairston and Hairston 1993, 1997, Chase 2000). This efficiency of zooplankton and its easy availability as food for fishes may explain why relatively few fishes have evolved herbivory, and mostly so for benthic algae or higher plants in freshwater.

The left side of the trade-off curve in Figure 8 has an interesting multimodal shape, with a local size minimum of small herbivores, an increase in minimum size towards omnivores, a decrease in minimum size towards low-level predators, and increase in minimum size towards top level predators. The right side of the trade-off curve has a local size maximum for large herbivores, a decrease in maximum size towards omnivores, and then a semi-log-linear increase of maximum size from low-level predators to top predators. The likely constraints associated with unused life-history space in the upper left and lower right corners of the graph have been discussed above.

Looking back at the box-plot of length versus productivity (Figure 6) there is an exponential (because the x-axis is log scale) increase in length from high to very low productivity with empty life-history space in the upper right and lower left corner of the graph.

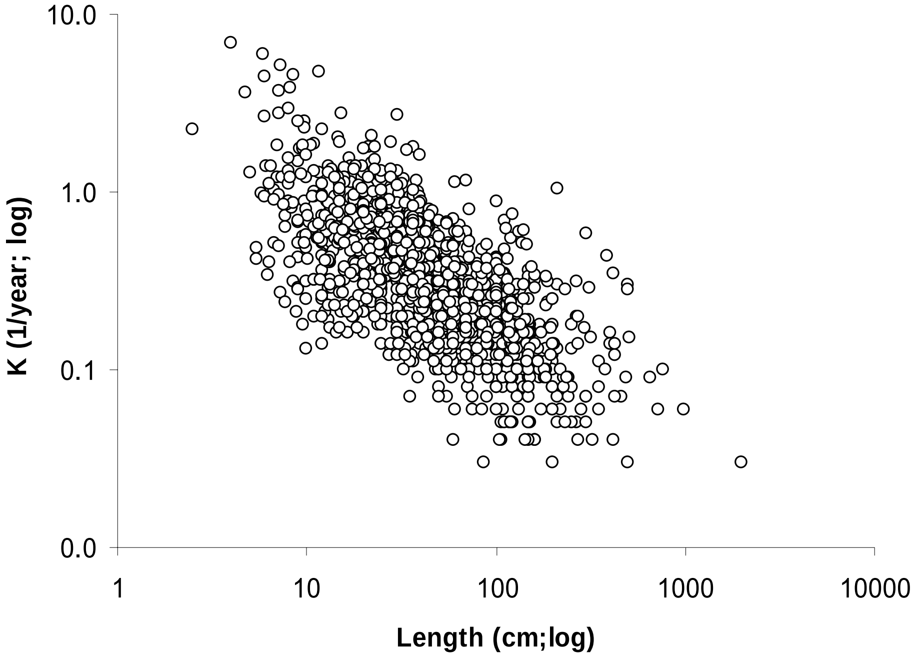


Figure 9. Growth parameter K versus maximum length for 1,368 species with available data.

Figure 9 shows a scatter plot of the von Bertalanffy growth parameter K (VBK) versus maximum length for 1,368 species with available data. Again the length-axis roughly represents the r-K continuum, from small r-selected to large K-selected species. VBK is used here as a proxy for productivity (see Table 6) and also roughly represents the r-K continuum, from r-selected species with high VBK to K-selected species with low VBK. As expected, this results in a negative log-linear orientation of the occupied life history space, where the scatter around a hypothetical regression line represents the plasticity of the life-history strategies or life-history tactics in the sense of Rochet (2000) in response to environmental influences. In fact Pauly and Binohlan (2000) show in a similar graph that part of the variance of natural mortality—which is highly correlated with VBK—versus length can be explained by environmental temperature.

An outline around the cloud of dots in Figure 9 gives the shape of the trade-off curve, here for the r-K continuum represented by two different parameters, roughly resembling an ellipse with r- selected species in the upper left and K-selected species in the lower right corner. Pauly et al. (2000) showed that the occupied life-history space is actually composed of smaller ellipses including points of populations of species, with the longer axes having a mean slope of -2, and the intercept with the Y-axis equal to $Ø' = \log K + 2 * \log L_{inf}$, where the asymptotic length L_{inf} is highly correlated with the maximum length used here (Froese and Binohlan 2000). The empty life-history spaces of small size and low productivity (lower left corner) and large size and high productivity (upper right corner) have been discussed above.

In the box-plot of trophic level versus productivity (Figure 7) despite the high variability there is a roughly linear increase in median trophic level from high to very low productivity; frequency distributions of trophic level within productivity groups are roughly normal; there is a large area of unused life-history space in the lower right low trophic level – low productivity corner, which was discussed above.

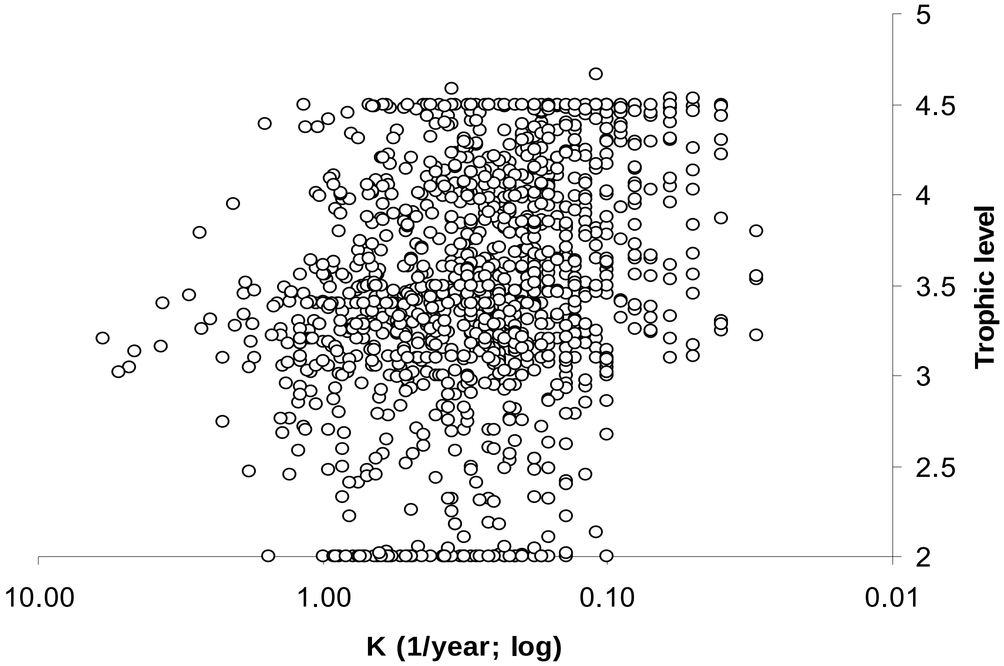


Figure 10. Trophic level versus growth parameter K for 1,176 species with available data. The graph has been inverted to facilitate comparison with Figure 8.

Figure 10 shows a scatter plot of trophic level versus the von Bertalanffy growth parameter VBK, again used as a proxy for productivity for 1,176 species with available data. An outline around the cloud of dots gives the shape of the trade-off curve. As discussed above, VBK is a rough representation of the r-K continuum with r-selected species having high and K-selected species having low VBK and thus the graph has been inverted along the x-axis to facilitate comparison with Figure 8. The sharp upper and lower boundaries of the trade-off curve are discussed with Figure 8. The shape of the left side shows an increase in maximum productivity from herbivores to low-level predators, and a subsequent decrease in maximum productivity towards top predators. The right side of the trade-off curve shows a decrease in minimum productivity from herbivores to low-level predators and about the same minimum productivity—though with high variance—from low-level to top predators. The overall shape of the trade-off curve is strikingly similar to the one in Figure 8, confirming that both size and productivity are parameters along the r-K continuum. The constraints associated with the unused life-history space in the lower left, upper left and lower right corners have been discussed above.

Life-history Strategies as a Function of Phylogeny

Intrinsic limits on possible phenotypes are set by genes, which modify existing forms through their mutations which are then subject to natural selection. Thus, phylogenetic relationships must be considered if comparative methods are to separate cross-taxonomic parallel or convergent adaptations in response to some aspect of the environment from those that are attributable to common ancestry. Only the former can be used for testing life-history theories (Pagel and Harvey 1988). In a different approach, Rochet (2000) distinguishes between life-history strategies evolved for a particular environment and tactics that provide the plasticity of these strategies to cope with environmental variability. In this study I explored traits and environmental aspects in respect to phylogeny at the Class level. I then used these results to detect potential 'phylogenetic bias' such as could be expected if distribution of available data by Class is different from the distribution of species by Class within a given category. In a form of 'natural bias' species numbers of Actinopterygii were 1-2 orders of magnitude higher than those in other Classes and they dominated in all environments considered in this study. I realize that there is also phylogenetic variation within classes, but at the scales used in this study I do not expect this to influence results (see also Winemiller and Rose (1992) who test for influence of phylogeny and come to a similar conclusion).

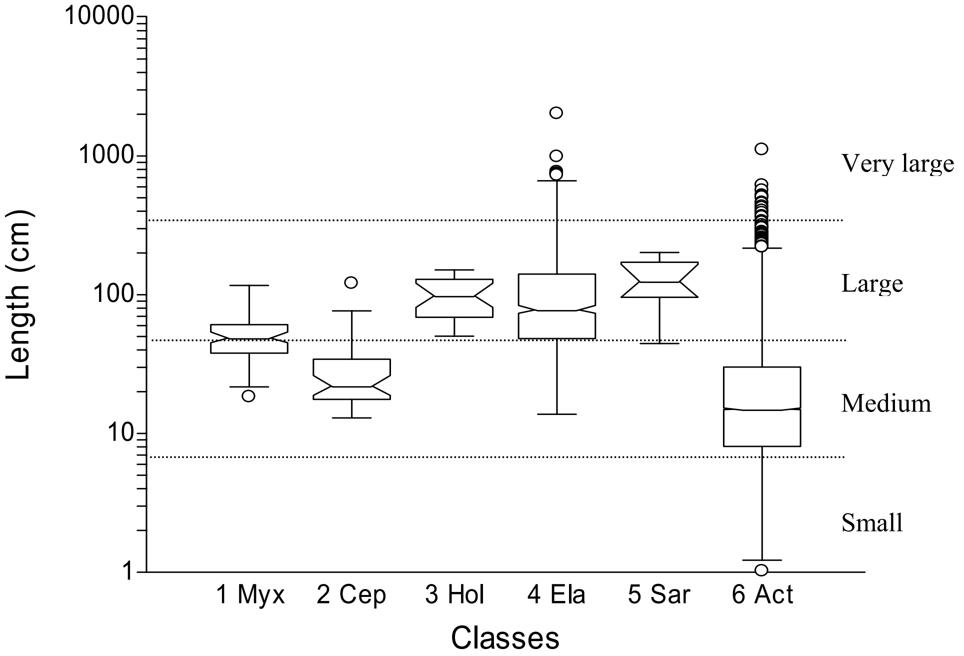


Figure 11. Distribution of maximum length by phylogenetic Class for 23,685 species of recent fishes with available data. 1 Myxini with n 69 (0.3%), median 49.0, 95% CL 43.0-54.0; 2 Cephalaspidomorphi with n = 40 (0.2%), median = 22.1, 95% CL = 19.5-30.0; 3 Holocephali with n = 24 (0.1%), median = 98.5 cm, 95% CL = 72.8-122; 4 Elasmobranchii with n = 672 (2.8%), median = 78.0 cm, 95% CL = 75.0-84.0; 5 Sarcopterygii with n = 11 (0.1%), median = 125, 95% CL = 90-170; and 6 Actinopterygii with n = 22,869 (96.6%), median = 15.0, 95% CL = 15.0-15.3; all lengths in cm maximum total lengths. Dotted lines indicate size groups used in this study (see Table 4).

The size of animals is determined by their interactions with the environment and related ecological and evolutionary processes (Cumming and Havlicek 2002). Figure 11 shows a box plot of maximum length distribution by phylogenetic Class. Note that median lengths in the recent representatives of basal Classes of hagfish to lobe-finned fishes are significantly larger than in modern ray-finned fishes. In comparison, the earliest fish-like animals ('conodonts') were apparently 4-40 cm long; fossil relatives of recent jawless fishes were also mostly medium-sized, but with some species reaching 150 cm. Among the extinct jawed fish groups, placoderms have reached well over 2 m in length and ‘spiny sharks’ ranged from 20 cm to 2 m length. Among the lobe-finned fishes extinct lungfishes and osteolepimorphans reached 4 m length. Primitive ray-finned fishes were similar in size and shape to many extant fishes; early Actinopterygii were relatively small (5-25 cm). Early Elasmobranchii were often large with about 2 m and up to 4 m, although some were as small as 15 cm and the extinct megatooth shark may have reached 16 m. Many early Holocephali were small, not exceeding 10 cm in length (Helfman et al. 1997).

In summary, compared with the fossil record, jawless fishes and chimaeras have lost species of small size whereas lobe-finned fishes have lost large-sized species. Sharks and rays as well as ray-finned fishes cover about the same size range today as in the fossil record. Moyle and Cech (2004) suggest that the diversity of recent sharks—such as their size distribution which includes very few small species—has been somehow limited by interactions with bony fishes; this is supported by Figure 11 where the predominance of modern ray-finned fishes in the ‘Medium’ size group has likely diminished the previous presence of the other Classes. Among recent fishes only Actinopterygii have species with less than 15 cm maximum length; only Elasmobranchii and Actinopterygii include species of more than 2 m length, but Actinopterygii do not reach the same maximum size as sharks do, probably because they lack the highly energy-efficient design of sharks (Helfman et al. 1997) and thus are constrained earlier on by the low amount of oxygen in water and the allometry between body weight and gill surface area (Pauly 1981). Note that the size groups derived in Table 4 and indicated by dotted lines in Figure 11 capture well the interquartile ranges of the Classes, with the exception of Myxini which have about equal numbers of medium-sized and large species. Note also that predominance of data for Holocephali, Elasmobranchii, or Sarcopterygii in a category to be analysed would introduce a ‘phylogenetic bias’ towards large size; however, the distribution of available size information (percentages in the legend of Figure 11) was very similar to the overall distribution of species by Class (percentages in Table 2), and thus I do not expect a phylogenetic bias in the analysis of size by environmental and other categories.

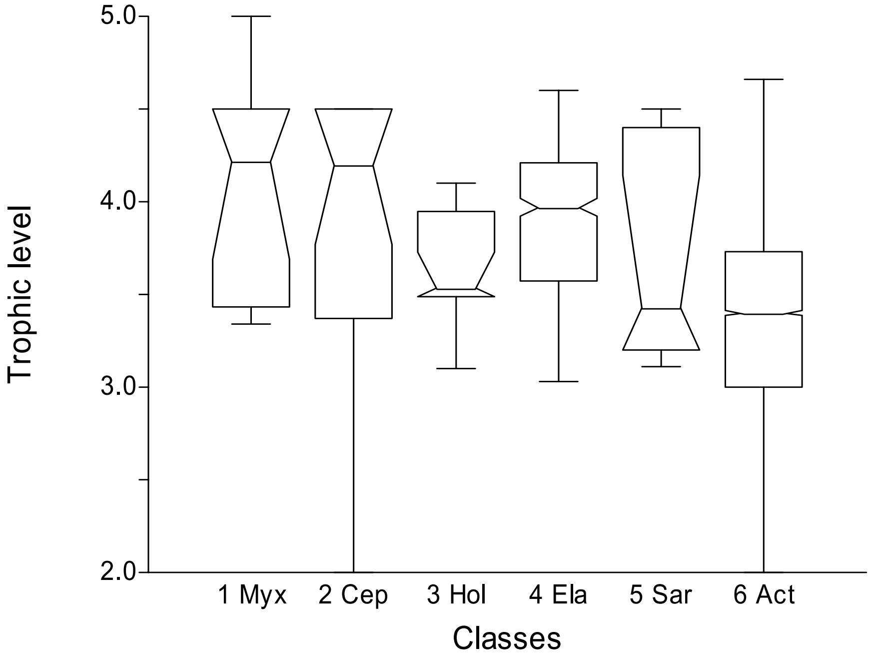


Figure 12. Trophic level by Class for 7,500 species with available data: 1 Myxini with n = 10 (0.1%), median = 4.22, 95% CL = 3.38-4.50; 2 Cephalaspidomorphi with n = 17 (0.2%), median = 4.20, 95% CL = 3.5-4.5; 3 Holocephali with n = 14 (0.2%), median = 3.54, 95% CL = 3.45-3.94; 4 Elasmobranchii with n = 432 (5.8%), median = 3.97, 95% CL = 3.89-4.01; 5 Sarcopterygii with n = 7 (0.1%), median = 3.43, 95% CL = 3.11-4.50; and 6 Actinopterygii with n = 7,020 (93.6%), median = 3.40, and 95% CL = 3.39-3.40.

Figure 12 shows the distribution of trophic levels by Classes for 7,500 species of fishes with available data. The null hypothesis that all Classes have species in all trophic categories is clearly rejected. Only Cephalaspidomorphi and Actinopterygii span the full range and include herbivorous/detritivore and omnivorous species as well as top predators. Fossil predecessors of todays jawless fishes were probably limited to planktivory, detrivory, parasitism and microcarnivory (Helfman et al. 1997) giving them a similar range of trophic levels as recent Myxini and Cephalaspidomorphi. Early Elasmobranchii were already large marine predators (Helfman et al. 1997). There is no evidence of herbivory in ancestors of recent hagfish, chimaeras, lungfishes or coelacanths.

Note that predominance of non-Actinopterygii in a group would introduce a ‘phylogenetic bias’ against herbivory and omnivory. However, the distribution of available trophic level information (percentages in the legend of Figure 12) was very similar to the overall distribution of species by Class (percentages in Table 2), and thus I do not expect a phylogenetic bias in the analysis of trophic level by environmental and other categories.

Table 10 shows Classes of fishes with productivity categories and number of species with available data, with the approximate intrinsic rate of population increase (r'_{max}). The table clearly shows the influence of phylogeny on productivity: Only ray-finned fishes spanned all productivity categories with species in the 'High' category, a majority of species in the 'Medium' category and mean $r'_{max} = 0.30$, which was significantly higher than that of all other Classes which had the majority of species in the 'Low' category and mean r'_{max} values of 0.08 - 0.15, with the exception of Sarcopterygii, which had only ‘Very low’ productivity with $r'_{max} = 0.025$. Note that the distribution of available productivity data differed from the overall distribution of species by Class (Table 2) with relatively more data for Elasmobranchii (25.7% versus 3.4%) and less for Actinopterygii (69.9% versus 96.1%). Thus, any analysis of productivity by environmental and other categories if dominated by data for non-

Actinopterygii and will have a 'phylogenetic bias' towards low productivity. However, the extended data set, which expanded the number of species with productivity estimates to 20,480, corrected this bias (see chapter *Phylogeny and Strategies Revisited*).

Table 10. Classes and productivity categories with number of species with available data, for altogether 2,932 species, with indication of approximate mean intrinsic rate of population increase (r'_{max}).

Class / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
Myxini			66		66	0.10	
Cephalaspidomorphi		7	10		17	0.15	0.120 – 0.187
Holocephali			37		37	0.10	
Elasmobranchii			580	212	792	0.08	0.078 – 0.082
Sarcopterygii				10	10	0.025	
Actinopterygii	410	1059	474	67	2,010	0.30	0.288 – 0.309

Above, I referred to the hypothesis of Hutchinson and MacArthur (1959) that high species richness, such as strikingly displayed here by Actinopterygii in comparison with the other Classes of fishes, is associated with relatively small body size and short generation time or high reproductive rate (Purvis and Hector 2000). Part one of this hypothesis was clearly supported by the significantly lower median length of Actinopterygii shown in Figure 11. Generation time is closely linked with age at first maturity and with intrinsic rate of population increase, which is highly correlated with the reproductive rate (see discussion of Table 8); r'_{max} of Actinopterygii in Table 10 is twice as high as that of the closest other Class, thus confirming part two of the hypothesis.

Table 11 shows a cross-tabulation of life-history strategies for 1,880 species with available data by phylogenetic Class. Below I explore the life-history strategies used by the members of the different Classes, and whether these can be considered representative for the Class as a whole, given that information was available for only 6 – 55% of the respective species.

For hagfishes (Myxini), combined data were available for only 10 (15 %) of the 69 recent species. Of eighty possible combinations of traits, only four were used in this Class: low-level to top predators of medium to large length and low productivity. Size and productivity were available for most hagfishes (see Figure 11 and Table 10) and confirmed the range of these traits in Table 11. Also, there was no evidence of herbivorous or omnivorous hagfishes. Thus, although the results in Table 11 were based only on 10 species, the listed life-history strategies will apply to the Class of Myxini as a whole.

For lampreys (Cephalaspidomorphi), combined data were available for 10 (24%) of 42 recent species. Of eighty possible combinations of traits, only six were present in this Class: herbivores / detrivores of medium size and low productivity and medium to large low-level to top predators of low to medium productivity, mostly parasitic adult lampreys. The length and trophic ranges were confirmed by Figure 11 and Figure 12, with data for 40 and 17 species, respectively. Table 10 confirmed the dominance of low productivity in this class, but added seven species with medium productivity. Thus, if more data were available we may expect an additional life-history strategy of mid-level predators with medium size and medium productivity (compare Table 20).

For chimaeras (Holocephali), combined data were available for 12 (32%) of 37 recent species. Of eighty possible combinations of traits only two were used: low- and mid-level predators of large size and low productivity. This result was confirmed by data in Figure 11, Figure 12 and Table 10, with data for 24, 14 and 34 species, respectively. Note, however, that very little is known about the biology of chimaeras. For example, the assignment of low productivity was mostly based on the assumption that female chimaeras produce less than 100 eggs per year. Chimaera eggs are large (10-17 cm long) and annual fecundity in some species may well be less than 10 eggs per female, which would put them in the very low productivity category. Thus, with better knowledge we may expect two more strategies with very low productivity. Most species (8, 67%) were low-level predators which is consistent with the general view of chimaeras feeding mostly on benthic invertebrates (Helfman et al. 1997).

For sharks and rays (Elasmobranchii), combined data were available for 316 (33%) of 965 recent species. Of eighty possible combinations of traits, sixteen were used: low-level to top predators of medium to very large size and very low to low productivity. This result was confirmed by Figure 11, Figure 12 and Table 10 with data for 672, 432 and 738 species, respectively. Thus, the results in Table 11 appeared to reflect correctly the life-history strategies available to the Class of Elasmobranchii as a whole. Independent of the trophic group there was a strong trend towards large size with very low or low productivity (263 species, 83%), consistent with the view that most elasmobranches live a 'Life in the slow lane' (Helfman et al. 1997).

For lungfishes and coelacanths (Sarcopterygii), combined data were available for 6 (55%) of the 11 recent species. Of eighty possible combinations of traits only three were found: low-level to top predators of large size and very low productivity. This result was confirmed by Figure 11, Figure 12 and Table 10 with data for 11, 7 and 10 species, respectively. Thus, the results in Table 11 appear to reflect correctly the life-history strategies used by the Class of Sarcopterygii as a whole.

For modern ray-finned fishes (Actinopterygii), combined data were available for 1,526 (5.5%) of the 27,662 recent species. Of eighty possible combinations of traits, forty-four were used, i.e., 3-20 fold more than in the other Classes. All expressions of all traits were present. For herbivores to mid-level predators there was a trend towards medium size with medium to high productivity and for large size with low to medium productivity. For top predators there was a trend towards large size with low to medium productivity. With the exception of one strategy used by lampreys, Actinopterygii were the only fishes using the 17 strategies from small herbivores with high productivity to medium-sized low-level predators with high productivity. Despite the low percentage of species with available data, the trends described above are likely to stand for the Class of Actinopterygii as a whole, although with more species added it is likely that some strategies adjacent to the ones found here will be added (compare Table 20). However, because of the under-representation of small and medium sized fishes pointed out in the discussion of Table 8, the numbers of species in these length groups are likely to increase.

No strategy was used by all Classes and there were only three life-history strategies that were used by four out of six Classes: low-level predators of medium to large length and low productivity and top-predators of large length and low productivity. Interestingly, while ray-finned fishes dominated in all three strategies, they tended to have higher species numbers in the adjacent strategies with higher productivity. This confirmed the observation by Helfman et al. (1997) that sharks consume about half of the oxygen of bony fish with similar size, i.e., everything else being equal Actinopterygii will tend to have higher metabolism and thus productivity.

Although the number of Actinopterygii contributing to this analysis was about four times higher than that of Elasmobranchii, sharks & rays had higher species numbers in nine strategies, six of which were of very low and the remainder of low productivity. This confirms the observation of Helfman et al. (1997) that “many aspects of the biology of sharks point to a strong emphasis on efficient energy use when compared with bony fishes,” including anatomical features such as fin and scale morphology but also lower resting and active metabolic rates and corresponding reduced energetic needs. Thus, there was evidence for a non-overlap of preferred life-history strategies between the two largest and thus most successful groups of recent fishes, with Elasmobranchii tending towards large size and low to very low productivity, and Actinopterygii tending towards medium size with medium to high productivity. Or put differently: the efficient energy use of sharks allows them to occupy positions in multidimensional life history space where bony fish have difficulties to persist. This confirms the finding of Winemiller and Rose (1992) who observed “evolutionary divergences in life-history strategies among higher taxa”.

Table 11. Cross-tabulated view of life-history strategies and phylogenetic Classes for 1,880 species. The last row gives for every Class number and percentage of species with available data; Myxini, Cephalaspidomorphi, Holocephali, Elasmobranchii, Sarcopterygii, and Actinopterygii.

Trophic group	Length group	Productivity	Myx	Ceph	Holo	Elasmo	Sarco	Actino
Herbivores	Small	High						2
	Medium	High						16
		Medium						31
		Low						3
	Large	High						4
		Medium		1				27
		Low						14
Omnivores	Small	High						3
	Medium	High						39
		Medium						26
		Low						3
	Large	Medium						29
		Low						14
Low-level predators	Small	High						22
		Medium						10
		Low						3
	Medium	High						184
		Medium		1				235
		Low	1	1		5		31
		Very low				2		2
	Large	High						14
		Medium						198
		Low	3		8	54		119
		Very low				28	4	23
	Very large	Very low				3		5
Mid-level predators	Medium	High						16
		Medium		1				49
		Low	1			3		7
		Very low				4		1
	Large	High						8
		Medium						108
		Low			4	59		65
		Very low				44	1	4
	Very large	Low				3		1
		Very low				5		2
Top predators	Medium	High						6
		Medium						10
		Low		2		5		1
	Large	High						10
		Medium						93
		Low	5	4		38		66
		Very low				40	1	12
	Very large	Medium						4
		Low				9		6
		Very low				14		
Total: n (%)			10 (15)	10 (24)	12 (32)	316 (33)	6 (55)	1526 (5.5)

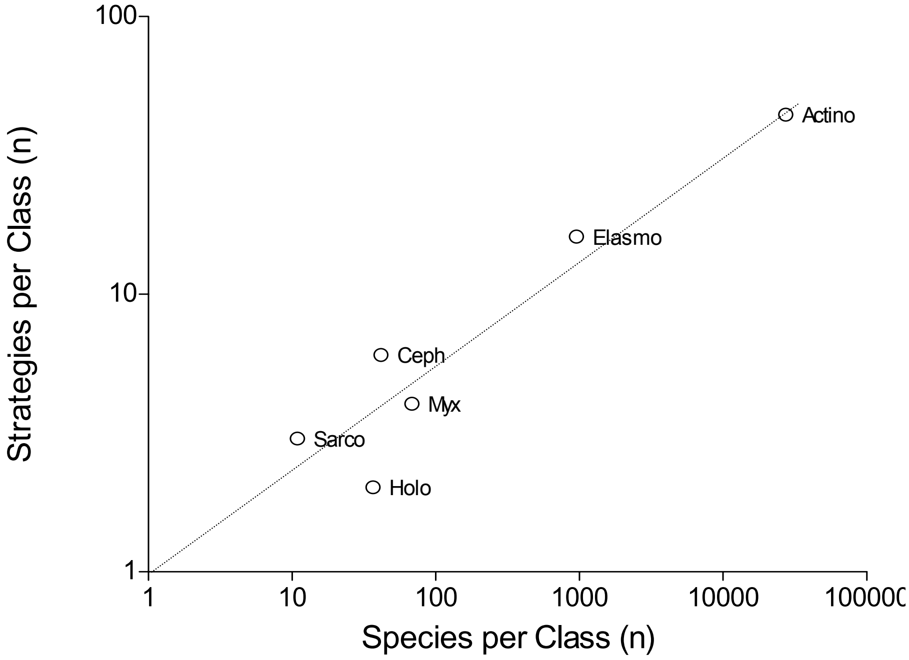


Figure 13. Number of strategies used by phylogenetic Classes plotted over number of recent species in the Class, with linear regression line forced through the origin; slope = 0.37. See Table 11 for abbreviations of Class names and respective numbers of species with available data.

Figure 13 shows the number of strategies used by a Class of fishes plotted over the respective number of recent species. The linearity of the relationship is striking, especially if we consider that the outlier Holocephali may have two more strategies (see discussion of Table 11), which would put them left of the Myxini and very close to the regression line. A linear regression analysis forced through the origin (because a theoretical Class with only one species can have one and only one strategy) explained 98% of the variance and resulted in the model:

$$\log \mathrm{Strat}_n = 0.3726 * \log \mathrm{Spec}_n$$

or

$$\mathrm{Strat}_n = \mathrm{Spec}_n^{0.37}$$

Equation 4. Number of strategies as a function of number of species, where Strat_n is the number of strategies and Spec_n is the number of species in a Class, with n = 6, $r^2 = 0.9754$, coefficient of variance = 0.1960, and 95% confidence limits of the slope = 0.3046 – 0.4406.

The explained variance is unusually high for multi-species comparisons and in part caused by the fact that species numbers span four orders of magnitude. There is also an aspect of probability theory: while the likelihood of a species being different and establishing a new strategy increases with the number of species in a Class—similar to the ‘selection probability effect’ of Huston (1997)—the likelihood of an ‘unused’ strategy becoming used decreases with the number of strategies that are already used. Also a Class cannot have more strategies than species, which is relevant for the Classes (Myxini, Cephalaspidomorphi, Holocephali, and Sarcopterygii) that have less recent species than the potentially available eighty strategies. Note Figure 81 and Equation 20 for a meta-analysis of these data in the context of all relationships between strategies per group and species per group.

In order to better understand the relationship between species richness and number of strategies I explored relationships between species richness and number of higher taxa.

Williams (1964) pointed out that "In almost every classification that has been proposed the number of genera with only a single species is greater than the number with two, the number with two greater than the number with three, and so on. [...] The same relation appears to exist also between genera and families, and between families and higher groups. [...] If we plot such a classification in form of a frequency distribution we get a hollow curve [...]." Yule (1924) suggested using logarithmic axes and fitting a straight line to the relationship. Figure 14 shows such a plot for all 4,812 Genera of recent fishes.

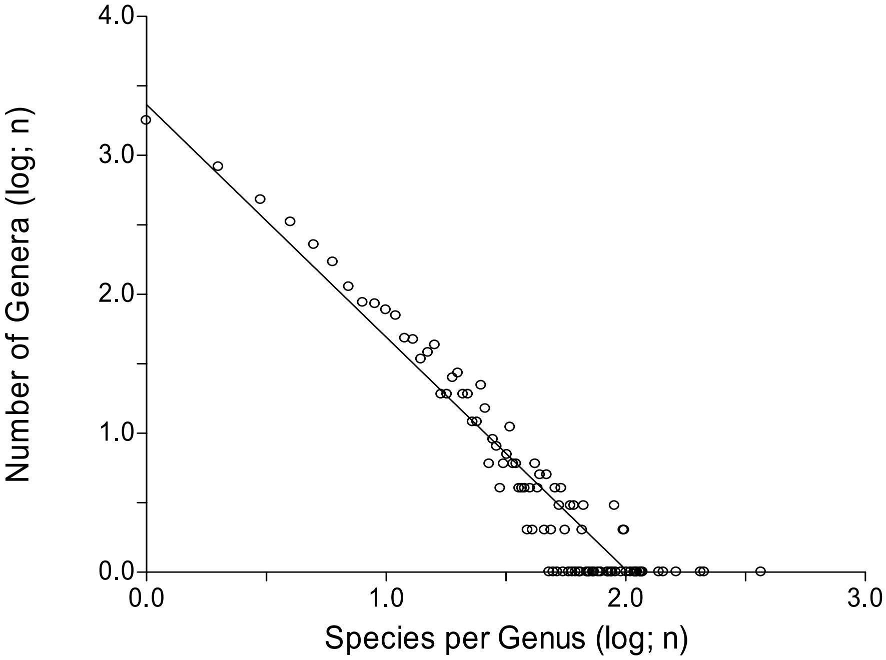


Figure 14. Frequency distribution of number of species per Genus for 4,812 Genera and 28,786 species of recent fishes. Intercept = 3.365 (3.179 – 3.550), slope = - 1.673 (-1.784 - -1.562), r^2 = 0.9047, coefficient of variation = 0.3624.

The straight line in Figure 14 explains 90% of the variance in the data. There are 1,775 Genera with only one species and 16 Genera with 101 to 368 species. The increased variance towards the lower right of the graph is partly an artefact because the likelihood that Genera have exactly the same number of species and thus show as a single dot in the graph decreases with the increase in number of species; however, it is also a reflection of several large Genera not yet being resolved taxonomically, i.e., more study is likely to split them into several Genera, such as is expected for *Barbus* (368 species) and *Haplochromis* (213 species), the two most specious Genera. Williams (1964) draws several conclusions from the fact that the number of higher taxa is highly predictable from the number of lower taxa: First, he concludes that higher taxa such as Genera and Families were "as real [...] as individuals and species", rather than mostly a matter of convenience for taxonomists to group species, as he had assumed previously. Second, since the classifications of 'lumpers' establishing few Genera per species and 'splitters' establishing many Genera, both could be fitted by the same mathematical function, albeit with different constants, he concludes that lumpers as well as splitters have worked consistently and described real differences between species, with the lumper focusing on fundamental differences further back in evolutionary time, whereas the splitter focuses on recently evolved differences. He stresses that a misfit (or increased variance) would result from combining classifications of lumpers and splitter, such as is the case in Figure 14 with 'lumper' Genera *Barbus* and *Haplochromis.* The underlying reasons for these scaling laws that govern patterns of taxonomic diversity are still a matter of debate.

As Gotelli (2002) put it: “Teasing apart the specific biological and statistical mechanisms responsible for these patterns is a task for the future.”

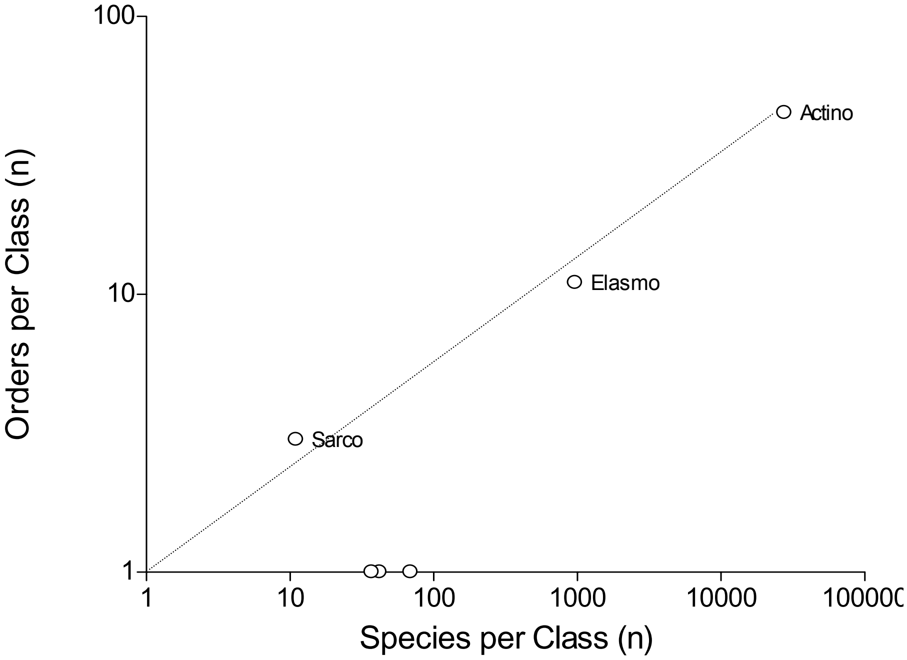


Figure 15. Number of Orders per Class plotted over Species per Class. Sarcopterygii, Elasmobranchii and Actinopterygii fall nearly on a hypothetical straight line through the origin; slope = 0.37. Myxini with 69, Cephalaspidomorphi with 42 and Holocephali with 37 species have only one recent Order and fall on the X-axis.

Figure 15 shows a plot of phylogenetic Orders over species per Class. The similarity with Figure 13 is striking. Myxini, Cephalaspidomorphi and Holocephali (on the X-axis) had fewer Orders than suggested by their species numbers. As discussed below, these ancient groups had several times more Orders in the fossil record. It seems that if the archetypal body plan of a Class allowed for the expression of a wide variety and range of traits then these will have evolved in numerous combinations expressed as Orders and strategies and used by numerous species. In particular, the bony skeleton especially of the jaws, movable fins, gas bladder, and wide variety of reproductive modes available to Actinopterygii have allowed them to evolve many more life-history strategies and species than the other Classes. In contrast, lack of jaws, paired fins and buoyancy organ and restriction to one reproductive mode clearly limits body plan options and life-history strategies for Myxini. This disparity in variety of body plans and strategies also becomes obvious when looking at recent species: while the relatedness of sharks (largest group within Elasmobranchii) is obvious from body form and life style, the relatedness of seahorses, eels, tunas and molas is not at all obvious.

The similarity between Figure 13 and Figure 15 as expressed by similar maximum number of groups (44 strategies and 45 Orders) and identical slopes is partly caused by the underlying probability for number of groups (strategies or Orders) as a function of the number of species in a Class. Also, the identical slopes suggest that the increase in overall trade-offs associated with not-yet-used strategies is similar to that for not-yet-used body plans that would constitute new Orders. To further explore this theme, I looked for similar relationships in other taxonomic groups.

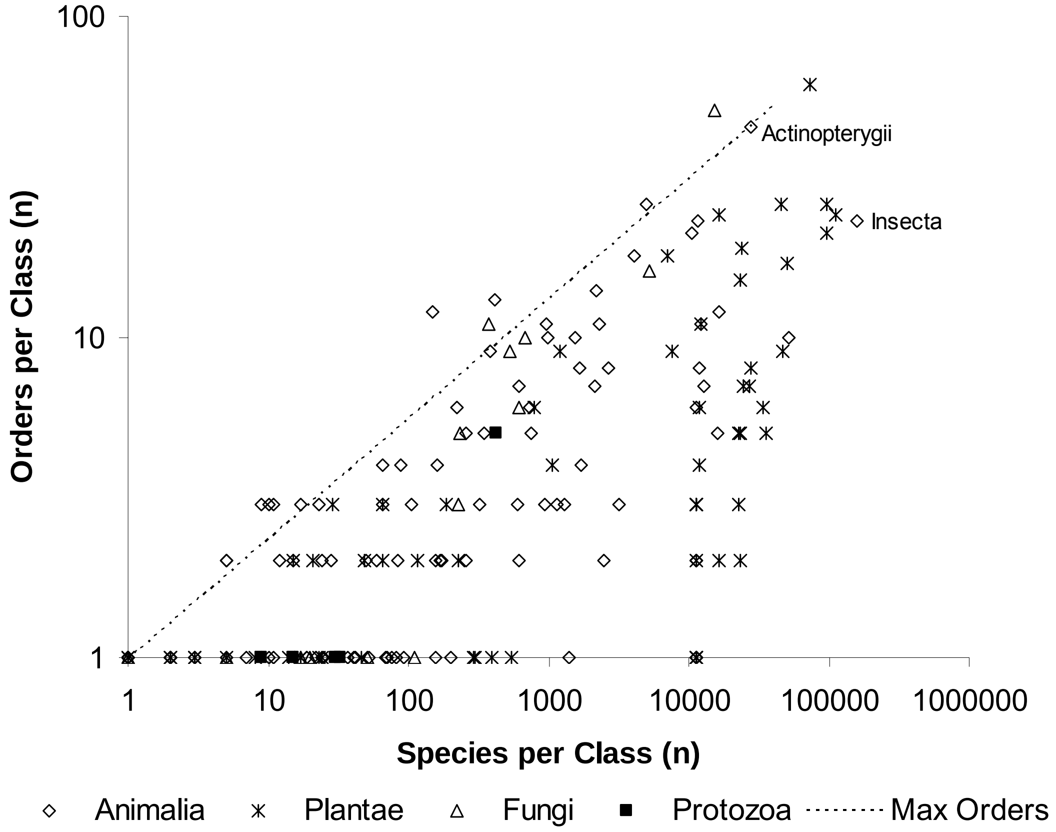


Figure 16. Number of Orders per Class plotted over species per Class for four Kingdoms and 415,000 species; the dotted line indicates the maximum number of Orders per species in a Class; slope = 0.37.

Figure 16 shows a plot of number of Orders per Class versus Species per Class for about 415,000 species from four Kingdoms: Bacteria, Fungi, Plants and Animals, based on the Species 2000 Annual Checklist (Froese and Bisby 2000), here from a preliminary version of the 2005 edition. An in-depth analysis of this graph is beyond the scope of this study, however, several properties are remarkable: Magnoliophyta (flowering plants; 61 Orders), Ascomycota (Fungi; 51 Orders) and Actinopterygii (Animalia; 45 Orders) together have the highest number of Orders and determine the upper-right end of a clear border line anchored in the origin of the graph; Protozoa have one point (black square) near the middle of that line. Also, Fungi, Plantae and Animalia have very similar upper limits to the number of species and number of Orders per Class. Insecta have the highest number of species (though here still largely under-represented) but relativly few Orders, probably both a result of this group being under-sampled and under studied. Across the four Kingdoms the relationship between Orders and Species per Class seems to be guided by the same underlying rules, resulting in similar variance and similar upper limit for maximum number of Orders per species in a Class, which is described by the following equation:

$$\text{Orders}_{max} = \text{Spec}_n^{0.3744}$$

Equation 5. Number of Orders as a function of number of species, where Orders_{max} is the maximum number of Orders per Class and Spec_n the number of Species per Class; the line was anchored in the origin of the graph and forced through the mean of the coordinates of the three Classes with highest Order numbers for Fungi, Plantae and Animalia.

From this relationship it can be deduced that Myxini, Cephalaspidomorphi and Holocephali have fewer Orders than suggested by their number of species (see discussion of fossil record below), and that 158 new species of Elasmobranchii or 1,574 new species of Actinopterygii need to be discovered before a new Order is likely to be established. Note that such suggestions are not unrealistic: for Elasmobranchii, Nelson (1984) recognized 763 species in 5 Orders; Nelson (1994) recognized 815 species in 9 Orders and FishBase 11/2004 recognized 965 species in 11 Orders compared to a maximum of 13 Orders predicted for 965 species by Equation 4. Similarly, for Actinopterygii Nelson (1984) recognized 20,850 species in 39 Orders compared to a predicted maximum of 41 Orders; Nelson (1994) recognized 23,681 species in 42 Orders; FishBase 11/2004 recognized 27,662 species in 45 Orders compared to a predicted maximum of 46 Orders. Thus, as the species of Elasmobranchii and Actinopterygii became more completely known and their relationships better understood, the number of Orders per species approached the maximum predicted by the relationship derived from Figure 16. Notably, the recognition of 150 new species of Elasmobranchii between 1994 and 2004 suggested an addition of one new Order and in fact two new Orders were recognized; the recognition of 6,812 new species of Actinopterygii between 1984 and 2004 suggested the addition of five new Orders and in fact six new Orders were recognized. Of course these predictions are statistical and must not be applied mechanistically. Also, I do not imply that all new Orders were based on new species. Still the close match of predictions and actual establishment of new Orders is striking. If we take the estimated number of one million known species of Insecta we can predict with some confidence that adequate taxonomic study will establish clearly more then the currently recognized 23 Orders, but not more than 176 Orders.

Building the Database for All Fishes

In the discussions of Table 8 and Table 11 I already pointed out that availability of information on diet and productivity was biased towards larger species. Table 12 further explores this bias: it is strongest in the combined group (column 5) where data are available for only 2% of the small and 37% of the medium sized fishes while the overall contribution of these groups is 17 and 67%, respectively. This confirms Winemiller and Rose (1992) who found their data set of 216 North American fish species to be biased towards larger, commercial species. In order to recognize the influence of this bias when comparing importance of and preference for certain life-history strategies I decided to use a modelling approach for trophic level and productivity to create an extended data set with life-history strategies for most species of fish. However, I continue to use observed data in direct comparisons of key traits with environmental and other parameters.

Table 12. Available information on trophic level and productivity by length group. Note bias towards large species when comparing percentages of species with length versus with all information.

Length group	**Species in length group**		**Species with trophic level**		**Species with productivity**		**Species with length, troph, productivity**	
	n	**(%)**	**n**	**(%)**	**n**	**(%)**	**n**	**(%)**
Small	4,09	17.3	483	6.6	92	3.5	40	2.1
Medium	15,892	67.1	4,637	63.6	1,068	40.7	686	36.5
Large	3,632	15.3	2,111	29.0	1,402	53.5	1,102	58.6
Very large	68	0.3	58	0.8	59	2.3	52	2.8
Total	23,685	100.0	7,289	100.0	2,621	100.0	1,880	100.0

Modelling Trophic Levels

For modelling of trophic levels, I followed the approach suggested by Pauly and Palomares (2000) and Pauly et al. (2001), who use available data for the closest relatives of a given species (congeners or members of the same Subfamily, Family or Order), calculate the slope of trophic level plotted over body length (see also Figure 5), and then use the body length of the species in question to derive an approximate estimate of trophic level. Notably, Pauly et al. (2001) anchore the regression line at length = 1 cm and trophic level = 3.0 based on the observation that during ontogeny trophic level changes from that of fish larvae which feed on small herbivorous zooplankton to that of adults which may range from herbivores to top predators, and that this pattern also applies to size groups of species (see Figure 8). The modelling steps used in this study were as follows:

For a species without food information

1) I identified the closest relatives with trophic level data (same Genus or Subfamily or Family or Order);
2) For the closest relatives with at least 3 trophic level records, I calculated the slope of trophic level versus body length from Equation 6:

$$b = (\text{troph} - 3) / \log(0.5 * L_{max})$$

Equation 6. Slope of trophic level as a function of body size, where troph is the trophic level and L_{max} is the maximum length reported for the respective species; half L_{max} is assumed as the typical size of fishes for which food information is available; the slope is anchored at troph = 3.0 and length = 1 cm.

3) Using the mean of the slopes obtained above and L_{max} for the species without trophic level, I computed the preliminary trophic level for that species from Equation 7.

$$\text{troph} = 3 + b_{mean} * \log(0.5 * L_{max})$$

Equation 7. Model for estimating trophic level, with parameters defined as above.

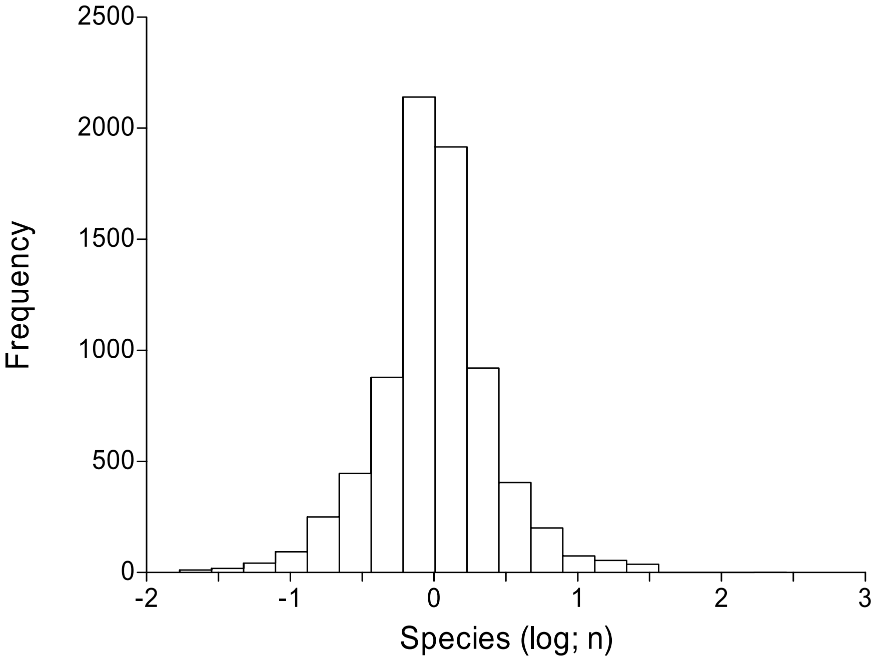


Figure 17. Frequency distribution of residuals of predicted versus observed trophic levels: the distribution is approximately normal with n = 7,485, mean = 0.000701, SD = 0.401, 95% CL = -0.00838 – 0.00978.

Figure 17 shows the frequency distribution of the residuals of predicted versus observed trophic level for 7,485 species with available data. Note that the residuals were about normally distributed, with a mean not significantly different from zero. About 68% of all predicted trophic levels fell within 0.4 units of the observed trophic level. Thus, the above method for predicting trophic levels provided reasonably accurate results.

Figure 18 shows the application of the above approach for 37 species of the Genus *Epinephelus* for which no food information was available (small black dots in Figure 18). Note that using the mean trophic level (here 3.9) of the species with food information would have put all species without trophic level in the 'Mid-level predator' category. The current approach put smaller species into the 'Low-level predator' category, thus providing a better interpretation of variance and trend in the available data.

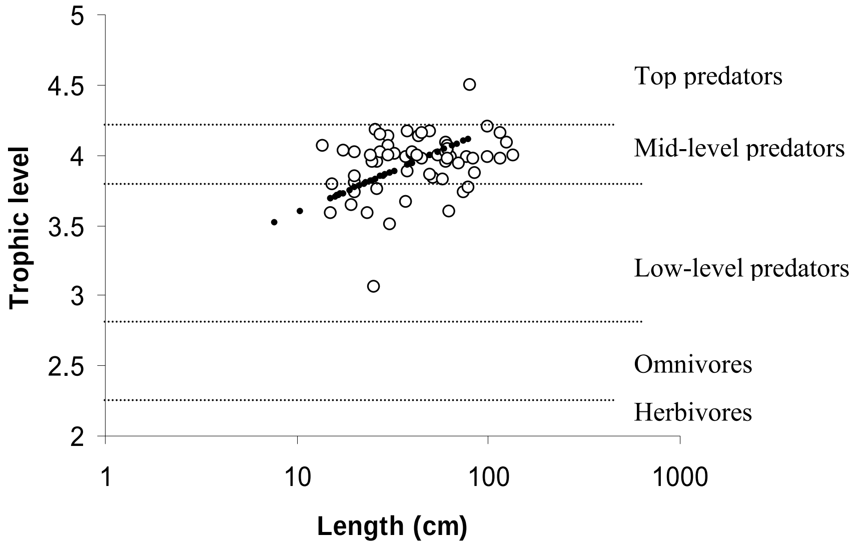


Figure 18. Trophic level of 97 species of Genus *Epinephelus* as a function of their body length (= ½ maximum length). Open circles are 60 observed values, black dots are 37 predicted values. The dotted lines indicate the classification into trophic groups, from herbivores below trophic level 2.2 to top predators above 4.2.

Modelling Productivity

In order to extend the productivity data set I derived preliminary values of the von Bertalanffy growth parameter K as described below and used these to derive preliminary productivity estimates.

Figure 19 shows the frequency distribution of available K values based on 5,850 growth studies for 1,404 species. K was roughly log-normal distributed. Mean K was 0.25 years^{-1}.

The method used here for estimating preliminary values of K for additional species was based on the observation by Pauly et al. (2000) that in plots of log K over log asymptotic length (L_{inf}), values for a given species form an ellipse, with the longer axis having a mean slope of about -2. For growth in length, Pauly et al. (2000) suggest naming the intersection of the ellipse axis with the ordinate Ø' and using it for comparing growth of species or for estimating the K corresponding to a given L_{inf}.

$$Ø' = \log L_{inf} + 2 \log K$$

Equation 8. Growth index Ø', where L_{inf} and K are parameters of the von Bertalanffy growth function.

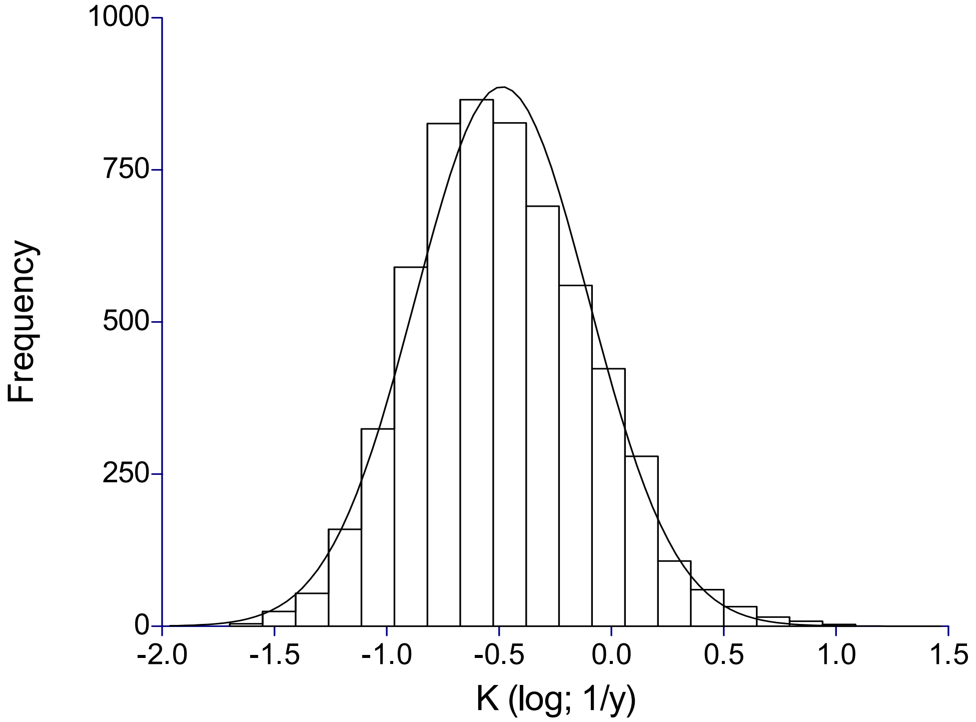


Figure 19. Frequency distribution of von Bertalanffy growth parameter K, with normal distribution line (mean = -0.488; SD = 0.386; n= 5850). Note that K is approximately log-normal distributed.

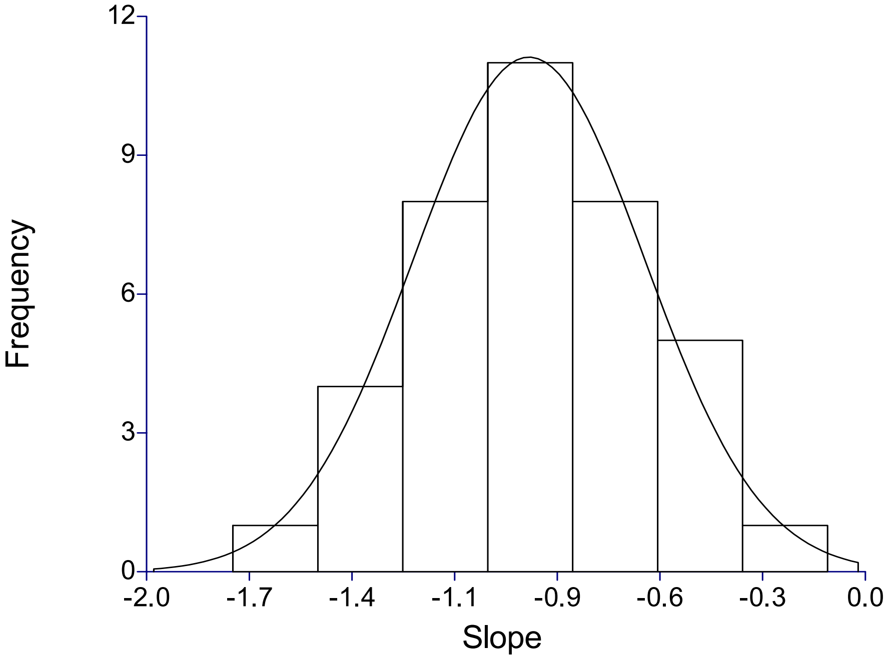


Figure 20. Frequency distribution of the slope when log K is plotted over log L_{inf} for 38 Families with at least 10 species with growth information; mean = -0.936, n = 38, SE = 0.0523, lower 95% CL = -1.041, upper 95% CI = -0.8300

For the purpose of this study I analysed plots of log K over log L_{inf} for 38 Families with at least 10 species with available growth parameters and fitted least squares regression lines to the data. The frequency distribution of the slopes is shown in Figure 20 and was normally distributed.

Ø' for families can thus be expressed as follows:

$$Ø'_{Family} = \log K + 0.94 * \log L_{inf}$$

Equation 9. Growth index Ø' for Families, where L_{inf} and K are parameters of the von Bertalanffy growth function.

Equation 9 was used to estimate $Ø'_{Family}$ for all Families for which at least one growth study was available. For species without growth information preliminary estimates of K were then obtained as follows:

1) Get maximum length from FishBase;
2) Transform length type to total length if different;
3) Calculate L_{inf} from maximum length based on the empirical equation of Froese and Binohlan (2000);
4) Get preliminary K from Equation 10.

$$\log K = Ø'_{Family} - 0.94 * \log L_{inf}$$

Equation 10. Estimating K from Ø' of the Family and L_{inf} of the species, with parameters as defined above.

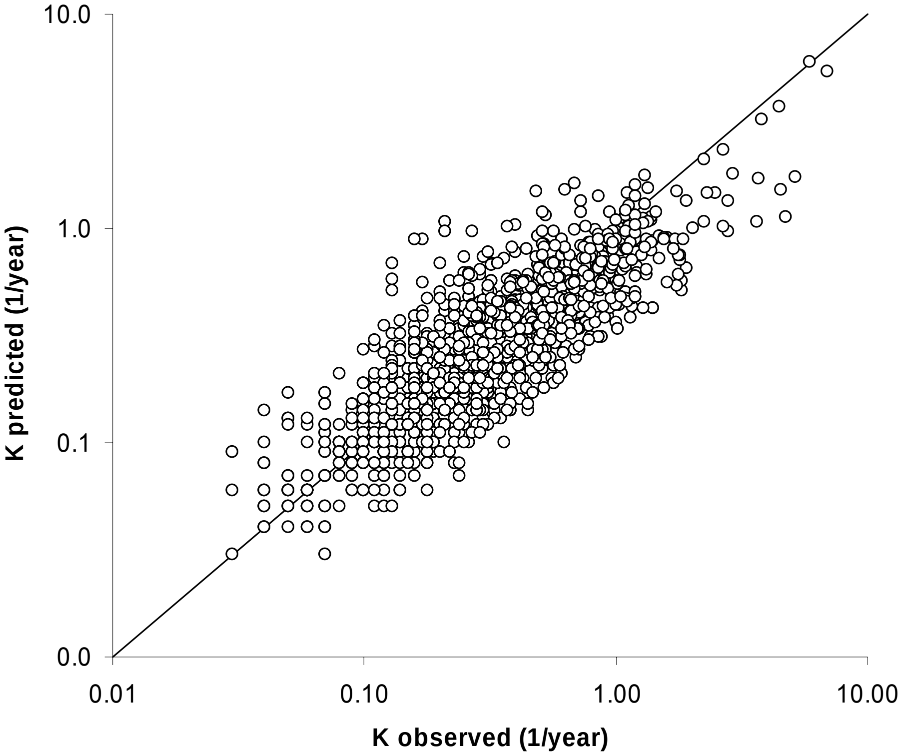


Figure 21. Predicted values of von Bertalanffy growth parameter K plotted over observed values for 1,311 species with available data. The line indicates the predicted = observed cases.

