

# Social induction of maturation and sex determination in a coral reef fish

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Labile maturation and sex determination should be advantageous where the probability of finding a mating partner is unpredictable. Here we tested the hypothesis that the presence of a potential mating partner induces maturation and sex determination in a coral-dwelling fish, *Gobiodon erythrosphilus*. In natural populations at Lizard Island (Great Barrier Reef), single individuals were less likely to be mature than paired individuals and they matured at a larger size, indicating plasticity in the timing of maturation. By manipulating group structure we demonstrated that both the timing of maturation and the sex of maturing individuals are socially controlled. Single juveniles did not mature, but maturation was rapidly induced by the presence of an adult partner. In addition, sex determination was found to be labile, with juveniles maturing into the opposite sex of the partner encountered. To our knowledge, this is the first experimental demonstration of social induction of maturation in conjunction with labile sex determination at maturation in vertebrates. This flexibility enables individuals to maximize their reproductive success in an environment where the timing of mate acquisition and the sex of their future partner are unpredictable.

**Keywords:** environmental sex determination; maturation; social conditions; phenotypic plasticity

## 1. INTRODUCTION

In most vertebrates, sex is genetically determined and maturation occurs according to a relatively fixed schedule. In many fishes, however, patterns of sexual development are highly flexible and can be influenced by local environmental conditions (Francis 1992; Devlin & Nagahama 2002). Flexible sexual development is particularly common in coral reef fishes, and many evolutionary ecologists have focused on this group to examine the adaptive significance of this plasticity (Warner 1975; St Mary 1997). Sex change (sequential hermaphroditism) is the most prevalent form of flexible sexual development in coral reef fishes and is usually mediated by local social conditions (Robertson 1972; Warner *et al.* 1975; Fricke & Fricke 1977; Ross 1990). Local social conditions have also been shown to influence the timing of maturation in some reef fishes (Fricke & Fricke 1977; Jones & McCormick 2002) and have been implicated in sex determination of others (Ochi 1989a; Hattori & Yanagisawa 1991; Kuwamura *et al.* 1994). However, few investigators have considered whether maturation and sex determination can be intimately linked. Decisions about when to mature, which sex to be and when to change sex may be influenced by the same local environmental conditions, and should not be considered in isolation.

The timing of maturation in species with flexible life histories can potentially be influenced by social interactions that may either suppress (delay) or induce (advance) reproductive development (Hofmann *et al.* 1999). Suppression of maturation is well known in fishes, particularly where juveniles cohabit with adults in discrete social groups (Fricke & Fricke 1977; Jones 1987). In these circumstances,

behavioural dominance by larger adult fishes can regulate the reproductive development of subordinate juveniles (Fricke & Fricke 1977; Sohn 1977; Borowsky 1978; Jones & Thompson 1980). Much less is known about the social conditions that may induce maturation. In many philopatric mammals, juveniles that leave their parents can accelerate maturation upon receiving stimulatory primers produced by an adult of the opposite sex (Bronson 1989). Whether such mechanisms occur in fish has not been determined.

The sex of an individual at maturation can be either genetically or environmentally controlled. Charnov & Bull (1977) predicted that sex should be environmentally determined when offspring enter an unpredictable, patchy environment where different sexes are favoured on different patches. Environmental sex determination (ESD) could occur early in juvenile ontogeny, or later when juveniles approach reproductive maturity and can more reliably assess the conditions likely to be experienced as an adult. Environmental conditions (pH, temperature, social conditions) have been shown to influence the juvenile sex of some freshwater fishes (Heiligenberg 1965; Rubin 1985; Francis & Barlow 1993; Devlin & Nagahama 2002) and temperature has been shown to determine sex in a small number of temperate marine fishes (Conover & Kynard 1981; Devlin & Nagahama 2002; Godwin *et al.* 2003). However, in general, ESD at or before maturation has not been well described in marine fishes. If sex determination is flexible and the adult environment unpredictable, individuals should delay choosing which sex to be until they are about to mature (Jones 1980).

