Chapter 1

Introduction

Introduction

A story, perhaps apocryphal, relates that the eminent British biologist, J.B.S. Haldane, was asked what his biological studies had told him about the nature of the Creator. He replied that it was an inordinate fondness for beetles, reflecting the numerous beetle species that had been described. Perhaps he should have added, the Creator also had a real affection for teleost fishes (Teleostei). There are approximately 30 000 species of teleosts (FishBase: http://www.fishbase.org) and they account for about 50% of all vertebrate species. Two teleost families, the Cyprinidae and the Gobiidae, are the largest vertebrate families in terms of number of species.

Although essentially excluded from the terrestrial environment, the teleosts have shown an exuberant adaptive radiation in the aquatic environment, occupying oceans, lakes, rivers, streams and even temporary pools (Wootton, 1998; Moyle & Cech, 2004; Helfman *et al.*, 2009). They occur from the Antarctic to the Arctic oceans, with species living in water that is at temperatures below 0 °C. In the tropics, they are found in waters

close to 40 °C. The altitudinal range of teleosts is about 11 000 m, from the abyssal depths of the oceans to the high plateaus of Tibet in Asia and the Andes of South America. Teleosts occur in waters with salinity ranging from close to distilled water in some streams in the Amazon region of South America to hypersaline waters, such as those found in desert pools.

In parallel to this wide adaptive radiation in habitats occupied, teleosts also show a wide radiation in modes of feeding (Gerking, 1994; Wootton, 1998). The group includes some species, the detritivores, which can survive on decaying organic matter. There are herbivorous teleosts ranging from species feeding on phytoplankton to species browsing on leaves, or even eating seeds and fruits. Carnivores range from scavengers to zooplanktivores to piscivores and include such strange diets as the scales or gill filaments of other fishes.

Teleosts also display a wide range of body forms (Videler, 1993), from the highly streamlined, fast-swimming tunas of the open oceans to the bizarre shape of the seahorses found in inshore habitats. A sector of the adaptive morphological space that is relatively poorly explored by teleosts is gigantism. Compared with the cartilaginous fishes (Chondrichthyes), especially the sharks and rays and the mammalian cetaceans, the median body size of teleostean species is relatively small. It is not clear why the teleosts have not explored the adaptive opportunities of large body size (Freedman & Noakes, 2002).

However, it is in their reproduction that the teleosts display perhaps their most striking diversity. No other vertebrates – indeed few other taxa – rival the teleosts in their extraordinary multiplicity of reproductive modes.

Reproductive modes of the teleosts

Reproduction is the central biological process by which genetic material is passed from one generation to the next. The reproductive biology of the teleosts shows high diversity, far more so than in other vertebrate groups (Table 1.1).

Gender systems of teleosts

About 88% of known teleosts are gonochoristic, with individuals being either male or female (Patzner, 2008). This is the usual condition in vertebrates. The sex of an individual can be determined genetically, known as genetic sex determination (GSD), as is found, for example, in mammals and birds. Sex may also be determined by the environmental conditions encountered in the early stages of development of the individual. This is environmental sex determination (ESD), which was first studied in reptiles (Bull, 1983). Sex in some teleosts is determined by interactions between genes and the environment. Sex determination in teleosts is described in Chapter 2. The differentiation of the gonads in gonochoristic teleosts is the subject of Chapter 3, while the production of the eggs and sperm by the differentiated gonads, the process of gametogenesis, is described in Chapter 4.

Functional hermaphroditism, which is extremely rare in other vertebrates, has been identified in about 2% of teleost species, representing approximately 30 families. Its taxonomic distribution in the teleosts suggests it has evolved independently in several teleost lineages (Patzner, 2008; Avise & Mank, 2009). Interestingly, in some gonochoristic teleost species, the gonad initially differentiates as an ovary, even in individuals that eventually become male. There seems to be indeterminacy in the teleostean gonad in

Table 1.1 Teleost sexuality and mating systems. (Source: Adapted from Wootton 1998. Reproduced with permission of Elsevier.)