Figure 21 shows predicted versus observed values of K for 1,311 species. The distribution around the 1:1 line seems reasonable. Very high values of K (>1.0) tended to be underestimated; however, this did not affect my analysis because all values above K = 0.42 (see below) were classified as high productivity.

As an example, Figure 22 shows a scatter plot of calculated and observed K values over maximum length for the Family Serranidae. While one can argue about the appropriateness of extending the regression line left beyond the available data, there is little doubt that these species will fall into the 'High' productivity category.

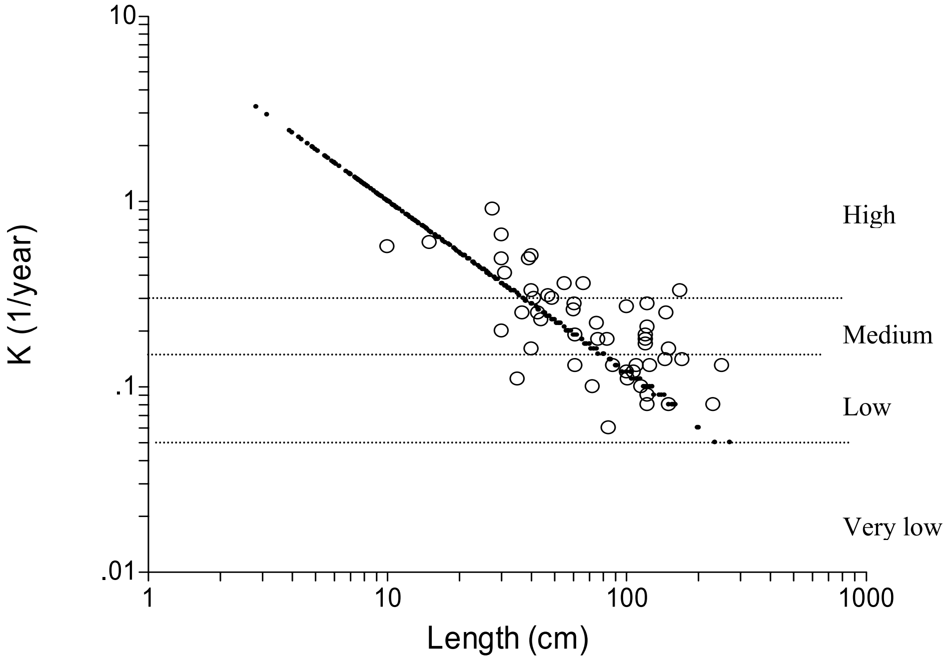


Figure 22. Von Bertalanffy growth parameter K plotted over maximum length for species of the Family Serranidae. Open circles are available data; small black dots are predicted K values. Dotted lines indicate the borders between productivity categories if derived from K.

I then explored how well the predicted values of K matched observed productivity categories. Table 13 shows median values and interquartile ranges of predicted K for 1,311 species for which observed productivity was available. When compared with the ranges in Table 6 (repeated in column 2), it becomes clear that predicted K, if used directly against the ranges in Table 6, overestimates medium and high productivity, underestimates low productivity and strongly underestimates very low productivity. For example, the predicted median K for species with very low productivity was 0.09, with IQR 0.06 – 0.14; with the ranges in column 2 these K values would result in an assignment of Low instead of Very low productivity. Thus, for the purpose of providing productivity estimates for the extended data set used in this study, I used the ranges shown in column 5 of Table 13 for assigning productivity to species.

Table 13. Median values and interquartile ranges of predicted von Bertalanffy growth parameter K for 1,311 species with observed productivity.

Productivity	**K** (Table 6)	**K_{pred}** (median)	**K_{pred}** (IQR)	**K range used**
High	>0.3	0.62	0.45-0.88	>0.42
Medium	0.16-0.30	0.26	0.18-0.39	0.18-0.42
Low	0.05-0.15	0.13	0.1-0.18	0.12-0.18
Very low	<0.05	0.09	0.06-0.14	<0.12

The above modelling exercise increased the number of species with information on length, trophic level and productivity to 20,480, i.e., 74% of all recent species of fishes and thus approaching a census of the largest group of vertebrates. As can be seen in Table 14, the distribution by length group (column 4) is now similar to the overall distribution (column 2). Note that the extended data set included the available data, i.e., all lengths (100%), 7,289 trophic levels (36%), and 2,621 productivities (13%) were based on observations.

Table 14. Comparison of length distribution of species with available data (column 3) and modelled data (column 4).

Length group	Species in length group n (%)		Species with length, troph, productivity n (%)		Species after modelling n (%)	
Small	4,093	17.3	40	2.1	3,233	15.8
Medium	15,892	67.1	686	36.5	13,929	68.0
Large	3,632	15.3	1,102	58.6	3,253	15.9
Very large	68	0.3	52	2.8	65	0.3
Total	23,685	100.0	1,880	100.0	20,480	100.0

Table 15 shows the number and percentage of species by life-history strategy and is a recreation of Table 8 using the extended data set. The number of strategies used has increased to fifty. New strategies were large herbivores with very low productivity (31 species); small omnivores with medium productivity (one species, *Rhodeus ocellatus* Knerr, 1866 of 6.5 cm TL, which would have joined the 235 species in the Omnivore-Medium-Medium strategy if it were 1 mm longer); large omnivores with high (7 species) and very low productivity (16 species); and small mid-level predators with high productivity (11 species). The new strategies seemed mostly reasonable if compared with species numbers in adjacent strategies; since productivity was roughly natural distributed (see Table 7) they provided the tails of natural distributions within the respective trophic and size groups. The above analysis of Table 8 was largely supported by the data in Table 15. However, among most trophic-length combinations, there was a shift towards higher productivity, suggesting that the available data were not only biased towards large but also towards temperate species (see discussion of Table 31 below). This was most visible in medium-sized low-level predators with high productivity, i.e., typical tropical fishes, which have increased from 9.8% (rank 3 in Table 8) to 33% (rank 1 in Table 15) of the species.

Table 15. Number and percentage of species by life-history strategy based on the extended data set with 20,480 species (continued on following page).

Trophic group	Length group	Productivity	Species n	%
Herbivores	Small	High	106	0.52
	Medium	High	494	2.41
		Medium	413	2.02
		Low	80	0.39
	Large	High	12	0.06
		Medium	101	0.49
		Low	58	0.28
		Very low	31	0.15
Omnivores	Small	High	330	1.61

Trophic group	Length group	Productivity	Species n	%
		Medium	1	0.00
	Medium	High	1211	5.91
		Medium	493	2.41
		Low	11	0.05
	Large	High	7	0.03
		Medium	65	0.32
		Low	76	0.37
		Very low	16	0.08
Low-level	Small	High	2710	13.2
predators		Medium	58	0.28
		Low	17	0.08
	Medium	High	6785	33.1
		Medium	2756	13.5
		Low	343	1.67
		Very low	55	0.27
	Large	High	60	0.29
		Medium	645	3.15
		Low	612	2.99
		Very low	214	1.04
	Very large	Very low	10	0.05
Mid-level	Small	High	11	0.05
predators	Medium	High	565	2.76
		Medium	432	2.11
		Low	80	0.39
		Very low	10	0.05
	Large	High	51	0.25
		Medium	368	1.80
		Low	310	1.51
		Very low	121	0.59
	Very large	Low	7	0.03
		Very low	9	0.04
Top	Medium	High	76	0.37
predators		Medium	98	0.48
		Low	27	0.13
	Large	High	38	0.19
		Medium	188	0.92
		Low	189	0.92
		Very low	91	0.44
	Very large	Medium	4	0.02
		Low	16	0.08
		Very low	19	0.09

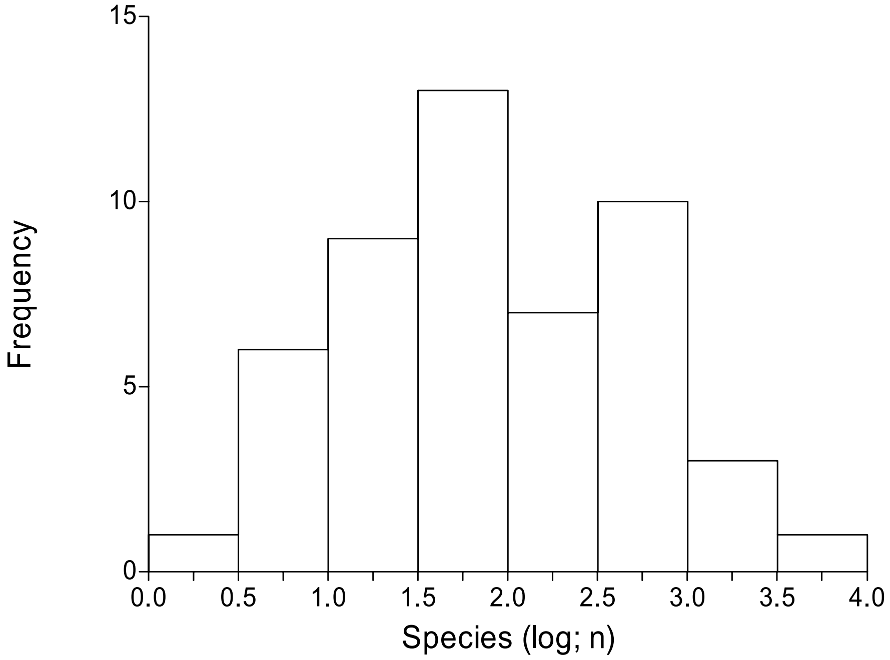


Figure 23. Frequency distribution of strategies that are used by a certain number of species: median = 78 species, 95% CL = 51-121, and IQR = 17-350.

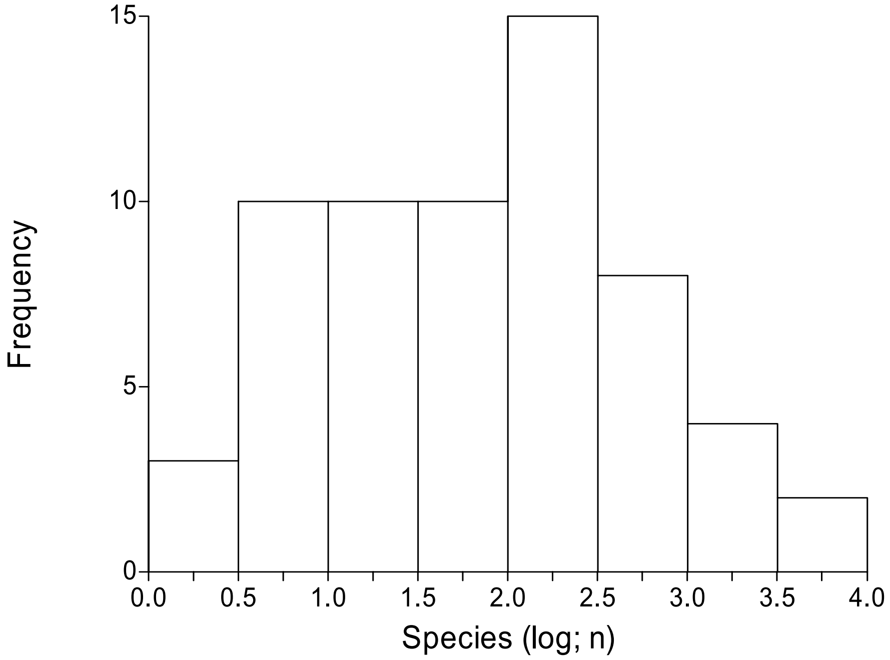


Figure 24. Frequency distribution of Orders containing a certain number of species: median = 64.5 species, 95% CL = 30 – 187, and IQR = 15 – 315.

Figure 23 shows the frequency distribution of strategies that are used by a certain number of species, ranging from 1 to 6,785 species per strategy. The data were very roughly log-normally distributed in the sense that there were few strategies used by few species and few strategies used by very many species, with a median of 78 species per strategy and 50% of the strategies being used by 17 to 350 species. Figure 24 shows a similar plot for the frequency distribution Orders containing a certain number of species. Note that the medians (78 and 65) are not significantly different, giving further support to the finding in the context of Figure 13 and Figure 15 that the distinctiveness of life-history strategies as used in this study is similar to that of Orders within phylogeny.

Table 16 shows life history strategies sorted by the number of species using them. It provides the following insights: Three strategies were used by 60% of all species, namely small to medium-sized low-level predators with medium to high productivity; thirty-four strategies were each used by less than 1% of the species; 15 strategies together were used by less then 1% of the species. The top 10 strategies contained no top predators, no very large species, and no low productivity. In contrast, the bottom 10 strategies contained all expressions of the three traits used for representing life-history strategies in this study, albeit in little-used combinations with presumably high trade-offs. Herbivores represented 5.9% of the species, i.e., more than the 2% predicted by Pauly (2000b), but still few compared with terrestrial vertebrate species where about 20% are herbivores (Brian R. Moore, Yale University, pers. comm. 2005). There was a roughly exponential decline of species per strategy, suggesting that that there was a roughly exponential increase in constraints associated with the lesser used strategies, as was suggested in the discussion of Figure 13 and Figure 16.

Table 16. Life history strategies sorted by the number of species using them, for 20,480 species based on the extended data set (continued on following page).

Trophic group	Length group	Productivity	Species n	%
Low-level pred.	Medium	High	6785	33.13
		Medium	2756	13.46
	Small	High	2710	13.23
Omnivores	Medium	High	1211	5.91
Low-level pred.	Large	Medium	645	3.15
		Low	612	2.99
Mid-level pred.	Medium	High	565	2.76
Herbivores	Medium	High	494	2.41
Omnivores	Medium	Medium	493	2.41
Mid-level pred.	Medium	Medium	432	2.11
Herbivores	Medium	Medium	413	2.02
Mid-level pred.	Large	Medium	368	1.80
Low-level pred.	Medium	Low	343	1.67
Omnivores	Small	High	330	1.61
Mid-level pred.	Large	Low	310	1.51
Low-level pred.	Large	Very low	214	1.04
Top predators	Large	Low	189	0.92
		Medium	188	0.92
Mid-level pred.	Large	Very low	121	0.59
Herbivores	Small	High	106	0.52
	Large	Medium	101	0.49
Top predators	Medium	Medium	98	0.48
	Large	Very low	91	0.44
Herbivores	Medium	Low	80	0.39
Mid-level pred.	Medium	Low	80	0.39
Top predators	Medium	High	76	0.37
Omnivores	Large	Low	76	0.37
		Medium	65	0.32

Trophic group	Length group	Productivity	Species	
			n	%
Low-level pred.	Large	High	60	0.29
	Small	Medium	58	0.28
Herbivores	Large	Low	58	0.28
Low-level pred.	Medium	Very low	55	0.27
Mid-level pred.	Large	High	51	0.25
Top predators	Large	High	38	0.19
Herbivores	Large	Very low	31	0.15
Top predators	Medium	Low	27	0.13
	Very large	Very low	19	0.09
Low-level pred.	Small	Low	17	0.08
Top predators	Very large	Low	16	0.08
Omnivores	Large	Very low	16	0.08
Herbivores	Large	High	12	0.06
Mid-level pred.	Small	High	11	0.05
Omnivores	Medium	Low	11	0.05
Mid-level pred.	Medium	Very low	10	0.05
Low-level pred.	Very large	Very low	10	0.05
Mid-level pred.	Very large	Very low	9	0.04
	Very large	Low	7	0.03
Omnivores	Large	High	7	0.03
Top predators	Very large	Medium	4	0.02
Omnivores	Small	Medium	1	0.00

Constraints in Life-history Space Revisited

Here I return to the theme of constraints and unoccupied life-history space using the extended data set which gives a better representation of the numbers of species using a given strategy. If we assume an inverse correlation between the constraints associated with a certain combination of traits and the number of species using that combination, then an exploration of the respective frequency distributions may reveal interesting patterns.

Table 17 shows a cross-tabulation of species numbers by size and trophic group.

Table 17. Cross-tabulation of numbers of species by length and trophic group, for 20,480 species based on the extended data set.

Length / Trophic group	Small	Medium	Large	Very large
Top predators	2	243	575	39
Mid-level	22	1,310	987	19
Low-level	3,584	11,452	1,691	10
Omnivores	352	1,767	170	0
Herbivores	133	1,120	209	0

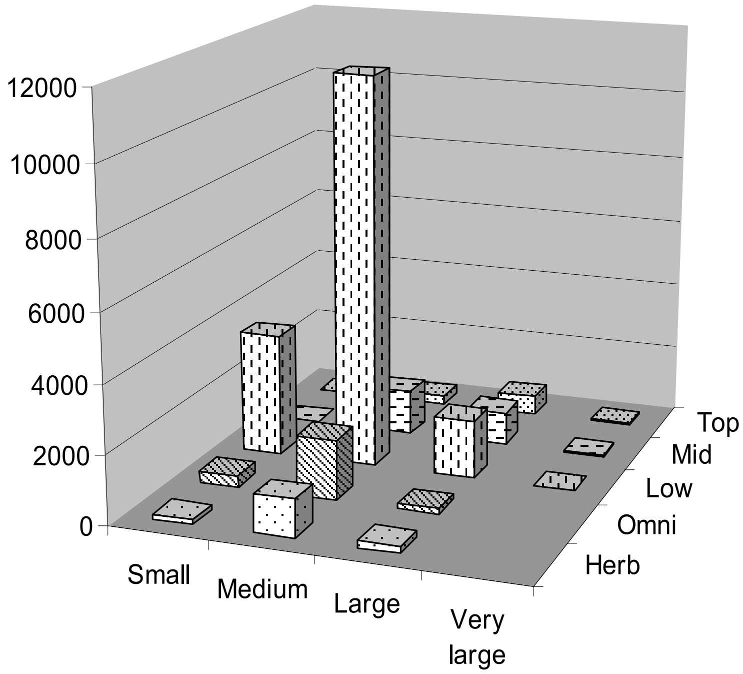


Figure 25. Three-dimensional bar-chart of data in Table 17, with length on the x-axis, trophic group on the y-axis, and species numbers on the z-axis.

Figure 25 presents the numbers of Table 17 in three-dimensional space, with the floor-area representing the life-history space and the columns showing its occupation by recent species. The overarching shape is a clear and dominant peak of species numbers of medium-sized low-level predators, with exponentially decreasing species numbers towards all adjacent combinations of size and trophic level. Less conspicuous patterns show a small increase in species numbers from large omnivores to large herbivores, and a clear increase—albeit in small absolute numbers—from very large low-level to top predators and thus a local optimum (Schaefer and Rosenzweig 1977) for very large top predators. Most likely the problems involved in overpowering a larger prey prevent small species from becoming mid-level and top-predators, with few exceptions that include parasitic fish. There are no very large herbivorous and omnivorous species, confirming the findings and discussion in the context of Table 9.

Table 18 shows a cross-tabulation of numbers of species by size and productivity groups.

Table 18. Cross-tabulation of numbers of species by size and productivity for 20,480 species based on the extended data set.

Length / Productivity	Small	Medium	Large	Very large
High	3,157	9,131	168	0
Medium	59	4,192	1,367	4
Low	17	541	1,245	23
Very low	0	65	473	38

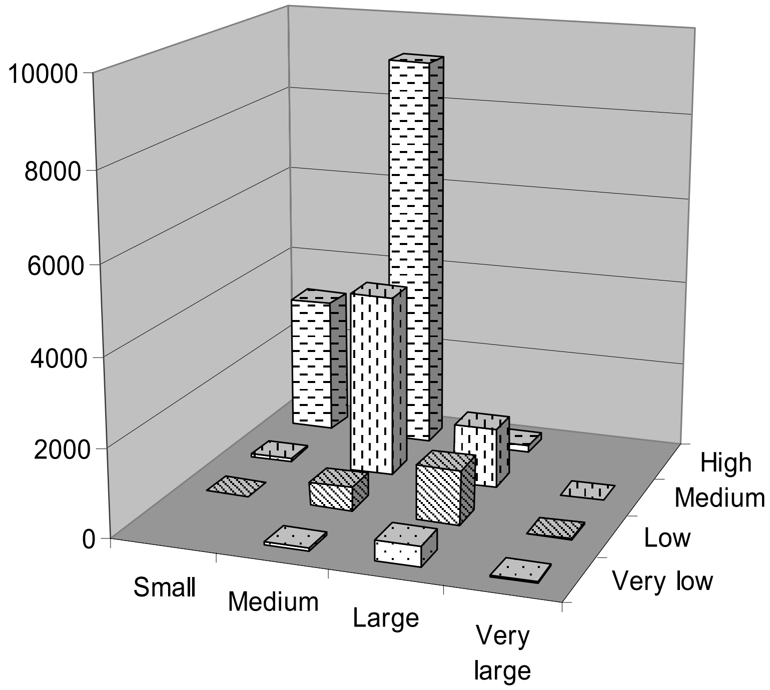


Figure 26. Three-dimensional bar chart of data in Table 18, with length on the x-axis, productivity on the y-axis and number of species on the z-axis.

Figure 26 presents the data from Table 18 in a three-dimensional bar chart. There is a clear and dominant peak of medium-sized species with high productivity, with exponential decline of species numbers in adjacent strategies. A less conspicuous pattern is the ‘against-the-trend’ increase in numbers of very large species from medium to very low productivity, i.e., there is a small but clear local optimum (Schaefer and Rosenzweig 1977) of very large species with very low productivity; high productivity is not used and probably constrained by the difficulties of oxygen supply to and heat management by very large animals. Conversely, there is a steep decrease in numbers of small species from high to low productivity; very low productivity is not used and probably constrained by the high metabolic level typical of small animals. Daniel Pauly (University of British Columbia, pers. comm. 2005) pointed out that low levels of predation will select for low productivity, e.g. in cave fishes. FishBase had productivity data for 21 species of cave fishes, with approximate mean $r'_{max} = 0.19$ (95% CL = 0.100 – 0.282), which is less than the 0.23 for all fishes with available data, though not significantly so.

Table 19 shows a cross-tabulation of numbers of species by trophic group and by productivity.

Table 19. Cross-tabulation of numbers of species by trophic group and productivity for 20,480 species based on the extended data set.

Trophic group / Productivity	Herbivores	Omnivores	Low-level	Mid-level	Top predators
High	612	1,548	9,555	627	114
Medium	514	559	3,459	800	290
Low	138	87	972	397	232
Very low	31	16	279	140	110

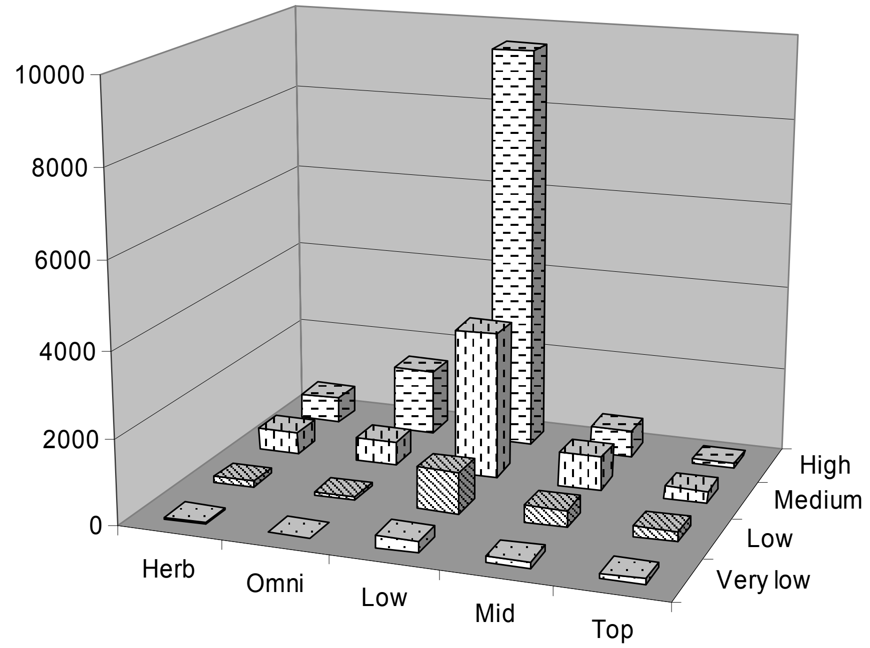


Figure 27. Three-dimensional bar chart of data in Table 19, with trophic groups on x-axis, productivity on y-axis, and numbers of species on z-axis.

Figure 27 presents the data from Table 19 in a three-dimensional bar chart. There is a clear and dominant peak of low-level predators with high productivity, with exponential decline of species numbers in adjacent strategies. All possible combinations of traits are used, but there is a clear decline in species numbers towards low and very low productivity in herbivores and omnivores, probably as a result of the energy-constraint proposed by herbivory theory.

In summary, the extended data set confirms the analysis of empty life-history space and trade-off curves presented in the context of Table 9. The dominant pattern seen in all three bar-graphs of an exponential stepwise decline in species numbers from one dominant peak to adjacent and then further outlying combinations confirms the spill-over theory of Matthews (1998), i.e., the fitness advantage of the dominant combination is 'eroded' by increased competition due to high number of species using the same strategy, and species evolved to make use of the ‘next best’, i.e., adjacent combination, and so forth. Also, there is evidence of ‘multiple optima’ in life history space (Schaefer and Rosenzweig 1977, Partridge and Sibly 1991).

Phylogeny and Strategies Revisited

The extended data set allows us to have a second look at the relationships between strategies and phylogeny. Table 20 shows a cross-tabulation of strategies and phylogenetic Classes, as a repetition of Table 11. Classes are now represented by 64 to 100 % of their species; especially the representation of Actinopterygii has increased from 5.5 to 71% percent of recent species. The discussion of the various groups presented with Table 11 is largely confirmed. The five new strategies are all used by Actinopterygii. Myxini use one more strategy of medium-sized top-predators with low productivity (4 species), which seems reasonable as all traits were already used by them, albeit not in this combination. Cephalaspidomorphi use three more strategies of medium-sized omnivores with medium to low productivity (one species each) and mid-level predator with low productivity (2 species), which is consistent with the already used strategies. Sarcopterygii add one strategy for the medium-sized *Protopterus amphibius* (Peters, 1844). Actinopterygii use six more strategies, albeit with low species numbers /1 – 31) and as a kind of continuation of adjacent strategies, e.g., the 14 large herbivores with low productivity in Table 11 have now increased to 58 species and are joined by a new strategy of large herbivores with very low productivity used by 31 species. Also, there are considerably higher numbers of small and medium-sized species compared to Table 11, as was expected.

There are two more strategies that are used by four out of six Classes: medium sized mid-level predators with low productivity and medium-sized top predators with low productivity. Interestingly, the observation made in Table 11 holds that Actinopterygii have the highest species numbers in these ‘multi-Class’ strategies, but have clearly higher species numbers in the adjacent strategies with higher productivity. There are still five (formerly 9) strategies in which Elasmobranchii have higher species numbers than Actinopterygii, confirming the previous evidence for a certain non-overlap of preferred life-history strategies between these two largest Classes of recent fishes.

In the overall analysis of number of strategies versus number of species (Figure 82) Myxini and Elasmobranchii were identified as outliers having significantly fewer strategies than predicted by their numbers of species. The main reason for this is, because of their phylogenetic constraints, 17 herbivorous and omnivorous strategies, 14 high productivity strategies, and several other combinations of strategies are not available to them. As a result they have evolved relatively more species using the strategies available to them.

Table 20. Cross-tabulated view of life-history strategies and phylogenetic Classes using the extended data set: Myxini, Cephalaspidomorphi, Holocephali, Elasmobranchii, Sarcopterygii and Actinopterygii. The last rows show the number of species and strategies per Class, and the respective numbers predicted by Equation 21; new strategies are marked in bold font. Table continued on next page.

Trophic group	Length group	Productivity	Myx	Ceph	Holo	Elasmo	Sarco	Actino
Herbivores	Small	High						106
	Medium	High						494
		Medium						413
		Low						80
	Large	High						12
		Medium		1				100
		Low						58
		Very low						**31**
Omnivores	Small	High						330
		Medium						**1**

Trophic group	Length group	Productivity	Myx	Ceph	Holo	Elasmo	Sarco	Actino
	Medium	High						1,211
		Medium		1				492
		Low		1				10
	Large	**High**						**7**
		Medium						65
		Low						76
		Very low						**16**
Low-level predators	Small	High						2,710
		Medium						58
		Low						17
	Medium	High						6,785
		Medium		4				2,752
		Low	7	2		74		260
		Very low				3	1	51
	Large	High						60
		Medium						645
		Low	20		18	145		429
		Very low				40	7	167
	Very large	Very low				5		5
Mid-level predators	**Small**	**High**						**11**
	Medium	High						565
		Medium		14				418
		Low	17	2		28		33
		Very low				5		5
	Large	High						51
		Medium						368
		Low			6	123		181
		Very low				59	1	61
	Very large	Low				6		1
		Very low				7		2
Top predators	Medium	High						76
		Medium						98
		Low	4	7		7		9
	Large	High						38
		Medium						188
		Low	18	4		47		120
		Very low				45	2	44
	Very large	Medium						4
		Low				9		7
		Very low				17		**2**
Species n (%)			64 (93)	36 (86)	24 (65)	620 (64)	11(100)	19,923 (71)
Strategies (n)			5	9	2	16	4	50
Predicted strategies (n)			14	9	6	36	2	49
Lower 95% CL (n)			7	2	-1	29	-5	42
Upper 95% CL (n)			21	15	12	42	9	56

Figure 28. Number of strategies used in a phylogenetic Order versus the number of species in the respective Order. The regression line was forced through the origin and has a slope of 0.43.

I used the extended data set to further explore the relationship between life-history strategies and higher taxa of fishes. Figure 28 shows the number of strategies per phylogenetic Order plotted over the respective number of species. There is a clear upper limit to the number of strategies per number of species in an Order, similar to the one found in Figure 16. Only few presumably specialized Orders have fewer strategies than suggested by their number of species, including several Orders with up to 50 species that use only one strategy. However, Orders with more than 100 species have at least five, and Orders with more than 1,000 species at least 10 strategies. A linear regression forced through the origin (because an Order with only one species can have one and only strategy) explains 94% of the variance and results in the model

$$\log \mathrm{Strat}_n = 0.4288 \log \mathrm{Spec}_n$$

or

$$\mathrm{Strat}_n = \mathrm{Spec}_n^{0.43}$$

Equation 11. Strategies per Order as a function of species per Order, where Strat_n is the number of strategies used in an Order, Spec_n is the number of recent species in an Order; $n = 61$, $r^2 = 0.9380$, coefficient of variation = 0.2845.

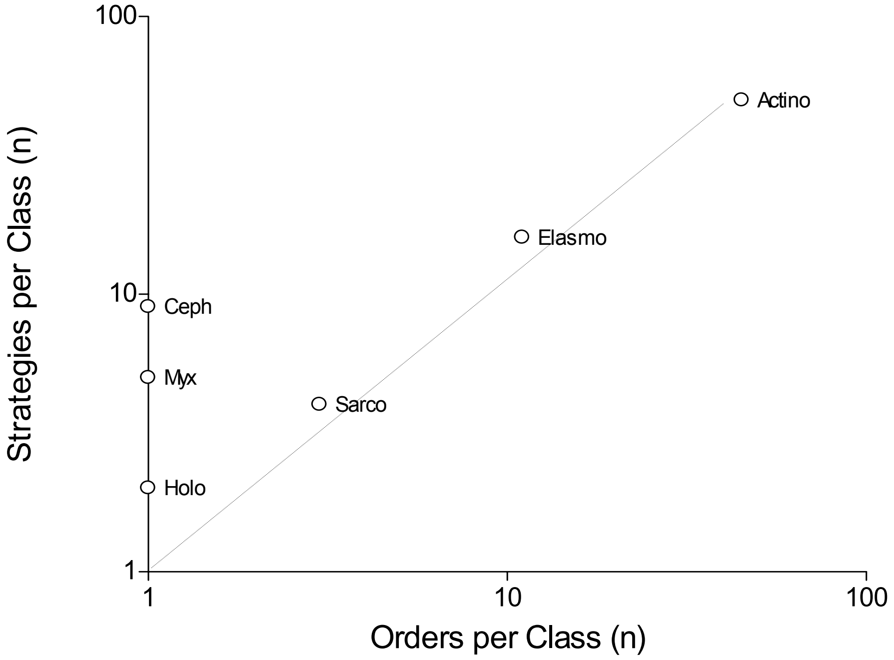


Figure 29. Number of strategies used in a phylogenetic Class plotted over the number of Orders in the respective Class: Myxini, Cephalaspidomorphi, Holocephali, Elasmobranchii, Sarcopterygii, and Actinopterygii.

The relationship in Figure 28 is similar to the one found in Figure 13, Figure 15 and Figure 16 and seems to point to a more general underlying phenomenon. As is shown in Figure 29 there is a close relationship between the number of Orders in a Class and the number of strategies used by the species in that Class. A linear relationship forced through the origin (because a theoretical Class with one species can have one and only one strategy and one Order) explains 76% of the variance and results in Equation 12.

$$\log Strat_n = 1.0753 * \log Ord_n$$

or

$$Strat_n = Ord_n^{1.08}$$

Equation 12. Strategies per Class as a function of Orders per Class, where $Strat_n$ is the number of strategies used in a Class and Ord_n is the number of Orders in the respective Class, with n = 6, $r^2 = 0.7556$, and coefficient of variation = 0.6042.

The 95% confidence limits of the slope in Equation 12 are 0.3727 – 1.778 i.e., the exponent is not significantly different from 1.0, or in other words, the number of Orders in a Class is a direct predictor of the number of strategies used in that Class. Phylogenetic Orders contain all Families, Genera and Species that share a common ancestor. Size, trophic level and productivity are not among the characters typically used by taxonomists when assigning species to higher taxa, i.e., although there is a correlation between these traits and morphology (see below), we can consider the assignment of Orders and strategies as independent from each other. Rather, I propose that the relationship follows the line developed in the discussion of Figure 13: a Class that has evolved a high number of successful Order-level archetypal ancestors (or body plans) is likely to express more life-history strategies; and the probability laws discussed with Figure 13 and Figure 16 also apply to Figure 28.

Myxini, Cephalaspidomorphi and Holocephali are outliers in Figure 29 as well as in Figure 15 above. Cephalaspidomorphi which have only one recent Order but seven strategies, have at least three more fossil Orders (Nelson 1994), which would bring them closer to the overall relationship. There is no evidence for extinct Orders of Myxini although six fossil Families and more than 50 Genera are generally recognized (Helfman et al. 1997). The unexpected high number of strategies of Myxini is partly an artifact of the length group assignment: as pointed out in the discussion of Figure 11 Myxini were the only Class split by a border line between length groups (here: medium and large), adding at least one of four strategies. Eight fossil Orders are known for Holocephali; for the other Classes the number of fossil Orders is not several times larger than the recent number (Nelson 1994), i.e., if fossil Orders were included in Figure 29 (and also additional strategies that such Orders may have had), the ancient Classes of Myxini, Cephalaspidomorphi and Holocephali are likely to move closer to the regression line whereas the position of the other Classes would not change much.

As a taxon, the Family level has undergone fewer changes than, e.g., the adjacent levels of Orders and Genera (Matthews 1998); most changes have involved raising of Subfamilies to Family level, and vice-versa (compare e.g. Nelson 1976, Nelson 1984 and Nelson 1994). Thus, if indeed the Family level is more stable than the Order level and more informative than the Class level, then it is of interest to see the relationship between strategies and Families.

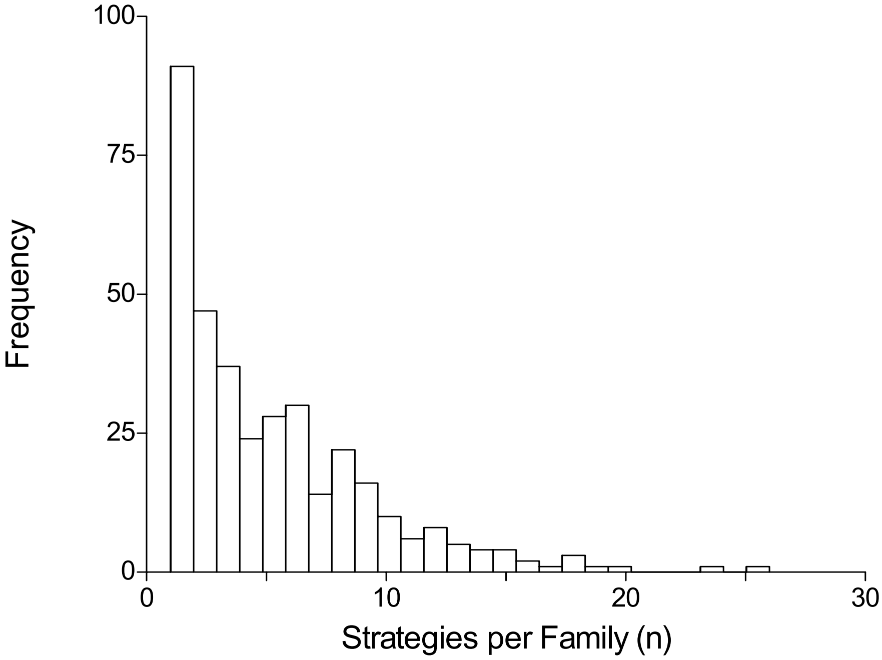


Figure 30. Frequency distribution of strategies per Family based on the extended data set for 20,480 species. Of 356 Families with strategies, 91 (26%) use only one strategy and 199 (56%) use 4 or fewer strategies.

Figure 30 shows the frequency distribution of strategies per Family. There is an exponential decline from 91 Families using only one strategy to few large Families using many strategies. Figure 31 shows the number of strategies plotted over species with assigned strategies per Family. A robust regression analysis forced through the origin results in Equation 13 and explains 96% of the variance:

$$\mathrm{Strat}_n = \mathrm{Spec}_n^{0.49}$$

Equation 13. Robust regression analysis of data shown in Figure 31, where Strat_n is the number of strategies used in a Family and Spec_n is the number of species with strategies in the respective Family, with n = 356, slope forced through origin = 0.4909, 95% CL of slope = 0.48 – 0.50, r^2 = 0.9575, and coefficient of variation = 0.2143.

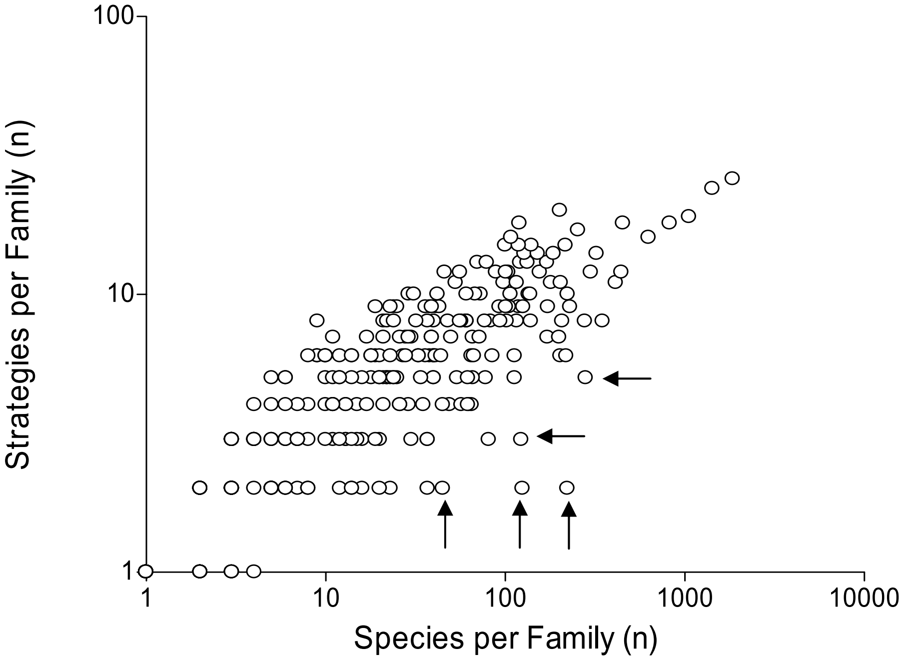


Figure 31. Strategies versus assessed species per Family using the extended data set for 356 Families and 20,480 species. Outliers identified by robust regression analysis are marked by arrows (see also Table 21).

There are 18 to 26 strategies used in the large top five families of Characidae (18), Gobiidae (19), Clupeidae (20), Cichlidae (24) and Cyprinidae (26). Families with fewer strategies than suggested by their number of assessed species were identified as outliers in robust regression analysis and are shown in Table 21 Fundulidae and Rivulidae are low-level predators of small to medium size with high productivity, i.e., they restrict themselves to two of the three most widely used strategies; Chaetodontidae are mostly medium-sized low-level predators of high productivity (the most widely used strategy), but some species are omnivores; Callionymidae are low-level predators of small to medium size and medium to high productivity, i.e., they restrict themselves to the top three strategies; Apogonidae restrict themselves to five strategies including ranks 1-3 and 7 in Table 21. Thus, other than may have been expected, Families that use fewer strategies than suggested by Equation 13 are not specialists in the sense that they are the dominant users of an otherwise rarely used strategy, but rather they seem to focus on the few most popular strategies. For a comparison of strategies by taxon see also Figure 79 below.

Table 21. Families that were identified as outliers in robust regression analysis of data shown in Figure 31.

Family	Species n	Assessed species n	 %	Strategies n
Fundulidae	45	45	100.0	2
Chaetodontidae	128	125	97.7	2
Rivulidae	245	222	90.6	2
Callionymidae	187	123	65.8	3
Apogonidae	334	281	84.1	5

A Chronology of Life-history Strategies

An interesting question is when life-history strategies were first 'invented' by species. Evolution rates are known to vary among traits, and for a given trait, between branches of the phylogeny and along them (Rochet 2000), i.e., any chronology of life histories can only be indicative of major trends. No comprehensive data on the first appearance of traits in the fossil record were available, but the age of the common ancestor of Orders of fishes is known (Preikshot et al. 2000) and can be used if the following assumptions are accepted for the purpose of this exploration: 1) life-history strategies visible in recent species of an Order have evolved early on, i.e., in early rather than late descendents of the common ancestor, and 2) life-history strategies used by extinct species are still present in recent species of the respective Order. There are 596 realized combinations of life-history strategies with Orders out of 3,100 possible combinations of 50 recent strategies with 62 Orders. While that list is interesting it is too long for presentation. Table 22 shows a shortened list with the oldest (years in bold) and second-oldest Orders that first used a certain strategy, with indication of the number of species in the respective Order that currently use the strategy, and the total number of recent species using the strategy. If several Orders of same age used a certain strategy, the Order with the highest number of recent species using the strategy was selected, under the assumption that this Order was most likely to have used the strategy early on.

Myxiniformes are the oldest Order and invented low-level to top predators of medium to large size with medium to low productivity. These strategies were adopted 145 – 200 million years later by two other old Orders, Petromyzontiformes and Chimaeriformes. Petromyzontiformes invented five new strategies: low- to mid-level predators of medium length and medium productivity plus one herbivorous and two omnivorous strategies. However, the latter three strategies are questionable: lampreys are not true herbivores in the sense of eating live plant material, but rather their ammocoetes larvae are detritivores and the adults are predators or non-feeding. Thus, the invention of true herbivory in fishes probably happened 300 million years later by Characiformes, Siluriformes and Cypriniformes, i.e., about 150 million years before present. If true this would mean that fish invented herbivory after terrestrial vertebrates, which did so about 290 million years ago (Rybczynski and Reisz 2001).

Polypteriformes are the first Order in the list with high productivity strategies, however, this is based on only three little-known species for which productivity was not known but modeled and may have been overestimated. The invention of high productivity probably happened 50 million years later by Cypriniformes and Characiformes.

Very large size was first invented by Acipenseriformes and Hexanchiformes, 200 and 195 million years ago, respectively. The famous extinct megatooth shark *Carcharodon megalodon* was probably 16 m long, but lived only 16 – 1.6 million years ago (Helfman et al. 1997).

Small size was first invented by Characiformes, Cypriniformes and Siluriformes 150 million years ago. The last strategy to be invented 15 million years ago by Perciformes, Family Istiophoridae was top predators of very large size and medium productivity.

Over 2/3 of recent life-history strategies were invented only 200-150 million years ago during several radiations of the Actinopterygii, including small size, very large size (invented in parallel by Elasmobranchii), high productivity, and true herbivory. As for the evolutionary history of the traits considered in this study, low-level to top predators were the original trophic groups from which omnivores and herbivores have evolved; medium to large length groups were the original sizes from which small and very large fishes have evolved; and low productivity was the original state of metabolism and population increase, from which very low as well as medium and high productivity have evolved.

Not all Orders that invented a successful strategy were able to benefit from it in the long-term. For example, Petromyzontidae first evolved low-level predators of medium size and medium productivity, a strategy now used by 2,756 species of which only 4 (0.15%) are Petromyzontidae. Other Orders were more successful, such as Siluriformes who first evolved medium-sized herbivores with medium productivity and still represent 201 (49%) of 413 recent species using that strategy.

If a high number of recent species using a certain strategy in an Order is indeed an indication of long usage or early invention of a strategy by an Order, then most inventions were made by Characiformes (10), Siluriformes (10), and Cypriniformes (9), i.e., Orders restricted to freshwater, where heterogeneity of the environment and isolation of adjacent ecosystems are known to favour speciation (Boyle and Cech, 2004).

Table 22. Chronology of life-history strategies presented in sequence of first (bold) and second appearance, using the age of the common ancestor of the Order where the strategy is still used by recent species. The last two columns give the number of species that use the strategy in the Order and altogether. Cases where the invention of strategies is questionable are marked with question marks. Table continued on next pages.

Common Ancestor (million years)	Trophic Group	Length Group	Productivity	Order	Species Order (n)	All Species (n)
600	Low	Medium	Low	Myxiniformes	7	343
455				Petromyzontiformes	2	
600	Low	Large	Low	Myxiniformes	20	612
400				Chimaeriformes	18	
600	Mid	Medium	Low	Myxiniformes	17	80
455				Petromyzontiformes	2	
600	Top	Medium	Low	Myxiniformes	4	27
455				Petromyzontiformes	7	
600	Top	Large	Low	Myxiniformes	18	189
455				Petromyzontiformes	4	
? 455	Herb	Large	Medium	Petromyzontiformes	1	101
150				Characiformes	26	
? 455	Omni	Medium	Medium	Petromyzontiformes	1	493
150				Cypriniformes	154	
? 455	Omni	Medium	Low	Petromyzontiformes	1	11
150				Cypriniformes	4	

Common Ancestor (million years)	Trophic Group	Length Group	Productivity	Order	Species Order (n)	All Species (n)
455	Low	Medium	Medium	Petromyzontiformes	4	2756
200				Polypteriformes	4	
455	Mid	Medium	Medium	Petromyzontiformes	14	432
150				Siluriformes	21	
400	Low	Medium	Very low	Lepidosireniformes	1	55
150				Siluriformes	1	
400	Low	Large	Very low	Ceratodontiformes	1	214
400				Lepidosireniformes	6	
400	Mid	Large	Low	Chimaeriformes	6	310
260				Lepisosteiformes	1	
400	Mid	Large	Very low	Lepidosireniformes	1	121
195				Hexanchiformes	1	
400	Top	Large	Very low	Coelacanthiformes	2	91
195				Hexanchiformes	3	
? 200	Omni	Medium	High	Polypteriformes	1	1211
150				Cypriniformes	362	
? 200	Low	Medium	High	Polypteriformes	2	6785
150				Cypriniformes	722	
200	Low	Large	Medium	Polypteriformes	6	645
150				Siluriformes	85	
200	Low	Very large	Very low	Acipenseriformes	3	10
155				Orectolobiformes	1	
200	Mid	Very large	Very low	Acipenseriformes	2	9
135				Carcharhiniformes	2	
200	Top	Large	Medium	Polypteriformes	2	188
150				Siluriformes	15	
195	Top	Very large	Low	Hexanchiformes	1	16
155				Squaliformes	2	
155	Mid	Medium	Very low	Squaliformes	2	10
135				Carcharhiniformes	3	
155	Mid	Very large	Low	Orectolobiformes	1	7
135				Carcharhiniformes	1	
155	Top	Very large	Very low	Squaliformes	1	19
150				Siluriformes	1	
150	Herb	Small	High	Siluriformes	27	106
150				Characiformes	6	
150	Herb	Medium	High	Characiformes	95	494
150				Cypriniformes	52	
150	Herb	Medium	Medium	Siluriformes	201	413
150				Cypriniformes	57	
150	Herb	Medium	Low	Siluriformes	76	80
15				Perciformes	4	
150	Herb	Large	High	Characiformes	5	12
150				Siluriformes	1	
150	Herb	Large	Low	Cypriniformes	36	58
150				Siluriformes	2	
150	Herb	Large	Very low	Siluriformes	18	31
150				Cypriniformes	12	

Common Ancestor (million years)	Trophic Group	Length Group	Productivity	Order	Species Order (n)	All Species (n)
150	Omni	Small	High	Cypriniformes	123	330
150				Siluriformes	56	
150	Omni	Small	Medium	Cypriniformes	1	1
150	Omni	Large	High	Characiformes	2	7
45				Beloniformes	1	
150	Omni	Large	Medium	Siluriformes	10	65
150				Characiformes	8	
150	Omni	Large	Low	Cypriniformes	39	76
150				Siluriformes	5	
150	Omni	Large	Very low	Cypriniformes	14	16
15				Perciformes	2	
150	Low	Small	High	Characiformes	395	2710
150				Cypriniformes	340	
150	Low	Small	Medium	Characiformes	4	58
150				Siluriformes	4	
150	Low	Small	Low	Siluriformes	2	17
150				Characiformes	1	
150	Low	Large	High	Siluriformes	3	60
140				Clupeiformes	1	
150	Mid	Small	High	Characiformes	1	11
15				Perciformes	10	
150	Mid	Medium	High	Characiformes	50	565
150				Siluriformes	13	
150	Mid	Large	High	Characiformes	2	51
150				Siluriformes	1	
150	Mid	Large	Medium	Siluriformes	22	368
150				Characiformes	3	
150	Top	Medium	High	Characiformes	1	76
140				Clupeiformes	1	
150	Top	Medium	Medium	Siluriformes	9	98
140				Clupeiformes	1	
150	Top	Large	High	Siluriformes	1	38
70				Aulopiformes	5	
15	Top	Very large	Medium	Perciformes	4	4

Life-history Strategies and Environment

Salinity

One of the broadest categories for classifying fishes is their salt tolerance (Berra 2001). Salinity not only affects the physiology of fishes but also defines large ecosystems such as the oceans, freshwater lakes and rivers, and brackish estuaries and peripheral seas. Salinity tolerance determines the ability of fishes to move between these different ecosystems. Freshwater and especially brackish estuaries will be more variable environments than other salinity groups and estuarine systems and brackish seas are often eutrophic. In the sense of succession theory, fresh- and brackish waters will be less mature ecosystems than marine waters. In this chapter, I explored correlations between life-history strategies and salinity.

Assigning fishes to categories of salinity tolerance is not as straightforward as it may seem. Table 23 shows how the categories were defined for the purpose of this study. Note that the categories 'Freshwater' and 'Fresh- and brackish waters' are largely the same as the categories 'Primary' and 'Secondary' freshwater fishes, respectively. However, the latter terms imply hypotheses about the dispersal of the respective species (Berra 2001). Stray occurrences of typical marine fish in estuaries or brackish seas like the Baltic suggest that most marine fishes have some tolerance for brackish waters, and thus the distinction between purely marine fishes and those with reported occurrences in brackish waters may be arbitrary (see also discussion in Winemiller and Rose (1992) who included estuarine fishes in the marine category) .

I used salinity assignments for 28,786 species of fishes as compiled in FishBase version 11/2004. FishBase assigns species to Freshwater Yes/No, Brackish water Yes/No and Saltwater Yes/No according to whether a species has been reported from such waters. I used the combinations in Table 23 to translate these assignments into salinity groups. With the exception of the diadromous group, these salinity tolerance groups can be taken as proxies for the respective aquatic ecosystems. Note that the null-hypothesis of species being evenly distributed across salinity tolerance groups is refuted by the species numbers in Table 23: There is an order of magnitude preference for either freshwater or marine salinity groups and only 86 species are restricted to brackish waters.

Table 23. Assignment of salinity tolerance groups for 28,786 species of fishes.

Freshwater	Brackish	Saltwater	Salinity tolerance	Species	
				n	%
Yes	No	No	Freshwater only	12,276	42.6
Yes	Yes	No	Fresh + brackish waters	678	2.4
Yes	Yes	Yes	Diadromous	709	2.5
No	Yes	No	Brackish waters only	86	0.3
No	Yes	Yes	Marine / brackish	1,327	4.6
No	No	Yes	Marine	13,710	47.6

For species richness by salinity tolerance groups, I suggest area as the structuring principle, ranking them from marine (70% of the surface of the earth) to freshwater (1%) to brackish (< 1%). Marine species have indeed the highest number of species and brackish waters the lowest. However, the number of freshwater fishes is much higher than suggested by the comparatively small area of their habitat. This may be explained by the heterogeneity of freshwater habitats when compared with the open oceans, and by the typical isolation of their ecosystems (lakes, river basins) when compared with continental shelf ecosystems or coral reefs. As Boyle and Cech (2004) put it: “Fresh water consists largely of thousands of distinct ‘islands’ in a sea of land, which helps to promote speciation.” Euryhaline species have to develop special mechanisms and invest more energy in osmoregulation, which—together with the small area—may explain the relatively low numbers of species in those categories. Succession theory predicts higher species numbers in the more mature marine environments and lower numbers in less mature brackish systems; these predictions are confirmed.

Table 24 shows the number of species by Class and salinity group for all 28,786 species of fishes. Ray-finned fishes (Actinopterygii) inhabit and dominate all salinity groups with 93.1-100% of the species. Actinopterygii are the only Class with species that are restricted to brackish waters. Species of sharks and rays (Elasmobranchii) occur in all salinities. Note that two rays fall into the Fresh- and brackish waters category, possibly a hint that the few freshwater elasmobranchs have evolved from marine ancestors that lost their connection to the sea (Berra 2001). Phylogeny clearly restricts life-history options with regard to salinity tolerance for the other Classes: lampreys (Cephalaspidomorphi) are anadromous or restricted to fresh and brackish waters, i.e., they depend on freshwater for reproduction and thus have no species in the ‘Marine only’ category. Lobefinned-fishes (Sarcopterygii) consist of lungfishes that are restricted to freshwater and coelacanths which are marine. Hagfishes (Myxini) are incapable of osmoregulation (Moyle and Cech 2004) and are restricted to marine waters. Holocephali live near the bottom in deep water and are stenohaline (Helfman et al. 1997).

Table 24. Classes of fishes with number of species by salinity tolerance.

Salinity	Myxini	Cephalaspido-morphi	Holo-cephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
Freshwater		30		24	9	12,213
Fresh & Brackish				2		676
Diadromous		12		16		681
Brackish						86
Marine & Brackish				90		1,237
Marine	69		37	833	2	12,768

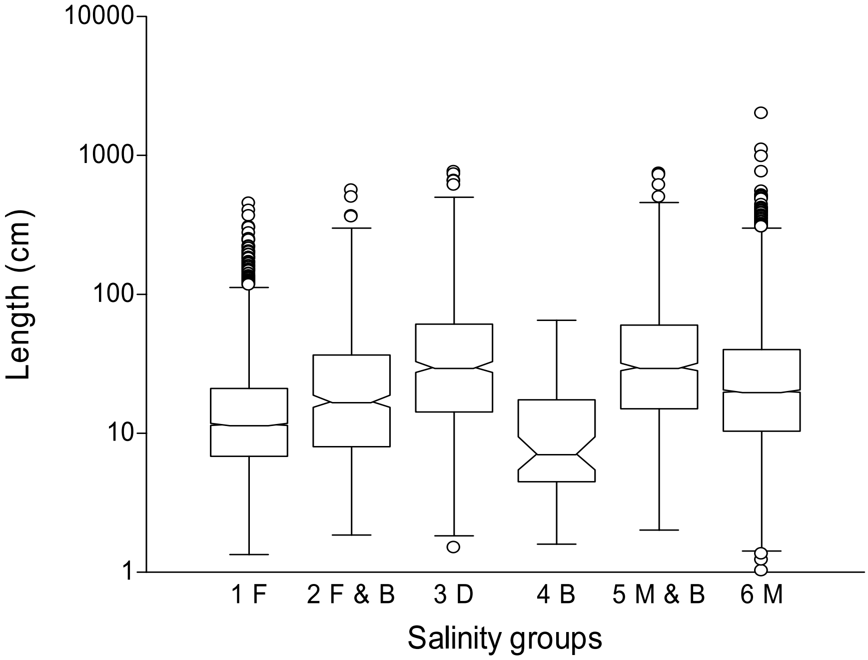


Figure 32. Distribution of maximum length by preferred salinity for 23,602 species with available data: 1 F is freshwater only with n = 9.973, median = 11.6 cm, 95% CL = 11.2-12.0 cm; 2 F&B is fresh-and brackish waters with n = 578, median = 17.0 cm, 95% CL = 15.0-18.3 cm; 3 D is diadromous with n = 652, median = 30.0 cm, 95% CL = 28.8-33.8 cm; 4 B is brackish waters only with n = 60, median = 7.2 cm, 95% CL = 6.0-10.4 cm; 5 M&B is marine and brackish waters with n = 1,224, median = 30.0 cm, 95% CL = 30.0-31.8 cm; and 6 M is marine only with 11,115, median = 20.1 cm, 95% CI = 20.0-21.0 cm.

Figure 32 shows maximum length distribution by salinity tolerance group. r-K theory predicts smaller size in the more variable freshwater and brackish environments. Median lengths are indeed significantly different and increase with salinity tolerance from freshwater to ‘fresh and brackish’ and marine environments, confirming the predictions of r-K theory and also the findings of Winemiller and Rose (1992). The largest and smallest fishes are marine.

Median length of diadromous fishes is not significantly different from that of ‘marine and brackish’ fishes, and their interquartile and adjacent value ranges are also nearly identical; median lengths of these two categories are significantly higher than all others, confirming the finding of Winemiller and Rose (1992) that highly migratory fishes are associated with large size. Diadromous fishes are migratory by definition and swimming speed is known to increase with body length (Weis 1973), putting smaller fishes at a disadvantage when, e.g., migrating long distances upstream.

Freshwater, estuaries and brackish peripheral seas such as the Baltic or the Black Sea are highly variable environments and less mature ecosystems for which r-K theory and succession theory predict selection for small size. As shown in Figure 32 fishes restricted to fresh or brackish waters are indeed significantly smaller in median length, interquartile range, and upper adjacent value than all other groups.

Knouft and Page (2003, their Figure 1) show frequency distribution of total length for 705 North American freshwater fishes; they do not give mean or median length but the figure shows strong peaks at slightly less than 10 cm total length. Welcomme (1999) finds that about 50% of the fishes present in any freshwater system do not grow larger than 15 cm in standard length, i.e., both studies are in reasonably good agreement with freshwater median length of 11.6 cm shown in Figure 32.

