FISH ON LINE

A guide to learning and teaching ichthyology using the FishBase Information System[1]

by

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Abstract

This guide provides a structure and case study material for a computer-based course in ichthyology for upper undergraduate and graduate students in biology or environmental science.

The key resource made accessible through this guide is FishBase, a large database on the biology of fish, available on the Internet (www.fishbase.org).

Following brief introductions to ichthyology and to FishBase, and to the use of the latter to teach the former, the key aspects of ichthyology are presented in five chapters covering Evolution and Classification; Morphology and Biodiversity; Reproduction; Physiology; and Fishes as Part of Ecosystems.

For each of these chapters, one or several 'Exercises' are presented describing how the relevant topics are covered in FishBase and describing how to access that information. 'Tasks for the Student' are provided, along with Internet links to relevant sources other than FishBase. For completing the exercises, students are adviced to also consult the theoretical background provided in the FishBase book (i.e., FishBase 2000: Concepts, design and data sources), which is also available online (http://www.fishbase.org/manual/English/contents.htm).

This is the second version of the guide, which expands that by Pauly *et al.* (2000). It is anticipated that this guide will continue to be updated as our experience with FishBase as a teaching tool improves. To this end, a final chapter describes how users (both students and teachers) may contribute to the updates that are anticipated for this guide, and to completing the coverage by FishBase of fishes at all levels of biological organization (i.e., individual, population, communitity, ecosystem).

CONTENTS

1. Introduction

1.1. What is ichthyology?

Ichthyology is commonly defined as ‘the study of fish’ or ‘that branch of zoology dealing with fish’. A fish is, literally, a vertebrate (i.e., animal with a backbone) that has gills, a body covered with scales, and lives in the water. However, some species are well known for their ability to leap clear of the sea surface and glide long distances using their fins as wings. In addition, other species can live out of the water for quite sometime, walk to migrate to other water bodies using auxiliary breathing organs, and some species have bodies without scales. Also, the word fish is sometimes used more broadly to include any edible animal living in water. Here, we limit ourselves to fish in the narrow sense; note that the term ‘fishes’ refers to more than one type (or species) of fish; ‘finfish’ refers to sharks, some rays and bony fishes, and ‘scalefish’ refers to fish bearing scales.

Ichthyology has a long documented history, dating thousands of years back to the ancient Egyptians, Indians, Chinese, Greeks and Romans (Cuvier 1828). This long, sustained interest in fish is due to their double role as highly speciose denizens of a fascinating, yet alien world and as human food since many thousands of years ago. It has generated, over the centuries, highly heterogeneous information – mainly taxonomic, but also referring to zoogeography, behavior, food, predators, environmental tolerances, etc.

This huge amount of information, embodied in a widely scattered literature, has gradually forced ichthyologists to specialize. Thus accounts on fish are now either global, but highly specialized (e.g., Eschmeyer’s *Catalog of fishes* (1998) or Pietsch and Grobecker’s *Frogfishes of the world* (1987) to name two outstanding representatives), or local and deep (e.g. Fryer and Iles’ *Cichlid Fishes of the Great Lakes of Africa* (1972) or Groot and Margolis’ *Pacific Salmon Life Histories* (1991).

Thus, with a few exceptions such as the massive *Diversity of fishes* (Helfman et al. 1997), texts are lacking which bring together, on a global basis, all aspects of ichthyology, such that they can be used for a specialized course, and/or independent learning.

1.2. What is FishBase?

FishBase is an information system available online at www.fishbase.org, covering all fishes of the world in a fashion that is both global and deep. FishBase, whose accompanying book is available in English, French and Portuguese, covers about 31,000 species of fish, i.e., most of the extant species in the world, and addresses the needs of a vast array of potential users, ranging from ichthyologists, fisheries biologists, ecologists and managers to biology teachers, administrators and the public at large. The features of FishBase that enable it to meet such a wide range of needs reside in its architecture, which makes extensive use of modern relational database techniques.

Other features of FishBase include:

- all information on a given species in the database is accessible through a unique scientific or common name or through common names in many languages;
- the wide use of multiple choice field structures standardize qualitative information;
- numeric fields record previously standardized quantitative information;
- numerous cross-relationships between data tables enable previously unknown relationships to be discovered; and
- complementary databases provided by colleagues and linked to FishBase contribute to making the combined package the most comprehensive data source of its kind.

1.3. Why use one to teach the other?

For teachers of aquatic biology, or of specialized ichthyology courses, the uses of FishBase will range from practical solutions to theoretical issues:

- FishBase is directly useable as data source (i.e., as an electronic encyclopedia on fish), thus complementing classical sources of information on fish, e.g., the Zoological Record or Aquatic Science and Fisheries Abstracts, and thus helps overcome the lack of scientific literature, especially in developing countries;
- the many pictures in FishBase can be used, just as those in taxonomic books, to provide students with a visual impression of the morphological and color diversity of fish, and/or of specific features of various groups;
- students will be able to assess the state of knowledge on various groups of fish, and thus obtain some guidance in identifying worthwhile projects; and
- the synoptical view that FishBase produces by assembling and structuring all available information on one species will help students to obtain material for study (see above) and, perhaps more importantly, to develop a sense of how scattered bits of information can be used to 'reconstruct' species, and to show how these fit into their environments. In other words, FishBase transforms information to knowledge and thus encourages a holistic view, as now required for most of what we do in the biological sciences.

Thus, a series of lectures on ichthyology may be conceived, based on the following elements:

- show FishBase pictures through an introductory lecture, to highlight the diversity and colorfulness of fish and similarity of external morphology in related groups (this hopefully would serve to generate interest in the course as a whole, and introduce fish classification);
- compare the early classification schemes in Cuvier (1828) with a recent one, e.g., that in the *Catalog of Fishes* (Eschmeyer 1998), 'hosted' by FishBase and largely identical with the widely used classification in Nelson (1994);
- introduce the species concept and its requirements (a formal description with figures, a binomen, a holotype, a type locality, etc.) and implications (synonymies, sister species, etc.), using FishBase as source of examples, and its Glossary for definition of terms;
- define the characteristics (meristics, morphometrics) through which fish species are usually defined and hence identified, and compare identification through keys with computer-based identification using the appropriate FishBase routine (see 'Quick Identification');
- show how museum and other occurrence records, as included in FishBase, can be used to define distribution ranges and habitats, which can then be used for answering high-order ecological questions;
- show how the latitudinal ranges of fish species can be used to test various hypotheses, e.g., on the relationship between fish biodiversity and shelf area (for neritic species) or land area (for freshwater species);
- define and illustrate various life history strategies, and analyze their frequency distribution throughout the world. Show, e.g., that salmon-type anadromy is extremely rare in subtropical or tropical species (it is well documented only in hilsa, *Tenualosa ilisha*, ranging from Iraq to Myanmar); show how students can

identify the relative frequencies of different strategies and draw inferences from these;

- let each student select a species, print out the relevant FishBase summary page and try to complement missing (black) items in the 'More Information' section, based on a literature review (and send the result to the FishBase Team); and
- show or let students derive quantitative relationships between different expressions of fish physiology (e.g., respiration, growth) and temperature (and hence latitude) and identify modifying factors (salinity, gill size, food type, etc.).

In the context of higher education, FishBase may also serve as background for Bachelor's or Master's theses, where data coverage of certain topics would first be checked and completed, and then data-mining techniques would be used to test relevant hypotheses.

2. Evolution and Classification

2.1. Phylogeny and Classification

There are different ways in which objects can be classified; the human mind is very good at generating criteria for classification. This is why the following list, assembled by the Argentinean author Jorge Luis Borges, and purportedly extracted from an ancient Chinese encyclopedia (Lakoff 1987), strikes us as funny: "[…] *it is written that animals are divided into*:

- *those that belong to the Emperor;*
- *embalmed ones;*
- *those that are trained;*
- *suckling pigs;*
- *mermaids;*
- *fabulous ones;*
- *stray dogs;*
- *those that are included in this classification;*
- *those that tremble as if they were mad;*
- *innumerable ones;*
- *those drawn with a very fine camel's hair brush;*
- *others;*
- *those that have just broken a flower vase;*
- *those that resemble flies from a distance."*

The two major criteria that are used to classify things (neither met by Borges' list), are *utility* or *affinity*:

- *Utility* generates classifications whose objects are easy *to find*. An example of such a classification would be a dictionary, whose entries are arranged alphabetically;
- *Affinity*, on the other hand generates classification wherein adjacent objects are straightforward *to compare* (because adjacent entries share important features).

In the European Middle Ages, animal books ('*Bestiarum*') were usually ordered alphabetically. However, such ordering eventually struck people as odd, especially as people realized, in the course of long debates on 'universals' (on whether names are 'natural' attributes of things, or not), that names are arbitrary labels.

Thus, authors gradually began seeking for natural classifications, wherein organisms are ordered by affinities, these affinities being initially conceived as reflective of the general rules which god used when creating these organisms.

The work of Linnaeus, whose *Systema Naturae*, the tenth edition (1758) of which still marks the beginning of zoological nomenclature, is an example of such attempts to identify the underlying affinities among plants and animals. The resulting 'natural' classifications have started to make sense, however, only since Darwin, in *The Origin of Species* (1859), provided a rationale for affinities, that is, shared ancestry. However, Darwin not only provided a basis for the affinities between organisms. He also provided a mechanism by which new species and higher taxa emerged out of common ancestors. This mechanism he called natural selection.

2.2. Darwin and Natural selection

Natural selection is the core of Charles Darwin's work and is best defined in his own terms: "*many of every species are destroyed either in egg or [young or mature (the former state the more common)]. In the course of thousand generations infinitesimally small differences must inevitably tell; when unusually cold winter, or hot or dry summer comes, then out of the whole body of individuals of any species, if there be the smallest differences in their structure, habits, instincts [senses], health, etc., <it> will on an average tell; as conditions change a rather larger proportion will be preserved: so if the chief check to increase falls on seeds or eggs, so will, in the course of 1,000 generations, or ten thousand, those seeds (like one with down to fly) which fly furthest and get scattered most ultimately rear most plants, and such small differences tend to be hereditary like shades of expression in human countenance*" (Darwin 1842).

Natural selection, thus, consists of three elements:

- organisms usually produce far more progeny than their habitat can accommodate;
- each member of the progeny differs in some *inheritable* attributes or properties;
- there is a tendency for those progeny with attributes or properties that are more suitable for the habitat in question to suffer a lower rate of mortality and thus for more of them to reach reproductive age than their sibling.

These three features jointly cause animals and plants, over evolutionary time, to 'track' fluctuation of their environment. In this process, and in conjunction with other mechanisms such as the '**founder effect**' and the effect of neutral selection, isolated populations can become so different from the mother species that their members will not be able to cross-mate if the barrier that once separated them disappears.

2.3. The species concept

Species are "*groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups*" (Mayr 1942, p. 120).

2.3.1. What's in a name?

Since species are the basic rank of biological nomenclature, naming species is very important and we now follow for this a model proposed by Linnaeus (see above), wherein the species is defined by a so-called *binomen* consisting of a *unique* genus name, which always starts with a capital letter, and a *species epithet* , which is *never* capitalized; usually, both are written in italics. With regard to the capitalization rule, simply recall that the binomen is the short version of an earlier mode of description wherein a whole paragraph was used to describe, and thereby define, a species. The binomen, thus, was the start of a sentence.

Important additions to a species name are the name of the author who first described a species and the year of that description; as in, for example, the Linnaean species *Salmo trutta* Linnaeus, 1758. At times you will encounter a species, e.g., *Oncorhynchus mykiss*, with an author's name and year in brackets, e.g., (Walbaum, 1792). This means that the species whose epithet is *mykiss* was originally described as a member of another genus, in this case, *Salmo.* However, due to better understanding of its relationships with other trout and salmon species, it was subsequently moved into the genus *Oncorhynchus*.

Also, many species have been described and named more then once. In that case, the oldest description takes preference, and the names given in later descriptions become 'junior synonyms.'

Another rule important to animal species names is that the genus part of the name must be unique to the animal kingdom. From the year 2000 on, it must also be unique among *all* organisms. Thus, when a generic name is coined, the author must verify that this name has never been used by any other zoologist, and, from 2000 on, by any botanist, bacteriologist, etc. This seemingly daunting task is not impossible. Global catalogues of organism names are now being created; the most important of these is the Catalogue of Life (see www.catalogueoflife.org).

2.3.1.1. Exercise

- In www.fishbase.org, go to 'Information by Country' and select your country and 'All fishes.' Look at the scientific names of ten species whose author name is in brackets and identify for each the original name and several synonyms. List and define the different kinds of synonyms.

  Example:

  Oreochromis niloticus (Linnaeus, 1758) [new combination, valid]

  Perca nilotica Linnaeus, 1758 [original combination, not valid]

  Tilapia nilotica (Linnaeus, 1758) [new combination, not valid]

  Tilapia nilotious (Linnaeus, 1758) [misspelling of new combination, not valid]

  Tilapia calciati Gianferrari, 1924 [original combination, junior synonym, not valid]

2.3.2. Subspecies vs. populations

Given the mechanism of natural selection, every fish population can be conceived as being a potential new species. All one needs to imagine is that populations become isolated from others long enough for their members to lose the ability to mate with those of other populations. However, as long as some members of each population continue to mate with members of other populations of the same species, a mating barrier will not emerge (only a small gene flow is required to prevent the emergence of a mating barrier). Thus populations, though they may be easy to define in terms of attributes such as number of scales or spines or body proportions, should not be given full taxonomic status, because (contrary to species) they usually do not maintain themselves over a long period. Not having taxonomic status also means they should not have formal names, such as the trinomen that are still frequently used today, e.g., *Oreochromis niloticus baringoensis* Trewawas, 1983. The third part of the trinomen refers to a subspecies, which is, in fact, a population, or, to use a term much used in earlier times, a 'race'. Fish taxonomists gradually do away with subspecies by either giving them species rank or making their names a synonym of the respective species. In our example, a taxonomist has to review the case and decide whether the individuals referred to as *Oreochromis baringoensis* Trewawas, 1983 are different enough to be recognized as a valid species, or if the population is well connected with others, in which case *Oreochromis niloticus baringoensis* Trewawas, 1983 becomes a junior synonym of *Oreochromis niloticus* (Linnaeus, 1758).

