Socially Controlled Sex Change in Fishes

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Glossary

11-Ketotestosterone Potent androgenic steroid hormone in teleost fishes inducing the development of secondary sexual characters often associated with territoriality and courtship in large males.

Arginine vasotocin Neuropeptide homolog of arginine vasopressin found in mammals. These hormones are released at the posterior pituitary gland, and also widely in the brain where they act as neuromodulators.

Aromatase Enzyme belonging to the cytochrome P450 family of proteins and plays a key role in the biosynthesis of estrogens through metabolism of androgens such as testosterone.

Estradiol 17β The most important circulating estrogen in both teleost fishes and mammals, produced in the ovaries and also other tissues including brain.

Gonadotropin-releasing hormone Neuropeptide hormone produced in the hypothalamus, released at the anterior pituitary gland to regulate gonadotropin secretion and is a key regulator of reproduction.

Gonochorism Sexual pattern in which individuals mature as one sex and remain that sex.

Initial phase First sexual phenotype seen in many protogynous species, often characterized by relatively drab colors and relatively low displays of aggression and courtship behavior.

Monoamine neurotransmitter A group of neurotransmitters that contain one amino group in their chemical structure.

Protandry Sexual pattern in which individuals mature as males and can then later change functional sex to become female.

Protogyny Sexual pattern in which individuals can mature as females and then later change functional sex to become secondary males. In monandric (one male) protogyny, all secondary males first pass through a female stage. In diandric (two males) protogyny, individuals can mature as either males or females and both can change from the initial phase to become the larger and typically colorful and aggressive terminal phase males.

Simultaneous hermaphroditism Sexual pattern characterized by individuals possessing both mature ovarian and spermatogenic tissue within the same functional gonad.

Steroid receptors Proteins that bind steroid hormones and then function as ligand-activated transcription factors to regulate gene expression in target cells.

Testosterone Important androgenic steroid hormone in all classes of vertebrates; critically, this steroid often functions as a biosynthetic intermediate in estradiol or 11-ketotestosterone production.

Introduction

This article focuses primarily on one of the more dramatic examples of reproductive adaptation to social environment seen in fishes and, indeed, any animal – socially controlled functional sex change. The adaptive significance (or why?) of sex change is generally better understood than the developmental and physiological mechanisms that underlie this process (i.e., how?). When individuals can reproduce more effectively as one sex when small or young and as the other sex when larger or older, then there is an obvious benefit in being able to change sex to maximize reproductive success for their body size. This is known as the 'size advantage model' of sex change and it has been quite successful in explaining patterns of sex change in many species.

While the size advantage model offers a compelling explanation for the presence of sex change in many species of fishes where this pattern is observed, it is equally striking that many species exhibit similar patterns of reproductive success across body size (especially mating advantages for large males) and should exhibit sex change according to the model, yet do not. This is true both

within the fishes and especially for other vertebrate groups where sexual lability is both much rarer and restricted to early developmental periods if it occurs. What accounts for this variation?

In mammals, the sex of an individual is determined by sex chromosomes at fertilization and specifically the presence or absence of the gene SRY (for 'Sex determining Region of the Y' chromosome). The testis or ovaries then arise relatively early in development and their hormonal secretions (particularly testicular androgens) organize other tissues including the brain. By contrast, the gonads develop relatively late in fishes as compared with other tissues and often well after individuals have spent considerable time as independently living miniature adults. But why does this matter in terms of environmental control of sex determination?

When the gonads develop very early, the brain is neither capable nor has the opportunity to gather and interpret environmental information that might be used to adaptively guide sex determination. By contrast, fishes often have ample opportunity to collect such information prior to gonadal development and, in the case of social influences, possess a well-developed brain to interpret it.

Sexual Patterns in Fishes

Fishes show the broadest range of sexual patterns of any group of vertebrates. With respect to sex determination, this variation ranges from strict gonochorism, where sex is determined by sex chromosomes, to simultaneous hermaphroditism, where individuals can alternate male and female function on a second-to-second basis. Between these extremes are species where:

1. sex is determined by social or physical factors prior to maturation, but then fixed after maturation;
2. species that mature as one sex, either male or female, and then change to become the other sex following maturation either as part of an ontogenetic sequence dependent on age or body size or in response to changes in their social environment; and
3. species that can undergo serial adult sex changes in both directions in response to social environment.