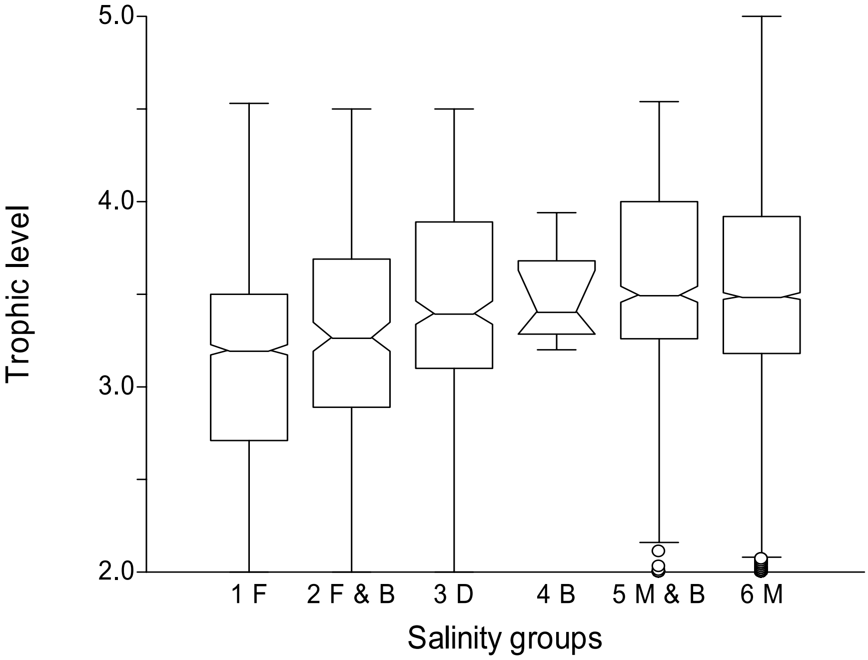


Figure 33. Distribution of trophic level by salinity tolerance group for 7,500 species with available data, where 1 F is freshwater only with n = 2,021, median = 3.2, 95% CL = 3.2-3.2; 2 F&B is fresh and brackish waters with n = 259, median = 3.3 and 95% CL 3.2-3.4; 3 D is diadromous with n = 387, median = 3.4, 95% CL = 3.3-3.5; 4 B is brackish only with n = 8, median = 3.4, 95% CL = 3.2-3.7; 5 M&B is marine and brackish waters with n = 719, median = 3.5, 95% CL = 3.5-3.6; 6 M is marine only with n = 4,106, median = 3.5, 95% CL = 3.46-3.5.

Figure 33 shows distribution of trophic level by salinity tolerance group for 7,500 species. Herbivory theory predicts more herbivores in freshwater. Odum's succession theory predicts higher median trophic levels in more mature marine waters. Indeed, median trophic level increases with salinity from freshwater to marine environments, thus supporting these predictions. Median trophic level in the brackish salinity group is not significantly different from the others but IQR and range of adjacent values is clearly narrower. Note, however, that trophic level was known for only eight species restricted to brackish waters.

Table 25 shows productivity groups by salinity tolerance group for 2,859 species with available data. r-K theory predicts higher productivity in the more variable freshwater and brackish environments. Succession theory also predicts higher productivity in the less mature freshwater and brackish ecosystems. In freshwater, fresh- and brackish and marine- and brackish groups, most species are of medium to high productivity ($r'_{max} = 0.29 – 0.34$) whereas in the marine group, most species are of low to medium productivity with r'_{max} = 0.19, which is significantly lower than in the other groups. This confirms the predictions of r-K theory and succession theory, and the findings of Winemiller and Rose (1992) that marine fish mature later and live longer (compare Table 6 for translating age at maturity and longevity into productivity) than freshwater fishes. The low to medium productivity (r'_{max} = 0.27) of diadromous fishes is probably a result of their overall larger size (see above). No productivity data were available for fishes restricted to brackish environments.

Table 25. Productivity by salinity tolerance group for 2,859 species with available data, with approximated intrinsic rates of population increase (r'_{max}) and 95% confidence intervals.

Salinity	High	Medium	Low	Very low	n	r'_{max}	95% CL
Freshwater	121	248	109	40	518	0.31	0.287 – 0.330
Fresh & Brackish	35	54	23	8	120	0.34	0.296 – 0.393
Diadromous	33	102	44	21	200	0.27	0.234 – 0.297
Marine & Brackish	74	172	79	38	351	0.29	0.268 – 0.320
Marine	147	490	912	182	1,670	0.19	0.178 – 0.196

Table 26 shows an analysis of food web complexity based on the extended data set. Succession theory predicts lower trophic diversity in the less stabilized freshwater and brackish ecosystems compared to the presumably more mature marine ecosystems. The marine salinity group has indeed the highest (31) and the brackish group the lowest (17) number of trophic levels; also the brackish group has the lowest trophic diversity, thus confirming the predictions of succession theory. Note, however, that trophic diversity of freshwater and mixed systems is not less than that of marine systems, suggesting that many marine ecosystems—such as upwelling areas—are not that stable.

Table 26. Analysis of food web complexity based on the extended data set; H' is trophic diversity and J' is evenness of the Shannon-Wiener index applied to trophic levels; trophic diversity in brackish waters is significantly less than in the other systems (t-test alpha = 0.05, P = 0.000, Power = 1.000).

Salinity	Trophic levels	Species	H'	J'
Freshwater	27	12,204	4.1	0.85
Fresh & Brackish	26	678	4.2	0.89
Diadromous	26	709	4.2	0.90
Brackish	17	86	3.3	0.81
Marine & Brackish	27	1,327	4.2	0.88
Marine	31	13,703	4.0	0.80

Table 27 gives an overview of the predictions of selection theories with regard to salinity groups. Symbols in parentheses indicate strategies whose predictions are in conflict with those of other strategies in the respective column; negative symbols without parentheses thus indicate 'unforced errors.' Only 4 (13%) of 32 predictions are not confirmed by the data. Succession and area theories predict relativly low number of species in freshwater, which is not supported by the data, with freshwater having the second highest species numbers of the examined salinity groups. Apparently heterogeneity of habitat and isolation of neighbouring ecosystems exert strong selection pressures in favour of high species numbers, outweighing the effects of relative small area and less mature ecosystems. Succession theory predicts higher trophic diversity in the relatively more mature marine environment compared to fresh and fresh & brackish environments, which is not supported by the data; apparently herbivory theory which predicts more herbivores, and thus higher trophic diversity in freshwater exerts stronger selection forces.

Table 27. Summary of predictions by selection theories as applicable to salinity groups, where '+' indicates values are on the predicted side if values are ranked and '+++' indicates that the difference from the other values is significant at the 95% level; '–' indicates that the values do not support the prediction; parentheses indicate conflict with other strategies. Data used were the overall number of species by salinity group, the box plots for observed size and trophic level, mean r'$_{max}$ of observed productivity, and Shannon-Wiener trophic diversity based on the extended data set.

Theory	Environment	Salinity	Species / Strategies	Size	Productivity	Trophic diversity
r-K	variable	Freshwater		+++	+	
		Fresh & brackish		+++	+	
		Brackish		+++	no data	
	stable	Marine		+++	+++	
Succession	less mature	Freshwater	(-)	+++	+	(-)
		Fresh & brackish	+	+++	+	-
		Brackish	+	+++	no data	+++
	mature	Marine	+	+++	+++	(-)
Herbivory	low pH	Freshwater				(+++)
	high pH	Marine				(+++)
Area	large	Marine	+			
	small	Freshwater	(-)			
		Brackish	+			
Heterogeneity	high	Freshwater	(+)			
		Marine	+			
	low	Brackish	+			
Isolation	high	Freshwater	(+)			
	low	Brackish	+			

Table 28 presents a cross-tabulation of number of species by life-history strategies and salinity groups for 20,480 species based on the extended data set. A null-hypothesis would suggest that distribution of species across salinity groups is the same for all 50 life-history strategies and follows the overall distribution shown in the *Species by salinity* row (see also Table 23). Cases where a strategy-salinity combination is used by more than twice the number of species as suggested by the overall distribution are highlighted in bold in the *Sal %* columns. Alternatively, the three highest percentages in the *Sal %* columns are in bold.

With regard to life-history strategies, parallel selection forces shown in Table 27 predict small size and high productivity for the freshwater group. This is confirmed by the extended data set. Predictions for species richness, number of strategies and trophic diversity are conflicting. The 8,541 species in the freshwater group use 44 out of 50 life-history strategies but 5 strategies are used by only one or two species, respectively. Used strategies are fewer than the 47 predicted by Equation 21 but still within the 95% confidence limits (see last rows in Table 28). Most species are small (20%) or medium-sized (35%) low-level predators with high productivity. Six of eight herbivorous strategies have more species in freshwater than suggested by the overall percentage of freshwater species; two of these strategies (Herb-Medium-Low and Herb-Large-Very low) have over 95% of their species in freshwater; of nine omnivorous strategies, eight have higher species numbers than suggested. In contrast, of 20 mid-level and top predator strategies all have lower species numbers than suggested, and six strategies all with very large size are not used at all.

For the fresh & brackish waters group, selection theories predict relatively low number of strategies and species, small size, and high productivity. This is confirmed by the data in the extended data set. A prediction for low trophic diversity is not supported by the data. The 528 species in the fresh- and brackish waters group use 36 of 50 strategies, which is similar to the 34 predicted by Equation 21. Most species are small low-level predators with high productivity (16%) or medium-sized low-level predators of high (31%) or medium (15%) productivity. Strategies that are highlighted in bold font in the *Sal %* column are represented by few species only and thus are unlikely to indicate significant preferences.

The diadromous salinity group does not match a specific environment, but rather includes species that migrate between freshwater, brackish and marine environments, and we can assume that evolution has acted more on the ability to migrate long distances and survive in these different environments than tightly adapting to any single environment. Diadromy can be viewed as a niche in its on right, with species adapted to migration, different salinities and different food items. Thus we would expect relatively low numbers of strategies and species, large size for efficient swimming, high productivity/metabolism for fast swimming and for dealing with different salinities, and high trophic diversity. These expectations are mostly confirmed by the extended data set. The 624 diadromous species use 43 of 50 strategies which is above the confidence limits (27 – 41) of Equation 21 and may suggest that several of the 13 strategies used by only one or two species may disappear, i.e., the respective species may be found to belong to one of the adjacent strategies if more and better data become available. Many species are medium-sized, low-level predators of medium (14%) or high (29%) productivity. Of the 26 strategies with higher species presence than suggested by the overall distribution of species by salinity group, 19 belong to the large or very large size groups; 8 of 10 top-predator strategies have higher presence than suggested. Thus, large and very large fishes in general, and especially top predators, show a preference for this salinity group, as already suggested by Figure 32, Figure 33 and Table 25. Also, trophic diversity in this group is high (see Table 26).

The marine and brackish water group is similar to the diadromous group and contains mostly marine species that regularly enter brackish waters. The 1,142 species use 40 of 50 strategies, same as predicted. Many species are medium-sized low-level predators of medium (14%) to high (32%) productivity. Of 21 strategies of mid- or top-level predators 17 show a stronger presence than suggested by overall distribution of species by salinity group. Large and very large mid- and top-level predators show a preference for this salinity group.

For the brackish salinity group, selection theories predict relatively few strategies and species, small size, high productivity, and low trophic diversity. This is confirmed by the extended data set. The 53 species in the brackish salinity group use only 8 of 50 strategies, with 4 strategies being used by only one species. The number of used strategies is smaller but not significantly different from the 12 predicted strategies. Most species are small (38%) or medium-sized (43%) low-level predators with high productivity. Small low-level predators with high productivity show a higher presence than suggested by overall salinity distribution. Herbivores and omnivores are represented by only three and two species, respectively; mid-level predators are presented by only one species, and there are no top-predators restricted to brackish waters.

For the marine salinity group, selection theories predict relatively high number of strategies and species, large size, and low productivity, which is supported by the data. The predictions for trophic diversity are conflicting. The 9,592 species in the marine group use 47 of 50 strategies, with 4 strategies being used by only one or two species. The number of used strategies is similar to the 48 predicted strategies. Many species are medium-sized low-level predators with medium (17%) or high (32%) productivity. Of 33 predator strategies 25 show a stronger presence in this group than suggested by overall salinity distribution. Four predator strategies have more than 80% of their species in the marine group.

In summary, the species-rich strategies of small- to medium-sized low-level predators have the highest species numbers across all salinity groups. Herbivores have a relative stronger presence in freshwater as predicted by herbivory theory, whereas predators have a relative stronger presence in marine waters. Large and very large predators show a preference for the diadromous and marine & brackish salinity groups. Small low-level predators with high productivity show a preference for brackish waters. Large herbivores with very low productivity (30 species) and medium-sized herbivores with low productivity (77 species) are mostly restricted to freshwater. No top-predators are restricted to brackish waters. As observed by Winemiller and Rose (1992), freshwater fishes have a more restricted range of strategies within life history space than marine fishes, with 44 versus 47 strategies, respectively. This difference is confirmed if we only include strategies used by at least three species, which then results in 39 freshwater and 43 marine strategies. Median sizes, productivity and trophic levels in estuaries versus other environments and in marine versus freshwater confirm predictions of r-K theory and succession theory. Note that in these cases—other than with climate zones and habitats discussed below—temperature ranges are similar across salinity groups and thus cannot explain the observed patterns.

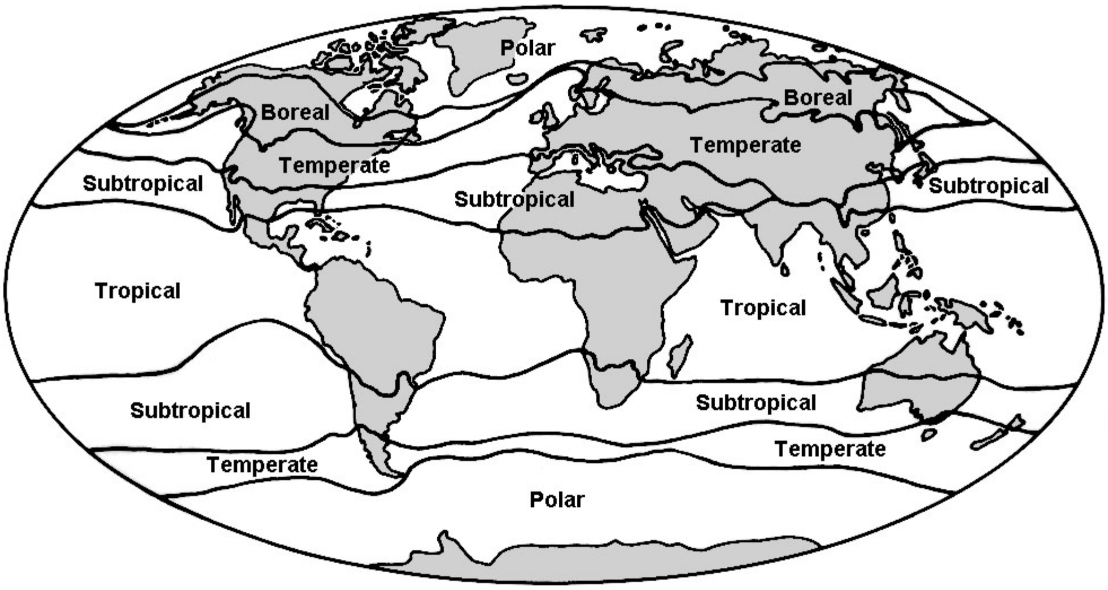
Table 28. Cross-tabulation of life-history strategies and salinity groups for 20,480 species based on the extended data set, where *n* is the number of species and *Sal %* the percentage of species associated with a certain strategy and salinity group. The *Species by salinity (%)* row gives the overall percentage of species by salinity group as derived in Table 23. If *Sal %* is more than twice the value of *Species by salinity (%)* then it is highlighted in bold font (Table continued on next page).

Salinity	**Freshwater**		**Fresh & Brackish**		**Diadromous**		**Brackish**		**Marine & Brackish**		**Marine**		**Species (%)**
Species by salinity (%)		**42.6**		**2.4**		**2.5**		**0.3**		**4.6**		**47.6**	**100**
Strategy (n)	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**Species (n)**
Herb-Small-High	39	36.8	2	1.9	1	0.9					64	60.4	106
Herb-Medium-High	273	55.4	9	1.8	4	0.8	3	0.6	20	4.0	185	37.4	494
Herb-Medium-Medium	311	75.3	15	3.6	11	2.7			10	2.4	66	16.0	413
Herb-Medium-Low	77	**96.3**	1	1.3							2	2.5	80
Herb-Large-High	7	58.3			1	**8.3**			1	8.3	3	25.0	12
Herb-Large-Medium	40	39.6	7	**6.9**	8	**7.9**			3	3.0	43	42.6	101
Herb-Large-Low	38	65.5	1	1.7	1	1.7			1	1.7	17	29.3	58
Herb-Large-Very low	30	**96.8**							1	3.2			31
Omni-Small-High	211	63.9	4	1.2	3	0.9	1	0.3	7	2.1	104	31.5	330
Omni-Small-Medium	1	**100.0**											1
Omni-Medium-High	843	69.6	32	2.6	13	1.1			34	2.8	289	23.9	1211
Omni-Medium-Medium	345	70.0	13	2.6	13	2.6	1	0.2	21	4.3	100	20.3	493
Omni-Medium-Low	8	72.7	1	**9.1**	1	**9.1**					1	9.1	11
Omni-Large-High	5	71.4							2	**28.6**			7
Omni-Large-Medium	25	38.5	6	**9.2**	9	**13.8**			7	**10.8**	18	27.7	65
Omni-Large-Low	44	57.9	1	1.3	7	**9.2**			5	6.6	19	25.0	76
Omni-Large-Very low	14	87.5			1	**6.3**					1	6.3	16
Low-Small-High	1622	59.9	83	3.1	37	1.4	20	**0.7**	52	1.9	896	33.1	2710
Low-Small-Medium	18	31.0	2	3.4	1	1.7			1	1.7	36	62.1	58
Low-Small-Low	9	52.9	1	**5.9**							7	41.2	17
Low-Medium-High	3024	44.6	166	2.4	181	2.7	23	0.3	364	5.4	3027	44.6	6785
Low-Medium-Medium	771	28.0	80	2.9	86	3.1	3	0.1	161	5.8	1655	60.1	2756
Low-Medium-Low	35	10.2	5	1.5	7	2.0			10	2.9	286	**83.4**	343
Low-Medium-Very low	5	9.1			3	**5.5**			4	7.3	43	78.2	55
Low-Large-High	2	3.3	3	**5.0**	4	**6.7**			6	**10.0**	45	75.0	60
Low-Large-Medium	138	21.4	22	3.4	48	**7.4**	1	0.2	94	**14.6**	342	53.0	645
Low-Large-Low	117	19.1	13	2.1	32	**5.2**			45	7.4	405	66.2	612

Salinity	**Freshwater**		**Fresh & Brackish**		**Diadromous**		**Brackish**		**Marine & Brackish**		**Marine**		**Species (%)**
Species by salinity (%)		**42.6**		**2.4**		**2.5**		**0.3**		**4.6**		**47.6**	**100**
Strategy (n)	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**n**	**Sal %**	**Species (n)**
Low-Large-Very low	57	26.6	12	**5.6**	18	**8.4**			15	7.0	112	52.3	214
Low-Very large-Very low			1	**10.0**	3	**30.0**					6	60.0	10
Mid-Small-High	2	18.2	3	**27.3**	1	**9.1**			2	**18.2**	3	27.3	11
Mid-Medium-High	191	33.8	6	1.1	18	3.2	1	0.2	31	5.5	318	56.3	565
Mid-Medium-Medium	77	17.8	11	2.5	22	**5.1**			29	6.7	293	67.8	432
Mid-Medium-Low	10	12.5			1	1.3			4	5.0	65	81.3	80
Mid-Medium-Very low					1	**10.0**					9	**90.0**	10
Mid-Large-High	5	9.8	1	2.0					9	**17.6**	36	70.6	51
Mid-Large-Medium	38	10.3	3	0.8	21	**5.7**			61	**16.6**	245	66.6	368
Mid-Large-Low	25	8.1	6	1.9	10	3.2			23	7.4	246	79.4	310
Mid-Large-Very low	3	2.5			3	2.5			20	**16.5**	95	78.5	121
Mid-Very large-Low					3	**42.9**			2	**28.6**	2	28.6	7
Mid-Very large-Very low			1	**11.1**	2	**22.2**			2	**22.2**	4	44.4	9
Top-Medium-High	13	17.1	1	1.3	1	1.3			5	6.6	56	73.7	76
Top-Medium-Medium	10	10.2			6	**6.1**			7	7.1	75	76.5	98
Top-Medium-Low	5	18.5			2	**7.4**					20	74.1	27
Top-Large-High	1	2.6	3	**7.9**	4	**10.5**			7	**18.4**	23	60.5	38
Top-Large-Medium	30	16.0	7	3.7	16	**8.5**			36	**19.1**	99	52.7	188
Top-Large-Low	13	6.9	4	2.1	11	**5.8**			21	**11.1**	140	74.1	189
Top-Large-Very low	7	7.7			6	**6.6**			9	**9.9**	69	75.8	91
Top-Very large-Medium											4	**100.0**	4
Top-Very large-Low	2	12.5	1	**6.3**	2	**12.5**			5	**31.3**	6	37.5	16
Top-Very large-Very low			1	**5.3**	1	**5.3**			5	**26.3**	12	63.2	19
Species (n)	8,541		528		624		53		1142		9,592		20,480
Strategies (n)	44		36		43		8		40		47		50
Predicted strategies (n)	47		34		36		12		40		48		
95% CL (n)	41 – 54		27 - 41		29 - 42		5 - 19		33 - 46		41 – 54		

Climate Zones

With few exceptions, fish, as ectotherms, have body temperatures that are close to that of the surrounding waters and there is evidence that many fish prefer water of particular temperatures (Reynolds and Casterlin 1979) because profound changes in physiology accompany environmental temperature changes (Crawshaw 1979). Figure 34 shows the climate zones used by FishBase. Temperature increases and environmental variability decreases from polar to tropical zones. The high-altitude zone will be cold, oligotrophic, highly variable and less mature. The deep water zone will be cold, oligotrophic (no primary production, instead 'marine snow'), relatively stable and mature.



WORLD CLIMATE

Figure 34. Climate zones of the world as used for the respective assignment of fishes in FishBase, modified after Bartholomew 1991.

Table 29 shows the number of species by climate zone as defined and classified in FishBase version 11/2004. Species increase in numbers from cold (polar/ boreal) to warm (tropical) zones, as has been found by many other studies across a wide range of taxa (e.g. Roy et al. for marine gastropods). This latitudinal diversity gradient may be caused by several factors such as increase in area, increase in temperature, increase in structural heterogeneity, and closeness to the center of fish biodiversity, but also by the 'mid-domain effect', which results in more species towards the middle in any very large system with clear borders, such as the poles along the latitudinal gradient (Gaston 2000), or Africa and the Americas with respect to species diversity across the Indo-Pacific (Bellwood and Hughes 2001). Note also low numbers of species restricted to high altitudes. The relatively high number of species in cold deep-waters may be explained by this environment having the largest area and being a mature ecosystem in the sense of succession theory.

The tropics have the largest climatically similar total surface area and thus tropical species tend to show limited adaptation to non-tropical environmental conditions; in contrast, because of strong seasonal fluctuations temperate species tend to have broader environmental tolerance, enabling them to venture into neighbouring polar/boreal or subtropical climate zones (Gaston 2000).

Table 29. Climate zones, abbreviations and respective species numbers for 28,786 species of fishes.

Climate zone	Abbreviation	Species	
		n	%
High altitude	1 high	60	0.2
Deep water	2 deep	3,723	12.9
Polar / boreal	3 pol/bor	261	0.9
Temperate	4 temp	3,317	11.5
Subtropical	5 sub	4,305	15.0
Tropical	6 tropical	17,120	59.5

Table 30 shows the number of species by climate zone and phylogenetic Class for all 28,782 species of fishes. Actinopterygii are represented with highest species numbers (88.4-98.4%) in all climate zones. Actinopterygii is the only Class with species occurring in high-altitude lakes; Cephalaspidomorphi are absent from deep waters; Myxini and Holocephali are absent from the polar / boreal zone; Sarcopterygii are absent from polar / boreal and temperate zones; and Holocephali are absent from polar / boreal and tropical waters, although they do appear in the deep-waters of those zones. Note that Elasmobranchii have nearly three times more species in deep waters than suggested by their overall proportion of species (9.4% versus 3.4%), although they are absent from depths below 3,500 m (Monty Priede, University of Aberdeen, pers. comm. 2001, confirmed by available depth distribution data in FishBase 11/2004).

Table 30. Phylogenetic Classes of 28,782 fish species by climate zone, with indication of number of species by Class.

Climate	Myxini	Cephala-spidomorphi	Holocephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
High altitude						60
Deep water	52		29	349	2	3,290
Polar/boreal		2		7		252
Temperate	10	33	4	76		3,194
Subtropical	6	5	4	266	1	4,023
Tropical	1	2		267	8	16,840

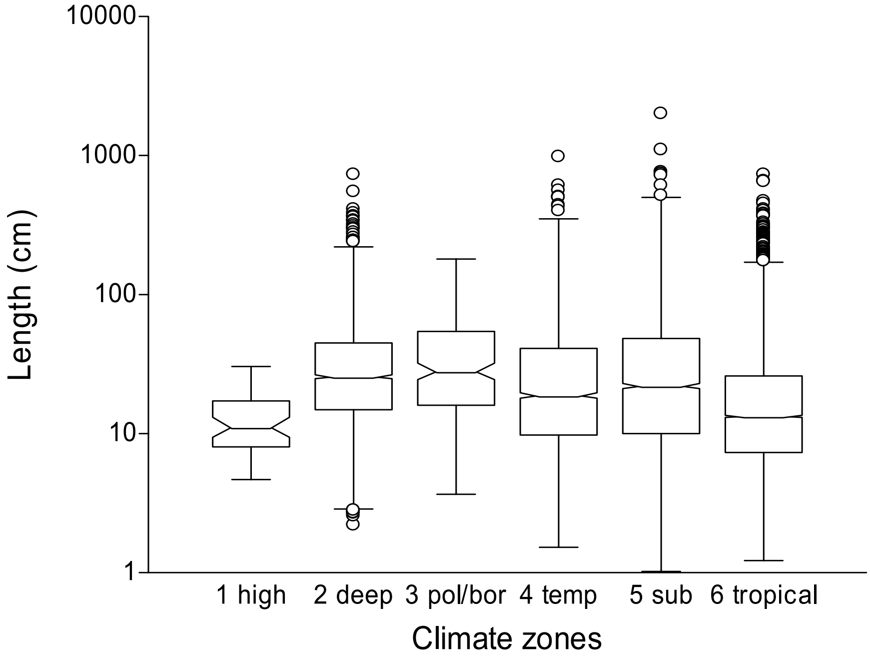


Figure 35. Maximum length distribution by climate zone for 23, 601 species of fishes with available data: 1 high altitude with n = 52, median = 11.1, 95% CL =8.70-14.2; 2 deep-water with n = 2,864, median = 25.6, 95% CL = 25.0-26.8 cm; 3 polar/boreal with n = 199, median = 28.0, 95% CL = 24.9-32.4; 4 temperate with n = 2,491, median = 18.8, 95% CL = 18.0-20.0; 5 subtropical with n = 3,384, median = 22.0, 95% CL = 20.7-24.0; 6 tropical with n = 14,611, median = 13.3, 95% CL = 13.0-13.5; all lengths in cm.

Figure 35 shows the distribution of maximum lengths by climate zone for 23,601 species with available data. r-K theory and succession theory predict selection for small species in the highly variable pole- and high-altitude zones and selection for large species in the tropical zones, whereas temperature theory predicts opposite selections. Trophy theory predicts selection for small size in oligotrophic high altitudes and deep waters whereas succession theory predicts selection for large size in deep waters.

Median lengths of high-altitude fishes are significantly lower than those of other groups, confirming the predictions of r-K, succession and trophy theory and suggesting that these combined selection forces outweigh selection for large size predicted by temperature theory. Median lengths of tropical fishes are significantly lower and median lengths of deep-water and polar/boreal fishes are significantly larger than in other groups, supporting the predictions of temperature theory and the findings of Vila-Gispert et al. (2002). No fishes with less than 2.2 cm maximum length occur in the cold water zones, probably because of constraints related to the high metabolic rates associated with small body size (Harrison 1996). Other than predicted by temperature theory there is no step-wise increase of median length from tropical to subtropical to temperate zones; rather, median length of subtropical fishes is significantly higher than those of temperate and tropical fishes; this may be caused by the practice of assigning species with seasonal migrations between temperate and tropical zones to the subtropical category (in FishBase 11/2004 there is only one climate zone per species); as has been shown before, highly migratory species, i.e. those with wide latitudinal ranges (Figure 73) or those within the diadromous salinity group (Figure 32) tend to be larger.

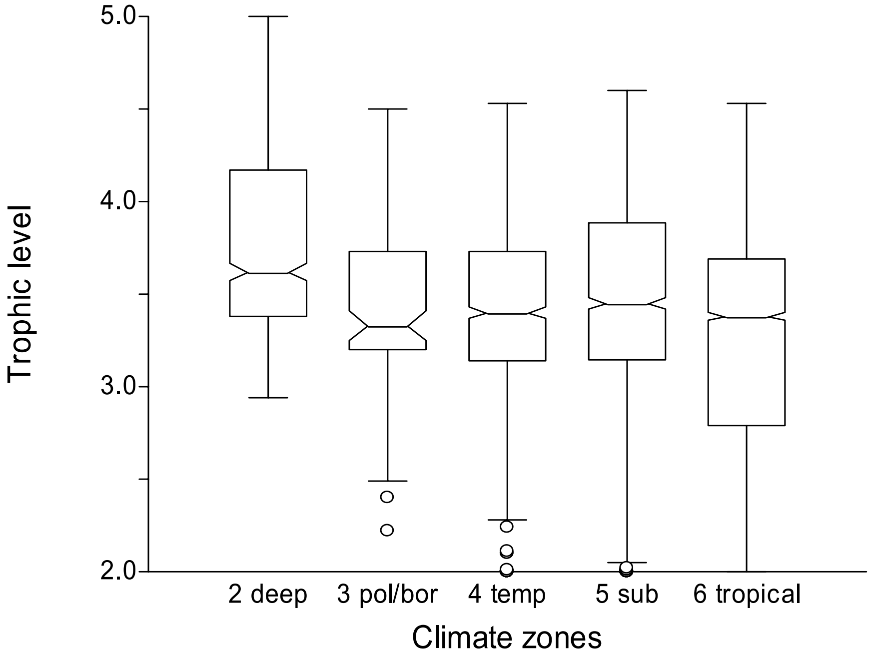


Figure 36. Trophic level by climate zone for 7,500 species of fishes with available data. No trophic data were available for high-altitude species. 2 deep water with n = 700, median = 3.62, 95% CL = 3.52-3.73; 3 polar / boreal with n = 107, median = 3.33, 95% CL = 3.29-3.47; 4 temperate with n = 912, median = 3.40, 95% CL = 3.38-3.42; 5 subtropical with n = 1,433, median = 3.45, 95% CL = 3.40-3.49; 6 tropical with n = 4,348, median = 3.38, and 95% CL = 3.35-3.40.

Figure 36 shows the distribution of trophic levels by climate zone for 7,500 species with available data. Herbivory theory predicts a decrease of median trophic levels towards the tropical zones, which is not supported by median trophic levels which, except for deep water, are not significantly different across zones. Note, however, the clear trend in the lower adjacent values with no herbivores in deep waters and only few in polar / boreal and temperate waters, as predicted (see also Froese and Sampang 2004).

Temperature is among the most important environmental variables and highly correlated with metabolism and its various expressions such as food consumption, growth and productivity (Beverton 1987, Wootton 1992, Moyle and Cech 2004) but also with latitudinal gradients of species diversity (Roy et al. 1998). Table 31 shows productivity by climate zone for 2,933 species with available data. Only one estimate of medium productivity was available for high-altitude fishes.

The deep sea is probably the most stable aquatic environment for which r-K theory thus predicts selection of slow development and late maturity, smaller reproductive effort, fewer young and long life. Temperature theory suggests selection for the same traits. Deep water species have indeed mostly (68%) low productivity with $r'_{max} = 0.13$, which is significantly lower than in all other environments and confirms the K-selected life history characteristics and the vulnerability to fishing pointed out by, e.g., Koslow et al. (2000) and Clark (2001).

Polar / boreal species have mostly (63%) medium productivity with $r'_{max} = 0.18$, which is significantly higher than in deepwater fishes and significantly lower than for the temperate, subtropical and tropical zones. The polar / boreal area is a highly variable, harsh zone for which r-K theory predicts selection of rapid development and early maturity, more young and short life. These attributes are indeed associated with medium productivity (see Table 6). In

Figure 32, polar/boreal fishes have the highest median length which seems to contradict these findings. Note, however, that this median length is only 28 cm which is consistent with medium productivity, and that there are only 11 fishes of more than 1 m total length and no fishes beyond 1.8 m length, i.e., compared with the other climate zones there seems to be a selection against large size and its associated life history traits, as suggested by r-K theory. Interestingly, there are also no fish smaller than about 4 cm and no fishes with high productivity, suggesting a lower physiological limit to r-selection in very cold environments. Temperature theory is not supported by these findings. Note, however, that Pauly (2000c) explicitly excluded environments with "temperatures of -2 to 3°C, wherein the phenomenon known as 'cold adaptation' (Wohlschlag 1961) induces stress similar to that caused by higher temperatures" (see also Pauly 1979 and Davies et al. 1993).

Temperate species have mostly low (35%) or medium (46%) productivity; subtropical species have mostly low (34%) or medium (39%) productivity; and tropical species have mostly low (26%), medium (38%) or high (25%) productivity. In other words, as predicted by temperature theory productivity as measured by approximate r'_{max} increased from deep water (0.13) to polar/boreal (0.18) to temperate (0.23) and subtropical (0.23) to tropical (0.30) zones. Similarly, Vila-Gispert et al. (2003) found a pattern of late maturation (= low productivity) in high latitudes and early maturation (= high productivity) in low latitudes.

Table 31. Productivity by climate zone for 2,933 species with available data, with approximated weighted means of intrinsic rate of population increase (r'_{max}).

Climate / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
High altitude		1			1	0.23	
Deep water	13	120	403	67	603	0.13	0.123 – 0.140
Polar / boreal		52	28	1	81	0.18	0.168 – 0.197
Temperate	67	252	198	34	551	0.23	0.217 – 0.251
Subtropical	108	302	273	93	776	0.23	0.217 – 0.248
Tropical	222	340	265	94	921	0.30	0.280 – 0.314

Table 32 shows an analysis of food web complexity based on the extended data set. Succession theory predicts fewer trophic levels and less trophic diversity in the presumably younger high-altitude systems and the more disturbed polar / boreal and temperate ecosystems. It also predicts more usage of trophic levels and higher trophic diversity in the mature and stabilized deep water ecosystems. High altitude and polar / boreal systems have indeed low numbers of trophic levels and trophic diversity, thus confirming succession theory. Other than predicted, deep water ecosystems use few trophic levels and have low trophic diversity; this is, however, caused by a physical limitation, i.e., the lack of light needed for photosynthesis and thus the lack of trophic levels below 3 (see Figure 36). If this is taken into account, then the 22 trophic levels indicate a complex food web in the upper trophic levels, as predicted by succession theory. Interestingly, evenness is lowest in the polar / boreal systems, indicating a trend towards few trophic levels, as is also visible in the narrow IQR and adjacent value ranges of this system shown in Figure 36.

Table 32. Analysis of food web complexity based on the extended data set; H' is trophic diversity and J' is evenness of the Shannon-Wiener index applied to trophic levels; diversity in high altitude, deep water and polar / boreal systems is significantly less than in the other systems (t-test alpha = 0.05, P=0.0121, Power = 0.890)

Climate	Trophic levels	Species	H'	J'
High altitude	16	60	3.8	0.95
Deep water	22	3,722	3.6	0.82
Polar / boreal	20	261	3.3	0.77
Temperate	28	3,306	4.0	0.83
Subtropical	27	4,282	4.3	0.90
Tropical	30	17,073	4.2	0.86

Table 33 gives an overview of predictions of selection theories with regard to climate zones. Symbols in parentheses indicate strategies whose predictions are in conflict with those of other strategies in the respective column; negative symbols without parentheses thus indicate ‘unforced errors.’ Nineteen (31%) of altogether 61 predictions are not confirmed by the data: Relatively low numbers of strategies and species are predicted for the deep sea because of low temperature and low heterogeneity, but succession and area theories predict relatively high numbers and prevail. Succession and r-K theories predict small size for polar / boreal and temperate zones and large size for the tropical zone, but temperature theory predicts the opposite trends and prevails; temperature theory predicts large size for the cold high-altitude zone, but r-K, succession, and trophy theories predict the opposite trend and prevail; trophy theory predicts small size for the oligotrophic deep waters, but r-K, succession and temperature theories predict large size and prevail. Succession and r-K theories predict high productivity in the polar / boreal and low productivity in the tropical zone, whereas temperature theory predicts the opposite trends and prevails. Succession and herbivory theories predict lower trophic diversity in the relatively less mature and cold temperate zone but this is not supported by the data. Succession theory predicts high trophic diversity in the relatively mature deep sea and herbivory theory predicts fewer herbivores and thus less trophic diversity because of cold temperature; trophic diversity in deep waters is indeed low. However, the causative factor is lack of light.

Table 33. Summary of predictions by selection theories as applicable to climate zones, where '+' indicates values are on the predicted side if values are ranked and '+++' indicates that the difference to the other values is significant at the 95% level; '–' indicates that the values do not support the prediction, with same amplification; parentheses indicate conflict with other strategies. Data used were the overall number of species by climate zone, the box plots for observed size and trophic level, mean r_{max} of observed productivity, and Shannon-Wiener trophic diversity based on the extended data set.

Theory	Environment	Climate	Species / Strategies	Size	Productivity	Trophic diversity
r-K	variable	high alt.		(+++)		
		pol/bor		(---)	(-)	
		temperate		(---)	(+)	
	stable	deep		(+++)	+++	
		tropical		(---)	(---)	
Succession	less mature	high alt.	+	(+++)		+++
		pol/bor	+	(---)	(-)	+++
		temperate	+	(---)	(+)	---
	mature	deep	(+)	(+++)	+++	(---)
		tropical	+	(---)	(---)	+++
Temperature	high temp.	tropical	+	(+++)	(+++)	
	low temp.	high alt.	+	(---)		
		deep	(-)	(+++)	+++	
		pol/bor	+	(+++)	(+)	
		temperate	+	(+++)	(-)	
Herbivory	high temp.	tropical				+++
	low temp.	high alt				+++
		deep				(+++)
		pol/bor				+++
		temperate				---
Trophy	oligotroph	high alt.		(+++)	no data	
		deep		(---)	+++	
Area	large	deep	(+)			
		tropical	+			
	small	high alt.	+			
Heterogeneity	high	tropical	+			
	low	high alt.	+			
		deep	(-)			
		pol/bor	+			
Closeness to Center	near	tropical	+			
	far	high alt.	+			
		pol/bor	+			
		temperate	+			

Table 34 shows a cross-tabulation of life-history strategies and climate zones for 20,482 species based on the extended data set. A null-hypothesis would suggest that the distribution of species by climate zone and strategy is the same as the overall distribution by climate zone shown in Table 29. Cases where a strategy is used by more than twice the percentage suggested by the overall distribution are highlighted in bold.

With regard to life-history strategies, parallel selection forces shown in Table 33 predict relatively low numbers of strategies and species and low trophic diversity for the high-altitude zone. This is confirmed by the extended data set. Predictions for size are conflicting. The 48 high-altitude species use 10 of 50 strategies, which is similar to the 11 strategies predicted by Equation 21 (see last rows in Table 34). Most species are medium-sized omnivores (10%) or low-level predators (25%). Mid- and top-level predators are absent. Thus, the extended data set suggests a flat trophic pyramid in oligotrophic high-altitude ecosystems.

For deep waters, selection theories predict low productivity. This is confirmed by the extended data set. Predictions for numbers of species and strategies, size and trophic diversity are conflicting. The 2,476 species restricted to deep waters use 31 of 50 strategies, which is below the 95% confidence limits of the 43 (37 – 50) strategies predicted by Equation 21 and outside the confidence limits of the probability plot (Figure 82). Deep water fishes have fewer life-history strategies available to them (no plants as food) and use the remaining strategies with more species than suggested by Equation 21. Most deep-water species are medium-sized low-level predators with medium (26%) and high (26%) productivity. This result contradicts the findings in Table 31 and overestimates medium and high productivity; this bias is caused by the modelling approach for the von Bertalanffy parameter K (see above) which is based on data available for family members; since deep-water fishes are poorly known, it were the 'shallower' and thus 'warmer' or ‘commercial’ family members with presumably faster growth and life cycles for which data were available and which then determined the growth and productivity assigned to the family members without data (see also discussion in Froese and Sampang 2004). Thus, the productivity assignments in Table 34 should be ignored in favor of the observed values presented in Table 31. There are no herbivorous deep-water fishes and only one omnivorous species which a more thorough study might reveal to be a low-level predator. Fifteen of twenty medium- to large-sized mid- to top-level predators of very low to low productivity show stronger presence than suggested by the overall species distribution. Thus, the data confirm the statements of Helfman et al. (1997) that, "all deep-sea fishes are carnivores..." and that, "biochemically, rates of enzymatic and metabolic activity and even levels of ATP-generating enzymes are lower in deep-sea fishes than in shallow-water relatives" (see also Vailliet et al. 2001).

For the polar / boreal climate zone, selection theories predict relatively low numbers of species and strategies and low trophic diversity. This is confirmed by the extended data set. Predictions for size and productivity are conflicting. The 179 polar / boreal species use 18 of 50 strategies, which is at the lower confidence limit of the 25 (18 – 31) predicted strategies. Polar / boreal fishes have fewer life-history strategies available to them (no herbivores) and use the remaining strategies with more species. The modelling exercise based on mean growth within a Family has put 28 species into the high productivity group. This is not supported by data in Table 31 and is probably a modelling bias as most growth estimates in the respective families are likely to stem from temperate areas without the constraints of very low temperature. Thus, two strategies (marked with question marks) are likely to disappear and the respective species are likely to fall into the adjacent strategies with medium productivity. In agreement with the observed data in Figure 33, the extended data set contains no herbivores and only two omnivorous species.

For the temperate zone, five of eleven predictions made by selection theories are not supported by the data, indicating that this zone is not easily classified in terms of environmental variability, ecosystem maturity, and temperature. The only uncontroversial prediction is that for relatively low numbers of species and strategies. The 2,301 temperate species use 44 of 50 strategies, which is similar to the predicted 43 (36 – 50) strategies. Most species are medium-sized low-level predators of medium (21%) and high (30%) productivity. All herbivorous strategies are represented by fewer species than suggested by the overall distribution of species by climate zone, confirming the findings of Figure 36.

The subtropical climate zone is transitional between the temperate and the tropical zones and has not been scored against predictions of selection theories. The 3,025 subtropical species use 48 of 50 strategies, which is within the confidence limits of the 44 (37 – 51) strategies predicted by Equation 21. Many species are medium-sized low-level predators with medium (15%) or high (29%) productivity. Five of six strategies with very large size are represented by more than twice the number of species than suggested by the overall distribution, confirming the findings in Figure 35.

For the tropical zone, selection theories predict relatively high number of species and strategies and high trophic diversity. These predictions are supported by the extended data set. Predictions for size and productivity are conflicting. The 12,453 tropical species use 48 of 50 strategies, which is the same as the 48 (41 – 54) strategies predicted by Equation 21. Many species are small low-level predators with high productivity (17%) and medium-sized low-level predators of medium (9%) and high (36%) productivity. All herbivores show higher presence (71-92%) then suggested by overall distribution of species by climate zone. All small mid-level predators with high productivity occur in this zone; of 14 strategies with high productivity 10 show higher presence of species than suggested by the overall distribution. In contrast, all top-predator strategies are represented with fewer species than suggested by overall distribution of species by climate zone.

In summary, the highest number of species and strategies occur in the tropical zone, which also supports more herbivores, more small species, and more high productivity species. Large and very large species occur largely in the subtropical zone; this includes species that migrate seasonally from temperate to tropical zones. Species numbers and numbers of used strategies decline towards the poles and the high-altitude zone; deep-waters have about the same number of species as the temperate or subtropical zone. There are no herbivorous and few omnivorous strategies in deep or polar waters, and as a result the remaining strategies are used by more species than suggested by the overall relationship between species and strategies (Equation 21). Medium-sized low-level predators of medium productivity present the highest number of species in all climate zones. With the exception of the temperate zone, selection theories correctly predicted predominant life-history strategies.

Table 34. Cross-tabulation of life-history strategies and climate zones for 20,482 species of fishes based on the extended data set, where *n* is the number of species and *Clim %* the percentage of species associated with a certain strategy and climate zone. The *Species by climate zone (%)* row gives the overall percentage of species by climate zone as derived in Table 29. If *Clim %* is more than twice the value of *Species by climate zone (%)* then it is highlighted in bold; otherwise, the three highest percentages are in bold (Table continued on next page).

Climate zone	**High altitude**		**Deep water**		**Polar / boreal**		**Temperate**		**Subtropical**		**Tropical**		**Total**
Species by climate zone (%)		0.2		12.9		0.9		11.5		15		59.5	100
Strategy	n	Clim %	n	Clim %	n	Clim %	n	Clim %	n	Clim %	n	Clim %	
Herb-Small-High							1	0.9	16	15.1	89	84.0	106
Herb-Medium-High	2	0.4					10	2.0	40	8.1	442	89.5	494
Herb-Medium-Medium	7	**1.7**					5	1.2	29	7.0	372	90.1	413
Herb-Medium-Low							3	3.8	4	5.0	73	**91.3**	80
Herb-Large-High									1	8.3	11	**91.7**	12
Herb-Large-Medium							4	4.0	16	15.8	81	80.2	101
Herb-Large-Low							4	6.9	13	22.4	41	70.7	58
Herb-Large-Very low							2	6.5	2	6.5	27	87.1	31
Omni-Small-High	1	0.3					19	5.8	34	10.3	276	83.6	330
Omni-Small-Medium									1	**100.0**			1
Omni-Medium-High	10	**0.8**					113	9.3	140	11.6	948	78.3	1211
Omni-Medium-Medium	5	**1.0**	1	0.2			74	15.0	86	17.4	327	66.3	493
Omni-Medium-Low					1	**9.1**	5	**45.5**	1	9.1	4	36.4	11
Omni-Large-High							1	14.3			6	85.7	7
Omni-Large-Medium							7	10.8	18	27.7	40	61.5	65
Omni-Large-Low					1	1.3	18	**23.7**	20	26.3	37	48.7	76
Omni-Large-Very low							11	**68.8**	2	12.5	3	18.8	16
Low-Small-High	1	0.0	107	3.9	3 ?	0.1	166	6.1	323	11.9	2110	77.9	2,710
Low-Small-Medium	1	**1.7**	11	**19.0**	4	**6.9**	11	19.0	11	19.0	20	34.5	58
Low-Small-Low			1	5.9			4	**23.5**	3	17.6	9	52.9	17
Low-Medium-High	12	0.2	650	9.6	25 ?	0.4	700	10.3	878	12.9	4520	66.6	6,785
Low-Medium-Medium	8	0.3	634	**23.0**	65	**2.4**	493	17.9	444	16.1	1114	40.4	2,758
Low-Medium-Low	1	0.3	128	**37.3**	12	**3.5**	77	22.4	57	16.6	68	19.8	343
Low-Medium-Very low			11	**20.0**			26	**47.3**	8	14.5	10	18.2	55
Low-Large-High			17	**28.3**			3	5.0	12	20.0	28	46.7	60
Low-Large-Medium			91	14.1	17	**2.6**	112	17.4	136	21.1	289	44.8	645
Low-Large-Low			177	**28.9**	17	**2.8**	114	18.6	134	21.9	170	27.8	612

Climate zone	**High altitude**		**Deep water**		**Polar / boreal**		**Temperate**		**Subtropical**		**Tropical**		**Total**
Species by climate zone (%)		0.2		12.9		0.9		11.5		15		59.5	100
Strategy	n	Clim %	n	Clim %	n	Clim %	n	Clim %	n	Clim %	n	Clim %	
Low-Large-Very low			36	**16.8**	2	0.9	51	**23.8**	57	26.6	68	31.8	214
Low-Very large-Very low			1	10.0			3	**30.0**	4	**40.0**	2	20.0	10
Mid-Small-High											11	**100.0**	11
Mid-Medium-High			94	**16.6**			27	4.8	50	8.8	394	69.7	565
Mid-Medium-Medium			104	**24.1**	5	1.2	55	12.7	65	15.0	203	47.0	432
Mid-Medium-Low			40	**50.0**	3	3.8	13	16.3	12	15.0	12	15.0	80
Mid-Medium-Very low			6	**60.0**			1	10.0	2	20.0	1	10.0	10
Mid-Large-High			11	**21.6**					13	25.5	27	52.9	51
Mid-Large-Medium			46	12.5	9	2.4	34	9.2	79	21.5	200	54.3	368
Mid-Large-Low			88	**28.4**	6	1.9	36	11.6	83	26.8	97	31.3	310
Mid-Large-Very low			32	**26.4**			10	8.3	34	28.1	45	37.2	121
Mid-Very large-Low			1	14.3					4	**57.1**	2	28.6	7
Mid-Very large-Very low			2	**22.2**			3	**33.3**	1	11.1	3	33.3	9
Top-Medium-High			28	**36.8**			1	1.3	9	11.8	38	50.0	76
Top-Medium-Medium			40	**40.8**	1	1.0	9	9.2	11	11.2	37	37.8	98
Top-Medium-Low			8	**29.6**			7	**25.9**	7	25.9	5	18.5	27
Top-Large-High			3	7.9			4	10.5	10	26.3	21	55.3	38
Top-Large-Medium			14	7.4	3	1.6	22	11.7	54	28.7	95	50.5	188
Top-Large-Low			61	**32.3**	4	**2.1**	30	15.9	51	27.0	43	22.8	189
Top-Large-Very low			30	**33.0**	1	1.1	7	7.7	24	26.4	29	31.9	91
Top-Very large-Medium									4	**100.0**			4
Top-Very large-Low							4	**25.0**	10	**62.5**	2	12.5	16
Top-Very large-Very low			3	15.8			1	5.3	12	**63.2**	3	15.8	19
Species (n)	48		2,476		179		2,301		3,025		12,453		20,482
Strategies (n)	10		31		18		44		48		48		50
Predicted strategies (n)	11		43		25		43		44		48		
95% CL lower	4		37		18		36		37		41		
95% CL upper	18		50		31		50		51		54		

Life-history Strategies and Aquatic Ecosystems

Zoogeographic Realms

Freshwater fishes are one of the most important groups for zoogeographical studies because their distribution is restricted to drainage systems within continents, with saltwater or mountain ranges acting as barriers (Berra 2001). All freshwater fishes contained in FishBase version 11/2004 have been assigned to one of the six realms following the revision of Berra (2001).

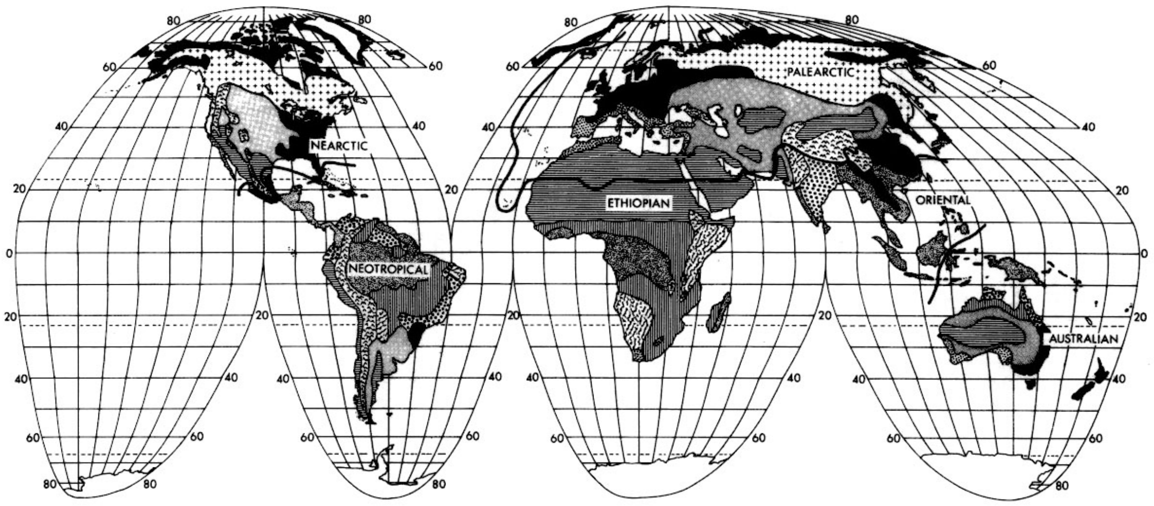


Figure 37. Map used by FishBase staff for assigning freshwater fishes to zoogeographic realms; modified after Berra (2001).

The Neotropical, Ethiopian, Oriental and Australian realms are dominated by tropical zones. The Palearctic realm is mostly boreal, temperate and subtropical; the tropical areas in northern Africa and the northern Arabian Peninsula are mostly deserts and support only few freshwater fishes. The Nearctic realm is similarly dominated by boreal, temperate and subtropical zones. The Nearctic and Palearctic realms have lower mean annual temperature and higher environmental variability than the tropical zones; because of the recent ice ages which affected the northern half of the Nearctic and Palearctic zone, these will also be relatively less mature ecosystems in the sense of succession theory. The Australian zone has the smallest area, whereas the other zones have about the same area.

Table 35 shows the distribution of 13,042 freshwater fishes by zoogeographical realm. The null hypothesis of even distribution of species across zoogeographic realms is rejected. Considering the principles governing species numbers, temperature explains lower species numbers in the temperate Palearctic and Nearctic realms compared to the more tropical realms; larger area explains the higher number of Palearctic compared to Nearctic fishes. Among the tropical realms, suitable area explains the ranking from Neotropical to Australian. In addition, the remarkably low number of species in the Australian zone is the result of past movements of continents (see Berra 2001 for review and discussion). An early attempt at estimating species numbers by zoogeographic realm was made by Moyle and Cech (1988) for 6,895 freshwater fish species, altogether. Their ranking was similar to the one in this study, with Neotropical and Ethiopian being the most species-rich and Australian being the most species-poor realms. However, they largely underestimated the number of Oriental species. A geographically more detailed discussion in Moyle and Cech (2000) results in the same ranking and in similar numbers as found in this study. Matthews (1998) also presents a detailed discussion and analysis of zoogeographic realms and geologic movement of land masses, albeit with numbers at the Family and not species level. As found in this study, the low number of species (2.4%) occurring in more than one realm strongly confirms the original concept of zoogeographic realms presented by Wallace (1860, 1876).

Table 35. Distribution of freshwater species by zoogeographic realm, with 13,354 records for 13,041 species, i.e., about 300 (2.4%) species occurred in more than one realm. Introduced species and questionable occurrences were excluded. The last column shows species numbers after Moyle and Cech (1988, 2000).

Zoogeographic realm	Abbr.	Species records	Percent	Moyle & Cech 1988	2000
Nearctic	1 Nea	1,052	7.9	950	1,061
Palearctic	2 Pal	1,397	10.5	420	>568
Neotropical	3 Neo	4,385	32.8	2,600	>3,600
Ethiopian	4 Eth	3,072	23.0	2,000	3,000
Oriental	5 Ori	2,821	21.1	700	>1,800
Australian	6 Aus	627	4.7	225	400

Table 36 shows the distribution of phylogenetic classes across zoogeographic realms for all 13,041 species of fishes that regularly occur in freshwater. Cephalaspidomorphi occur in all realms except the Ethiopian and Oriental realm. Elasmobranchii occur in all realms, albeit with few species. Lungfishes (Sarcopterygii) occur only in the Neotropical, Ethiopian and Australian realms. Actinopterygii occur in all realms with highest numbers of species records. Myxini and Holocephali do not enter freshwater.

Table 36. Phylogenetic Classes by zoogeographic realm, with 13,354 records for 13,041 species of fishes regularly found in freshwater.

Zoogeographic realm	Cephala-spidomorphi	Elasmobranchii	Sarcopterygii	Actinopterygii
Nearctic	24	2		1,026
Palearctic	17	3		1,377
Neotropical	2	22	1	4,360
Ethiopian		7	7	3,058
Oriental		10		2,811
Australian	3	6	1	617

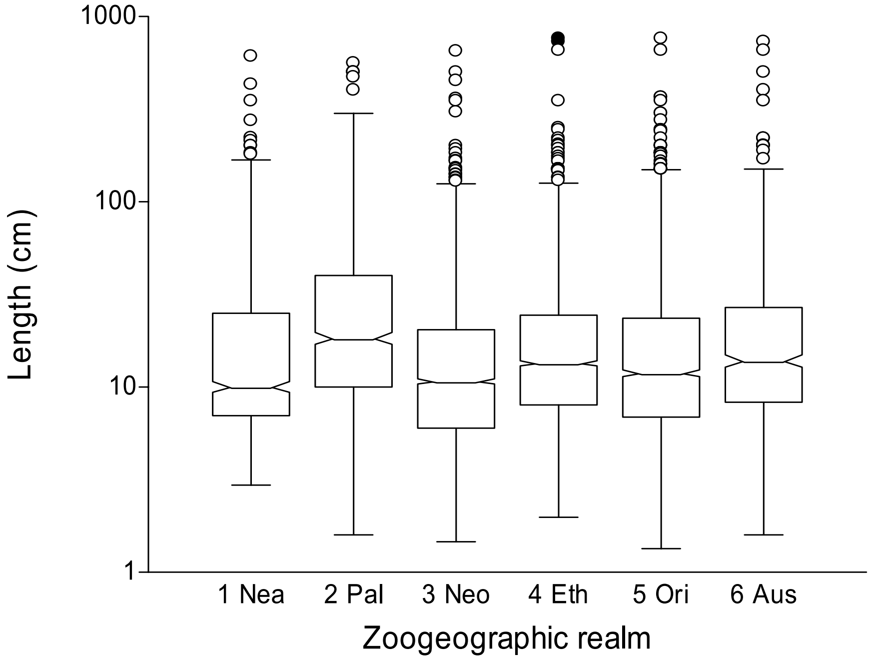


Figure 38. Length distribution with 11,210 records of freshwater fishes by zoogeographic realm: 1 Nearctic realm with n = 923, median = 10.0, 95% CL = 9.0–11.0; 2 Palearctic realm with n = 871, median = 18.3, 95% CL = 16.5–20.0; 3 Neotropical realm with n = 3,610, median = 10.7, 95% CL = 10.0–11.0; 4 Ethiopian realm with n = 3,030, median = 13.4, 95% CL = 12.8–13.9; 5 Oriental realm with n = 2,190, median = 11.9, 95% CL = 11.0–12.2; and 6 Australian realm with n = 586, median = 13.8, 95% CL = 12.2 – 14.6; all lengths in cm maximum total length.