2.3.3. Within-species diversity

Species differ as to the extent of their diversity. Some species consist of a single population of a few individuals – these are often endangered species. Others have wide ranges and a rich population structure. This situation tempted authors to name subspecies. However, it is often not objectively defined within-species diversity which motivated authors to define subspecies, but national or local research traditions, and the resources available for sampling specimens over large areas, and curate them. Thus, Berg (1965) established numerous subspecies and even lower taxa for the fishes of adjacent lakes and rivers of the former Soviet Union, while subspecies are rarely proposed by taxonomists working on the many coral reef species of the Indo-Pacific, although their distribution spans thousands of kilometres with many populations and limited gene-flow.

2.3.4. Common names

The common names of fish are what most people know about most fish. Thus, capturing the common names of fish in various languages captures most of what people who speak these languages know about fish. For this reason, FishBase includes about 280,000 names of fish in over 200 languages, ranging from widespread languages such as English or Spanish, to languages spoken by few speakers, such as Haida in Haida Gwaii, British Columbia. Anthropologists, notably Berlin (1966), have established that essentially all ethnic groups in the world spontaneously differentiate a similar number (about 500) of 'kinds' of organisms, the kinds roughly corresponding to genera, with important species being named, as well as some of their life history stages.

The sounds in fish names also generate interesting patterns. Thus, small fishes tend to have names containing high pitch sounds such as 'i' or 'ee', while large fish tend to have names with lower pitch sounds, such as 'a', or 'aa' (Berlin 1992; Palomares *et al*. 1999).

2.3.4.1 Exercises

- Identify a language with at least 50 different common names in FishBase. Relate the number of species with i/ee sounds in their names against the maximum length reported for those species, i.e., test the occurrence of a sound-size association for fish in the language in question. [Hints: use the Information by country/island search to get a list of common names (and the corresponding scientific names) by language; get maximum size information from the Species Summary page and see item (5) of www.fishbase.org/Tips.htm on how to export data to a spreadsheet (Excel format) for further analysis.]
- Find from FishBase, using search by **Common Name**, some blind species and some species that have the ability to 'fly' out of the water and the ability to 'walk' on land. [Hint: common names of species often contain the word that describes special abilities, characters or traits].

3. Biodiversity and Morphology

The diversity of fish is larger than for any other vertebrate group. Not only are there more species of fish (over 31,000) than of all other vertebrates taken together, but also the range of body shapes and sizes of fish is larger than for mammals, birds or reptiles. Consequently, the range of habitats occupied by fishes is larger than those occupied by other vertebrates.

3.1. Diversity of Indo-Pacific shore fishes

The triangle formed by Indonesia, the Philippines and New Guinea, previously referred to as the 'East Indies', form the center of marine fish biodiversity in the Indo-Pacific (Carpenter *et al*. 2008), with about 2,800 fish species naturally occurring there. These numbers drop with distance from this center to, e.g., about 500 species in Hawaii and 120 species in the Easter Islands. The number of endemic species, i.e., fishes that do not occur outside a given area, increases with distance from the center, which is compatible with the hypothesis that species evolved in the outer region and accumulated in the center. Another hypothesis holds that species evolved in the rich and stable habitats of the East Indies and were carried to the periphery by currents. Randall (1998) gives five explanations for the high fish biodiversity in the Indo-Pacific:

- Sea surface temperatures in the East Indies were more stable during the glacial periods and thus extinction rates were lower than at the periphery;
- Shelf area in the East Indies is much larger than that of the periphery, again making extinctions less likely;
- Dispersal of shore fishes to remote islands occurs during the planktonic larval phase (which lasts from several days to several weeks). However, the larval phase of many species is not long enough for long stretches of open ocean water, thus restricting their distribution;
- Existing current patterns support dispersal of fish larvae *from*, as well as convergence of larvae of species that have evolved in the periphery *towards* the East Indies;
- During the last 700,000 years, there have been at least three ice age events that reduced the water level in the East Indies and separated populations long enough for speciation to occur.

3.1.1. Exercises

- In FishBase, go to **Information by Country/Island**, select a number of islands along a North-South gradient in the Atlantic or a West-East gradient in the Pacific. Note the latitude or longitude, the area of the island, and the number of marine fishes. Sort the islands North to South or West to East. Discuss reasons for the observed trends in species numbers. [**Hint:** Use **Country info** to get coordinates and area, use **Marine** to get species numbers.]

- Use Randall's five explanations to discuss the pros and cons of the 'dispersal from center' *versus* the 'immigration from periphery' hypotheses.

3.2. The species-area relationship and latitudinal variations in diversity

The relationship between the number of species in an area (i.e., a river basin area, a lake, a shelf area) and the size of the area is known as species-area relationship and implies that the number of species in a given area increases with the size of the area. The latitudinal variation in diversity implies that the tropics are much richer in species than temperate and higher latitudes. These two general trends were the first 'diversity patterns' observed by ecologists for both aquatic and terrestrial ecosystems (see Rosenzweig 1995, Hawkins 2001), and a large number of hypotheses have been proposed for their explanation (e.g., Conor and McRoy 1979, Rosenzweig 1995, Anderson 1998, Hawkins 2001).

The species-area relationship is generally expressed as a power law (Arrhenius 1921) of the form:

$$S=c\cdot A^z \qquad \text{... 3.1)}$$

which, after logarithmic transformation of both S and A, takes the linear form:

$$\log_{10}(S)=\log_{10}(c) + z \log_{10}(A) \qquad \text{... 3.2)}$$

where S is species richness, A is the area of the ecosystem, and z and c are constants. For instance an analysis of a large number of lakes from Africa, USA and Canada, Europe and Asia, tropical Asia and tropical America as well as of rivers from Europe, Asia, Africa and South America (Table 3.1) indicates that, on a log-log plot, species richness was linearly related to lake and river basin area, respectively with the latter explaining more than 67% of the varability in species richness (Amarasinghe and Welcomme 2002). The exponent of the relationship between fish species richness and lake and river basin areas was larger in tropical than in temperate regions, a fact suggesting that freshwater fish species richness increases faster in the tropics than in temperate regions (Amarasinghe and Welcomme 2002).

Table 3.1. The relationships between number of fish species ($\log_{10}$) and river basin area ($\log_{10}$) in different geographical regions (from Amarasinghe and Welcomme 2002)

Continent	Species richness	R^2
Africa	$\log_{10}$(Species richness)=0.485 $\log_{10}$ (Area) – 0.561	0.88
Asia	$\log_{10}$ (Species richness)=0.263 $\log_{10}$ (Area) + 0.770	0.82
Europe	$\log_{10}$ (Species richness)=0.248 $\log_{10}$ (Area) + 0.428	0.67
South America	$\log_{10}$ (Species richness)=0.505 $\log_{10}$ (Area) – 0.491	0.91

3.2.1. Exercises

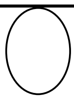
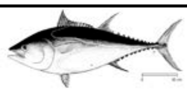
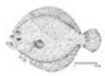
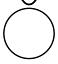
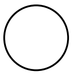
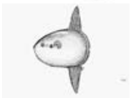
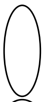
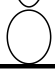
- FishBase provides a list of **All fishes** by country (all), and ecosystem (several) (i.e., **Information by Country / Island**, **Information by Ecosystem**). Select 10 marine ecosystems of different sizes (area). Get the list of all species and the number of species per ecosystem. Relate this to the area of the ecosystem. [**Hint:** for the ecosystem area, see http://www.seaaroundus.org/]. Compare the slope of the species-area relationship with the slopes shown in Table 3.1. Discuss the results in the form of a short essay.

- Select five tropical, subtropical, temperate and arctic/antarctic ecosystems (use **Information by Ecosystem**). Get the list of all species and the number of species per ecosystem. Compare the mean number of species per ecosystem type. [**Hint:** in Excel you can generate a file with columns entitled Ecosystem and Ecosystem type. Assign the dummy variables, 1 for tropical, 2 for temperate, and 3 for arctic/antarctic ecosystems. Use analysis of variance (ANOVA) from **Tools/Data analysis** to compare the means.] Discuss the results in relation to the latitudinal diversity pattern in the form of a short essay.

3.3. Diversity of shapes

The shapes of fish are also extremely diverse, and include – besides the torpedo shape perceived as ‘typical’ for fishes and termed ‘fusiform’ – shapes ranging from the serpentine (in the Anguilliformes and other orders) to the avian (in ‘flying fishes’), with the coelacanth, *Latimeria chalumnae* sporting limbs resembling, though not being used as, those of land-based tetrapods. Common basic shape categories of fish include: laterally flattened, ventrally flattened, torpediform or fusiform, arrow-like, eel-like, ribbon-like and spheroid shaped (e.g., Nikolsky 1963). Examples of the common categories of fish shapes are shown in Table 3.2.

Table 3.2. Common basic shape categories of fish.

Cross-section	Species	Scientific name	Common name	Body shape type
		*Thunnus thynnus*	Northern bluefin tuna	Torpediform
		*Psetta maxima*	Turbot	Ventrally flattened
		*Cepola macrophthalma*	Red bandfish	Ribbon-like
		*Anguilla anguilla*	European eel	Eel-like
		*Mola mola*	Ocean sunfish	Spheroid
		*Caranx ignobilis*	Giant trevally	Laterally flattened
		*Hyporhamphus dussumieri*	Dussumier's halfbeak	Arrow-like

Shape and other morphological features are the key characteristics still used to date for classifying fishes. Hence, understanding the classification of fishes requires a basic overview of their basic shapes. This can be obtained from the outline drawings included in FishBase, for each of the existing 500 fish families.

Body shape plays an important role in the way fish swim, prey and avoid predators and affects the way fish are caught by various fishing gears (e.g., trawls, gill and trammel nets, longlines, traps) and determines the size ranges caught by these fishing gears (i.e., gear size-selectivity; see Stergiou and Karpouzi 2003).

Apart from body shape, other external morphological features also exhibit a high variation, e.g., (a) the shape of the caudal fin – the main organ, acting with the caudal peduncle, which generates the required thrust for moving in the water (see, e.g., Weihs 1989) – can be rounded, truncated, pointed, or forked; (b) the mouth size ranges from small to very large and may be indicative of food preferences (see, e.g., Dabrowski and Bardega 1984) or the size of fish (see, e.g., Czerwinski et al. 2008); (c) the mouth shape ranges from an ellipse to a full circle (see also implications of shape to mouth volume in Muller 2009); and (d) the position of the mouth can be inferior, subterminal, terminal, or superior indicative of feeding ecology and/or habitat niche (see e.g., Langerhans et al. 2003).

3.3.1. Exercises

- Find from FishBase five species (not from the same genus) exhibiting the basic body shape types shown in Table 3.2. [**Hint:** use the **Identification** under **Tools**]. From the **Species Summary** page, find the habitat (e.g., pelagic, benthopelagic, demersal) of these species. Can you draw any inference, e.g., on the metabolic activity of the species, from these two sources of information?
- Find five species (not from the same genus) for each main type of caudal fin shape and mouth position. [**Hint:** use **Identification** under **Tools**]. From the **Species Summary** page, find information on the habitat and diet (from **More Information**) of these species. Can you draw any inferences, e.g., on the growth of these species, from these sources of information?

3.4. Diversity of scales

The body of fish is usually covered with scales, which provide protection. There are four basic types of scales:

- placoid scales (pointed, analogs of vertebrate teeth, e.g., in Elasmobranchii);
- cosmoid scales (probably evolved from the fusion of placoid scales, e.g., in the Family Ceratodontidae);
- ganoid scales (rhomboid shaped, modified cosmoid scales; e.g., in the Family Lepisosteidae); and
- elasmoid scales, separated into cycloid (circular with smooth edges) and ctenoid (circular with combed edges) scales, e.g., in Actinopterygii.

Scale size and morphology (especially of elasmoid scales) vary greatly from very small-sizes to highly modified scales (i.e., plates). There are many species that have no scales (e.g., the spotted torpedo, *Torpedo marmorata*, Family Gobiesocidae) and in some, e.g., flatfishes, scale type varies with sex and location on the body (dorsal *vs*. ventral).

Scales are of high practical importance to fisheries biology, notably because they (and other skeletal elements such as otoliths and rays) grow as fish grows. This leads to the formation of annual rings on the scales, much like in trees. The age of fish can be estimated from reading the number of annual rings on the scales (see Casselman 1979; Francis 1990). This results in length-at-age pairs which can be used to estimate growth in length (see section 3.8 on Diversity of growth).

3.4.1. Exercise

- Use Google images to find photos of the different types of scales. Then use the colour photos in FishBase to find several representative species for each scale type, as well as different variations in scale morphology. [**Hint:** many natural history museums whose collections are searchable online also contain photos of scales and otoliths of fish in their natural history collections.]

3.5. Diversity of color and sexual selection

Fish are beautiful; they have strange body shapes and vivid colors, the latter a major reason why people keep them in aquaria. Color patterns in fish have been long misunderstood. Some pre-Darwinian authors thought that god had given fish such marvelous colors so that predators would find it easier to see and catch them. We know, since Darwin, that such coloring, if it serves any function at all, must benefit directly the individuals sporting it, and not their predators. This is now obvious in the many color patterns that camouflage their owner, or confuse predators, by, e.g., displaying large eyes in the wrong places. Darwin also proposed a reason why non-camouflaging, striking coloring should exist, and that is *sexual selection*.

Essentially, the males entice the females to choose them by displaying nicer colors than other males; they compete in terms of their 'beauty', this being related to good genes (remember: Darwin did not know of genes and developing this part of his theory was very difficult for him). Recently, the Zahavi's complemented Darwin's version of sexual selection through a new concept, the *handicap principle*, which takes into account that the colors and other adornments which males use to entice females are costly to produce (Zahavi and Zahavi 1997). Hence, the color and other adornments represent a 'handicap' and the males capable of displaying these attributes thus should have really good genes for other life-supporting traits. We may call this 'truth in advertisement.'