Sexuality/mating system	Example
1. Sex determination	
(a) Genetic	Most teleosts
(b) Environmental	*Menidia menidia*
2. Gender systems	
(a) Gonochorism	Most teleosts
(b) Hermaphroditism	
(i) Simultaneous (synchronous)	
Self-fertilising	*Kryptolebias marmoratus*
Outcrossing	*Serranus fasciatus*
(ii) Sequential	
Protogynous	*Thalassoma bifasciatum*
Protandrous	*Amphiprion melanopus*
Serial (bidirectional)	*Gobiodon rivulatus*
3. Mode of fertilisation	
(a) External	Most teleosts
(b) Internal	*Poecilia reticulata*
(c) Buccal	*Oreochromis niloticus*
4. Mating system	
(a) Promiscuity	*Clupea harengus*
(b) Polygamy	
(i) Polygyny	*Oreochromis niloticus*
(i) Polyandry	*Amphiprion melanopus*
(i) Polygynandry	*Rhodeus amarus*
(b) Monogamy	*Amatitlania nigrofasciata*
5. Secondary sexual characteristics	
(a) Monomorphism	*Clupea harengus*
(b) Sexual dimorphism	
(i) Permanent dimorphism	*Betta splendens*
(i) Temporary dimorphism	*Gasterosteus aculeatus*
6. Spawning site preparation	
(a) No preparation	*Phoxinus phoxinus*
(b) Site prepared, but not defended	*Salmo salar*
(c) Site prepared, and defended	*Gasterosteus aculeatus*
7. Parental care	
(a) No care	Most teleosts
(b) Paternal care	*Gasterosteus aculeatus*
(c) Maternal care	
(i) Oviparity	*Oreochromis niloticus*
(i) Viviparity	*Poecilia reticulata*
(b) Biparental care	*Amatitlania nigrofasciata*
(c) Juvenile helpers	*Neolamprologus pulcher*

relation to development as an ovary or testis (Chapter 2), which predisposes them towards hermaphroditism.

Hermaphroditism in the teleosts can be simultaneous (synchronous) or sequential, the latter mode expressed as protandrous, protogynous or serial (bidirectional) hermaphroditism (Avise & Mank, 2009). The commonest forms of hermaphroditism are protandry and protogyny. In simultaneous hermaphroditism, the gonads

contain both male (spermatozoa) and female (eggs) haploid gametes at the same time. The co-occurrence of spermatozoa and eggs opens up the possibility of self-fertilisation by an individual, but this has been described for only two closely related species, the cyprinodont mangrove rivulus (*Kryptolebias marmoratus* and *Kryptolebias hermaphroditus*, Rivulidae) (Tatarenkov *et al.*, 2012). Other species with simultaneous hermaphroditism outcross, mating with other individuals. Protandry describes the situation in which an individual functions as a sexually mature male, producing spermatozoa, but at some point in its life history switches to perform as a female, spawning eggs. Protogyny is the reverse of this. When sexually mature, an individual is initially female, spawning eggs, but then later transforms into a male, producing spermatozoa. In serial species, the switch between male and female roles can take place more than once in a lifetime. Hermaphroditism is one of the subjects of Chapter 10.

Parthenogenesis, in which only the female genome is transmitted from generation to generation, also occurs in the teleosts, although it is rare (Chapter 10). A curious feature of parthenogenesis in most of the species that exhibit this mode of reproduction is that they require the presence of males from a closely related gonochoristic species. The male spermatozoon activates the development of the egg of the parthenogenetic female. Teleosts show two modified forms of parthenogenesis: gynogenesis and hybridogenesis. In hybridogenesis, the genetic material of the male is functional in the developing individual, but when that individual reproduces, only the female genome is transmitted to the progeny. In gynogenesis, the role of the spermatozoon is solely to activate the egg, and the genes of the male play no role in the development of the zygote. Thus, parthenogenetic females essentially parasitise the spermatozoa of the gonochoristic males.

Spawning dynamics

Two major temporal patterns of reproductive activity can be recognised in the life history of animals and plants, including teleosts (Roff, 1992, 2002; Stearns, 1992; Wootton, 1998; see Chapter 11). Semelparity describes the condition in which, after attaining sexual maturity, the individual breeds once and then dies. There is no significant post-reproductive survival. In semelparous organisms, the physiological changes associated with reproduction result in consequences that inevitably end in death. Iteroparity is the condition in which, after reproduction, there is some probability that the individual will survive to breed again. Frequently, reproduction takes place at yearly intervals.

