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Fish sex: why so diverse?

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DOI [10.1016/j.conb.2009.09.015](https://doi.org/10.1016/j.conb.2009.09.015)**Introduction**

In most animal species, males and females behave differently, especially when it comes to sex and related social behaviors. These behaviors evolved to ensure successful reproduction and typically include some genetically pre-programmed displays. There are ~25,000 known species of fishes, by far the largest group of vertebrates, and they express a remarkable variety of adaptive responses to aquatic habitats with associated ecological constraints [1]. Moreover, teleosts have evolved in a relatively short time (~200 My) [2] producing virtually every reproductive option open to vertebrates: they bear live young, brood offspring in their mouths or body cavities, lay eggs (sometimes even out of water) or simply release their gametes into the plankton. In addition, mating/brood-care systems range from monogamous bi-parental to polygamous non-parental. In some species, females can reproduce parthenogenetically, males may become pregnant, and fish of both genders can change sex [3,4]. This brief summary of the range of fish reproductive behaviors highlights why they offer so much as reproductive systems for analysis.

Here we address the following questions: 1) What is known about the physiological mechanisms underlying sex determination and sex-specific behaviors in teleost fish species? 2) How do different sensory inputs and mating systems interact to influence reproductive function? 3) How do the special cases of alternative reproductive tactics, sex-role reversal, and sex change in fish give insight into the vertebrate sexual brain? 4) How can genomic information and epigenetic change influence brain areas controlling reproduction?

Sex determination

Some sex-determining mechanisms have been conserved over vast stretches of evolutionary time. For example, in

birds and mammals, all extant species share a ZW system of female heterogamety (e.g., production of 2 kinds of gametes) and an XY system of male heterogamety. In both these cases, the different sexes are always represented by two different individuals (e.g., gonochorism, [1]). By contrast, fish show a wide variety of sex determination systems, some via sex-determining chromosomes, others via autosomal genes and still others via environmental or social signals [4–6]. Numerous studies have shown how morphological specialization and life-history differences between fish species translate directly into behavioral differentiation between the sexes. More subtle behavioral differences may arise as a consequence of the different reproductive roles taken by males and females. In gonochoristic fish species, all possible forms of genetic sex determination have been observed from male and female heterogamety with or without the influence of autosomal genes, to more complicated systems involving several loci but without sex chromosomes or with several pairs of sex chromosomes [7]. For example, in the striated spined loach (*Cobitis taenia*) sex is determined through multiple sex chromosomes where females have $X_1X_1X_2X_2$ while males have X_1X_2Y sex chromosomes [8].

In many fish species temperature and/or pH of the hatching water determines sex. In a mouthbrooding cichlid, *Oreochromis niloticus*, for example, Baroiller *et al.* [9] showed that housing mouthbrooding females in higher temperatures increased the male proportion in their brood from 33% to 81%. Phenotypic sex can also be fully reversed by hormone treatment in female Chinook salmon (*Oncorhynchus tshawytscha*) where a brief treatment with an aromatase (enzyme that converts T to E_2) inhibitor during sex differentiation causes chromosomally female animals to develop as normal males [10]. Nonetheless, the core of the vertebrate sex determination/differentiation cascade is conserved in fishes [11,12,1]. *Dmrt1*, named for a common DM domain is considered to be involved in sex determination and/or sex differentiation and its expression is central to the development of the male tetrapod phenotype. This gene has a similar role in sex determination in both hermaphroditic and gonochoristic fish [13–17]. In the medaka (*Oryzias latipes*) sex differentiation is chromosomal (male heterogamy XX-XY) and recently, functional and expression analyses have shown that *Dmrt1* is the master gene for male sex determination [18]. However, in many fish species, once sex has been determined, reproductive ability can be regulated through social cues (e.g., [19]).

How do social and environmental signals regulate reproduction? Little is known about the actual pathways

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through which social signals act, but the final common output pathway requires hypothalamic gonadotropin-releasing hormone (GnRH1) signaling. The GnRH1-containing neurons are known to have a variety of inputs that are sexually dimorphic, change with reproductive status, and include many well-known neurotransmitters as well as other signaling molecules [20]. Ultimately GnRH1 expression depends on the integration of this wide variety of input signals and regulates reproduction.