The aim of this study was to test the hypothesis that the presence of a suitable sexual partner induces maturation and controls sex determination in the obligate coral-dwelling goby, *Gobiodon erythrosphilus*. Coral colonies inhabited by *G. erythrosphilus* form discrete patches of

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habitat that provide the gobies with shelter and sites for reproduction. The social structure of *G. erythrospilus* consists primarily of breeding pairs occupying large corals and single juveniles inhabiting smaller corals (Munday *et al.* 1998). Coral colonies are a limited resource (Munday *et al.* 2001) and only corals above a certain size can support a breeding pair (Hobbs & Munday 2004). Adults are capable of changing sex in either direction (bi-directional sex change) enabling any adult to form a breeding pair with any other individual (Munday *et al.* 1998). This flexibility is believed to be advantageous because of the low density of available mates and the risk of predation associated with searching for a breeding partner (Munday 2002).

For a juvenile to reproduce it must first find a single partner occupying a coral colony large enough to support a breeding pair. However, there are few opportunities for this, as most coral colonies large enough to support a breeding pair are already occupied by an adult pair (Munday *et al.* 1998; Hobbs & Munday 2004). Consequently, the timing of pair formation and the sex of the future partner are likely to be unpredictable. If so, it would be advantageous for a juvenile to remain immature until another single individual is located in a suitably sized coral and then mature into the sex opposite to that of the prospective partner.

To determine if *G. erythrospilus* exhibits plasticity in timing of maturation, and whether this timing is influenced by social conditions, we used a combination of field observations and manipulative experiments. If juvenile *G. erythrospilus* can delay maturity until a partner is encountered we predicted that single fish would mature at larger sizes than paired fish. To investigate this, we first examined the reproductive state of single and paired fish from a range of sizes in the natural population. We then used a manipulative field experiment to test for induction of maturation in the presence of a prospective adult partner. We predicted that single juveniles would remain immature, but that juveniles placed with a single adult would mature. Finally, we tested for flexibility in sex determination at maturation. If the sex at maturation was determined by social conditions, we predicted that a juvenile placed with an adult male would mature as a female, whereas a juvenile placed with an adult female would mature as a male.

## 2. MATERIAL AND METHODS

To determine if the social environment influences the timing of maturation in *G. erythrospilus*, we examined size and maturity in 54 single and 96 paired *G. erythrospilus* from a natural population. Single and paired fish were collected randomly from colonies of *Acropora nasuta* on six reefs within the lagoon of Lizard Island (Great Barrier Reef: 14°40' S, 145°28' E). Fish were anaesthetized using clove oil (Munday & Wilson 1997), removed from their coral colony and measured (total length (TL) to the nearest 0.1 mm), and fixed in 4% formaldehyde, 5% acetic acid, 1.3% calcium chloride (FAACC) in preparation for histological analysis of the gonads. The maturity status of all fish was determined on the basis of the most advanced stage of germ cell development in the gonad. Females with gonads containing vitellogenic oocytes were classified as mature and males with gonads containing spermatozoa were considered mature (West 1990; Cole & Hoese 2001). Immature fish lacked these advanced stages of germ cell

development. The proportions of mature and immature fish in each size class were compared among single and paired fish to determine if there was plasticity in the timing of maturation.

To test whether the presence of a potential mating partner induces maturation and determines the sex adopted, we conducted a manipulative field experiment. Juveniles were placed on coral colonies, either by themselves or paired with an adult female or an adult male. If maturation is induced by the presence of an adult, we expected that single juveniles would remain immature, whereas those in the presence of an adult would mature. In addition, if the sexual identity of the potential mating partner determines the sex adopted by the maturing individual, we predicted that a juvenile would mature into a male in the presence of an adult female and a female in the presence of an adult male.

To establish the experiment, fish were collected randomly from reefs around Lizard Island, anaesthetized, tagged with visible implant fluorescent elastomer (VIFE tags: Northwest Technologies) and sex and maturity determined by the shape of the genital papillae (Munday *et al.* 1998; Munday 2002). The genital papilla of juveniles is distinctively small, translucent and undeveloped, whereas the papilla of adult females is typically short and square, with fimbriate edges, and the papilla of adult males is larger, elongated and conical in shape. Histological examination of the gonads from 30 juveniles, 30 adult females and 30 adult males confirmed that the genital papillae could be used to accurately identify sex and maturity of *G. erythrospilus*.