Within a breeding season, two temporal patterns of spawning occur in female teleosts (Wootton, 1998; Patzner, 2008). In total spawners, the female spawns all her eggs over a short period of time and no further eggs are shed in that breeding season. If the female is semelparous, she then dies. If iteroparous, her ovaries regress and become quiescent until the physiological (Chapter 5) and environmental conditions (Chapter 6) induce the recrudescence of the ovaries (Chapter 3), leading to the production of eggs for the next breeding season. In batch spawners, the female spawns eggs in batches (or clutches) at intervals during the breeding season, which is typically of an extended duration. The interval between spawnings varies. In some species, the female may spawn at daily intervals, but in others, spawning takes place at intervals of several days. There are two types of batch spawner. Some species have determinate fecundity. The females have all the eggs that are going to be spawned during that breeding season present in the ovaries at the start of the breeding season and there is no

addition to the pool of eggs available to be spawned in that season. Other species have indeterminate fecundity. Here, the pool of eggs that can be spawned can be replenished during the breeding season.

In short-lived fishes, the females may be batch spawners, but may not survive to breed in the next breeding season. They thus share the characteristics of semelparous and iteroparous species. However, in such species, there is usually the physiological capacity to survive to the next breeding season if environmental conditions are benign. Such species can be described as showing abbreviated iteroparity.

Modes of fertilisation

The vast majority of teleost species have external fertilisation (Patzner, 2008). The eggs and sperm are released into the water, where fertilisation takes place. In about 500–600 species, fertilisation takes place internally within the female (Chapter 10). The male introduces the spermatozoa into the gonoduct of the female, using an intromittent organ. This is analogous to the mode of fertilisation seen in the cartilaginous fishes, the Chondrichthyes, and in mammals and a few other vertebrates. In most teleosts with internal fertilisation, some development of the fertilised egg takes place within the ovary of the female, but in a few species the eggs are deposited soon after fertilisation (Chapter 10). In some cichlid species in which the female broods the fertilised eggs in her buccal cavity (Chapter 8), the female lays the eggs and then sucks them into her buccal cavity and also sucks in the male's spermatozoa, so the eggs are fertilised within the buccal cavity.

Mating systems

Teleosts also show diversity in the social contexts in which mating occurs (Chapter 8; Taylor & Knight, 2008; Patzner, 2008). These contexts differ in the extent to which they allow some selection of partners by the mating fish. In promiscuity, males potentially fertilise the eggs of several females, and the eggs of a female may be fertilised by several males, with minimal selection of partners. Polygamy refers to the social situation in which an individual mates with several partners, but with the possibility of some selection of the partner at each spawning. Males in polygynous species mate with several females, but each female spawns with only one male. Females in polyandrous species mate with several males, but each male spawns with only a single female. In this system, the male may assume the parental role (Chapter 9). A form of promiscuity, but with the possibility of mate selection, is polygynandry. A male will spawn with several females and a female with several males over the course of a breeding season, but with mate choice operating. In monogamy, a single male and female form a mating pair and show some degree of bonding with the mate. This type of mating system is particularly associated with species in which parental care follows the fertilisation of eggs. The pair bond may be long-lasting or more temporary, only persisting for a single breeding attempt. Even in socially monogamous systems, both males and females may take part in extra-pair spawnings, so socially monogamous matings systems may not be genetically monogamous.

Where a pair bond forms, if only for as long as it takes for successful spawning, the bond may be subverted by other males, who take advantage of the pairing to steal or 'sneak' fertilisations by depositing sperm close to, or at, the site of spawning. The sneaking males are demonstrating an alternative mating tactic (see Chapters 8 and 11).

Secondary sexual characteristics

Sexually mature males and females may differ in appearance, either permanently or only in the breeding season. In sexually monomorphic species, there are no obvious differences between sexually mature males and females, although one or both sexes may produce pheromones (Chapters 5 and 8) to attract mates. The sexual dimorphism may only be present during the breeding season, and outside of breeding, males and females are indistinguishable. However, in some species, the sexual dimorphism is permanent, so sexually mature males and females can be reliably identified.

Parental care

The majority of teleost species show no post-fertilisation care of their progeny. However, in a number of teleost lineages, parental care has evolved, taking different forms in different lineages (Chapter 9). Perhaps the commonest form is paternal care, in which the male cares for one of more clutches of fertilised eggs. An extreme form of this is seen in the pipefishes and seahorses (Syngnathidae). The female transfers eggs to a brood pouch on the abdomen of her male partner and the eggs develop in the male's pouch in a form of male pregnancy (Chapter 10).