The article primarily focuses on the latter two patterns where sex determination occurs in adults and is under social control. Many species that undergo sex change also exhibit alternate male phenotypes; these are fascinating reproductive adaptations, but a full treatment is beyond the scope of this article.

Socially controlled sex change was first described and is best characterized in tropical marine fishes associated with coral reefs. This is because sex change is relatively common in four families that are conspicuous and important parts of the reef fish community. These families are the wrasses (Labridae), parrotfishes (Scaridae), damselfishes (Pomacentridae including the anemonefishes, subfamily Amphiprioninae), and the gobies (Gobiidae). Socially controlled sex change is also found in some temperate species where studies have focused on wrasses and gobies.

Male-to-female adult sex change is termed protandry and is seen in several families of fishes. Socially controlled protandry is best described in the anemonefishes, an Indo-Pacific group of 26 species (25 in *Amphiprion* and one species of *Premnas*). The anemonefishes have been an object of fascination due to both the symbiotic relationship they show with large tropical sea anemones and their recognition as stars in the movie *Finding Nemo* that featured Nemo, a 'boy' anemonefish, being raised by his single father Marvin. However, had the movie been biologically accurate, Nemo's father would have likely changed sex to become female following the disappearance of Nemo's mother and Nemo would have been like other anemonefishes, developing as an immature female who would likely have matured into a functional male to form a breeding pair in the social group (**Figure 1**). This pattern of a breeding pair and up to several immature females forming social groups has now been described for several anemonefish species. The gonadal structure of males consists of peripheral active spermatogenic tissues surrounding immature ovarian tissue (oocytes in the previtellogenic stage of development, **Figure 2**). This pattern is interesting because it illustrates the fundamentally female-first pattern of development in sex changing fishes even when the adult sex change pattern is male-to-female (we can only speculate as to why the movie makers decided not to have Nemo's father change sex!).

The maturation of juveniles and sex change by breeding males appears to be prevented by aggressive dominance of large females in anemonefishes. In the cinnamon anemonefish, *Amphiprion melanopus*, dominant females rapidly and aggressively approach their male pair mates approximately 150 times a day. Disappearance or experimental removal of these females eliminates this inhibition and both the behavior and gonadal structure of the male begin to change rapidly. Male cinnamon anemonefish made experimentally dominant show significant increases in aggressive behavior within 1 day of the removal of their dominant female pair mates and extensive changes in gonadal structure with proliferation of oogonial-like cells by 10 days later. Replacement of spermatogenic tissue with ovarian tissue is complete by 20 days.