A null hypothesis about size distributions of freshwater fishes according to their zoogeographic realms would assume that these large realms would provide similar types of habitats suitable for small to large fishes, and that thus there will be no significant difference in length distributions. Figure 38 shows the length distribution of 11,210 records of freshwater fishes by zoogeographic realm with significantly different median lengths, thus refuting the null-hypothesis. Temperature theory predicts selection for larger species in the colder Nearctic and Palearctic realms whereas r-K and succession theories predict selection for smaller size in these more variable and less mature areas. Palearctic fishes have indeed a significantly higher median length then the other realms, in support of temperature theory. Nearctic fishes have a significantly lower median length than Palearctic, Ethiopian, and Australian fishes, which is in support of r-K theory and also suggests that environmental variability affecting freshwater fishes is higher in the Nearctic than in the Palearctic realm, which may indeed be the case because of the North-South orientation of mountain chains in North America, which allow cold air to reach further South. Also, in the Palearctic realm boreal and temperate areas are larger than in the Nearctic realm; the subtropical area is also larger but consists mainly of species-poor deserts. As shown in Table 37 the Nearctic realm has relatively more tropical species (22%) than the Palearctic realm (6.8%). As shown in Figure 35 the median length of tropical fishes is significantly lower than that of boreal, temperate or subtropical fishes. Interestingly, Knouft and Page (2003) find an evolutionary trend of decreasing body size in five out of nine families of North American freshwater fishes, which they relate to “the high percentage of small streams in North America.”

Neotropical, Ethiopian, Oriental and Australian realms have very similar distributions of lengths, although the slightly lower median lengths of Neotropical and Oriental fishes are significant. This was predicted by both r-K and temperature theory.

Table 37. Cross-tabulation of species records by zoogeographic realm and climate zone.

Zoogeographic realm	polar boreal	temperate	subtropical	tropical
Nearctic	19	553	243	233
Palearctic	35	876	373	93
Neotropical	1	115	309	3920
Ethiopian			70	3001
Oriental		96	503	2213
Australian		51	81	493

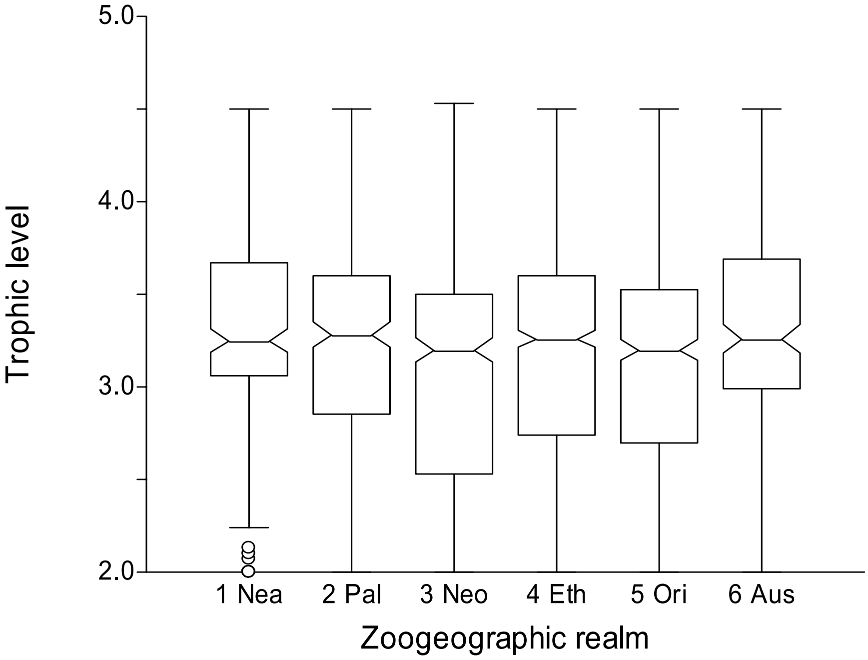


Figure 39. Distribution of trophic levels by zoogeographic realm for 2,700 records of freshwater fishes with available data. 1 Nearctic realm with n = 231, median = 3.3, 95% CL = 3.2-3.3; 2 Palearctic realm with n = 296, median = 3.3, 95% CL = 3.2-3.4; 3 Neotropical realm with n = 545, median = 3.2, 95% CL = 3.1-3.2; 4 Ethiopian realm with n = 891, median = 3.3, 95% CL = 3.2-3.3; 5 Oriental realm with n = 534, median = 3.2, 95% CL = 3.2-3.3; and 6 Australian realm with n = 203, median = 3.3, 95% CL = 3.2-3.3.

Figure 39 shows the distribution of trophic levels by zoogeographic realm. Herbivory theory predicts more herbivorous species in the tropical realms. This is supported by the tendency in the lower inter-quartile ranges (IQRs) towards more omnivorous/herbivorous species in the Neotropical, Ethiopian and Oriental realms and fewer omnivorous species in the Nearctic realm. Surprisingly, the Australian realm does not follow this pattern and has clearly a smaller fraction of omnivorous/herbivorous species than the other tropical realms.

Table 38 shows the distribution of 868 records of freshwater fishes by productivity and zoogeographic realm. Temperature theory predicts selection for smaller species with faster growth and thus higher productivity (see Table 6) in the tropical realms. In contrast, if the tropical freshwater realms indeed provide more environmentally stable environments than the Nearctic and Palearctic realms, then r-K theory predicts selection for slow development, late maturity and long life, i.e., traits that are associated with low productivity. With opposing selection pressures we would expect intermediate results. This is indeed what the data show: Across all realms, highest numbers of species are found in the medium productivity group, suggesting that opposing selection pressures are indeed at work and prevent strong responses in one or the other direction. However, the colder Nearctic and Palearctic realms have second-most species in the low productivity group with r'_{max} of 0.28 and 0.23, respectively, which is significantly lower than the tropical realms, which have second-most species in the high productivity group with $r'_{max} = 0.30 – 0.37$, suggesting that selection forces resulting from differences in temperature are stronger than those resulting from environmental variability.

Table 38. Distribution of species by zoogeographic realm and productivity with 868 records for freshwater fishes with available data, with indication of the approximated r'_{max}.

Zoogeographic realm / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
Nearctic	28	88	44	7	167	0.28	0.241 – 0.309
Palearctic	20	110	70	12	212	0.23	0.201 – 0.250
Neotropical	36	78	21	25	160	0.30	0.258 – 0.338
Ethiopian	45	62	21	14	142	0.36	0.309 – 0.401
Oriental	40	49	19	11	119	0.37	0.314 – 0.416
Australian	20	26	15	7	68	0.33	0.266 – 0.401

Table 39 shows an analysis of food web complexity using the extended data set. Succession theory predicts fewer trophic levels and lower trophic diversity for the less stabilized ecosystems of the Nearctic and Palearctic realms. This is true for the Nearctic realm which has the lowest trophic diversity, but not for the trophic diversity of the Palearctic realm nor for numbers of trophic levels in general, which are about the same across all realms. The Nearctic realm also has the lowest evenness, suggesting a preference of species for few trophic levels and confirming the narrow IQR and adjacent value ranges of this realm in Figure 39.

Table 39. Analysis of food web complexity using the extended data set; H' is trophic diversity and J' is evenness of the Shannon-Wiener index applied to trophic levels.

Realm	Trophic levels	Species	H'	J'
Nearctic	26	1,052	3.6	0.77
Palearctic	27	1,397	4.0	0.83
Neotropical	27	4,385	4.1	0.86
Ethiopian	26	3,063	4.0	0.84
Oriental	26	2,821	4.0	0.85
Australian	26	627	4.0	0.84

Table 40 presents an overview of predictions by selection theories as they apply to zoogeographic realms. Symbols in parentheses indicate strategies whose predictions are in conflict with those of other strategies in the respective column; negative symbols without parentheses thus indicate ‘unforced errors.’ Of 61 predictions 27 (44%) are not supported by the data: r-K and succession theories predict relatively small size and high productivity for the more variable and less mature Palearctic realm whereas temperature theory predicts large size and low productivity and prevails; in contrast, temperature theory also predicts relatively large size in the Nearctic realm whereas r-K and succession theory predict relatively small size and prevail. As discussed above, the Nearctic realm is more variable and less boreal/temperate than the Palearctic realm, which may explain these results. r-K and succession theories predict large size and low productivity in the tropical realms, whereas temperature theory predicts small size and high productivity and prevails. Succession and herbivory theories predict relatively low trophic diversity in the Palearctic realm; however, trophic diversity and evenness in this realm is about the same as in the tropical realms; this result is unexpected and needs further research.

Succession and temperature theory predict relatively high number of species in the Australian realm, whereas area, size and separation from the continental center of freshwater fish biodiversity predict lower numbers and prevail. As Berra (2001) observed: “The Australian freshwater fauna is depauperate, as expected of an island, and dominated by peripheral groups.”

Table 40. Summary of predictions by selection theories as applicable to zoogeographic realms, where ‘+’ indicates values are on the predicted side if values are ranked and ‘+++’ indicates that the difference to the other values is significant at the 95% level; ‘–‘ indicates that the values do not support the prediction, with same amplification; parentheses indicate conflict with other strategies. Data used were the overall number of species by zoogeographic realm, the box plots for observed size and trophic level, mean r_{max} of observed productivity, and Shannon-Wiener trophic diversity based on the extended data set.

Theory	Environment	Realm	Species / Strategies	Size	Productivity	Trophic diversity
r-K	variable	Nearctic		(+++)	(---)	
		Palearctic		(---)	(---)	
	stable	Neotropical		(-)	(-)	
		Ethiopian		(-)	(-)	
		Oriental		(-)	(-)	
		Australian		(-)	(-)	
Succession	less mature	Nearctic	+	(+++)	(---)	+
		Palearctic	+	(---)	(---)	-
	mature	Neotropical	+	(-)	(-)	+
		Ethiopian	+	(-)	(-)	+
		Oriental	+	(-)	(-)	+
		Australian	(-)	(-)	(-)	+
Temperature	low temp.	Nearctic	+	(---)	(+++)	
		Palearctic	+	(+++)	(+++)	
	high temp.	Neotropical	+	(+++)	(+)	
		Ethiopian	+	(+++)	(+)	
		Oriental	+	(+++)	(+)	
		Australian	(-)	(+++)	(+)	
Herbivory	low temp.	Nearctic				+
		Palearctic				-
	high temp.	Neotropical				+
		Ethiopian				+
		Oriental				+
		Australian				+
Area	small	Australian	(+)			
Closeness to Center	far	Australian	(+)			

Table 41 shows a cross-tabulation of life-history strategies with zoogeographic realms with 9,652 (74%) records of freshwater fishes based on the extended data set. Freshwater fishes use 49 of 50 strategies, i.e., only very large top predators with medium productivity do not occur in freshwater. A null-hypothesis would suggest that the distribution of species by realm and strategy is the same as the overall distribution by realm shown in row *Records by realm %* of Table 41 and in Table 35. Cases where a strategy is used by more than twice the percentage suggested by the overall distribution are highlighted in bold.

For the Nearctic realm selection theories predict relatively low numbers of species and strategies and low trophic diversity. These predictions are supported by the extended data set. The 876 Nearctic species use 32 of 49 strategies, which is near the lower confidence limit of the 38 (31 – 45) strategies predicted by Equation 21. Apparently Nearctic fishes have fewer strategies available to them (narrower size range in Figure 38 and less trophic diversity visible in Figure 39 and Table 39) resulting in the remaining strategies being used by more species than predicted by the overall relationship between species and strategies. Predictions for size and productivity were conflicting. Most species are small low-level predators with high productivity (18%) or medium-sized low-level predators with medium (15%) or high (35%) productivity. Medium-sized top predators with low productivity (seven species) only occur in this realm. Of 20 predatory strategies used in this realm, 19 are represented with more species than suggested by the overall distribution of species by realms.

For the Palearctic realm, selection theories predict relatively low numbers of species and strategies and low trophic diversity. Except for trophic diversity, these predictions are supported by the extended data set. The 840 Palearctic species use 34 of 49 strategies, which is similar to the 38 (31 – 44) strategies predicted by Equation 21. Predictions for size and productivity were conflicting. Many species are medium-sized low-level predators with medium (20%) or high (26%) productivity. Of 25 strategies involving large or very large size, 19 are used in this realm and 13 of these show higher species record numbers than suggested by overall distribution of species by realm, including 8 cases with more than twice the number of suggested species records, thus confirming the large median size shown in Figure 38.

For the Neotropical realm, selection theories predict relatively high numbers of species and strategies and high trophic diversity. These predictions are supported by the extended data set. Predictions for size and productivity are conflicting. The 2,867 Neotropical species use 41 of 49 strategies, which is similar to the 44 (37 – 51) predicted strategies. Most species are small (27%) or medium-sized (25%) low-level predators with high productivity. All eight herbivorous strategies are used, including three with higher and three with twice as high species numbers than suggested by overall distribution of species by realm, supporting the trend towards low trophic levels seen in Figure 38. Six (86%) large top-predators with high productivity also belong to this realm.

For the Ethiopian realm, selection theories predict relatively high numbers of species and strategies and high trophic diversity. These predictions are supported by the extended data set. Predictions for size and productivity are conflicting. The 2,761 Ethiopian species use 42 of 49 strategies, which is similar to the 44 (37 – 51) predicted strategies. Many species (46%) are medium-sized low-level predators with high productivity. All eight herbivorous strategies are used, including two with higher and two with twice as high species numbers than suggested by overall distribution. Medium sized top-predators with medium and high productivity have most of their species in this realm.

For the Oriental realm, selection theories predict relatively high numbers of species and strategies and high trophic diversity. These predictions are supported by the extended data set. Predictions for size and productivity are conflicting. The 1,779 Oriental species use 40 of 49 strategies, which is close to the 42 (35 – 49) strategies predicted by Equation 21. Most species are small, low-level predators with high productivity (16%) and medium-sized low-level predators with medium (12%) and high (33%) productivity. Another strategy with many species is that of medium-sized omnivores with high productivity (12%).

For the Australian realm, selection theories predict high numbers of species and strategies and high trophic diversity. Except for high numbers of species and strategies and percentage of herbivores these predictions are supported by the extended data set. Predictions for size and productivity are conflicting. The 529 Australian species use 34 of 49 strategies, which is the same as predicted by Equation 21. Many species are medium-sized low-level predators with high productivity (43%). Of 17 herbivorous and omnivorous strategies only 10 are used, and of these, 7 are used by fewer species than suggested by overall distribution, confirming the finding in Figure 39. Of 24 used predatory strategies 8 have higher and 13 have twice as high species numbers than predicted by overall distribution of species by realm.

In summary, the results obtained with the extended data set confirm the trends in Figure 38, Figure 39 and Table 38 and support the non-conflicting predictions of selection theories. The similarities in species richness between the mostly temperate Nearctic and Palearctic realms and between the mostly tropical Neotropical and Ethiopian realms, are striking, given support to Hubbell’s (2001) assertion that species richness in large, similar areas will be governed by general rules resulting in similar species richness and overall abundance of individuals. Zoogeographic realms are confirmed as useful units for global grouping of freshwater fishes.

Table 41. Cross-tabulation of life-history strategies and zoogeographic realm with 9,652 records of freshwater fishes, where *n* is the number of species and *Hab %* the percentage of species records associated with a certain strategy and realm. The *Records by realm (%)* row gives the overall percentage of species by habitat as derived in Table 35. If *Rlm %* is more than twice the value of *Species by realm (%)* then it is highlighted in bold (Table continued on next page).

Zoogeographic realm	**Nearctic**		**Palearctic**		**Neotropical**		**Ethiopian**		**Oriental**		**Australian**		**Total**
Species by realm (%)		7.9		10.5		32.8		23		21.1		4.7	100
Strategy	n	Realm %	n	Realm %	n	Realm %	n	Realm %	n	Realm %	n	Realm %	
Herb-Small-High	3	7.0			33	**76.7**	1	2.3	5	11.6	1	2.3	43
Herb-Medium-High	5	1.7	6	2.1	122	42.5	108	37.6	41	14.3	5	1.7	287
Herb-Medium-Medium	3	0.9	8	2.4	235	**70.4**	33	9.9	51	15.3	4	1.2	334
Herb-Medium-Low	1	1.3			77	**97.5**	1	1.3					79
Herb-Large-High					3	37.5	4	**50.0**	1	12.5			8
Herb-Large-Medium	4	6.5	5	8.1	16	25.8	30	**48.4**	6	9.7	1	1.6	62
Herb-Large-Low			4	9.8	3	7.3	16	39.0	17	41.5	1	2.4	41
Herb-Large-Very low			1	3.2	18	58.1	3	9.7	9	29.0			31
Omni-Small-High	8	3.8	17	8.1	81	38.6	14	6.7	88	41.9	2	1.0	210
Omni-Small-Medium									1	**100.0**			1
Omni-Medium-High	70	7.9	70	7.9	304	34.5	218	24.7	207	23.5	12	1.4	881
Omni-Medium-Medium	11	3.0	60	16.4	155	42.3	39	10.7	69	18.9	32	8.7	366
Omni-Medium-Low	1	10.0	5	**50.0**	3	30.0	1	10.0					10
Omni-Large-High					2	40.0			3	**60.0**			5
Omni-Large-Medium	2	5.1	3	7.7	14	35.9	8	20.5	9	23.1	3	7.7	39
Omni-Large-Low	8	14.3	17	**30.4**	1	1.8	9	16.1	17	30.4	4	7.1	56
Omni-Large-Very low	5	**33.3**	6	**40.0**			1	6.7	3	20.0			15
Low-Small-High	157	9.2	65	3.8	769	44.9	367	21.4	288	16.8	68	4.0	1,714
Low-Small-Medium	4	**20.0**			12	60.0	2	10.0			2	**10.0**	20
Low-Small-Low	3	**30.0**			4	40.0	2	20.0	1	10.0			10
Low-Medium-High	303	9.1	217	6.5	715	21.5	1275	38.3	594	17.8	226	6.8	3,330
Low-Medium-Medium	131	13.9	168	17.8	104	11.0	251	26.6	215	22.8	74	7.8	943
Low-Medium-Low	10	**20.8**	21	**43.8**	8	16.7	4	8.3	1	2.1	4	8.3	48
Low-Medium-Very low	1	11.1	2	**22.2**	3	33.3	1	11.1	2	22.2			9
Low-Large-High			1	11.1	2	22.2	1	11.1	5	**55.6**			9
Low-Large-Medium	29	14.6	35	17.7	18	9.1	79	39.9	21	10.6	16	8.1	198
Low-Large-Low	30	**18.5**	39	**24.1**	4	2.5	46	28.4	30	18.5	13	8.0	162
Low-Large-Very low	19	**20.0**	18	18.9	3	3.2	26	27.4	19	20.0	10	**10.5**	95

Zoogeographic realm	**Nearctic**		**Palearctic**		**Neotropical**		**Ethiopian**		**Oriental**		**Australian**		**Total**
Species by realm (%)		7.9		10.5		32.8		23		21.1		4.7	100
Strategy	n	Realm %	n	Realm %	n	Realm %	n	Realm %	n	Realm %	n	Realm %	
Low-Very large-Very low	2	**50.0**	1	**25.0**					1	25.0			4
Mid-Small-High					1	16.7	1	16.7	3	**50.0**	1	**16.7**	6
Mid-Medium-High	1	0.5	3	1.4	72	32.7	118	**53.6**	18	8.2	8	3.6	220
Mid-Medium-Medium	19	15.6	17	13.9	17	13.9	36	29.5	20	16.4	13	**10.7**	122
Mid-Medium-Low	2	**18.2**	7	**63.6**							2	**18.2**	11
Mid-Medium-Very low			1	**100.0**									1
Mid-Large-High					3	50.0	1	16.7	1	16.7	1	**16.7**	6
Mid-Large-Medium	7	11.7	6	10.0	14	23.3	15	25.0	13	21.7	5	8.3	60
Mid-Large-Low	8	**20.5**	9	**23.1**	3	7.7	9	23.1	4	10.3	6	**15.4**	39
Mid-Large-Very low			1	16.7			2	33.3	1	16.7	2	**33.3**	6
Mid-Very large-Low					2	40.0	1	20.0			2	**40.0**	5
Mid-Very large-Very low			2	**40.0**			1	20.0	1	20.0	1	**20.0**	5
Top-Medium-High					1	6.7	11	**73.3**	2	13.3	1	6.7	15
Top-Medium-Medium					5	38.5	8	**61.5**					13
Top-Medium-Low	7	**100.0**											7
Top-Large-High					6	**85.7**					1	**14.3**	7
Top-Large-Medium	10	**17.2**	10	17.2	22	37.9	10	17.2	4	6.9	2	3.4	58
Top-Large-Low	11	**31.4**	11	**31.4**	6	17.1	3	8.6	2	5.7	2	5.7	35
Top-Large-Very low			1	7.1	3	21.4	3	21.4	4	28.6	3	**21.4**	14
Top-Very large-Low			3	**50.0**	1	16.7	1	16.7	1	16.7			6
Top-Very large-Very low	1	**16.7**			2	33.3	1	16.7	1	16.7	1	**16.7**	6
Species (n)	876		840		2867		2761		1779		529		9,652
Strategies (n)	32		34		41		42		40		34		49
Predicted strategies (n)	38		38		44		44		42		34		
95% CL lower	31		31		37		37		35		27		
95% CL upper	45		44		51		51		49		41		

Oceans

The world's oceans cover about 71% of the Earth's surface and contain most of its water. For the purpose of this study I considered the Arctic and Antarctic Oceans, the Atlantic, Indian and Pacific Ocean, and also the Mediterranean. Note that as used here, the Atlantic includes the Baltic and the Mediterranean the Black Sea. The polar oceans have the lowest temperature and the Indian Ocean—which is mostly tropical—the highest. Environmental variability is highest in the polar oceans and arguably least in the mostly tropical Indian Ocean and subtropical Mediterranean. Because of ice ages and high seasonal variability the polar oceans will be less mature than the tropical oceans in the sense of succession theory. The Mediterranean is the youngest sea and therefore expected to be less mature than the tropical oceans.

Table 42 shows the number of species records by ocean, with 22,426 records for 15,865 species of marine and diadromous fishes, i.e., several thousand species occur in more than one ocean. The null hypothesis of even distribution of species across oceans is clearly refuted: in accordance with temperature theory, the polar oceans have an order of magnitude fewer species than those including tropical waters. Among the non-polar oceans, species numbers decline roughly with area from the Pacific Ocean to the Mediterranean Sea, with the exception of the Indian Ocean, which has more species than the larger Atlantic, probably because of its mostly tropical area and the larger extent of species-rich tropical coral reefs, which in the Atlantic are restricted mostly to the Caribbean. Also, the Indian Ocean is adjacent to the center of marine fish biodiversity in the Philippine-Malaysian-Indonesian triangle (Randall 1998, Carpenter and Springer 2005).

Table 42. Number of species records by ocean, with 22,426 records for 15,865 species. Introduced species and questionable occurrences were excluded.

Ocean	Abbr.	Records	Percent
Arctic Ocean	Arc	130	0.6
Antarctic	Ant	366	1.6
Atlantic Ocean	Atl	4,894	21.8
Mediterranean Sea	Med	607	2.7
Indian Ocean	Ind	5,966	26.6
Pacific Ocean	Pac	10,463	46.7

Table 43 shows the distribution of phylogenetic Classes of fishes across oceans for all 15,865 species occurring in oceans. Myxini, Cephalaspidomorphi, Elasmobranchii and Actinopterygii are present in all oceans. Holocephali are missing from the polar oceans, and coelacanths (Sarcopterygii) have only been found in the Indian and western Pacific Oceans. Actinopterygii dominate in all oceans with 86.1 – 95.6% of the species, followed by Elasmobranchii with 3.1 – 13.0% of the species.

Table 43. Species records by phylogenetic Class and ocean, with 22,426 records for 15,865 species.

Ocean / Class	Myxini	Cephala-spidomorphi	Holocephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
Arctic Ocean	1	2		4		123
Antarctic Ocean	1	1		14		350
Atlantic Ocean	28	4	15	399		4,448
Mediterranean Sea	1	3	1	79		523
Indian Ocean	3	2	12	356	1	5,592
Pacific Ocean	45	6	22	551	1	9,839

Figure 40 shows length distribution by ocean with 19,379 records for 13,124 species with available data. The null-hypothesis of similar length distribution in all world oceans is rejected by significant differences in median length, most notably in the Mediterranean Sea, which has the highest median length, the widest interquartile range, and the highest adjacent length. It is the youngest and smallest of the marine areas considered and maybe does not belong into this comparison of Oceans. The Mediterranean is a subtropical sea which already suggests a higher median length of species (see Figure 35). Also, 29% of Mediterranean species are migratory—probably including many visitors from the Atlantic—compared with 14% of migratory Atlantic species, and migratory species tend to be larger (see Figure 59). The Mediterranean has dried out in the past eliminating many species, and full re-colonization especially by warm water fishes has been hampered by cooler temperatures in the Strait of Gibraltar (Helfman et al. 1997).

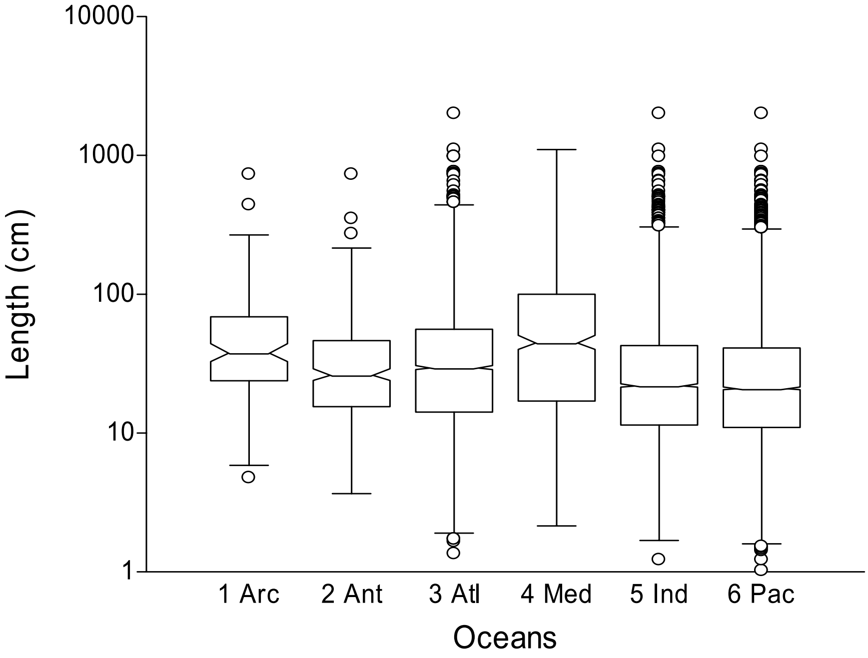


Figure 40. Length distribution by ocean with 19,379 records for 13,124 species of marine and diadromous fishes: 1 Arctic Ocean with n = 125, median = 38.0, 95% CL = 32.4-48.0; 2 Antarctic Ocean with n = 315, median = 26.4, 95% CL = 23.8-29.3; 3 Atlantic Ocean with n = 4,299, median = 29.7, 95% CL = 28.0-30.0; 4 Mediterranean Sea with n = 577, median = 45.0 95% CL = 40.0-50.0; 5 Indian Ocean with n = 5,388, median = 22.0, 95% CL = 21.0-23.0; and Pacific Ocean with n = 8,675, median = 21.0, 95% CL = 20.4-22.0; all length in cm maximum total length.

Temperature theory predicts that median length will be higher in the cold Arctic and Antarctic oceans. However, because of high environmental variability r-K theory predicts life history traits associated with smaller size. Arctic fishes have a significantly higher median length than the other oceans thus supporting the temperature hypothesis. Antarctic fishes have a similar median length to that found in the other large oceans suggesting that r-selection here counterbalanced the influence of temperature selection. Note also that fishes with less than 4 cm maximum length are conspicuously absent from the Arctic and Antarctic, and there is also an apparent limit for maximum size, confirming the findings in polar/boreal waters as discussed in the context of Figure 35.

Fishes of the Atlantic Ocean have a significantly higher median length than those of the Indian and Pacific oceans, probably because the Atlantic has fewer tropical fishes, which tend to be smaller. Length distribution in the Indian and Pacific Oceans is very similar as was expected because there is no clear border between these Oceans and many species have an Indo-Pacific range.

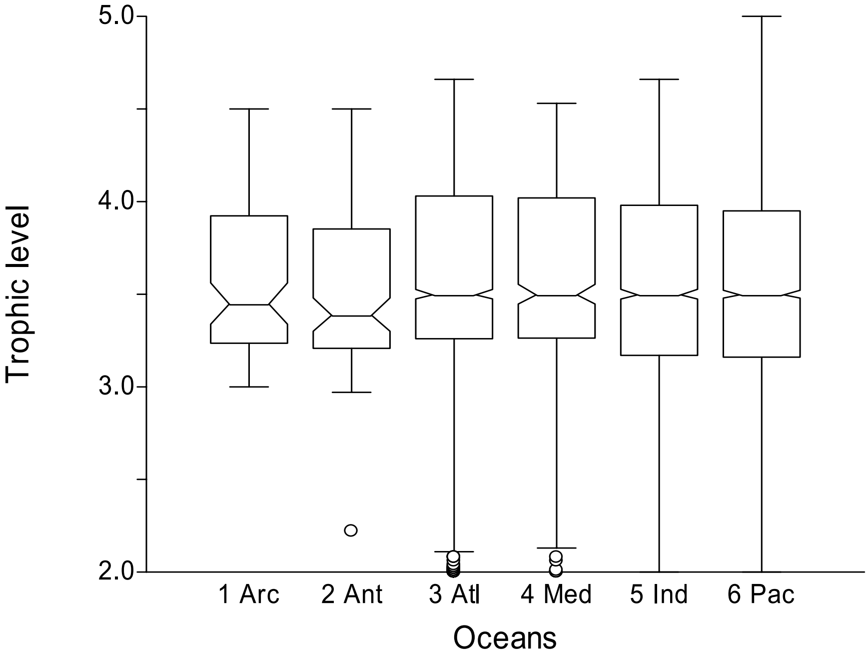


Figure 41. Trophic level by ocean with 8,758 records for 5,268 species: 1 Arctic Ocean with n = 94, median = 3.5, 95% CL = 3.3-3.5; 2 Antarctic Ocean with n = 126, median = 3.4, 95% CL = 3.3-3.5; 3 Atlantic with n = 2,198, median = 3.5, 95% CL = 3.5-3.54; 4 Mediterranean Sea with n = 496, median = 3.5, 95% CL = 3.5-3.6; 5 Indian Ocean with n = 2,334, median = 3.5, 95% CL = 3.49-3.5, and 6 Pacific Ocean with n = 3,510, median = 3.5, 95% CL = 3.46-3.5.

Figure 41 shows trophic levels by ocean, with 8,758 records for 5,268 species. Herbivory theory predicts fewer herbivores in the polar and more in the tropical oceans. Indeed, with the exception of the algae-eating *Notothenia coriiceps* Richardson, 1844, there are no herbivorous or omnivorous species in the polar oceans. Surprisingly, as a result the median trophic level in the polar oceans is not higher but lower than in the tropical oceans, though not significantly. This is also visible in the upper IQRs and adjacent values, i.e., there are also fewer top predators in the polar oceans. This result is supported by succession theory which predicted low trophic diversity in the less stable polar oceans. For the other oceans, median trophic levels and IQRs are very similar.

Table 44 shows the distribution of productivity by ocean with 3,893 records for 2,330 species with available data. Temperature theory predicts lower productivity in the polar oceans and higher productivity in the mostly tropical Indian Ocean. In contrast, r-K theory predicts higher productivity in the highly variable polar environments and less productivity in the more stable Indian Ocean. As a result of these opposing selection pressures, we expect intermediate productivity across the oceans.

The polar oceans have no species with high productivity in agreement with temperature theory and $r'_{max} = 0.18$ for both oceans, which is significantly lower than the other oceans, except for the Atlantic where the 95% confidence limits overlap with those of the Arctic. The differences in r'_{max} between the non-polar oceans are not significant.

Table 44. Productivity of marine and diadromous fishes by ocean, with 3,893 records for 2,330 species with available data, with indication of the approximate r'_{max}.

Ocean / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
Arctic Ocean	1	32	27	1	61	0.18	0.152 – 0.203
Antarctic Ocean		54	27	4	85	0.18	0.164 – 0.194
Atlantic Ocean	122	465	498	128	1,213	0.21	0.196 – 0.218
Mediterranean Sea	39	138	79	47	303	0.23	0.207 – 0.255
Indian Ocean	122	277	324	123	846	0.23	0.210 – 0.241
Pacific Ocean	168	451	594	172	1,385	0.21	0.201 – 0.223

Table 45 shows an analysis of food web complexity using the extended data set. Temperature theory predicts absence of herbivorous and omnivorous species in the cold polar oceans, which is confirmed and reflected in the low number of trophic levels and the corresponding low trophic diversity (see also Figure 41). Change of ice-cover in evolutionary time and high annual environmental variability suggest less stabilized ecosystems in the polar oceans in the sense of succession theory and thus also less complex food webs.

Table 45. Analysis of food web complexity using the extended data set; H' is trophic diversity and J' is evenness of the Shannon-Wiener diversity index applied to trophic levels; trophic diversity of the Arctic and Antarctic Oceans is significantly lower than in the other oceans (t-test alpha = 0.05, P = 0.000, Power = 1.000).

Oceans	Trophic levels	Species	H'	J'
Arctic Ocean	16	130	3.46	0.86
Antarctic	18	366	3.25	0.78
Atlantic Ocean	29	4,893	4.09	0.84
Mediterranean Sea	26	607	4.10	0.87
Indian Ocean	29	5,964	4.10	0.84
Pacific Ocean	31	10,458	4.01	0.81

Table 46 presents an overview of predictions by selection theories as they apply to oceans. Symbols in parentheses indicate strategies whose predictions are in conflict with those of other strategies in the respective column; negative symbols without parentheses thus indicate ‘unforced errors.’ Of 70 predictions 26 (37%) are not supported by the data: r-K and succession theories predict relatively small size and high productivity for the more variable and less mature polar oceans, whereas temperature theory predicts large size and low productivity and prevails; succession and temperature theory predict relatively small size for the Mediterranean and succession theory in addition predicts low trophic diversity, none of which is supported by the data, probably because many large predatory fishes from the

Atlantic regularly visit the Mediterranean and immigration of small warm-water species is hampered by colder waters in the Strait of Gibraltar (Helfman et al. 1997). Interestingly, this gap of small warm-water fishes is now filled by Lessepsian migrants (Por 1978), which were excluded from this analysis.

Table 46. Summary of predictions by selection theories as applicable to oceans, where ‘+’ indicates values are on the predicted side if values are ranked and ‘+++’ indicates that the difference to the other values is significant at the 95% level; ‘–‘ indicates that the values do not support the prediction, with same amplification; parentheses indicate conflict with other strategies. Data used were the overall number of species by ocean, the box plots for observed size and trophic level, mean r_{max} of observed productivity, and Shannon-Wiener trophic diversity based on the extended data set.

Theory	Environment	Ocean	Species / Strategies	Size	Productivity	Trophic diversity
r-K	variable	Arctic		(-)	(-)	
		Antarctic		(-)	(---)	
	stable	Atlantic		(-)	(-)	
		Mediterranean		(+)	(-)	
		Indian Ocean		(-)	(-)	
		Pacific		(-)	(-)	
Succession	less mature	Arctic	+	(-)	(-)	+++
		Antarctic	+	(-)	(---)	+++
		Mediterranean	(+)	(-)	(+)	(---)
	mature	Atlantic	+	(-)	(-)	+++
		Indian Ocean	+	(-)	(-)	+++
		Pacific	+	(-)	(-)	+++
Temperature	low temp.	Arctic	+	(+)	(+)	
		Antarctic	+	(+)	(+++)	
	high temp.	Atlantic	+	(+)	(+)	
		Mediterranean	(-)	(-)	(+)	
		Indian Ocean	+	(+)	(+)	
		Pacific	+	(+)	(+)	
Herbivory	low temp.	Arctic				+
		Antarctic				+
	high temp.	Atlantic				+
		Mediterranean				(+)
		Indian Ocean				+
		Pacific				+
Area	small	Arctic	+			
		Mediterranean	(+)			
	large	Atlantic	+			
		Pacific	+			
Closeness to center of biodiversity	far	Arctic	+			
		Antarctic	+			
		Atlantic	+			
		Mediterranean	(+)			
	near	Indian Ocean	+			
		Pacific	+			

Table 47 shows as cross-tabulation of 49 life-history strategies and number of species that use a strategy in a respective ocean, with 16,928 records based on the extended data set. Small omnivores with medium productivity (one species) are not suggested to occur in marine environments (see also Table 28). There is no evidence for the occurrence of high productivity species in the polar oceans (see Table 44) and the respective records in Table 47 are likely to stem from a bias in the modelling approach with respect to cold-water species (see discussion of Table 34); thus these records are marked with a question mark and are excluded from the discussion below.

For the Arctic Ocean selection theories predict relatively low numbers of species and strategies, large size, low productivity, and low trophic diversity. These predictions are confirmed by the extended data set. The 122 species in the Arctic Ocean use 19 of 49 strategies, which is similar to the 21 (14 – 27) strategies predicted by Equation 21. Most species are medium-sized low-level predators with medium productivity (34%) or large low-level predators with low productivity (14%). There are no herbivorous or omnivorous strategies confirming the finding in Figure 41. There are only two small species, but 52 large and 2 very large species, confirming the high median length in Figure 40.

For the Antarctic Ocean selection theories also predict relatively low numbers of species and strategies, large size, low productivity, and low trophic diversity. These predictions are confirmed by the extended data set. The 250 Antarctic fishes use 21 of 49 strategies, which is at the lower confidence limit of the 28 (21 – 35) predicted strategies and indicates that the fewer strategies available to them (no herbivory) resulted in more species using the available strategies. Most species are medium-sized low-level predators with medium (44%) or high (18%) productivity. As pointed out in Figure 41, there are no herbivores and only one omnivorous species. Only one of six strategies with very large size is used. The similarity between strategies used in the Antarctic and Arctic oceans is striking: of 19 strategies used in the Arctic, 16 are also used in the Antarctic Ocean. Interestingly, these are widely used strategies not restricted to the polar oceans. Rather, about 2/3 of all strategies are apparently not suitable for this type of environment, notably those with low trophic level, small or very large size, or high productivity.

For the Mediterranean, selection theories predict relatively low numbers of species and strategies, which is supported by the extended data set. The other predictions are less clear and more difficult to assess, because the high number of large predatory visitors from the Atlantic masks effects of selection on resident species. The 549 Mediterranean species use 36 of 49 strategies, which is similar to the 35 (28 – 41) strategies predicted by Equation 21. Many species are medium-sized low-level predators with medium (15%) or high (20%) productivity or large low-level predators with low (7%) or medium (11%) productivity. Of 21 strategies with large or very large size 14 are represented by more species than suggested by overall distribution of species by oceans, thus confirming the larger median length in Figure 40.

Atlantic, Indian and Pacific Ocean fishes use 46-48 of 49 strategies, all similar to the numbers of strategies suggested by Equation 21. Many species are medium-sized low-level predators with medium or high productivity. No major differences in the use of strategies are apparent between these oceans.

In summary, the extended data set confirms the findings of Figure 40, Figure 41 and Table 44. Polar oceans and Atlantic, Indian and Pacific oceans, respectively, are similar with regard to preferred life-history strategies.

Table 47. Cross-tabulation of life-history strategies and Oceans with 16,928 records of marine and diadromous fishes, where *n* is the number of species records and *Oc %* the percentage of species records associated with a certain strategy and ocean. The *Records by ocean (%)* row gives the overall percentage of species by ocean as derived in Table 42. If *Oc %* is more than twice the value of *Species by ocean (%)* then it is highlighted in bold; otherwise the three highest percentages are in bold font (Table continued on next page).

Oceans	**Arctic**		**Antarctic**		**Atlantic**		**Mediterranean**		**Indian Ocean**		**Pacific**		**Total**
Records by ocean (%)		0.58		1.63		21.8		2.71		26.6		46.7	100
Strategy	n	Oc %	n	Oc %	n	Oc %	n	Oc %	n	Oc %	n	Oc %	
Herb-Small-High					1	1.4			16	22.5	54	**76.1**	71
Herb-Medium-High					41	13.5	4	1.3	110	36.2	149	49.0	304
Herb-Medium-Medium					26	21.3	2	1.6	41	33.6	53	43.4	122
Herb-Medium-Low									2	**50.0**	2	50.0	4
Herb-Large-High					3	**42.9**			3	**42.9**	1	14.3	7
Herb-Large-Medium					14	17.5	3	3.8	29	36.3	34	42.5	80
Herb-Large-Low					10	31.3	2	**6.3**	8	25.0	12	37.5	32
Herb-Large-Very low					1	**100.0**							1
Omni-Small-High					17	12.1	2	1.4	49	35.0	72	51.4	140
Omni-Medium-High					49	10.6	5	1.1	181	39.0	229	49.4	464
Omni-Medium-Medium					39	19.2	3	1.5	73	36.0	88	43.3	203
Omni-Medium-Low					1	33.3					2	**66.7**	3
Omni-Large-High									1	33.3	2	**66.7**	3
Omni-Large-Medium					18	29.5	1	1.6	19	31.1	23	37.7	61
Omni-Large-Low			1	1.8	10	17.5	1	1.8	22	38.6	23	40.4	57
Omni-Large-Very low					1	20.0			2	40.0	2	40.0	5
Low-Small-High	1	0.1	5	0.4	227	17.1	39	2.9	396	29.9	658	49.6	1326
Low-Small-Medium	1	1.9	2	**3.8**	12	22.6	2	3.8	5	9.4	31	58.5	53
Low-Small-Low					3	33.3					6	**66.7**	9
Low-Medium-High	10	0.2	45	0.9	893	17.5	107	2.1	1575	30.9	2473	48.5	5,103
Low-Medium-Medium	41	1.4	109	**3.8**	689	24.1	84	2.9	675	23.6	1259	44.1	2,857
Low-Medium-Low	8	**2.1**	5	1.3	118	30.6	3	0.8	64	16.6	188	48.7	386
Low-Medium-Very low	3	**4.8**			15	23.8	2	3.2	8	12.7	35	55.6	63
Low-Large-High			1	1.2	28	32.6	2	2.3	21	24.4	34	39.5	86
Low-Large-Medium	12	**1.5**	14	1.7	232	28.8	59	**7.3**	186	23.1	303	37.6	806
Low-Large-Low	17	**2.3**	22	3.0	225	30.6	40	**5.4**	153	20.8	279	37.9	736

Oceans	Arctic		Antarctic		Atlantic		Mediterranean		Indian Ocean		Pacific		Total
Records by ocean (%)		0.58		1.63		21.8		2.71		26.6		46.7	100
Strategy	n	Oc %	n	Oc %	n	Oc %	n	Oc %	n	Oc %	n	Oc %	
Low-Large-Very low	1	0.5	3	1.4	42	19.8	12	**5.7**	54	25.5	100	47.2	212
Low-Very large-Very low					9	36.0	3	**12.0**	6	24.0	7	28.0	25
Mid-Small-High									3	37.5	5	62.5	8
Mid-Medium-High					113	20.4	7	1.3	162	29.2	272	49.1	554
Mid-Medium-Medium	1	0.2	10	1.8	140	25.2	16	2.9	149	26.8	240	43.2	556
Mid-Medium-Low	2	**2.4**			16	19.0	1	1.2	24	28.6	41	48.8	84
Mid-Medium-Very low					3	18.8			7	**43.8**	6	37.5	16
Mid-Large-High			1	1.3	16	20.8	3	3.9	25	32.5	32	41.6	77
Mid-Large-Medium	5	1.0	7	1.4	139	26.9	24	4.7	133	25.8	208	40.3	516
Mid-Large-Low	4	0.9	7	1.6	132	30.0	21	4.8	108	24.5	168	38.2	440
Mid-Large-Very low	1	0.5	3	1.4	47	22.7	17	**8.2**	54	26.1	85	41.1	207
Mid-Very large-Low					7	33.3	3	**14.3**	5	23.8	6	28.6	21
Mid-Very large-Very low					4	18.2	2	**9.1**	7	31.8	9	40.9	22
Top-Medium-High					28	29.5			24	25.3	43	45.3	95
Top-Medium-Medium	1	0.7	2	1.4	52	37.7	3	2.2	26	18.8	54	39.1	138
Top-Medium-Low					8	26.7			10	33.3	12	40.0	30
Top-Large-High			1	1.6	18	29.5	8	**13.1**	11	18.0	23	37.7	61
Top-Large-Medium	5	**1.8**	2	0.7	85	29.9	18	**6.3**	72	25.4	102	35.9	284
Top-Large-Low	7	**2.3**	6	1.9	101	32.8	22	**7.1**	72	23.4	100	32.5	308
Top-Large-Very low			2	1.1	54	30.3	14	**7.9**	49	27.5	59	33.1	178
Top-Very large-Medium					4	**40.0**			3	30.0	3	30.0	10
Top-Very large-Low	1	**2.2**			14	31.1	6	**13.3**	12	26.7	12	26.7	45
Top-Very large-Very low	1	**1.7**	2	**3.4**	17	28.8	8	**13.6**	14	23.7	17	28.8	59
Species (n)	122		250		3,722		549		4,669		7,616		16,928
Strategies (n)	19		21		46		36		46		48		49
Predicted strategies (n)	21		28		45		35		46		47		
95% lower CL	14		21		38		28		39		40		
95% upper CL	27		35		52		41		53		54		

Habitats

Life history traits are shaped by the specific niche in which a species has evolved. In this chapter, I explore the influence of environmental characteristics related to depth, degree of association with the bottom, and association with reefs. The classification of habitats follows that used in FishBase 11/2004, with definitions given in Froese et al. (2000). The demersal, benthopelagic and pelagic categories correspond to the benthic, epibenthic and pelagic water column categories, respectively, of Winemiller and Rose (1992).

In the sense of r-K and succession theories, the deep-sea habitats are more stable and mature than the euphotic habitats; among the euphotic habitats, the pelagic zone is more stable and mature than the others; the benthopelagic habitat is the most fluctuating and least mature because while it is not depth-restricted within the euphotic zone, species in shallow waters such as freshwater are typically classified as benthopelagic. In terms of temperature theory the deep sea habitats are coldest and the reef-associated habitat is warmest, because in the latter group most data stem from reef-associated fishes in the tropics. The demersal, benthopelagic and pelagic habitats have similar intermediate temperatures. In terms of herbivory theory, the demersal and benthopelagic habitat have the lowest pH because they include most freshwater habitats. With regard to nutrient concentrations, the deep-sea and the pelagic habitats are oligotrophic. Pelagic, bathypelagic and bathydemersal habitats have the largest area; the reef-associated habitat has the smallest area. In terms of heterogeneity, reef-associated, demersal and benthopelagic habitats rank highest and pelagic and bathypelagic rank lowest. Because of freshwater habitats and continental shelves separated by deep oceans, the demersal and benthopelagic habitats provide highest isolation, followed by the reef-associated habitat; pelagic and bathypelagic habitats provide least isolation. The reef-associated habitat is mostly tropical and thus has a larger proportion of its area close to the center of marine fish biodiversity around the equator and especially to the Indo-Malay-Philippines Archipelago (Carpenter and Springer 2005).

Table 48 shows the distribution of 28,786 species by preferred habitat. The majority of species (89%) are associated with the sea, lake or river bottom. Succession and area theories predict high species numbers in the large and relativly mature deep-sea and pelagic habitats, whereas temperature (for deep-sea habitats), heterogeneity and isolation theories predict relatively low species numbers, and prevail. Among the remaining habitats, the demersal and benthopelagic groups have the highest area and species numbers; the reef-associated group has the smallest area and species number, however, the species number is higher than suggested by the relativly small area because of high habitat heterogeneity and closeness to the center of marine fish biodiversity (Smith and Tyler 1972, Bellwood and Hughes 2001).

Table 48. Distribution of 28,786 species by preferred habitat.

Habitat	Abbr.	Species	Percent
bathydemersal	1 batdem	2,113	7.3
bathypelagic	2 batpel	1,279	4.4
reef-associated	3 reef	4,244	14.7
demersal	4 dem	10,475	36.5
benthopelagic	5 bentpl	8,799	30.6
pelagic	6 pelagic	1,876	6.5

Table 49 shows the distribution of all 28,785 species of fishes by preferred habitat and phylogenetic Class. Actinopterygii are present and dominate in all habitats with 82.8 – 99.3 % of the species. Interestingly, Elasmobranchii contribute four times more species in the bathydemersal habitat than suggested by their overall contribution to species of fishes (13.6% versus 3.4%); yet they have failed to evolve species capable of roaming the vast abyssal plains in 4,000 m depths, as yet-to-be-discovered physiological or life-history constraints limit their presence to depths above 3,500 m (Monty Priede, University of Aberdeen, pers. comm. 2001, supported by depth range data in FishBase). Myxini and Holocephali are restricted to demersal and bathydemersal habitats. Cephalaspidomorphi and Sarcopterygii are demersal. Elasmobranchii and Actinopterygii are the only Classes present in bathypelagic, reef-associated, benthopelagic and pelagic habitats.

Table 49. Distribution of species by preferred habitat and by phylogenetic Class, for 28,785 species.

Habitat / Class	Myxini	Cephala-spidomorphi	Holocephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
bathydemersal	47		29	287		1,750
bathypelagic				29		1,250
reef-associated				106		4,137
demersal	22	42	8	445	11	9,953
benthopelagic				64		8,732
pelagic				34		1,840

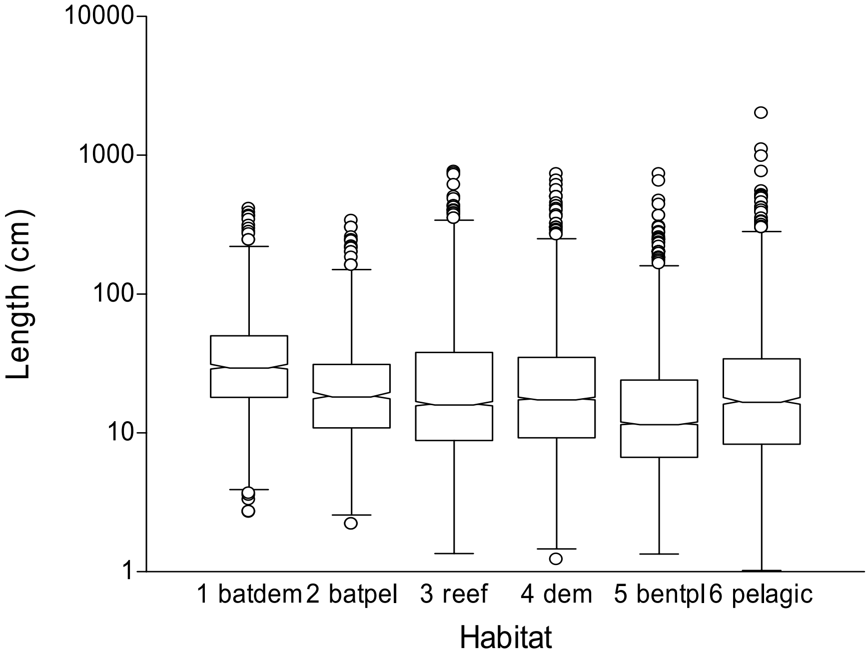


Figure 42. Length distribution of 23,685 fishes by habitat: 1 bathydemersal with n = 1600, median = 30, 95% CL = 29.3-30.9; 2 bathypelagic with n = 1010, median = 18.5, 95% CL = 17.6-19.9; 3 reef-associated with n = 3981, median = 16.2, 95% CL = 15.3-17.5; 4 demersal with n= 8341, median = 17.7, 95% CL = 17.0-18.0; 5 benthopelagic with n = 7099, median = 11.7, 95% CL = 11.2-12.0; and 6 pelagic with n = 1654, median = 17.0, 95% CL = 15.9-18.2; all lengths are maximum total lengths in cm.

Figure 42 shows the length distribution by preferred habitat for 23,685 species. r-K and succession theories predict larger size in deep-sea and pelagic habitats and smaller size in the benthopelagic habitat. Bathydemersal fishes have indeed significantly larger and benthopelagic species significantly lower median lengths than the other groups; bathypelagic species have significantly higher median length than reef-associated fishes and higher median lengths than demersal fishes, i.e., all in support of r-K and succession theories. However, median length of pelagic fishes is not significantly different from reef-associated and demersal species, suggesting that other selection forces are at work or that the pelagic environment is not as stable as has been assumed.

Temperature theory predicts larger size in the deep sea habitats and smaller size in reef-associated fishes. Deep sea fishes have indeed larger size, and median length of reef-fishes is smaller than that of demersal and pelagic fishes, though not significantly. Thus, temperature theory is not refuted by the data.

Trophy theory predicts small size in oligotrophic deep-sea and pelagic habitats. This is not supported by the data.

Note the restricted size ranges of both deep-water groups; especially the lower adjacent lengths are clearly above those of all other groups. Thus, being very small seems to be a disadvantage in cold waters, as has been shown and discussed in the context of Figure 35. The smallest and largest fish are found in pelagic habitats.

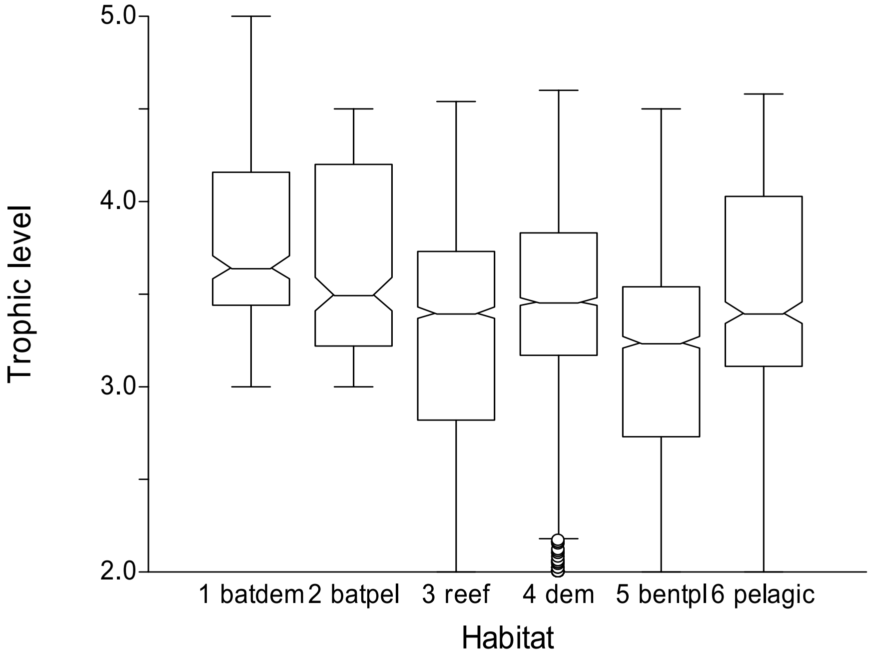


Figure 43. Trophic level of 7,500 species by preferred habitat: 1 bathydemersal with n = 324, median = 3.7, 95% CL = 3.6-3.8; 2 bathypelagic with n = 291, median = 3.5, 95% CL = 3.4-3.7; 3 reef-associated with n = 2,149, median = 3.4, 95% CL = 3.4-3.4; 4 demersal with n = 2,509, median = 3.5, 95% CL = 3.4-3.5; 5 benthopelagic with n = 1,623, median = 3.2, 95% CL = 3.2-3.3; and 6 pelagic with n = 604, median = 3.4, 95% CL = 3.4-3.5.

Figure 43 shows the distribution of trophic level by preferred habitat for 7,500 species with available data. Bathydemersal species have a significantly higher median trophic level than non-deep-sea species; there are no herbivores or omnivores in the deep-sea habitats as already shown in Figure 36 and predicted by herbivory theory, although the primary reason is lack of light and not low temperature. In the euphotic zone, benthopelagic species have a significantly lower median trophic level and the lowest interquartile ranges. As explained above, many shallow-water freshwater species have been assigned to this category, and as shown in Figure 33, freshwater fishes have the lowest median trophic level. Median trophic levels of reef-associated, demersal and pelagic fishes are not significantly different, although the upper interquartile range of pelagic fishes suggests a large number of mid- and top-level predators.

Table 50 shows the number of species by preferred habitat and by productivity group for 2,932 species with available data. Succession and r-K theories predict lower productivity in the relatively stable and mature deep-sea habitats and higher productivity in the variable benthopelagic habitat, which includes most freshwater fishes. Temperature theory predicts low productivity in the deep-sea and high productivity in the reef-associated habitat. Trophy theory predicts lower productivity in the oligotrophic deep-sea and pelagic habitats.

Productivity of bathydemersal fishes with $r'_{max} = 0.11$ is significantly lower than that of all other habitats, and $r'_{max} = 0.31$ of benthopelagic fishes is is significantly higher than that of demersal fishes, confirming the predictions of r-K, succession, temperature and trophy theories. Productivity of bathypelagic, demersal and reef-associated fishes is not significantly different. Unexpectedly, the pelagic habitat has mostly species with medium and high productivity and the highest $r'_{max} = 0.36$ in contrast to the predictions made by r-K, succession and trophy theories. Except for live-bearing sharks, pelagic species rarely exercise parental care as a means of reducing offspring mortality, which then is a function of external factors (predation on eggs and larvae and larval-food availability) which affect the offspring but not the parents. Under such conditions ‘bet-hedging’ theory (Stearns 1976) predicts an inversion of r-K traits, i.e., in a stable environment a selection for early maturity, larger reproductive effort, and shorter life, such as are associated with medium and high productivity. Or expressed differently, if an environment that appears stable with regard to its impact on adult mortality provides highly unpredictable conditions for the survival of offspring, then overall, such an environment may not be perceived as stable but as variable in the sense of r-K theory. Similarly, if pelagic fishes have learned to detect and follow concentrations of food items such as produced by upwelling events or fronts, then they may not perceive their environment as oligotrophic in the sense of trophy theory.

Table 50. Number of species by habitat and productivity group for 2,932 species with available data, with indication of the approximate r'_{max}.

Habitat / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
bathydemersal		60	334	50	444	0.11	0.104 – 0.114
bathypelagic	9	45	31	9	94	0.22	0.179 – 0.256
reef-associated	64	171	151	45	431	0.24	0.219 – 0.261
demersal	125	404	476	139	1,144	0.21	0.196 – 0.220
benthopelagic	123	249	131	29	532	0.31	0.286 – 0.328
pelagic	89	137	44	17	287	0.36	0.328 – 0.390

Table 51 shows an analysis of the food web complexity using the extended data set. Absence of light excludes primary productivity and thus trophic levels below 3.0 in the bathydemersal and bathypelagic habitats, resulting in fewer trophic levels and less trophic diversity (see also Figure 43). Deep-sea habitats are comparatively stabilized ecosystems for which succession theory predicts complex food webs; this is confirmed by the fact that 19 of 21 possible upper trophic levels are used in both of these habitats. Note low evenness in bathydemersal species, suggesting preference for few trophic levels.

Table 51. Analysis of food web complexity using the extended data set; H' is trophic diversity and J' is evenness of the Shannon-Wiener diversity index applied to trophic levels. Bathydemersal and bathypelagic habitats have significantly less trophic diversity than the other systems (t-test alpha 0.05, P = 0.006, Power = 0.968).

