



SYMPOSIUM

Phylogenetic Patterns and Phenotypic Plasticity of Molluscan Sexual Systems

Rachel Collin¹

Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Republic of Panama

From the symposium “Phenotypic Plasticity and the Evolution of Gender” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2013 at San Francisco, California.

¹E-mail: collinr@si.edu

Synopsis Molluscs show a wide diversity of sexual systems and strategies. There are both gastropod and bivalve families that are each primarily dioecious, simultaneous hermaphrodites, or sequential hermaphrodites, and other families in which almost every sexual strategy occurs. The multiple evolutionary transitions of sexual systems within molluscs would allow comparative analyses of the associated ecological factors, but data on all but a few groups are too sparse to draw many solid conclusions. The phylogenetic distribution of sexual systems in the Mollusca shows that gastropods and bivalves demonstrate different patterns, possibly associated with the presence/absence of copulation. The distribution of change of sex suggests that, in gastropods, sequential hermaphrodites do not evolve from simultaneous hermaphrodites, and that sex reversal (flip-flopping) occurs in free-spawners but not in copulators. Three well-studied protandrous gastropod groups (calyptraeids, coralliophilids, and patellogastropods) show similar responses to environmental conditions and associations with conspecifics. They all have the following attributes: (1) they are sedentary, (2) they live in groups, patches, or aggregates, and (3) size at sex change varies among sites and among aggregates. In addition the available experimental evidence suggests that (4) the presence of females or large individuals represses growth and sex change of males, and (5) behavior seems to mediate the repressive influence of large females. Available data from other species tend to support these patterns. Finally, the repression of growth of males by females in protandry likely facilitates the evolution of dwarf males.

“The molluscs are a large and diverse group including more known sex-changers than any other except perhaps the fishes. In this group especially the terminology is confusing, as are some of the life cycles.”

David Policansky (1982)

Introduction

Sex and sex allocation in animals are often divided into two general categories. Species are either dioecious, made up of individuals of separate sexes (males and females), or hermaphrodites in which each individual acts both as male and female sometime during its lifespan. Hermaphrodites are often further categorized as simultaneous hermaphrodites in which animals function both as males and females

at the same time, or as sequential hermaphrodites, in which animals change from one sex to the other. Finally hermaphroditic animals can produce both male and female gametes from a single gonad or like some lepetelloidean gastropods they can possess a separate testis and ovary, each with their own ducts (Ponder and Lindberg 1997). By categorizing sexual systems in this way we emphasize that sequential and simultaneous hermaphroditism are more similar and more closely related to each other than they are to dioecy. Of course, after closer investigation, nothing in biology is easily and neatly categorized, and the same is true of sex allocation. Almost every possible combination of strategies occurs among marine invertebrates, and molluscs are no exception (Coe 1943, 1944). Molluscan sexual systems include

dioecy, protandrous sex change (male first), simultaneous hermaphroditism, sex reversal (flip-flopping), and species that are comprised of a mix of individuals displaying more than one of these strategies (Coe 1943, 1944; Ghiselin 1969; Policansky 1982; Wright 1988; Heller 1993).

The rampant diversity of molluscan sexual systems can be understood in several different ways. The phylogenetic distribution of sexual systems suggests that they are subject to different phylogenetic, constructional, or adaptive constraints in particular clades. This results in some clades that show no variation and others that encompass wide diversity. Such patterns are well known from other metazoan phyla (e.g., barnacles: Yusa et al. 2013, this issue; fishes: Erisman et al. 2013, this issue). The phylogenetic distribution of sexual systems in molluscs can be used to gain insight into the ecological and morphological factors that constrain or promote the diversity of sexual systems.

Optimality theory has also been used to predict the conditions under which different sexual systems will be favored and to explain the relative effort expended on male and female functions (Charnov 1982). This approach focuses on the roles of phenotypic plasticity and intraspecific variation in male and female functions in hermaphrodites. By predicting the optimal timing of sex change in sequential hermaphrodites, and the timing and relative allocation to each sex in simultaneous hermaphrodites, this approach emphasizes the continuity between simultaneous and sequential hermaphroditism (Leonard 2013, this issue).