The most common form of socially mediated sexual plasticity seen in reef fishes is female-to-male sex change or protogyny. Protogyny can take two forms. In monandric (one male) protogyny, all individuals mature as females and only later potentially change to become males. In diandric protogyny, individuals develop initially as immature females, but may mature into the initial phase (IP) as either males or females and either of these
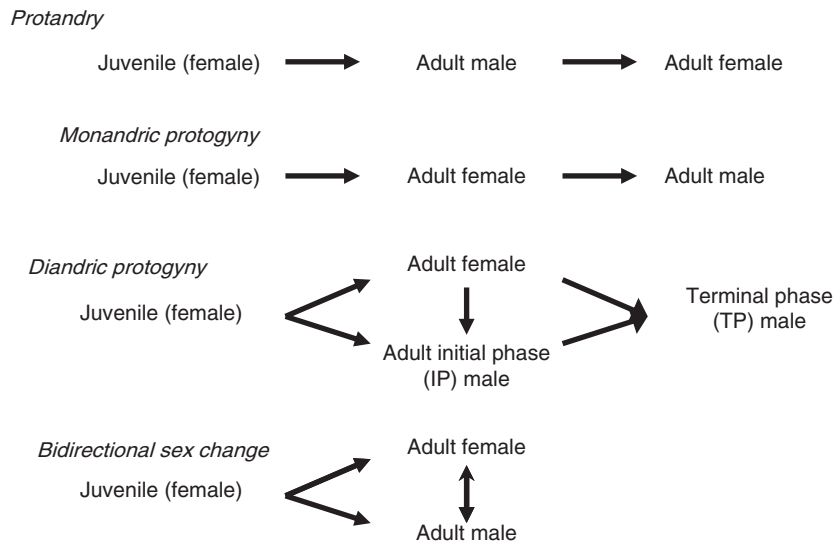
Figure 1 Sex change patterns in fishes. Modified from Godwin J (2010) Neuroendocrinology of sexual plasticity in teleost fishes. *Frontiers in Neuroendocrinology* 31(2), 203–216, with permission from Elsevier.
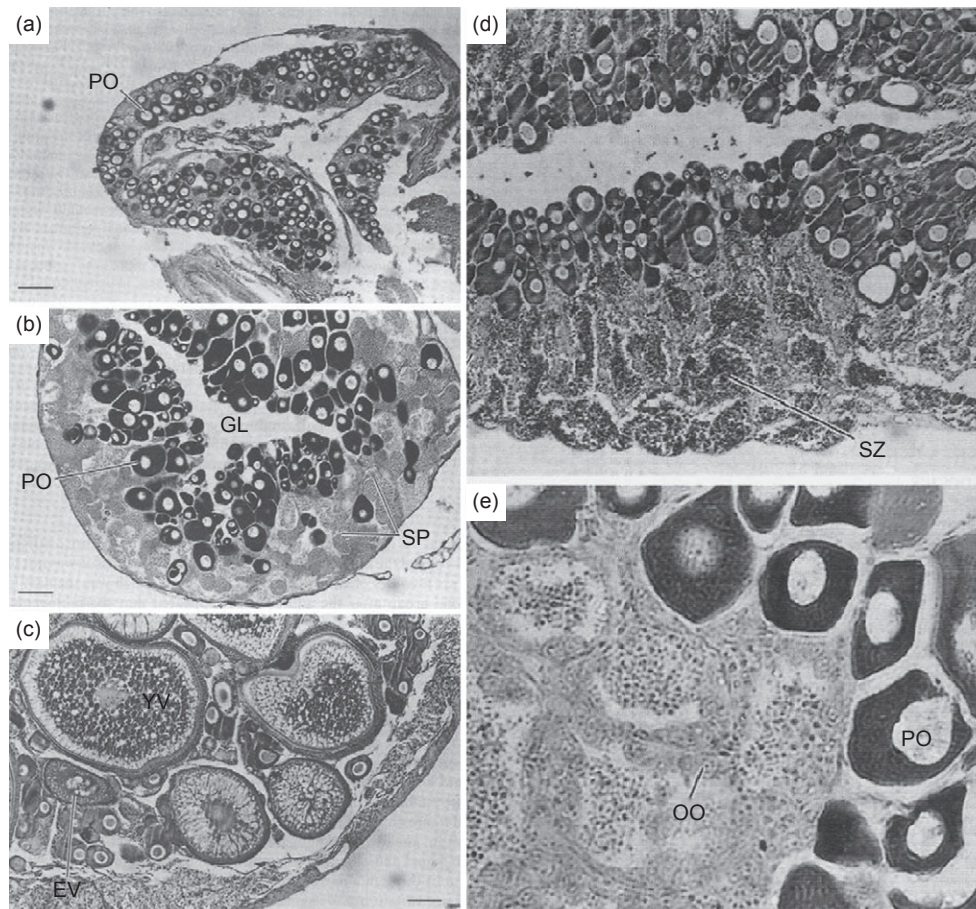