Juvenile *G. erythrospilus* were placed on isolated coral colonies alone ( $n = 43$ ), with an adult female ( $n = 28$ ), or with an adult male ( $n = 24$ ). *G. erythrospilus* are known to mature between 25 and 35 mm TL (Munday *et al.* 1998) and fish in this size range, exhibiting an immature-shaped genital papilla, were used because they were likely to be physiologically capable of maturing. Adults were between 35 and 45 mm TL with distinct male- or female-shaped genital papillae. Juveniles placed singly or with an adult did not differ in size ( $t = 1.29$ , d.f. 17,  $p = 0.214$ ), thereby eliminating the possibility that juvenile size, rather than its social conditions, determined patterns of maturity. Gobies were transplanted to suitably sized coral colonies that had been cleared of other resident gobies and invertebrates. Single juveniles, and juveniles partnered with adults, were placed on similar sized corals (range: 14.6–19.5 cm mean diameter) to ensure that coral size did not influence maturation ( $t = 0.70$ , d.f. 11,  $p = 0.49$ ).

All fish remaining in the corals were re-collected after 6 weeks, killed with clove oil anaesthetic, and fixed in FAACC. The gonads of all fish were removed, embedded in paraffin wax and serially sectioned at 5  $\mu$ m, stained with Mayer's alum haematoxylin and Young's eosin–erythrosin and inspected under a light microscope. Maturity and sex were assigned on the basis of the most advanced gamete stage present. A  $\chi^2$ -test of independence was used to compare the number of juveniles that matured versus the number that remained immature in single fish and those paired with an adult. Only those juveniles that remained in the original experimental social conditions (i.e. remained single or remained with the tagged adult) were included in the statistical analysis.

## 3. RESULTS

The reproductive status of *G. erythrospilus* collected from natural populations indicated considerable plasticity in the size at maturity. The smallest mature individual was 25.2 mm TL, and the largest immature individual was 44 mm TL. Therefore, maturation occurred over a 19 mm size range (38% of the total body size range).

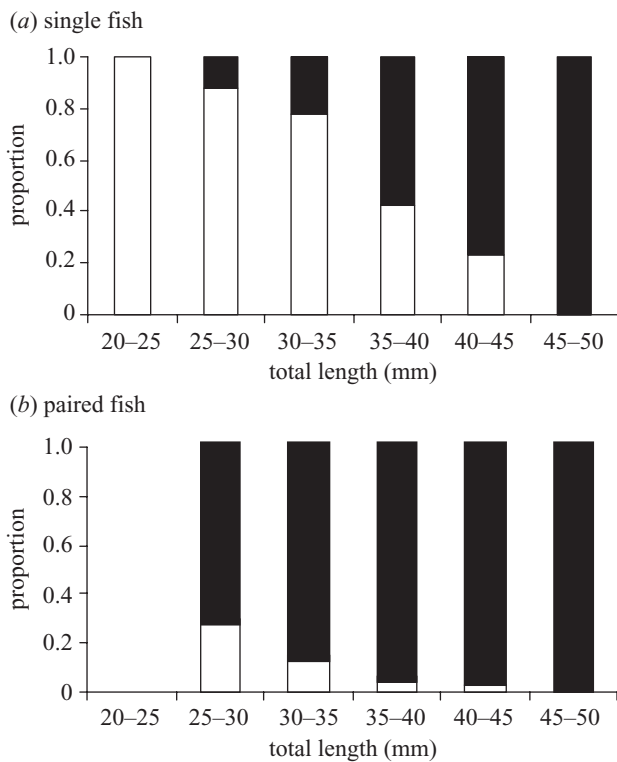


Figure 1. The proportion of immature (□) and mature (■) individuals in each size class for (a) single ( $n = 54$ ) and (b) paired ( $n = 96$ ) *Gobiodon erythrospilus*.