Habitat	Trophic levels	Species	H'	J'
bathydemersal	19	2,113	3.42	0.80
bathypelagic	19	1,279	3.79	0.89
reef-associated	28	4,242	4.13	0.86
demersal	30	10,475	4.18	0.85
benthopelagic	26	8,727	4.04	0.86
pelagic	27	1,871	4.15	0.87

Table 52 presents an overview of predictions by selection theories as they apply to aquatic habitats. Symbols in parentheses indicate strategies whose predictions are in conflict with those of other strategies in the respective column; negative symbols without parentheses thus indicate ‘unforced errors.’ Of 57 predictions 17 (30%) are not supported by the data: predictions for number of species and strategies by succession and area theories are in conflict with those of temperature, heterogeneity and isolation theories and the latter three prevail; predictions by r-K and succession theories for relatively larger size and by trophy theory for relatively smaller size in the presumably more stable, mature, and oligotrophic pelagic habitat all are not supported by the data as pelagic median length is not significantly different from median lengths in demersal and reef habitats; also predictions by trophy theory for relatively small size in the deep-sea are not supported by the data. Predictions by r-K, succession and trophy theory for relatively low productivity in pelagic fishes and by succession theory for relatively high trophic diversity in the deep-sea are also not supported by the data.

Table 52. Summary of predictions by selection theories as applicable to aquatic habitats, where '+' indicates values are on the predicted side if values are ranked and '+++' indicates that the difference to the other values is significant at the 95% level; '–' indicates that the values do not support the prediction, with same amplification; parentheses indicate conflict with other strategies. Data used were the overall number of species by ocean, the box plots for observed size and trophic level, mean r_{max} of observed productivity, and Shannon-Wiener trophic diversity based on the extended data set.

Theory	Environment	Habitat	Species / Strategies	Size	Productivity	Trophic diversity
r-K	variable	benthopelagic		+++	+	
	stable	bathydemersal		(+++)	+++	
		bathypelagic		(+++)	+	
		pelagic		(-)	---	
Succession	less mature	benthopelagic	(-)	+++	+	+
	mature	bathydemersal	(-)	(+++)	+++	(---)
		bathypelagic	(-)	(+++)	+	(---)
		pelagic	(-)	(-)	---	+
Temperature	low temp.	bathydemersal	(+)	(+++)	+++	
		bathypelagic	(+)	(+)	+	
	high temp.	reef-associated	(+)	+	+	
Herbivory	low temp.	bathydemersal				(+)
		bathypelagic				(+)
	high temp.	reef-associated				+
Trophy	oligotrophic	bathydemersal		(---)	+++	
		bathypelagic		(-)	+	
		pelagic		(+)	---	
Area	small	reef-associated	(-)			
	large	bathydemersal	(-)			
		bathypelagic	(-)			
		pelagic	(-)			
Heterogeneity	high	reef-associated	(+)			
		demersal	+			
		benthopelagic	(+)			
	low	bathypelagic	(+)			
		pelagic	(+)			
Isolation	high	demersal	+			
		benthopelagic	(+)			
		reef-associated	+			
	low	bathypelagic	(+)			
		pelagic	(+)			
Closeness to center	near	reef-associated	(+)			

Table 53 shows a cross-tabulation of life-history strategies and habitats for 20,480 species based on the extended data set. A null-hypothesis would suggest that the distribution of species by habitat and strategy is the same as the overall distribution of species by habitats shown in Table 48. Cases where a strategy is used by more than twice the percentage suggested by the overall distribution are highlighted in bold; otherwise the three highest percentages are in bold font. In the bathydemersal habitat there are three strategies with high productivity, which is not supported by the data shown in Table 50; as discussed above, this high productivity may result from a bias in relation to cold water species in the approach used to create the extended data set; these strategies are marked with a question mark and excluded from the discussion below

For the bathydemersal habitat, selection theories predict relatively low productivity, which is supported by the extended data set. Predictions for number of species and strategies, size and trophic diversity are conflicting. The 1,409 bathydemersal species use 23 (3 high productivity strategies excluded) of 50 strategies, which is significantly lower than the 41 (34 – 48) strategies predicted by Equation 21 and which is one of the outliers in Figure 82. No plants are available as food to deep-sea species and the remaining strategies are used by relatively more species than predicted by Equation 21. Many species (>27%) are medium-sized low-level predators of medium productivity; of eight 'predator-low-productivity' strategies, six have more than twice as many species as suggested by overall distribution of species across habitats; similarly, seven of eight 'predator-very low-productivity' strategies have higher species numbers, confirming the trend towards low productivity ($r'_{max} = 0.11$) seen in Table 50.

For the bathypelagic habitat, selection theories predict relatively low productivity, which is supported by the extended data set. Predictions for number of species and strategies, size and trophic diversity are conflicting. The 846 bathypelagic species use 25 of 50 strategies, which is significantly less than the 38 (31 – 45) strategies predicted by Equation 21 and which is one of the outliers in Figure 82. Similar to bathydemersal species, no plants are available as food and the remaining strategies are used by relatively more species than predicted by Equation 21. Also, while data in Table 50 confirm the occurrence of high productivity in this group, for reasons discussed above, the species numbers in these strategies are too high when compared with Table 50 and are thus marked with a question mark. No herbivorous or omnivorous strategies are used. Many species (> 26%) are medium-sized low-level predators with medium productivity.

For the reef-associated habitat, selection strategies predict relatively small size, high productivity, and high trophic diversity. The predictions are supported by the extended data set. Predictions for number of species and strategies are conflicting. The 3,463 reef-associated species use 45 of 50 strategies, which is the same as predicted. Most species are small low-level predators with high productivity (12%) or medium-sized low-level predators with medium (10%) or high (33%) productivity. Of 17 herbivorous and omnivorous strategies, 15 are used and 10 of these have higher species numbers than suggested by overall distribution. Small herbivores with high productivity have 48 (45%) of their species in this habitat. Also, 38% of very large top predators with low (6 species) and 42% with very low (8 species) productivity are reef-associated.

For the demersal habitat, selection theories predict relatively high numbers of species and strategies. This prediction is supported by the extended data set. The 7,196 demersal species use 48 of 50 strategies, which is similar to the 47 (40 – 54) strategies predicted by Equation 21. Most species are small low-level predators with high productivity (11%) or medium-sized low-level predators with medium (15%) to high (32%) productivity. Medium-sized herbivores with low productivity (71 species), large herbivores with very low productivity (18 species) and medium-sized low-level predators with very low productivity (39 species) have 58-89% of their species in this habitat.

For the benthopelagic habitat, selection theories predict small size, high productivity and low trophic diversity. These predictions are supported by the extended data set. Predictions for number of species and strategies are conflicting. The 6,079 benthopelagic species use 47 of 50 strategies, which is the same as predicted. Most species are small low-level predators with high productivity (20%) or medium-sized low-level predators with high (35%) productivity. All 17 herbivorous and omnivorous strategies are used, 12 of which with higher species numbers than predicted by overall distribution. In contrast, of 33 predatory strategies 31 are used and 28 of these have lower species numbers than suggested by overall distribution, thus confirming the lower trophic levels and trophic diversity of this habitat as discussed in the context of Figure 43 and Table 51.

For the pelagic habitat, selection theories predict relatively low productivity and high trophic diversity. Of these, the predictions for low productivity are not supported by the extended data set. Predictions for number of species and strategies and size are conflicting. The 1,487 pelagic species use 41 of 50 strategies, which is the same as predicted. Most species are small low-level predators with high productivity (16%) or medium-sized low-level predators with high productivity (42%). Very large top predators with medium productivity have all their (4) species in this habitat. Of 10 top-predator strategies, 8 have higher species numbers than suggested by overall distribution of species by habitat; conversely, of 16 herbivorous and omnivorous strategies only 12 are used and 8 have lower than suggested species numbers, thus confirming the under representation of herbivores in this habitat as shown in Figure 43.

In summary, Winemiller and Rose's (1992) point that fishes with divergent life-history strategies coexist in the same habitats, but may perceive the environment very differently from another is confirmed. r-K theory correctly predicts the life-history traits associated with the relatively stable bathydemersal habitat and the relatively variable reef habitat; 'bet-hedging' theory correctly predicts the life history traits associated with the relatively stable pelagic habitat if the assumption of relatively higher variability of offspring mortality in this habitat is accepted. Deep sea fishes have fewer strategies available to them and as a result the remaining strategies are used by more species then suggested by the overall relationship between species and strategies.

Table 53. Cross-tabulation of life-history strategies and habitats for 20,480 species of fishes, where *n* is the number of species and *Hab %* the percentage of species associated with a certain strategy and habitat. The *Species by habitat (%)* row gives the overall percentage of species by habitat as derived in Table 48. If *Hab %* is more than twice the value of *Species by habitat (%)* then it is highlighted in bold; otherwise the three highest percentages are in bold font (Table continued on next page).

Habitats	**bathydemersal**		**bathypelagic**		**reef-associated**		**demersal**		**benthopelagic**		**pelagic**		**Total**
Species by habitat (%)		7.3		4.4		14.7		36.5		30.6		6.5	100
Strategy	n	Hab %	n	Hab %	n	Hab %	n	Hab %	n	Hab %	n	Hab %	
Herb-Small-High					48	**45.3**	34	32.1	24	22.6		0.0	106
Herb-Medium-High					150	**30.4**	137	27.7	199	40.3	8	1.6	494
Herb-Medium-Medium					58	14.0	199	48.2	147	35.6	9	2.2	413
Herb-Medium-Low					2	2.5	71	**88.8**	7	8.8			80
Herb-Large-High					4	**33.3**	4	33.3	1	8.3	3	**25.0**	12
Herb-Large-Medium					36	**35.6**	18	17.8	34	33.7	13	12.9	101
Herb-Large-Low					15	25.9	6	10.3	35	60.3	2	3.4	58
Herb-Large-Very low							18	**58.1**	13	41.9			31
Omni-Small-High					46	13.9	154	46.7	122	37.0	8	2.4	330
Omni-Small-Medium									1	**100.0**			1
Omni-Medium-High					248	20.5	310	25.6	580	47.9	73	6.0	1,211
Omni-Medium-Medium					78	15.8	198	40.2	201	40.8	16	3.2	493
Omni-Medium-Low					1	9.1	6	54.5	4	36.4			11
Omni-Large-High					1	14.3	3	42.9	2	28.6	1	**14.3**	7
Omni-Large-Medium					17	26.2	19	29.2	16	24.6	13	**20.0**	65
Omni-Large-Low					16	21.1	17	22.4	39	51.3	4	5.3	76
Omni-Large-Very low					1	6.3	6	37.5	8	50.0	1	6.3	16
Low-Small-High	34 ?	1.3 ?	66 ?	2.4 ?	419	15.5	771	28.5	1186	43.8	234	8.6	2,710
Low-Small-Medium	3	5.2	6	**10.3**	3	5.2	32	55.2	12	20.7	2	3.4	58
Low-Small-Low			1	5.9	3	17.6	9	52.9	4	23.5			17
Low-Medium-High	358 ?	5.3 ?	228 ?	3.4 ?	1143	16.8	2309	34.0	2128	31.4	619	9.1	6,785
Low-Medium-Medium	377	13.7	221	8.0	358	13.0	1091	39.6	621	22.5	88	3.2	2,756
Low-Medium-Low	99	**28.9**	21	6.1	47	13.7	141	41.1	28	8.2	7	2.0	343
Low-Medium-Very low	5	9.1	5	**9.1**	4	7.3	39	**70.9**	1	1.8	1	1.8	55
Low-Large-High	14 ?	**23.3 ?**			8	13.3	19	31.7	13	21.7	6	10.0	60
Low-Large-Medium	51	7.9	24	3.7	97	15.0	302	46.8	117	18.1	54	8.4	645
Low-Large-Low	143	**23.4**	25	4.1	72	11.8	241	39.4	117	19.1	14	2.3	612
Low-Large-Very low	25	11.7	7	3.3	27	12.6	123	57.5	31	14.5	1	0.5	214

Habitats	**bathydemersal**		**bathypelagic**		**reef-associated**		**demersal**		**benthopelagic**		**pelagic**		**Total**
Species by habitat (%)		7.3		4.4		14.7		36.5		30.6		6.5	100
Strategy	n	Hab %	n	Hab %	n	Hab %	n	Hab %	n	Hab %	n	Hab %	
Low-Very large-Very low							5	50.0	1	10.0	4	**40.0**	10
Mid-Small-High					3	27.3	6	54.5	2	18.2			11
Mid-Medium-High	17	3.0	65 ?	**11.5 ?**	97	17.2	142	25.1	154	27.3	90	**15.9**	565
Mid-Medium-Medium	38	8.8	61	**14.1**	85	19.7	183	42.4	34	7.9	31	7.2	432
Mid-Medium-Low	37	**46.3**	1	1.3	5	6.3	28	35.0	4	5.0	5	6.3	80
Mid-Medium-Very low	4	**40.0**	2	**20.0**			4	40.0					10
Mid-Large-High	6	11.8	6 ?	**11.8 ?**	6	11.8	12	23.5	9	17.6	12	**23.5**	51
Mid-Large-Medium	19	5.2	15	4.1	105	28.5	147	39.9	48	13.0	34	9.2	368
Mid-Large-Low	65	**21.0**	15	4.8	61	19.7	122	39.4	34	11.0	13	4.2	310
Mid-Large-Very low	26	**21.5**	3	2.5	33	27.3	51	42.1	6	5.0	2	1.7	121
Mid-Very large-Low	1	14.3			2	28.6	2	28.6	1	14.3	1	14.3	7
Mid-Very large-Very low	2	**22.2**			3	**33.3**	4	44.4					9
Top-Medium-High			23 ?	**30.3 ?**	16	21.1	12	15.8	12	15.8	13	17.1	76
Top-Medium-Medium	5	5.1	30	**30.6**	9	9.2	31	31.6	8	8.2	15	15.3	98
Top-Medium-Low	6	**22.2**	1	3.7	4	14.8	13	48.1	2	7.4	1	3.7	27
Top-Large-High			3 ?	7.9 ?	10	26.3	2	5.3	5	13.2	18	**47.4**	38
Top-Large-Medium	7	3.7	3	1.6	51	27.1	56	29.8	31	16.5	40	**21.3**	188
Top-Large-Low	44	**23.3**	8	4.2	36	19.0	63	33.3	28	14.8	10	5.3	189
Top-Large-Very low	21	**23.1**	6	6.6	21	23.1	30	33.0	6	6.6	7	7.7	91
Top-Very large-Medium											4	**100.0**	4
Top-Very large-Low					6	**37.5**	4	25.0	2	12.5	4	**25.0**	16
Top-Very large-Very low	2	10.5			8	**42.1**	2	10.5	1	5.3	6	**31.6**	19
Species (n)	1409		846		3463		7196		6079		1487		20,480
Strategies (n)	26		25		45		48		47		41		50
Predicted strategies (n)	41		38		45		47		47		41		
95% CL lower	34		31		38		40		40		34		
95% CL upper	48		45		52		54		53		48		

Life-history Strategies and Functional Morphology

Functional morphology is often referred to as ‘biomechanics’ when muscle-bone levers or strengths are assessed, or as ‘hydromechanics’ when the interactions of the structures of a fish with flowing water are analysed. Here I use it in a more general sense for pointing out the relationship between, e.g., body shape and locomotion, and between brain size and sensory capabilities.

Body shape

Most of the characteristics we recognize as fish-like are adaptations to allow the most efficient use of the aquatic medium by mobile vertebrate predators (Webb 1975, Moyle and Cech 2004). Other shapes may have evolved to permit usage of space-limited micro-habitats (Matthews 1998). An interesting question is whether some of the life-history strategies identified in this study are related with certain body shapes.

Nelson (1994) provided drawings of body forms for most Families of fishes, and Lagler et al. (1977) defined basic fish morphologies and standardized the respective terminology. FishBase 11/2004 contained direct assignments of fishes to classifications of lateral body shape into eel-like, elongated, fusiform and short and/or deep. Table 54 shows number of species by body shapes for 7,657 species of fishes with available data. Eel-like fishes are eels, morays, lampreys, hagfishes and other very elongated fishes; this extreme shape is used by relativly few species. Elongated fishes include sharks and sturgeons, but also loaches and blennies; this is the body shape adopted by the highest number of species. Fusiform is the typical spindle-like fish form with maximum depth at approximately one-third of total length, such as found in tunas, mackerels, snappers, perches or groupers. Short and/or deep is the body form of, e.g., box fishes, puffers, molas, flatfishes and butterfly fishes. The null hypothesis of similar distribution of body shapes is rejected by the clear differences in the numbers in Table 54. An alternative hypothesis would suggest that, because of the physics related to movement in water (see e.g. Videler 1993) and the fact that sustained swimming speed increases (Froese et al. 2000) and minimum energy expenditure decreases (Weihs 1973) with body length, most fish will be more or less elongated, which indeed applies to 77% of the species with available data (see Table 54).

Table 54. Body shape for 7,657 species of fishes with available data.

Body shape	Abbr.	Species	Percent
eel-like	eel	874	11.4
elongated	elong	3,216	42.0
fusiform	fusi	1,799	23.5
short & deep	short	1,768	23.1

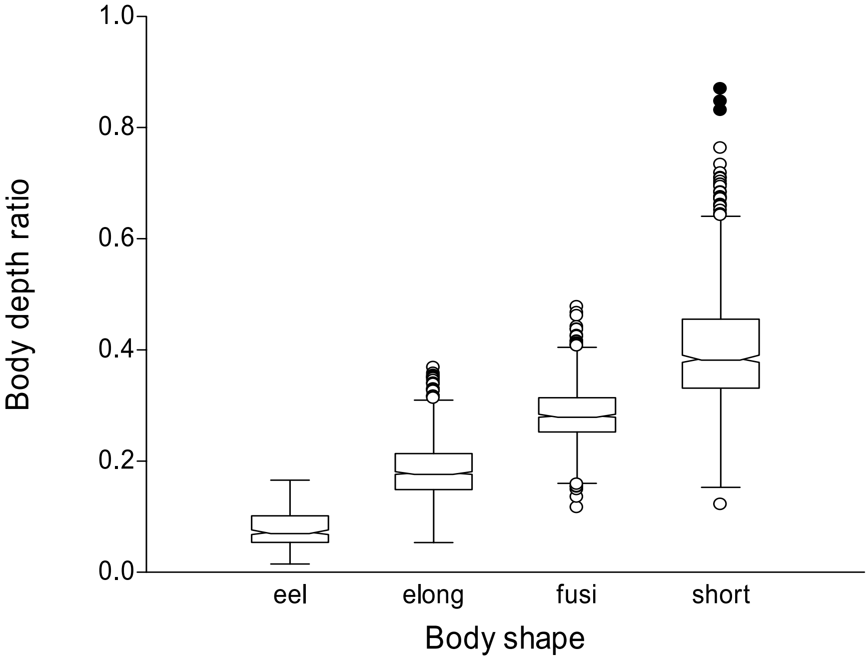


Figure 44. Ratio of body depth to total length by body shape for 4,296 species of fishes with available data: eel-like fishes with n = 321, median = 0.072, 95% CL = 0.067-0.076, IQR = 0.054-0.10; elongated fishes with n = 1,701, median = 0.178, 95% CL = 0.176-0.182, IQR = 0.149-0.213; fusiform fishes with n = 1,360, median = 0.281, 95% CL = 0.279-0.284, IQR = 0.252-0.313; and short and/or deep fishes with n = 887, median = 0.384, 95% CL = 0.376-0.392.

FishBase 11/2004 contained morphometric measurements of various proportions of the fish body. Figure 44 shows the ratio of maximum body depth to total length by body shape for 4,269 species of fishes with available data. Median ratios are significantly different and interquartile ranges do not overlap, i.e., the manual assignment of body shapes by FishBase staff (mostly from looking at drawings or photos) was reasonably accurate. For the purpose of this study, I classified fishes with a ratio of less than 0.12 as eel-like, with less than 0.24 as elongate, with less than 0.35 as fusiform, and those above 0.35 as short and/or deep. Applying this to the available measurements increased the total number of species with body shapes to 10,189 species.

FishBase also contained length-weight relationships for many species. Kulbicki et al. (2005) point out the relationship between body shape and the parameters of the length-weight relationship. In order to further increase the number of species with shape information I explored the relationship between body shape and the parameter *a* of the Length-Weight relationship $W = a * L^b$ where W is weight in grams, L is length in cm, and a and b are parameters (Ricker 1975). The parameter a can be used as a condition factor if $b = 3.0$ (Fulton 1911); in that case, a can be interpreted as the fraction of the volume L^3 occupied by the volume of the fish.

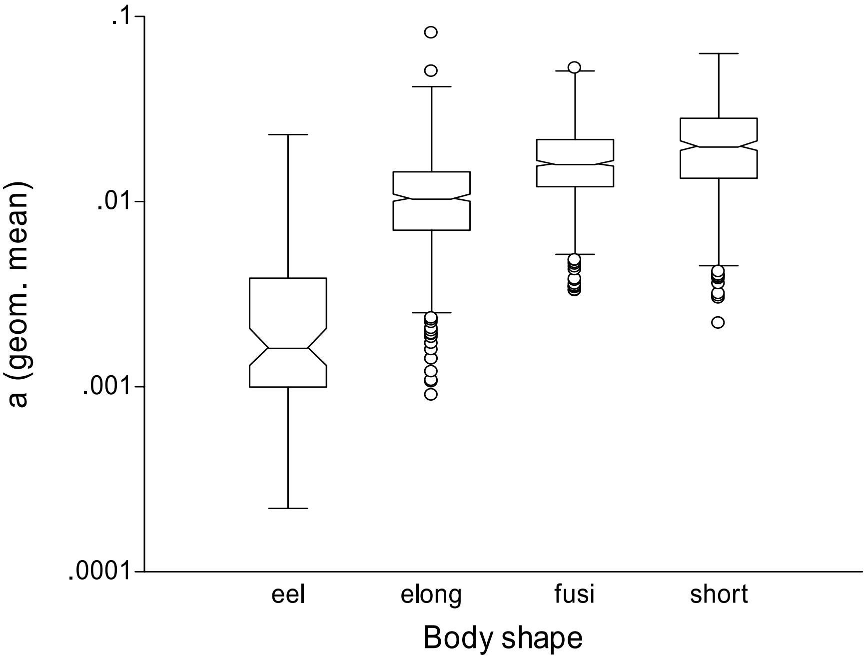


Figure 45. Geometric mean of the length-weight parameter *a* by body shape for 1,805 species of fishes with available data: eel-like fishes with n = 85, median = 0.0016; 95% CL = 0.0013-0.0019; IQR = 0.0010-0.0039; elongated fishes with n = 637, median = 0.0105; 95% CL = 0.0099-0.0110; IQR = 0.0070-0.0158; fusiform fishes with n = 699, median = 0.0160, 95% CL = 0.0153-0.0167; IQR = 0.0120-0.0216; and short and / or deep fishes with n = 384, median = 0.020, 95% CL = 0.019-0.022; IQR = 0.013-0.028; note that only studies were included where *b* was > 2.8 and < 3.2.

Figure 45 shows the distribution of a by body shape for 1,805 species with available data, and where $2.8 < b < 3.2$. For the purpose of this study, I classified fishes with geometric mean $a < 0.005$ as eel-like, with $0.005 <= a < 0.014$ as elongated, with $0.014 <= a < 0.019$ as fusiform, and with $a >= 0.019$ as short and / or deep. This procedure increased the number of species with available body shape information to 10,669, see Table 55.

Table 55. Updated number of species by body shape, for 10,669 species.

Body shape	Abbr.	Species	Percent
eel-like	eel	1,079	10.1
elongated	elong	4,728	44.3
fusiform	fusi	2,688	25.2
short & deep	short	2,174	20.4

Phylogenetic ‘baggage’ may constrain morphological diversification within a taxon (Matthews 1998). Table 56 shows number of species by body shape and phylogenetic Class for 10,669 species of fishes with available data. Actinopterygii are present and dominate with 91.8-100% in all shape categories similar to their overall contribution of 96.1% to numbers of fishes (see Table 2), i.e., although body shape information is available for only 37% of all fish species, there is no evidence for a ‘phylogenetic bias’ in available data on body shape.

Actinopterygii are the only Class with fusiform and short and/or deep shapes. Myxini and Cephalaspidomorphi are constrained to eel-like bodies and Holocephali, Elasmobranchii (most rays are classified under ‘other’ body shape not included here) and Sarcopterygii have elongated bodies. The data in Table 56 indicated that eel-like and elongated forms are primitive body shapes whereas fusiform and short and/or deep body shapes are modern inventions of teleosts. This is consistent with the thoracic or jugular position of the pelvic fins typically associated with short and/or deep body forms and which are considered 'derived' features (Moyle and Cech 2004).

Table 56. Body shape and phylogenetic Class for 10,666 species with available data.

Body shape / Class	Myxini	Cephalaspido-morphi	Holocephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
eel-like	38	17				1,024
elongated			18	360	10	4,338
fusiform						2,687
short & deep						2,174

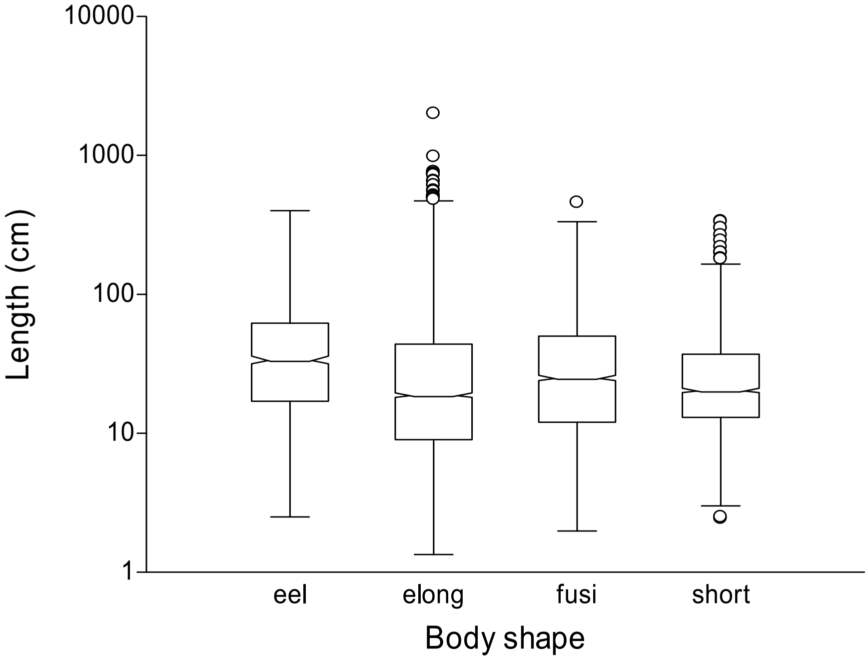


Figure 46. Distribution of maximum lengths by body shape for 10,333 species of fishes with available data: eel-like fishes with n = 1,031, median = 33.7, 95% CL = 30.5-36.6; elongated fishes with n = 4,555, median = 18.8, 95% CL = 18.0-20.0; fusiform fishes with n = 2,645, median = 25.0, 95% CL = 24.4-26.0; and short and/or deep fishes with n = 2,102, median = 20.3, 95% CL = 20.0-22.0; all lengths are total lengths in cm.

Figure 46 shows the distribution of length by body shape for 10,333 species of fishes with available data. The null-hypothesis of similar length distribution is refuted: median length decreases significantly from eel-like over fusiform to elongate and to short and/or deep. IQR and adjacent value ranges are widest in elongated fishes and narrowest in short and/or deep fishes. The largest as well as the smallest fishes are elongated.

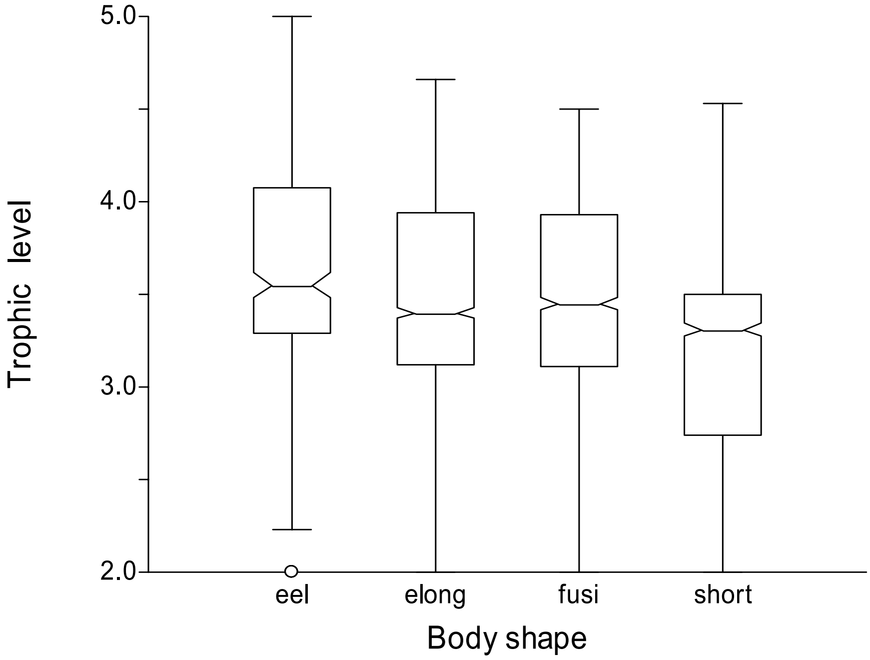


Figure 47. Distribution of trophic levels by body shape for 5,054 species with available data: eel-like fishes with n = 333, median = 3.55, 95% CL = 3.50-3.73; elongated fishes with n = 2,046, median = 3.4, 95% CL = 3.40-3.44; fusiform fishes with n = 1,496, median = 3.45, 95% CL = 3.40-3.49; and short and/or deep fishes with n = 1,179, median = 3.31, 95% CL = 3.28-3.34.

Figure 47 shows the distribution of trophic level by body shape for 5,054 species with available data. The null-hypothesis of similar distribution of trophic levels across body shapes is refuted. Eel-like fishes have the significantly highest median trophic level with few omnivorous and very few detritivore species and short and/or deep fishes have the significantly lowest median trophic level. Elongated and fusiform fishes have similar trophic levels with overlapping confidence limits. Overall, there is thus a slight increase in median trophic level with elongation in body shape. Herbivorous and omnivorous species have a clear preference for the short and/or deep body shape, as indicated by the lower IQR range in that group.

Table 57 shows number of species by body shape and productivity for 1,989 fishes with available data. All productivity groups are present with all body shapes, but the null-hypothesis of similar distribution of productivity across body-shapes is not supported: eel-like and elongated fishes have highest species numbers in the low productivity group with r'_{max} values of 0.20 – 0.21, whereas fusiform and short and/or deep fishes have highest numbers in the medium productivity group with r'_{max} values of 0.30 – 0.33. Note that this result is not biased by phylogeny: While fusiform and short and/or deep body forms are only used by Actinopterygii, and thus these r'_{max} values are similar to the overall value for Actinopterygii of 0.3 (see Table 10), the other two body shapes are also dominated by Actinopterygii with 91.8 - 94.9% of the data, i.e., the low r'_{max} values of 0.20 – 0.21 in these groups stem from the fact that Actinopterygii in these groups also have lower productivity.

Productivity is a proxy for metabolism which is inversely correlated with body weight (see Figure 3). Eel-like fishes have less body weight than suggested by their length, i.e., in this group, productivity will be biased towards higher productivity which is associated with smaller body size. In contrast short and/or deep fishes have more body weight than suggested by their length and here results will be biased towards lower productivity. Despite these biases, eel-like fishes have the lowest and short and/or deep fishes have the highest r'_{max} values. This is consistent with eel-like fishes having the largest and short & deep fishes having the smallest median body length in Figure 46, i.e., the observed difference in productivity for these two groups is largely a result of their difference in size. This is, however, not the case for elongated and fusiform fishes, where the latter have significantly larger median length. Here the data for productivity suggest that fusiform fishes have higher metabolic rates than elongated fishes of the same body weight.

Table 57. Fishes by body shape and productivity, for 1,989 species with available data. Approximate r'_{max} by body shape is as follows: eel-like = 0.20; elongate = 0.21, fusiform = 0.30 and short and/or deep = 0.33.

Shape	High	Medium	Low	Very low	n	r'_{max}	95% CL
eel-like	11	48	69	5	133	0.20	0.167 – 0.229
elongated	124	298	381	178	981	0.21	0.194 – 0.222
fusiform	116	321	124	17	578	0.30	0.282 – 0.319
short & deep	71	163	58	5	297	0.33	0.298 – 0.353

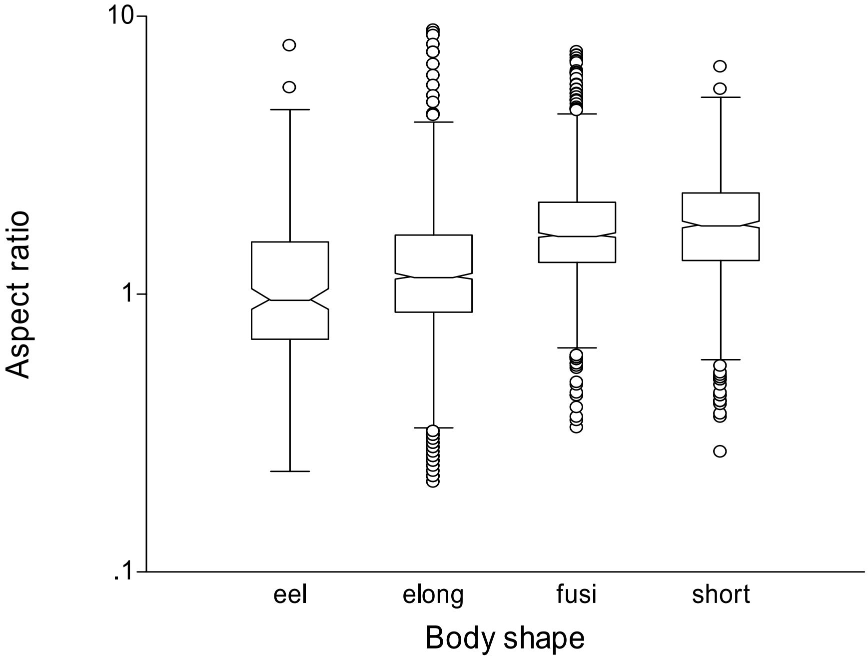


Figure 48. Aspect ratio of caudal fin by body shape for 4,813 species with available data: eel-like fishes with n = 218, median = 0.96, 95% CL = 0.87 – 1.09; elongated with n = 1,842, median = 1.16, 95% CL = 1.13 – 1.19; fusiform with n = 1,737, median = 1.63, 95% CL = 1.59 – 1.66; and short and/or deep fishes with n = 1,016, median = 1.78, 95% CL = 1.72 – 1.82.

Pauly (1989) showed that the aspect ratio of the caudal fin of fishes, i.e., the ratio of the square of the height of the caudal fin divided by the actual surface of the fin is closely correlated with the average level of activity. Figure 48 shows the distribution of aspect ratios by body shape. There is a significant increase in median aspect ratios from eel-like over elongate and fusiform to short and/or deep body shapes. Low aspect ratios are found in bottom-dwelling eel-like fishes such as eels and morays, and also in less active elongated fishes such as bottom-dwelling gobies or pikes, barracudas, and other lurking predators. High aspect ratios are often found in constantly active fusiform fishes such as jacks, tunas, and fusiliers. Short and/or deep body forms are common in damsel fishes, butterfly fishes, surgeon fishes and angelfishes, which have aspect ratios around 2, resulting in the highest median aspect ratio in this group despite a lack of very high aspect ratios, as can be seen by only two points beyond the adjacent range in short and/or deep body shapes in Figure 48. The average level of activity is correlated with metabolism (Pauly 1989), which is correlated with productivity. Thus, the results in Figure 48 confirm the increase in productivity shown in Table 57. I am not aware of other studies relating body shape to size, trophic level and productivity, i.e., I could not compare these results with those of other authors.

Table 58 shows a cross-tabulation of life history strategies and lateral body shape for 9,149 species based on the extended data set. The 750 eel-like fishes use 31 of 50 strategies, which is close to the lower confidence level of the 37 (30 – 44) strategies predicted by Equation 21 and may suggest that not all 50 strategies are truly available to the members of this group; this is indeed the case for lower trophic levels and very small size, not available to Myxini and Cephalaspidomorphi, which are restricted to this group. Many eel-like fishes are medium-sized low-level predators with medium (12%) to high (34%) productivity. Large omnivore, low- and mid-level predators with high productivity have more than 50% of their species with this body shape, thus confirming the findings in Figure 46 and Figure 47. This rare combination of large size and high productivity may now be explained by body shape as follows: Productivity is inversely related with body weight (see also Figure 6), and eel-like fishes have the least weight per length (see Figure 45 and discussion of Table 57) thus making it easier for species in this group to use high productivity. Finally, of 17 herbivorous and omnivorous strategies, 16 have fewer species than suggested by overall percentage of eel-like fishes, confirming the under-representation of these trophic groups in Figure 47.

The 4,005 elongated fishes use 48 of 50 strategies, which is similar to the 45 (38 – 52) strategies predicted by Equation 21. Most species are small low-level predators with high productivity (11%) or medium-sized low-level predators with medium (15%) to high (28%) productivity. Nine strategies are apparently preferred by elongated fishes and have 80% or more of their species with this body shape; interestingly, four of these strategies have small and four have very large size, reminding us that elongated body shapes are used by sharks as well as blennies and gobies.

The 2,506 fusiform fishes use 42 of 50 strategies, which is similar to the 43 (37 – 50) strategies predicted by Equation 21. Many are medium-sized low-level predators with medium (13%) or high (31%) productivity, confirming the observed trends in Figure 46, Figure 47 and Table 57. Half of the large mid-level predators with medium productivity are fusiform.

The 1,888 fishes with short and/or deep body shapes use 39 of 50 strategies, which is similar to the 42 (35 – 49) strategies predicted by Equation 21. Most species are medium-sized omnivores with high productivity (10%) and medium-sized low-level predators with medium (15%) or high (37%) productivity, confirming the observed trends in Figure 46, Figure 47 and Table 57. Of 13 used herbivorous or omnivorous strategies, 10 have higher species numbers than suggested by overall percentage of this shape, confirming the trend towards lower trophic levels seen in Figure 47.

In summary, size, trophic level and productivity are related with body shapes and there is evidence that some life-history strategies are mostly associated with specific body shapes, as indicated by the bold numbers in Table 58. However, these are mostly strategies used by few species; there is no evidence for preference of body shapes in the most widely used strategies, such as low-level predators with medium size and medium to high productivity.

Table 58. Cross-tabulation of life-history strategies with lateral body shapes for 9,149 species based on the extended data set, where *n* is the number of species and *Shp %* the percentage of species associated with a certain strategy and body shape. The *Percent of body shapes* row gives the overall percentage of species by body shape as derived in Table 55. If *Shp %* is more than twice the value of *Percent of body shapes* then it is highlighted in bold; otherwise the three highest percentages are in bold. The last column gives the number of species associated with a strategy. The last three rows show predictions of number of strategies with confidence limits based on Equation 21. Table continues on next page.

Shapes	eel-like		elongated		fusiform		short / deep		Total
Species by shape (%)		10.1		44.3		25.2		20.4	100
Strategy	n	Shp %	n	Shp %	n	Shp %	n	Shp %	
Herb-Small-High			31	**88.6**	4	11.4			35
Herb-Medium-High	4	1.7	102	43.2	54	22.9	76	32.2	236
Herb-Medium-Medium	1	0.8	44	33.3	35	26.5	52	39.4	132
Herb-Medium-Low			3	42.9	2	28.6	2	28.6	7
Herb-Large-High			1	10.0	4	40.0	5	**50.0**	10
Herb-Large-Medium	2	2.7	16	21.6	26	35.1	30	**40.5**	74
Herb-Large-Low			13	37.1	14	40.0	8	22.9	35
Herb-Large-Very low			1	20.0	4	**80.0**			5
Omni-Small-High			79	79.0	17	17.0	4	4.0	100
Omni-Small-Medium					1	**100.0**			1
Omni-Medium-High	12	2.4	154	31.2	145	29.4	182	36.9	493
Omni-Medium-Medium	2	1.1	65	37.1	35	20.0	73	**41.7**	175
Omni-Medium-Low			3	**100.0**					3
Omni-Large-High	2	**66.7**					1	33.3	3
Omni-Large-Medium	4	7.5	11	20.8	19	35.8	19	35.8	53
Omni-Large-Low	1	2.0	29	58.0	12	24.0	8	16.0	50
Omni-Large-Very low			4	44.4	4	44.4	1	11.1	9
Low-Small-High	29	4.1	429	60.8	176	24.9	72	10.2	706
Low-Small-Medium			8	61.5	3	23.1	2	15.4	13
Low-Small-Low			6	85.7	1	14.3			7
Low-Medium-High	256	8.9	1135	39.5	784	27.3	700	24.3	2,875
Low-Medium-Medium	89	6.9	594	46.3	320	24.9	280	21.8	1,283
Low-Medium-Low	11	7.6	81	55.9	31	21.4	22	15.2	145
Low-Medium-Very low	1	3.3	19	63.3	6	20.0	4	13.3	30
Low-Large-High	18	**54.5**	8	24.2	2	6.1	5	15.2	33

Shapes	eel-like		elongated		fusiform		short / deep		Total
Species by shape (%)		10.1		44.3		25.2		20.4	100
Strategy	n	Shp %	n	Shp %	n	Shp %	n	Shp %	
Low-Large-Medium	66	14.6	154	34.1	140	31.0	92	20.4	452
Low-Large-Low	29	9.1	170	53.1	83	25.9	38	11.9	320
Low-Large-Very low	14	10.6	76	57.6	30	22.7	12	9.1	132
Low-Very large-Very low			8	**100.0**					8
Mid-Small-High			4	80.0			1	20.0	5
Mid-Medium-High	25	10.0	90	36.1	76	30.5	58	23.3	249
Mid-Medium-Medium	24	9.8	92	37.7	87	35.7	41	16.8	244
Mid-Medium-Low	15	30.0	25	50.0	7	14.0	3	6.0	50
Mid-Medium-Very low			5	71.4	1	14.3	1	14.3	7
Mid-Large-High	21	**52.5**	12	30.0	3	7.5	4	10.0	40
Mid-Large-Medium	44	16.2	69	25.4	135	**49.6**	24	8.8	272
Mid-Large-Low	18	8.5	111	52.1	71	33.3	13	6.1	213
Mid-Large-Very low	5	5.1	64	65.3	28	28.6	1	1.0	98
Mid-Very large-Low			4	80.0			1	20.0	5
Mid-Very large-Very low			7	**100.0**					7
Top-Medium-High			16	64.0	3	12.0	6	24.0	25
Top-Medium-Medium	3	7.7	17	43.6	12	30.8	7	17.9	39
Top-Medium-Low	6	**37.5**	4	25.0	5	31.3	1	6.3	16
Top-Large-High	9	**28.1**	14	43.8	9	28.1			32
Top-Large-Medium	15	9.3	59	36.4	68	42.0	20	12.3	162
Top-Large-Low	18	12.0	84	56.0	34	22.7	14	9.3	150
Top-Large-Very low	5	6.8	50	68.5	13	17.8	5	6.8	73
Top-Very large-Medium	1	**25.0**	3	75.0					4
Top-Very large-Low			14	**87.5**	2	12.5			16
Top-Very large-Very low			17	**100.0**					17
Species (n)	750		4,005		2,506		1,888		9,149
Strategies (n)	31		48		42		39		50
Predicted strategies (n)	37		45		43		42		
95% CL lower	30		38		37		35		
95% CL upper	44		52		50		49		

Brain Size

The brains of fishes have evolved to suite their various life history modes and environments (Albert et al. 1997). An interesting question is whether some of the life-history strategies identified in this study are associated with relativly larger or smaller brain sizes.

FishBase 11/2004 contained encephalization coefficients (brain weight in milligrams divided by body weight in grams) for 1,051 species, mostly based on a data set assembled by Bauchot and Bauchot (1978) and archived in FishBase (Pauly et al. 2000).

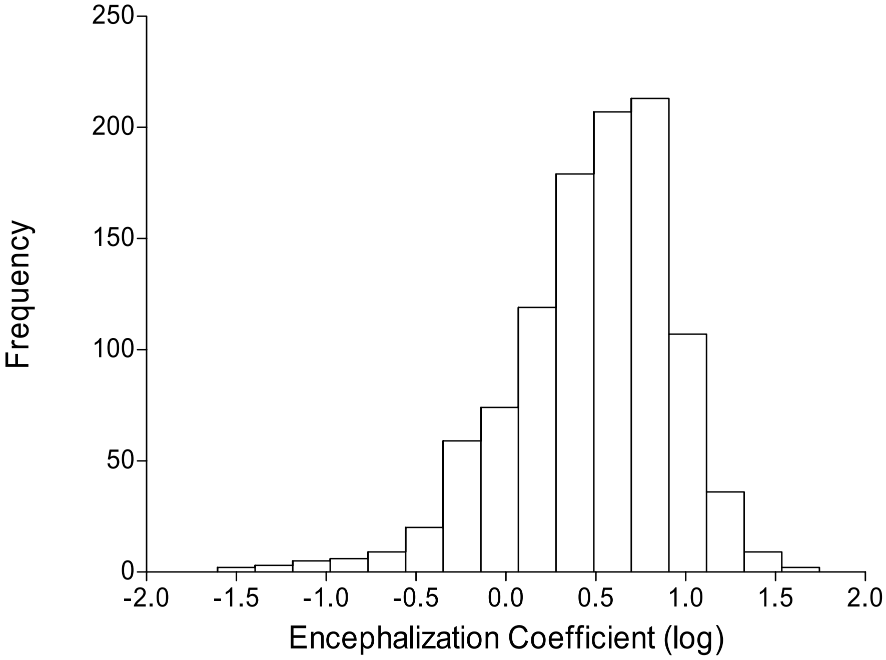


Figure 49. Relative brain size for 1,051 species with available data: median = 3.46 (log 0.539); 95% CL = 3.17-3.69 (log 0.502-0.567); IQR = 1.67-6.19 (log 0.223-0.792); adjacent range = 0.235-44.1 (log -0.629-1.64); with brain weight in mg and body weight in g.

Figure 49 shows relative brain size for 1,051 species with available data. The encephalization coefficient is roughly log-normal distributed but clearly skewed to the left side.

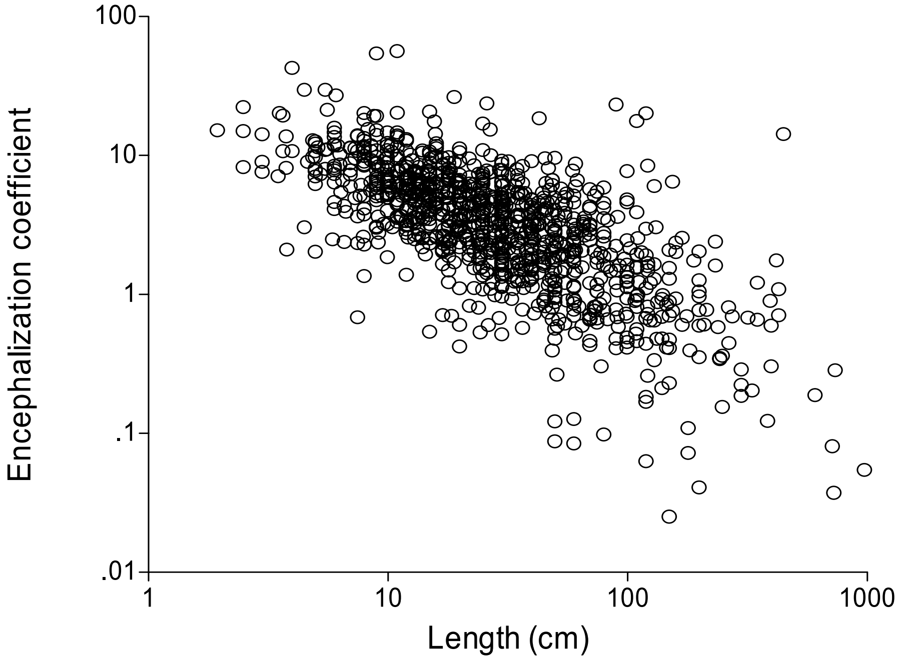


Figure 50. Relative brain size versus length for 1,037 species with available data. The decrease of relative brain size with increase in length is significant and the model log Enz = 1.534 – 0.730 = log Length (n = 1,037, r2 = 0.4821, CV = 0.6898) explains 48% of the variance.

Figure 50 shows the correlation between relative brain size and body length for 1,037 species with available data. Despite high variance, relative brain size clearly decreases with increase in length. A previous analysis of this data set (Albert et al. 1997, Pauly et al. 2000) showed that dots above the cloud belong mostly to electro-sensing Elasmobranchii and Actinopterygii, whereas many of the dots below the cloud belong to Cephalaspidomorphi, Sarcopterygii, and bathypelagic Actinopterygii.

The strong correlation between relative brain size and length makes correlation with trophic level and productivity difficult to interpret, as these traits are also correlated with length. I therefore adopted a correction for body weight used by Albert et al. (1997):

$$\text{Standardized Encephalization Index (SEC)} = \text{brain weight} / (\text{body weight})^{2/3}$$

Equation 14. Standardization of relative brain weight for effect of body weight, with brain weight in mg and body weight in g.

Figure 51 shows the frequency distribution of the standardized Encephalization Coefficient (SEC), which is similar to that of the Encephalization Coefficient, i.e., roughly log-normal distributed but skewed to the left. Figure 52 shows a plot of SEC over length; as intended there is no remaining relationship.

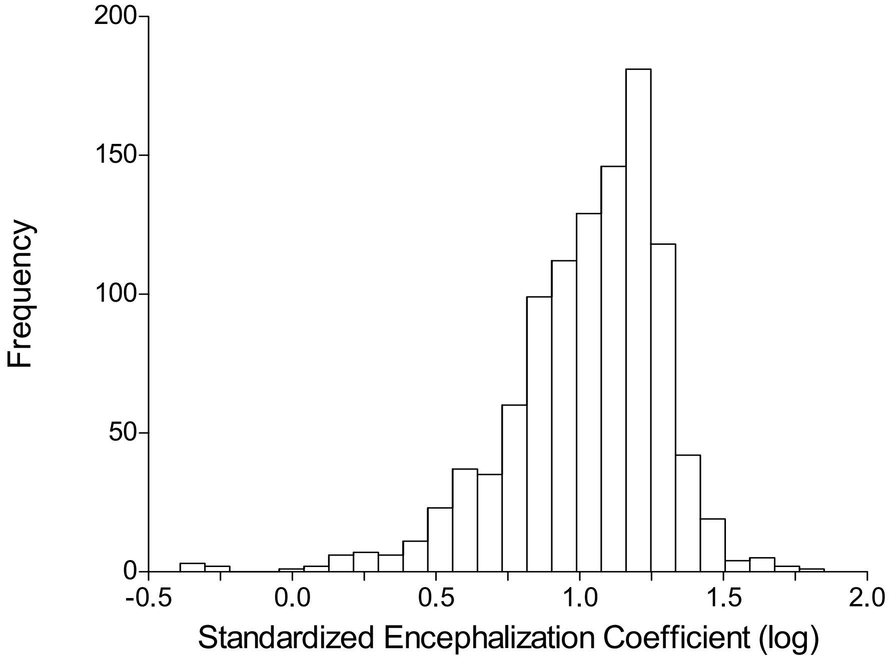


Figure 51. Frequency distribution of the standardized Encephalization Coefficient (brain weight / (body weight)$^{2/3}$) for 1,051 species with available data: median = 11.76, 95% CL = 11.11-12.20, IQR = 7.57 - 16.23.

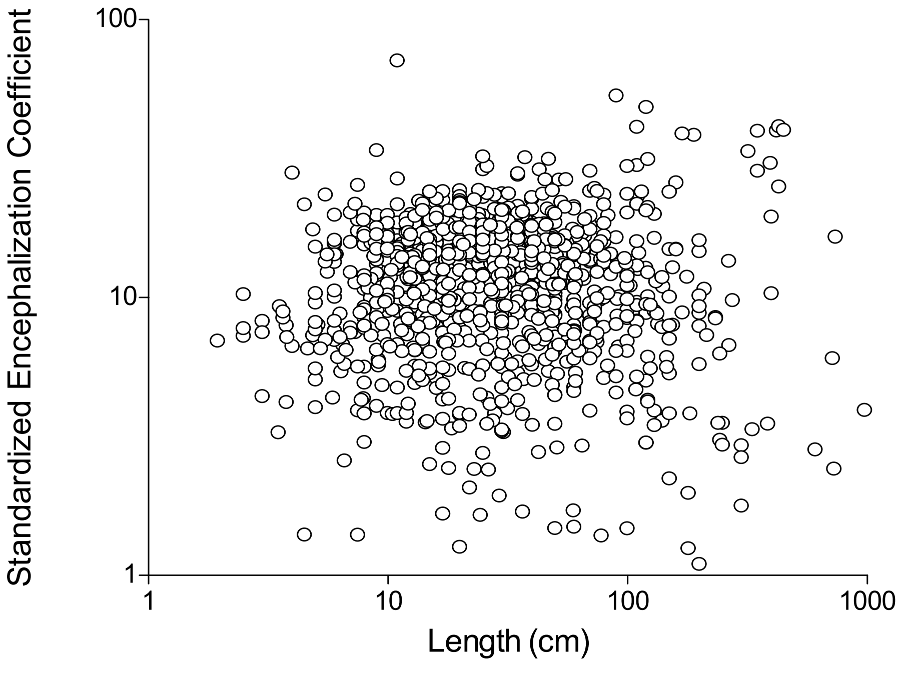


Figure 52. Standardized Encephalization Coefficient plotted over body length, for 1,037 species with available data.

For the purpose of this study I classified relative brain sizes within the interquartile range of median SEC (Figure 51) as normal, larger sizes as large, smaller sizes as small, and sizes below the lower adjacent range as very small; there were no species with brain sizes beyond the upper adjacent range. Table 59 shows the number of species by these categories.

Table 59. Standardized relative brain size for 1,051 species with available data.

Brain size	Species	Percent
Large	262	24.9
Normal	526	50.0
Small	237	22.6
Very small	26	2.5

Table 60 shows standardized relative brain size (SEC) by phylogenetic Class for 1,051 species with available data. Actinopterygii dominate in species numbers in all groups. Large brain size is found only in Elasmobranchii and Actinopterygii, mostly in species with highly developed capabilities for electro-sensing (Moller 1995, Albert et al. 1999); Elasmobranchii have most of their species with available data in this group; both Classes have also species in the normal, low, and very low brain size groups. With one exception for one species of Sarcopterygii with small brains, phylogeny apparently restricts the primitive Classes of Myxini, Cephalaspidomorphi and Sarcopterygii to very small brain sizes.

Table 60. Relative brain size by phylogenetic Class for 1,051 species with available data.

Brain size / Class	Myxini	Cephala-spidomorphi	Elasmo-branchii	Sarcopterygii	Actinopterygii
Large			21		241
Normal			7		519
Small			3	1	233
Very small	2	3	1	1	19

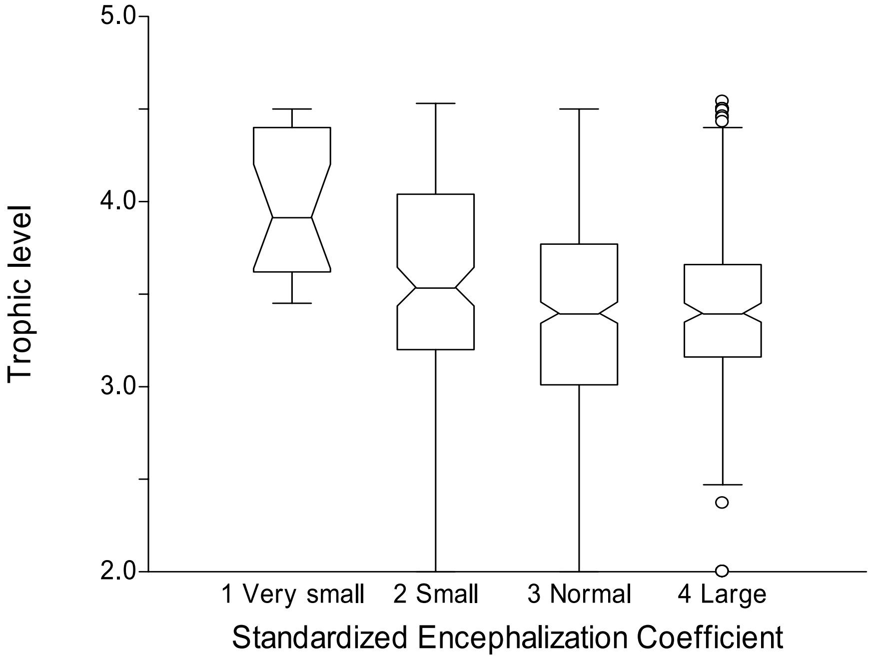


Figure 53. Distribution of trophic level by relative brain size for 840 species with available data: very small brain size with n = 19, median = 3.92, 95% CL = 3.62-4.37; small brain size with n = 159, median = 3.54, 95% CL = 3.45-3.62; normal brain size with n = 428, median = 3.40, 95% CL = 3.35-3.43; and large brain size with n = 234, median = 3.40, 95% CL = 3.25-3.45.

Figure 53 shows the distribution of trophic levels by relative brain size for 840 species with available data. There is a significant decrease in median trophic levels with increase in standardized relative brains size from very small to small and to normal and large brains. Very small brain size is restricted to mid-level and top predators. With one exception, large brains have not been found in herbivores and rarely in omnivores. In other words, mid-level and top predators may have small to large brains, but they are the only trophic group that can also have very small brains. In contrast, herbivores and omnivores typically have normal brain sizes, and apparently they have no need to develop large brains e.g. for detection and hunting for food; however, they can also not afford to have very small brains because presumably they need to support the sensory organs needed to avoid predation.

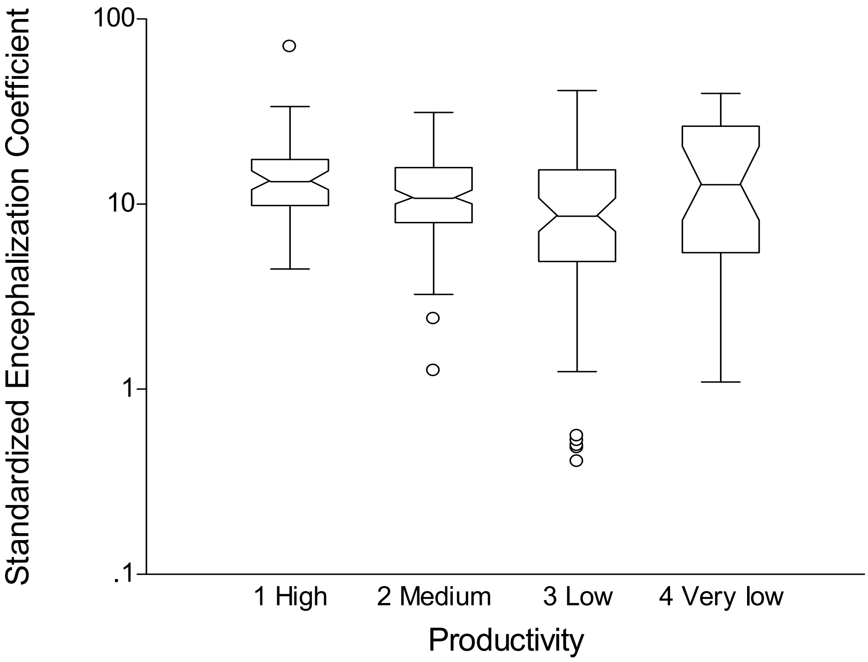


Figure 54. Standardized relative brain size by productivity for 315 species with available data: 1 High productivity with n = 59, median = 13.5, 95% CL = 11.2-15.3; 2 Medium productivity with n = 154, median = 10.9, 95% CL = 10.1-12.1; 3 Low productivity with n = 73, median = 8.75, 95% CL = 7.61-11.3; and 4 Very low productivity with n = 29, median = 13.0, 95% CL = 6.01-19.4.