Figure 2 Gonad structure in the anemonefish *Amphiprion melanopus* for juvenile nonbreeders (a), breeding males (b), breeding females (c), and a sex changing fish 10 days after removal of the dominant female ((d) – low magnification, (e) – higher magnification). Abbreviations: EV, early vitellogenic oocyte; GL, gonadal lumen; PO, previtellogenic oocyte; SP, spermatogenic tissue (multiple stages); SZ, spermatozoa; OO, presumptive oogonia appearing as ovary develops during sex change. Scale bars = 100 mm. Reproduced from Godwin J (1994) Histological aspects of protandrous sex-change in the anemonefish *Amphiprion melanopus* (Pomacentridae, Teleostei). *Journal of Zoology* 232: 199–213.
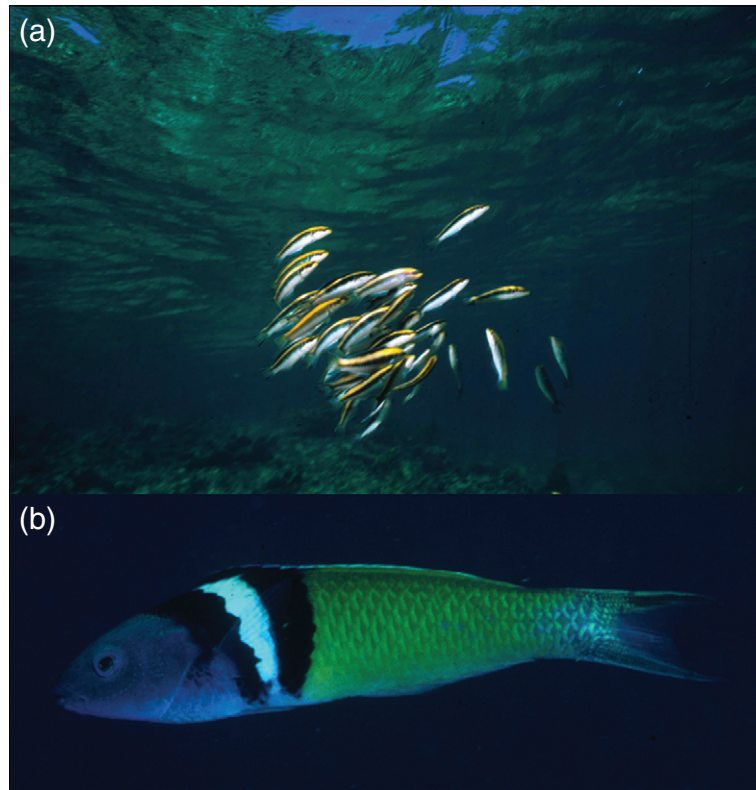
Figure 3   Initial phase and terminal phase males of the bluehead wrasse, *Thalassoma bifasciatum.*

phenotypes can then undergo change to the typically brightly colored terminal phase males (**Figures 1 and 3**). Monandric protogyny occurs in some damselfishes and is common in gobies and groupers with both monandric and diandric protogyny occurring in wrasses and parrotfishes. As predicted by the size advantage model discussed earlier, the adaptive significance of both monandric and diandric protogyny appears to be the high levels of reproductive success that accrue to large males who monopolize access to females or spawning territories.

Perhaps the most dramatic examples of sexual plasticity are seen in gobies and some serranid fishes. A number of serranid species are simultaneous hermaphrodites, maintaining both mature ovarian and testicular tissue in the same gonad. The hamlets (genus *Hypoplectrus*) are native to the Caribbean Sea and alternate female and male behavior and spawning on a second-to-second timescale in a behavior termed 'egg trading'. Other species of small serranid sea basses maintain gonads with mature tissue of both sexes and may lose the ovarian tissue when they become socially dominant members of social groups able to monopolize mating.

A number of goby species are protogynous. However, gobies also show an additional degree of flexibility in species that exhibit bidirectional sex change. Species of *Gobiodon* and *Paragobiodon* are obligate residents of branching corals in the west Pacific that can change sex in either direction. This flexibility allows any two individuals to

form a mating pair on a coral, likely a strong advantage for a very small bodied species in which traveling large reef areas in search of mates could be very dangerous (**see also Hormonal Control of Reproduction and Growth**: Endocrine Regulation of Fish Reproduction; Endocrine Control of Sex Differentiation in Fish).

