

Social and Neural Modulation of Sexual Plasticity in Teleost Fish

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Teleost fish · Sex reversal · Alternative mating tactics · Neuroendocrine system

Abstract

Teleost fishes are the 'champions' of sexual plasticity among vertebrates. Several species have two male reproductive morphs with distinct suites of behavioral, somatic, neuronal, endocrinological, and life history traits. Here, we consider recent studies of the social and neural modulation of sexual plasticity for such species with a focus on two neuropeptides, gonadotropin releasing hormone (GnRH) and arginine vasotocin (AVT, teleostean analogue of mammalian arginine vasopressin). The major premise of this review is that phenotypic changes in GnRH and AVT expression in the brain can orchestrate events leading to changes in either sexual status or the expression of morph specific display behaviors important in reproduction.

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Introduction

Teleost fishes exhibit a wide range of reproductively active phenotypes; they are the 'champions' of sexual plasticity among vertebrates [reviews: Taborsky, 1994; Grober, 1998; Foran and Bass, 1999]. This includes species with hermaphroditic individuals that can either permanently transform sequentially from male to female (protandry) or

female to male (protogyny), to those where individuals can change gender on the order of minutes (simultaneous hermaphrodites). In some cases, including both hermaphroditic and non-hermaphroditic species, one sex (usually males) may display two or more mating tactics. Two male reproductive phenotypes or 'morphs' can represent either sequential life history stages for one individual as exhibited by some protogynous species, or distinct developmental trajectories. In all cases, each male morph displays a distinct suite of behavioral, somatic, neuronal, endocrinological and life history traits [Bass, 1992, 1993].

Complementary Explanations for Phenotypic Characters

Complementary hypotheses can be proposed to explain an existing phenotype [Sherman, 1988; Bass, 1998]. The temporal scales for such explanations range from the duration of an action potential to the maintenance of a behavior or neural circuit over a single life history stage or geological time. An existing phenotype is operationally defined by behavioral and structural characters that exist within a current ecological environment [Bass, 1998]. Behavioral characters, like reproductive tactics, are the measurable actions taken by individual organisms. Structural characters, like those of the nervous system, are typically given either a genetic, psychological, physiological, morphological, or biochemical signature depending on the disciplinary approach used to characterize them. The ecological environment includes abiotic and biotic factors such as

spawning sites and conspecifics respectively. Multiple, but complementary, explanations can be provided for the existence of any behavioral phenotype including mechanisms, life history, fitness, and evolutionary history. The focus here is on mechanisms; for an extended discussion of others, see Bass [1998].

Mechanisms are processes that contribute to the current maintenance of any one character in a particular environment; they are designated as either structural-behavioral, behavioral-ecological, or ecological-structural. Whatever the time frame applied to existing mechanisms, whether nanoseconds or hours, they are operative within a single life history stage.

Mechanisms of Sexual Plasticity

Examples of social modulation of reproductive tactics among teleost fish are abundant [see Taborsky, 1994]. Given the goals of this symposium, we focused our discussion on behavioral-ecological and structural-behavioral mechanisms modulating sexual plasticity among teleosts. For a more complete commentary of these and other explanations see Bass [1998], Grober [1998], Bass et al. [1999] and Foran and Bass [1999]. We also focused our discussion on two broadly defined groups of teleosts: (1) species where single individuals exhibit either sex or role change, namely sequential male reproductive phenotypes among hermaphroditic species and (2) species where juveniles permanently adopt one of two or more developmental trajectories that lead to alternative male reproductive tactics. We chose these examples, in part, because they have been the focus of our own research programs. However, these two groups also show the most extreme examples of sexual plasticity among vertebrates and thus maximize the chances of establishing testable hypotheses about the mechanisms underlying the divergence in brain phenotypes among members of one sex.