Here I aim to show how both approaches can lead to insights or suggest fruitful areas for future study of molluscan sexual systems. I briefly outline the phylogenetic distribution of sexual systems in the Mollusca in general, followed by some ideas generated by these patterns. I describe three well-studied protandrous gastropod groups and summarize what we know about the role of phenotypic plasticity. Finally, I discuss how the mechanisms and plasticity in regularly protandrous gastropods could be taken to an extreme to produce dwarf males both in gastropods and in bivalves.

Phylogenetic patterns

Is dioecy ancestral in the Mollusca?

It seems likely that dioecy is the ancestral condition in the Mollusca (Fig. 1). Dioecy is the most common sexual system among extant species and occurs in seven of the eight extant classes. Solenogastres appear to be exclusively simultaneous

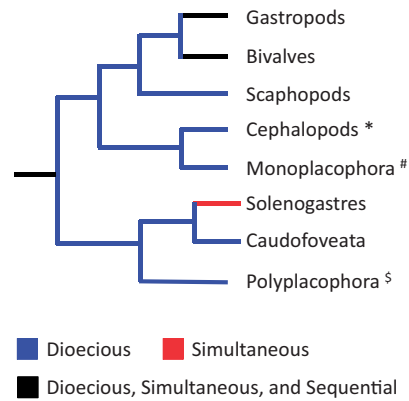


Fig. 1 The distribution of sexual systems in the Mollusca. Phylogeny from Kocot et al. (2011) and Smith et al. (2011). *One known case of sequential. #One known case of simultaneous. §One genus with some simultaneous hermaphrodites. Data from Eernisse (1988); Lamprell and Scheltema (2001); Haszprunar and Schaefer (1996).

hermaphrodites, but this strategy is unknown in the Caudofoveata and scaphopods, both of which are dioecious (Lamprell and Scheltema 2001). Monoplacophorans, which are generally dioecious, are known to include at least one simultaneous hermaphrodite, *Micropilina arntzi* (Haszprunar and Schaefer 1996). Chitons are also most commonly dioecious, but simultaneous hermaphroditism occurs in two small species of brooding *Lepidochitona* (Eernisse 1988). Sequential hermaphroditism has yet to be documented in chitons. Among the diverse and well-studied molluscs, both simultaneous and sequential hermaphroditism are common and well-documented both in gastropods and bivalves (Coe 1943, 1944; Ghiselin 1969; Policansky 1982; Wright 1988; Heller 1993) and generally occur in derived clades of each group. The basal clade of bivalves, the protobranchs, are dioecious supporting the idea that dioecy is ancestral in bivalves. In gastropods, the most basal extant clade, the patellogastropods, have species with all three sexual systems (Coe 1944). The other basal groups, Cocculiniformia and Vetigastropoda, show variation in aspects of sexual morphology that seem to be conserved in most other clades: some clades in the Cocculiniformia are simultaneous hermaphrodites with two separate gonads (one male and one female) (Ponder and Lindberg 1997), but some show protandrous simultaneous hermaphroditism (PSH) in which the testis develops before the ovary (Huys et al. 2002), and copulatory structures and internal or semi-internal fertilization have evolved independently at least six times in the Vetigastropoda (Kano 2008). Cephalopods, in contrast to gastropods and bivalves, are exclusively dioecious

with the possible exception of a single squid species, *Ancistrocheirus lesueurii*, for which there is evidence of protandry (Hoving et al. 2006).

It should be noted that the clades that lack documented diversity in sexual systems are also those that lack feeding larvae. With the exception of cephalopods these are basal clades with low extant diversity and little information available on their sexual systems and reproduction. Strathmann (1978) suggested that the absence of feeding larval stages in these and some other invertebrate clades could be explained by the progressive loss of adaptive types over evolutionary time. A similar scenario could explain the observed distribution of sexual systems, although the selective factors that would result in repeated losses and failures to regain hermaphroditism are difficult to imagine.