Paired fish were more likely to be mature and they matured at a smaller size than solitary individuals (figure 1). The vast majority (91%,  $n = 96$ ) of paired fish were mature, whereas only 52% ( $n = 54$ ) of single fish were mature ( $\chi^2 = 31.25$ , d.f. 1,  $p < 0.001$ ). Most of the paired individuals in the smaller size classes were mature, while most singles in the same size classes were immature (figure 1). The proportion of single fish that were mature increased with body size (figure 1). The social history of these fish before collection was not known; therefore, some of the mature individuals in the single population may have recently separated from a partner, whereas some immature paired fish may have only recently encountered a partner. Approximately 80% of immature singles were females, with the remainder having bisexual gonads. There were only eight immature individuals in pairs and all of these were female.

Experimental manipulation confirmed that maturation is induced when a juvenile comes in contact with a single adult. All nine juveniles that stayed single were still immature at the end of the experiment (figure 2 and figure 3*a,b*). Eight of these were immature females and one was an immature bisexual at the end of the experiment. By contrast, 21 out of 22 juveniles placed with an adult had matured by the end of the experiment ( $\chi^2 = 22.44$ , d.f. 1,  $p < 0.001$ ; figure 2). Growth of single juveniles (mean increase in TL over 42 days:  $5.3 \text{ mm} \pm 2.4 \text{ s.d.}$ ) was slightly greater than for juveniles placed in pairs (mean increase in TL over 42 days:  $4.6 \text{ mm} \pm 2.0 \text{ s.d.}$ ), but this trend was not statistically significant (ANOVA:  $F = 0.8$ , d.f. 29,  $p = 0.4$ ).

There was clear ESD at maturation, with juveniles maturing into the sex opposite to that of the adult partner. In 12 cases a juvenile remained paired with an adult male

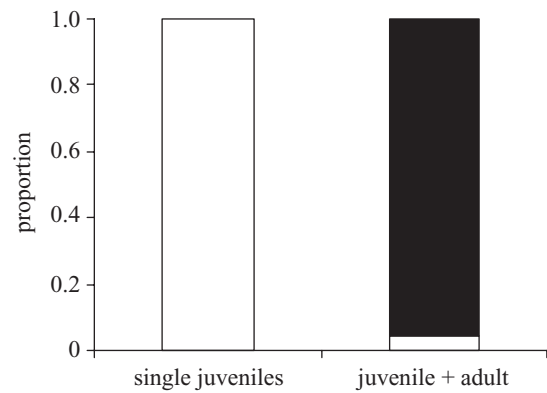


Figure 2. The proportion of juvenile *Gobiodon erythrospilus* that remained immature (□) or matured (■) when placed on corals singly ( $n = 9$ ) or paired with an adult ( $n = 22$ ) for 42 days.

and in 11 of these cases the juvenile matured into an adult female (figure 3*c* and figure 4*a*). In the one other case the juvenile remained an immature female. In 10 cases a juvenile remained paired with an adult female and in six of these cases the juvenile developed into an adult male (figure 3*d* and figure 4*b*). In the other four cases the adult female changed sex to an adult male and the juvenile matured into an adult female. Therefore, in all but one instance, the juveniles matured into the sex opposite to that of the adult.

#### 4. DISCUSSION

Juvenile *G. erythrospilus* exhibited a high level of plasticity in the timing of maturation and patterns of sex determination in response to social conditions. Experimental manipulations demonstrated that contact with a potential mating partner determines both the timing of maturation and the sex of a maturing individual. Social suppression of maturation is well known in coral reef fish, but this is the first experimental demonstration that social stimulation can also induce maturation in reef fishes.