Sensory inputs regulating reproduction

Sensing potential mates in water offers special challenges. Underwater optics and lighting are limiting, chemical signals can diffuse quickly, and other modalities such as weak electrical signaling and sound have distance limitations. Nonetheless, teleost fish have adapted to nearly every kind of water habitat imaginable, including very cold (-17°C) and very hot (38°C) water, low pressure at the water's surface and enormous pressures at 9000 m in depth, and in currents as different as a stagnant swamp to raging torrents. This diversity of habitats has result in a spectacular range of adaptations in teleost vision, particular in those species where seeing is the most important sense.

Vision

Among teleosts, cichlid fish species have been well studied and, in particular, for *Astatotilapia burtoni*, a cichlid fish endemic to Lake Tanganyika in the African Rift Valley, the visual system is well understood. *A. burtoni* has both rods (500 nm) and cone vision with cells tuned to λ_{max} values of 454 nm, 523 nm, and 562 nm [(for review see 21)]. In this species, visual cues play a role in female mate choice [22] and in male assessment of dominance and fighting ability [23,24]. When a non-dominant male sees a larger more dominant competitor, he stops displaying and courting females, turns off his body coloration, and acts submissively towards the more dominant individual [24]. Visual information is processed by the standard vertebrate pathway: From the eye to the nuclei of the accessory optic tract, the dorsal thalamus, the ventral thalamus, the pretectal region, and the optic tectum [25]. But exactly how and where reproductive information is collected and processed is not known. No sensory system operates in isolation, so olfactory, mechanosensory, and auditory pathways collaborate to provide information about reproduction.

Olfaction, mechanosensation, electroreception, and audition

The most ancient of the sensory systems (>500 My) are chemosensation, olfaction, and gustation, which are the major sensory pathways for detection and identification of chemical stimuli in the environment [26]. In teleost fish, paired olfactory organs are unlike terrestrial vertebrates since there is no direct contact between the olfactory and respiratory systems [26]. In crucian carp (*Carassius car-*

assius) the olfactory system detects preovulatory pheromones reflected in key amino acids in the water [27,28]. Treatment with preovulatory pheromones stimulates testicular hormone production in goldfish that in turn evokes increased milt production and courtship behaviors towards females [29]. Similar findings have been shown in the Rose bitterling (*Rhodeus ocellatus ocellatus*) [30], common carp (*Cyprinu carpio*) [29], and crucian carp (*C. carassius*) [31].

The fish mechanosensory system or lateral line organ, present in all fishes and aquatic amphibians [32–34], detects near field water movements relative to the skin surface [35]. Some fish even use self-induced water motions to detect stationary objects with the aid of the lateral line. This ability is well developed in the blind Mexican cavefish (*Astyanax mexicanus*), which when confronted with a new object, accelerates and then glides past it in close proximity. Environmental information is collected by analyzing distortions of the self-induced flow field using the lateral line [36,37]. In the hime salmon (*Oncorhynchus nerka*), sexual behavior depends on the use of body vibration and electromyographic activity of the trunk muscles of both males and females. These vibrations act as timing cues not only to synchronize the chain reaction of sexual behaviors but also to synchronize gamete release [38]. When using the lateral line, displacement of hair cells by viscous drag due to water movements causes modulation of the spontaneous primary afferent discharges sent to the mechanosensory processing centers in the hindbrain [39,40].

Electric fish generate weak electric organ discharges from a muscle-derived electric organ and use these fields for electrolocation and communication. Use of weak electrical signals has evolved twice, in the mormyriforms and the gymnotiforms [41]. In both of these groups of fishes, electric fields are used for sophisticated communication between individuals and the detection and identification of nearby objects [42]. The electrical organs are distributed over the entire body surface of fish and can be classified into two major classes: tuberous organs, specialized to high-frequency self-generated electrical fields and ampullary organs, specialized for the detection from external sources, like those generated from other animals [43]. The information gathered by these specialized organs is processed in the posterior lateral line lobe that projects to multiple brain areas [44].