Figure 54 shows standardized encephalization coefficient (SEC) by productivity group for 315 species with available data. There is a clear, though not significant, decline in SEC with decrease from high to low productivity: this is apparent in median SEC as well as in upper and lower IQRs; also, the range of available brain sizes increases from high to low productivity. The increase in median SEC and IQRs in the very low productivity group may be the result of a phylogenetic bias because of the relativly high number of Elasmobranchii with available data in this category (see Table 60 and discussion of Table 10). Froese and Pauly (2000) explored a correlation between oxygen consumption and relative brain size that was corrected for the effect of body size and concluded “that despite a fair amount of variance, the hypothesis that large brains require more oxygen and are therefore more common in active fish with higher metabolic rates, cannot be refuted.” This interpretation seems also reasonable for the pattern shown in Figure 54.

Table 61 shows the median standardized relative brain size (SEC) by life history strategy for 948 species with available data; note that size was excluded because SEC was corrected for size. The null-hypothesis of even distribution of encephalization coefficients across strategies is rejected with 3 of 18 coefficients being significantly different from overall median SEC: Top predators with low productivity have significantly smaller brains and low-level predators with high productivity have significantly larger brains, which is consistent with the trends in Figure 53 and Figure 54. Herbivores with medium productivity have significantly smaller brains; this result is not obvious from the trends in Figure 53 and Figure 54 and needs further research.

Table 61. Strategies with associated median standardized encephalization coefficient (SEC), 95% confidence limits of the median, and number of species with available data: overall median =11.9, 95% CL = 11.2 - 12.5, n = 948. Strategies where the confidence limits do not overlap with those of the overall median are highlighted in bold.

Strategy Troph-Productivity	**Median SEC**	**95% CL**	**Species (n)**
Herb-High	11.2	9.78 - 13.4	34
Herb-Low	13.2		5
Herb-Medium	**9.57**	**7.96 - 10.4**	**34**
Omni-High	13.2	12.2 – 14.6	48
Omni-Medium	11.4	6.94 – 14.3	22
Omni-Low	11.2		5
Low-High	**14.0**	**12.6 - 14.7**	**332**
Low-Medium	11.9	10.7 – 13.2	188
Low-Low	9.64	7.61 – 13.1	44
Low-Very low	8.55	3.91 – 14.0	15
Mid-High	13.7	10.4 – 16.6	31
Mid-Low	9.78	6.92 – 14.7	23
Mid-Medium	10.3	8.64 – 11.8	67
Mid-Very low	9.35	5.40 – 29.7	13
Top-High	10.7	7.05 – 16.7	9
Top-Medium	10.5	7.84 – 13.5	34
Top-Low	**8.34**	**3.49 – 10.1**	**26**
Top-Very low	10.6	6.01 – 16.4	18

In summary, size, trophic level and productivity all are related to relative brain size. Top predators with low productivity tend to have relatively small brains, whereas the many low-level predators with high productivity, such as reef-associated fishes, tend to have relatively large brains.

Life-history Strategies and Behaviour

A variety of behavioural traits of fishes have been analysed in the context of life history strategies of fishes, mostly related to reproduction such as duration of spawning season, number of spawning bouts, clutch size, and parental care, but also migratory behaviour and latitudinal range (e.g. Winemiller and Rose 1992, Vila-Gispert et al. 2002). In this chapter I will explore parental care, latitudinal range and migratory behaviour and their respective relationships with the life-history strategies identified in this study.

Reproductive guild

Balon (1975, 1990) suggested a classification for reproductive guilds in fishes based on the type of parental care with the choices *nonguarders*, *guarders*, and *bearers*, and the pattern of care for the eggs or young, with the choices *open substratum egg scatterers* (nonguarders that leave eggs after spawning in the water column or on any substrate, e.g., rocks, gravel, sand, plant, etc.), *brood hiders* (nonguarders that deposit eggs in inconspicuous places, e.g., caves, rock interstices, gravel depressions, inside live invertebrates, etc.), *clutch tenders* (non-nesters that guard eggs at the water surface, on underside of objects or any substrate, e.g., rocks, plants, etc.), *nesters* (fish which deposit and often guard eggs in nests, e.g., mucus bubbles, rocks, gravel, sand, holes, base of sea anemones, plants, etc.), *external brooders* (fish which incubate eggs externally on parental body, e.g., pouch, mouth, gill cavities, pelvic fins, etc.), and *internal live bearers* (fish which fertilize eggs internally, with development taking place inside the maternal body) (Torres 2000). FishBase 11/2004 contained such records for over 5,000 species, i.e., 17% of all fishes. As is shown in Table 62, most fishes for which data were available scatter their eggs in open water or over substratum without parental care; this reproductive mode is widespread in bony fish and thus the number one rank is probably correct. Because live bearers and external brooders are relatively well-known groups, the data for them are more complete than those for nesters, clutch tenders and brood hiders, and thus their ranking in Table 62 does not reflect the true frequency of types of parental care.

Table 62. Number and percentage of species by type of parental care for 5,120 species with available data.

Parental Care Type		Species	Percent
Bearers	Internal live bearers	855	16.7
	External brooders	806	15.7
Guarders	Nesters	529	10.3
	Clutch tenders	309	6.0
Nonguarders	Brood hiders	215	4.2
	Open water/substratum egg scatterers	2,406	47.0

For the purpose of this study, I focused on reproductive guilds as shown in Table 63, which is a summary of Table 62 with slightly more (20%) available data, but the same comment applies: while nonguarders are probably the largest guild among fishes, the percentage of bearers is likely to be overestimated.

Table 63. Number and percentage of species by reproductive guild for 5,740 species with available data.

Reproductive guild	Species	Percent
bearers	1,656	28.9
guarders	991	17.3
nonguarders	3,093	53.8

Table 64 shows the number of species by reproductive guild and Class. Bearers are found among Elasmobranchii, Actinopterygii and also Sarcopterygii (*Latimeria*). Guarders are only found among Sarcopterygii and Actinopterygii. Nonguarding occurs in all Classes shown here and is the only mode used by Cephalaspidomorphi and Holocephali (Breder and Rosen 1966, Helfman et al. 1997). Reproductive behaviour of hagfish (Myxini) remains largely unknown. Fertilisation is external and females produce batches of relativly large eggs covered by a horny shell. The eggs attach to each other and to the ocean floor (Breder and Rosen 1966, Helfman et al. 1997) and from this information it may be deduced that no guarding takes place.

Within Elasmobranchii, 56% are bearers, confirming the estimate of Helfman et al. (1997) that “about 40% of all living elasmobranches are oviparous.” Note that more data have been available for Elasmobranchii (13.8%) than their overall contribution to species of fishes (3.4%, see Table 2), i.e., relationships with size, trophic level and productivity of bearers and nonguarders will be slightly biased towards large size, high trophic level and low productivity (see Figure 11, Figure 12, and Table 10). Within Actinopterygii 25% are bearers, 20% are guarders and 55% are nonguarders. However, since only 18% of recent Actinopterygii are included and bearers are covered more completely than the other guilds, these percentages are only indicative in the sense that most Actinopterygii will be non-guarders, confirming the observation of Helfman et al. (1997) that internal gestation occurs only in few bony fish and mouth brooding and attachment of eggs to the body are restricted to few Families. Because the data in Table 64 are more complete for bearing than for guarding, I expect guarding to be found more common than bearing among Actinopterygii once more data become available.

Table 64. Numbers of species by reproductive guild and Class for 5,740 species with available data.

Reproductive guild / Class	Cephala-spidomorphi	Holocephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
bearers			439	1	1,216
guarders				5	985
nonguarders	18	37	350	1	2,679

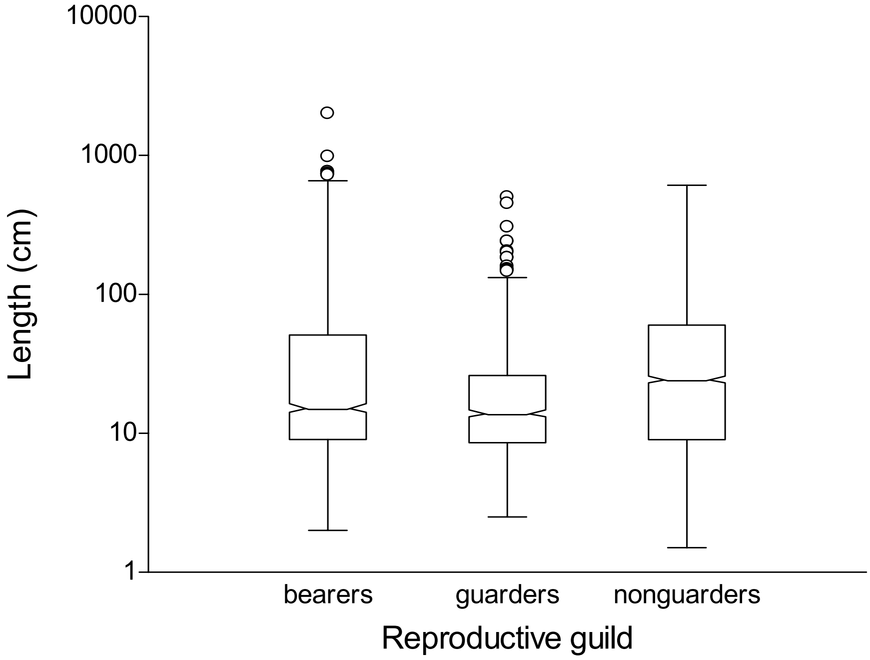


Figure 55. Distribution of length by reproductive guild for 5,202 species with available data. Bearers with n = 1,428, median = 15.2, 95% CL = 14.6-16.7; guarders with n = 945, median = 13.9, 95% CL = 12.9-14.8; nonguarders with n = 2,829, median = 24.4, 95% CL = 22.2-25.0; all lengths are maximum total length in cm.

Figure 55 shows the distribution of length by reproductive guild for 5,202 species with available data. Median lengths of bearers and guarders are similar and significantly smaller than nonguarders. This confirms the results of Winemiller and Rose (1992) and the suggestion by Mahon (1984) that increasing survival of juveniles by parental care may be a viable tactic of small fish to overcome the constraints imposed by small body size on number of eggs or pups. It does not support Goodwin et al. (2005) who found no relationship between mean body size and reproductive mode in about 300 genera of fishes.

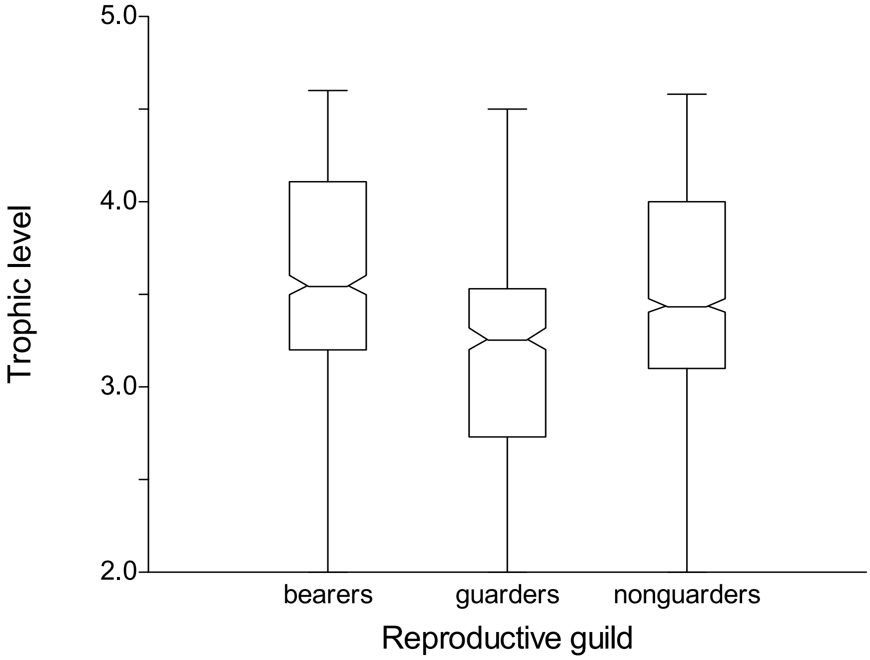


Figure 56. Distribution of trophic levels by reproductive guild for 2,705 species with available data. Bearers with n = 740, median = 3.55, 95% CL = 3.5-3.6; guarders with n = 460, median = 3.26, 95% CL = 3.21-3.31; and nonguarders with n = 1,505, median = 3.44, 95% CL = 3.4-3.5.

Figure 56 shows the distribution of trophic levels by reproductive guild for 2,705 species with available data. The adjacent values are similar for all guilds and range from herbivores to top predators. However, guarders have significantly lower trophic levels than bearers, which include many sharks, and nonguarders, which include many large predatory fish. This confirms the results of Winemiller and Rose (1992) who found a pattern of "little parental care in association with piscivory" and "more parental care in association with feeding on invertebrates and omnivory."

Table 65 shows the distribution of productivity by reproductive guild for 1,810 species with available data. Bearers have mostly low or very low productivity with r'_{max} of 0.12; this reflects the fact that bearers typically have small numbers of offspring which limits their productivity (see Table 6), unless they produce multiple batches per year, as is common in small tropical live bearers such as Poeciliidae. Guarders have mostly medium (52%) and high (25%) productivity with r'_{max} of 0.33, which confirms the short life spans and fast growth (see Table 6) that Winemiller and Rose (1992) found in association with highly developed parental care (note that the 'adult growth rate' of Winemiller and Rose (1992) is expressed as 'mean increment in millimetres TL per year of life over an average adult life span', which is inversely related to von Bertalanffy growth). Nonguarders have mostly low (48%) and medium (36%) productivity with r'_{max} of 0.23, which confirms the finding of Winemiller and Rose (1992) that, "fishes with no parental care tended to long life spans" (see Table 6).

Table 65. Productivity by reproductive guild for 1,810 species with available data, with indication of approximated mean intrinsic rate of population increase (r'_{max}).

Reproductive guild / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
bearers	33	44	272	210	559	0.12	0.107 – 0.134
guarders	41	85	30	7	163	0.33	0.289 – 0.367
nonguarders	142	386	527	33	1,088	0.23	0.216 – 0.241

Above analyses included 82% of Elasmobranchii but only 18% of Actinopterygii species, thus distorting results towards large size, high trophic level and low productivity of bearers. I therefore repeated these analyses for Actinopterygii only.

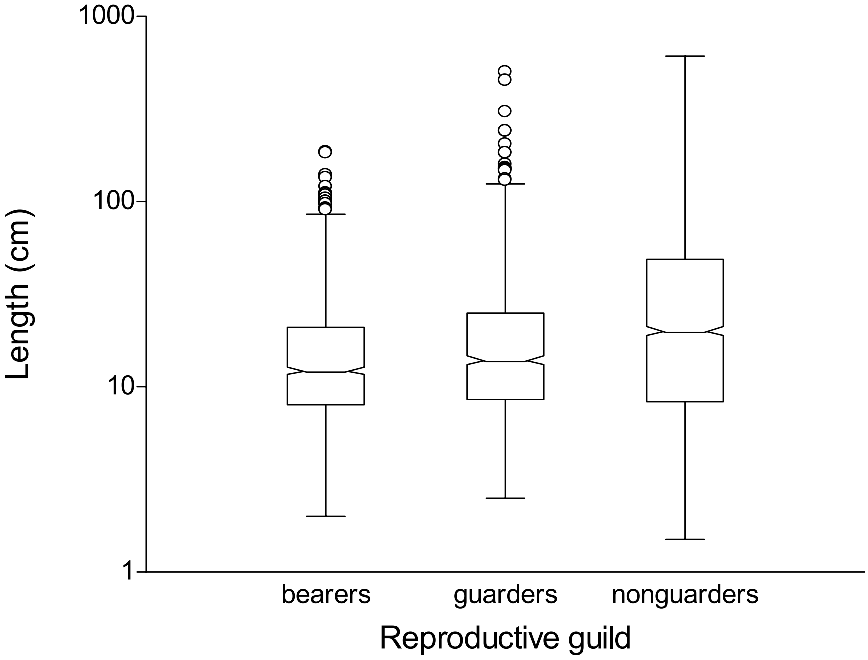


Figure 57. Distribution of length by reproductive guild for 4,599 species of Actinopterygii with bearers n = 1,117, median = 12.2, 95% CL = 11.7-12.8; guarders with n = 940, median = 13.9, 95% CL = 12.6-14.6; and nonguarders with n = 2,542, median = 20.0, 95% CL = 19.2-21.2; length is maximum total length in cm.

Figure 57 shows the distribution of maximum length by reproductive guild for 4,599 species of Actinopterygii. Median length as well as upper IQR and upper adjacent values increase with decrease in parental care confirming the results of Winemiller and Rose (1992) and Mahon (1984). Median length of bearers is significantly lower than in Figure 55, where Elasmobranchii contributed about a quarter of the species in this group. The median length of bearers is 12 cm and bearers beyond 100 cm length are rare in Actinopterygii. Similarly, the median length of guarders is about 14 cm and guarding in Actinopterygii beyond one meter length occurs but is rare. Lower adjacent values are slightly higher for bearers and guarders, suggesting that there may be a minimum size limit of about 2-2.5 cm maximum total length for live bearing and efficient guarding. The smallest live bearer in FishBase 11/2004 is the poeciliid *Pseudopoecilia austrocolumbiana* Radda, 1987 with 2 cm total length, and the smallest guarder is the Emerald clingfish *Acyrtops beryllinus* (Hildebrand & Ginsburg 1926) with 2.5 cm total length.

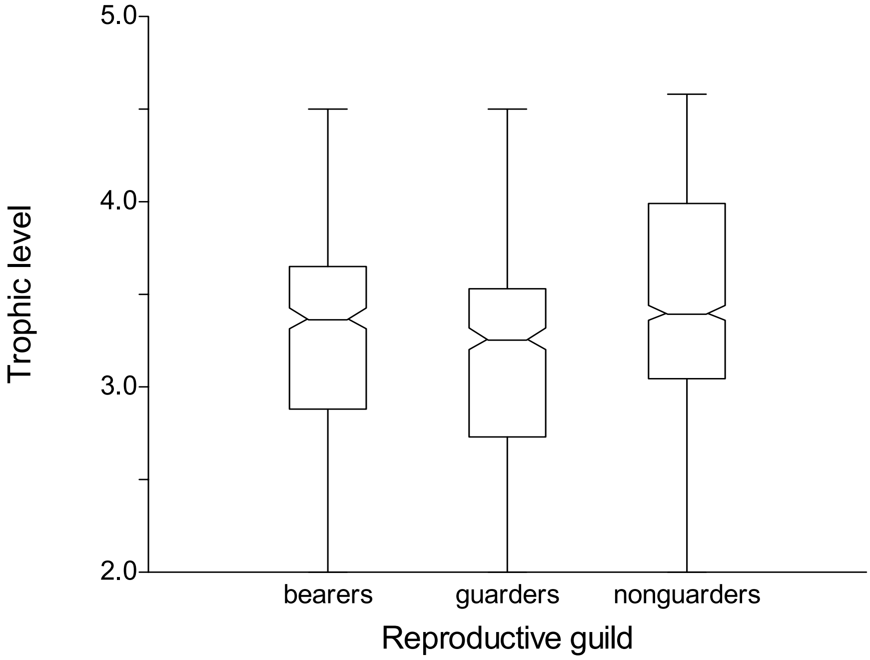


Figure 58. Distribution of trophic levels by reproductive guild for 2,276 species of Actinopterygii: bearers with n = 459, median = 3.37, 95% CL = 3.3-3.4; guarders with n = 456, median = 3.26, 95% CL = 3.22-3.31; and nonguarders with n = 1,361, median = 3.4, 95% CL = 3.35-3.4.

Figure 58 shows the distribution of trophic levels for 2,276 species of Actinopterygii. Median trophic level for bearers is significantly lower than in Figure 56 where Elasmobranchii were included, but still higher than that of guarders and not significantly different from guarders and nonguarders. Median trophic level of nonguarders is significantly higher than that of guarders, confirming the findings of Winemiller and Rose (1992) of little parental care in association with piscivory. Nevertheless, all guilds cover the trophic spectrum from herbivores to top predators.

Table 66 shows the number of species by reproductive guild and productivity group for 1,045 species of Actinopterygii. The dominance of low and very low productivity in the bearer guild of Table 65 has disappeared, but low productivity remains the category with most species resulting in $r'_{max} = 0.24$, which is significantly lower than r'_{max} of guarders and nonguarders; this was to be expected because the limited number of pups constrains the maximum rate of population increase of bearers (see Table 6). Guarders and non-guarders have most species in the medium productivity category with r'_{max} of 0.34 and 0.30, respectively. The low number (1.2%) of guarders with very low productivity—compared to 14% in bearers and 3.1% in nonguarders—may indicate a lower limit to metabolism or activity (both correlates of productivity, see Figure 3 and Figure 4) in association with guarding. Winemiller and Rose (1992) and McCann and Shuter (1997) use the presence or absence of guarding as a measure of high or low juvenile survival. High juvenile survival will increase r_{max}; however, guarding is typically associated with lower fecundity, which decreases r_{max}; thus, we would expect the difference between r'_{max} of guarders and nonguarders to be insignificant, which is indeed the case.

Table 66. Number of species by reproductive guild and productivity for 1,045 species of Actinopterygii, with indication of approximate r'_{max} .

Reproductive guild / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
bearers	33	44	78	25	180	0.24	0.204 – 0.277
guarders	41	85	30	2	158	0.34	0.298 – 0.377
nonguarders	142	382	161	22	707	0.30	0.281 – 0.316

Table 67 shows a cross-tabulation of strategies and reproductive guilds for 4,747 species using the extended data set. The 1,355 bearers use 42 of 49 strategies which is similar to the 41 (34 – 47) strategies predicted by Equation 21. Many species are small (12%) or medium-sized (34%) low-level predators with high productivity. Most large and very large species have higher representation than suggested by the overall distribution of species by reproductive guild (Table 63 and second row in Table 67), which is a reflection of live-bearing sharks being included here.

The 876 guarders use 38 of 49 strategies, which is the same as predicted. Most guarders are small low-level predators with high productivity (13%) or medium-sized low-level predators with medium (13%) or high (36%) productivity. Several herbivorous and omnivorous strategies are used by more than twice the percentage of species suggested by the overall distribution, confirming the trends in Figure 56 and Figure 58.

The 2,516 nonguarders use 47 of 49 strategies, which is not significantly different from the 43 (37 – 50) strategies predicted by Equation 21. Many species are small low-level predators with high productivity (12%) or medium-sized low-level predators with medium (12%) or high (24%) productivity. Large herbivorous and omnivorous strategies and also most top predators have more species than suggested by the overall distribution, confirming the findings in Figure 55 and Figure 56.

In summary, the extended data set confirms the trends found with available data. However, because the extended data set covers only 1/6 of the species and is slightly biased towards Elasmobranchii, the percentages of species using a certain strategy are likely to change once more data on reproductive mode become available.

Table 67. Cross-tabulation of life history strategies and reproductive guilds with respective numbers and percentages for 4,747 species using the extended data set. Percentages of species that are more than twice the overall percentage of Table 63 are highlighted. Number of predicted strategies and confidence limits in the bottom rows are estimated from Equation 21 (Table continued on next page).

Reproductive guild	bearers		guarders		nonguarders		Total
Species by guild %		28.9		17.3		53.8	100
Strategy	n	Guild%	n	Guild%	n	Guild%	
Herb-Small-High	2	20.0	4	**40.0**	4	40.0	10
Herb-Medium-High	43	33.3	56	**43.4**	30	23.3	129
Herb-Medium-Medium	12	21.4	16	28.6	28	50.0	56
Herb-Medium-Low	1	12.5	6	**75.0**	1	12.5	8
Herb-Large-High	1	16.7	1	16.7	4	66.7	6
Herb-Large-Medium	9	26.5	5	14.7	20	58.8	34
Herb-Large-Low					7	**100.0**	7
Herb-Large-Very low			1	**100.0**			1

Reproductive guild	**bearers**		**guarders**		**nonguarders**		**Total**
Species by guild %		28.9		17.3		53.8	100
Strategy	n	Guild%	n	Guild%	n	Guild%	
Omni-Small-High	2	8.0	9	**36.0**	14	56.0	25
Omni-Small-Medium					1	**100.0**	1
Omni-Medium-High	52	25.4	71	34.6	82	40.0	205
Omni-Medium-Medium	4	5.1	11	14.1	63	80.8	78
Omni-Medium-Low			2		3	60.0	5
Omni-Large-Medium	3	10.0	4	13.3	23	76.7	30
Omni-Large-Low	1	5.6			17	94.4	18
Omni-Large-Very low					4	**100.0**	4
Low-Small-High	160	28.2	114	20.1	293	51.7	567
Low-Small-Medium	2	9.5	8	38.1	11	52.4	21
Low-Small-Low	8	53.3	2	13.3	5	33.3	15
Low-Medium-High	463	33.5	313	22.6	607	43.9	1,383
Low-Medium-Medium	65	13.9	110	23.6	291	62.4	466
Low-Medium-Low	68	49.6	6	4.4	63	46.0	137
Low-Medium-Very low	7	50.0	4	28.6	3	21.4	14
Low-Large-High	1	7.7	4	30.8	8	61.5	13
Low-Large-Medium	12	7.8	29	19.0	112	73.2	153
Low-Large-Low	67	26.4	10	3.9	177	69.7	254
Low-Large-Very low	55	55.6	7	7.1	37	37.4	99
Low-Very large-Very low	5	**62.5**			3	37.5	8
Mid-Small-High	2	50.0	1	25.0	1	25.0	4
Mid-Medium-High	68	43.9	14	9.0	73	47.1	155
Mid-Medium-Medium	5	6.4	21	26.9	52	66.7	78
Mid-Medium-Low	4	14.8	6	22.2	17	63.0	27
Mid-Medium-Very low	5	**100.0**					5
Mid-Large-High	1	5.9	2	11.8	14	82.4	17
Mid-Large-Medium	4	4.4	10	11.1	76	84.4	90
Mid-Large-Low	43	23.6	8	4.4	131	72.0	182
Mid-Large-Very low	58	**69.9**	1	1.2	24	28.9	83
Mid-Very large-Low	5	**71.4**			2	28.6	7
Mid-Very large-Very low	7	**77.8**			2	22.2	9
Top-Medium-High	1	7.1	3	21.4	10	71.4	14
Top-Medium-Medium			2	20.0	8	80.0	10
Top-Medium-Low	4	44.4			5	55.6	9
Top-Large-High	1	3.6	1	3.6	26	92.9	28
Top-Large-Medium	1	1.2	8	9.6	74	89.2	83
Top-Large-Low	31	30.1	3	2.9	69	67.0	103
Top-Large-Very low	47	**77.0**	1	1.6	13	21.3	61
Top-Very large-Medium					4	**100.0**	4
Top-Very large-Low	9	**64.3**	2	14.3	3	21.4	14
Top-Very large-Very low	16	**94.1**			1	5.9	17
Species (n)	1,355		876		2,516		4,747
Strategies (n)	42		38		47		49
Predicted strategies (n)	41		38		43		
95% CL lower	34		31		37		
95% CL upper	47		45		50		

Distributional range

The area or geographical range that is occupied by a species is related to its life-history strategy, such as in migratory species. However, there are many widespread species that are non-migratory. I see the area occupied by a species as a result rather than a component of its life-history strategy. Distributional range is thus discussed below in the chapter *How to Measure Success of Life-history Strategies*.

Migratory behaviour

Most fish migrations relate to reproduction and separation of life stages, but many are also in response to seasonal change of environmental conditions and to movement and abundance of food organisms (Moyle and Cech 2004). It is thus interesting to see whether some of the life-history strategies identified in this study are preferred by migratory or non-migratory species. Table 68 shows the number and percentage of species by migratory behaviour for 3,791 species with available data. Migrations are defined as cyclical and predictable and covering more than 100 km; amphidromous species migrate regularly between freshwater and the sea (in both directions) but for feeding, not for breeding as in anadromous and catadromous species (Riede 2004); otherwise the terms are used in their regular sense (Lagler 1977). Except for anadromous and catadromous species, numbers are underestimates because, for most species, migratory behaviour is either not known or not stated explicitly in the literature. As predicted by McDowall (1987), the 239 catadromous plus anadromous fishes represent less than one percent of the 28,000 recent species of fishes.

Table 68. Migratory behaviour for 3,776 species with available data.

Migratory behaviour	Abbr.	Species (n)	(%)
potamodromous	1 pot	533	14.1
catadromous	2 cat	68	1.8
anadromous	3 ana	171	4.5
amphidromous	4 amp	335	8.9
oceanodromous	5 oc	714	18.9
non-migratory	6 non	1955	51.8

Table 69 shows the number of species by migratory behaviour and phylogenetic Class based on data in FishBase 11/2004. Except for the catadromous and anadromous groups, the species numbers are underestimates, but the overall assignment of Classes to migratory categories appears to be correct: The seven Elasmobranchii in the potamodromous group are freshwater rays in South America; otherwise Elasmobranchii migrate in the oceans for feeding, mating and spawning and several species enter freshwater for feeding; in addition, there may be non-migratory Elasmobranchii such as home-ranging small reef sharks. About 2.3% of the available data refer to Elasmobranchii, which is close to their overall contribution to fishes of 3.4%. Thus, I do not expect a ‘phylogenetic bias’ in migratory behaviour data.

Only Actinopterygii are represented in all categories with highest species numbers in each. Myxini are non-migratory (Bo Fernholm, Swedish Museum of Natural History, pers. comm. 2004). Coelacanths are thought to be home-ranging and lungfishes are not known to migrate, so Sarcopterygii are also restricted to the non-migratory group. The assignment of Holocephali as a Class to the oceanodromous—rather than non-migratory—group is probably correct, although data are available for only two species. Cephalaspidomorphi are anadromous but several species are landlocked and thus non-migratory or potamodromous.

Table 69. Number of species by migratory behaviour and phylogenetic Class for 3,776 species with available data.

Migratory behaviour / Class	Myxini	Cephala-spidomorphi	Holocephali	Elasmo-branchii	Sarco-pterygii	Actino-pterygii
potamodromous		5		7		521
catadromous						68
anadromous		12				159
amphidromous				25		310
oceanodromous			2	53		659
non-migratory	69	12			2	1,872

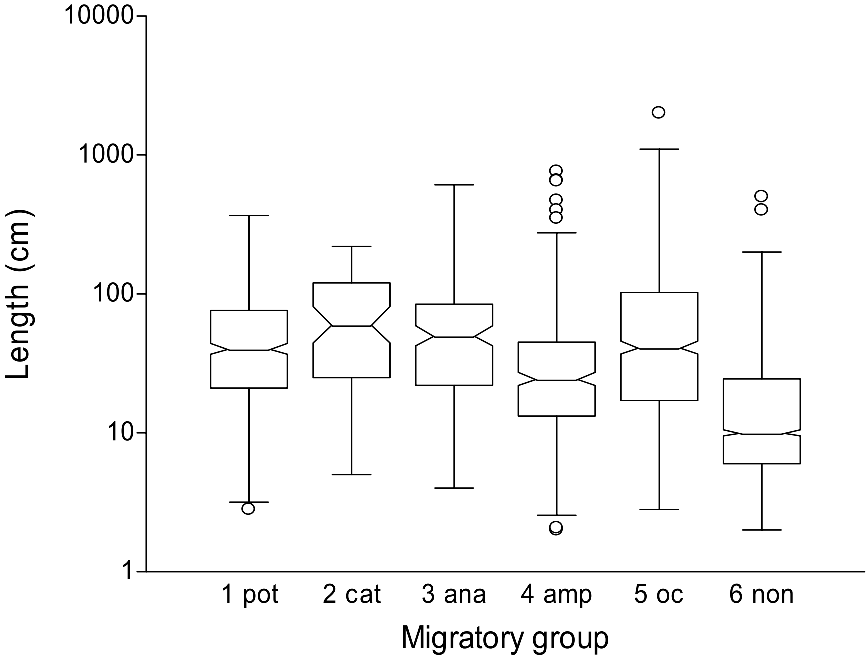


Figure 59. Distribution of maximum total lengths by migratory behaviour for 3,616 species with available data: 1 potamodromous with n = 511, median = 40.3, 95% CL = 37.0-46.0; 2 catadromous with n = 66, median = 60, 95% CL = 40-81; 3 anadromous with n = 162, median = 50, 95% CL = 45-60; 4 amphidromous with n = 313, median = 24.4, 95% CL = 20.7-29.9; 5 oceanodromous with n = 694, median = 41.1, 95% CL = 36.6-48.8; and 6 non-migratory with n = 1870, median = 10, 95% CL = 10-11; all lengths in cm.

Figure 59 shows the distribution of maximum length by migratory groups for 3,616 species with available data. Median length of non-migratory fishes is significantly lower than those of all migratory groups; this confirms the finding of Winemiller and Rose (1992) that "less-migratory fishes tended to be smaller." Amphidromous species have a significantly lower median length than potamodromous, catadromous, anadromous and oceanodromous species which have similar lengths, confirming the finding of Winemiller and Rose (1992) that highly migratory fishes were associated with large body sizes; this is also confirmed by Reynolds et al. (2005) who found larger size in anadromous fishes. The largest fish are oceanodromous and the smallest are amphidromous or non-migratory.

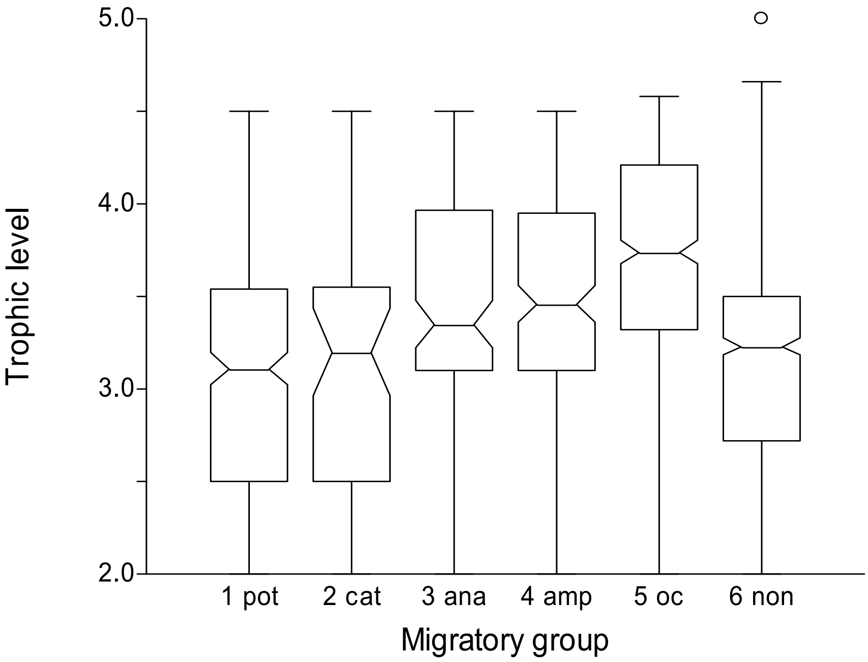


Figure 60. Trophic level by migratory group for 1,896 species with available data: 1 potamodromous with n = 351, median = 3.1, 95% CL = 3-3.2; 2 catadromous with n = 49, median = 3.2, 95% CL = 2.9-3.4; 3 anadromous with n = 113, median = 3.4, 95% CL = 3.3-3.5; 4 amphidromous with n = 180, median = 3.5, 95% CL = 3.4-3.5; 5 oceanodromous with n = 483, median = 3.7, 95% CL = 3.6-3.9; and 6 non-migratory with n = 720, median = 3.2, 95% CL = 3.2-3.3.

Figure 60 shows the trophic level by migratory group for 1,896 species with available data. Overall, interquartile ranges are wide and confidence limits of median trophic level overlap for many groups, suggesting that there is no strong relationship between migratory behaviour and trophic level. Oceanodromous species have a significantly higher median trophic level than all other groups. Amphidromous species have a significantly higher median trophic level than potamodromous and non-migratory species. Herbivorous and omnivorous species are less represented in the anadromous, amphidromous and oceanodromous groups. The outlier near trophic level 5 in the non-migratory group is a deep-water hagfish reported to feed on whale flesh, probably from carcasses.

Table 70 shows productivity by migratory behaviour for 960 species with available data. Most potamodromous, catadromous, anadromous, oceanodromous and non-migratory species have low to medium productivity with r'_{max} ranging from 0.20 to 0.30. Only in the amphidromous group most species are of medium and high productivity with $r'_{max} = 0.35$ being significantly higher than in catadromous, anadromous and oceanodromous fishes. This is probably due to amphidromy being more common in warm waters, because the associated energy cost for osmoregulation are relatively lower with higher metabolic rates. Indeed, while the overall contribution of tropical fishes with migratory information is 59%, their contribution to amphidromous species is 75%.

Table 70. Productivity by migratory behaviour for 960 species with available data, with approximate mean r'_{max}.

Migratory behaviour / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
potamodromous	30	84	47	12	173	0.27	0.236 – 0.305
catadromous	2	12	9	4	27	0.20	0.124 – 0.265
anadromous	11	49	23	10	93	0.24	0.196 – 0.279
amphidromous	28	29	14	13	84	0.35	0.286 – 0.414
oceanodromous	55	155	88	38	336	0.26	0.233 – 0.282
non-migratory	61	84	98	4	247	0.30	0.271 – 0.336

Table 71 shows a cross-tabulation of life-history strategies with migratory behaviour for 3,249 species of fishes based on the extended data set. A null-hypothesis would suggest that the distribution of species by migratory group and strategy is the same as the overall distribution shown in Table 68. Cases where a strategy is used by more than twice the percentage suggested by the overall distribution are highlighted in bold. Note, however, that because of the low number of species with migratory data, conclusions drawn from this table have to be viewed as very preliminary and incomplete.

The 463 potamodromous species in the extended data set use 35 of 49 strategies, which is similar to the 33 (26 – 40) strategies predicted by Equation 21. Many species are medium-sized low-level predators with medium (12%) to high (15%) productivity or large low-level predators with low (9%) to medium (8%) productivity. Of 15 herbivorous or omnivorous strategies, 13 are used by more species than suggested by the overall distribution of species by migratory groups; of these, 8 have 50-100% of their species in this group. Conversely, of 21 mid- and top-level predator strategies, only 10 are used and, of these, 8 are used by fewer species than suggested, thus confirming the relatively low trophic levels of potamodromous fishes in Figure 60.

The 64 catadromous fishes in the extended data set use 21 of 49 strategies, which is at the upper confidence limit of the 14 (7 – 21) strategies predicted by Equation 21, suggesting that some of the 10 strategies used only by one or two species may disappear, i.e., the respective species being merged with adjacent strategies already used by other species, if more and better data become available. Large low-level predators with very low productivity are present with 10 times more (= 11) species than suggested by overall distribution.

The 157 anadromous fishes in the extended data set use 24 of 49 strategies, which is similar to the 23 (16 – 30) strategies predicted by Equation 21. Most species are medium-sized low-level predators with medium (15%) to high (19%) productivity and large low-level predators with low (12%) to medium (14%) productivity.

The 298 amphidromous species use 36 of 49 strategies, which is at the upper confidence limit of the 29 (23 – 36) strategies predicted by Equation 21 and may suggest that some of the 16 strategies used only by one or two species may disappear if more and better data become available. Most species are medium-sized low-level predators with medium (15%) or high (38%) productivity.

The 660 oceanodromous species use 38 of 49 strategies, which is similar to the 36 (29 – 43) strategies predicted by Equation 21. Many species are medium-sized low-level predators with medium (14%) or high (23%) productivity. Of 21 mid- and top-level predator strategies, 16 have higher species numbers than suggested by the overall distribution of species by migratory groups. Eleven predators have 50 - 100% of their species in this group, thus confirming the high trophic levels of oceanodromous fishes shown in Figure 60.

The 1,607 non-migratory species in the extended data set use 33 of 49 strategies, which is significantly fewer than the 41 (35 – 48) strategies predicted by Equation 21. Indeed there are 16 strategies that contain only migratory species. If we only look at those cases where at least 25% of the species using these strategies have been assessed with regard to their migratory behaviour, we obtain 10 strategies that are probably exclusively migratory and thus not available to the non-migratory group members, explaining their relatively low number of strategies.

Most non-migratory species are small low-level predators with high productivity (24%) and medium-sized low-level predators of medium (13%) or high (26%) productivity. Of six small-size strategies, five are represented by more species than suggested by the overall distribution of species by migratory groups and have 67 – 92% of their species in this group, thus confirming the low median size found in Figure 59. In strategies where more than 100 species have been assessed with regard to their migratory behaviour, percentages of non-migrants range from 84% in small low-level predators with high productivity to 23% in large low-level predators with medium productivity. There are no strategies with only non-migrants.

The exclusively migratory strategies identified above are large herbivores with very low, low and high productivity; large omnivores with high productivity; very large low-level to top predators with very low productivity; large top predators with high productivity and very large top predators with medium productivity. The most notable common feature of these strategies is the large to very large size which has already been identified as a characteristic of migratory fishes.

In summary, there are indeed several life-history strategies that are preferred by migratory fishes, and some strategies are only used by migrators. In contrast, there are no strategies that are used only by non-migratory species.

Table 71. Cross-tabulation of life-history strategies and migratory behaviour for 3,249 species of fishes, where *n* is the number of species and *Hab %* the percentage of species associated with a certain strategy and habitat. The *Species by migratory group (%)* row gives the overall percentage of species by habitat as derived in Table 48. If *Mig %* is more than twice the value of *Species by habitat (%)* then it is highlighted in bold. The last column shows the percentage of species that have been assessed per strategy.

Migratory group	**potamo-dromous**		**catadromous**		**anadromous**		**amphi-dromous**		**oceano-dromous**		**non-migratory**		**Total**	**Assessed (%)**
Migratory Species %		14.1		1.8		4.5		8.9		18.9		51.8	100	15.9
Strategy	n	Mig %	n	Mig %	n	Mig %	n	Mig %	n	Mig %	n	Mig %		
Herb-Small-High							1	**25.0**			3	75.0	4	3.8
Herb-Medium-High	14	21.2	2	3.0			2	3.0	1	1.5	47	71.2	66	13.4
Herb-Medium-Medium	19	**57.6**					5	15.2	2	6.1	7	21.2	33	8.0
Herb-Medium-Low	1	**100.0**											1	1.3
Herb-Large-High	1	**33.3**			2	**66.7**							3	25.0
Herb-Large-Medium	18	**58.1**	2	**6.5**	4	**12.9**	2	6.5	1	3.2	4	12.9	31	30.7
Herb-Large-Low	19	**82.6**	1	**4.3**			1	4.3	2	8.7			23	39.7
Herb-Large-Very low	9	**90.0**	1	**10.0**									10	32.3
Omni-Small-High	2	8.0									23	**92.0**	25	7.6
Omni-Medium-High	28	12.4	1	0.4	3	1.3	12	5.3	11	4.9	171	75.7	226	18.7
Omni-Medium-Medium	28	**34.1**	4	**4.9**	2	2.4	3	3.7	4	4.9	41	50.0	82	16.6
Omni-Medium-Low	1	**33.3**			1	**33.3**					1	33.3	3	27.3
Omni-Large-High	2	**66.7**							1	33.3			3	42.9
Omni-Large-Medium	11	**44.0**	4	**16.0**	3	**12.0**	1	4.0	4	16.0	2	8.0	25	38.5
Omni-Large-Low	16	**59.3**	3	**11.1**			4	14.8	1	3.7	3	11.1	27	35.5
Omni-Large-Very low	2	**50.0**					1	**25.0**			1	25.0	4	25.0
Low-Small-High	17	3.7	3	0.7	1	0.2	23	5.0	28	6.1	387	84.3	459	16.9
Low-Small-Medium									1	12.5	7	**87.5**	8	13.8
Low-Small-Low	1	**33.3**									2	66.7	3	17.6
Low-Medium-High	67	8.6	3	0.4	29	3.7	114	14.6	151	19.3	419	53.5	783	11.5
Low-Medium-Medium	57	13.1	9	2.1	23	5.3	46	10.6	94	21.7	205	47.2	434	15.7
Low-Medium-Low	3	6.1	3	**6.1**	3	6.1	3	6.1	6	12.2	31	63.3	49	14.3
Low-Medium-Very low			1	**14.3**	2	**28.6**	1	14.3	1	14.3	2	28.6	7	12.7
Low-Large-High	2	**28.6**					3	**42.9**	2	28.6			7	11.7
Low-Large-Medium	38	22.8	5	3.0	22	**13.2**	10	6.0	54	32.3	38	22.8	167	25.9
Low-Large-Low	42	28.2	3	2.0	18	**12.1**	4	2.7	33	22.1	49	32.9	149	24.4

Migratory group	**potamo-dromous**		**catadromous**		**anadromous**		**amphi-dromous**		**oceano-dromous**		**non-migratory**		**Total**	**Assessed (%)**
Migratory Species %		14.1		1.8		4.5		8.9		18.9		51.8	100	15.9
Strategy	n	Mig %	n	Mig %	n	Mig %	n	Mig %	n	Mig %	n	Mig %		
Low-Large-Very low	15	**30.6**	11	**22.4**	8	**16.3**	3	6.1	7	14.3	5	10.2	49	22.9
Low-Very large-Very low	1	12.5			3	**37.5**			4	**50.0**			8	80.0
Mid-Small-High							1	**100.0**					1	9.1
Mid-Medium-High	3	5.9			1	2.0	4	7.8	29	**56.9**	14	27.5	51	9.0
Mid-Medium-Medium	8	11.1	1	1.4	3	4.2	12	16.7	11	15.3	37	51.4	72	16.7
Mid-Medium-Low							1	4.2	2	8.3	21	**87.5**	24	30.0
Mid-Medium-Very low			1	**50.0**					1	**50.0**			2	20.0
Mid-Large-High	1	9.1							10	**90.9**			11	21.6
Mid-Large-Medium	8	10.7			7	**9.3**	9	12.0	33	**44.0**	18	24.0	75	20.4
Mid-Large-Low	10	16.9	3	5.1	3	5.1	4	6.8	25	**42.4**	14	23.7	59	19.0
Mid-Large-Very low					1	5.0	6	**30.0**	8	**40.0**	5	25.0	20	16.5
Mid-Very large-Low							1	**25.0**	3	**75.0**			4	57.1
Mid-Very large-Very low					2	**50.0**	1	**25.0**	1	25.0			4	44.4
Top-Medium-High	1	25.0					1	**25.0**	2	**50.0**			4	5.3
Top-Medium-Medium							1	**20.0**			4	80.0	5	5.1
Top-Medium-Low					2	**25.0**					6	75.0	8	29.6
Top-Large-High							1	9.1	10	**90.9**			11	29.0
Top-Large-Medium	7	8.5			7	8.5	7	8.5	53	**64.6**	8	9.8	82	43.6
Top-Large-Low	8	11.1	1	1.4	7	**9.7**	3	4.2	28	**38.9**	25	34.7	72	38.1
Top-Large-Very low	2	8.0	2	**8.0**			4	16.0	12	**48.0**	5	20.0	25	27.5
Top-Very large-Medium									4	**100.0**			4	100
Top-Very large-Low							2	15.4	9	**69.2**	2	15.4	13	81.3
Top-Very large-Very low	1	7.7					1	7.7	11	**84.6**			13	68.4
Species (n)	463		64		157		298		660		1,607		3,249	20,480
Strategies (n)	35		21		24		36		38		33		49	50
Predicted strategies (n)	33		14		23		29		36		41			
95% CL lower	26		7		16		23		29		35			
95% CL upper	40		21		30		36		43		48			

Life-history Strategies and Human Impact on Fishes

Resilience to Fishing Pressure

The time a population needs to replenish itself when numbers of individuals have been drastically reduced, e.g. by fishing, can be calculated from its intrinsic rate of population increase, which is the numerical equivalent of the productivity categories used in this study (see Table 6). As pointed out in the discussion of Table 6, data on intrinsic rate of population increase are available for only very few commercial species. In agreement with Musick (1999), I propose that productivity can be viewed as resilience against fishing pressure, and thus species with strategies with medium or high productivity will be able to withstand medium to high fishing pressure, whereas species with low or very low productivity may not be able to withstand any directed fishing pressure and will already be endangered if they are part of the 'by-catch.' As Adams (1980) puts it, fisheries based on more r-selected (= high productivity) species, if not carefully managed, are likely to be of a "boom and bust" nature; fisheries based on more K-selected (= medium to low productivity) species will be more predictable and thus easier to manage, but will require a long period of recovery once overfished; and extremely K-selected (= very low productivity) species would not be suitable for commercial fisheries.

Froese and Pauly (2003) provide a first analysis of productivity / resilience and status of fished stocks. They find a preliminary positive correlation between productivity and number of years that a stock withstood full exploitation before collapse. Jennings et al. (1998) show that after accounting for differences in fishing mortality, species with relative late maturity and lower rates of population increase have decreased more in abundance than their closest relatives.

Murphy (1968) stressed that, "it is common knowledge that many long-lived organisms [...] reproduce over many years but only rarely reproduce successfully." Winemiller and Rose (1992) based on Southwood (1977) further explore this theme and make an interesting point: If environmental conditions essential for growth and survival of larvae are periodic and occur at frequencies smaller than the normal life span then selection will favour the strategy of production of a large number of eggs without parental care released in phase with the optimal conditions. If such environmental conditions are not available every year or are typically so short, localized and difficult to predict that they are missed by most spawners, then most females will only produce surviving offspring in the exceptional years where optimal environmental conditions are widespread and last long enough. In other words, reproductive life spans of highly fecund fishes will have evolved to be longer than the frequency of exceptionally good conditions for the survival of larvae, such as is visible in the resulting large year classes. These relationships may be called the 'reproductive longevity' hypothesis. Humans are unnatural predators in that they do not selectively target young, sick or stray individuals, but rather first and foremost remove the large and successful specimens. Fishing thus drastically reduces the average life span of stocks, curtailing the life history strategy of highly fecund fishes and making them a misfit for their environment and their populations prone to collapse, as is indeed happening on a global scale (Jackson et al. 2001, Longhurst 2002, Myers and Worm 2003, Froese 2004a,b).

Some corollaries to the 'reproductive longevity' hypothesis can be tested. For example, as already pointed out by Williams (1964) the number of eggs released by a female is inversely related with the likelihood of finding optimal conditions for survival, i.e., the higher the fecundity, the higher the typical mortality of eggs and larvae. In that case there should be no correlation between fecundity and the number of offspring surviving to maturity. Froese and Luna (2004) have tested this and found indeed no such relationship for 49 species of bony fish with available data.

Another implication of the ‘reproductive longevity’ hypothesis is that reproductive life span should be longer then the frequency of exceptionally good environmental conditions. Sinclair et al. (1985) showed that survival of Pacific mackerel *Scomber japonicus* larvae in the California current was higher during El Niño events. During the period they analysed (1928-1965), time between major El Niño events was 4 to 7 years (n = 5, mean = 5.4, 95% CL = 4.0 – 6.8). Based on data in FishBase, Pacific mackerel off California mature at 2 years and their maximum age is 8 to 14 years. Thus, the maximum reproductive life span is 6 – 14 years. Not all fish will reach maximum age; assuming mean reproductive life span to be half of the maximum results in 3 – 7 life-time spawning seasons per female on average, i.e., most females have a good chance to spawn at least once with exceptionally good conditions.

FishBase 11/2004 contains a recruitment time series for the Hokkaido stock of the Pacific herring (*Clupea pallasii*) from 1907 to 1954 based on Myers et al. (1995). This time series shows very pronounced peaks in recruitment with 3-9 years (n=7, mean = 5.6, 95% CL = 3.6-7.6) inbetween. Maximum age for the area is given as 18 years. Based on growth parameters and the given size at first maturity of 28-30 cm TL, age at first maturity can be assumed to be 4 years, resulting in a maximum reproductive period of 14 years. If we again assume half of that as mean reproductive period, an average female will have 7 spawning seasons and thus a good chance of hitting the exceptional year with high chance of reproductive success.

El Niño events are known to result in lower recruitment of the Peruvian anchoveta *Engraulis ringens* (e.g. Mendelsohn and Mendo 1987). The typical period of El Niño events is 3 – 7 years (e.g. Brainard and McLain 1987). Since these events normally only last one year, the reproductive period of Peruvian anchoveta can be expected to be at least two years. Based on data in FishBase 11/2004 Peruvian anchoveta reach 3 years maximum age and mature with one year. A mean reproductive period of one year means that an average female reaching first maturity in an El Niño year has a second chance to spawn at the end of her reproductive life.

These three examples are obviously not enough to make a strong case in support for the ‘reproductive longevity’ hypothesis and more research is needed. Froese and Binohlan (2000) have shown a strong positive correlation between asymptotic length and length at first maturity in iteroparous fishes, which implies that there is a similarly strong positive correlation between maximum age and age at first maturity and thus with reproductive period. Maximum age is one of the parameters used to determine productivity and resilience in this study (see Table 6), with higher age being associated with lower productivity and resilience. The ‘reproductive longevity’ hypothesis presents an explanation why, contrary to intuition, an extended reproductive period is not an indication of more, but rather of less productivity, and a reduced resilience to fishing.

Status of Threat

Fishes and especially freshwater fishes are among the most threatened vertebrate groups (Bruton 1995). It is thus interesting to explore whether there is a relationship between life-history strategies as defined in this study and status of threat.

Table 72 shows 1,027 species of fishes listed in the respective categories of threat in the IUCN Red List (IUCN 2000). Note that extinction risk of the vast majority of fishes has not yet been assessed and thus the numbers below underestimate the problem. Also, although the threat to marine fishes is becoming increasingly clear (e.g., Roberts et al. 1998, Sadovy 2001) only 253 marine or diadromous species are included in the IUCN (2000) Red List, i.e., the numbers mostly represent freshwater fishes. Froese and Torres (1999) presented a detailed analysis of the fishes in the 1996 release of the IUCN Red List, which is not very different from the 2000 release used here.

Table 72. Threatened fishes in the 2000 IUCN Red List (1,027 species). The 'Lower risk' category includes near-threatened and conservation dependent species; the 'Extinct' category includes species that are extinct in the wild but may survive in breeding programs.

Threat	Abbr.	Species	Percent
Lower risk	1 Low	155	15.1
Vulnerable	2 Vul	459	44.7
Endangered	3 End	161	15.7
Critically endangered	4 Crit	160	15.6
Extinct	5 Ext	92	9.0

Table 73 shows the number of threatened species by category of threat and phylogenetic Class. No threatened species are reported for Myxini and Holocephali. Note that because of their overall lower species numbers, Cephalaspidomorphi, Elasmobranchii and Sarcopterygii are more threatened at the Class-level than Actinopterygii. Also, relatively fewer Actinopterygii have been assessed, resulting in a slight phylogenetic bias towards the other Classes.

Table 73. Threatened fishes by phylogenetic Class, with percentage of threatened species in the respective Class and category of threat; no threatened species were reported for Myxini and Holocephali.

Threat / Class	Cephala-spidomorphi		Elasmo-branchii		Sarco-pterygii		Actino-pterygii	
	n	%	n	%	n	%	n	%
Lower risk	5	12.0	42	4.4			108	0.4
Vulnerable	2	4.8	25	2.6			432	1.6
Endangered	1	2.4	18	1.9			142	0.5
Critically endangered			7	0.7	1	9.1	152	0.6
Extinct	1	2.4					91	0.3

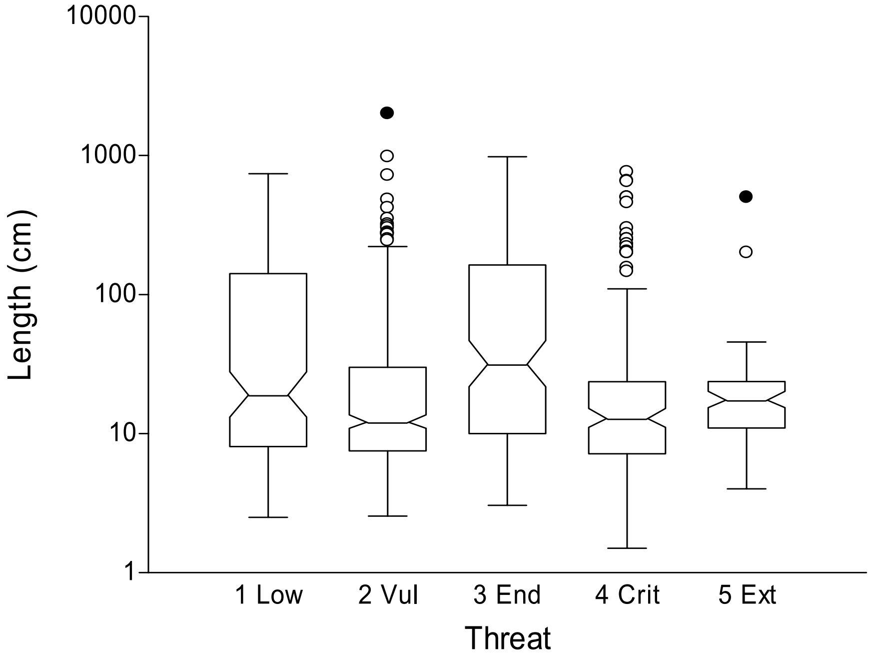


Figure 61. Length distribution by category of threat for 879 species with available data: 1 Lower risk with n = 144, Median = 19.2, 95% CL = 12-31.7; 2 Vulnerable with n = 382, median = 12.2, 95% CL = 10.3-14; 3 Endangered with n = 132, median = 31.9, 95% CL = 16.5-64; 4 Critically endangered with n = 142, median = 13.0, 95% CL = 11.0-14.4; and 5 Extinct with n = 79, median = 17.6, 95% CL = 12.7-19.0; all lengths are maximum total lengths in cm.

Figure 61 shows the distribution of maximum length by category of threat. There is no apparent correlation between median lengths and threat, which is increasing from ‘Lower risk’ to ‘Extinct’, confirming the findings of Reynolds et al. (2005) of “… no significant increase in body size between threatened and less-threatened native species.” However, in a more detailed analysis Froese and Torres (1999) found “a clear increase in the relative number of threatened fishes above 100 cm [..] maximum length, to a point where most very large freshwater fishes are threatened.” This finding is confirmed in the analysis of Table 75 below.