In maternal care, the female takes care of the developing eggs. The nature of the maternal care depends on the mode of fertilisation. If the eggs were fertilised externally, the female must protect the eggs from adverse environmental conditions. Incubation in the buccal cavity is one solution to this problem. The female scoops up the eggs in her mouth and the eggs complete their development in their mother's buccal cavity. A second form of maternal care is seen in viviparous species in which the eggs are fertilised and develop in the ovaries of the female (Chapter 10). In some species, the female provides only protection, but in other species, the female provides the developing eggs with nutrients in a way that is analogous to pregnancy in mammals.

In a few species with external fertilisation, there is biparental care, with the female and male cooperating in care of the young. In this situation, the female and male may show some division of labour, often with the male protecting the area around the eggs and the female tending to the eggs and young stages. An even rarer form of parental care has been described for a few cichlid species. The parents are helped in the care of a current brood by juveniles from a previous spawning. This phenomenon of juvenile helpers has been well studied in birds, but less so in teleosts.

Reproductive guilds

The diversity of modes of reproduction has also been described by reproductive guilds on the basis of the nature of the spawning site (Balon, 1975). This classification into reproductive guilds overlaps, to some extent, with the reproductive modes already defined. A simplified version of the original classification is shown in Table 1.2.

Reproductive diversity in teleosts: an explanatory framework

What explains the extraordinary diversity of reproductive modes shown by teleosts? Why has such diversity evolved? It is not yet possible to provide a comprehensive explanation for the extraordinary variability in teleost mating systems and modes of reproduction (Chapter 13). However, two, inter-related explanatory frameworks can be

Table 1.2 Breeding sites of teleosts, based on reproductive guilds defined by Balon (1975). (Source: Balon 1975. Reproduced with permission of Canadian Science Publishing.)

Reproductive guild	Example
1. Non-guarders of eggs and young	
(a) Open substrate spawners	
(i) Pelagic spawners	
Pair spawners	*Zebrasoma scopas*
Group spawners	*Mycteroperca rosacea*
Mass spawners	*Theragra chalcogramma*
(b) Benthic spawners	
(i) Spawners on coarse substrates	
Pelagic free embryo and larvae	*Morone saxatilis*
Benthic free embryo and larvae	*Phoxinus phoxinus*
(ii) Spawners on plants	
Non-obligatory	*Rutilus rutilus*
Obligatory	*Esox lucius*
(iii) Spawners on sandy substrates	
(c) Brood hiders	
(i) Benthic spawners	*Oncorhynchus nerka*
(ii) Cave spawners	*Astyanax jordani*
(iii) Spawners on invertebrates	*Rhodeus amarus*
(iv) Beach spawners	*Leuresthes tenuis*
(v) Annual fishes	*Nothobranchius kadleci*
2. Guarders	
(a) Substrate spawners	
(i) Rock spawners	*Stegastes leucostictus*
(ii) Plant spawners	*Pomoxis annularis*
(iii) Terrestrial spawners	*Copella arnoldi*
(iv) Pelagic spawners	*Channa punctata*
(b) Nest spawners	
(i) Rock and gravel nesters	*Ambloplites rupestris*
(ii) Sand nesters	*Hypsophrys nicaraguensis*
(iii) Plant material nesters	*Hoplosternum littorale*
Gluemakers	*Gasterosteus aculeatus*
Non-gluemakers	*Micropterus dolomieu*
(iv) Bubble nesters	*Betta splendens*
(v) Hole nesters	*Cottus gobio*
(vi) Miscellaneous materials nesters	*Lepomis macrochirus*
(vii) Anemone nesters	*Amphiprion melanopus*
3. Bearers	
(a) External bearers	
(i) Transfer brooders	*Oryzias latipes*
(ii) Forehead brooders	*Kurtus gulliveri*
(iii) Mouthbrooders	*Oreochromis niloticus*
(iv) Gill-chamber brooders	*Amblyopsis rosae* (?)
(v) Skin brooders	*Antennarius commerson*
(vi) Pouch brooders	*Hippocampus zosterae*
(b) Internal bearers	
(i) Viviparous	*Poecilia reticulata*

?, indicates uncertainty with this mode of bearing.

identified: phylogenetic relationships and adaption by natural selection. Phylogenetic lineages map the evolutionary relationships between species. Essentially, they map the changes in the gene pool represented by the lineage. This means that the adaptive responses by a population to its physical and social environment are likely to be constrained to a lesser or greater extent by its genetic inheritance (Taylor & Knight, 2008).