Some teleost fish species generate acoustic signals for vocal communication. Carp (*Cyprinus carpio*), cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) use sound and can readily discriminate its amplitude and direction. The Hawaiian sergeant fish (*Abudefduf abdominalis*) produces sounds at close distances to the intended receiver with different pulse characteristics that are associated with aggression, nest preparation, and courtship

behaviors [45]. The plainfin midshipman (*Porichthys notatus*), a territorial fish uses vocalizations to court females and defend a territory against conspecific intruders. There is a direct relationship between rhythmic, patterned output of a brainstem pacemaker circuit and the physical attributes of species- and sex-specific vocalizations [46].

How did these sensory systems contribute to the evolution of mating?

Mating systems

Understanding the evolution of neural control of reproduction requires comparing model organisms with a variety of reproductive systems. Since teleost fish have the widest range of reproductive behaviors and mating systems among vertebrates [(c.f., 47)], these species offer unique opportunities to study both the evolution and the function of the variation in neural pathways involved in mating systems. In addition to primary reproductive strategies, alternative reproductive tactics abound, typically in species where males compete for access to mating territories to gain access to females. Smaller males with a reduced competitive ability may use one of multiple alternative tactics to achieve fertilization of part of the clutch [48]. In one cichlid, *Telmatochromis vittatus*, 4 alternative reproductive tactics exist [49]. Adult males can be: 1) territorial and defend a nest; 2) 'pirates' that displace territorial males; 3) satellite males, submissive to territorial and pirate males; and 4) sneaker males, who parasitize spawnings by releasing sperm when the territorial or pirate is absent [50]. In some species, younger males adopt a sneaker strategy until they grow big enough to become territorial (e.g., *Pomatochistus microps*) [51]. Interestingly, though, sneaker and territorial tactics may produce equivalent fitness (*Lepomis*, *Oncorhynchus*) [52]. Despite having mature gonads, males using alternative reproductive tactics do not show secondary sex characters typical of the dominant males of the species and the effects of high levels of circulating androgens are somehow differentially suppressed [53]. It is not known in these morphs how different aspects of male reproductive physiology including control of gonadal maturation, expression of secondary sexual characteristics, and activation of male sexual behavior are suppressed. For example, androgen profiles vary according to male mating tactics and courting males consistently have higher levels of 11KT (a fish-specific androgen) but not of T than non-courting males [(c.f., 54)].

Sex-role reversal occurs when females compete more intensely than males for access to mates, and hence such females have higher potential reproductive rates than males [55]. Male pregnancy in pipefishes and seahorses (*Syngnathidae*) suggests that females compete most intensely for access to males, because males limit female reproduction. Mayer *et al.* [56] measured plasma levels of androgens in three species of pipefish to discover

whether sex-role reversal and male pregnancy was correlated with circulating hormone levels. In pipefish, males had higher levels of 11KT, typical for normal teleosts, while levels of 17 β -estradiol were higher in males than in females, markedly different from that of the typical teleost pattern. Although few studies have looked at the hormonal correlates of sex-role reversal, reversal of sex roles is not typically associated with dramatic endocrinological differences [55].

In addition to the gonochoristic varieties described above, some fish species are sequential hermaphrodites, in which individuals at a stage of their life cycle or social status change sex [57]. There are simultaneous hermaphroditic species as well as parthenogenic species where all individuals reproduce asexually (e.g., Amazon mollie: *Poecilia Formosa*) [48,58,59]. The change of sex in sequential hermaphrodites may be genetically controlled or triggered by external events, such as the loss of a dominant male from a harem or it may be affected by the combination of these two mechanisms [60]. However, most sex changing fish rely on social cues to initiate and orchestrate the development of the dominant phenotype [61], which requires correlated changes in a suite of characters including brain, behavior, hormones, gonads, genitalia, and other secondary sexual characters [62]. In the dramatic case of some wrasse species, removal of a dominant male from his harem produced sex change of the largest female, who assumed male coloration in four days and full gonadal maturation including the production of mature sperm in eight days [63]. The mechanisms of sex change are not understood and typical hormonal interventions (e.g., gonad removal) have no effect [64].