The contrast between previous reports of suppression of maturation in reef fishes and induction of maturation in *G. erythrospilus* may be related to differences in the social conditions of juveniles. In site-attached species where juveniles occur in the same social groups as adults, the timing of maturation is often socially determined and dependent on an individual's size relative to others in the social group (Fricke & Fricke 1977; Fricke 1979; Kuwamura *et al.* 1994; Buston 2003). In these species, juvenile maturation is usually suppressed by the aggressive behaviour of larger adults in the social group. For example, in anemonefishes maturity occurs only when an individual becomes the largest or second largest in a social group, either through the disappearance of a larger individual or through migration into another social group (Fricke 1979; Ochi 1989*a,b*). In contrast, juveniles of *G. erythrospilus* rarely occur in the same social groups as adults. Juveniles occur singly in small coral colonies and in order to reproduce they must move to find a breeding partner. Induction of maturation would be advantageous under these conditions because it would facilitate continued somatic growth while the juvenile was still single, thus providing benefits to future reproductive success through the size–fecundity relationship. We detected a slightly faster growth rate in single juveniles compared

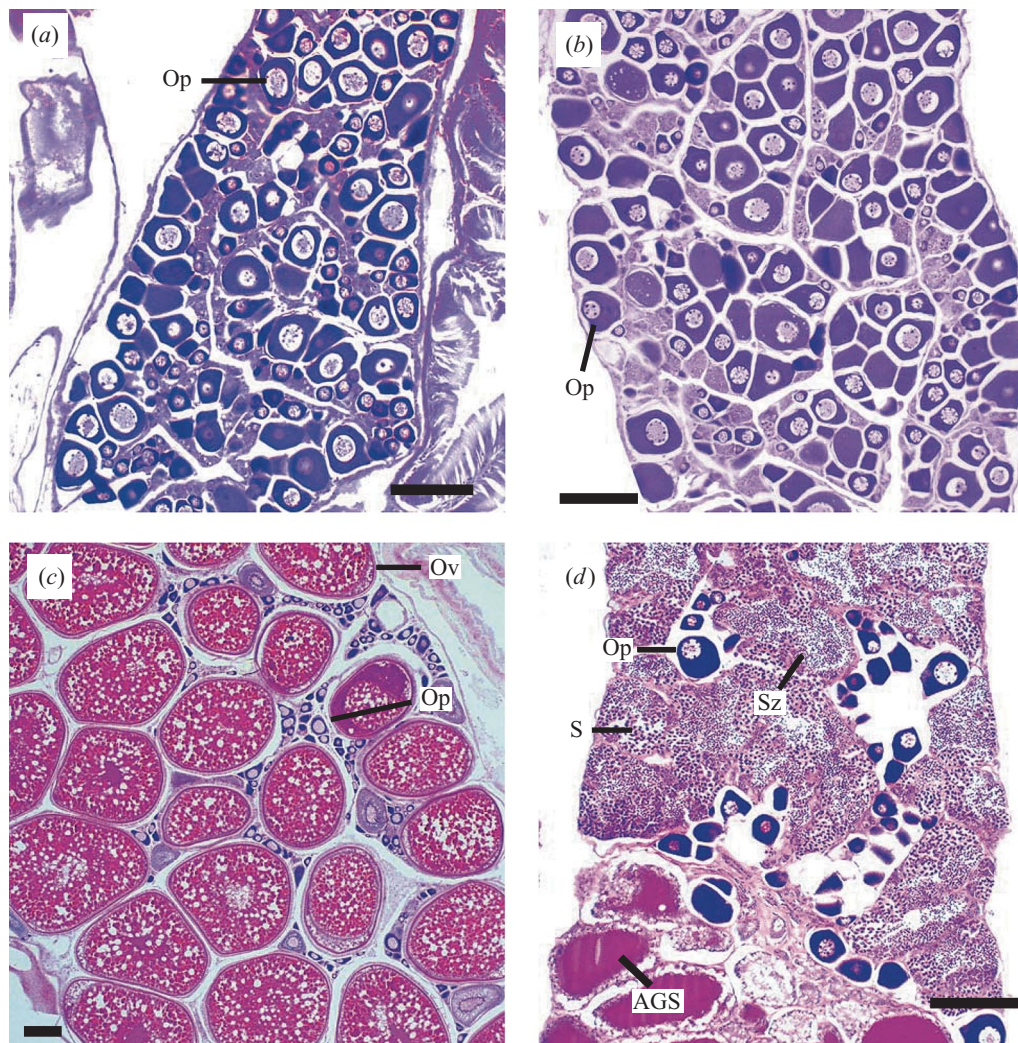


Figure 3. Longitudinal sections of gonads from: (a) a typical juvenile before experimental manipulation (immature female); (b) a juvenile that had remained single for 42 days (immature female); (c) a juvenile paired with an adult male for 42 days (juvenile became a mature female); (d) a juvenile paired with an adult female for 42 days (juvenile became a mature male). Op = previtellogenic oocytes, Ov = vitellogenic oocyte, S = spermatoocytes, Sz = spermatozoa, AGS = accessory gonad structure. Scale bar, 0.1 mm.

with juveniles placed in pairs, which would support this hypothesis, but the trend was not statistically significant, probably because the experiment was not conducted over a time period long enough to achieve a significant difference in body size. Investing energy into growth while single would be particularly advantageous in pair-forming gobies, because reproductive success of a breeding pair depends on the body size of both partners (Kuwamura *et al.* 1993). Further work is required to establish whether induction of maturation is characteristic of social organizations in which juveniles inhabit different habitats from adults.