Steroid Hormone Patterns

The effects of androgens in a sex changing species were examined as early as 1962 in the wrasse *Coris julis*, but measurements of circulating levels of sex steroid hormones had to wait for the development of a technique termed 'radioimmunoassay' (RIA). Early studies using RIA showed that plasma levels of the primary estrogen in fishes (and mammals) 17-beta estradiol (E_2) were elevated in female saddleback wrasses (*Thalassoma duperrey*) and declined dramatically at the onset of sex change at the same time that oocytes in the gonad degenerated (**Figure 4**). Levels of E_2 remained very low across sex change and in terminal phase (TP) males. By contrast, a key androgen in fishes 11-ketotestosterone (11KT), was present at low levels in females and across sex change, only becoming elevated in TP males. Importantly, significant increases over female 11KT levels appeared to follow rather than precede or accompany the appearance of mature spermatogenic tissues.
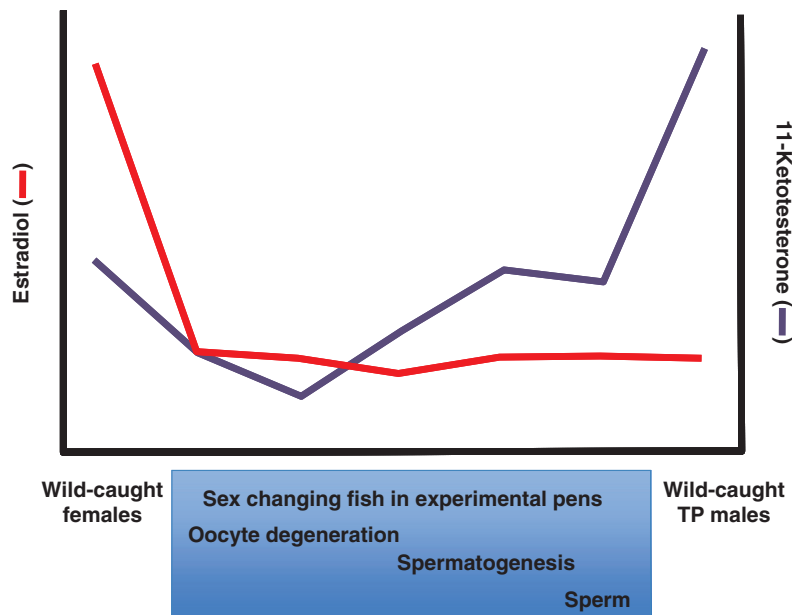
Figure 4 Relative steroid hormone levels in the plasma of saddleback wrasses shown for natural females and TP males as well as females undergoing socially induced sex change in experimental pens. Redrawn from Nakamura M, Kobayashi Y, Miura S, Alam MA, and Bhandari RK (2005) Sex change in coral reef fish. *Fish Physiology and Biochemistry* 31: 117–122.

Similar sex steroid hormone patterns are seen in the stoplight parrotfish (*Sparisoma viride*) and several other sex changing species that have been examined, including goby and grouper species. In an interesting twist, the anemonefish

A. melanopus also shows higher plasma E$_2$ levels in females and higher 11KT levels in males despite the direction of sex change being male-to-female and females being the larger and aggressively dominant sex (**Figure 5**).
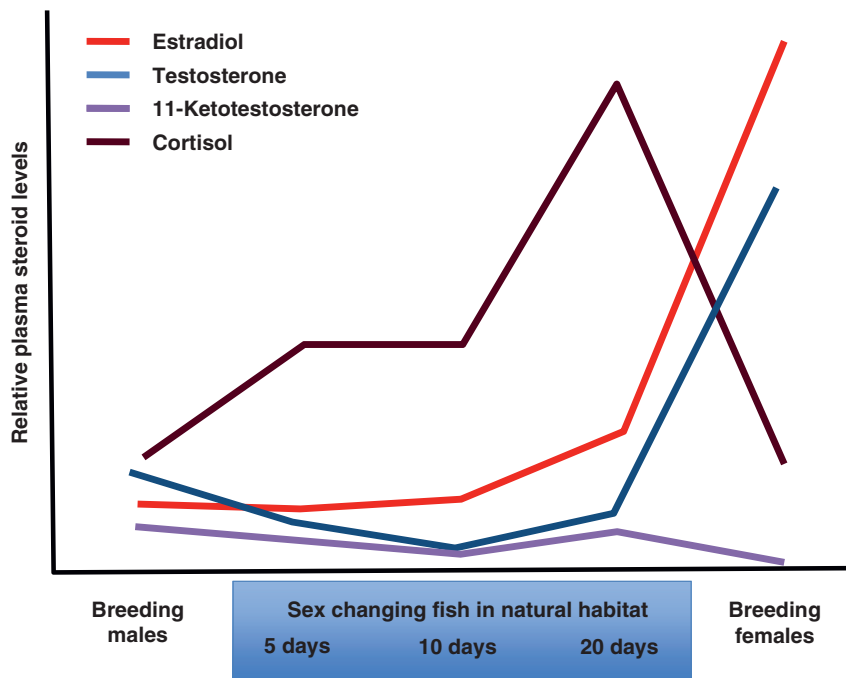