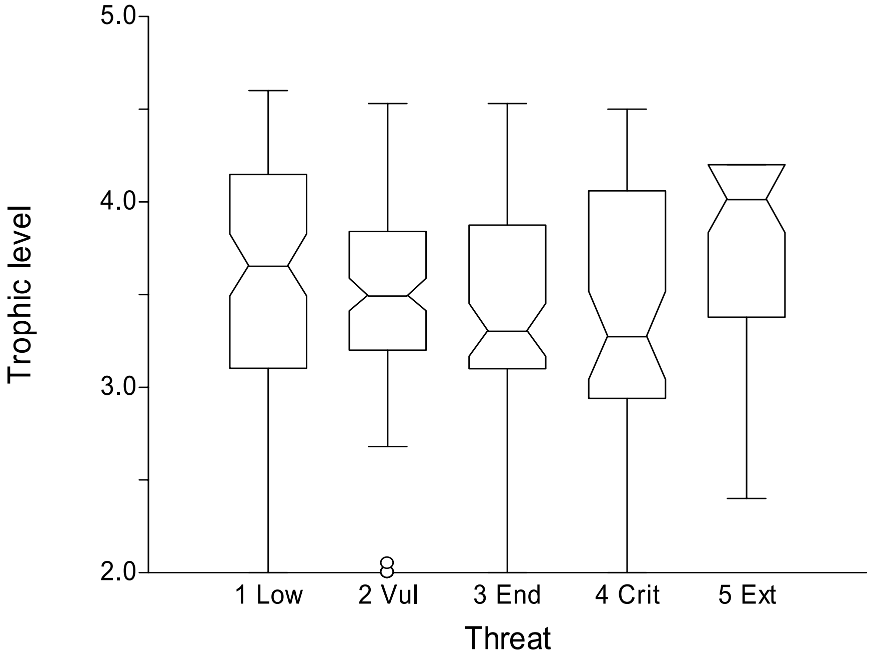


Figure 62. Distribution of trophic levels by category of threat for 403 species with available data: 1 Lower risk with n = 96, median = 3.66, 95% CL = 3.4-3.8; 2 Vulnerable with n = 131, median = 3.5, 95% CL = 3.38-3.5; 3 Endangered with n = 73, median = 3.31, 95% CL = 3.2-3.46; 4 Critically endangered with n = 55, median = 3.28, 95% CL = 3.2-3.6; and 5 Extinct with n = 48, median = 4.02, 95% CL = 3.6-4.2.

Figure 62 shows the distribution of trophic levels by categories of threat for 403 species with available data. Confidence limits are broad and overlapping, confirming the finding of Reynolds et al. (2005) that "the mean trophic level did not differ between threatened and less-threatened species" of fishes. However, there is a trend of decreasing median trophic level from Lower risk towards Critically endangered. This confirms the finding of Froese and Torres (1999) that "there are considerably more [..] herbivorous threatened species than suggested by their contribution [..] to all fishes." The Extinct category has the highest median trophic level, however, the confidence limits overlap with the Lower risk category, making this result difficult to interpret.

Table 74 shows the number of species by category of threat and productivity group. Productivity is also a measure of resilience, i.e., how fast a population or species can recover from events that have drastically reduced the number of specimens (Musick 1999). This is confirmed with lowest numbers of threatened species in the high productivity group, and highest numbers in the low or very low productivity group, with the exception of the Extinct category for which only 4 records are available. Overall mean r'_{max} is 0.14 (n = 226, 95% CL = 0.115 – 0.161) for threatened fishes. This is significantly lower than mean r'_{max} = 0.23 (n = 2,747, 95% CL = 0.228 – 0.244) for all non-threatened fishes with available productivity data. This also confirms the finding of Winemiller and Rose (1992) that, "the opportunistic suite of life history characteristics allows fishes to rebound from local disturbances …" (note that their 'opportunistic suite' is identical with high productivity as used in this study). It also confirms the finding of Reynolds et al. (2005) that threatened species show a tendency towards later age at maturity (which is inversely correlated with r'_{max}, see Table 6).

Table 74. Productivity of species by category of threat for 226 species with available data, with approximate mean r'_{max} .

Threat / Productivity	High	Medium	Low	Very low	n	r'_{max}	95% CL
Lower risk	2	6	18	31	57	0.10	0.058 – 0.133
Vulnerable	6	24	26	21	77	0.17	0.128 – 0.213
Endangered	7	5	25	25	62	0.15	0.097 – 0.210
Critically endangered		4	13	9	26	0.09	0.066 – 0.122
Extinct		2	1	1	4	0.15	0.000 – 0.308

Table 75 shows a cross-tabulation of strategies and categories of threat for 805 species with data in the extended data set. The 805 threatened species use 38 of 49 strategies. The numbers of strategies used per category of threat are similar to those predicted by Equation 21, except for the Extinct category, in which significantly fewer strategies are used.

Because of the incomplete assessment (only 3.9% of species with strategies are assessed and threatened) there is no apparent pattern distinguishing between the different categories of threat. The last column in Table 75 integrates species numbers across categories and shows percentage of species in a strategy that are threatened. Cases where this percentage is twice the overall percentage of 3.9% are highlighted in bold. In the following strategies, 20% or more of the species are threatened: very large low-level predators with very low productivity (80%); very large mid-level predators with low (57%) and very low (100%) productivity; large top predators with very low productivity (23%) and very large top predators with low (56%) and very low (53%) productivity. Of 13 strategies involving large or very large size and low or very low productivity, 10 have more threatened species than suggested by overall percentage of threatened species. Conversely, of 9 strategies involving high productivity 7 have fewer threatened species than suggested.

In summary, assessment of fishes as to their status of threat is incomplete and biased towards freshwater and non-Actinopterygii. A preliminary analysis shows that mean productivity or resilience of threatened fishes is significantly lower than that of non-threatened fishes with available data, confirming the results of Cheung et al. (2005). Life-history strategies that combine large size and low productivity contain several times more threatened species than suggested by the overall average.

Table 75. Cross-tabulation of life-history strategies with categories of threat for 805 species based on the extended data set, where *n* is the number of species and *Thr %* the percentage of species associated with a certain strategy and threat. The *Species by threat (%)* row gives the overall percentage of species by threat as derived in Table 72. If *Thr %* is more than twice the value of *Species by threat (%)* then it is highlighted in bold. The last column gives the percentage of species that are threatened in a certain strategy (Table continued on next page).

Categories of threat	Lower risk		Vulnerable		Endangered		Critically endangered		Extinct		Total	Percent
Species by threat (%)		15.1		44.6		15.7		15.6		9	100	3.9
Strategy	n	Thr %	n	Thr %	n	Thr %	n	Thr %	n	Thr %		
Herb-Small-High					1	**100.0**					1	0.9
Herb-Medium-High	3	27.3	1	9.1	2	18.2	5	**45.5**			11	2.2
Herb-Medium-Medium	2	28.6	3	42.9	2	28.6					7	1.7
Herb-Large-Medium			1	**100.0**							1	1.0
Herb-Large-Low			1	**100.0**							1	1.7
Omni-Small-High	3	**37.5**	3	37.5	1	12.5	1	12.5			8	2.4
Omni-Medium-High	2	4.9	23	56.1	5	12.2	9	22.0	2	4.9	41	3.4
Omni-Medium-Medium	5	22.7	10	45.5	3	13.6	4	18.2			22	4.5
Omni-Medium-Low	1	**100.0**									1	**9.1**
Omni-Large-Medium					1	**100.0**					1	1.5
Omni-Large-Low	1	**33.3**			2	**66.7**					3	3.9
Omni-Large-Very low			1	**100.0**							1	6.3
Low-Small-High	19	16.1	53	44.9	12	10.2	27	22.9	7	5.9	118	4.4
Low-Small-Medium			2	**100.0**							2	3.4
Low-Small-Low			1	**100.0**							1	5.9
Low-Medium-High	32	13.4	124	52.1	19	8.0	41	17.2	22	9.2	238	3.5
Low-Medium-Medium	10	11.5	42	48.3	11	12.6	12	13.8	12	13.8	87	3.2
Low-Medium-Low	2	**33.3**	1	16.7	3	**50.0**					6	1.7
Low-Medium-Very low			4	**100.0**							4	7.3
Low-Large-High			1	**100.0**							1	1.7
Low-Large-Medium	1	12.5	5	62.5	1	12.5	1	12.5			8	1.2
Low-Large-Low	8	20.5	14	35.9	13	**33.3**	3	7.7	1	2.6	39	6.4
Low-Large-Very low	7	20.0	8	22.9	17	**48.6**	3	8.6			35	**16.4**

Categories of threat	Lower risk		Vulnerable		Endangered		Critically endangered		Extinct		Total	Percent
Species by threat (%)		15.1		44.6		15.7		15.6		9	100	3.9
Strategy	n	Thr %	n	Thr %	n	Thr %	n	Thr %	n	Thr %		
Low-Very large-Very low	2	25.0	2	25.0	3	**37.5**	1	12.5			8	**80.0**
Mid-Medium-High	2	5.1	2	5.1	3	7.7	4	10.3	28	**71.8**	39	6.9
Mid-Medium-Medium	5	**55.6**	1	11.1			1	11.1	2	22.2	9	2.1
Mid-Medium-Low			1	**100.0**							1	1.3
Mid-Large-Medium			5	83.3			1	16.7			6	1.6
Mid-Large-Low	5	20.0	8	32.0	6	24.0	6	24.0			25	8.1
Mid-Large-Very low	7	**53.8**	3	23.1	3	23.1					13	**10.7**
Mid-Very large-Low	1	25.0			1	25.0	2	**50.0**			4	**57.1**
Mid-Very large-Very low	1	11.1			5	**55.6**	2	22.2	1	11.1	9	**100.0**
Top-Medium-High							1	**100.0**			1	1.3
Top-Large-Medium			5	62.5	2	25.0	1	12.5			8	4.3
Top-Large-Low	2	**40.0**	3	60.0							5	2.6
Top-Large-Very low	9	**42.9**	8	38.1	1	4.8	3	14.3			21	**23.1**
Top-Very large-Low	2	22.2	1	11.1	4	**44.4**	2	22.2			9	**56.3**
Top-Very large-Very low	7	**70.0**	3	30.0							10	**52.6**
Species (n)	139		340		121		130		75		805	
Strategies (n)	25		31		24		21		8		38	
Predicted strategies (n)	22		31		21		21		16			
95% CL lower	15		24		14		14		9			
95% CL upper	29		37		27		28		22			

How to Measure Success of Life-history Strategies

Measuring the success of life-history strategies is not straightforward. One could take the duration of successful usage of a strategy in evolutionary time as a measure (see Table 22), which would make the five low-productivity strategies first used by Myxiniformes 600 million years ago the most successful. Or one could use the current number of species using a strategy as a measure, which would make the three strategies of low-level predators of small to medium size with medium to high productivity the most successful (see Table 16). Or one could use the intrinsic rate of population increase (Partridge and Sibly 1991) which, in this study, is highly correlated with productivity (see Table 6) and which would make the 14 strategies with high productivity the most successful. In this chapter I explore the usefulness of independent estimates of abundance and area of occupancy as measures of success.

Abundance

Fitness is typically defined at the level of the individual, where the individual with the highest number of surviving descendants at a certain time in the future is considered to have the highest fitness. If we apply this scheme to the level of species, we could compare the fitness of the ancestors of our recent species and measure their fitness as the number of individuals of their species existing in a given recent year. As opposed to those of terrestrial vertebrates, numbers of individual fishes are not known. However, one can approximate this number by taking the unfished global biomass of the respective species and divide it by mean weight at first maturity to obtain a proxy for abundance.

Unfortunately, there is no large enough compilation of unfished biomasses of fishes. Therefore, I assumed a positive correlation between unfished biomass and highest catch ever reported in the catch statistics published by FAO from 1950 to present (FAO 2002). Note that such assumption is not unreasonable, as the highest catch can be expected to be smaller than but close to unfished biomass. Jackson et al. (2001) came to a similar conclusion and used ‘peak in landings’ as proxy for baseline biomass if no better data were available. To account for the fact that commercial species typically exist in several distinct stocks with distinct histories of exploitation, I took ‘species by FAO statistical area’ as a substitute for stocks for the purpose of this study. The procedure used was then as follows:

1) From FAO catch statistic data for 1950 to 2002, determine for every species and FAO area the maximum catch and the number of years for which catch data were available;
2) For every species, add up the maximum catch as well as the number of years with available catch data across the different FAO areas;
3) In order to exclude species that are not fully exploited yet (see left side of frequency distribution of maximum catches in Figure 63), exclude species with less than 10 years of reported catch or less than 100 tons of maximum catch (10 years is the median number of years in which maximum catch was reached by FAO species and areas);
4) For the remaining 557 species, calculate length at first maturity from maximum length (Froese and Binohlan 2000), get length-weight relationships from FishBase (was available for 451 species; for the remaining species mean LW-parameters were taken from the Genus (61 cases), the Family (36 cases), and the Order (9 cases), respectively) and calculate weight at first maturity;
5) Divide maximum catch by weight at first maturity to get the respective number of individuals (Figure 64);
6) Plot number of individuals against trophic group, length group, and productivity.

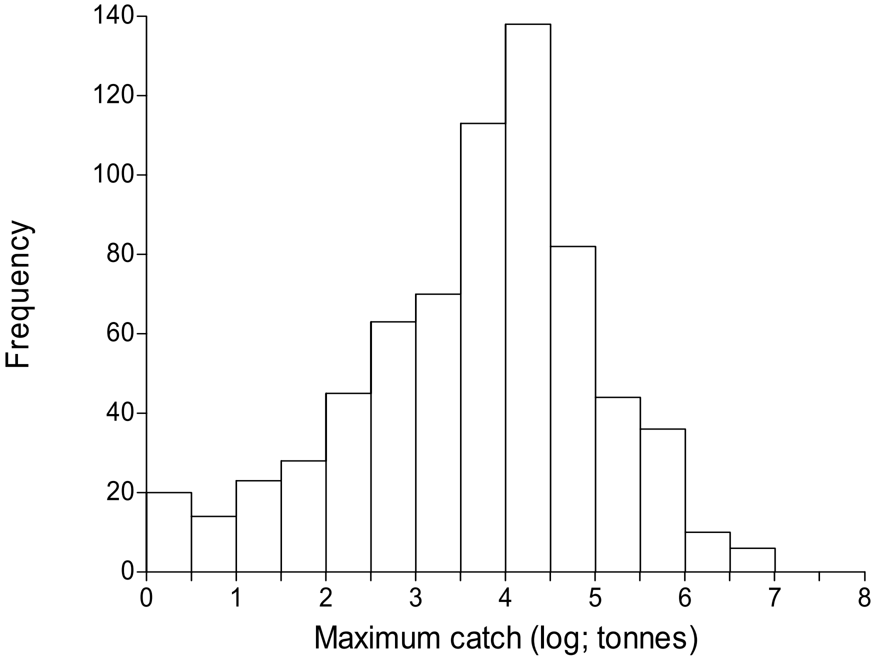


Figure 63. Frequency distribution of maximum catches in FAO statistics for 694 fish species; median = 7,732 tonnes. Note well-formed log-normal shape of right side of curve; left side of curve is distorted, probably by maximum catch data for species that are not yet fully exploited.

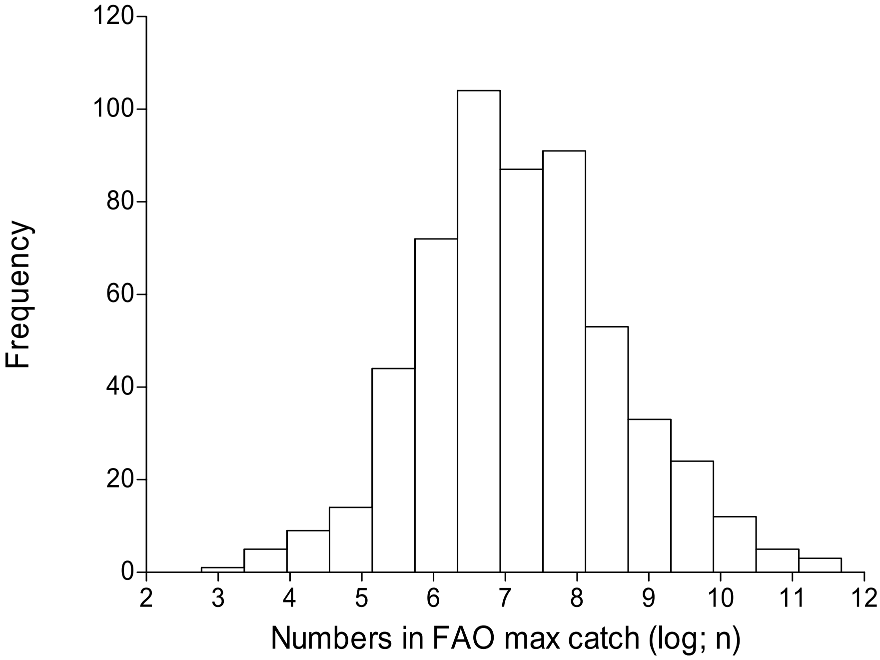


Figure 64. Frequency distribution of number of individuals in maximum FAO catches for 557 fish species, with median = 12 million individuals. Species with catches of less than 100 tons or less than 10 years with reported catch have been excluded.

Figure 63 shows the frequency distribution of maximum catches in FAO statistics for 694 species of fishes. The left-side tail is probably caused by maximum catches of species that are not yet fully exploited and thus their maximum catch has not yet reached the highest level.

This was corrected by excluding species with maximum catches of less than 100 tons or less than 10 years with reported catch. Figure 64 shows the resulting frequency distribution for 557 species, which is roughly symmetrical. Note, however, that the log scale of the x-axis normalizes an otherwise strongly right-skewed distribution, confirming the observation of Garthside (1928, unpublished thesis, cited in Williams 1964) that "we are forced to conclude that, despite the large number of individuals that characterize some species, the great bulk of species occur in relatively small numbers."

Connolly et al. (2005) studied the abundance of wrasses and parrotfishes at 100 sites in the Indo-Pacific and found an "excellent fit of the truncated log-normal distribution", where the truncation of the left side of the curve is caused by the fact that rare species are less likely to be sampled. Hubbell (2001) presents a unified theory of biodiversity and biogeography and predicts frequency plots of log-abundance to be negatively skewed, i.e., there will be more low-abundance or rare species than predicted by a log-normal distribution; according to him the extent of the negative skewness depends on the size of the community and the immigration rate, i.e., the relative number of new species entering the community. If we apply this interpretation to Figure 64, it means that the skewed left side of the graph is caused by the fact that new species—that are not yet fully exploited—are continuously entering FAO catch statistics, which is indeed the case (Froese and Kesner-Reyes 2002, Froese and Pauly 2003).

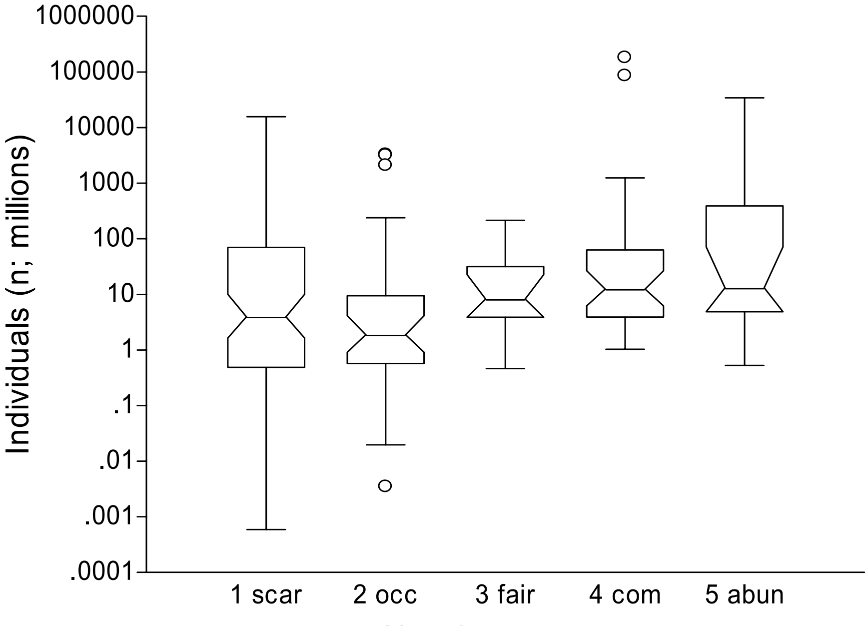


Figure 65. Number of individuals in FAO maximum catches by abundance in ecosystems, with 172 cases for 133 species with available data. Scarce with n = 74, median = 4.06, 95% CL = 1.527 – 12. 44; occasional with n = 34, median = 1.941, 95% CL = 0.776 – 5.118; fairly common with n = 11, median = 8.372, 95% CL = 0.609 – 31.53; common with n = 36, median = 12.774, 95% CL = 4.237 – 37.348; and abundant with n = 17, median = 13.365, 95% CL = 5.503 – 245.1.

FishBase 11/2004 contained indications of abundance by ecosystems, with the following categories; scarce (very unlikely); occasional (usually not seen); fairly common (chances are about 50%); common (usually seen); and abundant (always seen in some numbers). These categories have been adopted from bird watchers and their applicability to commercial fishes (in contrast to fishes caught by anglers or observed by divers) can be debated. Nevertheless, I explored the relationship between these independent estimates of abundance and the ones derived from FAO maximum catches.

Figure 65 shows the distribution of individuals by abundance categories for 133 species with available data. Despite the small number of available data and the high variance there is a clear increase in median individual numbers with abundance categories from occasional to abundant. The higher median and very high variance in the scarce category likely stems from the fact that some commercial fishes—such as those from deep waters or open oceans—are rarely observed, and that species that are abundant in one ecosystem may be scarce in another. Thus, for the purpose of this study I assume that individuals in FAO maximum catches can be used as a proxy for abundance of species.

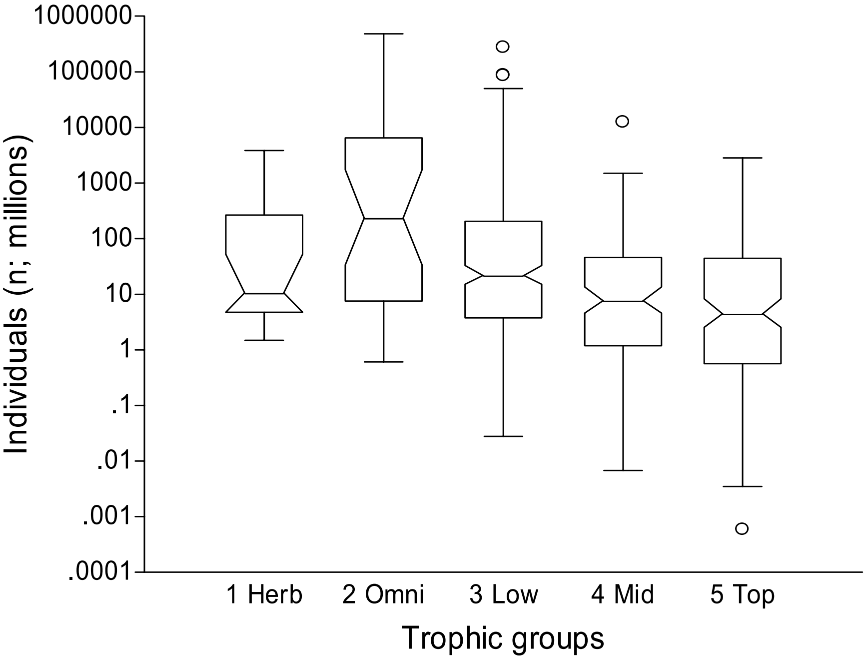


Figure 66. Number of individuals in FAO maximum catches of 557 fish species by trophic groups: 1 Herbivores with n = 16, median = 10.76, 95% CL = 4.69 – 141.9; 2 Omnivores with n = 29, median = 240.4, 95% CL = 18.0 – 2984; 3 Low-level predators with n= 265, median = 22.20, 95% CL = 13.37 – 42.80; 4 Mid-level predators with n = 113, median = 7.83, 95% CL = 4.29 – 13.79; and 5 Top predators with n = 134, median = 4.55, 95% CL = 2.24 – 7.10; with individual numbers in millions; for 33 species trophic level was not observed but derived from closest relatives as explained in the chapter *Building the Database for All Fishes.*

In Figure 66, I plotted the distribution of numbers of individuals by trophic groups as defined in Table 5. Median individual numbers decline from omnivores to top predators; herbivores have lower individual numbers than suggested by that trend. Decrease in abundance with increase in trophic level is expected as a direct result of the trophic biomass pyramid: Since biomass decreases about 10 fold per increase in trophic level, and as predatory fish tend to be larger then their prey (Pauly 2000a), it follows that there must be fewer predators than prey. See also Matthews et al. (1994) who observed an order of magnitude difference in abundance of *Micropterus* spp. and their potential prey.

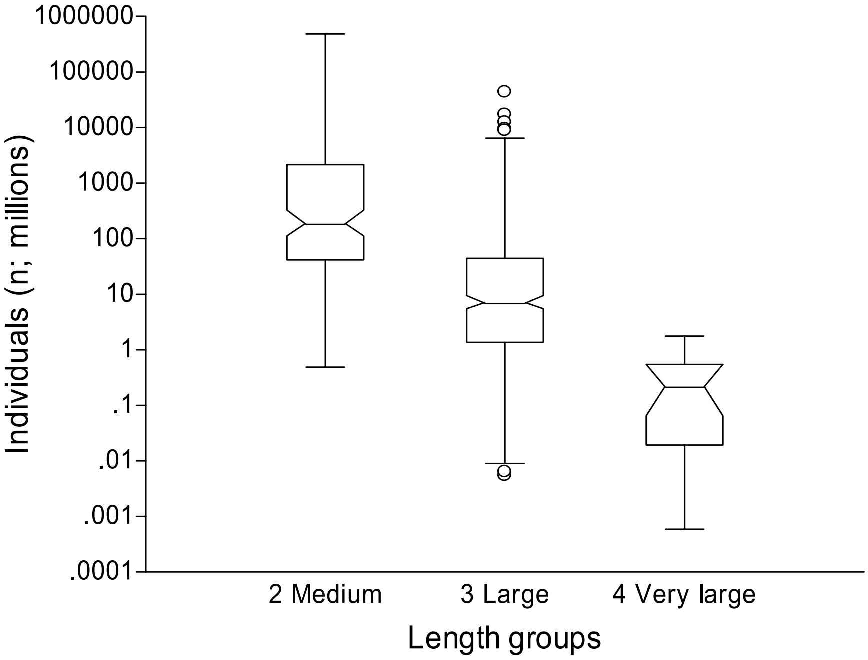


Figure 67. Number of individuals in FAO maximum catches by length group for 557 species of fishes: 2 Medium length (6.6 – 46 cm TL, n = 135, median = 190.3, 95% CL = 116.4 – 476.4), 3 Large length (>46 – 323 cm TL, n = 404, median = 7.16, 95% CL = 5.50 – 9.03) and 4 Very large length (> 323 cm TL, n = 18, median = 0.22, 95% CL = 0.022 – 0.51); individual numbers in millions.

Figure 67 shows the distribution of numbers of individuals by length groups as defined in Table 4. Small fishes (< 6.6 cm maximum length) were not present in the catch data. Median numbers of specimens decrease and are significantly different between size groups. This decrease in abundance with increase in body size has been found in many natural assemblages of animals and a linear negative relationship is the typical pattern of large-scale interspecific compilations such as used here (Blackburn and Gaston 1997). This has been linked with metabolic rate in that maintenance of a certain number of large animals requires more energy than the same number of small animals; if small and large animals have the same access to energy and if energy is a limiting factor, which will be true at least for the most abundant species in a given ecosystem (Blackburn et al. 1993), then the abundance of large species must be less (Damuth 1975). Productivity as used in this study is a proxy for metabolic rate (Figure 3) and thus this reasoning also explains the decrease of abundance with decrease in productivity shown in Figure 68 below.

Blackburn and Gaston (1997) stressed that the observed trend of decreasing abundance with size can also be explained by just looking at extremes of species density: At very high density, more small than large species can obviously be packed in a given area; conversely, at very low densities the likelihood of finding a mate and reproducing within the lifetime of an individual drastically decreases; as shown elsewhere in this study, large species tend to be more migratory (Figure 32 and Figure 59) and longer lived (K as shown e.g. in Figure 22 is a proxy for maximum age t_{max} = 3/K (Taylor 1958)) and thus are more likely to persist at low densities.

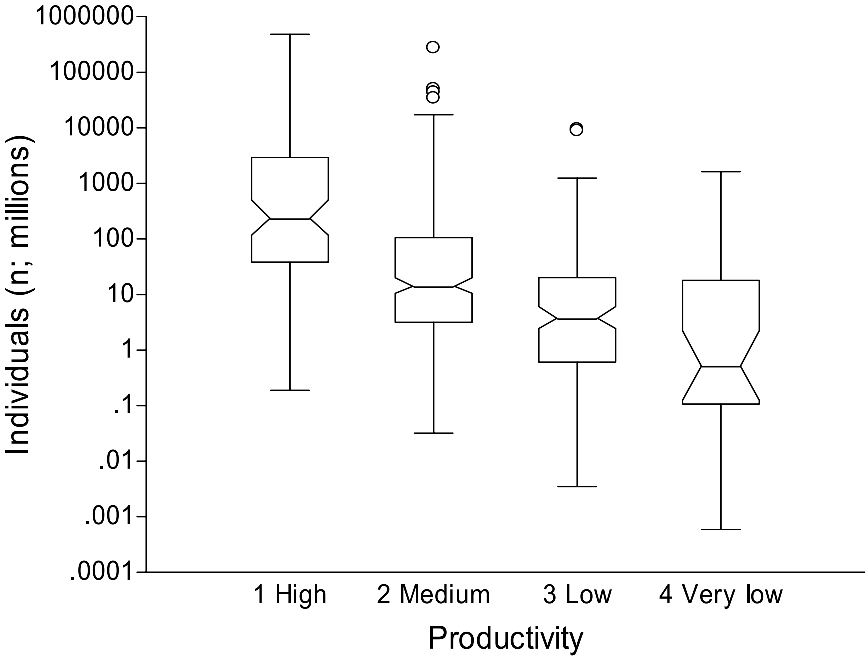


Figure 68. Number of individuals in FAO maximum catches by productivity groups for 557 species of fishes. Median numbers of specimens were significantly different for 1 High productivity (n= 86, median = 240.9, 95% CL = 155.7 – 755.5), 2 Medium productivity (n = 292, median = 14.4, 95% CL = 9.32 – 24.1), and 3 Low productivity (n = 148, median = 3.83, 95% CL = 1.99 – 5.85); the confidence limits of 4 Very low productivity (n = 31, median = 0.526, 95% CL = 0.212 – 5.61) overlap with those of Low productivity; individual numbers in millions.

The above figures show that small to medium sized species relatively low in the food web with medium to high productivity have the highest numbers of individuals; conversely, large top predators with low productivity have significantly smaller numbers of individuals. These surprisingly clear and expected trends increase confidence that numbers of individuals can indeed be derived from FAO maximum catches. Trophic level, maximum length and productivity can then be used to predict number of individuals. The following model (multiple regression analysis in Hintze (2001)) explains 47% of the variance:

log Individuals = 5.904 - 2.570 * Log Length - 0.0198 * Troph + 0.5480 * (1 if Productivity=High; else 0) + 0.2292 * (1 if Productivity=Medium; else 0) + 0.0952 * (1 if Productivity=Low; else 0)

Approximate 95% lower and upper confidence limits (CL) can be obtained from

Log lower CL = log Individuals * (1 – 1.96 * 0.8348)
Log upper CL = log individuals * (1 + 1.96 * 0.8348)

Equation 15. Estimating abundance from maximum length, trophic level and productivity, where n = 557, r^2 = 0.4668, coefficient of variation = 0.8348, with individuals in millions.

In combination with the area of occupancy (IUCN 1994, see below), this equation could eventually be used for estimating density, i.e., whether a species is likely to be abundant or rare.

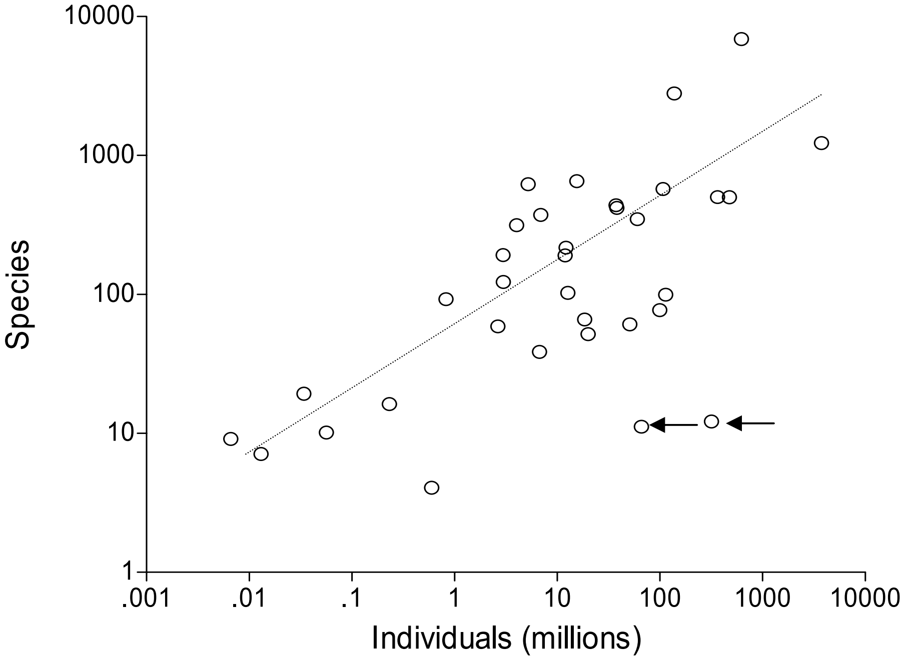


Figure 69. Number of species using a strategy versus geometric mean of individuals per species associated with a strategy. The two points on the lower right (arrows) were identified as outliers (robust weight 0.003 and 0.071) and were excluded from the regression.

I have established above that certain combinations of size, trophic level, and productivity are likely to result in higher number of individuals for the species that have adopted that strategy. An interesting question is whether such strategies are more attractive, i.e., are used by a higher number of species. Figure 69 shows a positive correlation between the numbers of species using a strategy versus the mean abundance (number of individuals per species) associated with that strategy. A linear regression analysis explained 62% of the variance and can be expressed by the model:

$$\log \text{Species} = 1.718 + 0.437 * \log \text{Individuals}$$

Equation 16. Number of species as a function of mean abundance per strategy, with n= 32, r^2 = 0.6216, coefficient of variation = 0.2214. The two data points on the lower right in Figure 69 were identified as outliers in robust regression analysis (robust weight = 0.003 and 0.071) and were excluded from the regression.

In this context a statement of Williams (1964) is of interest: “Both very small and very large numbers within a species may bring dangers. In bisexual animals, low numbers result in a difficulty in finding a mate, hence very rare animals are usually also very localized. On the other hand, large numbers bring the dangers of increase or concentration of enemies, or of epidemic diseases; and also dangers of starvation, particularly when the food supply itself fluctuates in abundance, either seasonally or over longer periods.” Thus, while the relationship shown in Figure 69 holds, it is also apparent that most strategies have intermediate abundance and number of species, and very low and very high abundances are in fact rare, as was already shown by the frequency distribution in Figure 64.

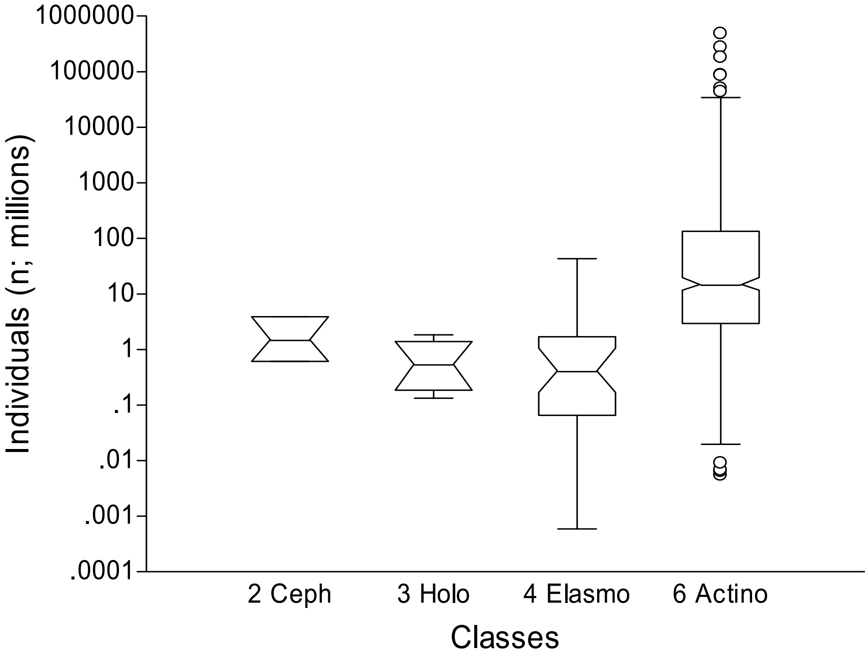


Figure 70. Numbers of individuals per species in FAO maximum catches by phylogenetic Class: Cephalaspidomorphi with n = 2, median = 2.24; Holocephali with n = 4 and median = 0.559; Elasmobranchii with n = 31, median = 0.421, 95% CL = 0.0889 – 1.50; Actinopterygii with n = 520, median = 15.1, 95% CL = 10.2 – 24.2; individual numbers in millions.

Figure 70 shows the distribution of numbers of individuals per species in FAO maximum catches by phylogenetic Class. No maximum catch data were available for Myxini and Sarcopterygii, and Cephalaspidomorphi and Holocephali were represented by only 2 and 4 species, respectively. While Elasmobranchii are heavily fished, their overall contribution to world fisheries is much less then that of Actinopterygii (Bonfil 1994) and data at the species level were only available for 31 species showing relatively low numbers of individuals. As expected, Actinopterygii had the highest species numbers and significantly more individuals per species than any of the other Classes.

In summary, FAO maximum catches can be used to estimate natural abundances of fishes. Abundance increases with productivity and decreases with size and trophic level. Life-history strategies that are associated with high abundances are used by more species than other strategies.

Area of Distribution

Another potential measure of success of life-history strategies is the mean area of occupancy per species associated with a strategy, thus inverting the argument for threat associated with small and shrinking areas of occupancy (IUCN 1994). Since information on area of occupancy was not directly available for most fishes, I used latitudinal range as a proxy for overall range, similar to Winemiller and Rose (1992) and many other authors.

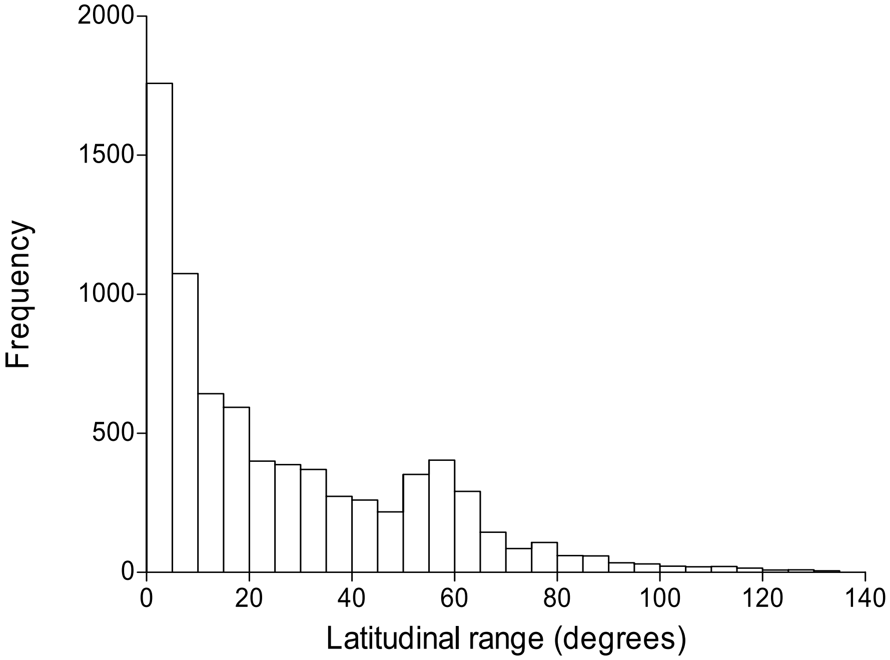


Figure 71. Frequency distribution of latitudinal range for 7,639 marine and freshwater species of fishes.

Figure 71 shows the frequency distribution of latitudinal ranges of species for 7,639 marine and freshwater fishes with available data. The graph has a bimodal, composite distribution and is difficult to interpret in this format.

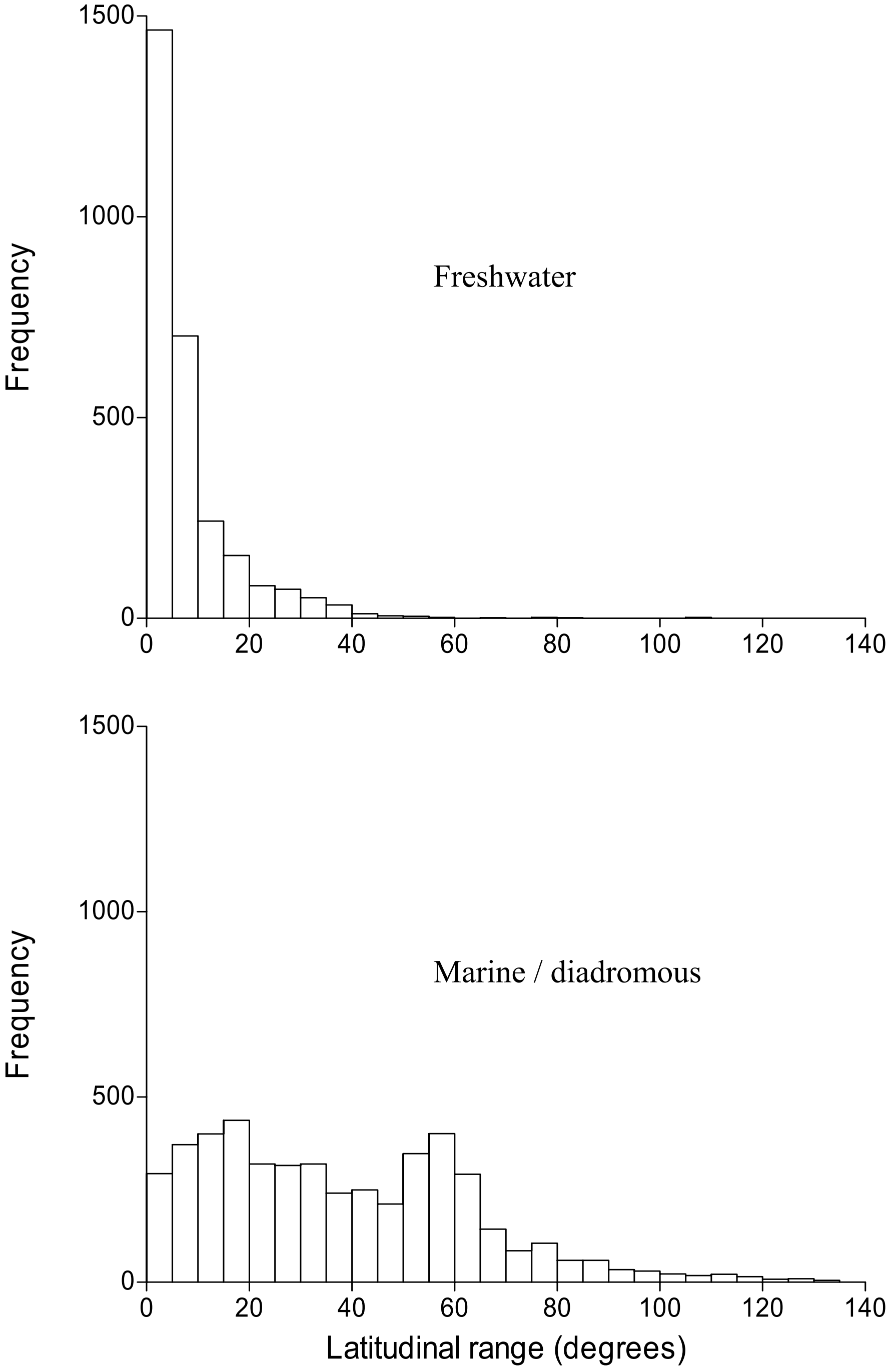


Figure 72. Frequency distribution of latitudinal range for 2,833 primary freshwater (upper) and 4,806 marine and diadromous (lower) fish species. Median range for primary freshwater fishes is 5 degrees (n = 2,833, 95% CL = 5 – 6) and for marine and diadromous fishes 35 degrees (n = 4,806, 95% CL = 34 – 36).

Figure 72 shows separate frequency distributions for 2,833 primary freshwater and 4,806 marine and diadromous fishes. The distributions for freshwater and marine fishes are significantly different: primary freshwater fishes show a steep and roughly exponential decline from many species with narrow ranges (median range = 5 degrees) to few species with wide ranges, with very few species having ranges beyond 60 degrees. This corresponds to most freshwater lakes and ecotopes within river basins having less than 5 degree latitudinal range. In contrast, marine and diadromous fishes show a bimodal distribution with a first peak around 15 – 20 degrees and a second peak between 55 and 60 degrees, with a median range of

35 degrees and many species having ranges beyond 60 degrees. With continuous north-south orientation of most continental coast lines, marine fishes are less restricted by geographic boundaries with respect to latitudinal ranges. Instead, preferred temperature provides a physiological barrier as already demonstrated by the successful assignment of most species to climate zones (see Figure 34). The range of the first peak roughly corresponds to the latitudinal range of the temperate and subtropical climate zones, whereas the range of the second peak is slightly larger than the latitudinal range of the tropical zone.

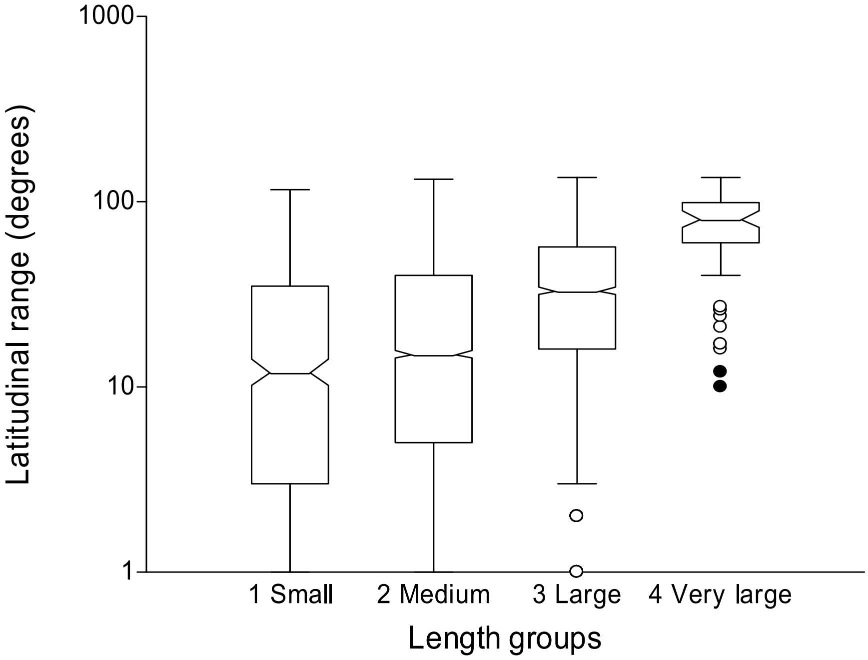


Figure 73. Latitudinal range by length group for 7,363 species of fishes. Median latitudinal range increase significantly from Small (n = 553, median = 12, 95% CL = 10 – 15) and Medium (n = 4,842, median = 15, 95% CL = 14 – 15) to Large (n = 1,910, median = 33, 95% CL = 31 – 34) and Very large (n = 58, median = 80.5, 95% CL = 72 – 86).

Figure 73 shows latitudinal ranges by length groups. There is a clear and significant increase in median latitudinal range with size from small to very large species confirming the finding by Taylor and Gotelli (1994) and Goodwin et al. (2005) that body size and range size are positively correlated. Notably, with few exceptions very large fishes apparently cannot exist with latitudinal ranges of less than 10 degrees. This confirms the positive correlation of maximum length with latitudinal range found by Winemiller and Rose (1992); surprisingly, in their Table 2 length at maturity is negatively correlated with latitudinal range. However, this negative sign in front of the 0.36 value for the correlation of latitudinal range and length at maturity was a printing error (K. Winemiller, Texas A&M University, pers. comm. 2005).

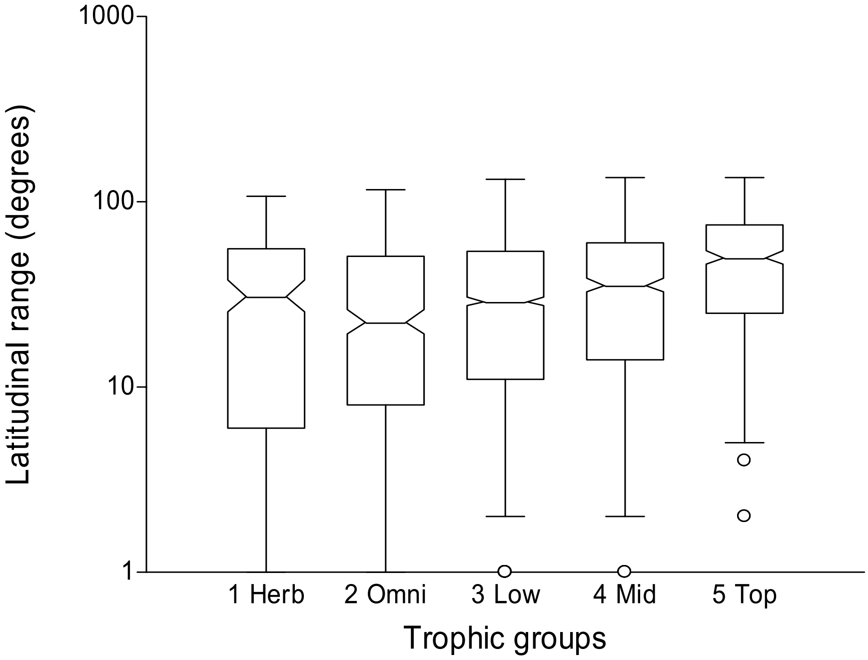


Figure 74. Latitudinal range by trophic groups for 4,058 species of fishes. With the exception of 1 Herbivores (n = 312, median = 31, 95% CL = 23 – 37) the median range increase significantly from 2 Omnivores (n = 368, median = 22.5, 95% CL = 17 – 27) to 3 Low-level predators (n = 2207, median = 29, 95% CL = 27 – 31), 4 Mid-level predators (n = 746, median = 35.5, 95% CL = 32 – 39) and 5 Top predators (n = 425, median = 50, 95% CL = 43 – 56).

Figure 74 shows the distribution of latitudinal ranges by trophic groups for 4,058 species with available data. While the maximum ranges are very similar across groups, the median latitudinal range increases significantly from omnivores to top predators. Notably, predators and especially top predators do not have very narrow ranges. Herbivores have the widest interquartile range and confidence limits for the median, suggesting that they have no strong preference with regard to latitudinal ranges.

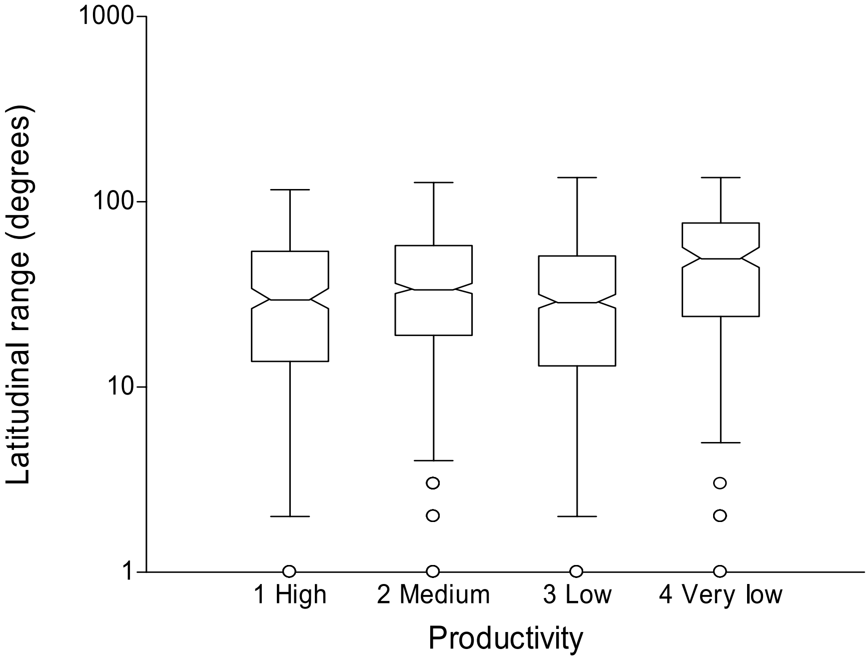


Figure 75. Latitudinal range by productivity for 1,891 species of fishes. Confidence limits for latitudinal range overlap for 1 High (n = 294, median = 30, 95% CL = 25 – 34) with 2 Medium (n = 758, median = 34, 95% CL = 32 – 36) and 3 Low productivity (n = 627, median = 29, 95% CL = 25 – 31); however, median latitudinal range is significantly higher for 4 Very low productivity (n = 212, median = 50, 95% CL = 42 – 58).

Figure 75 shows the distribution of latitudinal ranges by productivity groups for 1,891 species with available data. Ranges of species with high to low productivity are similar. However, species with very low productivity have significantly higher median latitudinal ranges.

A robust multiple regression (Hintze 2001) predicting latitudinal range from trophic level, maximum length, and productivity explained only 14% of the variance; when tolerance for saltwater (Yes/No) was included 32 % of the variance was explained and resulted in the model

$$\log \text{LatRange} = 1.030 + 0.3114 * \log \text{MaxLength} - 0.006520 * \text{Troph} + 0.1282 * (1 \text{ if Productivity=High; else } 0) + 0.0590 * (1 \text{ if Productivity = Medium; else } 0) - 0.06354 * (1 \text{ if Productivity = Low; else } 0) - 0.3525 * (1 \text{ if Saltwater = No; else } 0)$$

Equation 17. Latitudinal range as a function of length, trophic level, productivity and salinity tolerance, with n = 1541, r^2 = 0.3161 and coefficient of variance = 0.1772 and where LatRange is the latitudinal range in degrees, MaxLength is the maximum total length in cm, and troph is the trophic level.

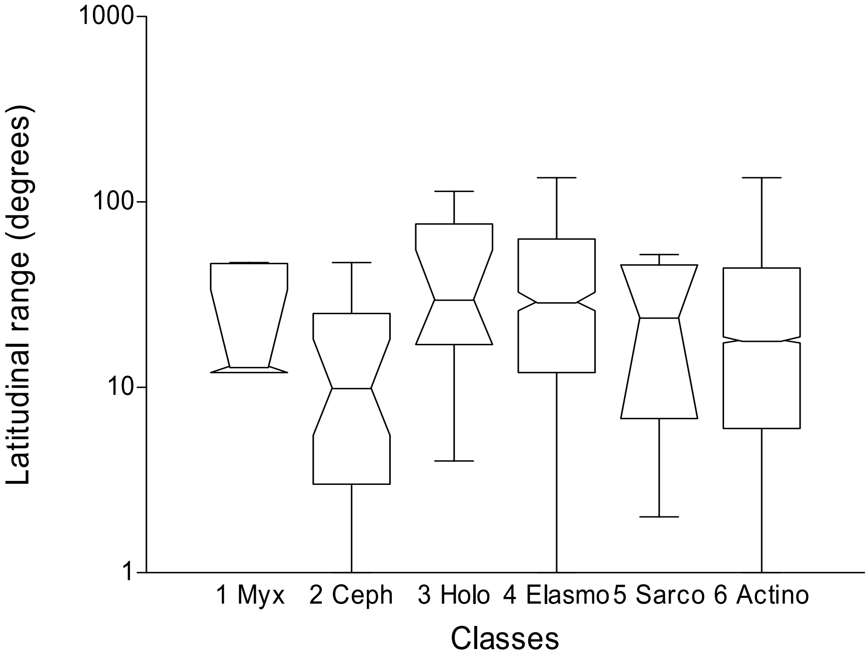


Figure 76. Latitudinal range by phylogenetic Class for 7,639 species of fishes: 1 Myxini (n = 5, median = 13), 2 Cephalaspidomorphi (n = 31, median = 10, 95% CL = 4–22), 3 Holocephali (n = 15, median = 30, 95% CL = 17–76), 4 Elasmobranchii (n = 511, median = 29, 95% CL = 25–33), 5 Sarcopterygii (n = 5, median = 24) and 6 Actinopterygii (n = 7072, median = 18, 95% CL = 17–18).

Figure 76 shows the distribution of latitudinal ranges by phylogenetic Class for 7,639 species with available data. Confidence limits for median latitudinal range are very wide and overlapping for the species-poor Classes of Myxini, Cephalaspidomorphi, Holocephali and Sarcopterygii. The restriction of Myxini to ranges beyond 10 degrees latitudinal range may stem from the fact that data for only 5 species were available. Median latitudinal range was significantly larger for Elasmobranchii than for Actinopterygii, reflecting the previously discussed trends in the sense that Elasmobranchii tend to be large to very large marine mid- to top predators with low to very low productivity.

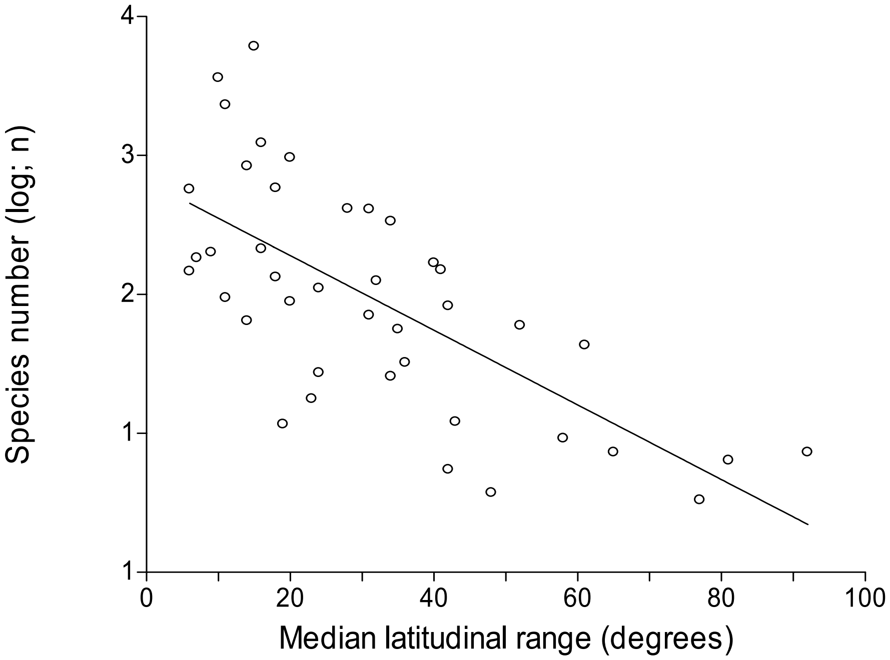


Figure 77. Number of species per life-history strategy versus respective median latitudinal range. The regression line is described by the model log Species = 2.964 – 0.02351 * LatRange with n = 41, r^2 = 0.4787 and coefficient of variance = 0.2391.

An interesting question is whether life-history strategies associated with large latitudinal ranges are used by more species than other strategies, and the answer is no. Figure 77 shows a plot of species per life-history strategy versus respective median latitudinal range. The linear regression line explains 48% of the variance. Most species are associated with life-history strategies that have median latitudinal ranges between 5 and 20 degrees; thereafter species numbers gradually decline with further increase in latitudinal range.

In summary, large and very large top predators with very low productivity such as sharks tend to have broader latitudinal ranges than small to medium-sized omnivores or low-level predators with low to high productivity. Herbivores do not show a clear preference and may have narrow ranges, such as the algae-scrapping ‘mbuna’ cichlids of Lake Malawi, or very wide ranges such as the algae-eating damsel fishes of the Indo-Pacific. Overall, most species have latitudinal ranges between 5 and 20 degrees.