Genomic and epigenetic regulation

Teleost fish have experienced extremely rapid genomic evolution, with notably fast-paced genic and genomic duplication [65,66]. Genome-wide duplications increase the potential for evolutionary flexibility in sex-determining and other sexually dimorphic pathways [67] but the diversity of specific strategies through which this has happened is staggering. The genetic mechanisms underlying development or modification of reproductive systems are due to 1) changes in protein or mRNA concentration and targeting; 2) modification of protein trafficking and/or retention; or 3) post-translational modifications. As shown above, measurements of protein or mRNA level changes have been extensively studied in fish species in relation to sex, sex change, and changes in social system (e.g., AVT, GnRH, serotonin, dopamine, etc.) [20,68]. However, changes in protein processing and post-translational processes have not been analyzed in fish reproduction *in vivo*.

microRNAs (miRNAs) are another possible regulator of reproductive action. These small non-coding RNAs control the stability or translation of mRNA transcripts and

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are a recently discovered mechanism. In multicellular organisms, numerous miRNA genes can act post-transcriptionally to modulate the expression of more than a third of the coding mRNAs [69] and these miRNAs are expressed in adult neurons providing local translational control of plasticity [70,71]. For example, miRNAs are key regulators in the circadian-timing process: miR-219-1 is a clock controlled gene that plays a role in regulating the length of the circadian day, while miR-132 is light inducible and modulates the phase-shifting capacity of light [72].

Another potential avenue for regulation of sex and reproductive behavior is the methylation of coding DNA [73]. DNA methylation occurs in the genomes of a wide array of bacteria, plants, fungi, and animals [74] and the methylation of cytosine bases represents an important epigenetic mark that affects gene expression in diverse taxa [74,75]. DNA methylation in vertebrates typically occurs at cytosine-phosphate-guanine sites (CpG) and is catalyzed by DNA methyltransferase [76]. In honeybees (*Apis mellifera*)

different levels of methylation have been associated with different castes within the hive [77] and Kucharski *et al.* [78] showed that downregulation of a key DNA methyltransferase (Dnmt3) in developing bees resulted in profound changes in developmental trajectories, suggesting that DNA methylation is widespread and may play a crucial role in the unfolding of life-history strategies. In rats, maternal behavior towards pups resulted in stable alterations of DNA methylation and chromatin structure, providing a mechanism for the long-term effects of maternal care on gene expression in offspring [79].

Conclusion

Fish express extremely diverse sex determination systems, mating systems, sensory systems, and reproductive tactics that have evolved multiple times and account for their evolutionary success. The fine-tuning of each of these pathways is unlikely to be genetically determined but shaped by experience, ongoing behavior, the reproductive axis as well as neural and epigenetic changes (Figure 1).

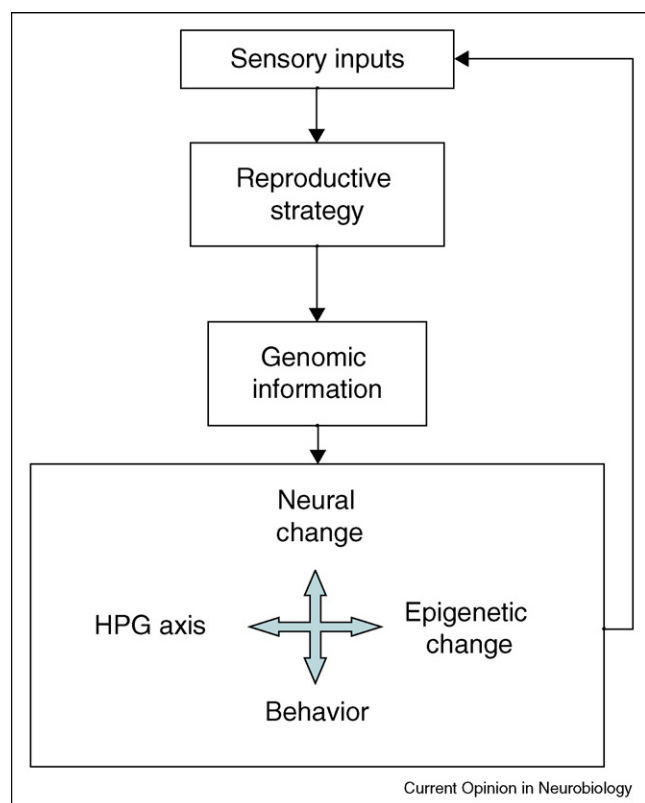
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References