Figure 5 Relative steroid hormone levels in plasma of the anemonefish *Amphiprion melanopus* in natural males and females and as males underwent protandrous sex change following experimental female removals from social groups. Relative levels of different hormones are depicted approximately to scale except for cortisol, where levels were substantially higher. Redrawn from Godwin JR and Thomas P (1993) Sex change and steroid profiles in the protandrous anemonefish *Amphiprion melanopus* (Pomacentridae, Teleostei). *General and Comparative Endocrinology* 91(2): 144–157.

The role of steroid hormones in the control of sex change is supported by many experiments manipulating either steroid hormones directly or their synthesis. Androgen administration is effective for inducing male sex determination in a wide range of fishes and this approach is widely used in aquaculture to produce faster-growing males. Beginning in 1955 with bluehead wrasses, androgen administration has also been used to successfully induce sex change in a number of sex changing species. These include a number of wrasses, the stoplight parrotfish *S. viride,* the blackeye goby *Coryphopterus nicholsi,* and several species of groupers.

Blocking estrogen synthesis has similar effects to androgen administration in inducing female-to-male sex change. A key regulatory step in estrogen synthesis is the enzyme aromatase, a protein in the cytochrome P450 family of proteins. Fishes express two forms of this enzyme, known as gonadal and brain aromatase. Aromatase and estrogens generally appear to play key roles in sex determination in a range of species. Manipulations of estrogen signaling and aromatase activity are effective in manipulating the occurrence of sex change in several wrasse and grouper species as well as two goby species. For example, inhibiting aromatase action in the blackeye goby *C. nicholsi* induces sex change as effectively as 11KT implants. The bidirectionally sex changing gobies in the genus *Gobiodon* are especially interesting in this respect. As noted above, these gobies can change sex in either direction to form heterosexual pairs on the corals where they reside. Implants of the aromatase inhibitor fadrozole induce females to become males and males to remain male even when paired with a larger male. Conversely, E_2 implants induce sex change in males paired with other males while E_2-implanted females paired with other females do not change sex. Also consistent with a dominant role for estrogenic signaling in regulating sex change was a study where co-administering E_2 with androgens in three-spot wrasses blocked the female-to-male sex change that would otherwise occur. Taken together, these studies suggest that estrogenic inhibition may be the critical controlling factor for gonadal sex change.

The environmental cues for socially controlled sex change must clearly first be perceived in the brain. Consistent with this expectation, the more rapid decreases in brain aromatase activity seen in the brain compared to the ovaries of sex changing *Lythrypnus dalli* gobies suggest that a key early event in the sex change process is reduced estrogen signaling to neural structures.

Other Steroid Hormones and Sex Change

Because the social regulation of sex change is often closely related to aggressive behavioral dominance, there has been interest in the potential role of stress hormones. The key stress-related steroid in fishes is cortisol, as in humans, and is synthesized in the interrenal gland. Subordinate social status is quite often characterized by elevated cortisol levels in fishes and other species and elevated cortisol levels can inhibit reproductive function. These relationships led Perry and Grober to develop a model of the mediation of socially controlled sex change through the endocrine stress axis. This model was not supported in studies in anemonefish (*A. melanopus*) or the sandperch *Parapercis cylindrica*, where experimental increases in cortisol did not prevent sex change. However, stress effects can be exquisitely time sensitive and animals show physiological adaptation to chronic stressors in sometimes subtle ways, so more work remains to be done regarding the potential role of the endocrine stress axis in mediating sex change (**see also Social and Reproductive Behaviors**: Dominance Behaviors, **Hormonal Responses to Stress**: Impact of Stress in Health and Reproduction).

Neural Mechanisms of Sex Change

It has become clear that the often dramatic changes in behavior that accompany sex change are key parts of the change in sexual phenotype and may play an important role in stimulating the gonadal sex change process. This appreciation of the role of behavioral change as well as development of new techniques have shifted much of the focus in recent studies of sex change to neural and neuroendocrine mechanisms which may translate changes in social environment to changes in the gonads and other parts of the sexual phenotype.