Behavioral-Ecological Mechanisms

In the context of the present discussion, behavioral-ecological mechanisms would include the influence of conspecific and heterospecific interactions on the expression of a reproductive phenotype. Studies of hermaphroditic teleosts are exemplary in this regard. We originally chose the bluehead wrasse (*Thalassoma bifasciatum*) as a study species [Grober and Bass, 1991] because of an especially rich literature that considered behavioral ecological, life history and fitness explanations for the existence of sex and role reversal in this group [see Warner and Swearer, 1991 and references therein]. *T. bifasciatum* has two male phenotypes: (1) larger terminal phase (TP) males have blue heads, a black-white-black banding behind the head, and green

bodies; (2) smaller initial phase (IP) males, like females, have a yellow – white coloration pattern. All individuals first reproduce as either IP males or females. TP males develop from either sex changing IP females or role changing IP males. Aside from body coloration, IP and TP individuals exhibit dramatic differences in body size, reproductive behavior, and fecundity [Petersen et al., 1992; Warner and Schultz, 1992]. TP males are highly territorial on the reef, actively court and gain preferential access to females, and may mate with up to 100 females per day. IP males are non-territorial (like females) and mate in large aggregations (~50 IP males per female) or sneak spawn with a TP male/female pair. This difference in access to females may explain the much higher gonosomatic index (GSI, gonad weight/body weight) in IP males, which is probably a response to the intense sperm competition associated with mass spawnings. Finally, IP females show no breeding site defense and little aggression towards IP fish, and they visit TP male or IP male spawning sites.

Studies in wrasses, and hermaphroditic species in general, highlight the potential role of social cues in the regulation of sexuality within individual members of a social group. Sex or role change is rapid and occurs even in gonadectomized individuals [Warner and Swearer, 1991; Godwin et al., 1996]. Development of permanent changes in body coloration does however appear to be dependent on gonadal steroids [Godwin et al., 1996; also see Grober et al., 1991]. The removal of the TP male from a social group acts as the behavioral trigger for both sex and role change. Within the first day after TP male removal, the largest IP fish (either male or female) initiates behavioral sex/role change, as evidenced by increased aggression towards other IP fish and courtship directed towards smaller females. Three to four days later the levels of these behaviors exceed those produced by ‘ruling’ TP males, suggesting that focal females are acting overly male in an effort to suppress sex change in other members of the social group. What is so compelling about this transformation is that the sex changing fish are not capable of producing sperm at the time they are expressing a complete repertoire of male sexual behavior, including spawning. This suggests that these fish are using sexual behavior to manipulate the behavior and reproductive potential of other members of the group.

The potential influence of social cues in the regulation of sexual status or role within a social group is not as well understood among species where individuals adopt one of two or more developmental pathways leading to alternative male morphs. Midshipman fish (*Porichthys notatus*) have type I and type II male reproductive morphs [Bass, 1992, 1996]. Type I males build nests under rocky shelters in the

intertidal zone, guard eggs, and court gravid females with a long duration (minutes to hours) call known as a 'hum' [Brantley and Bass, 1994; Bass et al., 1999]. Underwater playback experiments using synthetic signals that mimic natural hums show that the hum functions, in part, as an advertisement call [McKibben and Bass, 1998, 2001a]. On average, type II males are 50% smaller and have a nine-fold larger gonosomatic index than type I males (similar to the IP-TP dimorphism in wrasses) and neither build nests nor guard eggs. Type II males, like IP males, do not court females. Neither type II males nor females produce hums, although they infrequently produce brief duration (~50–150 ms) 'grunts' in non-spawning contexts. Type I males also produce grunts in agonistic contexts, although here too they differ from type II males and females because they produce grunts in long duration trains [Brantley and Bass, 1994; Bass et al., 1999]. Type I males alone also produce 'growls' that are intermediate in their physical attributes between hums and grunts and are also produced in agonistic contexts [Bass et al., 1999]. Developmental studies support the hypothesis that type I males, compared to type II males, show delayed maturity characterized by increased body growth and elaboration of vocal control mechanisms that function in mate attraction (see later section). Type II males, by contrast, exhibit gonadal investment and reproduction beginning at a younger age [Bass et al., 1996].