1. Schartl M: **Sex chromosome evolution in non-mammalian vertebrates.** *Current Opinion in Genetics and Development* 2004, **14**:634-641.
2. Taylor JS, de Peer YV, Meyer A: **Genome duplication, divergent resolution and speciation.** *Trends in Genetics* 2001, **17**:299-301.
3. Helfman GS, Collette BB, Facey DE: *The Diversity of Fishes.* Oxford: Blackwell Science; 1997.
4. Magurran AE, Garcia CM: **Sex differences in behaviour as an indirect consequence of mating system.** *Journal of Fish Biology* 2000, **57**:839-857.
5. Baroiller JF, D'Cotta H, Saillant E: **Environmental effects on fish sex determination and differentiation.** *Sexual Development* 2009, **3**:118-135.
6. Luckenbach JA, Borski RJ, Daniels HV, Godwin J: **Sex determination in flatfishes: mechanisms and environmental influences.** *Seminars in Cell and Developmental Biology* 2009, **20**:256-263.
7. Baroiller JF, D'Cotta H: **Environment and sex determination in farmed fish.** *Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology* 2001, **130**:399-409.
8. Saitoh K: **Multiple sex-chromosome system in a loach fish.** *Cytogenetic and Genome Research* 1989, **52**:62-64.
9. Baroiller JF, Chourrout D, Fostier A, Jalabert B: **Temperature and sex chromosomes govern sex ratios of the mouthbrooding cichlid fish *Oreochromis niloticus*.** *Journal of Fish Biology* 1995, **273**:216-223.
10. Piferrer FC, Callard GV: **Inhibition of DNA synthesis during premeiotic stages of spermatogenesis by a factor from testis-associated lymphomyeloid tissue in the dogfish shark (*Squalus acanthias*).** *Biology of Reproduction* 1995, **53**:390-398.
11. Smith CA, McClive PJ, Western PS, Reed KJ, Sinclair AH: **Evolution: conservation of a sex-determining gene.** *Nature* 1999, **402**:601-602.
12. Zarkower D: **Establishing sexual dimorphism: conservation amidst diversity?** *Nature Reviews Genetics* 2001, **2**:175-185.

Figure 1



Theoretical pathway of the interaction between sensory inputs, reproductive strategy, genomic information, the brain, and behavior. The signals received by the sensory system will generate behavioral outputs based on the reproductive strategy of the species as well as the encoded genomic information. Once this signal is passed on, neural change, epigenetic change, the HPG axis, and behavior will change depending on the state of each. The behavioral output will then in turn influence how sensory inputs are interpreted.