The idea is that sporting highly symmetrical patterns, as, for example, in the emperor angelfish, *Pomacanthus imperator*, implies that the fish in question had a harmonious development since development problems, due to genetic problems, parasites or disease (also indicative of 'bad genes') would always lead to asymmetries. In addition, for colors that do not necessarily camouflage the fish, sporting them indicates that the fish in question has been able to evade predators. Some fish, however, imitate the color patterns of other species to fool prey or predators (mimicry), sometimes making them conveniently 'disappear' in the habitat they occupy.

3.5.1. Exercises

- Read Chapter XII, 'Secondary sexual characters of fishes, amphibians and reptiles', in Charles Darwin's *Descent of Man*, Vol.2. Give a one-page summary of the argument and re-express the main line of Darwin's argument using fish other than the ones in that chapter.
- Give examples from FishBase for species that use color patterns for (a) camouflage, (b) predator confusion, and (c) sexual selection.
- Give one example of mimicry in fishes. Explain the benefits gained. [**Hint:** common names of such species often contain the words 'mimic' or 'false'].
- Find from FishBase 10 pelagic species, 10 reef-associated and 10 bathydemersal species. Compare their colouration from the different photos from the **Species Summary** page and write a paragraph to describe this.

3.6. Diversity of sizes

Size is the most important attribute of individual organisms; it determines what can be their food, and the extent to which they can be the prey of other organisms. Size also determines how much food an animal requires, how fast it can swim, and to a large extent, where it can live. In fact, size is related to a plethora of biological, demographic, ecological, fisheries, and management parameters (Figure 3.1), which are often true within and between species. This shows that "[...] *marine fishes have been shaped by strong constraints, which once overcome, have produced strongly convergent features and hence predictable patterns* [...]" (Cury and Pauly 2000). In addition, length can generally be easier obtained than any other parameter and thus length records are available in most laboratories studying fish.

FishBase provided the opportunity to explore a large number of the relationships enumerated in Figure 3.1 (see, Froese and Binohlan 2000) which illustrates FishBase's capacity to transform information, i.e., each individual points, observations or records, to knowledge, i.e., the form resulting from the relationship of these individual points.

Maximum length (L_{max}) is available for the vast majority of species (i.e., for 26,074 species in FishBase as of April 2010). The L_{max} of fish ranges from less than 1 cm (e.g., 0.8 cm SL for the plainchin dreamarm, *Leptacanthichthys gracilispinis* and 1 cm TL for *Photocorynus spiniceps*) to 1,100 cm TL for the king of herrings, *Regalecus glesne*, and to 2,000 cm in the whale shark, *Rhincodon typus* (Figure 3.2). The L_{max} appears roughly log-normally distributed, but is actually right-skewed towards large fishes (Figure 3.2; Froese 2006). Fifty percent of fishes have L_{max} between 9 and 33 cm, and 90% of fishes between 4 and 96 cm (Froese 2006).

The maximum weight of fish also varies greatly but it is available for much less species (for 1727 species as of April, 2010) than L_{max}. It varies from about 1 g, such as in the lemon tetra, *Hyphessobrycon pulchripinnis*, to 4 t for the basking shark, *Cetorhinus maximus*, and 34 t for the whale shark, *Rhincodon typus*.

This diversity of size allowed widely different environments to be colonized, ranging from temporary puddles to the central gyres of the open ocean. However, colonizing these environments required other adaptations, involving growth and mortality rates, and their various correlates, discussed in the sections below.

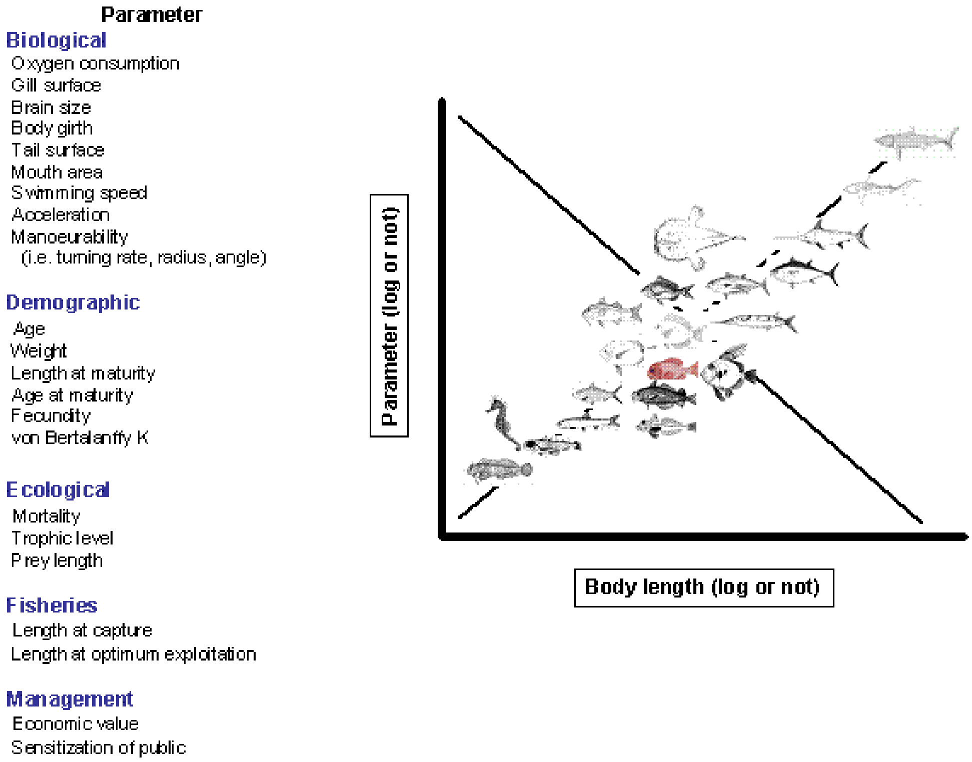


Figure 3.1. Relationship between length and other parameters in fishes (from Stergiou 2005a).

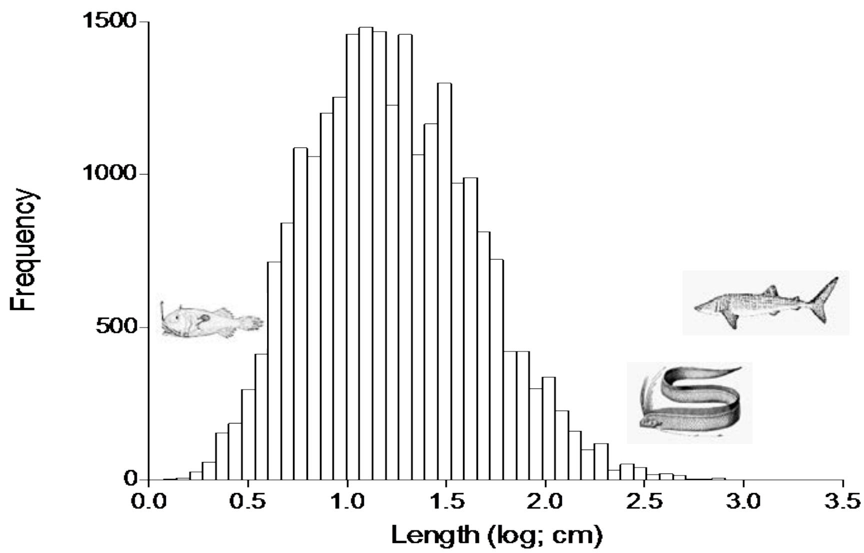


Figure 3.2. Frequency distribution of maximum lengths in 23,685 species of fishes (from Froese 2006). The depicted species are from left to right: plainchin dreamarm, *Leptacanthichthys gracilispinis*, king of herrings *Regalecus glesne*, and whale shark, *Rhincodon typus*.

3.6.1. Exercise

- Write down 20 marine and freshwater fish species that you know from your country. Next to the name of each species write its maximum length based on your knowledge or guess. Use FishBase to check your guesses.

3.7. The length-weight relationship (L-W)

The relationship between weight (W) and length (L) in fishes has the form:

$$W=a\,L^b \qquad \text{…. 3.3)}$$

which after logarithmic transformation of both length and weight takes the linear form:

$$\log_{10}(W)=\log_{10}(a) + b\cdot\log_{10}(L) \qquad \text{... 3.4)}$$

wherein $\log_{10}(a)$ is the intercept and (b) the slope or regression coefficient.

Length-weight (L-W) relationships are very useful for fisheries and ecological research because they are used: (a) to convert growth-in-length equations to growth-in-weight, for stock assessment models; (b) for the estimation of the biomass of a species from length frequency distributions from both onboard surveys and underwater (‘eyeballing’) observations; (c) as an estimate of the condition of fish; and (d) for between-region comparisons of life histories of a certain species. As a result, L-W relationships are an important component of FishBase (see The LENGTH-WEIGHT Table; Binohlan and Pauly 2000), which, in April 2010, contained 9,166 records for 3,426 species of fishes.

The analysis of a large number of L-W relationships from FishBase (Froese 2006) shows that the values of the slope b generally ranges between 2 and 4, with 90% of the values ranging from 2.7 to 3.4 (Figure 3.3). Values of b smaller, equal and larger than 3 indicate isometry, negative allometry and positive allometry, respectively. When b=3, small individuals have the same shape and condition as large ones. On the other hand, when b>3, large specimens increase in height or width faster than in length, either as the result of a change in body shape with size (an infrequent case), or because the large specimens in the sample are in better condition than the small ones. Conversely, when b<3, either the large specimens have changed body shape, i.e., become more elongated, or the small specimens were in better nutritional condition at the time of sampling. We point out that values of b<2.5 or >3.5 are often derived from samples with narrow size ranges (Carlander 1977; Froese 2006), although there are species with truly and strongly allometric growth (e.g., the red bandfish, *Cepola macrophthalma*, with an exponent of b~2.0, and the blackfin icefish, *Chaenocephalus aceratus* with an exponent of b~3.7).

The parameters a and b of the L-W relationship vary with the size range of the sample and thus, their use should be limited within this range. They also generally vary with sex, season and area.

The plot of $\log_{10}a$ *vs.* b for all species with available L-W relationships (Figure 3.4) shows that the variation in $\log_{10}a$ is largely a function of the body shape of the respective species (Froese 2006). This plot, referred to as the ‘Froese plot’ by Karachle and Stergiou (2008), can be used to identify outliers, i.e., points that deviate from the (straight) regression line.

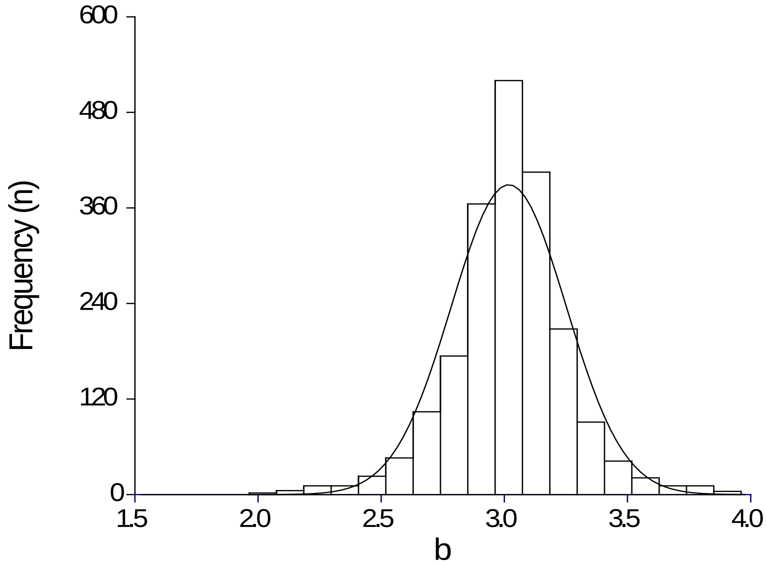


Figure 3.3. Frequency distribution of mean exponent b based on 5,079 records for 2,054 species, with normal line overlaid (from Froese 2006).

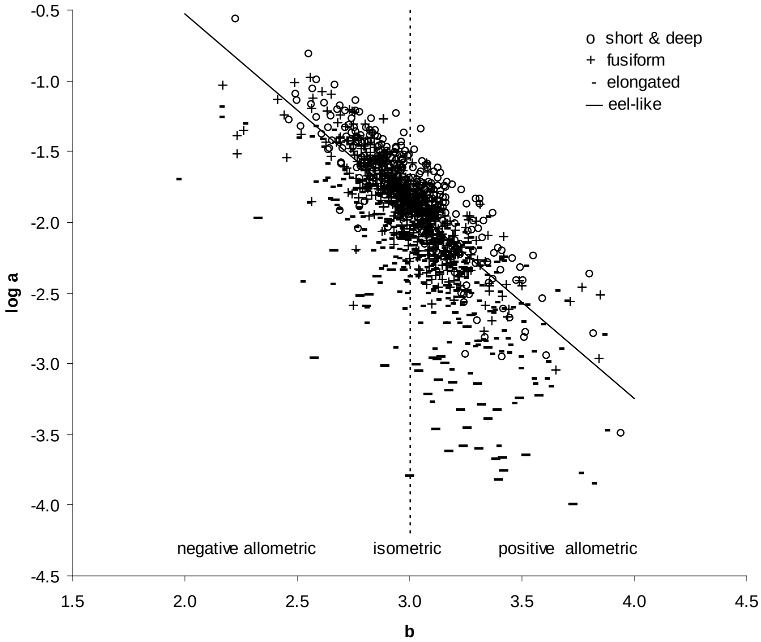


Figure 3.4. Scatter plot of mean $\log_{10}$a (cm; TL) over mean b for 1,232 fish species with body shape information (see legend). Areas of negative allometric, isometric and positive allometric change in body weight relative to body length are indicated. The regression line is based on robust regression analysis for fusiform species (n=451) (from Froese 2006).