The hypothalamus serves as a critical integrative center for both the reproductive axis and sexual behavior and is the site of gonadotropin-releasing hormone (GnRH) neurons which project to the pituitary gland. This brain region has, therefore, been a logical starting point for investigations of the neural mediation of sex change. Both correlative and experimental approaches support a role for the GnRH system in the sex change process. Working with bluehead wrasses in the early 1990s, Matthew Grober and colleagues described greater numbers of immunoreactive GnRH neurons in the hypothalamus of TP males than in that of females and that these numbers were increased in females by 11KT treatment. This pattern of greater numbers of GnRH neurons in males than females is also seen in the Ballan wrasse (*Labrus berggylta*) and in the protandrous anemonefish *Amphiprion bicinctus* (despite females being larger and aggressively dominant in anemonefishes). Expression of GnRH has not been closely monitored through the sex change process in any species, but findings from the cichlid *Astatotilapia burtoni* suggest that this would likely be informative. *A. burtoni* shows socially regulated sexual

development that involves rapid activation of preoptic area GnRH neurons when changes in social conditions are perceived. This rapid activation of GnRH neurons underlies the rapid activation of the HPG axis when subordinate males ascend to social dominance.

What mechanisms might induce a change in the activity of GnRH neurons? Changes in neural estrogen signaling due to reductions in brain aromatase activity at the onset of sex change and a potential role for stress hormones were discussed above. Another intriguing possibility is the monoamine neurotransmitters – serotonin, noradrenaline, and dopamine which have been shown to vary in areas of the forebrain important for reproduction and sexual behavior, and their roles further confirmed by manipulation experiments.

Before leaving the discussion of neural mediation of gonadal sex change, this article discusses some recent work suggesting that the variation in target tissue responsiveness to gonadotropins is the critical change at the time of sex change. The bidirectionally sex changing goby *Trimma okinawae* expresses both ovarian and testicular tissues, but with only one type being mature and active at a given time. Kobayashi and colleagues found that the active portion of the gonad expressed gonadotropin receptors at much higher levels than the inactive portion and that this higher expression was associated with greater responsiveness to gonadotropin. Exposure to visual cues that induce a change to the opposite sex reversed the pattern of gonadotropin receptor expression within approximately 12 h.

Neural Bases of Behavioral Sex Change

Successful sex change requires coordinated changes in a suite of phenotypic features. Behavioral sex change in fishes is often very rapid, occurring within one to several days in anemonefishes and blue-banded gobies and within minutes of dominant male removal with cleaner and bluehead wrasses studied in nature. This short timescale suggests gonadal change does not drive behavioral change. Indeed, the reverse may be true. The role of the gonads, neural mediators of behavioral sex change, and potential connections between the behavioral and gonadal sex change are discussed in this section.

Surgically removing the gonads from female bluehead wrasses does not prevent behavioral sex change when those females are made socially dominant. While the gonads are not necessary for the behavioral components of sex change in this species, ovariectomized females do not develop TP male coloration on becoming dominant. This is presumably because they lack a source of 11KT, which can induce the development of these colors when administered even to subordinate, ovariectomized females. This lack of necessity for gonads in behavioral sex change is consistent with often very rapid time course of this process and highlights

the fact that important changes in steroid hormone signaling do not need to occur in the gonad itself.

What neural mechanisms do mediate behavioral changes during the sex change process? Two areas of focus have been monoamine neurotransmitters and neuropeptide hormones. Changes in monoamines were mentioned above and in saddleback wrasses (*T. duperrey*) changes are especially pronounced during the first week of sex change when social dominance for sex changing females is being established. During the first week in experimental groups, dominance interactions develop accompanied by a number of alterations in monoaminergic signaling, although the patterns are complex across brain nuclei. In bluehead wrasses, serotonergic manipulations can decrease aggression in both laboratory and wild TP males, but no studies have closely examined the behavioral effects of manipulating monoamines during the sex change process in wrasses.