13. Marchand O, Govoroun M, D'Cotta H, Lareyre J-J, Bernot A, Laudet V, Guegeun Y: **DMRT1 expression during gonadal differentiation and spermatogenesis in the rainbow trout, *Oncorhynchus mykiss***. *Biochimica et Biophysica Acta (BBA): Gene Structure and Expression* 2000, **1493**:180-187.
14. Brunner B, Hornung U, Shan Z, Nanda I, Kondo M, Zend-Ajusch E: **Genomic organization and expression of the doublesex-related gene cluster in vertebrates and detection of putative regulatory regions for DMRT1**. *Genomics* 2001, **77**:8-17.
15. He CL, Du JL, Wu GC, Lee YH, Sun LT, Chang CF: **Differential Dmrt1 transcripts in gonads of the protandrous black progy, *Acanthopagrus schlegelii***. *Cytogenetic and Genome Research* 2003, **101**:2462-2465.
16. Volf J-N: **Genome evolution and biodiversity in teleost fish**. *Heredity* 2005, **94**:280-294.
17. Kobayashi Y, Kobayashi T, Nakamura M, Sunobe T, Morrey CE, Suzuki N, Nagahama Y: **Characterization of two types of cytochrome P450 aromatase in the serial-sex changing gobioid fish, *Trimma okinawae***. *Zoological Science* 2004, **21**:417-425.
18. Matsuda M: **Sex determination in the teleost medaka, *Oryzias latipes***. *Annual Reviews of Genetics* 2005, **39**:293-307.
19. Davis MR, Fernald RD: **Social control of neuronal soma size**. *Journal of Neurobiology* 1990, **21**:1180-1188.
20. Fernald RD: **Social regulation of the brain: sex, size and status**. *The Genetics and Biology of Sex Determination*. Wiley; 2002: 382 pp.
21. Fernald RD: **Principles of sensory regeneration**. In *Regeneration of Vertebrate Sensory Receptor Cells*. Edited by Bock GR, Marsh J, Wheland J. New York: Wiley; 1991:318-329.
22. Clement TS, Grens KE, Fernald RD: **Female affiliative preference depends on reproductive state in the African cichlid fish, *Astatotilapia burtoni***. *Behavioral Ecology* 2005, **16**:83-88.
23. Grosenik L, Clement TS, Fernald RD: **Fish can infer social rank by observation alone**. *Nature* 2007, **445**:429-432.
24. Chen, Fernald 2009, in preparation.
25. Ebbesson SOE: **On the organization of central visual pathways in vertebrates**. *Brain, Behavior and Evolution* 1970, **3**:178-194.
26. Hara TJ: **The diversity of chemical stimulation in fish olfaction and gustation**. *Reviews in Fish Biology and Fisheries* 1994, **4**:1-35.
27. Stacey NE, Kyle AL: **Effects of olfactory tract lesions on sexual and feeding behavior in the goldfish**. *Physiology and Behavior* 1983, **30**:921-928.
28. Stacey N: **Hormones, pheromones and reproductive behavior**. *Fish Physiology and Biochemistry* 2003, **28**:229-235.
29. Sorensen PW: **Hormonally derived sex pheromones in goldfish: a model for understanding the evolution of sex pheromone systems in fish**. *The Biological Bulletin* 1992, **183**:173-177.
30. Kawabata K, Tsubaki K, Tazaki T, Ikeda S: **Sexual behavior induced by amino acids in the role bitterling *Rhodeus ocellatus ocellatus***. *Bulletin of the Japanese Society of Scientific Fisheries (Japan)* 1992, **58**:839-844.
31. Bjerselius R, Olsen KH: **A study of the olfactory sensitivity of crucian carp (*Carassius carassius*) and goldfish (*Carassius auratus*) to 17alpha, 20beta-dihydroxy-4-pregnen-3-one and prostaglandin F2alpha**. *Chemical Senses* 1993, **18**:427-436.
32. Flock AMB, Wersall JMD: **A study of the orientation of the sensory hairs of the receptor cells in the lateral line organ of fish, with special reference to the function of the receptors**. *The Journal of Cell Biology* 1962, **15**:19-27.
33. Lannoo MJ: **Neuromast topography in urodele amphibians**. *Journal of Morphology* 1987, **191**:247-263.
34. Northcutt RG: **Distribution and innervation of lateral line organs in the axolotl**. *Journal of Comparative Neurology* 1992, **325**:95-123.
35. Coombs S: **Nearfield detection of dipole sources by the goldfish (*Carassius auratus*) and the mottled sculpin (*Cottus bairdi*)**. *Journal of Experimental Biology* 1994, **190**:109-129.