Much of what we know about social modulation of sexual status/plasticity among species with a pattern of social organization like that of midshipman comes from studies of adult behaviors. Although this would include behaviors such as the attempts of type I males to steal nests from each other or of sneaker and satellite males to steal fertilizations from a type I male, the individual male traits that contribute to the final outcome of such events await definition [Brantley and Bass, 1994]. Fortunately, the social structure of midshipman has a striking resemblance to that of bluegill sunfish [*Lepomis macrochirus*; Gross, 1991; also see Neff, 2001 and references therein]. Studies in sunfish provide important insights into mechanisms that are likely to operate among other species like midshipman that have alternative male morphs. Sunfish have small males that are several years younger than the larger, nest-building and egg-guarding, parental males. Small males can further exhibit two reproductive morphs/tactics that represent sequential life history tactics, namely sneakers that quickly move in and out of nests trying to fertilize the eggs of a spawning pair and larger satellites or female mimics that are closer in size to gravid females and spend more time in a nest with the spawning pair. Thus, bluegills have three male mating tactics [midshipman may also have two size-dependent small

male morphs; see size distribution histogram in Brantley et al., 1993]. Both small male morphs gain access to eggs, although they differ in the amount of time they are in the nest with a spawning pair. Parental males account for about 80% of the egg fertilizations [see Neff, 2001]. Cuckolding males (sneakers and satellites) compete with parentals in about 20% of their mating opportunities, whereas cuckolders are always in competition with parentals [see Fu et al., 2001]. As in midshipman, a transformation of small males to parental males has not been definitively ruled out, although both growth and aging data make it unlikely [Gross, 1982].

Structural-Behavioral Mechanisms

Structural-behavioral mechanisms establish a causal relationship between structural characters and behavioral actions. We have focused many of our studies on the identification of the neuroendocrine correlates of both alternative mating tactics and sex/role change in teleosts. What are the neuroendocrine mechanisms associated with these events which are induced by changes in environmental (social) cues? Gonadotrophin releasing hormone (GnRH) and arginine vasotocin (AVT) are the two neuropeptides that have been most studied in the context of sexual plasticity among teleost fish [Foran and Bass, 1999; also see Hoffmann and Fernald, 2000 for studies of somatostatin in the cichlid *Haplochromis burtoni*]. As summarized in tables 1 and 2, intra- and intersexual dimorphisms in the GnRH and/or AVT brain phenotype have now been identified mainly in the forebrain's preoptic area (POA) and anterior hypothalamus across a number of species [updated from Foran and Bass, 1999]. Our initial investigations of wrasses focused on GnRH-immunoreactivity (ir) in the central nervous system mainly because a number of studies in other vertebrates suggested that GnRH initiated a cascade of events leading to sexual maturation. We first identified intra- and intersexual dimorphisms in the number of GnRH-positive neurons in the POA of wrasses and then showed that gonadal steroids (androgens) could influence the final determination of that number [Grober and Bass, 1991; Grober et al., 1991]. This was an especially important finding given the well established role of steroid hormones, gonadotropins and the POA in determining the temporal onset of sexual maturation of behavior and reproductive systems. The GnRH work was then extended to studies of midshipman fish, showing that the GnRH-POA phenotype is transformed at the time of sexual maturation [Grober et al., 1994]. There are increases in the number and size of GnRH-POA neurons at the time of juvenile-adult transformations for all adult reproductive morphs (number and soma size), consistent with all morphs

Table 1. Sexual dimorphisms of preoptic GnRH neurons in teleost fishes

Species	Male morph(s)	Male life history	Male GSI ⁷	Cell size	Cell No.
Plainfin Midshipman ¹ , <i>Porichthys notatus</i>	type I (territorial/courting) and type II (non-territorial/non-courting) male morphs	permanent, early diverging developmental trajectories	TII > TI	TI > TII and female	none
Swordtails ² , <i>Xiphophorus maculatus</i>	'small' (S) and 'large' (L) male morphs	permanent, early diverging developmental trajectories	S > L	none	S > L
African cichlid ³ , <i>Haplochromis burtoni</i>	conditional/male status, territorial/courting (T) or non-territorial/non-courting (NT)	change in adult status based on social conditions	T > NT	T > NT	none
Bluehead wrasse ⁴ , <i>Thalassoma bifasciatum</i>	protogynous hermaphroditism, terminal phase (TP) and initial phase (IP) males	single, permanent, sex/role change for IP male and females into TP male	IP > TP	none	TP > IP and female
Anemone fish ⁵ , <i>Amphiprion melanopus</i>	protrandrous hermaphrodite, a colony with one reproductive male (R) and several non-reproductive individuals (NR)	permanent, one-time, adult male to female sex change	R > NR	female > R and NR male ⁸	R > NR and female
Ballan wrasse ⁶ , <i>Labrus berggylta</i>	protogynous hermaphroditism, male defends harem of females	permanent, one-time, adult female to male sex change		none ⁹	male > female ¹⁰