The manner in which sexual systems are documented may result in the apparent dominance of dioecy. Since the scaphopods, Caudofoveata and Solenogastres are under-studied and seldom reared in the laboratory, the apparent absence of diversity in sexual systems may simply be due to a lack of information about all but a handful of species. There is also a bias in the detection of different kinds of hermaphroditism; anatomical examination of only a single individual is usually sufficient to detect simultaneous hermaphroditism. Sequential hermaphroditism is more difficult to detect. Differences in the sizes of males and females sometimes in combination with biased sex ratios are cited as indications of sex change and have been used to successfully infer sex change by the earliest workers on invertebrate sex change (e.g., Bacci 1947; Orton 1920). Such distributions do not rule out sexual dimorphisms or selective mortality. In addition, protandrous species that have been examined in detail often show considerable overlap in size between males and females, often with clear biases only in the smallest and largest size categories (e.g., Collin 2006). Therefore, large sample sizes are required to detect sex change in this way. In many taxa “rare” cases of individuals with both male and female gametes in the gonad have been explained as occasional abnormal sexual development (e.g., Coe 1943). In some species these cases may account for a significant percentage of the population and should be examined in more detail as potential indicators of sex change or the presence of an alternate sexual strategy. Overall, these biases in detection suggest that the distribution of simultaneous hermaphroditism is well documented, but that many cases of sequential hermaphroditism may have gone undetected (Policansky 1982).

Phylogenetic distribution of sexual systems

The distribution of sexual systems among gastropods and bivalves suggests both evolutionary flexibility and evolutionarily conservatism, but the patterns shown in each group are quite different. In bivalves the vast majority of species are thought to be dioecious (Coe 1943), although the difficulty of sexing live individuals and following them through time may underestimate the number of sex changers (as described above). In contrast to gastropods, sex change in bivalves often occurs in the same clades as simultaneous hermaphroditism and there are few families made up entirely of sex changers. Although sex change is most commonly protandrous a number of species can change from one sex to the other and back again (sex reversal). The clades of bivalves that are not strictly dioecious tend to show significant variation in sexual systems among species (e.g., oysters, scallops, galeommatoidaeans) as well as pronounced phenotypic plasticity in response to environmental conditions. For example galeommatoidaeans include protandrous hermaphroditic and sequential hermaphroditic species, as well as species with parasitic dwarf males (Jespersen and Lützen 2006; Fox et al. 2007; Goto et al. 2007; Goto et al. 2011). Likewise, populations of oysters like *Ostrea nomades* are often made up of individuals that are pure males, pure females, and simultaneous hermaphrodites at any one time (Siddiqui and Ahmed 2002) but may have the potential to change sex between seasons. These systems, similar to some of the sexual systems found in plants, appear to evolve along a continuum of relative allocation to male and female function (Fig. 2).

Hermaphroditic bivalves can be fully simultaneously hermaphroditic but more generally show some kind of sex change or gradation between the sexes (Coe 1943). Histological examination of the gonads show that numerous species have a tendency toward protandry whereby animals develop functioning male gonads before female function is achieved. This protandrous simultaneous hermaphroditism (PSH) is often, confusingly, referred to as protandry in the literature on bivalves and pulmonates. If male function is subsequently lost, it is usually after a significant period when the animal functions as both sexes, either simultaneously or during the course of the same reproductive season. In other cases the gonad reverts to undifferentiated cells during the non-reproductive period and sex is re-determined during the next breeding season. In general, the bivalve gonad is primarily ambisexual, with gametes of the different sexes maturing in response to various cues (Coe 1943). Unfortunately, the cues and details