36. Weissert R, von Campenhausen C: **Discrimination between stationary objects by the blind cave fish *Anoptichthys jordani***. *Comparative Physiology, A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 1981, **143**:375-381.
37. Hassan ES: **On the discrimination of spatial intervals by the blind cave fish (*Anoptichthys jordani*)**. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology* 1986, **159**:701-710.
38. Satou M, Shiraishi A, Matsushima T, Okumoto N: **Vibrational communication during spawning behavior in the hime salmon (landlocked red salmon, *Oncorhynchus nerka*)**. *Journal of Comparative Physiology A* 1991, **168L**:417-428.
39. Maruska KP: **Morphology of the mechanosensory lateral line system in elasmobranch fishes: ecological and behavioral considerations**. *Environmental Biology of Fishes* 2001, **60**:47-75.
40. Denton EJ, Gray JAB: **Mechanical factors in the excitation of the lateral lines of fishes**. In *Sensory Biology of Aquatic Animals*. Edited by Atema J, Fay RR, Popper AN, Tavolga WN. New York, NY, Berlin: Springer-Verlag; 1988:595-618.
41. Zakon HH, Zwickl DJ, Lu Y, Hillis DM: **Molecular evolution of communication signals in electric fish**. *The Journal of Experimental Biology* 2008, **211**:1814-1818.
42. Zakon HH, Lu Y, Zwickl DJ, Hillis DM: **Sodium channel genes and the evolution of diversity in communication signals of electric fishes: convergent molecular evolution**. *PNAS* 2006, **103**:3675-3680.
43. Nelson ME, Maciver MA: **Prey capture in the weakly electric fish *Apteronotus albifrons*: sensory acquisition strategies and electrosensory consequences**. *The Journal of Experimental Biology* 1999, **202**:1195-1203.
44. Maler L, Sas EKB, Rogers J: **The cytology of the posterior lateral line lobe of the high-frequency weakly electric fish (Gymnotidae): Dendritic differentiation and synaptic specificity in a simple cortex**. *The Journal of Comparative Neurology* 1981, **195**:87-139.
45. Maruska KP, Boyle KS, Dewan LR, Tricas TC: **Sound production and spectral hearing sensitivity in the Hawaiian sergeant damselfish, *Abudefduf abdominalis***. *The Journal of Experimental Biology* 2007, **210**:3990-4004.
46. Goodson JL, Bass AH: **Vasotocin innervation and modulation of vocal-acoustic circuitry in the teleost *Porichthys notatus***. *Journal of Comparative Neurology* 2000, **422**:363-379.
47. Demski L, Schwanzel-Fukuda M (Eds): *The Terminal Nerve (Nervus terminalis), Structure, Function and Evolution*, 519. NY: Annual Reviews of the National Academy of Science; 1987:469.
48. Oliveira RF, Canario AVM, Bshry R: **Hormones, behaviour and conservation of littoral fishes: current status and prospects for future research**. *Behavior and Conservation of Littoral Fishes* 1999, **149**:178.
49. Ota K, Kohda M: **Description of alternative male reproductive tactics in a shell-brooding cichlid, *Telmatochromis vittatus*, in Lake Tanganyika**. *Journal of Ethology* 2006, **24**:9-15.
50. Fitzpatrick JL, Desjardins JK, Milligan N, Montgomerie R, Balshine S: **Reproductive-tactic-specific variation in sperm swimming speeds in a shell-brooding cichlid**. *Biology of Reproduction* 2007, **77**:280-284.
51. Magnhagen C: **Alternative reproductive behaviour in the common goby, *Pomatoschistus microps*: an ontogenetic gradient?** *Animal Behaviour* 1992, **44**:182-184.
52. Gross MR: **Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes**. In *Fish Reproduction: Strategies and Tactics*. Edited by Wootton R, Potts G. London: Academic Press; 1984:55-75.
53. Taborbky M: **Sneakers, satellites and helpers: parasitic and cooperative behavior in fish reproduction**. *Advances in the Study of Behavior* 1994, **23**:1-100.
54. Brantley RK, Wingfield JC, Bass AH: **Sex steroid levels of *Porichthys notatus*, a fish with alternative reproductive**