Phylogenetic relationships of the teleosts

There is still uncertainty about the details of the phylogeny of the teleost fishes, but some of the major trends are recognised (Nelson, 2006; Helfman *et al*., 2009; Orti & Li, 2009). The teleosts belong to the actinopterygian lineage of jawed vertebrates. Early in the evolutionary history of the jawed vertebrates, the Gnathostomata, two lineages separated approximately 450 million years ago (mya) during the Silurian Period, the cartilaginous fishes (Chondrichthyes) and the bony fishes (Osteichthyes). The Chondrichthyes are restricted to the aquatic and largely to the marine environment. Interestingly, they all have internal fertilisation, which is more commonly found in fully terrestrial vertebrates, which cannot use the ambient water to transfer the spermatozoa to the eggs. Chondrichthyian fishes show a range of care for their offspring, ranging from spawning eggs protected by an egg capsule to viviparity with placenta-like structures, by which the female provides nourishment for the developing embryos. There are no reports of chondrichthyian fishes showing any parental care once the eggs have been laid or the female has given birth. In the osteichthyan lineage, there was a further splitting of the lineages during the Silurian Period. One lineage, the lobe-finned fishes, the Sarcopterygii, now has few aquatic representatives, just the coelacanths (Actinistia) and lungfishes (Dipnoi), but it is the lineage that probably gave rise to all the terrestrial vertebrates, the amphibians, reptiles, birds and mammals. The second lineage evolved as the ray-finned fishes, the Actinopterygii. The sturgeons and paddlefish (Acipenseriformes) are living representatives of the evolutionarily more primitive representatives of the Actinopterygii (Fig. 1.1).

Of the contemporary teleost groups, the freshwater Osteoglossomorpha are the earliest to appear in the fossil record and probably appeared 250–290 mya during the Triassic Period (Fig. 1.2). The marine Elapomorpha, which includes the eels (Anguilliformes) and tarpons (Elopiformes), originated 230–260 mya. The Clupeomorpha, which includes the herrings (Clupeiformes), is a largely marine group. However, the related Ostariophysii, which includes the characins (Characiformes), the carps (Cypriniformes) and catfishes (Siluriformes), is the dominant freshwater teleost group on all the continents. The Ostario-Clupeamorpha have their origins about 200–240 mya. Some 80–110 mya ago, the Euteleostei evolved. The more primitive representatives of the Euteleostei include the salmon and trout (Salmoniformes) and the pikes and pickerels (Esociformes). The major radiation of the teleosts in terms of number of species occurred 55–125 mya with the appearance of the Acanthomorpha. There are around 16 000 living species of the Acanthomorpha, representing approximately 86% of all non-ostariophysan teleosts. The radiation of the Acanthomorpha in the early Eocene, about 55 mya, has been described as 'the most dramatic evolutionary radiation ever seen in vertebrate history' (Maisey, 1996). Some of the better-known orders in the Acanthomorpha include the cods (Gadiformes), the atherinids (Atheriniformes), the toothcarps (Cyprinodontiformes), the perches (Perciformes) and the flatfishes (Pleuronectiformes). Curiously, although the evolutionary history of the teleosts coincides in time, to a large extent, with that of mammals, the teleosts are still often referred to as lower vertebrates and a common misconception is that they are an evolutionarily primitive group (Fig. 1.2).
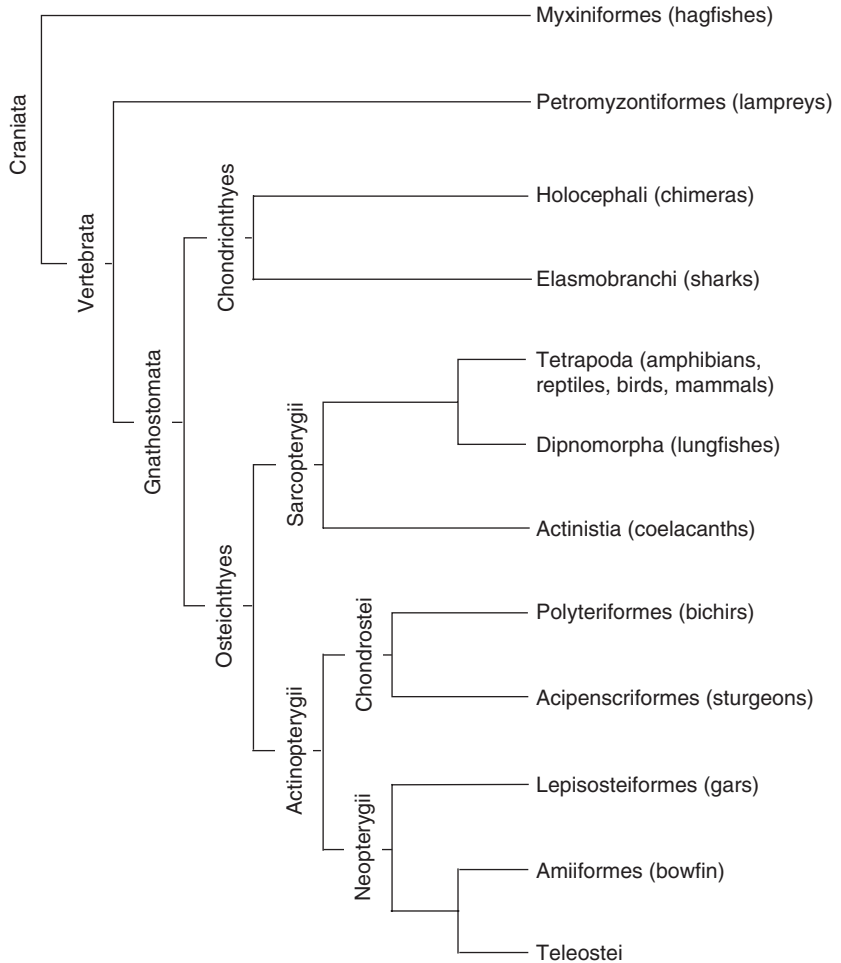
Figure 1.1 Phylogenetic relationships of the vertebrates showing the relationship of the teleosts to other vertebrates. (Source: Adapted from Nelson 2006. Reproduced with permission of John Wiley & Sons.)