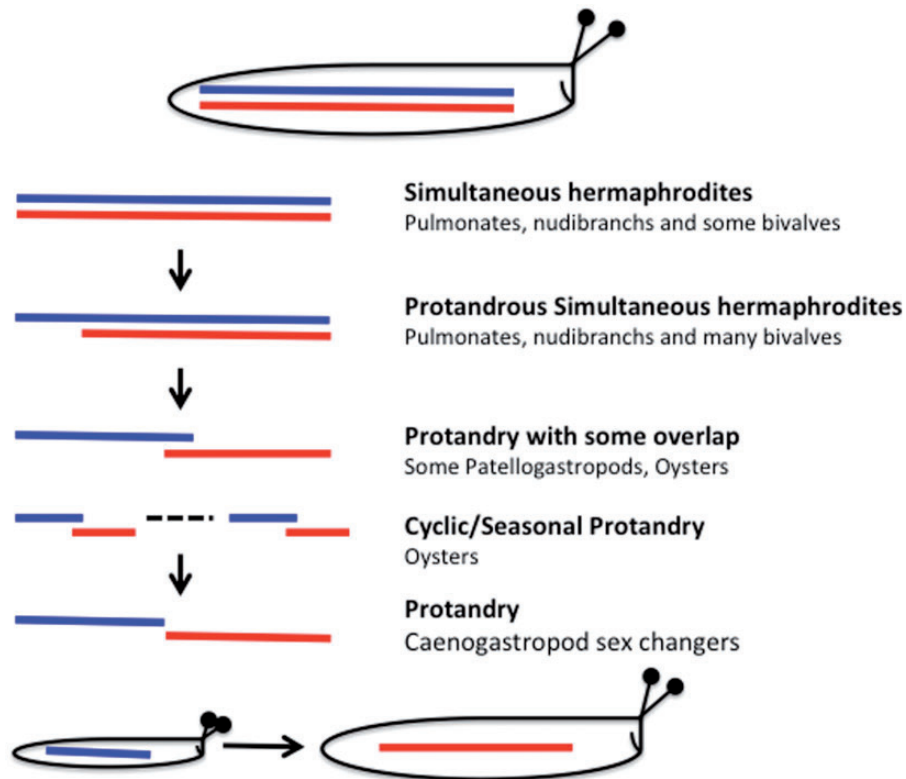


Fig. 2 A schematic showing the hypothesized easiest series of transitions between simultaneous and sequential hermaphrodites. The horizontal position of the colored lines indicates the point in life when each sex is expressed. Red lines indicate female function and blue lines indicate male function.

that control switching have not been investigated experimentally and merely are inferred from population samples. Recent advances in following the sex of individuals (Bauer 1987; Lee et al. 2012), as well as the application of genetic approaches (Guo et al. 1998; Yusa 2007), hold promise for increased understanding of sex expression in bivalves.

Gastropods are probably ancestrally dioecious, but hermaphroditism is equally common, among extant taxa. The distribution of sexual systems is clearly phylogenetically conserved at the familial and super-familial levels. One of the two major crown-group gastropod clades, the heterobranchs, are almost entirely simultaneous hermaphrodites and possess both male and female copulatory structures during most of their lives (for more nuances see Heller 1993). Like most hermaphroditic bivalves, many species develop male function earlier than they do female function, and sexual function can change during each reproductive season (Heller 1993). Detailed behavioral studies of pulmonates and nudibranchs have shown that the sex role an individual plays during copulation can also change. Although heterobranchs are morphologically simultaneous hermaphrodites in that they usually possess

the reproductive structures of both sexes, allocation of energy to each sex, as well as behavioral decisions about which sexual role to play, can vary in response to a number of environmental conditions (e.g., Leonard 1991, 2010).

The other major gastropod crown clade, caenogastropods, are primarily dioecious. Several caenogastropod families have evolved protandry independently and simultaneous hermaphroditism is rare. Unlike bivalves in which non-dioecious families are sexually flexible, these gastropod families are often exclusively protandrous. These include the well-studied calyptraeids, as well as the poorly understood hipponicids, epitonids, vermetids, and eulimids. As far as we know, in the well-studied species, sex change is always protandrous, does not involve an intermediate hermaphroditic stage, and occurs only once. There is some circumstantial evidence that sex reversal (flip-flopping) occurs in the vermetid *Serpulorbis arenarius* (Calvo and Templado 2005). There is also an interesting case of recent innovation in an otherwise conservative group. All littorinids were thought to be dioecious until close examination of *Mainwaringia rhizophila* showed this species to be protandrous (Reid 1986). As littorinids

are some of the most intensively studied gastropods it seems unlikely that this conclusion, that protandry in *M. rhizophila* is a recent evolutionary innovation, will change with additional sampling.