¹ Grober et al., 1994; ² Halpern-Sebold et al., 1986; ³ Davis and Fernald, 1990; Francis et al., 1993; ⁴ Grober and Bass, 1991; ⁵ Elofsson et al., 1997; ⁶ Elofsson et al., 1999; ⁷ Gonosomatic index (gonad weight/body weight); ⁸ explained by differences in body size; ⁹ postspawning males > prespawning males and females; ¹⁰ explained by differences in body size among males only; thus, no difference in cell number between males and females of similar body size.

being sexually mature. Together, these studies support the hypothesis that changes in preoptic GnRH expression play a pivotal role in the initiation of sexual maturation or transformation among either juveniles (as shown for midshipman) or adults (as shown for wrasses).

More recently, studies have also implicated a role for the arginine vasopressin (AVP) – oxytocin family of preoptic neuropeptides in mediating the expression of reproductive plasticity among teleosts. The teleost homologues of AVP and oxytocin are arginine vasotocin (AVT) and isotocin respectively. A number of studies, mainly in mammalian species, had implicated the role of AVP in determining the expression of a variety of adult social and reproductive behaviors including both mating and parental care [reviews: Moore, 1992; Insel and Young, 2001; Goodson and Bass, 2001a]. Grober and Sunobe [1996] first investigated possible changes in the size of AVT-immunoreactive (ir) cells in the forebrain preoptic area following single and serial sex change in the marine goby, *Trimma okinawae* (table 2). Females had significantly larger AVT-ir cells than males and the area of these cells was greatest following male to female transformations, whereas female to male transformations resulted in a significantly smaller mean cell size. A subset of individuals that underwent female to male and then back to

female transitions also showed the female-typical AVT-ir phenotype, that is larger cells [also see Reavis and Grober 1999 and table 2 for studies in another goby, *Lythrypnus dalli*].

A recent study of bluehead wrasse demonstrates both sexual status and transformation dependent changes in the AVT-POA phenotype using in situ hybridization to identify cells labeled with a degenerate probe complementary to AVT mRNA [Godwin et al., 2000; table 2]. TP males had significantly more AVT neurons than females, whereas IP males had intermediate values that were not significantly different from either TP males or females; these differences were however dependent on body size allometry. Godwin et al. [2000] also determined the relative abundance of AVT mRNA on the basis of grain counts. As with cell number, AVT mRNA content per neuron was significantly greater in TP males than females. IP males also had two-fold greater levels than females, while sex reversed females showed four-fold the levels of females and resembled TP male values by 2–3 days following removal of TP and IP males from a social unit. Unlike cell number, these differences could not be explained by variation in body size. Almost complete gonadal transformation occurs by 5 days with complete reversal by 7–10 days. The time course of AVT expression

Table 2. Sexual dimorphisms of preoptic AVT neurons in teleost fishes

Species	Male morph(s)	Male life history	Male GSI ⁶	Cell size	Cell No.
Plainfin Midshipman ¹ , <i>Porichthys notatus</i>	type I (territorial/courting) and type II (non-territorial/non-courting) male morphs	permanent, early diverging developmental trajectories	TII > TI	TI and female > TII ⁷	TII number/body mass > TI and female
Saddleback wrasse ² , <i>Thalassoma duperrey</i>	protogynous hermaphroditism, terminal phase (TP) and initial phase (IP) males	single, permanent, sex/role change for IP male and females into TP male	IP > TP	TP > IP and female	TP > IP and female
Bluehead wrasse ³ , <i>Thalassoma bifasciatum</i>	protogynous hermaphroditism, terminal phase (TP) and initial phase (IP) males	single, permanent, sex/role change for IP male and females into TP male	IP > TP	not available ⁸	TP > female ⁷ ; IP = TP, female
Marine goby ⁴ , <i>Trimma okinawae</i>	serial sex change, territorial males	reversible changes, e.g. female to male to female		females > males	not available
Bluebanded goby ⁵ , <i>Lythrypnus dalli</i>	protogynous hermaphroditism	permanent, one-time, adult female to male sex change		males > females	not available