Environmental sex determination is predicted when offspring are dispersed into unpredictable patchy environments and different patches confer advantages on different sexes (Charnov & Bull 1977). Multiple pathways of juvenile sexual development have been described in many reef fishes (Robertson & Warner 1978; Jones 1980; Cole & Robertson 1988; Ochi 1989*a,b*; Hattori 1991; Sadovy & Colin 1995); however, the mechanisms responsible for these multiple pathways have rarely been elucidated. This study demonstrated that the immediate social environment is responsible for determining the sex of maturing

individuals. Juveniles matured into the sex opposite to that of the partnering adult, even when the adult had changed sex. Similar mechanisms are likely to operate in other species of reef fishes, particularly highly site-attached species, such as anemonefishes (Ochi 1989*a,b*; Hattori & Yanagisawa 1991), other coral-dwelling gobies (Kuwamura *et al.* 1994; Nakashima *et al.* 1995) and possibly some damselfishes (Cole 2002).

Labile sex determination at maturation would be advantageous for *G. erythrospilus* because breeding opportunities are limited and unpredictable. These limitations result from the high saturation of suitable host corals (Munday 2002) and the unpredictable nature of adult mortality. Just as bi-directional sex change in adult *G. erythrospilus* enables mature individuals to mate with any other individual encountered (Munday *et al.* 1998), flexibility in sex determination enables a juvenile to form a breeding pair with any partner encountered. In addition, flexibility in sex determination enables maturation to be induced by the presence of an adult of either sex, unlike other vertebrates where induction of maturation occurs only in the presence of an adult of the opposite sex (Bronson 1989).

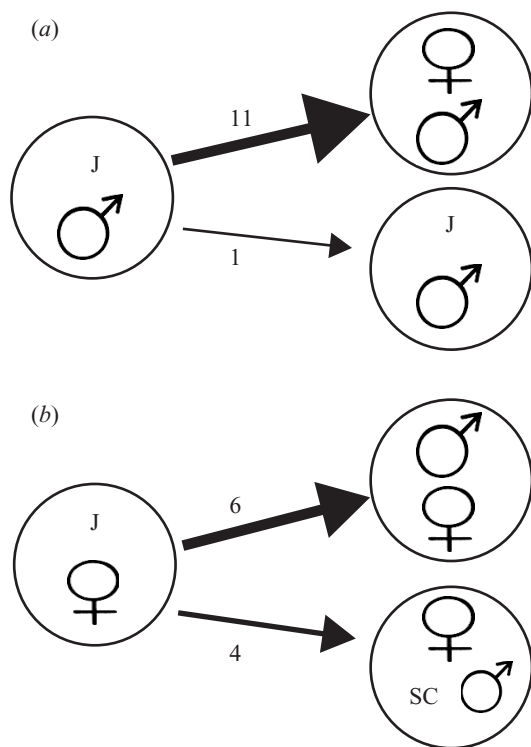


Figure 4. Sexual development of juveniles when placed with: (a) an adult male; (b) an adult female. Numerals and arrow thickness indicate the number of juveniles that progressed along a particular pathway of sexual development. The sexual status of juveniles is represented by the uppermost symbol within each circle. J, juvenile; SC, adult sex change from female to male.