A second focus for studies of the neural mechanisms mediating behavioral sex change has been on neuropeptide hormones, especially arginine vasotocin (AVT). The first study to show differences in AVT neurons across sexual phenotypes in a sex changing fish was in the goby *T. okinawae*. In bluehead wrasse, TP males have significantly higher abundances of AVT mRNA in the preoptic area of the hypothalamus compared with females and these levels increase rapidly during experimentally induced sex change. Both the gonads and social interactions are changing as a female wrasse undergoes sex change; therefore, to tease these two factors apart, levels of AVT neurons in females changing sex with and without gonads and females that remain as subordinate females were compared. Social status affected AVT mRNA abundance, while gonadal status did not (Figure 6). Behavioral effects of AVT also appear to depend on sexual phenotype. Neither courtship nor territorial behavior could be induced by AVT injections in females or female-mimic IP males. However, injection of AVT increases courtship in TP males and induces nonterritorial TP males to establish territories.

This difference in responsiveness to AVT across sexual phenotypes is not surprising. In mammals, arginine vasopressin, the mammalian homolog of AVT, is more strongly implicated in male-typical socio-sexual behavior, while oxytocin, the homolog of the teleost isotocin, is implicated primarily in mediating female-typical socio-sexual behavior. The best data on the effects of isotocin in fishes come from an experiment by James Goodson and Andrew Bass, who examined neural responsiveness with a non-sex changing species, the plainfin midshipman *Porichthys notatus*. They found that the brains of large territorial males were strongly responsive to AVT while those of females and smaller nonterritorial type II males were not responsive at all. By contrast, the brains of females and type II males were strongly responsive to isotocin, while the large territorial type I males were completely unresponsive. The only data available
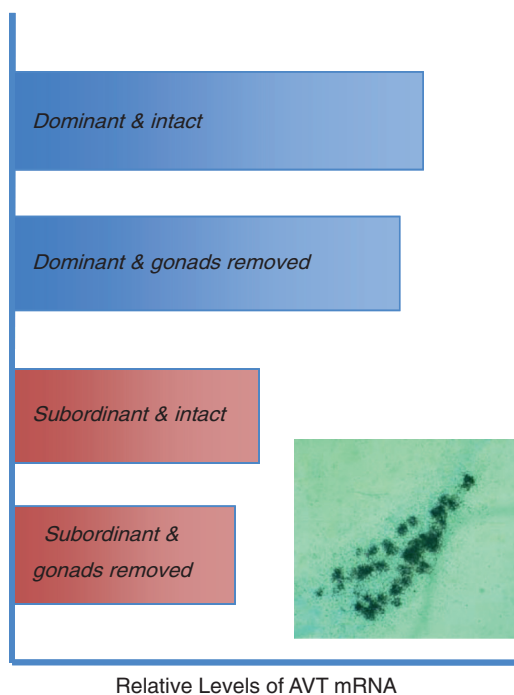
Relative Levels of AVT mRNA

Figure 6 Social status influences AVT mRNA levels in the preoptic area of the hypothalamus in bluehead wrasses while gonadal status does not. Dominant individuals were the largest in their social groups while subordinants were not. Intact animals underwent sham operations to control for the surgical procedure. Inset shows AVT mRNA in the preoptic area visualized by the technique of *in situ* hybridization. Data from Semsar K and Godwin J (2003) Social influences on the arginine vasotocin system are independent of gonads in a sex-changing fish. *Journal of Neuroscience* 23: 4386–4393.

regarding isotocin neuron patterns in sex-changing species come from blue-banded gobies, where more isotocin neurons were found in females than males. Further exploration of isotocin actions in sex changing fishes would be valuable.

Summary

Our understanding of the physiological basis of sex change has increased rapidly in recent years. This is due to both technical advances in endocrine techniques and especially molecular biology as well as the identification and exploitation of powerful model systems such as sex changing wrasses and bidirectionally sex changing gobies. Estrogen synthesis through the aromatase enzyme and the actions of the neuropeptides GnRH and AVT appear especially important in regulating sex change, but other physiological mediators are undoubtedly important contributors to the process. The discovery of these mechanisms and development of synthetic models of the mechanistic basis of sex change from the perception of changed social environment to gonadal change should be the next stage in study of this fascinating reproductive adaptation.

See also: **Hormonal Control of Reproduction and Growth**: Endocrine Control of Sex Differentiation in Fish; Endocrine Regulation of Fish Reproduction. **Hormonal Responses to Stress**: Hormone Response to Stress; Impact of Stress in Health and Reproduction. **Social and Reproductive Behaviors**: Dominance Behaviors.

Further Reading

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