¹ Foran and Bass, 1998; ² Grober, 1998; ³ Godwin et al., 2000; ⁴ Grober and Sunobe, 1996; ⁵ Reavis and Grober, 1999; ⁶ Gonosomatic index; ⁷ explained by differences in body size; ⁸ differences in mRNA abundance in cells; IP and TP > females.

suggests that AVT may be involved in producing early behavioral transformations, prior to changes in gonad structure and androgen synthesis.

While there are species-typical patterns in the divergence of the GnRH and AVT phenotypes either within or between sexes, dimorphisms in the GnRH phenotype are consistently linked to a divergence in gonadal investment and reproductive tactic (table 1). By contrast, the mechanistic significance of divergent AVT phenotypes among teleosts (table 2) remains somewhat more elusive, excepting perhaps for midshipman (see below). Deciphering the significance of such divergence is one of the challenges remaining for workers in this field [see Foran and Bass, 1999 for more discussion of species-typical patterns of variation].

Midshipman, like wrasses, exhibit sex and male morph-specific phenotypes for AVT-ir neurons (number and size) in the POA [Foran and Bass, 1998]. AVT-ir neurons are larger in type I males and females compared to type II males. Differences in AVT cell size among morphs can be explained by divergent body sizes. However, type II males have more AVT-ir neurons per gram body weight compared to type I males (on average almost a six-fold difference). To begin to assess the role of environmental factors on brain patterns of AVT expression, Foran [1998] matched juvenile males according to body size and raised them in flow-through seawater tanks in either sparse or dense populations (density was defined relative to their natural habitat). The results showed that juveniles raised in captivity develop

into one of the two male morphs – the dimorphisms were entirely similar to morph divergence among field caught animals. Pairs of adults of each morph matched for body size also exhibit differences in AVT-ir cell number; thus, animals raised under more dense social conditions consistently had more AVT-ir neurons in the POA.

Functional interpretations of the significance of morph and sex specific differences in neuropeptide phenotypes must rely, in part, upon neurophysiological studies. Towards this goal, Goodson and Bass [2000a, b] have now shown that AVT and isotocin can modulate the patterned output of a male morph and sex-typical behavior, in this case the vocalizations of midshipman fish. Midshipman, as many other sonic fish, produce sound by the contraction of paired skeletal muscles attached to the walls of their swimbladder [review: Bass and Baker, 1991]. These muscles are innervated by ventral occipital nerve roots that are the homologues of the hypoglossal nerve of tetrapods [Bass and Baker, 1997]. Intracellular recording and staining, along with transneuronal biocytin transport, identifies an extensive pacemaker-motoneuron circuit in the caudal hindbrain that establishes the physical attributes of vocalizations such as fundamental frequency and duration [Bass and Baker, 1990; Bass et al., 1994]. A rhythmic, vocal motor volley can be monitored by intracranial recordings from the sonic occipital nerves (fictive vocalization).

Sites of dense AVT-ir in midshipman brain include the POA/anterior hypothalamus (POA-AH) [Goodson and

Bass, 2000a]. Electrical brain stimulation of the POA-AH, as well as a number of other sites, can activate a patterned output from the hindbrain vocal pattern generator. Electrical stimulation in the POA-AH, coupled with pressure injections of AVT or isotocin, showed that fictive vocalization in type I males was either inhibited or facilitated by AVT or AVT antagonists respectively; isotocin had no significant effect. By contrast, isotocin was the active substance in both type II males and females; fictive vocalization was either inhibited or facilitated by isotocin or oxytocin antagonists respectively. Thus, AVT and isotocin are implicated in the short-term modulation of vocal behavior that is differentially expressed among the three reproductive morphs [Goodson and Bass, 2000b]. Other studies show that AVT's action is site specific. Thus, AVT influences the initiation rather than patterning of calls in a midbrain vocal center [Goodson and Bass, 2000a].