A key feature of the evolution of teleosts is that at some point in the early evolutionary history of the teleost lineage, there was a whole genome duplication (WGD; Finn & Kristoffersen, 2007), which results in each gene being duplicated. This duplication raises the possibility that one of the genes will acquire a new function, neo-functionalism. This WGD may help to account for the extraordinary diversity of teleosts and some of their unusual traits compared with other lineages of jawed vertebrates.

Life-history theory

Life-history theory attempts to account for the adaptive relationship between life-history traits and the physical and social environments encountered. The life-history traits typically considered include age and size at sexual maturity, size of eggs, fecundity and parental care (Chapter 11). There have been several approaches to this problem, each of which has provided valuable insights into the evolution of life-history traits.
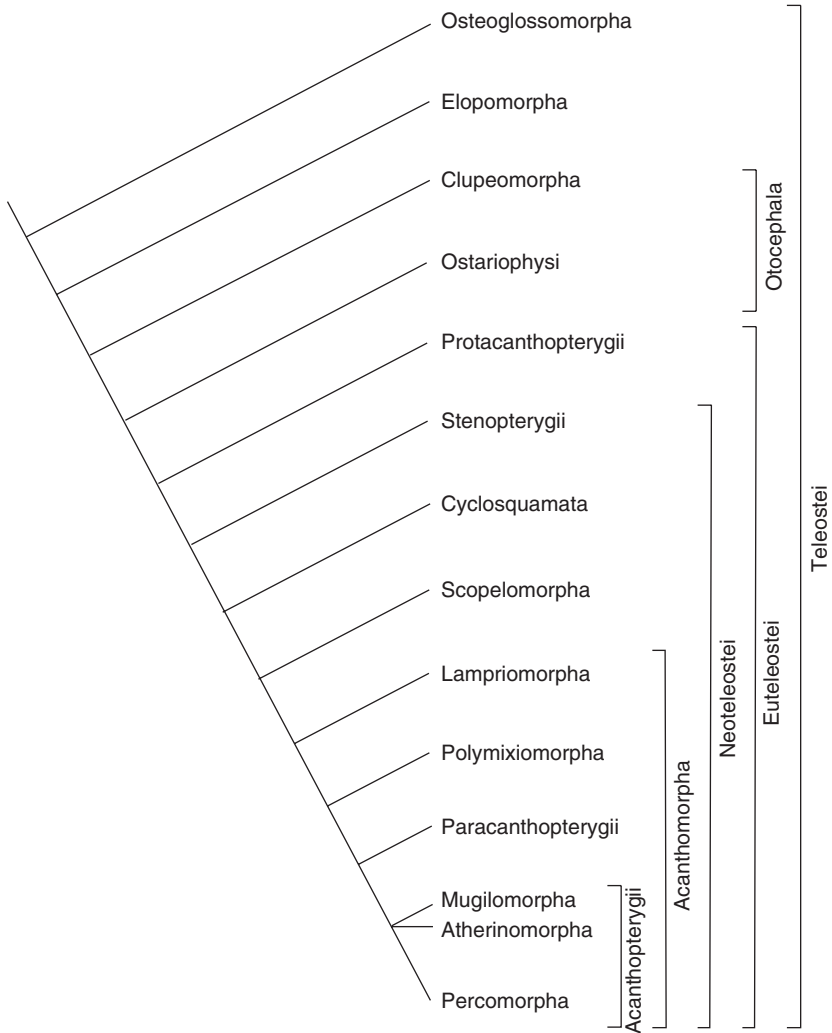
Figure 1.2 Phylogenetic relationships within contemporary teleosts. (Source: Adapted from Helfman *et al.* 2009. Reproduced with permission of John Wiley & Sons.)