3.7.1. Exercises

Table 3.3. Mean fork length-at-age

- Based on the data in Table 3.3, estimate the parameter a and b of a length-weight relationship of the form $W=a \cdot L^b$. The procedure to apply is the linear regression routine in Excel (or another spreadsheet or statistical software) after taking the logarithm of the length and weight observations. Results should be presented with estimates of the precision of the a and b parameters. [**Hint:** The regression function in Excel is found in the **Data Analysis** option under the **Tools** menu.]

of the St. Lawrence River population of muskellunge, *Esox masquinongy*, adapted from Scott and Crossman (1973, p. 367).

Age (year)	Mean length (FL; cm)	Mean weight (g)	Cohort strength (N)[a]
2	47.6	635	1005
3	58.7	1452	822
4	69.0	2631	674
5	79.8	3946	552
6	82.4	4491	452
7	87.6	5352	370
8	95.6	7167	303
9	105.6	9662	248
10	113.7	11476	203
11	112.5	12701	166
12	109.3	11295	136

[a)] hypothetical data

- Find one L-W relationship for each species per basic shape type used in exercise 3.3.1 (Diversity in shapes). Plot on the same graph the theoretical regression lines for the length ranges of all species per shape type, as reported in the LENGTH-WEIGHT Table [**Hint:** in Excel, generate a series, named **Length**, starting from 1 up to the maximum length of the largest species you have selected, using step size 1 cm. In the next column, generate a series, named **Weight,** i.e., for each cell of the weight series, estimate the weight corresponding to each length using the L-W equation available for each species]. Compare the L-W relationships and discuss the results.
- Find from FishBase all L-W relationships of the gila trout, *Oncorhynchus gilae*, the European hake, *Merluccius merluccius* and the cod, *Gadus morhua*. Plot $\log_{10}a$ *vs.* b for all relationships per species. Fit a linear regression to each. [**Hint:** The regression function in Excel is found in the **Data Analysis** option under the **Tools** menu.]. Check for points that deviate from the regression line.

3.8. Diversity of growth

Growth is the increase in size (i.e., length and weight) with time, and, the change in size per unit of time is called growth rate. The most commonly used equation to describe growth in fishes is the von Bertalanffy growth equation, which has the form:

$$L_t = L_\infty \left[1 - e^{-K(t - t_0)} \right] \qquad \text{… 3.5)}$$

where L_t is the mean length predicted at age (t); L_∞ ('L-infinity'), the mean size the fish would reach if they were to grow indefinitely (i.e., for a very long time); K is the rate at which L_∞ is approached (with dimension 1/time); and t_0 is the (usually negative) age the fish would have at length zero if they always grew as predicted by the equation (which they don't).

The L_∞ values estimated for fishes range from 1 cm in some short-lived gobies to around 14 m in long-lived whale sharks, as can be expected given their maximum size (see section 3.6 above). K values range from 8.5 $year^{-1}$ for small-sized, fast growing species such as the delicate round herring, *Spratelloides delicatulus*, to 0.02 $year^{-1}$, for the Adriatic halibut, *Hippoglossus hippoglossus*.

Parameters of the von Bertalanffy growth function are very important for ichthyology, and fisheries biology and ecology. They are used in life-history studies, in stock assessment and in ecological models. These parameters are usually estimated either from: length-at-age data (directly from readings of daily, monthly or annual rings from skeletal elements, i.e., otoliths and scales,); length-frequency data; or mark-recapture data. For species without available growth parameters in FishBase, e.g., rare species or species which are not exploited by commercial fishing, L_∞ can be estimated from the empirical relationship presented in Froese and Binohlan (2000):

$$\log_{10} L_\infty = 0.044 + 0.9841 \log_{10} L_{max} \qquad \text{… 3.6)}$$

which was based on 551 data sets from FishBase and where the resulting r^2 is 0.959 (s.e.=0.074).

The VBGF parameter K can be estimated using three different approaches. In cases where there are no VBGF parameters available, maximum age can be used with the empirical relationship:

$$K \approx 3/(t_{max}) \qquad \text{… 3.7)}$$

In cases where no growth studies are available, but length at first maturity (L_m) is available with age at first maturity (t_m), K can be estimated from the empirical relationship:

$$K \approx \log_e (1 - L_m/L_\infty)/(t_m) \qquad \text{… 3.8)}$$

where L_∞ is estimated using equation 3.6. Finally, in cases where growth parameter estimates are available for different populations or for closely related species, K can be estimated from L_∞ through the growth coefficient index (Ø') and the empirical relationship from Pauly *et al.* (1998):

$$Ø' = \log_{10} K + 2 \cdot \log_{10} L_\infty \qquad \text{… 3.9)}$$

In spite of the wide diversity of fish sizes mentioned above, clear patterns do emerge. One is that tropical fish tend to be smaller and faster-growing than their cold-water counterparts and that their natural mortality tends to be higher (see section 3.9). This is due to high temperature elevating the metabolic rates of tropical fish relative to their cold-water counterparts (Pauly 1998). Thus, when one estimates the parameter of the von Bertalanffy growth equation in tropical fish, one usually ends up with relatively low values of L_∞ and high values of K, at least as compared with their cold water analogs.

3.8.1. Exercises

- Estimate the von Bertalanffy growth parameters (L_∞, K and t_0) for the muskellunge *Esox masquinongy*, based on the age-length data pairs in Table 3.3. [**Hints:** The von Bertalanffy equation can be linearized through the expression $L_{t+1}=a+b \cdot L_t$ wherein L_t and L_{t+1} are the length at successive ages. Once a and b have been estimated by linear regression (see section 3.7), L_∞ and K can be estimated from $L_\infty=a/(1-b)$ and $K=-\log_e(b)$; t_0 can then be obtained by solving the von Bertalanffy equation for a few L_t and t data pairs and averaging the solutions. See also Froese and Palomares (2000) where this method is used for a re-interpretation of published data on the coelacanth, *Latimeria chalumnae*. Alternatively, a non-linear fitting routine, such as ‘Solver’, built in Excel can be used to solve simultaneously for L_∞, K and t_0 (see the Excel manual on how to use Solver).]
- Identify two families, one tropical, one temperate, whose representatives have similar maximum sizes, and compare the distribution of their growth parameters on an auximetric plot. Discuss how it is possible to compare growth parameters even of very different life forms, e.g., jellyfishes, with fish (see Palomares and Pauly 2009).
- Find from FishBase five species, each having more than 10 sets of von Bertalanffy growth parameters. [**Hint:** use commercial species, check for growth parameters in the **Species Summary** page, **More Information** link]. For each species, plot $\log_{10}K$ vs. $\log_{10}L_\infty$. Fit the five regression lines [**Hint:** The regression function in Excel is found in the **Data Analysis** option under the **Tools** menu.]. Compare the five slopes. Discuss the results.

3.9 Diversity of ages, longevity, senescence and mortality

Longevity (or lifespan) is defined as the oldest fish ever recorded for an unexploited species or stock, and can be approximated by the maximum known age. The latter also varies greatly in fishes, from very few months, in, e.g., seven-figure pygmy goby, *Eviota sigillata*, to 140 years for warty oreo, *Allocyttus verrucosus*, 149 years for orange roughy, *Hoplostethus atlanticus*, and 157 years for shortraker rockfish, *Sebastes borealis*. Fish are exceptional among vertebrates (Table 3.4) in terms of their lifespan. They are characterized by many species with lifespans more than 100 years (Reznick *et al.* 2002). Reznick *et al.* (2002) attribute this to the fact that fishes are characterized by 'indeterminate growth' (depicted in the von Bertalanffy growth equation; see section 3.8), which allows for a substantial increase in fecundity with age (see section 4).

Table 3.4. Known supercentenarian vertebrate species (i.e., species with longevity >100 years).

Group	Common name	Scientific name	Longevity (years)	Reference
Mammals	blue whale	*Balaenoptera musculus*	110+	Haley (1978)
	fin whale	*B. physalus*	114+; 116+	Bobick and Peffer (1993); Haley (1978)
	bowhead whale	*Balaena mysticetus*	100	Reznick *et al.* (2002)
	killer whale	*Orcinus orca*	100+, 90+	MacDonald (1984); Bobick and Peffer (1993)
	humans	*Homo sapiens*	100+, 116+, 122.5+	Nowak (1991); Bobick and Peffer (1993); Alaro *et al.* (1998)
Reptiles	Aldabra tortoise	*Geochlone gigantea*	152+	Burton and Burton (1975); Goin *et al.* (1978)
Fishes	lake sturgeon	*Acipenser fulvescens*	152	Anderson (1954)
	beluga	*Huso huso*	118	Carey and Judge (2002)
	white sturgeon	*Acipenser transmontanus*	100+	Anderson (1988)

Lifespan is the result of mortality caused by the combined action of intrinsic and extrinsic sources (Partridge and Barton 1996; Reznick *et al.* 2002). Although long lifespans is not synonymous to senescence, the former can only be achieved with "the combination of low extrinsic mortality rates and deferred senescence" (Reznick *et al.* 2002).

The loss of individuals due to natural intrinsic and extrinsic causes, such as predation (the main cause of natural mortality), starvation, diseases, genetic anomalies, etc, is known as natural mortality (M). However, humans use fish for food and other purposes (e.g., recreation, aquaria), which cause additional mortality. The mortality caused by all forms of fishing is known as fishing mortality (F). The sum of natural and fishing mortality is called total mortality (Z).

Natural mortality is one of the most difficult parameters to estimate because nowadays most fish stocks, commercial or not, are affected directly or indirectly by fishing. As a result, most of the available estimation methods provide estimates of Z rather than M. Thus M is often estimated from empirical equations, which relate existing M values for several unexploited stocks to other parameters. Two of the most commonly used empirical methods are those of Hoenig (1983), which relates M to maximum age, t_{max}, for unexploited stocks (thus Z=M) and was based on data for 84 stocks of 53 fish species:

$$\log_e Z = 1.46 - 1.01 \cdot \log_e T_{max} \qquad \ldots 3.10)$$

and Pauly's (1980) equation, which relates M to L_∞, K and mean temperature (T) in the habitat of the stock and was based on data from 175 stocks:

$$\log_e M = -0.0152 - 0.279 \cdot \log_e L_\infty + 0.6543 \cdot K + 0.463 \cdot \log_e(T) \qquad \ldots 3.11)$$

The natural mortalities experienced by fish, which are also a function of their size and age, range from values which exterminate an entire cohort in less than a year, e.g., in the Lake Tanganyika sprat, *Stolothrissa tanganicae* (M=5.2 $year^{-1}$), to values which suggest an average life expectancy of over 20 years, e.g., in the lake sturgeon, *Acipenser fulvescens* (M=0.06 $year^{-1}$). These enormous differences in natural mortalities and lifespans allow fish to respond differently to habitat variations. Small, short-lived fish track such variations, for example, when growing up in temporary puddles and laying desiccation-proof eggs before they dry up, thus being able to live through dry periods, or by spawning every year, but producing a successful cohort only once every 5-10 years (as may happen in such long-lived fish as cod, *Gadus morhua*).

3.9.1. Exercises

- Reznick *et al.* (2002) reports 13 fish species with ages>100 years. Table 3.4 shows some of them. Find from FishBase as many fish species as possible with ages>100 years and fill Table 3.4. [**Hint:** Size is related to age. A list of growth parameters available in FishBase can be accessed under the **Information by Topic** section of the FishBase search page.]
- Estimate the value of natural mortality (*M)* from the relative abundance in Table 3.3 (4^{th} column). [**Hints:** M can be estimated as the slope (with sign changed) of the regression of $\log_e(N)=a+b \cdot t$, where *N* is the number of fish in a cohort, and t their age. The regression function in Excel is found in the **Data Analysis** option under the **Tools** menu.]
- Compare natural mortality (M) estimates for 10 species of tropical fish, ranging between 50 and 100 cm maximum length, with 10 species of fish with similar sizes from cold waters and test for a temperature effect. [**Hint:** temperature and M values maybe found in the **Life history tool** available from the bottom of the Species Summary page.]
- Select 10 commercial stocks (from different species) for which there are available records of maximum age (t_{max}) and von Bertalanffy parameters. Estimate their natural mortality (M) using Hoenig's (1983) and Pauly's (1980) empirical formulas. Compare and discuss the results.
- Select 30 stocks from different species for which there are records of natural mortality (M), maximum age (t_{max}) and maximum length (L_{max}). Plot $\log_{10}M$ *vs.* $\log_{10}t_{max}$ and $\log_{10}M$ *vs.* $\log_{10}L_{max}$. Fit the regression lines. Discuss the results.

[**Hint:** The regression function in Excel is found in the **Data Analysis** option under the **Tools** menu.]

3.10. Diversity of habitats: inferences from occurrence records

Fish inhabit more diverse habitats than any other group of vertebrates, ranging from Himalayan or Andean brooks at 4000 meters to abyssal depths at 10 kilometers, thus spanning an extremely high range of pressures. The range of temperatures that can be tolerated is also very large, from -2ºC as for the antarctic fish *Pagothenia borchgrevinki* (which sport anti-freeze substances in their blood; see Eastman and Devries 1985); to up to 40ºC for the natron tilapia, *Oreochromis alcalicus*, which lives at the edge of a hot spring in Lake Nakuru in Kenya. (This does not consider the temperature tolerance of deep-sea vent fishes, which have not yet been studied in detail; see however Somero 2005 for a discussion on thermal limits of aquatic animals).

Because fish occur only in habitats which they can tolerate, and tend to be abundant in those habitats to which they are best adapted, occurrence records kept by museums can be used to reconstruct the habitat preferences of fishes whose ecology is otherwise unknown. Such records have been named *bioquads* because they refer to biodiversity and consist of four key elements: (a) the name of the organism; (b) the place where it was caught; (c) the source or person who sampled or identified it; and (d) the date (Pauly and Froese, 2001). FishBase makes wide use of bioquads for documenting the distribution of fish and this can be emulated by ichthyology students who may assemble bioquads from FishBase and other sources, notably, the Internet.

