The remarkable reproductive diversity of teleost fishes

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Abstract

Teleosts display the most striking reproductive diversity of all vertebrates. However, no convincing hypothesis has yet been proposed to explain why they have evolved this remarkable variability in their modes of reproduction. Some of the features of the reproductive biology of teleosts are briefly reviewed and unique characteristics of the group that may have made possible the evolution of their remarkable reproductive diversity are considered. These include whole genome duplication, the mode of differentiation of the gonads, and the organisation of the brain–pituitary relationship.

Keywords: alternative mating tactics, hermaphroditism, mating system, self-fertilisation, sex determination, unisexuality, viviparity

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Introduction

Teleost fishes are an evolutionary puzzle. They display virtually every mode of reproduction found in vertebrates (Desjardins and Fernald 2009). Yet why this group has evolved such exuberant variation in its reproduction has still to be convincingly explained (Wootton and Smith 2015). In this brief review I summarise some of the features of the reproductive biology of teleosts and suggest unique characteristics of the group that may have made possible the evolution of this remarkable reproductive diversity.

Modes of reproduction in teleosts

Gender systems

In terms of sex determination, about 88% of known teleosts are gonochorists, with individuals either male or female (Patzner 2008). Gonochorism is the usual condition in vertebrates. The sex of an individual can be determined genetically, known as genetic sex determination (GSD). Sex can also be determined by the environmental conditions encountered in the early stages of development of the individual; termed environmental sex determination (ESD). Sex in some teleosts is determined by interactions between genes and the environment. Functional hermaphroditism, which is extremely rare in other vertebrate groups, has been identified in about 2% of teleost species, representing approximately 30 families. Its taxonomic distribution in the teleosts suggests hermaphroditism has evolved independently in several teleost lineages (Patzner 2008; Avise and Mank 2009; Erisman *et al*. 2013). Interestingly, in some gonochoristic teleost species, the gonad initially differentiates as an ovary even in individuals that eventually become male and there seems to be indeterminacy in the teleostean gonad in relation to development as an ovary or testis, which predisposes them towards hermaphroditism. Hermaphroditism in the teleosts can be simultaneous (synchronous) or sequential, the latter mode expressed as protandrous, protogynous or serial (bi-directional) hermaphroditism (Avise and 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 *K. 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.

Parthenogenesis, in which only the female genome is transmitted from generation to generation, also occurs in the teleosts, although it is rare. A curious feature of parthenogenesis in most teleost biotypes that exhibit this mode of reproduction, such as the Amazon molly (*Poecilia formosa*), is that they require the presence of males from a closely related gonochoristic species (Lampert and Schartl 2008; Pandian 2011; Wootton and Smith 2015). 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 (Wootton and Smith 2015). Thus, parthenogenetic females essentially parasitise the spermatozoa of the gonochoristic males (Neaves and Baumann 2011).

Spawning dynamics

There are two major temporal patterns of reproductive activity that can be recognised in the life history of teleosts (Stearns 1992; Wootton 1998; Roff 2002). Semelparity describes the condition in which, after attaining sexual maturity, the individual breeds once and then dies without 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. In this case, reproduction typically 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 and environmental conditions induce the recrudescence of the ovaries 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 water, where fertilisation takes place. In about 500-600 species, fertilisation takes place internally within the female. The male introduces the spermatozoa into the gonoduct of the female, using an intromittent organ (Wourms 1981). 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. In some cichlid species in which the female broods the fertilised eggs in her buccal cavity, 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 (Fryer and Iles 1972).

Mating systems

Teleosts also show diversity in the social contexts in which mating occurs (Patzner 2008; Wootton and Smith 2015). 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 only with 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. 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 (Wootton and Smith 2015).

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 (Taborsky 2008).

Secondary sexual characteristics

Sexually mature males and females may differ in appearance, either permanently or only in the breeding season (Helfman *et al*. 2009; Wootton and Smith 2015). In sexually monomorphic species, there are no obvious differences between sexually mature males and females, although one or both sexes may produce pheromones 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 (Pandian 2011).

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 (Mank *et al*. 2005). 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 (Kolm 2009).

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 (Kolm 2009). 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. In some viviparous species, the female provides only protection, but in others provides the developing eggs with nutrients in a way analogous to pregnancy in mammals (Wourms 1981).

In a few species with external fertilisation, there is bi-parental care, with the female and male co-operating 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 (Smith and Wootton 1995). 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 (Wong and Balshine 2011).

Unique characteristics of teleosts

Species number

In terms of number of species, teleosts are by far the most speciose of the vertebrates, with about 30,000 species, representing approximately half of all vertebrates (Helfman *et al*. 2009). Associated with this diversity is the extremely wide range of aquatic habitats that teleosts occupy (Wootton, 1998; Helfman *et al*. 2009). The reproductive diversity of teleosts may, therefore, simply reflect the reproductive adaptations that are required for them to occupy this range of habitats.