Given the sensitivity of AVT neuronal phenotypes to the influences of circulating sex steroids [see Goodson and Bass, 2001a, for recent review], we expect that short term changes in AVT/isotocin modulation of vocal motor behavior will in turn be influenced by an individual's hormonal profile. Knapp et al. [1999] showed that circulating levels of gonadal steroids vary among type I males depending on their parental care status. Thus, plasma levels of the potent teleost androgen 11-ketotestosterone were highest among males in nests either without any eggs or with only recently fertilized eggs compared to males in nests containing mostly hatched embryos [Knapp et al., 1999; also see Brantley et al., 1993 for a comparative survey of androgen levels among teleosts with alternative tactics, including midshipman]. Only about half of the males in the 'no eggs' or 'eggs only' groups had detectable levels of testosterone, whereas no males in the 'embryos' group had detectable levels. Type I males guard eggs in their nest while continuing to acoustically court females on successive nights [Brantley and Bass, 1994]. However, as type I males begin to invest in parental care, we expect an increase in the production of agonistic grunt trains that are displayed when a type I male is defending his nest against an intruder male [Brantley and Bass, 1994]. Shifting levels of androgens throughout the breeding season might, in turn, lead to changes in AVT/IT profiles that influence calling phenotypes linked to courtship versus paternal care and nest defense.

Summary

In summary then, studies of adult reproductive morphs in both midshipman and wrasses show that:

- (1) Divergent male phenotypes (type I and II males, TP and IP males) represent either non-sequential, mutually exclusive growth patterns (midshipman) or sequential life history stages (wrasse).
- (2) Divergent reproductive tactics among sexually mature males are paralleled by alternative phenotypes for neurons within the neuroendocrine axis, e.g. GnRH or AVT neurons of the preoptic area.
- (3) Divergent reproductive tactics among sexually mature males are paralleled by alternative phenotypes for neurons that can determine tactic-specific display behaviors, e.g. vocal behaviors among midshipman.
- (4) Reproductive maturation is not obligatorily linked to the expression of neuronal, in this case vocal and neurochemical (AVT and isotocin), secondary sex characteristics: sexual maturation of type II or IP males may not involve the expression of type I or TP male-specific traits.
- (5) Although type II male and female midshipman, like IP male and female wrasses, have morph-specific spawning tactics, they are convergent in a number of traits. Among midshipman, this includes vocal motor phenotype, neurochemical phenotypes (GnRH; isotocin modulation of vocal pattern generator), circulating levels of sex steroids (testosterone), large investment in gonad, absence of parental care behaviors, and dependence on type I males for nest construction. Among wrasses, this includes neurochemical phenotypes (GnRH and AVT), large investment in gonad, and absence of territoriality.

Future Challenges

Ultimately, the performance of an existing behavioral phenotype is dependent on the interactions between different classes of mechanisms (i.e. behavioral – ecological, structural – behavioral, ecological – structural). One of the more daunting challenges facing us is to specify how these mechanisms do indeed lead to context-dependent, behavioral expression. The pursuit of such research programs demands a multidisciplinary, neuroethological approach where neural and hormonal mechanisms are specifically linked to social modulation of naturally selected behaviors.

Recent studies have begun to make significant headway in this endeavor. Social modulation of neuropeptide and hormonal mechanisms hold great promise in this regard. The AVT studies in wrasses and other species, while still correlational, are one case in point. What is necessary here

is to identify one or more relevant stimuli that lead to sex or role change and then delineate the neural pathway(s) mediating that signal, and its linkage to changes in either AVT containing neurons and or receptors. As for midshipman, the demonstration of such mechanistic linkages are closer at hand. Hence, the detection of conspecific vocalizations should first lead to central encoding of relevant behavioral parameters at identified sites in the brain [e.g. Bass et al., 2000; Bodnar and Bass, 2001; McKibben and Bass, 2001b]. This, in turn, should lead to an interface between the central

auditory system and both the vocal and neuroendocrine (in this case, AVT) axes of the brain [Bass et al., 1994, 2000; Goodson and Bass, 2000b, 2001b], and the subsequent production of an appropriate context-dependent, morph-typical behavioral response.

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