Demographic life-history theory addresses the effects of age-specific mortality rates on reproductive traits (Roff, 1992, 2002; Stearns, 1992). It seeks to define the combination of life-history traits that will maximise fitness in a given environment, taking into account trade-offs between traits such as that between age and size at first maturation, or between egg size and fecundity. The approach has been used with particular effect to analyse life-history traits of salmonids (Schaffer, 1979, 2004) and cyprinodonts, especially the guppy (*Poecilia reticulata*) (Reznick, 1996; Reznick *et al.*, 2002a).

A second approach has been to deduce what combination of life-history traits would be adaptive given a set of environmental conditions. This is called the templet model of life histories. The first and most influential example of this model of life histories is the concept of r- and K-selection. This model relates the intensity of density dependence in populations to life-history traits. This approach has been developed by

considering other dimensions such as habitat productivity when accounting for the evolution of life-history traits (Southwood, 1988). A scheme that has been applied to terrestrial plants defines three dimensions: a 'disturbance' axis, an 'adversity' axis and a 'biotic interactions' axis. Attempts to apply templet models to teleosts have had limited success (Persat *et al.*, 1994).

A third approach, related to templet models, which has been applied to describing life-history traits in teleosts, is the application of multivariate statistics to define clusters of species that share similar combinations of life-history traits. These combinations can then be related to the environments in which the various clusters tend to occur. An influential example of this approach identified three life-history strategies (Winemiller & Rose, 1992). These represent end points in a continuum, but do capture important combinations of life-history variables. The initial analysis used data on marine and freshwater fishes from North America, but it ranged across many teleost lineages, so the strategies do not reflect phylogenetic constraints. The 'periodic strategy' is characterised by species with delayed maturation, large size at sexual maturation and high fecundities. Some of these species have total spawning, ensuring that eggs are produced in a period most suitable for the development of the early life stages. By contrast, the 'opportunistic strategy' is characterised by early maturation, small adult size, batch spawning over an extended breeding season and rapid early growth. Species with an 'equilibrium strategy' tend to have a small to medium body size, low fecundities, large eggs and some form of parental care.

Finally, an additional approach to understanding life-history evolution comes from identifying regularities in the relationships between life-history traits, termed 'invariants' (Charnov, 1993). The adaptive significance of these different models of life-history evolution is discussed in Chapter 11.

Aims of the volume

The lack of information on the reproductive biology of teleosts and the remaining uncertainty about the phylogenetic relationships within the teleost lineage preclude a comprehensive synthesis of phylogenetic and adaptive influences on their diverse reproductive biology. This book attempts to establish a framework in which such a synthesis could be achieved. It describes the reproductive biology, using, wherever possible, phylogenetic information and life-history theory as means to interpret the information. The pages also celebrate the diversity of modes of reproduction of the teleosts.