However, species richness alone is an unsatisfactory explanation for their reproductive diversity, since it still begs the question of why the teleosts have speciated to such a spectacular degree in comparison with other vertebrates. Indeed, this speciosity may be a potent manifestation of underlying mechanisms that have likewise driven the diversification of reproductive modes. Thus there are distinctive characteristics of the teleosts that may have facilitated the evolution of their reproductive diversity.

Whole genome duplication

A key feature of the evolution of the teleosts is that in the early Devonian, after their divergence from the Sarcoptergygii (lobe-finned fishes), and early in the evolutionary history of the teleost lineage, there was a whole genome duplication (WGD) (Amores *et al*. 1998; Finn and Kristoffersen 2007; Santini *et al*. 2009), which resulted in each gene being duplicated. Genome duplication presents the opportunity for one of the replicated genes to acquire a new function, termed 'neo-functionalism'. WGD may help to account for the extraordinary species diversity of teleosts, as well as some of their unusual traits compared with other lineages of jawed vertebrates, by making available a reservoir of genetic variation with the possibility of duplicated genes evolving separate functions and hence opening up the possibility of diversity in reproductive modes (Meyer and Schartl 1999; Le Comber and Smith 2004). Within the teleosts, extremely quick genomic evolution has occurred, with rapid duplication of genes and genomes (Desjardins and Fernald 2009; Mank and Avise 2009), strongly implying that genetic variation leads to reproductive diversity.

An example of the impact of WGD is in the evolution of pelagic eggs. The ancestral spawning habit of teleost fishes is benthic eggs. Pelagic eggs need hydration to float and this state is primarily achieved in teleosts through the presence of high concentrations of free amino acids (FAA), which increase the osmolality of the ooplasm resulting in water uptake. During oogenesis, FAAs in the oocyte are derived from the proteolysis of vitellogenin, which is the main source of the proteins and lipids needed by the developing embryo and which is synthesised in the liver of a female before transport to the ovary in the blood supply (Wootton and Smith 2015). The evolution of an effective means of hydrating the oocyte was essential for the teleosts to invade the open ocean, because there are no surfaces on which eggs can be deposited, so the eggs have to be pelagic. Duplication of a vitellogenin gene through WGD appears have allowed the specialisation of a vitellogenin whose neo-function is to be proteolysed to FAA (Finn and Kristoffersen 2007), thereby permitting spawning in open water and invasion of the pelagic environment.

Gonad differentiation

The mode of differentiation of the gonads in teleosts differs from the majority of vertebrates. The gonads of vertebrates have two cellular components; the somatic cells and the germ cells. It is the latter that give rise to the gametes. In most lineages of jawed vertebrates, the somatic cells have two embryological origins. One population originates from the cells of the walls of the peritoneum, lining the coelomic cavity. This population forms the cortex of the developing gonad. The second population, which forms the medulla of the gonad, is derived from mesonephric blastema, a feature of the developing kidney. In females, the medulla component of the gonad degenerates, while the cortical component expands and gives rise to the ovaries. In males, the development of the testes involves the medulla, while the cortex degenerates (Atz 1964; Merchant-Larios 1978; Nakamura *et al*. 1998). In terms of the embryological tissues involved, the cortex has a mesodermal origin, while the medulla has an endodermal origin (Francis 1992). It has been argued that the position of cells, cortical or medullary, determines whether they develop as cells characteristic of males or females, though recent evidence from studies on the mouse suggest that the outcome is determined by each cell rather than by the position of the cells (Maatouk and Capel 2008).

In teleosts, the gonadal somatic cells are derived only from the peritoneal cells; both ovaries and testes develop from the gonadal cortex and hence have a mesodermal origin. Thus the somatic tissues of the ovaries and testes of teleosts have a common embryological origin (Nakamura *et al.* 1998). There is a correlation between this distinctive mode of development of the gonads in teleosts and the relative sensitivity of the developing gonad to factors that cause changes in sex of the differentiating gonad, for example the presence of exogenous hormones (Francis 1992). The evidence suggests that teleosts tend to show a protogynous pattern of sexual development, even in gonochorists (Francis 1992). In some teleostean lineages, males pass through a stage in which the gonad develops as a proto-ovary, before switching to differentiate as testis. The position of the cells in the gonadal anlagen is not a factor in their pattern of differentiation. A consequence is that in many teleost species the gonads remain bipotential until later in development than in other vertebrates. An outcome is that the developmental 'decision' to become a functional male or a functional female is delayed and remains plastic (Adkins-Regan 2005).

Allied to this gonadal bipotentiality, teleosts tend to retain a sexually bipotential brain. There is evidence that the sexual behavioural dimorphism seen in teleosts is a consequence of the activational effects of hormones rather than the structural organisation of the brain (Adkins-Regan 2005). A further possible factor is that in teleosts there is adult neurogenesis, which may make flexibility in reproductive behaviour more possible (Adkins-Regan 2005).