The most basal clade of gastropods, the “true” limpets or patellogastropods, show a pattern different from that of other gastropods; protandrous sex change has evolved from dioecy in several apparently independent lineages (D. R. Lindberg, personal communication; Branch 1974; Nakano and Ozawa 2004, 2007). Unlike protandry in hermaphroditic caenogastropods in which gonads with simultaneous oogenesis and spermatogenesis are seldom if ever observed, mixed gonads have been reported in several patellogastropods (e.g., Orton 1928; Branch 1974; Creese et al. 1990; Cunha et al. 2007). This suggests greater evolutionary flexibility in the design of patellogastropod gonads and sexual systems compared with caenogastropods or heterobranchs.

Few generalizations can be made about the ecological factors that favor sex change in gastropods and bivalves. However, protandry does occur in particularly sedentary gastropods; hipponicids are physically permanently attached to the substrate; eulimids, coralliophilids, and epitomidids are closely associated with host animals. PSH sex change occurs in the most sedentary or cemented bivalves (oysters, rock scallops, giant clams) (Lauren 1982; Dolgov 1992) as well as those that are closely associated with hosts (e.g., Tsubaki and Kato 2012). These commensal and parasitic molluscs are often very small, so sex change is also associated with small size in these taxa. As all species in some families change sex, an association with size, independent of phylogeny, cannot be demonstrated in those groups. In clades that are sexually variable, for example in the patellogastropods, it is the larger species that change sex. Particularly large bivalves like *Tridacna* and geoducks also exhibit PSH (Dolgov 1992; Gribben and Creese 2003). This suggests that factors that select for large body size may also select, directly or indirectly, for protandry.

Two interesting patterns that have not received much previous attention are evident from the phylogenetic distribution of sex change in molluscs. First, in gastropods sequential hermaphrodites do not evolve from simultaneous hermaphrodites. It seems intuitively likely that continued selection for early male function and later female function in simultaneous hermaphrodites would lead to PSH and eventually select for animals that are first male and then female, with or without a minimal intervening hermaphroditic stage (Fig. 2). This scenario predicts that discrete protandry should occur on the twigs of

clades that are primarily made up of simultaneous hermaphrodites. It is possible that such species exist in the heterobranchs or that protandry is behavioral rather than morphological in this clade, but there is no evidence that such a pattern is common. The predicted pattern is also clearly not supported by the caenogastropods or patellogastropods. Patellogastropods have evolved protandry at least five times (D. R. Lindberg, personal communication; Branch 1974; Nakano and Ozawa 2004, 2007) from dioecy. The evolutionary history of protandry in caenogastropods is not clear due to the unresolved relationships at the base of the group and our poor knowledge of the distribution of protandry in some of the groups. In fact, the dense distribution of protandry in basal caenogastropods does not exclude the possibility that this is the ancestral state of caenogastropods. This hypothesis cannot be ruled out without formal phylogenetic analyses.

The second noteworthy pattern is that sex reversal (flip-flopping) occurs in free-spawners but not in copulators. In none of the protandrous caenogastropods is there good experimental evidence for sex reversal after the initial sex change. The only study to suggest such an event was of the vermetid *Serpulorbis arenarius* in which an individual brooding egg capsules was found to have a testis (Calvo and Templado 2005). Vermetids live cemented to the substrate and do not copulate, instead sperm is passed via spermatophores that are caught by the filter-feeding females. The other gastropod taxon in which morphological sex reversal occurs are the patellogastropods. There are several lines of evidence for this. In *Patella vulgata* among others, there are often low numbers of males in the largest size class (e.g., Orton et al. 1956; Le Quesne and Hawkins 2006). In fact at three intensively surveyed sites in the Orkney Islands, the largest animals were males, even though there was a female-biased sex ratio in the large animals (Baxter 1983). This pattern has been considered to reflect the presence of “true” males that never change sex (e.g., Orton 1928). However, this pattern could also be interpreted as the result of a low frequency of sex reversals from female back to male. Histological studies provide data consistent with sex reversal for *Patella kermadecensis* in which several large females had small pockets of sperm in their gonads (Creese et al. 1990). Finally, in *Patella ferruginea* and *P. vulgata* tracking individual limpets showed reversal from female to male in a small number of individuals (Le Quesne and Hawkins 2006; Guallart et al. 2013). Patellogastropods are free-spawners and therefore offer good support to the observation that sex

reversal, which is common in free-spawning bivalves, is associated with free spawning or the lack of accessory, copulatory structures. Janthinids lack copulatory structures and have been suggested to have a single sex change (Graham 1954) or to make multiple switches (Laursen 1953). Epitonids are also reported as protandrous and lack copulatory structures (Collin 2000), so discovery of sex reversal in this group would further support this pattern.