3.10.1. Exercises

- Select a species in FishBase and print a point map as well as the point information. See whether you can find additional points in ichthyological museum collections. Identify problematic records. Infer from the habitat (i.e., occurrence records) or the ecological requirements of that species. [**Hint:** links to point maps are available from the **Species Summary** page. Point information details are shown by clicking on a point (or dot) in a map. Further details on how point maps are created are also available at the AquaMaps website at www.aquamaps.org.]
- Find from FishBase 20 species inhabiting very deep waters (e.g., bathypelagic, bathydemersal). [**Hint:** use the **Information by Country / Island**, **Biodiversity**, **Deep-water** link.] Compare their morphology and identify special adaptations in morphology for deep-water life.

3.11. Diversity of food and feeding habits

Given the diversity of their sizes and habitats, it is obvious that fish should also have a wide diversity of food and feeding habits. Thus fish range from feeding on microscopic phyto- and zooplankton to engulfing entire adult fishes, such as is done by whale sharks or gulpers, respectively. Attempts to link fish to their ecosystems have led to a huge number of studies on their food and feeding habits. Unfortunately, some of these are largely useless because they are reported using the wrong units, i.e., frequency of occurrence of certain items in a number of stomachs sampled. Still, there are enough studies in which the proper units have been used (contribution in weight, energy or volume to total stomach contents) for a clear idea to emerge of what fish generally eat in their typical habitat. Given knowledge of the average trophic level of their diet items (Table 3.5), the trophic level of fish whose stomach content has been studied can thus be computed, which allows evaluation of the position the consumers occupy in the food web (see section 6.1 on Food webs and trophic levels).

Table 3.5. Hierarchy of food items, simplified from the FishBase table used to compute trophic levels (TL) from diet composition data. Therein, the TL of a consumer is 1 + (mean TL of the prey items).

Food I	Food II	Food III[a]	TL
Detritus	Detritus	debris; carcasses	1.0
Plants	Phytoplankton	blue-green algae; dinoflagellates; diatoms; green algae; other phytoplankton	1.0
	other pla nts	benthic algae/weeds; periphyton; terrestrial plants	1.0
zoobenthos	sponges/tunicates	sponges; ascidians	2.0
	Cnidarians	hard corals and other polyps	2.5
	Worms	Polychaetes; other annelids; non-annelids	2.1
	Mollusks	chitons; bivalves; gastropods; octopi;, other mollusks	2.5
	benthic crustaceans	ostracods;; isopods; amphipods; other small forms	2.5
		shrimps; lobsters; crabs stomatopod; other large forms	2.6
	Insects	Insects	2.2
	Echinoderms	sea stars/brittle stars; sea urchins; sea cucumbers; etc	2.4
	other benthic inverts	Other benthic invertebrates	2.5
zooplankton	jellyfish/hydroids	jellyfish/hydroids	3.0
	planktonic crustaceans	copepods; cladocerans; mysids; euphausiids; etc.	2.1
	other planktonic inverts	n.a./other planktonic invertebrates	2.2
	finfish	fish larvae	2.5
Nekton	Cephalopods	squids/cuttlefish	3.5
	Finfish	Bony fish and small sharks or rays	3.2
Others	Herps	Salamanders/newts; toads/frogs; turtles and other reptiles	2.6
	Birds	sea and shore birds	3.6
	Mammals	Small cetaceans and pinnipeds	4.1

a) in FishBase, these food items have distinct trophic levels (and associated standard errors), not presented here

3.11.1 Exercises

- Find published studies on the diet composition of six different species of fish: two mainly herbivores; two omnivores, and two typical carnivores. Construct a common table including all prey items from all six fish species. In this table the presence of a prey item in the diet of each of the six species is marked with 1 and its absence with 0. Subject this table to cluster and multidimensional scaling in order to separate the six species into groups characterised by a similar diet. [**Hint:** for multivariate analysis, use specialised statistical software such as PRIMER]. Discuss results in the form of a short essay.

- Select five species from FishBase and find their main prey items and predators from the **Species Summary** page (**More Information, Prey items** and **Predators** links). For each species construct a simplified food web. [**Hint:** select commercially important species.]

4. Reproduction

4.1. The reproductive load concept

Fish usually reproduce when they have reached about half of the maximum size they are likely to reach (L_{max}). The size at which maturity is first reached is called size at first maturity (L_m), and the fraction L_m/L_{max}, called *reproductive load*, tends to be higher in small than in large fish. Thus, a goby with L_{max}=10 cm will have a value of L_m=7 cm, while in a basking shark with L_{max}≈10 m, L_m will be about 4 m. Given that fish of different sizes have different growth rates, their different L_m values imply very different ages at first maturity (t_m).

L_m is available for few species when compared to the total number of fish species. Froese and Binohlan (2000) developed the following empirical equation based on available data from 467 fish stocks **(r^2=0.89, s.e.=0.127)** in FishBase:

$$\log_{10}(L_m) = -0.0782 + 0.8979 \cdot (\log_{10} L_\infty) \quad \text{... 4.1)}$$

For species with no available L_m information, equation 4.1 can be used for the estimation of L_m (and its standard error, s.e.) from the available L_∞ values of the species and the s.e. of the slope of equation 4.1. Such 'quick' estimates are useful for fisheries management in data-sparse situations (see section 6.5 on Fisheries Management).

4.1.1. Exercises

- Find from FishBase 20 species with maximum lengths L_{max}<50 cm, 50<L_{max}<100 and L_{max}>100 cm with at least one record of L_m. Estimate the L_m/L_{max} ratio. Estimate the mean ratio for the three size classes. Compare the means. [**Hint:** In Excel use ANOVA from **Tools/Data analysis** to compare the three means.]
- Find from FishBase 10 species with no record of L_m but with at least one available set of von Bertalanffy growth parameter. Estimate the species' L_m from their L_∞ using equation 4.1.

4.2. Small eggs and no worries

Fish differ from most other vertebrates in that for most species, parental care is very limited or non-existent. The typical bony fish produces a large number of small eggs which hatch and become part of the zooplankton, and which must beware of their parents (or other members of their species) if these are zooplankton feeders.

The high fecundity of bony fish (see Nellen 1986) has led many to believe that they can be exploited very strongly, i.e., that there will always be some recruits even if the parental stock is much reduced. This is called the 'million egg fallacy' (see Froese and Luna 2004). and it has caused untold damage to fisheries, especially cod fisheries. Still, it is useful to know the relationship between numbers of eggs spawned and the weight of the mothers.

4.2.1. Exercises

- A given fish species capable of reaching 50 cm, has the following fecundity-length relationship: $f=0.03 \cdot L^{3.5}$, where f is the number of eggs in a ripe female and L its length in cm. The same species has the length-weight relationship $W=0.01 \cdot L^{3.0}$ where W is in g and L in cm. Use these relationships to calculate the relative fecundity of the largest females, and compare this with the relative fecundity of a female near first maturity, near 60% of L_{max}.
- Redo the above calculations, but with exponents of 2.5 and 4.5 for the fecundity-length relationships. What are the implications of the results for the usefulness of marine protected areas, where female fish can get old (and hence large)?

4.3. Large eggs and parental investment

There are a number of fish which give birth to live young or which construct nests for their eggs, or which practice buccal incubation, e.g., in the Nile tilapia. Some other fish, notably the cartilaginous sharks and rays, give birth to fully-formed pups or produce very large eggs from which fully-formed young are hatched.

4.3.1. Exercise

- Write a one-page essay on why most fish species broadcast their eggs and exert no parental care, given the fact that parental care reduces the mortality of the young and is practiced by several successful groups of fishes. [Note: a number of studies have been published on this, e.g., Smith 1977, Perrone and Zaret 1979, Barlow 1981, King and McFarlane 2003.

4.4. Variations on the basic theme

As noted by Darwin, fish are extremely labile in their sex determination, i.e., there are lots of fish which change sex (e.g., anemonefishes, wrasses, parrot fishes, groupers), at least, far more than in other vertebrate classes (see Warner 1988, Ross 1990). These are called hermaphrodites. In some fishes the different life (and sex) stages differ so much in color and/or form that they were originally described as different species, e.g., the protogynous hermaphrodite Mediterranean rainbow wrasse, *Coris julis* (see Bruslé 1987), or even different families, e.g., the case of larval and juvenile forms of whalefishes (see Paxton *et al*. 2001). Fish also give us neat examples of parasitic males (Taborsky 1998 lists 140 fish species in 28 families exhibiting forms of parasitism), and other strange behaviors.

4.4.1. Exercise

- Give one example of a hermaphroditic species where subsequent development phases look very different.
- Write a one-page essay about the different forms of hermaphroditism that exist and their distribution among fish families, and latitudinally.
- Write a one-page essay on the group(s) in which parasitic males occur and give possible reasons for their preponderance among these groups.

5. Physiology

The basic building blocks of fish bodies are proteins. Proteins have structure at several levels. The primary structure is determined by a sequence of the component amino acids, themselves with a structure determined by their sequence of atoms of carbon, hydrogen, etc. The secondary structure of most protein is a primary coil, similar to a braid. A third-level structure can emerge when the braids fold onto themselves, with various loops weakly connected by hydrogen bonds. It is this tertiary structure which determines the external shape of a protein, e.g., of an enzyme and hence how it will lock into 'receptors', often other molecules on the surface of cells.

5.1. Metabolism, gills and size

Thermal noise is ubiquitous above absolute zero (0 Kelvin) and one of its effects is to destroy the tertiary structure of protein, thus rendering it ineffective. As a result, animals must break down such denatured molecules into their constituent parts and re-synthesize them. This is the reason why it costs energy to maintain a living body, even when it 'does' nothing, nor grows. In mammals and birds, which maintain more or less constant internal body temperatures, the enzyme systems are geared such that the rate of synthesis matches a certain level of thermal noise, i.e., that which occurs at 37 to 38°C. In fish, which except for large scombroids and some large sharks, cannot maintain a constant body temperature, different external temperatures thus imply different levels of thermal noise and hence rates of protein denaturation. Thus, metabolic rate must vary with temperature and it does so essentially as a function of the need to re-synthesize protein.

However, it must be understood that the oxygen *consumed* by a fish is not its oxygen *demand* but the oxygen *supplied* to it via its gills, i.e., the fish would use more oxygen if it could get it. Hence, the amount of oxygen consumed by a fish is an imperfect measure of its real 'need' for oxygen. Gill size grows in proportion to a power of body weight that is less than one, i.e., the bigger the fish of a given species becomes, the smaller the gill area per body weight becomes. Hence, big fish, given a certain level of activity, will tend to run out of oxygen faster than small fish of the same species, other things being equal.

5.1.1. Exercise

- Choose a species from Table 5.1. Estimate for that species the exponent of a log-log relationship between gill area and body weight, and between oxygen consumption and body weight, and plug into this equation the value for the maximum size reported for that fish in a given habitat. [**Hint:** maximum lengths by locality are found using the **Max. size & age** link in the **Species Summary** page.]

Table 5.1. Ten species in FishBase with growth parameters, at least one length-weight relationship and three records each of gill area and oxygen consumption per unit body weight.

Common name	Scientific name
Sea trout	*Salmo trutta trutta*
Goldfish	*Carassius auratus auratus*
Blackfin icefish	*Chaenocephalus aceratus*
Flounder	*Platichthys flesus*
Walleye	*Stizostedion vitreum*

Mrigal	*Cirrhinus mrigala*
Skipjack tuna	*Katsuwonus pelamis*
Tench	*Tinca tinca*
Common carp	*Cyprinus carpio carpio*
Roach	*Rutilus rutilus*

- Compute the gill area per unit weight and oxygen consumption per unit weight at which the fish stops growing. [**Hint:** L_{max} and L_{∞} may have something to do with this.]

5.2. Diversity of brain sizes

The brain size per body weight of adult animals is related to the sensory and behavioral capabilities of the species to which they belong. For example, fishes with well-developed electrosensing capabilities are known to have large brains. On the other hand, the brain is the body organ with the highest energy and oxygen demand, and thus, fishes as well as other animals have evolved brain sizes that are neither too small nor too large respective to the niches they occupy in nature. Brain size of tropical coral reef fish, for example, have been found to be related to their ability to avoid predators (see Bauchot *et al.* 1977, Bauchot *et al*. 1989; see also Packard 1972 for a similar example on cephalopods). More recent studies also show that large-brained predators feed on equally large-brained prey implying that brain size may be related to trophic interactions and may be used to better understand how ecosystems function (see Kondoh 2010). [Note as an aside that it is not true that people (at least most) use only 10% of their brain's capacity].

5.2.1. Exercise

- Based on your general knowledge about the fish and their habitat, rank the following groups according to their brain size: coral reef fish, deep sea fish, herrings, sharks, coelacanths. Explain in a few sentences why you ranked each group as you did.
- For the groups listed above, find typical examples, look at their brain size compared to other fishes, and use these data to test your hypothesis about their respective groups. [**Hint:** common names often contain parts of a group's scientific name].

5.3. Fish vision and sleep

One main brain activity of most vertebrates is the processing of sensory, mainly visual, information. Sleep may have evolved as a response to the need to refresh memory circuits (Kavaneau 1998). This is consistent with the fact that genetically blind fishes that live in caves do not need sleep because their need for processing sensory information is almost nil (Kavaneau 1998). [For other potential non-sleeping fish species see Kavaneau (1998).]

5.3.1. Exercise

- Find from FishBase 30 blind fish species. From the **Species Summary** page extract information related to **Habitat** and **Diet** (**More Information** link) and check their colouration from the available photos. Construct a table with these parameters, draw conclusions and write an essay.