Relationship between brain and pituitary

In vertebrates, the brain does not communicate directly with the gonads to control reproduction. Instead, neurohormones produced in the brain, especially the hypothalamus affect the pituitary, the major endocrine organ in vertebrates. Under the influence of these neurohormones, some pituitary cells produce hormones, which are secreted into the blood stream to be transported to the target organs. In the case of the reproductive system, the gonads are the targets. This arrangement is called the brain-pituitary-gonad reproductive axis (BPG axis), or, to emphasise the role of the hypothalamus of the brain, the HPG axis (Meccariello *et al*. 2014). In the ovary, the thecal and granulosa cells of the ovarian follicle complex are the target cells. In the testes, the Leydig and Sertoli cells are the main target cells (Wootton and Smith 2015). Modulation and modification of the activity of the BPG reproductive axis can take place at a variety of levels in the axis, including the brain, the pituitary and the gonads (van der Kraak *et al.* 1998).

In comparison with the other jawed vertebrates, the teleosts have an idiosyncratic organisation of the brain–pituitary relationship (Zohar *et al*. 2010; Kah and

Dafour 2011). In teleosts, hypophysiotropic neurons from the brain pass into the pituitary and release their neurohormones close to the pituitary cells (gonadotropes) that synthesise the hormones (Sherwood and Adams 2005; Levavi-Sivan *et al*. 2010). In other jawed vertebrates, in contrast, the neurohormones are released into the blood stream and pass into the pituitary in a hypophysial portal system. The adaptive significance of the difference between teleosts and other vertebrates is unclear, but the direct neural connection in teleosts probably allows a faster and more precise control over the secretion of pituitary hormones. Another endocrinological difference is that teleosts produce a non-aromatisable androgen, 11 ketotestosterone (11-KT), which characterises the male and is particularly important in the regulation of male reproductive behaviour (Adkins-Regan 2005; Munakata and Kobayashi 2010).

Conclusions

The unusual reproductive diversity of the teleosts demands explanation. In this brief review three features of the teleosts are proposed as contributing to this diversity (Fig. 1). Whole genome duplication generates a pool of duplicated genes that can evolve new functions. The outcome is an enhanced capacity for rapid genomic evolution, potentially encompassing a broad range of reproductive roles. While the functional significance of the idiosyncratic organisation of the brain–pituitary relationship in teleosts has yet to be fully appreciated, it appears to permit a finely-tuned system for controlling pituitary hormone secretion. The outcome is a highly adaptable neuroendorine system that is responsive to social and environmental factors, which may permit the evolution of reproductive tactics unavailable to other jawed vertebrates. The mode of gonad differentiation in teleosts, with gonadal somatic cells in males and females having a common mesodermal origin, generates an inherently protogynous pattern of sexual development, irrespective of mode of sex determination. An outcome of this bipotentiality is the unusual frequency of hermaphroditism in teleosts, a reproductive strategy rarely expressed in other vertebrates. This lability of the gonads may also facilitate the evolution of multiple alternative mating tactics within species.

While these distinctive characteristics of teleost reproduction have been dealt with separately, the interactions of these features may be the key to teleost reproductive diversity. For example, whole genome duplication may be pivotal in facilitating how rapidly the neuroendocrine system is able to respond to selection in generating variation in reproductive patterns. Similarly, the bipotentiality of the teleost gonads and brain may make regulatory mechanisms in the neuroendocrine system more responsive to selection for flexibility in mating behaviour.

How might an understanding of these distinctive features of teleost biology be used to explain why the teleosts among all other vertebrates have evolved such an extraordinary diversity of reproduction? Two inter-related explanatory frameworks offer a means to tackle the question: phylogenetic relationships and adaption by natural selection. Phylogenetic lineages map the evolutionary relationships among species and hence 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 (Wootton and Smith 2015). Within these constraints the suite of traits expressed by an individual that determine how it spreads its reproduction over its lifetime is summarised by its life-history strategy. Life-history theory predicts that selection will favour a pattern of allocation of resources to reproduction over the lifetime of an individual that will maximise the contribution of offspring to the next generation (Roff 1992; Stearns 1992).

The challenge is to develop a coherent hypothesis of how the distinctive features of teleost reproduction identified here, and perhaps others yet to be recognized, can explain the diversity of reproductive modes. This will be achieved by using emerging phylogenetic information about the relationships within the teleost lineage, as well as the large and disparate literature on the reproductive biology of teleosts, interpreted in the context of life-history theory.

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Figure caption

Figure 1 Distinctive features of teleost reproduction, their functional significance and the potential evolutionary outcomes for reproductive diversity. Arrows indicate proposed impacts.