6 Neurobiology of behaviour

- tactics, and a review of the hormonal basis for male dimorphism among teleost fishes. *Hormones and Behavior* 1993, **27**:332-347.
55. Eens M, Pinxten R: **Sex-role reversal in vertebrates: behavioural and endocrinological accounts.** *Behavioral Processes* 2000, **51**:135-147.
56. Mayer I, Rosenqvist G, Borg B, Ahnesjö I, Berglund A, Schulz RW: **Plasma levels of sex steroids in three species of pipefish.** *Canadian Journal of Zoology* 1993, **71**:1903-1907.
57. Godwin J: **Social determination of sex in reef fishes.** *Seminars in Cell and Developmental Biology* 2009, **20**:264-270.
58. Hubbs CL, Hubbs LC: **Apparent parthenogenesis in nature, in a form of fish of hybrid origin.** *Science* 1932, **76**:628-630.
59. Scharl M, Wilde B, Schlupp I, Parzefall J: **Evolutionary origin of a parthenoform, the Amazon Molly *Poecilia Formosa*, on the basis of a molecular genealogy.** *Evolution* 1995, **49**:827-835.
60. Warner RR, Robertson DR, Leigh EG: **Sex change and sexual selection.** *Science* 1975, **190**:633-638.
61. Warner RR: **Sex change and the size-advantage model.** *Trends in Ecology and Evolution* 1988, **3**:133-136.
62. Grober MS: **Neuroendocrine foundations of diverse sexual phenotypes in fish.** In *Sexual Orientation: Toward Biological Understanding*. Edited by Ellis L, Ebertz L. WestPort, CT: Praeger Press; 1997.
63. Warner RR, Swearer SE: **Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum*.** *The Biological Bulletin* 1991, **181**:199-204.
64. Godwin J, Crews D, Warner RR: **Behavioural sex change in the absence of gonads in a coral reef fish.** In *Proceedings of the Royal Society, B* 1996, **263**:1683-1688.
65. Taylor JS, Braasch I, Frickey T, Meyer A, de Peer YV: **Genome duplication, a trait shared by 22,000 species of ray-finned fish.** *Genome Research* 2003, **13**:382-390.
66. Vandepoele K, De Vos W, Taylor JS, Meyer A, de Peer YV: **Major events in the genome evolution of vertebrates: paraneome age and size differ considerably between ray-finned fishes and land vertebrates.** *PNAS* 2003, **101**:1343-1638.
67. Mank JE, Promislow DEL, Avise JC: **Evolution of alternative sex-determining mechanisms in teleost fishes.** *Biological Journal of the Linnean Society* 2006, **87**:83-93.
68. Grober MS, Sunobe T: **Serial adult sex change involves rapid and reversible changes in forebrain neurochemistry.** *Neuroreport* 1996, **25**:2867-2878.
69. Lewis B, Burge C, Bartel D: **Conserved seed pairing, often flanked by adenosines indicates that thousands of human genes are MicroRNA targets.** *Cell* 2005, **120**:15-20.
70. Martin KC, Kosik KS: **Synaptic tagging— who's it? *Nature Reviews Neuroscience* 2004, **3**:813-820.**
71. Cheng H-YM, Papp JW, Varlamova O, Dziema H, Russell B, Curfman JP, Nakazawa T, Shimizu K, Okamura H, Impey S, Obrietan K: **microRNA modulation of circadian-clock period and entrainment.** *Neuron* 2007, **54**:813-829.
72. Aubin-Horth N, Renn SCP: **Genomic reaction norms: using integrative biology to understand molecular mechanisms of phenotypic plasticity.** *Molecular Ecology* 2009, **18**:3763-3780.
73. Klose RJ, Bird AP: **Genomic DNA methylation: the mark and its mediators.** *Trends in Immunology* 2006, **31**:89-97.
74. Suzuki MM, Bird A: **DNA methylation landscapes: provocative insights from epigenomics.** *Nature Reviews Genetics* 2008, **9**:465-476.
75. Hendrich B, Tweedie S: **The methyl-CpG binding domain and the evolving role of DNA methylation in animals.** *Trends in Genetics* 2003, **19**:269-277.
76. Jones PA, Takai D: **The role of DNA methylation in mammalian epigenetics.** *Science* 2001, **293**:1068-1070.
77. Elango N, Hunt BG, Goodisman AD, Yi SV: **DNA methylation is widespread and associated with differential gene expression in castes of the honeybee, *Apis mellifera*.** *PNAS* 2009, **106**:11206-11210.
78. Kucharski R, Maleszka J, Foret S, Maleszka R: **Nutritional control of reproductive status in honeybees via DNA methylation.** *Science* 2008, **319**:1827-1830.
79. Weaver ICG, Cervoni N, Champagne FA, D'Alessio AC, Sharma S, Seckl JR, Dymov S, Szyf M, Meaney MJ: **Epigenetic programming by maternal behavior.** *Nature Neuroscience* 2004, **7**:847-854.