Impact

As can be seen from the signs of the factors in Equation 17 and also from Figure 69 and Figure 77, latitudinal range and number of individuals show opposite trends in their correlation with number of species associated with strategies and thus counter-balance each other. This seems to make sense: A strategy associated with very wide ranges but very low abundances and also a strategy with very high abundance but very narrow distribution would appear less desirable than an intermediate strategy maximizing the combination of abundance and range rather than the parts. A multiple regression of number of species versus mean number of individuals and median latitudinal range associated with a strategy explained 56% of the variance and is described by the model:

$$\log \mathrm{Spec}_n = 2.938 - 0.02218 * \mathrm{LatRange} + 0.06867 * \log \mathrm{IndivN}$$

Equation 18. Number of species using a strategy as a function of abundance and latitudinal range, with n = 31, $r^2 = 0.5596$, coefficient of variance = 0.2354, where Spec_n is the number of species, LatRange is the median latitudinal range, and IndivN is the geometric mean of individuals associated with a strategy.

In order to establish a single measure for the relevance or impact of a strategy I combined number of individuals and latitudinal range as follows:

1) I used estimates of abundance as derived from FAO maximum catches and latitudinal range as available for 557 species.
2) I normalized the log values for individuals and latitudinal range by dividing the values by the respective maximum value.
3) I defined the combined value for individual numbers and range of a species as Impact = log normalized latitudinal range * log normalized number of individuals.

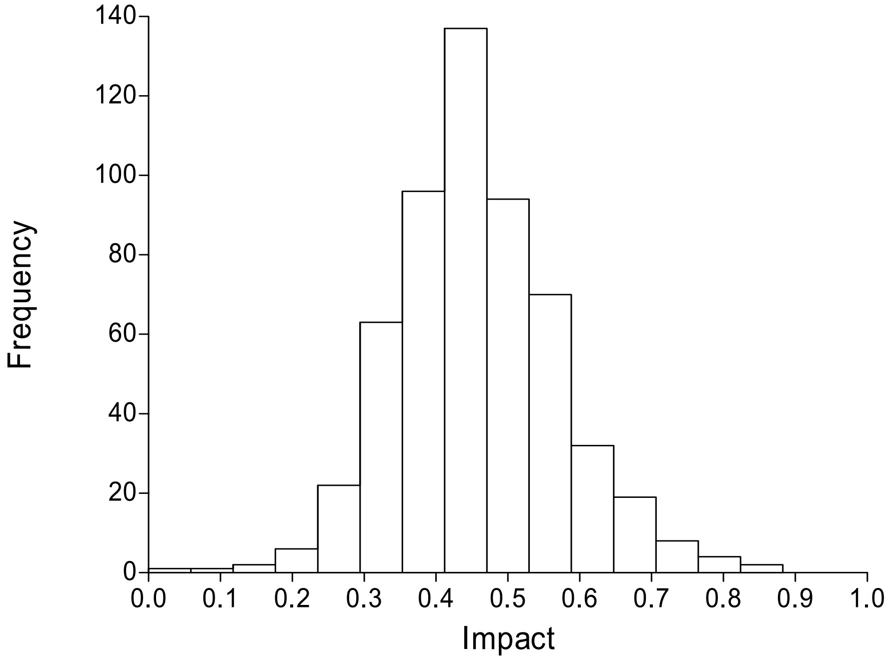


Figure 78. Frequency distribution of Impact for 557 species with available data, mean = 0.457, 95% CL = 0.447-0.466. Note that normality is rejected by formal tests but is still assumed for the purposes of this study.

The frequency distribution of Impact is shown in Figure 78 and is roughly normally distributed although slightly skewed to the right. I assumed normal distribution for the purpose of this study. Table 76 gives an overview of the descriptive statistics with mean individuals, median latitudinal range and mean impact for 49 strategies with available data. The impact of most strategies is not significantly different from the overall mean. Only two strategies have significantly higher impact: medium-sized low-level predators with high productivity and medium-sized omnivores with high productivity. The first is the strategy with highest rank in Table 16 used by 33% of the species; the second has rank 4 and is used by 6% of the species.

In summary, in this chapter I have shown that there are strong correlations between the life-history strategies derived by combining size, trophic level and productivity and the independently derived estimates for abundance and distributional range. Recent species show preference for strategies associated with high abundances or small to medium ranges. When abundance and range are combined into a single measure of 'Impact' most strategies have a mean impact that is not significantly different from the overall mean, i.e., abundance and range counterbalance each other. Only two strategies show significantly higher impact than other strategies: medium-sized low-level predators with high productivity, which also is the strategy preferred by the highest number of species, and medium-sized omnivores with high productivity, which ranks 4 in the list of preferred strategies. Note, however, that this analysis excluded the many small fishes for which no FAO catch data were available.

Table 76. Forty-nine life-history strategies with mean number of individuals, median latitudinal range, mean impact and associated number of species. Overall mean impact is 0.445, n=34, 95% CL = 0.419–0.471 (Table continued on next page).

Trophic group	Length group	Productivity	Individuals geom. mean, 95% CL, (n) millions		Latitudinal range median, 95% CL*, (n) degrees		Impact mean, 95% CL, (n)		Species n, %	
Herbivores	Small	High			35	25 - 46 (19)			108	0.44
	Medium	High	370	21.6 - 6382 (3)	6	5 - 11 (94)	0.46	0.386 - 0.535 (3)	248	1.00
		Medium	38.8	0.06 - 23358 (2)	28	17 - 41 (165)	0.52	0.327 - 0.713 (2)	615	2.48
		Low			7	3 - 54 (13)			301	1.22
	Large	High	323	(1)	26	9 - 30 (3)	0.48	(1)	4	0.02
		Medium	12.9	5.61 - 29.8 (8)	36	23 - 54 (36)	0.48	0.429 - 0.524 (8)	66	0.27
		Low	2.69	1.80 - 4.01 (2)	31	16 - 54 (43)	0.45	0.388 - 0.516 (2)	131	0.53
		Very low			46	(1)			12	0.05
Omnivores	Small	High			16	10 - 30 (39)			343	1.39
		Medium			4	(1)			10	0.04
	Medium	High	3808	854 - 16980 (12)	6	5 - 9 (229)	0.60	0.531 - 0.669 (12)	815	3.29
		Medium	483	24.9 - 9394 (5)	13	10 - 17 (240)	0.50	0.367 - 0.634 (5)	1,145	4.65
		Low	67.3	(1)	11	6 - 16 (49)	0.49	(1)	169	0.68
	Large	Medium	18.8	2.44 - 144 (11)	34	21 - 53 (32)	0.47	0.372 - 0.564 (11)	54	0.22
		Low			14	9 - 30 (43)			121	0.49
		Very low			8	4 - 70 (6)			17	0.07
Low-level predators	Small	High			11	10 - 15 (449)			2,770	11.2
		Medium			9	4 - 15 (53)			327	1.32
		Low			4	3 - 8 (3)			18	0.07
	Medium	High	633	273 - 1466 (40)	10	9 - 11 (1346)	0.54	0.494 - 0.582 (40)	4,108	16.6
		Medium	141	59.9 - 329 (44)	15	14 - 17 (1834)	0.50	0.464 - 0.531 (44)	6,465	26.1
		Low	61.3	35.7 - 105 (3)	16	13 - 18 (421)	0.26	0.005 - 0.522 (3)	1,597	6.45
		Very low			23	2 - 28 (19)			39	0.16
	Large	High	51.8	4.66 - 575 (7)	43	22 - 60 (19)	0.50	0.424 - 0.567 (7)	28	0.11
		Medium	15.8	10.2 - 24.4 (104)	34	31 - 39 (277)	0.45	0.434 - 0.472 (104)	512	2.07
		Low	5.29	2.46 - 11.4 (57)	20	18 - 24 (523)	0.41	0.378 - 0.438 (57)	1,289	5.23
		Very low	12.4	1.85 - 82.4 (9)	24	19 - 31 (100)	0.42	0.355 - 0.494 (9)	194	0.78

Trophic group	**Length group**	**Productivity**	**Individuals geom. mean, 95% CL, (n) millions**		**Latitudinal range median, 95% CL*, (n) degrees**		**Impact mean, 95% CL, (n)**		**Species n, %**	
	Very large	Very low	0.06	(1)	48	26 - 124 (10)	0.40	(1)	10	0.04
Mid-level	Small	High			16	4 - 29 (2)			12	0.05
predators	Medium	High	109	23.70 - 501.81 (9)	32	17 - 42 (71)	0.52	0.454 - 0.588 (9)	216	0.87
		Medium	38.1	13.6 - 107 (11)	18	16 - 24 (321)	0.46	0.410 - 0.504 (11)	833	3.38
		Low			18	12 - 22 (88)			228	0.92
		Very low			42	10 - 92 (7)			14	0.06
	Large	High	20.4	3.71 - 111 (4)	19	12 - 29 (14)	0.40	0.280 - 0.525 (4)	27	0.11
		Medium	7.02	3.51 - 14.0 (48)	41	37 - 49 (145)	0.44	0.414 - 0.469 (48)	253	1.02
		Low	4.10	1.93 - 8.70 (35)	31	27 - 36 (325)	0.42	0.393 - 0.445 (35)	610	2.46
		Very low	3.03	0.12 - 74.0 (4)	52	35 - 59 (82)	0.46	0.331 - 0.589 (4)	113	0.46
	Very large	Low	0.01	(1)	79	63 - 82 (5)	0.32	(1)	7	0.03
		Very low	0.01	(1)	77	12 - 92 (7)	0.20	(1)	9	0.04
Top	Medium	High	101	0.15 - 68704 (2)	65	6 - 72 (11)	0.56	0.469 - 0.648 (2)	18	0.07
predators		Medium	116	59.1 - 227 (3)	20	13 - 36 (63)	0.43	0.224 - 0.632 (3)	160	0.65
		Low			24	12 - 33 (26)			57	0.23
	Large	High	6.83	1.20 - 38.8 (8)	58	20 - 73 (11)	0.47	0.414 - 0.522 (8)	22	0.09
		Medium	12.2	6.56 - 22.8 (52)	42	36 - 55 (112)	0.48	0.458 - 0.504 (52)	150	0.61
		Low	2.90	1.28 - 6.55 (43)	40	34 - 46 (186)	0.41	0.388 - 0.439 (43)	280	1.13
		Very low	0.84	0.17 - 4.21 (11)	61	44 - 74 (60)	0.43	0.350 - 0.512 (11)	85	0.34
	Very large	Medium	0.61	0.27 - 1.38 (4)	85	10 - 95 (5)	0.45	0.421 - 0.485 (4)	5	0.02
		Low	0.24	0.04 - 1.26 (6)	81	60 - 113 (15)	0.38	0.307 - 0.445 (6)	16	0.06
		Very low	0.03	0.00 - 0.30 (5)	92	69 - 110 (16)	0.38	0.303 - 0.457 (5)	18	0.07

* For latitudinal ranges based on less then 7 records the minimum and maximum values are shown instead of the 95% confidence limits.

Some Meta-Analyses

Critique of Data and Methods

Data and methods used in this study were not free of errors and biases, which I discuss below.

Maximum reported total length of a species was taken as a proxy for maximum size, which is typically given as maximum body weight. Total length overestimates weight in eel-like fishes or those with very long tails or caudal fins; it underestimates weight in spherical and short & deep fishes. Also, in rare fishes, maximum length is based on the few specimens deposited in museums and may be underestimated; in fishes with a long history of exploitation maximum size is based on historical records whereas recent stocks have been modified by fisheries towards smaller sizes and earlier maturity. In FishBase 11/2004 length data were available for over 23,000 species of fishes, 15 times more than for maximum weight, making it the preferred measure of size despite the above short-comings. A similar decision for use of length instead of weight was made by Winemiller and Rose (1992), Vila-Gispert et al. (2002), and other authors.

Trophic level as available in FishBase 11/2004 was only rarely based on representative studies of diet composition. In most cases it was based on few unquantified reported food items which have been transformed to trophic levels with the help of a Monte Carlo routine and a standardised assignment of trophic levels to types of food items (Pauly and Palomares 2000). These standardised assignments result in an artificial upper limit to trophic levels, visible in the peak near 4.5 in Figure 2. Also, trophic level does not distinguish between true herbivores feeding on living plants and detritivores feeding on mixed debris consisting mainly of dead plant matter but also containing some animal remains, all of it partly pre-digested by bacteria; this made it difficult to distinguish between true herbivorous strategies and detrivore strategies, which are, e.g., used by ammocoetes larvae of lampreys and thus may be much older. Despite of these shortcomings, trophic level is now widely accepted as a useful ecological parameter (e.g. Pauly et al. 1998, Pauly and Watson 2005) and in FishBase 11/2004 it was available for over 7,500 species making it a parameter of choice, rather than using broadly defined discrete groups of detritivores/herbivores, omnivores, invertebrate feeders and piscivores (Winemiller and Rose 1992), but see below comments on classification of trophic levels.

Estimates of the maximum intrinsic rate of population increase (r_{max}) are only known for a few dozen fish species. Productivity as used in this study is a proxy for r_{max} based on an empirical approach suggested by Musick (1999), which includes assumptions about the correlation of traits (see columns in Table 6). Productivity was often determined from one parameter only, such as low fecundity in sharks or maximum age or age at maturity in many temperate bony fishes. However, the positive correlation of productivity with independent estimates of metabolism (Figure 3) and activity (Figure 4) confirm the usefulness of this parameter. In FishBase 11/2004 productivity estimates were available for over 2,800 species, i.e., 10 times more than for metabolism, two times more than for activity (which because of the method was also limited to fishes with well developed caudal fins and certain types of swimming, (Pauly 1989)), and two orders of magnitude more than for r_{max}, making it the parameter of choice.

For the purpose of defining discrete life history strategies, I transferred the continuous parameters (length and trophic level) into classes of values. This had the advantage of easy communication and simple graphic representation, e.g. in box plots. It has the disadvantage of arbitrary classification of species near the class-borders, i.e., a few millimetres increase in length would change a species assignment from small to medium size. Where appropriate, I used the continuous variables, especially when other parameters were discrete, such as reproductive modes or migratory behaviour.

The grouping of length from small to very large using logarithmic-scale standard deviations is original as far as I know. The resulting length classification fitted the length frequency distribution (Figure 1) and also the evolutionary grouping of length by phylogenetic Class (Figure 11) well.

Grouping of trophic levels followed an approach used by Palomares (2000) to transform trophic levels into the widely used categories of herbivores, omnivores, and several levels of predators and captured the peaks in the frequency distribution of trophic levels well (Figure 2).

The above comments on data and methods make it clear that the assignment of species to traits and to life-history strategies in this study is subject to errors and biases, and can only be preliminary. Special attention was given to potential phylogenetic bias, resulting from 'unnatural' distribution of available data with respect to Classes of fishes. Among others, an extended data set was used to detect phylogenetic biases as well as such caused by data being mostly available for medium to large sized, commercial fishes from shallow, temperate northern-hemisphere areas. Such biases have been taken into account when the respective results were presented. Unbiased errors in a data set of this size are likely to balance each other. Thus, while the assignment to strategies may be erroneous for several species, the trends and statistically significant results presented in this study are expected to hold even if such errors are detected and corrected and if additional data become available.

General Properties of Life-History Strategies

Over 2/3rd of recent life-history strategies were 'invented' only 200-150 million years ago during several radiations of Actinopterygii. New inventions include small size, very large size (invented in parallel by Elasmobranchii), high productivity and true herbivory as opposed to detrivory (Table 22).

There is evidence for an exponential increase in trade-offs associated with life-history strategies (Table 16). Matthews (1998) explain this as follows: A successful strategy with few constraints will be used by many species until competition for similar resources increases and becomes a constraint in its own right, to a point where another strategy with originally more trade-offs becomes attractive because it has less competition. This 'spill-over' effect continues until physical or physiological boundaries are reached that prevent the usage of certain potential life-history strategies, such as very large size and high productivity.

Families that have many species but use few strategies only are not specialists in the sense that they are the dominant users of an otherwise rarely used strategy (Figure 31 and Table 21); rather, they make more-than-expected use of the few most popular strategies, possibly an indication that in their respective area, this niche has not yet been occupied to the extent that competition makes it less attractive.

Similarly, strategies used by polar species are widely used ones not restricted to cold waters. Rather, most other strategies with presumably higher trade-offs are not suitable for the polar zones, notably those with low trophic level, small or very large size, or high productivity (Table 47).

Testing of Selection Theories

Nine selection theories (Table 1) were tested as to their ability to correctly predict adaptation of life-history traits such as numbers of species and strategies, size, productivity and trophic level in response to environmental conditions in freshwater versus marine habitats, climate zones, zoogeographic realms, oceans, and habitat types.

r-K theory made 48 predictions altogether for size and productivity based on environmental conditions being classified as relatively variable or stable. Of these predictions 19 (39.6%) were supported by the data, which is less than 50% correct predictions expected by chance. r-K theory mostly failed when its predictions were in conflict with those of temperature theory (25 cases). It also wrongly predicted larger size and lower productivity for pelagic versus benthopelagic habitats, on the assumption that pelagic habitats of mostly marine species were more stable than benthopelagic habitats which included many freshwater species. r-K theory sometimes prevailed when in conflict with temperature theory (4 cases), trophy theory (3 cases), and succession plus temperature theories (1 case). The strongest overlap was with succession theory, with 46 (95.8%) of 48 predictions being identical. Of 25 predictions for size 11 (44%) were supported by the data; of 23 predictions for productivity 8 (34.7%) were supported by the data. Under a more appropriate ‘all else being equal except variability of the environment’ scenario where only cases not in conflict with the predictions of other strategies were considered, 92.3% of 13 predictions were correct (see Table 77).

Succession theory made 98 predictions altogether for numbers of species and strategies, size, productivity, and trophic diversity based on environmental conditions being classified as relatively less or more mature. Of these predictions 54 (mean = 56.5%) were supported by the data, which is not significantly more than random prediction (t-value = 1.260, n = 5 environmental scenarios, probability level 56.46 > 50 = 0.1382, power (0.05) = 0.2766). Succession theory failed when its predictions were in conflict with those of temperature theory (27 cases), heterogeneity plus isolation theories (3 cases), herbivory theory (5 cases), trophy theory (1 case), area and closeness to center theories (1 case), and r-K theory (1 case). It also wrongly predicted low trophic diversity in relatively less mature fresh & brackish water habitats, temperate climate zones, and the Palearctic realm and relatively larger size and lower productivity in more mature pelagic habitats. Succession theory prevailed when in conflict with temperature theory (2 cases), trophy theory (4 cases), and temperature plus heterogeneity theories (1 case). Of the 25 predictions for size 10 (40%) were supported by the data; of the 23 predictions for productivity 9 (39.1%) were supported by the data. The strongest overlap (95.8%) was with r-K theory (see above). Of the 25 predictions on numbers of species and strategies 19 (76%) were supported by the data; the highest overlap was with temperature theory (15 matches, 60%) followed by area (13 matches, 52%) and closeness to center (10 matches, 40%) theories. Of the 25 predictions for trophic diversity, 16 (64%) were supported by the data and 15 (60%) overlapped with those of herbivory theory. Altogether, correctness of predictions ranged from 76% for species numbers to 39% for productivity. If only no-conflict cases are considered, then 91.8% of 49 predictions were correct.

Temperature theory made 59 predictions altogether for numbers of species and strategies, size and productivity based on relatively high versus low mean environmental temperatures. Of these predictions 52 (mean = 89.1%) were supported by the data, which is significantly more than random predictions (t-value = 8.933, n = 4 environmental scenarios, probability level 89.09 > 50 = 0.0015, power (0.05) = 1.000). Temperature theory failed when its predictions were in conflict with succession and area theories (1 case), r-K and succession theories (2 cases), r-k, succession and trophy theories (1 case), area and closeness to center theories (1 case), succession, area and closeness to center theories (1 case), and r-K theory (1 case). Thus, in all but one case, it took more than one conflicting theory to overturn the predictions of temperature theory. It prevailed when in conflict with r-K and succession theory (26 cases), r-K theory (1 case), succession and area theories (2 cases), trophy theory (3 cases), and area theory (1 case). If only no-conflict cases are considered, then 95% of 20 predictions were correct.

Herbivory theory made 22 predictions altogether for relatively fewer herbivores and thus lower trophic diversity based on environmental temperature and pH. Of these predictions, 20 (mean = 92.7%) were supported by the data, which is significantly more than random predictions (t-value = 9.428, n = 5 environmental scenarios, probability level 92.66 > 50 = 0.0004, power (0.05) = 1.000). Herbivory theory predicted lower trophic diversity in temperate climate zones, which is not supported by the data in Table 32; note, however, the trend to fewer herbivores visible in Figure 36. It also predicted lower trophic diversity and fewer herbivores in the Palearctic realm, which is not supported by the data in Table 39 and Figure 39. Herbivory theory prevailed when in conflict with succession theory (6 cases). If only no-conflict cases are considered, then 87.5% of 16 predictions were correct.

Trophy theory made 9 predictions altogether for relatively small size and low productivity in oligotroph environments. Of these predictions, 5 (mean = 58.3%) were supported by the data, which is not significantly different from random predictions (t-value 1.0; n = 2 environmental scenarios, probability level 58.30 > 50 = 0.25, power (0.05) = 0.135). Correct predictions overlapped with those of temperature, r-K and succession theories. Trophy theory failed when in conflict with temperature, succession and r-K theories (3 cases). Also, the predicted relatively lower productivity for the pelagic realm was not supported by the data. If only no-conflict cases are considered, then 3 of 4 predictions were correct.

Area theory made 15 predictions altogether for numbers of species and strategies based on the relative surface area of the respective environments. Of these predictions, 10 (mean = 73.3%) were supported by the data, which is not significantly more than random predictions (t-value = 1.2005, n = 5 environmental scenarios, probability level 73.33 > 50 = 0.1481, power (0.05) = 0.2606). Area theory failed when in conflict with heterogeneity and isolation theories (2 cases), temperature, heterogeneity, isolation and closeness to center theories (1 case), temperature, heterogeneity and isolation theories (2 cases), and temperature theory (1 case). It prevailed when in conflict with temperature and heterogeneity theories (1 case) and temperature theory (1 case). If only no-conflict cases are considered, then all of seven predictions were correct.

Heterogeneity theory made 12 predictions altogether for numbers of species and strategies based on relative structural diversity of habitats. Of these predictions 11 (91.7%) were supported by the data. Heterogeneity theory failed when in conflict with succession and area theories (1 case). It prevailed when in conflict with succession and area theories (2 cases), area theory (1 case) and succession theory (1 case). If only no-conflict cases are considered, then all of six predictions were correct.

Isolation theory made 7 predictions altogether on numbers of species and strategies based on isolation of ecosystems from gene flow from neighbouring ecosystems. All predictions were supported by the data. Isolation theory prevailed when in conflict with succession and area theories (3 cases) and succession theory (1 case).

Closeness to center of biodiversity theory made 12 predictions altogether on numbers of species and strategies, all of which were supported by the data. It prevailed when in conflict with succession and temperature theories (1 case), temperature theory (1 case), and area theory (1 case).

When looking specifically at scenarios with opposing selection forces, r-K theory prevailed in 7 (20%) of 35 cases, succession theory prevailed in 9 (18.4%) of 49 cases, temperature theory prevailed in 33 (84.6%) of 39 cases, trophy theory prevailed in two (40%) of five cases, area theory prevailed in three (37.5%) of eight cases, heterogeneity prevailed in five (83.3%) of six cases and herbivory (6), isolation (4) and closeness to center (3) theories prevailed in all (100%) of their cases.

In summary, with the likely exception of trophy theory, selection theories made mostly (87.5 – 100%) correct predictions when cases of conflicting selection forces where excluded, confirming similar findings by many other authors (e.g. Adams 1980, Winemiller and Rose 1992, Vila-Gispert et al. 2002), albeit with a much larger data set. If conflicting selection forces where allowed, predictions by r-K, trophy and area theories were not significantly different from random predictions. In cases of conflicting predictions, r-K, succession, trophy and area theories were likely to lose out with success rates of 18.4 to 40%, whereas the remaining theories were likely to prevail with success rates of 83.3 to 100%. Especially, with regard to selection for size and productivity, temperature theory prevailed when in conflict with r-K and/or succession theory in 20 (87%) of 23 cases.

Table 77. Summary of correctness of predictions of selection theories, with number of predictions made with and without conflicts with other theories, and the respective percentages of predictions that were supported by the data. 'No conflict' results are highlighted in bold to facilitate comparison.

Theory	Category	Species / Strategies	Size	Productivity	Trophic diversity	Total
r-K	Predictions (n)		25	23		48
	Correct (%)		44.0	34.8		39.6
	No conflict (n)		5	8		13
	Correct (%)		**100**	**87.5**		**92.3**
Succession	Predictions (n)	25	25	23	25	98
	Correct (%)	76.0	40	39.1	64.0	55.1
	No conflict (n)	17	5	8	19	49
	Correct (%)	**100**	**100**	**87.5**	**84.2**	**91.8**
Temperature	Predictions (n)	20	20	19		59
	Correct (%)	85.0	85.0	94.7		88.1
	No conflict (n)	14	1	5		20
	Correct (%)	**100**	**100**	**80**		**95.0**
Herbivory	Predictions (n)				22	22
	Correct (%)				90.9	90.9
	No conflict (n)				16	16
	Correct (%)				**87.5**	**87.5**
Trophy	Predictions (n)		5	4		9
	Correct (%)		40	75.0		55.6
	No conflict (n)		0	4		4
	Correct (%)			**75.0**		**75.0**
Area	Predictions (n)	15				15
	Correct (%)	66.7				66.7
	No conflict (n)	7				7
	Correct (%)	**100**				**100**
Heterogeneity	Predictions (n)	12				12
	Correct (%)	91.7				91.7
	No conflict (n)	6				6
	Correct (%)	**100**				**100**
Isolation	Predictions (n)	7				7
	Correct (%)	100				100
	No conflict (n)	3				3
	Correct (%)	**100**				**100**
Closeness to center of biodiversity	Predictions (n)	12				12
	Correct (%)	100				100
	No conflict (n)	9				9
	Correct (%)	**100**				**100**

Correlations of Life-history Strategies with Functional Morphology, Behaviour, and Resilience

In this chapter I summarize the correlations of life-history strategies with functional morphology, behaviour and resilience to anthropogenic stress. Some patterns can already be seen from Table 78, which gives an overview of trends in median values for size and trophic level and approximate mean r'_{max} for productivity. For example, productivity increases with body shape from eel-like (low) to short and/or deep (high), with brain size from very small (low) to normal and large (high), and with migratory behaviour from catadromous (low) to amphidromous and non-migratory (high). Size decreases with migratory behaviour from catadromous (large) to non-migratory (small to medium), and increase with parental care from bearers to nonguarders. Trophic level decreases with increase in brain size, i.e., top predatory bony fish such as pikes tend to have small brains.

Table 78. Correlations of life-history traits with regard to body shape, brain size, reproductive guild, migratory behaviour and status of threat. Plus signs indicate rank of respective values from high (many signs) to low; when the difference to the closest value was significant, signs and numbers are in bold font.

	Length (median; cm)		**Trophic level** (median)		**Productivity** (r'_{max})	
Body shape						
eel-like	**++++**	**33.7**	**++++**	**3.55**	+	0.20
elongate	**+**	**18.8**	++	3.40	++	0.21
fusiform	**+++**	**25.0**	+++	3.45	+++	0.30
short & deep	**++**	**20.3**	**+**	**3.31**	++++	0.33
Standardized relative brain size (SEC)						
very small	used for standardization		**++++**	**3.92**	+	0.10
small			**+++**	**3.54**	++	0.23
normal			++	3.40	+++	0.30
large			++	3.40	+++	0.30
Reproductive guild (only Actinopterygii)						
bearers	+	12.2	++	3.37	+	0.24
guarders	++	13.9	+	3.26	+++	0.34
nonguarders	**+++**	**20.0**	+++	3.40	++	0.30
Migratory behaviour						
catadromous	++++++	60	+++	3.2	+	0.19
anadromous	+++++	50	++++	3.4	++	0.24
oceanodromous	++++	41.1	++++++	3.7	+++	0.26
potamodromous	+++	40.3	++	3.1	++++	0.27
amphidromous	**++**	**24.4**	+++++	3.5	++++++	0.36
non-migratory	**+**	**10**	+++	3.2	+++++	0.30
Status of threat						
not listed	+++	15.9	+++	3.40	**++++++**	**0.23**
lower risk	+++++	19.2	+++++	3.66	+++	0.10
vulnerable	+	12.2	++++	3.50	+++++	0.17
endangered	++++++	31.9	++	3.31	++++	0.15
critically end.	++	13.0	+	3.28	++	0.09
extinct	++++	17.6	++++++	4.02	++++	0.15

Interesting are also the 'non-groups', such as Actinopterygii without parental care having higher trophic levels and significantly larger size, non-migratory fishes having significantly smaller size, and non-threatened fishes having significantly higher productivity and thus resilience against human-caused stresses.

Additional patterns are revealed by the extended data sets: Herbivorous and omnivorous fishes have mostly short and/or deep body shapes, whereas large mid-level predators with medium productivity often have fusiform body shapes. Top predators with low productivity have significantly smaller and low-level predators with high productivity have significantly larger brains than overall median relative brain size (SEC). Large herbivores and omnivores but also most top predators are nonguarders. Several life-history strategies are exclusively migratory, including most large herbivorous, large omnivorous with high productivity, and most large top predator strategies. Life-history strategies that combine large size and low productivity contain several times more threatened species than suggested by their percentage of all fish species.

The respective chapters contain more detailed presentations of these trends and a discussion of the results with regard to other publications.

The scale of nature is not linear but logarithmic

As Williams (1964) already put it, "it has become more and more apparent that in most biological problems involving frequency distributions [..] the variation [..] is geometric and not arithmetic [..]. Thus we get the log-normal distribution." Of the continuous variables used in this study, most (oxygen consumption, aspect ratio, *a*, *K*, length, species numbers, brain size, maximum catch, individual numbers, and latitudinal range) were approximately log-normal distributed, and only two (*b*, trophic level) were approximately normally distributed, where one can argue that *b,* as the exponent of the length-weight relationship, belongs into the log-normal group, and trophic level is also kind of 'log-normal', with available energy diminishing by factor 10 with each increase in trophic level (Daniel Pauly, University of British Columbia, pers. comm., 2005). Thus, key traits and properties of fishes and probably of living organisms in general show exponential rather than linear change.

Competition

Matthews (1998) presented a graph (his Fig. 9.5, p. 498) showing a hypothetical decrease in magnitude of competition for resources (food, shelter) between two individual animals as a function of their relatedness, from siblings of the same size and cohort to relatedness at the level of Species, Genus, Family, Order, Class or Phylum. Here I test this hypothesis with the following assumptions:

1) Two individuals using the same life-history strategy at the same place and time are likely to compete for resources;
2) Two individuals using different life history strategies at the same place and time are less likely to compete for resources; and
3) The more strategies that are used by a taxon the less likely two individuals of this taxon occurring at the same place and time are to compete for resources.

Figure 79 shows the median number of strategies used by Species (one by definition), Genera (1), Families (4), Orders (7), and Classes (7). Median numbers of strategies increase and are significantly different from Genus, to Family to Order. This supports the hypothetical decrease in competition with decrease in relatedness suggested by Matthews (1998). Notably,

Figure 79 even supports the different slopes suggested by Matthews (1998), i.e., a modest (here: not significant decrease) slope from Species to Genus (sub-Genus in Matthews 1998); a steep slope from Genus to Order (here: significant decrease), and a modest slope from Order to Phylum (here: non-significant decrease from Order to Class).

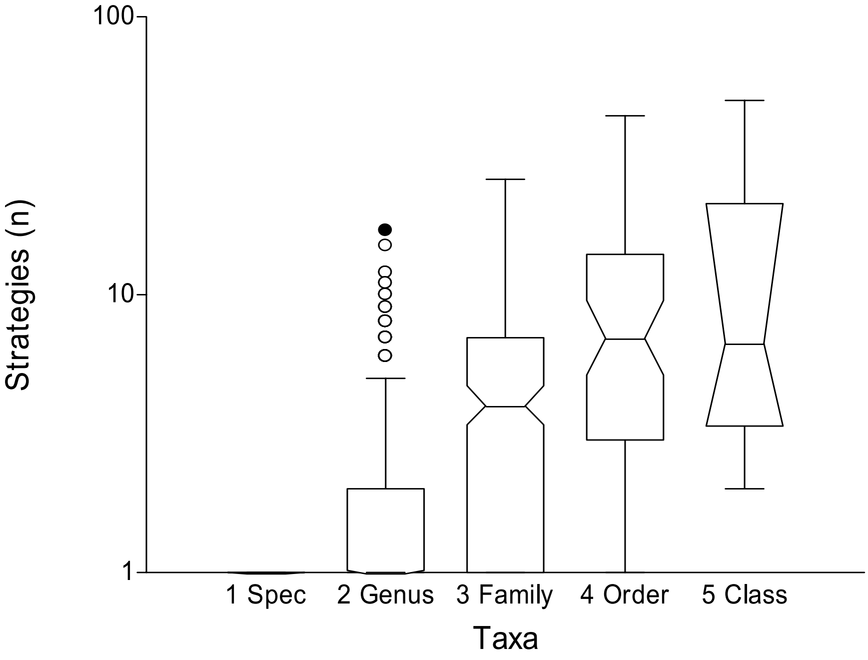


Figure 79. Distribution of number of strategies by taxon: 1 Spec = Species, with n = 20,479 and median = 1, 95% CL 1-1; 2 Genus with n = 3,777, median = 1, 95% CL 1-1; 3 Family with n = 356, median = 4, 95% CL = 3-4; 4 Order with n = 61, median = 7, 95% CL = 5-11; and 5 Class with n = 6, median = 7, 95% CL = 2-50.

Number of Higher Taxa and Strategies as a Function of Species Richness

Functions describing the relationships between taxonomic groups and subgroups, such as Genera and species, are of importance to ecologists requiring quick and robust estimates of local taxonomic richness and to theoretical and empirical ecologists studying the causes and consequences of biological diversity. Enquist et al. (2002) showed for woody plant communities from around the world that the relationships between the number of species and the number of Genera and Families, respectively, are described by simple power functions with exponents of 0.94 for Genera and 0.68 for Families. Here I repeat this exercise for fishes with climate zones, continents, oceans, zoogeographic realms, and habitat types as representatives of large aquatic ecosystems (Table 79).

Table 79. Taxonomic richness and number of life-history strategies in large aquatic ecosystems.

Ecosystem	Classes	Orders	Families	Genera	Species	Strategies
high altitude	1	8	12	31	48	10
deep water	5	39	167	683	2476	31
polar/boreal	3	14	37	99	178	18
temperate	5	42	180	901	2301	44
subtropical	6	48	230	1247	3025	48
tropical	6	43	219	2271	12451	48
Nearctic	3	24	47	173	876	32
Palearctic	3	22	56	266	840	34
Neotropical	3	21	54	535	2867	41
Ethiopian	3	21	52	409	2761	42
Oriental	2	17	60	408	1779	40
Australian	3	16	45	158	529	34
Arctic	4	15	24	67	122	19
Antarctic	3	20	44	130	250	21
Atlantic	5	52	259	1303	3722	46
Mediterranean	5	38	131	335	549	36
Indian Ocean	5	47	231	1390	4669	46
Pacific	6	50	268	1945	7616	48
bathydemersal	4	30	116	397	1409	26
bathypelagic	2	22	73	279	846	25
reef-associated	2	28	120	742	3463	45
demersal	6	50	227	1958	7196	48
benthopelagic	2	38	169	1056	6079	47
pelagic	2	28	128	545	1487	41

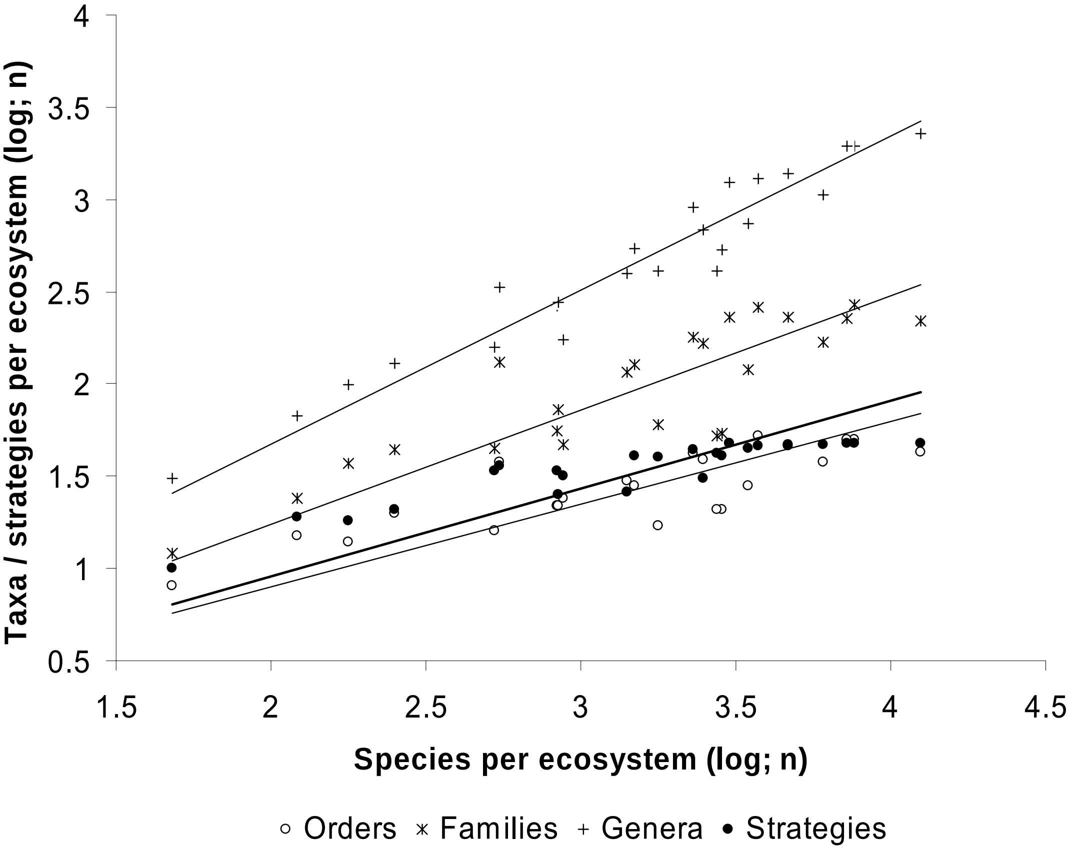


Figure 80. Number of higher taxa and life-history strategies per ecosystem as a function of species richness. Regression lines were forced through the origin. Orders n = 24, slope = 0.450, 95% CL = 0.429 – 0.470, r^2 = 0.989; Families n = 24, slope = 0.619, 95% CL = 0.593 – 0.645, r^2 = 0.991; Genera n = 24, slope = 0.836, 95% CL = 0.819 – 0.853, r^2 = 0.998; and life-history strategies (bold line) n = 24, slope = 0.477, 95% CL = 0.458 – 0.497, r^2 = 0.991.

Figure 80 shows a plot of higher taxa per large aquatic ecosystem as a function of respective species richness. Note that the slopes found here for Genera (0.84) and Families (0.62) are similar to those found for woody plant communities by Enquist et al (2002). The data for life-history strategies (black dots) are not fitted well by the straight (bold) line, a theme that I will return to. The interesting point here is that the slope for life-history strategies is not significantly different from that for Orders, i.e., both seem to express a similar degree of organizational and behavioural distinctiveness between species, as has already been pointed out in the context of Figure 29.

Enquist et al. (2002) compared their slopes for Genera and Families with those derived from communities randomly assembled from species pools of different sizes. They found that such hypothetical communities were characterized by significantly steeper slopes than observed and concluded that ‘real’ communities are more taxonomically similar than expected by chance, a pattern that was already described by Elton (1946). This is consistent with other findings that an increase in species richness is accompanied by an increase in total morphological or character diversity (= number of life-history strategies), although at an ever-slowing rate leading to a relative increase in taxonomic and life-history similarity, i.e., more species belong to the same higher taxa and use the same life-history strategies (Hubbell 2001, Webb 2000).
Enquist et al. (2002) suggest two mechanisms for the higher-than-expected similarity among species within a given ecosystem: First, they suggest that higher taxa vary widely in their

ability to colonize new sites, i.e., species of taxa with life history strategies with fewer dispersal limitations will be more frequent. Second, ecosystems will have characteristics that are more favourable to some higher taxa than to others, i.e., species of taxa with life-history strategies that suit the conditions of a given ecosystem will be more frequent. Or put differently: the null-model of Enquist et al. (2002) assumed that all species and higher taxa have the same likelihood of occurring in a given ecosystem. In reality, the likelihood of, e.g., tropical taxa such as Epinephelidae occurring in polar oceans, primarily freshwater taxa such as Cyprinidae occurring in marine ecosystems, or deepwater taxa such as Bathylagidae occurring in coral reefs, is zero. This high diversity of aquatic ecosystems and fish taxa (see Table 79) may explain why the slopes between Families and Genera versus species richness found in this study are similar but less steep than those of Enquist et al. (2002), who analysed 227 one-tenth hectare sites of woody plant communities, with a maximum of 275 species, 175 Genera and 50 Families per site.

Relationship between Numbers of Species and Numbers of Strategies

The strong correlation between number of species in a group and the number of strategies used in that group has been striking.

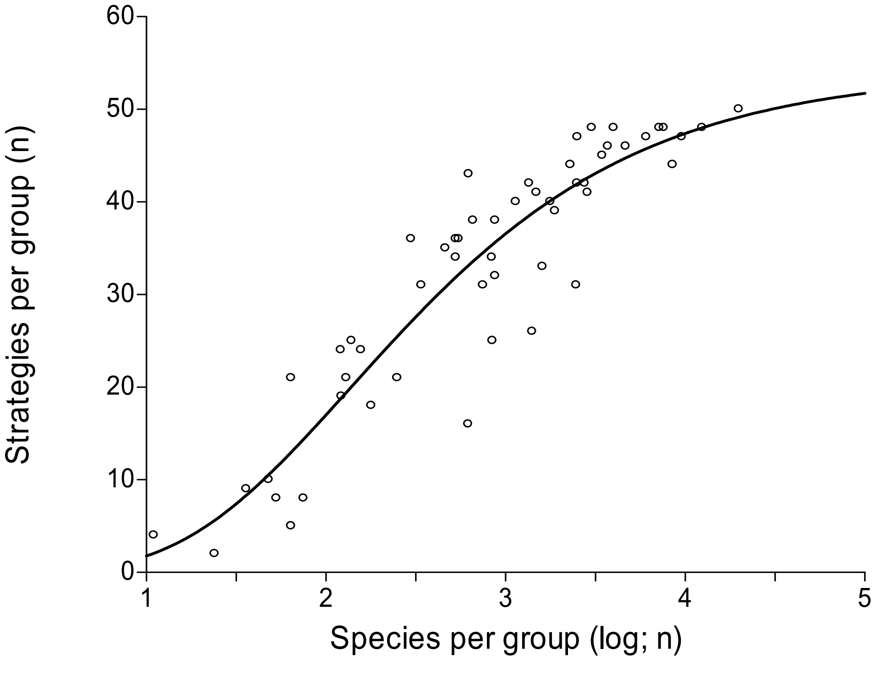


Figure 81. Number of strategies per group as a function of species per group, for 10 phylogenetic, environmental, morphological, behavioural and human impact groups analysed in this study. The fitted line is a Gompertz growth curve.

Figure 81 shows the number of strategies versus number of species for the various groups of environmental and other parameters analysed in this study. A simple semi-log linear regression would result in Equation 19 and explain 84% of the variance with only two parameters (Wilson 1964).

$$\mathrm{Strat}_n = -14.53 + 16.35 * \log(\mathrm{Spec}_n)$$

Equation 19. Linear regression of number of strategies as a function of number of species per group, where Strat_n is the number of strategies and Spec_n the number of species in a group, with 10 groups and n = 54 cases, $r^2 = 0.8355$, 95% CL of the intersect = -20.54 – -8.518, 95% CL of the slope = 14.33 – 18.37.

However, a linear fit does not capture the lower and upper limit constraints, i.e., that there cannot be more strategies than species and that there cannot be more than the maximum of 80 strategies per group. Sigmoid growth models such as the logistic or the Gompertz model accommodate such constraints, albeit with three parameters. Here I chose a modified Gompertz model (I use natural logarithm of Spec_n instead of Spec_n) because, other than the Logistic model, it does not assume a symmetric point of inflection.

$$\mathrm{Strat}_n = 54.08 * \mathrm{EXP}(-\mathrm{EXP}(-0.4705 * (\ln(\mathrm{Spec}_n) - 4.916)))$$

Equation 20. Modified Gompertz function of number of strategies, where Strat_n is the number of strategies and Spec_n the number of species in a group, for 10 groups with n = 54 cases, $r^2 = 0.8536$, 95% CL of the first parameter $\alpha = 43.98 – 64.19$, second parameter 95% CL $\kappa = 0.2827 – 0.6582$, and third parameter 95% CL $\gamma = 4.417 – 5.414$.

In a Gompertz growth model the first parameter α represents the final size achieved, i.e., here the maximum number of strategies if new groups with more species were added, which is estimated at 54 (44-64) strategies. For the strategies used in this study it means that, based on the available data, not more than 54 of the available 80 strategies are likely to be used even if the about 5,000 species of recent fishes missing from the extended data set were added. Also, the Gompertz model has an inflection point where the number of new strategies per new species is maximum, here at $\gamma = e^{4.916}$ ($e^{4.417} – e^{5.414}$) = 137 (83 – 225) species and at α / e = 54.08 / 2.718 = 20 (16 – 24) strategies. The inflection of the curve makes sense: In small groups, the number of strategies is limited by the fact that there cannot be more strategies than species; once this constraint is overcome ($\mathrm{Spec}_n >> \max. \mathrm{Strat}_n$) the relative number of new strategies per additional species increases until a) the ‘viability’ of new strategies decreases—such as combinations of very small size and very low productivity (see Table 9)—and b) the probability that new species will use new strategies decreases once more of the available strategies are used than unused. Because of the decrease in ‘viability’ of strategies we would expect the maximum number of viable strategies to be less than the maximum number of possible combinations (here: 50 out of 80) and the inflection point to be below half of the viable strategies (here: 20 instead of 25).

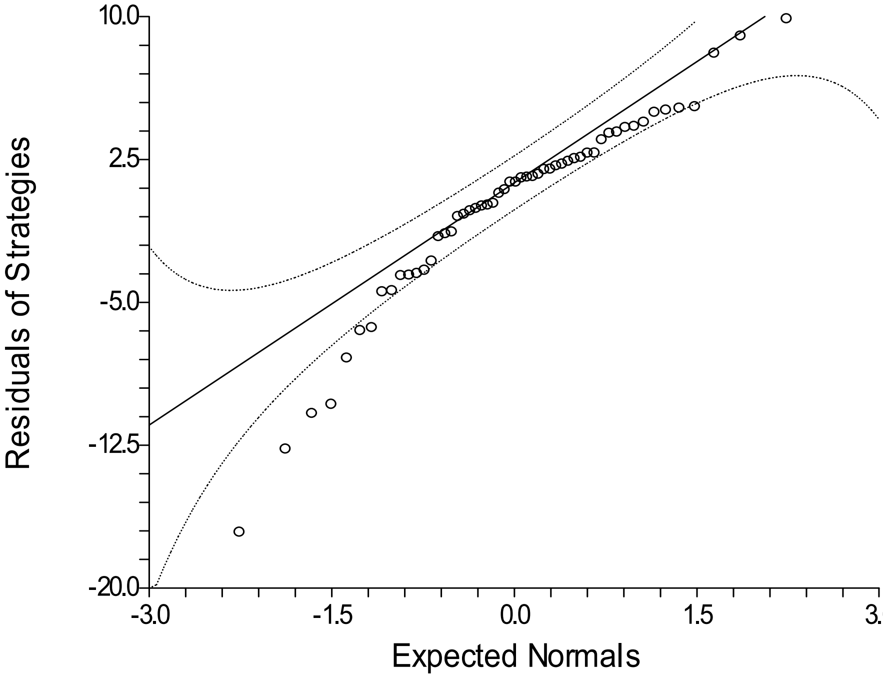


Figure 82. Normal probability plot of residuals of strategies. Note 7 points with residuals outside of 95% confidence limits.

Figure 82 shows a normal probability plot of residuals of number of life history strategies as predicted by Equation 20. Seven points have residuals outside of the 95% confidence limits, and in all cases they have fewer strategies than predicted by their species numbers. These are the Myxini and Elasmobranchii among Classes, the deep-sea fishes among climate and habitat groups, the non-migratory fishes among migratory groups, and the extinct fishes among threatened groups. These cases are discussed in more detail in the respective chapters. Mostly, they are true outliers in the sense that the number of strategies available to them is limited either by phylogeny (no herbivores among sharks and hagfish) or by environmental constraints (no plants and thus no herbivores in the deep sea). These points do not belong into a model that assumes 54 strategies being available in principle to each group member. I therefore recalculated the Gompertz model without these seven points.

$$\mathrm{Strat}_n = 51.88 * \mathrm{EXP}(-\,\mathrm{EXP}(-\,0.5460 * (\ln(\mathrm{Spec}_n) - 4.653)))$$

Equation 21. Number of life-history strategies as a function of number of species per group, where Strat_n is the number of strategies and Spec_n the number of species in a group, for 10 groups with n = 47 cases, r^2 = 0.9403, 95% CL of the first parameter α = 47.22 – 56.54, second parameter 95% CL κ = 0.0.4141 – 0.6779, and third parameter 95% CL γ = 4.415 – 4.892. The approximate lower and upper 95% confidence limits of the estimate can be obtained as estimate +/- 6.83 (mean of difference between estimate and 95% confidence limits determined by modified bootstrap method in Hintze (2001)).

Equation 21 explains 94% of the variance and is suggested as an appropriate model for predicting number of life history strategies as a function of number of species in the respective group.

Note that one consequence of fewer available strategies is that more species have to share the same strategy, which explains why the outliers in Figure 82 all had fewer strategies than predicted and thus fell below the straight line.

In conclusion, the principles governing species numbers (see discussion of Table 23) fully explain the numbers observed in zoogeographic realms and oceans as well as in most other environmental groupings used in this study.

More Research Needed

A study on biodiversity of fishes is necessarily incomplete. Below I list several researchable questions that can be answered with the data at hand, but which were peripheral to the current study, and thus will be explored in future studies.

The data at hand can be used to test hypotheses about macro-evolutionary patterns such as the uneven relationship between numbers of species per Order or Class versus the evolutionary time elapsed since the appearance of the respective common ancestor, and the associated rates of speciation and extinction (e.g. Nee 2004). Similarly, hypotheses about macro-ecological patterns can be tested, such as numbers of species per Family or Order in relation to body size, trophic level, or productivity (e.g. Owens et al. 1999).

Rapoport’s rule suggests a decline in mean or median latitudinal extent towards lower latitudes resulting in larger ‘species pools’ and thus higher diversity towards the equator (Stevens 1989, Gaston et al. 1998). Roy et al. (1998) refuted Rapoport’s rule for marine gastropods; instead they found a high correlation between diversity and sea surface temperature. Winemiller and Rose (1992) found that marine fishes at higher latitudes tended to be associated with smaller ranges in latitude. These hypotheses can be tested with the over 7,000 marine and freshwater fish species for which latitudinal and temperature data are available here.

FishBase contains data on swimming modes of fishes (Froese et al. 2000) following the classification of Lindsey (1978). A future analysis is likely to find a correlation between swimming modes and each of the key traits (length, trophic level and productivity).

In log-log plots of abundance over body mass, typically, a slope of -0.75 is found (Damuth 1987). Blackburn and Gaston (1997) discuss causes that might be responsible for the observed variance of the slope. In Figure 67, I plot abundance over length and readily find the negative slope. Repeating this graph using e.g. body weight at first maturity for the 557 species with abundance data would allow determining the magnitude of the slope and compare it with the literature.

Human uses of fishes include aquaculture and introductions. It would be interesting to see which strategies are preferred by fishes used in aquaculture, and by invasive fishes.

In a study of butterflies, Kotiaho et al. (2005) found that narrow niche breadth, restricted resource distribution, poor dispersal ability, and short flight period are characteristics of threatened species. They used these characteristics to identify species that are likely to be threatened, but not included in the current Red List. The data available in this study can be used for a similar analysis and prediction for fishes: for example, species with very low productivity and narrow latitudinal range can be expected to be threatened by extinction (Musick 1999, IUCN 2000, Cheung et al. 2005).

Several of the environmental parameters used in this study are likely to provide more insights if analysed jointly towards their impact on life history strategies. Thus, the analysis of a multidimensional ‘super matrix’ of strategies versus all or most other parameters will be the subject of a future study.

In the chapter on resilience to fishing pressure, I proposed that the normal life span of highly fecund fishes will be longer than the frequency of favourable conditions for the survival of eggs and larvae such as manifest in outstanding year classes. This hypothesis can be tested based on age data in FishBase and occurrence of ‘outstanding’ year classes in fisheries time series data.

Jennings et al. (1998) propose a potential rate of population increase (r’) as surrogate for the intrinsic rate of population increase with

$$r' = \ln(\text{Fecundity}) / \text{Age at maturity}$$

Equation 22. Potential rate of population increase (r’) of Jennings et al. (1998).

While this equation reduces the importance of fecundity by using the natural logarithm of fecundity rather than absolute fecundity, it still results in a positive relationship with, e.g., fishes with 1 million eggs per female and year having twice the resilience to fishing then fishes with annual fecundity of 1,000 eggs, given same age at first maturity. In contrast, Froese and Luna (2004) showed that there is no relationship between fecundity and intrinsic rate of population increase in fishes that produce more than 1,000 eggs per female and year. Meanwhile the concept of potential rate of population increase of Jennings et al. (1998) has been taken up by subsequent works (Frisk et al. 2001). There seems to be a need to formally demonstrate that the potential rate of population increase of Jennings et al. (1998) is not a replacement for intrinsic rate of population increase and not a reliable indicator for resilience to fishing.

Summary

The purpose of this study was to explore life-history strategies of recent fishes based on a data set that was two orders of magnitude larger than those used in previous studies, and which in several traits and environmental parameters approached a census of recent fishes and their environment. Below I summarize the key findings.

Size

Fishes can be conveniently grouped into size classes from small to very large, using standard deviation of the log-normal distribution of maximum length. These size classes capture well the differences in size distribution among the recent phylogenetic Classes of fishes. Size was strongly correlated with most life-history traits of fishes and also with morphological characters, with behaviour and with preferred environmental conditions. Size was found to be a good predictor of placement on the r-K continuum, with small fishes being mostly r-selected and large fishes being mostly K-selected.

Productivity

Productivity as used in this study was derived from available data on growth, age at maturity, maximum age, and fecundity constraints. It was positively correlated with metabolism and level of activity and taken as a proxy for maximum intrinsic rate of population increase and thus as an indicator for placement of species on the r-K continuum. It was strongly correlated with most life-history traits of fishes and also with morphological characteristics, with behaviour and with preferred environmental conditions. Notably, productivity was negatively correlated with status of threat and resilience to fishing.

Trophic level

The position of species in the food web was shown to restrict life-history options. For example, there were no herbivorous fishes in polar or deep waters and no top-predator fishes in high-altitude lakes. The addition of trophic level as orthogonal axis on the r-K continuum opened a new dimension of life-history space and revealed unoccupied regions such as the combination of small size and high productivity with either herbivory or top-predatory, and the combination of very large size and very low productivity with herbivory.

Life-history Strategies

Discrete classes of size, trophic level and productivity were used to define 80 potential combinations representing major life history strategies. Only 50 of these combinations were used by recent species of fishes, with an exponential decline in species numbers from the most to the least used strategies. This decline was interpreted as an exponential increase in constraints associated with less-used strategies. Analysis of trade-off or constraint curves in life-history space revealed unoccupied areas as well as local maxima, i.e., areas occupied by more species than the surrounding space. Such a local optimum was occupied by very large top predators with very low productivity. Low-level predators of small to medium size and medium to high productivity were the three strategies used by 60% of the species altogether. Strategies used in extreme environments such as the deep and polar seas or high-altitude lakes were not ‘specialist strategies’ but rather among the 10 most-used strategies, suggesting that constraints imposed by extreme environments excluded strategies that had a high degree of inherent constraints. The number of strategies used by phylogenetic, environmental, morphological or behavioural groupings of fishes was highly predictable from the number of species in the respective groups. A preliminary chronology of life-history strategies showed that over 2/3rd of recent strategies were invented only 200-150 million years ago during several radiations of the Actinopterygii, including small size, very large size (invented in parallel by Elasmobranchii), high productivity, and true herbivory. As for the evolutionary history of the traits, low-level to top predators were the original trophic groups from which omnivores and herbivores have evolved; medium to large length groups were the original sizes from which small and very large fishes have evolved; and low productivity was the original state of metabolism and population increase, from which very low as well as medium and high productivity have evolved.

Influence of Phylogeny on Life-history Strategies

Phylogeny clearly restricted the life-history options available to species with respect to size, place in the food web and productivity. The most specious Class (Actinopterygii) had relatively smaller size, higher productivity and wider trophic diversity. There was evidence for a certain non-overlap of preferred life-history strategies between the two largest recent Classes, with Elasmobranchii tending towards large size and low to very low productivity, and Actinopterygii tending towards medium size with medium to high productivity. The strategies defined in this study were very similar to phylogenetic Orders in their ability to create functionally related groups of species, albeit without the requirement of common ancestry.

Selection Theories

Nine selection theories were tested as to their ability to correctly predict adaptation of life-history traits in response to environmental conditions such as salinity, climate, zoogeographic realm, ocean basin, and habitat type. Predictions were 88 – 100% correct when cases where different theories predicted different adaptations were excluded. When conflicting cases were included, predictions of r-K, ecosystem succession, trophy and area theories were not better than random, whereas predictions by temperature, herbivory and other theories were still correct in 88 – 100% of the cases. In conflicting cases, predictions by temperature theory usually prevailed over those by r-K and succession theories.

Correlations with Functional Morphology, Behaviour and Resilience

Life-history strategies were examined with respect to their correlations with body shape, brain size, reproductive guild, migratory behaviour and status of threat. Productivity increased with body shape from eel-like to short and/or deep, with brain size from very small to normal and large, and with migratory behaviour from catadromous to amphidromous and non-migratory. Size decreased with migratory behaviour from catadromous to non-migratory, and with parental care from nonguarders to bearers (in Actinopterygii). Trophic level decreased with increase in brain size, i.e., top predatory bony fishes such as pikes tend to have relatively small brains; in contrast, electro-sensing sharks have very large brains. Non-threatened fishes had significantly higher productivity than threatened fishes. Several life-history strategies are only used by migratory species. Life history-strategies that combine large size and low productivity contain much higher percentages of threatened species than other strategies.

Success of Life-history Strategies

Independent estimates of abundance and distributional range of species were used as indicators of success of life-history strategies. Species showed preferences for strategies that were associated with high abundance or small to medium ranges. When abundance and range were combined into a single measure of success (Impact), most strategies were associated with impacts that were not significantly different from the overall mean. Only medium-sized low-level predators and omnivores with high productivity had significantly higher impact; these two strategies were among the top-four and were used by 39% of the species.

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