5.4. Fish sounds

Fishes having good audition, and water being a good medium for the dispersion of sounds, fishes are thus able to produce different types of sounds, viz.: grating sounds produced by rubbing certain body parts, drumming, cavitation, and percussion, as well as hydrodynamic, pneumatic, stringed, and respiratory sounds (see Kasumyan 2008). These sounds maybe produced both passively and/or activiely as an expression of different behaviors, e.g., 'agonistic' sounds used in aggression, threat, submission, escape, distress (see Ladich 1997) when alarmed, netted, or in intraspecific competition or when defending its territory (see Amorim 2006). The main sound production organs are the swim bladder (see Yan *et al*. 2000) and the teeth, mainly the pharyngeal ones (Demski *et al*. 1973, Rice and Lobel 2005). Vocal fishes use sounds to distinguish their own when closely related species are present, notably during the mating season, e.g., African mormyrids living in low visibility freshwaters where visual recognition is not viable (Amorim 2006). Because of this mating vocalisation, it has been suggested that conservation measures, e.g., closure of fishing in spawning sites, can be based on hydroacoustic surveys (Luczkovich *et al*. 1999). The intensity and frequency of sounds produced by fish are closely related to the size of fish, and may have individual qualities (Kasumyan 2008), i.e., bigger, and thus better sounding individuals, are stronger and fitter and are therefore desirable mates (Amorim 2006). FishBase (**Information by topic**, **Physiology/Behaviour, Fish sounds**) lists the species that produce sound together with accompanying information (i.e., type of sound produced, sound production organ, sonic mechanism, behavioural context, reference and remarks).

5.4.1. Exercise

- Select 50 sound-producing species and prepare a table listing the types of produced sound, the sound production organ, the sonic mechanism and the behavioural context. Summarise the results in the form of a short essay.

5.5. Food consumption

Like other heterotrophic organisms, fish need food to survive and grow. Within ecosystems, trophic (feeding) relationships and energy flows largely define the function of various species. There are two ways of presenting species-specific consumption:

- At the individual level, i.e., as the consumption of a particular food type by a fish of a certain size, in the form of a daily ration (R_d); or
- At the population level, i.e., as the consumption (Q) by an age-structured population of weight (B), in the form of population-weighted consumption per unit biomass (Q/B).

There are a number of methods that can be used to estimate the daily ration of fish: studying the changes in stomach content in the course of a day, direct observation of captive fish, etc. One of these techniques is to infer ration from daily oxygen consumption, which is justified since the oxygen consumed is ultimately combined with the food consumed to generate ATP (adenosine triphosphate, the substance used to fuel internal metabolism). This is illustrated through an example for red piranha, *Pygocentrus nattereri*, adapted from Pauly (1994):

Data were analyzed using a multiple (log) linear regression which yielded, for prediction of the metabolic rate (C, in mgO_2h^{-1}) in small *Pygocentrus nattereri*, the model:

$$C=0.387 \cdot W^{0.539} \cdot O_2^{1.13} \qquad \ldots 5.1)$$

where W is the live weight of the fish in g, and O_2 is the oxygen content of the water, in mg 1^{-1}. The overall fit is good (R=0.950); the standard errors of the exponents are 0.163 and 0.205, respectively, for 4 degrees of freedom. Given the small range of weights considered here, the relatively large standard errors about the estimates, and the low number of degrees of freedom, it would not be appropriate to assume that the slope linking O_2 consumption and body weight is, in *P. nattereri*, significantly different from that proposed by Winberg (1960) for most fishes larger than guppies, i.e., 0.7-0.8. This implies that the equation above can be used only for a small range of weights, here 20 to 160 g.

For a 100 g fish in water with 6 mg $O_2 1^{-1}$, the equation above predicts an O_2 consumption of 35 mg$\cdot h^{-1}$, i.e., 841 $mgO_2 \cdot day^{-1}$. An estimate of daily energy consumption (Q) can be obtained from this using the approach of Wakeman *et al.* (1979), wherein:

$$R_d=(\Delta W+RESP)/0.75 \qquad \ldots \text{eq. } 5.2)$$

where R_d is the daily ration, i.e., daily energy consumption in kcal, ΔW the energy content of the (daily) growth increment, and RESP is the oxygen consumption. The first derivative (i.e., growth rate) of the von Bertalanffy equation in terms of wet weight is:

$$dW/dt=3KW((W_\infty/W)^{1/b}-1) \qquad \ldots 5.3)$$

This, solved for W_∞=756 g, K=0.893/365=0.00245 day^{-1}, and b=3, gives for a 100 g fish a daily growth increment of 0.706 g, corresponding to 0.706 kcal if the calorific value of fish wet weight is set equal to unity (Brett and Blackburn 1978). The available information on body composition of red piranha flesh (Junk 1976, in Smith 1979) is 8.2 % fat, 15.0 % protein, and 4.4 % ash, not very different from values reported from other fishes (Bykov 1983). Thus, if an oxycaloric equivalent of 0.00325 $kcal \cdot mg^{-1}$ O_2 is assumed, as in other fishes (Elliot and Davidson 1975), the above estimate of 841 mg O_2 day^{-1} becomes 2.733 kcal day^{-1}. Thus:

$$R_d=(0.706 + 2.733)/0.75 \quad \ldots 5.4)$$

or 4.585 kcal day^{-1} for a 100 g piranha. Food conversion efficiency (K_1=(dW/dt)/R_d; Ivlev 1966) would then be K_1=0.154.

5.5.1. Exercise

- Compute for species in Table 5.1, the gill area per unit weight and oxygen consumption used only for maintenance. [**Hint:** fish cease growing when they approach W_∞ and conversion between total and fork length can be done from a picture or using the link L-L relationship in the ‘More Information’ link in the Species Summary page].

5.6. Estimating food consumption from empirical models

The method outlined above to deal with the ration of fishes led to point estimates, pertaining to a single size or age (group). A fish population consists, however, of different size (age) groups, with small sizes and ages being far more abundant than large sizes and ages. Thus, drawing inferences from one (or several) ration estimate(s) pertaining to a given size (range) of fish, to a population containing a multitude of size groups, requires a knowledge of the size (age) structure of the population. An approach for performing this inference is given in FishBase.

A large number of such inferences, from ration to population weighted food consumption estimates (Q/B), have been performed in recent years, notably Palomares and Pauly (1998). These estimates of Q/B can be used in the context of empirical models to predict Q/B from other, easy-to-estimate parameters. One such equation is:

$$\log_{10} Q/B = 7.964 - 0.204 \log W_\infty - 1.965 T' + 0.083 A + 0.532 h + 0.398 d \qquad \text{… 5.5)}$$

where Q/B is the food consumption, W_∞ is the asymptotic weight in grams, $T'=1000/(°C+273)$, A is the aspect ratio of the caudal fin=h^2/s, h=1 and d=0 for herbivores, h=0 and d=1 for detritivores, and h=0 and d=0 for carnivores.

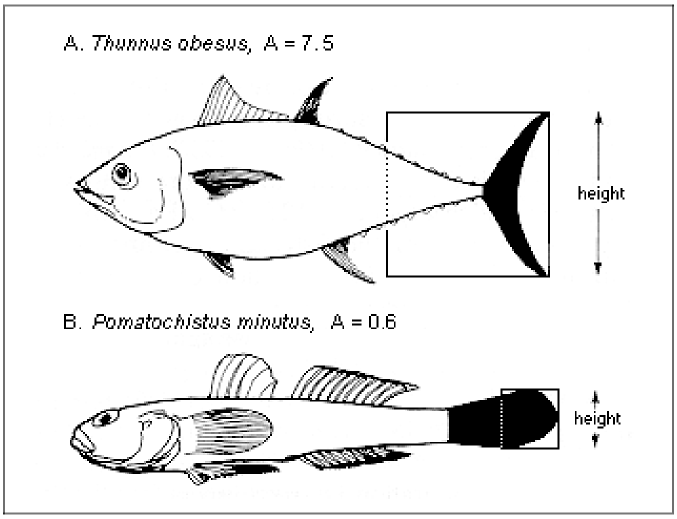


Figure 5.1. Aspect ratio (A) of the caudal fin (see section 3.3 on Diversity of shapes)

Here, one key input is the aspect ratio of the caudal fin defined as in Figure 5.1. Fish with tails with high aspect ratio consume more food than fish with low aspect ratio tails, other things being equal. Needless to say, equation 5.5 cannot be used for fish (e.g., eels) which do not use their caudal fin as their main propulsive organ. Other approaches can be used in such cases.

5.6.1. Exercises

- Identify through FishBase, pictures of three species of fish covering a wide range of caudal fin aspect ratio: one with an aspect ratio of around 1; one with an aspect ratio of around 3-4, and one with an aspect ratio of above 7. [**Hint:** using a square grid on a transparency and counting the number of square units or cells occupied by the caudal fin to estimate the fin area should help.]

- Use the aspect ratio, the body size, and the temperature of the habitat to infer Q/B given equation (5) above, and (a) a herbivorous diet; or (b) a carnivorous diet. [**Hint:** the equation is also implemented in the Life-history tool available from the bottom of the Species Summary pages]

6. Fish as part of exploited ecosystems

6.1. Food webs and trophic levels

Fish populations do not live by themselves. Rather, they are embedded in ecosystems where they perform their roles as consumers and prey of other organisms, including larger fishes. The position of an organism in the food web is depicted by its trophic level, which is estimated as follows:

$$\mathbf{TROPH_i = 1 + \sum_{j=1}^{G} DC_{ij} * TROPH_j} \qquad \text{... 6.1)}$$

where $TROPH_i$ is the trophic level of species (i), $TROPH_j$ is the trophic level of prey (j), DC_{ij} is the contribution of prey (j) in the diet of species (i) and G is the total number of prey.

Trophic levels in aquatic environments generally range from 2, for herbivores and detritivores, to 5.5, for specialised predators of marine mammals, such as the polar bear, *Ursus maritimus* and the killer whale, *Orcinus orca*. The trophic levels of fishes generally range from 2 (e.g., the detritus feeding blue-barred parrotfish) to 4.7 (e.g., the piscivorous striped marlin), whereas those of marine mammals range from 3 (e.g., the predominantly seagrass feeding dugong) to 5.5 (e.g., the carnivorous killer whale), those of cephalopods from 3.2 (e.g., the planktivorous Patagonian squid) to 4.5 (e.g., the piscivorous greater hooked squid), and of marine birds from 2.6 (e.g., the gastropod feeding Mediterranean gull) to 4.9 (e.g., the petrel preying brown skua; see Pauly *et al.* 2001; Froese *et al.* 2005; Karpouzi 2005).

It is important to compare the consumption patterns of humans in the terrestrial and aquatic realms in terms of trophic levels. The terrestrial animals consumed by humans have usually trophic level 2 (e.g., cows, pigs, chickens, lamb). In contrast, humans have a strong preference for large-sized fishes such as flatfishes, hakes, cods, tunas, swordfishs, all of which have trophic levels higher than 4. This is the equivalent of consuming the terrestrial predators of lions and tigers (i.e., dragons?).

Trophic level has gained wide acceptance as an ecological indicator for ecosystem management. One measure, the marine trophic index, has been selected by the Conference of the Parties to the Convention of Biological Diversity as 1 of 8 biodiversity indicators (see Pauly and Watson 2005). Its strength as an ecological indicator lies in its efficiency in capturing/expressing fishing-induced effects at the community or ecosystem level, either directly: (a) for identifying the **'fishing down the marine food webs'** process (Pauly *et al.* 1998; see section 6.6, Effects of fishing on ecosystems) and (b) for estimating the trophic impact of different fishing gears (see section 6.3, Trophic signatures), or indirectly (c) for estimating other indicators (e.g., Primary Production Required to support fisheries, Pauly and Christensen 1995; 'Fishery in Balance' index, Pauly *et al.* 2000).

6.1.1. Exercises

- Find published studies on the diet composition of three different species of fish: one mainly herbivore; one omnivore, and one typical carnivore. Compute their trophic levels using the classification of diet items and trophic levels in Table

3.5. [**Hint:** see Boxes 25-26 of the FishBase book at http://www.fishbase.org/manual/English/contents.htm].

6.2. Trophic levels and sizes of fish

The role of fishes within ecosystems is largely a function of their size: small fish are more likely to have a vast array of predators than very large ones. On the other hand, various anatomical and physiological adaptations may lead to dietary specialization, enabling different fish species to function as herbivores, with a trophic level of 2.0, or carnivores, with trophic levels typically ranging from 3.0 to about 4.5.

Moreover, trophic levels change during ontogeny of fishes. Larvae, which usually feed on herbivorous zooplankton (TL=2.0) consequently have a trophic level of about 3.0. Subsequent growth enables the juveniles to consume larger, predatory zooplankton and small fishes or benthic invertebrates; this leads to an increase in trophic level, often culminating in values around 4.5 in purely piscivorous, large fishes.

6.2.1. Exercise

- Find from FishBase 10 small-, 10 medium- and 10 large-sized species with information on trophic level. Plot trophic level *vs*. L_{max}.
- Assemble diet composition studies for different sizes of the same species of fish, preferably in the same population, and show trophic level changes with ontogeny.

6.3. Trophic signatures

The plot of the number of species in an ecosystem per trophic level class is called **trophic signature** (Froese *et al.* 2005). Trophic signatures are useful for comparing different ecosystems in terms of the embedded functional groups. Thus, the analysis of different ecosystems shows that although the numbers of species present in these ecosystems differ, most ecosystems are dominated by omnivorous species (trophic level class 3-3.5) (Froese *et al.* 2005).

6.3.1. Exercise

- Select one tropical, one temperate and one arctic ecosystem. Extract all the fish species and their trophic levels. [**Hint:** use the **Information by Ecosystem** routine.] Construct their trophic signatures. Compare them and discuss the results.

6.4. Formal description of food webs

For formal descriptions of the role of fish in ecosystems and their responses to changes in fishing, and other changes, see the Ecopath with Ecosim modeling tool at www.ecopath.org. There is a strong link between Ecopath and FishBase, i.e., the trophic ecology suite of tables enables FishBase to construct trophic pyramids, species ecology matrices and list parameters useful in constructing ecosystem models for a given area or ecosystem.

6.4.1. Exercise

- Identify a marine ecosystem that interests you and draw a food web incorporating the diet information on major fish and invertebrates in that ecosystem. [**Hint:** use the **Information by Ecosystem** routine.]