This study demonstrated that maturation and sex determination are extremely flexible in *G. erythrosphilus*. Plasticity in the timing of maturation allows single juveniles to remain immature and this may result in an increased allocation of energy into growth until a partner is obtained. The presence of an adult induces maturation, and labile sex determination enables a juvenile to form a breeding pair with any adult encountered. Flexibility in juvenile sexual development appears to be advantageous because it provides a means of rapidly responding to breeding opportunities when they arise. We predict that flexibility in the sexual development of juveniles in response to variable social conditions is widespread in reef fish and it requires further investigation.

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## REFERENCES

- Borowsky, R. 1978 Social inhibition of maturation in natural populations of *Xiphophorus variatus* (Pisces: Poeciliidae). *Science* **201**, 933–935.
- Bronson, F. H. 1989 *Mammalian reproductive biology*. University of Chicago Press.
- Buston, P. 2003 Social hierarchies: size and growth modification in clownfish. *Nature* **424**, 145–146.
- Charnov, E. L. & Bull, J. 1977 When is sex environmentally determined? *Nature* **266**, 828–830.
- Cole, K. S. 2002 Gonad morphology, sexual development, and colony composition in the obligate coral-dwelling damselfish *Dascyllus aruanus*. *Mar. Biol.* **140**, 151–163.
- Cole, K. S. & Hoese, D. F. 2001 Gonad morphology, colony demography and evidence for hermaphroditism in *Gobiodon okinawae* (Teleostei, Gobiidae). *Environ. Biol. Fish.* **61**, 161–173.
- Cole, K. S. & Robertson, R. D. 1988 Protogyny in the Caribbean reef goby, *Coryphopterus personatus*: gonad ontogeny and social influences on sex-change. *Bull. Mar. Sci.* **42**, 317–333.
- Conover, D. O. & Kynard, B. E. 1981 Environmental sex determination: interaction of temperature and genotype in a fish. *Science* **213**, 577–579.
- Devlin, R. H. & Nagahama, Y. 2002 Sex determination and sex differentiation in fish: an overview of genetic, physiological and environmental influences. *Aquaculture* **208**, 191–304.
- Francis, R. C. 1992 Sexual lability in teleosts: developmental factors. *Q. Rev. Biol.* **67**, 1–18.
- Francis, R. C. & Barlow, G. W. 1993 Social control of primary sex differentiation in the Midas Cichlid. *Proc. Natl Acad. Sci. USA* **90**, 10 673–10 675.
- Fricke, H. W. 1979 Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos*. *Z. Tierpsychol.* **50**, 313–326.
- Fricke, H. W. & Fricke, S. 1977 Monogamy and sex change by aggressive dominance in a coral reef fish. *Nature* **266**, 830–832.
- Godwin, J., Luckenbach, J. A. & Borski, R. J. 2003 Ecology meets endocrinology: environmental sex determination in fishes. *Evol. Dev.* **5**, 40–49.
- Hattori, A. 1991 Socially controlled growth and size-dependent sex change in the anemonefish, *Amphiprion frenatus* in Okinawa, Japan. *Jpn. J. Ichthyol.* **38**, 165–177.
- Hattori, A. & Yanagisawa, Y. 1991 Life history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. *Environ. Biol. Fish.* **31**, 139–155.
- Heiligenberg, W. 1965 Colour polymorphism in the males of an African Cichlid fish. *J. Zool.* **146**, 95–97.
- Hobbs, J.-P. A. & Munday, P. L. 2004 Intraspecific competition controls spatial distribution and social organisation of the coral-dwelling goby *Gobiodon histrio*. *Mar. Ecol. Prog. Ser.* **278**, 253–259.
- Hofmann, H. A., Benson, M. E. & Fernald, R. D. 1999 Social status regulates growth rate: Consequences for life-history strategies. *Proc. Natl Acad. Sci. USA* **96**, 14 171–14 176.
- Jones, G. P. 1980 Growth and reproduction in the protogynous hermaphrodite *Pseudolabrus celidotus* (Pisces: Labridae) in New Zealand. *Copeia* **1980**, 660–675.
- Jones, G. P. 1987 Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* **68**, 1534–1547.
- Jones, G. P. & McCormick, M. I. 2002 Interaction between energetic and numerical processes in the ecology of coral reef fish populations. In *Coral reef fishes. Dynamics and diversity in a complex ecosystem* (ed. P. Sale), pp. 221–238. San Diego: Academic Press.
- Jones, G. P. & Thompson, S. M. 1980 Social inhibition of maturation in females of the temperate wrasse *Pseudolabrus celidotus* and a comparison with the blennioid *Tripterygion varium*. *Mar. Biol.* **59**, 247–256.
- Kuwamura, T., Yogo, Y. & Nakashima, Y. 1993 Size-assortive monogamy and paternal egg care in a coral goby *Paragobiodon echinocephalus*. *Ethology* **95**, 65–75.
- Kuwamura, T., Nakashima, Y. & Yogo, Y. 1994 Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. *Behav. Ecol.* **5**, 434–438.