6.5. Fisheries management: keep it simple

6.5.1. L_m and minimum landing sizes

The mass removal of immature individuals has detrimental effects for the stocks, the communities, the ecosystems and their supported fisheries (e.g., Froese 2004). The removal of immature fish contributes to the decline of these stocks bringing about growth overfishing (Pauly 1979). Compare this to the idea of 'eating babies' before they even grow to become adults and having their own babies, i.e., 'forgone' production (Jensen *et al.* 1988). Catch consisting of immature, small-sized individuals is usually valued at relative low prices, i.e., fish feed. Thus, growth overfishing has important economic repercussions because, small fishes, if allowed to grow and be caught later at a much larger size, represent production valued at much higher prices (Jennings *et al.* 1999).

One technical managerial measure against growth overfishing is the establishment of Minimum Landing Sizes (MLS) for the main commercial stocks, i.e., landing of individuals with sizes smaller than MLS is not allowed. In order for such MLS to be ecologically meaningful they must be harmonized with the life-history of the species (i.e., being at least equal or slightly larger than L_m: all fish should be allowed to spawn at least once). This is especially crucial for large-sized, high trophic level species, e.g., sharks, tunas, trevallies, jacks, whose stocks are prone to overfishing.

Table 6.1. Minimum Landing Sizes (MLS) for 13 fish species in Greek waters (from Stergiou *et al.*, 2009).

Species	MLS
Boops boops	11.0
Mullus surmuletus	11.0
Mullus barbatus	11.0
Pagellus erythrinus	15.0
Serranus cabrilla	8.3
Diplodus annularis	12.0
Merluccius merluccius	20.0
Diplodus sargus	23.0
Pagrus pagrus	18.0
Spondyliosoma cantharus	8.7
Oblada melanura	9.5
Dentex dentex	8.4

6.5.1.1. Exercise

- Find one L_m value for the Mediterranean Sea for each species in Table 6.1. If more than one value is available per species, estimate the mean and its s.e. Compare the L_m (mean+/-s.e., if available) with the minimum landing size (MLS) of the species. Discuss the results. [**Hint:** L_m can be estimated using equation 4.1 (section 4.1 on the Reproductive load concept).]

6.5.2. Three simple management indicators

Froese (2004) suggested that the following three, simple to estimate, indicators can be used for the management of fisheries resources in order to rebuild and maintain healthy spawning stocks.

Indicator 1: ‘let them spawn’. This refers to the percentage (i.e., 100%) of mature specimens in the catch and aims at letting fish spawn at least once before they are caught.

Indicator 2: ‘let them grow’. This refers to the percentage of fish caught at optimum length, L_{opt}, i.e., the length at which the number of fish in a given unfished year-class multiplied with their mean individual weight is maximum and where the maximum yield and revenue can be obtained. L_{opt} is typically a bit larger than L_m and can be estimated from growth and mortality parameters (Beverton 1992):

$$L_{opt}=L_{\infty}\cdot(3/(3+M/K)) \qquad \text{… 6.2)}$$

It can also be estimate from the empirical equation of Froese and Binohlan (2000), which was based on data from FishBase. The aim here is to catch all fish (100%) within, e.g., $L_{opt}\pm10\%$.

Indicator 3: ‘let the megaspawners live’. This refers to the percentage of old, large-sized fish in the catch, i.e., fish of a size > L_{opt} +10%. The aim here is to implement a fishing strategy for which no (0%) mega-spawners are caught. If such a strategy does not exist, and thus the catch reflects the age and size structure of the stock, values of 30–40% megaspawners in the stock represent a healthy age structure, whereas values of <20% should be alarming.

6.5.2.1. Exercise

- Find from the literature five published length-frequencies. Enter the length-frequencies in the ‘Length–Frequency Wizard’ and estimate the values of Froese’s three indicators. Discuss the results.

6.6. Effects of fishing on ecosystems

The marine ecosystems of today are impoverished versions of their former, pristine counterparts in terms of diversity and biomass. Annual global fisheries landings have been diminishing in the past decades, and many stocks are threatened by biological or economic extinction. Fishing affects all levels of biological organization, i.e., from individuals to ecosystems (e.g., Jennings and Kaiser 1998; Pauly *et al.* 1998, 2002; Jackson *et al.* 2001; Stergiou 2002; Myers and Worm 2003). For instance, fishing removes the largest individuals, which represent 'stored' biomass. Fishing (notably dredging and trawling) also removes structure-forming benthic fauna (e.g., corals, sponges, molluscs, worms), which is replaced, if at all, by algae or gelatinous ooze (see e.g., 'then and now comparisons' by Elliott Norse of the Marine Conservation Biology Institute). In addition, fishing indirectly increases eutrophication of the water column and increases the ecosystem's production to biomass (P/B) ratio driving the ecosystem to be energetically sub-optimal and immature. These effects induce ecological adaptations and evolutionary trends favoring species generally characterized by low longevities, small sizes and thus small lengths at first maturity, low trophic levels, high growth rates and high productivity, i.e., resilient species, e.g., anchovies.

One of the effects of fishing on ecosystems that has gained large attention both by scientists and media in recent years is the '**fishing down the food webs**' process (Pauly *et al.* 1998), which gave 'flesh and bones' into what most fisheries scientists intuitively had in their minds, i.e., that expansive fishing tends to remove larger, higher-trophic level species, and progressively lowers the mean trophic level of fishery landings. Thus, 'fishing down the food webs' implies a gradual reduction in abundance of large, long-lived, high trophic level organisms, and which are replaced by smaller, short-lived, low trophic level fish (e.g., species considered as fish feed) and invertebrates (e.g., jellyfish).

6.6.1. Exercise

- Use the national statistical fisheries data of your country for the last 30 years, or the capture fisheries data from the Food and Agriculture Organization (FAO) for your country. [**Hint**: use (1) the FishStat Plus software, v. 2.31, www.fao.org or (2) the catch data by EEZ from the *Sea Around Us* Project web site, www.seaaroundus.org]. Use FishBase to find the trophic level of all fish species composing these landings. Construct the frequency distribution of the production by trophic level class. Test for 'fishing down' and discuss the results. [**Hint**: A routine on **Catch analysis** is available under the **Tools** section of the FishBase search page.]

6.7. Effects of aquaculture on ecosystems

Aquaculture, the production of which has drastically increased in the last decades, is considered by many as the solution to the crisis of the world fisheries (see section 6.6 on Effects of fishing on ecosystems). Yet, aquaculture has also potentially deleterious impacts at all levels of biological organization (i.e., individuals, populations, communities, and ecosystems). Such impacts are directly related to the use of food, hormones, chemicals, and antibiotics, as well as to the degree of crowding in farming facilities, geographic origin and ecological function of the cultured species (e.g., Naylor *et al.* 2002; CIESM 2007). In addition, aquaculture has indirect effects related to the origin of the aquaculture feed, which is composed of high levels of fish meal and oil.

Aquaculture was originally devoted to low trophic level invertebrates, i.e., detritivorous and/or herbivorous bivalves like mussels or oysters (Bardach *et al.* 1972). Nowadays, it has become increasingly based on high trophic level fish, e.g., carnivorous fish like salmon. This is known as ‘farming up food webs’ (Pauly *et al.* 2001). Pauly *et al.* (2001) show that the mean weighted trophic level of mariculture products in countries such as Chile, Canada, Norway and the UK, increased since 1970. The same is also true of the Mediterranean Sea (Stergiou *et al.* 2008).

Culture of high trophic level species raises ecological concerns since it requires large quantities of fish, which are turned into feed, and can thus contribute to overfishing. It also raises socioeconomic and ethical concerns, i.e., large quantities of fish which were before consumed directly by humans are used for the production of relatively small quantities of high-valued fish destined for affluent consumers.

6.7.1. Exercise

- Find the aquaculture production of 3 European, Asian and South and North American countries. [Hint: see Exercise 6.6.1]. List the species used for aquaculture per country. Find their trophic levels from FishBase. Construct the frequency distribution of the trophic levels of cultured species. Discuss the results.

6.8. FishBase, archaeology and shifting baselines

Existing frescos, such as the 'Little Fisherman from Thera (Santorini)' (Figure 6.1), and other paintings have, apart from their historic, cultural and artistic value, an untold ecological one (Stergiou 2005b). Because of their bright colors and fine, detailed representations, it is possible for the specialist to identify, at the species level, many of the marine organisms (e.g., echinoderms, cephalopods, fishes, dolphins) depicted in the frescoes (Economidis 2000; Eleftheriou 2004).

Figure 6.1. The 'Little Fisherman from Thera (Santorini)'.

In addition, there are many descriptions of various aspects of marine life and biodiversity, and fishing methods in the writings of many 'classic' writers (e.g. the Homer' rhapsode; Aristotle who wrote that larger fishes prey upon smaller ones, implies that trophic level increases with size; the poet Oppianos who refered to many fishing gears) (Stergiou 2005b). The evaluation of written, pictorial, and archaelogical information is critical for establishing 'baselines' (Pauly 1995) and reconstructing the history of marine animal populations (Stergiou 2005b).

6.8.1. Exercise

- Identify the species depicted in the fresco 'The little fisherman' (Figure 6.1). Estimate the size of each individual fish. [**Hint**: make the assumption that the height of the boy is about 1.6 m]. Construct the length frequency of the 'sample'. Compare the maxiumum size with that reported in FishBase.
- Read Aristotle's book '*The history of Animals*', Book VIII. Find at least 5 quotes that are related to fish and can be included in FishBase. [**Hint**: Aristotle's books are available free on the Internet.]

7. Contributing to FishBase

The FishBase project is a large, international, non-profit venture which started in 1989 and whose latest product, FishBase Online (see www.fishbase.org) covers essentially all the fish in the world - at least in terms of nomenclature. In terms of biology and ecology the coverage is, however, rather spotty and it is paradoxically in the well-studied temperate areas that the coverage is most incomplete, at least relative to the available literature. The reason for this is that FishBase was funded by the European Commission to cover countries in Africa, the Caribbean and the Pacific ('ACP') that are associated with the European Union.

For FishBase to realize its potential as the integrated, computerized system of fish most useful to the global ichthyological community, it requires input from users, including students. Thus you are encouraged to contribute to FishBase, notably by sending reprints or photocopies of material used for your analyses, as well as other information which you think should be incorporated (with complete sources!). You are also welcome to submit photos. The section of the FishBase book on 'How to become a collaborator and why' discusses details on the manners in which such contributions are acknowledged (see also the Collaborators Table); also note that you retain all rights to any submitted photo.

Students usually ask 'simple' but rather hard to answer questions, such as for instance 'is this shark species dangerous?' or 'does this species have a gas bladder?' or 'what is the natural mortality of this species?' Answering these questions is often difficult because it involves context-free information. Checking FishBase for such questions will generally get you an answer (e.g., the mortality of shark), but you won't really 'learn' much from it. It is by putting the answer in context that you generate knowledge. The FishBase book and this online guide provide context, and thus enable a deeper use of FishBase.

Some questions might not be answered through FishBase (e.g., that about the gas bladder). This only shows that FishBase is not yet complete. FishBase is the result of the hard work of the FishBase team and of its more than 1,200 collaborators. So become a collaborator and contribute to its growth – together, we can solve the gas bladder problem!

7.1. Exercise

- Do a gap analysis on the information for all fish species inhabiting the fresh and marine waters of your country or any country of your preference. A gap analyis helps identify priorities for future research in a geographic region by estimating how many species out of the total number of species occurring in a country or region are covered in FishBase with respect to the various FishBase topics (e.g., photos, common names, ecology, growth, L-W relationships, maturity, diet, reproduction, spawning). [**Hint**: use the **Information gaps** routine under the **Tools** section of the FishBase search page.]
- Use Google Scholar (or any other search engine), to see if there are available published sources on the gaps identified above.
- Select one of the topics (e.g., growth, feeding habits), and write a short review (i.e., collect all available papers on all species on this topic for the selected

country/region and tabulize the quantitative information which is used in FishBase).

- Submit it to a primary journal (e.g., Acta Ichthyologica et Piscatoria, which has a FishBase Section).

8. Acknowledgements

We wish to thank Ms. Donna Shanley for creating a first workable draft out of a jumble of text notes, references and Internet URLs. Without her dedication and skill, the making of this guide would have continued to be postponed forever.

9. Appendix

9.1. Classification-related topics covered in FishBase:

FishBase terms:	To search for terms included in the FishBase online glossary, go to www.fishbase.org and use the **Glossary** search by either typing in a term or browsing the index provided. Note that here, and for nearly all other terms in the glossary, you can click on the hypertext link to the *Encyclopedia Britannica* online.
Classification:	The Role of Taxonomy; The FAMILIES Table; Genera and Species in a Classification.
Darwin, Charles:	See **Box 9** in The Expeditions Table.
Species concept:	Eschmeyer's Genera of Fishes; Eschmeyer's Species of Fishes.
	Go to www.fishbase.org, use the **Scientific name** search either by typing in the genus and species names or by browsing the provided index and select the **Summary** button. In the **Species Summary** page, click on the **Synonyms** link, e.g., *Oncorhynchus mykiss*
Subspecies:	The STOCKS Table.
	Go to www.fishbase.org and search for *Oreochromis niloticus*.
Population:	The STOCKS Table.
Threatened species:	See **Status** field in The STOCKS Table.
	Go to www.fishbase.org, use the **Information by country/island** search, type in the country of interest and select the **Threatened** button.
Common names:	See **Figure 8** in The COMMON NAMES Table.
	Go to www.fishbase.org and use the Common name search by typing in the name or by browsing the provided index. If a list of species is returned, click on the species of interest to access the **Species Summary** page. Then click on the **Common names** link, e.g., click on the Haida name 'Skaagwun'.
Max. length (L_{max}):	The POPCHAR Table.
	Go to www.fishbase.org to search for a species as described above. Once in the **Species Summary** page, click on the **Max. age & size** link to obtain a list of maximum lengths, e.g., *Salmo trutta*.

9.2. Biodiversity-related topics in FishBase:

Distribution: The FAOAREAS Table; The COUNTRIES Table; The COUNTREF Table; The OCCURRENCES Table. Plots occurrence records, families by FAO area, species by FAO area, species by climate, etc. using the **Biodiversity Maps** routines in www.fishbase.org.