- Munday, P. L. 2002 Does habitat availability determine geographical-scale abundances of coral-dwelling fishes? *Coral Reefs* **21**, 105–116.
- Munday, P. L. & Wilson, S. K. 1997 Comparative efficacy of clove oil and other chemicals in the anaesthetisation of *Pomacentrus amboinensis*, a coral reef fish. *J. Fish Biol.* **51**, 931–938.
- Munday, P. L., Caley, M. J. & Jones, G. P. 1998 Bi-directional sex change in a coral-dwelling goby. *Behav. Ecol. Sociobiol.* **43**, 371–377.
- Munday, P. L., Jones, G. P. & Caley, M. J. 2001 Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology* **82**, 2177–2189.
- Nakashima, Y., Kuwamura, T. & Yogo, Y. 1995 Why be a both-ways sex changer? *Ethology* **101**, 301–307.
- Ochi, H. 1989a Acquisition of breeding space by nonbreeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. *Ethology* **89**, 279–294.
- Ochi, H. 1989b Mating behaviour and sex change of the anemonefish, *Amphiprion clarkii*, in the temperate waters of southern Japan. *Environ. Biol. Fish.* **26**, 257–275.
- Robertson, D. R. 1972 Social control of sex-reversal in a coral-reef fish. *Science* **177**, 1007–1009.
- Robertson, R. D. & Warner, R. R. 1978 Sexual patterns in the Labroid fishes of the Western Caribbean, II: The parrotfishes (Scaridae). *Smithson. Contrib. Zool.* **255**, 1–26.
- Ross, R. M. 1990 The evolution of sex-change mechanism in fishes. *Environ. Biol. Fish.* **29**, 81–93.
- Rubin, D. A. 1985 Effect of pH on sex ratio in cichlids and a poeciliid (Teleostei). *Copeia* **1985**, 233–235.
- Sadovy, Y. & Colin, P. L. 1995 Sexual development and sexuality in the Nassau grouper. *Environ. Biol. Fish.* **46**, 961–976.
- Sohn, J. J. 1977 Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. *Science* **195**, 199–201.
- St Mary, C. 1997 Sequential patterns of sex allocation in simultaneous hermaphrodites: do we need models that specifically incorporate this complexity? *Am. Nat.* **150**, 73–97.
- Warner, R. R. 1975 The adaptive significance of sequential hermaphroditism in animals. *Am. Nat.* **109**, 61–82.
- Warner, R. R., Robertson, R. D. & Leigh, E. G. Jr 1975 Sex change and sexual selection. *Science* **193**, 633–638.
- West, G. 1990 Methods of assessing ovarian development in fishes: a review. *Mar. Freshwat. Res.* **41**, 122–199.