9.3. Brain size-related topics covered in FishBase:

Brains: See **Box 33** and **Figure 50** in The BRAINS Table.

In the **Species Summary** page, click on the **Brains** link to obtain brain weight measurement data. Click on the **Relative brain weight** graph link to obtain a plot of encephalization coefficients' (i.e., relative brain weight, accounting at least in part for difference in body weights). [**Hint**: To get a list of species with brain weight measurements, use the **Information by Topic** search, click on the **Brains** option. To see the Relative brain weight graph for a family, go to **Information by Family** search and choose the **Graphs** option. In the **Graphs by Family** page make sure that the family of interest is selected, choose the **Relative brain weight** option and click on the **View graph** button.]

9.4. Size, growth and mortality-related topics covered in FishBase:

Auximetric grid:	Go to www.fishbase.org, use the **Information by Family** search, select a family, click on the **Graphs** option, select **Auximetric graph**, click on **View graph**.
Morphology:	The MORPHOLOGY Table.
Biodiversity:	The OCCURRENCES Table.
Shapes (Fam. picts.):	Go to www.fishbase.org, use the **Information by Family** search by choosing the Family of interest from the drop-down list and select the **Family information** button. In the **Families** page, click on the **Pictures** link to view the outline drawing representative of the Family.
Shapes (swim. mode):	See **Figures 52** and **53** in The SWIMMING and SPEED Tables.
	[Note: Information on swimming modes is currently available only in the CD-ROM version. However, some biological information are available in the **Species Summary** page under the **Biology** field and in the **Key Facts** page. Swimming mode can also be inferred from the aspect ratio or the shape of the caudal fin. To make a list of species with such information, use the **Information by topic** search in www.fishbase.org, click on the **Swim. type** option and jot down the scientific name(s) of the species of interest. Then open the **Species Summary** and **Key Facts** page for that species or look at its **Picture**.]
Sizes (lengths):	See **Box 5 and Figure 7** in The SPECIES Table; **Box 14 and Figure 16** and in The POPCHAR Table; **Figure 35** in The ECOLOGY Table; **Max. size** field in the **Species Summary** page; click on the **AgeSize** link for further information, e.g., in cod or click on the **Life-history tool** link in the **Tools** section of the **Species Summary** page to display size-related parameters, as in the example for, *Oncorhynchus mykiss*.
	Sizes are expressed in lengths and/or weights. A graph comparing the constants *a* and *b* of available length-weight relationships for fish families is available through the **Information by family** search, **Graphs** option. In the **Graphs by family** page, click on the **Length-weight (a vs b)** option, and then on the **View graph** button.
Growth:	See POPULATION DYNAMICS and link to The POPGROWTH Table and discussion on Auximetric Analyses.
	Download "Color versions of the graphs contained in Pauly D. 1998. Tropical fishes: patterns and propensities. J. Fish Biol. (53(A): 1-17" from www.FishBase.org/Download/TropicalPaper.zip.
	In the **Species Summary** page, click on the Growth link to obtain a list of growth and mortality parameters for different populations of a species, e.g., for *Gadus morhua*, then click on the Auximetric graph link to view a plot

of growth coefficients *vs*. body lengths, e.g., for the cod.

Life span: See **Figure 20** in The POPGROWTH Table; **Box 19 and Figures 27 and 28** in section on Natural Mortality; **Sizes (lengths)** above; **Life span** field in the Key Facts page, e.g., for the rainbow trout.

Graphs comparing estimates of natural mortality and growth (L_∞ and K) for species in a family are available through the **Information by family** search, Graphs option. In the **Graphs by Family** page, choose either the **M vs. K** or the **M vs Linf** graph options then click on the **View graph** button.

9.5. Distribution and occurrence-related topics covered in FishBase:

Biodiversity:	See **Biodiversity maps** in www.aquamaps.org.
Environmental Information:	Under The SPECIES Table, see **Box 5 and Figure 7** in Environmental Information.
	See **Biology**, **Environment** and **Climate zone** fields in the **Species Summary** page, e.g., for *Pagothenia borchgrevinki*.
Habitat and feeding:	See **Box 23 and Figure 35** in The ECOLOGY Table.
	See **Main food**, **Trophic level** and **Food consumption** fields in **Key facts** page, e.g., for *Oncorhynchus mykiss*; click on **Diet** link to obtain detailed information of food items.
	To make a list of species with habitat and feeding information, use the **Information by topic** search in www.fishbase.org and click on the **Diet** option.
Occurrence:	The OCCURRENCES Table and see also The INTRODUCTIONS Table.
	To obtain a list of species with introductions information, use the **Information by topic** search in www.fishbase.org and click on the **Introductions** option. See also **Biodiversity Maps** and plot, e.g., occurrence records by museum, familes by FAO area, species by climate zone.

9.6. Morphology-related topics covered in FishBase:

Morphology: See links to information on MORPHOLOGY AND PHYSIOLOGY.

Reproduction: See links to information on REPRODUCTION and spawning.

To make a list of species with morphology and reproduction information, use the **Information by topic** search in www.fishbase.org, and select the appropriate topic button. [Note: Information on morphology is currently available only in the CD-ROM version of FishBase. However, some biological information are available in the **Species Summary** page under the **Biology** field and in the **Key Facts** page. To make a list of species with morphology information, use the **Information by topic** search in www.fishbase.org, click on the **Morphology** option and jot down the scientific name(s) of the species of interest. Then open the **Species Summary** and **Key Facts** page for that species or look at its **Picture**.]

9.7. Food and feeding habits-related topics covered in FishBase:

Trophic Ecology:	See **Box 21** and links to information on diet composition, food items, predators, daily ration and food consumption in TROPHIC ECOLOGY. See **Box 23** in The ECOLOGY Table. See **Box 24** in The FOOD ITEMS Table. See **Boxes 28-29 and Figure 41** in The PREDATORS Table. See also **Box 12 in** FAO Statistics. [Note: information contained in the Ecology table is available only in the CD-ROM version of FishBase. However, some ecological information are available in the **Species Summary** page under the **Biology** and **Environment** fields and in the **Key Facts** page. To make a list of species with such information, use the **Information by topic** search in www.fishbase.org, select the **Ecology** button and jot down the scientific name(s) of the species of interest. Then open the **Species Summary** and **Key Facts** page for that species.]

9.8. Reproduction-related topics covered in FishBase:

Reproductive load:	See **Box 31 and Figures 43-44** and The MATURITY Table; see text after item (h) under **Fields** in The POPGROWTH Table; see also **Fecundity-**related fields in The SPAWNING Table. Use the **Key facts** (from the **Key facts** link in the **Species Summary** page or from the **Scientific name** search selecting the **Key facts** button) and/or **Species Summary** pages to obtain more information on reproduction. In the **Key Facts** page, click on the **Growth & mortality data** link and in the resulting list, click the **Reproductive load graph** link to view a plot of Lm/L_∞ *vs*. L_∞. This graph is also available in the **Species Summary**, through the **Growth** link. Go to the **Information by family** search in www.fishbase.org and click on the Graphs option to access the **Reproductive load graph** for the family of your interest. Through the same path, look at the **Lm vs Linf** graph.
Egg sizes:	ICHTHYOPLANKTON and see **Egg diameter** field in The EGGS Table; refer to 4.3.1 Exercise.

9.9. Reproductive strategies (sex change)-related topics covered in FishBase:

Hermaphroditism: See discussion on **Mode** field and pay particular attention to **Box 30** and **Figure 42** in The REPRODUCTION Table.

See **Biology field** in **Species summary** page for the Mangrove rivulus and click on the **Reproduction** link for more information.

To list species with information on reproduction in FishBase, use the **Information by topic** search in www.fishbase.org and click on the **Reproduction** option.

9.10. Metabolism-related topics covered in FishBase:

Gill area and size:	See **Figures 54-55** in The GILL AREA Table and the The OXYGEN Table.

To list species with gill area information in FishBase, use the **Information by topic** search in www.fishbase.org and click on the **Gill area** option. Click on the species of interest then click on the **Gill area vs body weight graph** link.

To view a graph of the relationship between gill area and fish body weights, go to the **Information by family** search, **Graphs** option. In the **Graphs by Family** page, click on the **Gill area** graph option then on the **View graph** button.

9.11. Ration-related topics covered in FishBase:

Daily ration:	The RATION Table and see links to food consumption in TROPHIC ECOLOGY. In the **Species Summary** page, click on the **Ration** link for more information. To list species with daily ration information in FishBase, use the **Information by topic** search in www.fishbase.org and click on the **Ration** option.

9.12. Food consumption-related topics covered in FishBase:

Food consumption:	www.FishBase.org/manual/FishBaseThe_POPQB_Table.htm. To get a list of species with food consumption information, use the **Information by topic** search in www.fishbase.org and select the **Food consumption** button. Or look for a particular species using the **Scientific name** search and select the **Key Facts** or **Species Summary**, click on the **Food consumption** link to get more information on food consumption.

9.13. Food web-related topics covered in FishBase:

Food webs:	See **Box 21** in Trophic Ecology; see also **Box 23** in The ECOLOGY Table.
Ecopath parameters:	Use the **Information by Ecosystem** search in www.fishbase.org and select the **Ecopath parameters** button to get a list of species ordered by habitat type and size occurring in the given ecosystem. The list indicates for which of these species Ecopath-related parameters, i.e., growth parameters, Q/B, diet and predator information, are available. It is also possible to output the list as an Excel file.
Trophic levels & catches:	In the **Species Summary** page, click on link to **FAO stats** for information on mean trophic levels and catches. [Note: FAO catches is only available in the CD-ROM version. To list species with available catch data in the FishBase CD-ROM, use the **Information by topic** search and click the FAO catches option. Or search the FAO Fishery Statistics online database at http://www.fao.org/fishery/statistics/programme/3,1,1/en].
Diets:	In the **Species Summary** page, click on links to **Diet** and **Predators**. [Note: links to **Diet** and **Food consumption** are also available in the **Key facts** page.] To list species with available diet data in FishBase, use the **Information by topic** search and click on the **Diet** option.

9.14. List of symbols and abbreviations:

A	area of the ecosystem.
ATP	Adenosine triphosphate, the substance used to fuel internal metabolism.
B	age-structured population of weight.
b	slope or regression coefficient in the length-weight relationship equation.
C	parameter of the von Bertalanffy equation, modified to express seasonal growth oscillations, and expressing the amplitude of such oscillations. In practice, C ranges from C = 0 (no oscillations) to C = 1, when dl/dt = 0 at the winter point (WP).
c	constant in species-area relationship.
°C	degree Celsius, used for expressing temperature.
DC_{ij}	contribution of prey (j) in the diet of species (i).
dl/dt	growth rate in length; first derivative of the VBGF for length.
dW/dt	growth rate in weight; first derivative of the VBGF for weight.
ΔW	energy content of the (daily) growth increment.
F	instantaneous rate of fishing mortality (time-1), i.e., F= Z – M. Also: absolute fecundity.
f	number of eggs in a ripe female ovary in fish.
FL	fork length; the length of a fish, measured from the tip of the snout to the tip of the shortest central rays of the caudal fin.
G	specific growth in weight, defined by ln W2 – ln W1 / Δt where W1 and W2 are successive weights, and the Δt the growing period; used for fish larvae; also: total number of prey.
g	gram.
K	parameter of the VBGF, of dimension time-1, and expressing the rate at which the asymptotic length (or weight) is approached.
L	symbol for the individual body length of a fish.
L_∞	asymptotic length (also Linf): a parameter of the VBGF, expressing the mean length the fish of a given stock would reach if they were to grow for an infinitely long period.
L_m	mean length at first maturity of the fish of a given population.
L_{max}	maximum individual length on record for a species or one of its populations (depending on context).
log	base 10 logarithms (also log10).
$log_{10}(a)$	intercept in the length-weight relationship equation.
log_e	base e logarithms (also ln).
L_{opt}	percentage of fish caught at optimum length.
L_t	mean length at age t predicted by the VBGF.
M	instantaneous rate of natural mortality (time-1), i.e., M=Z – F.
Ø’	a growth coefficient index, equal to log K + 2 log10L∞, where K and L∞ are parameters of the VBGF.
Q	amount of food consumed by a population of fish over a specified period; also: metabolic rate, i.e., O2 consumption.
Q/B	amount of food consumed per unit weight of an age-structured population of fish; generally expressed on an annual basis.
R_d	daily ration, i.e. the amount of food consumed by a fish of a given weight in one day, and often expressed as % of its own weight.
RESP	oxygen consumption.
S	species richness.
SL	standard length; the length of a fish, measured from the tip of the snout to the tip of the hypural bone, or of the fleshy part of the caudal peduncle (i.e., excluding the caudal fin).
T	temperature (in °C).

t	metric ton, a unit of weight. Also: age, a unit of time.
t_0	a parameter of the VBGF expressing the theoretical "age" the fish of a given stock would have at length zero if they had always grown as predicted by that equation. The parameter t0, which usually takes negative values, is often omitted from stock assessment models incorporating the VBGF.
TL	total length; the length of a fish, measured from the tip of the snout to the tip of the longest rays of the caudal fin (but excluding filaments), when the caudal fin lobes are aligned with the main body axis. Also: trophic level.
t_m	mean age at first maturity of the fish of a given population.
t_{max}	maximum age reached by the fish of a given species or population (i.e., longevity); hence also: age at exit (or de-recruitment) from a population.
$TROPH_i$	trophic level of species (i).
$TROPH_j$	trophic level of prey (j).
VBGF	von Bertalanffy Growth Function, used to describe the growth in length or weight of fish.
W	symbol for the individual live body weight of a fish.
W_∞	asymptotic weight (also Winf): a parameter of the VBGF expressing the mean weight the fish of a given stock would reach if they were to grow for an infinitely long period. Also: the weight corresponding to $L\infty$.
Z	instantaneous rate of total mortality (time-1), i.e., the sum of natural mortality (M) and fishing mortality (F).
z	constant in species-area relationship.

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