Social and environmental control of sex change—three case studies of gastropods

Many organisms alter their sex allocation in response to intraspecific associations and interactions. This is particularly true in animals that change sex; fishes and molluscs both have been shown to respond to interactions with conspecifics (Charnov 1982; Munday et al. 2006). Socially-mediated sex change has been inferred from size distributions and sex distributions for most protandrous gastropods and bivalves. Differences among populations in the size at which sex change, coincident with differences in maximum body size, are usually considered to be an indicator of socially-mediated sex change. These patterns are sometimes combined with anatomical data that suggest indeterminate, transitional, or simultaneous hermaphroditic stages in what appears to be an otherwise dioecious species. In rare species that live in isolated groups or patches a non-random distribution of sexes may also suggest socially-mediated protandry, in which the first animal in the patch becomes a female and subsequent recruits are induced to develop as males (e.g., some barnacles; Yusa et al. 2013, this issue). Unfortunately, few experiments have been conducted with molluscs to unequivocally document sex change, to test the social and environmental factors that influence sex change, or to identify the mechanism by which these cues are transmitted. Below I review the recent experimental data on three well-studied cases of sex change in gastropods and show that, although these groups have evolved sex change independently, they have some characteristics in common. They all have the following attributes: (1) they are sedentary, (2) they live in groups, patches, or aggregates, and (3) size at sex change varies among sites and among aggregates. In addition, the available experimental evidence suggests that (4) the presence of females or large individuals represses growth and sex change of males, and (5) behavior seems to mediate the repressive influence of large females.

Case 1: Slipper limpets (Calyptraeidae)

Calyptraeids (*Crepidula*: slipper snails; *Crucibulum*: cup-and-saucer snails; and *Calyptraea*: hat snails) are sedentary protandrous filter feeders. All species in the family are thought to change sex, and sex change was first documented in *Crepidula* a hundred years ago (Orton 1909). As is expected for protandry, females are larger than males, but in natural populations there is usually a large range of overlap in size between the sexes (Collin 1995, 2006; Hoagland 1978; Hoch and Cahill 2012). Although sex ratio is predicted to be biased towards the first sex in sex changers (Charnov 1982), this is not always the case in calyptraeids in which sex ratios can range from as few as 10% to as many as 90% males (Collin 2006). The sex ratio and size distribution of males and females can vary seasonally, among sites, or among years (Hendler and Franz 1971; Hoagland 1978; Collin 2006; Richard et al. 2006; Hoch and Cahill 2012).

As sedentary animals that copulate, it is thought that most calyptraeids mate with close neighbors. Genetic paternity studies in *Crepidula fornicata* and *Crepidula coquimbensis* show that this is largely true (Dupont et al. 2006; Proestou et al. 2008; Brante et al. 2011). Many of the species live in small groups or aggregates, either because they specialize in patchy habitats like the inside of shells inhabited by hermit crabs, or because their limitation to soft substrates result in animals stacking on top of each other. It seems likely that interactions with other animals in the patch would influence reproductive success and therefore the best time to change sex. This is supported by the observations that in any group the largest is almost always female and the smaller animals almost always male (Collin 2006; Hoch and Cahill 2012).

Experimental manipulations of the social environment for several species of *Crepidula* show that growth and sex change in small males are repressed by the presence of a larger male or a female (Warner et al. 1996; Collin et al. 2005). Preliminary data suggest that this effect is mediated by physical contact and that contact with conspecific mucus and waterborne cues do not produce the same effect (Carrillo and Collin, in preparation). Data on individual growth trajectories of *Crepidula* cf. *marginalis* (Fig. 3A) raised alone show that growth rate increases at the time of sex change (Fig. 4) and also that individuals differ considerably in their propensity to grow and change sex when raised under standardized conditions (Fig. 4). These animals were collected from the field as juveniles or as very small males and it is possible that these differences are the result of their early life experience,

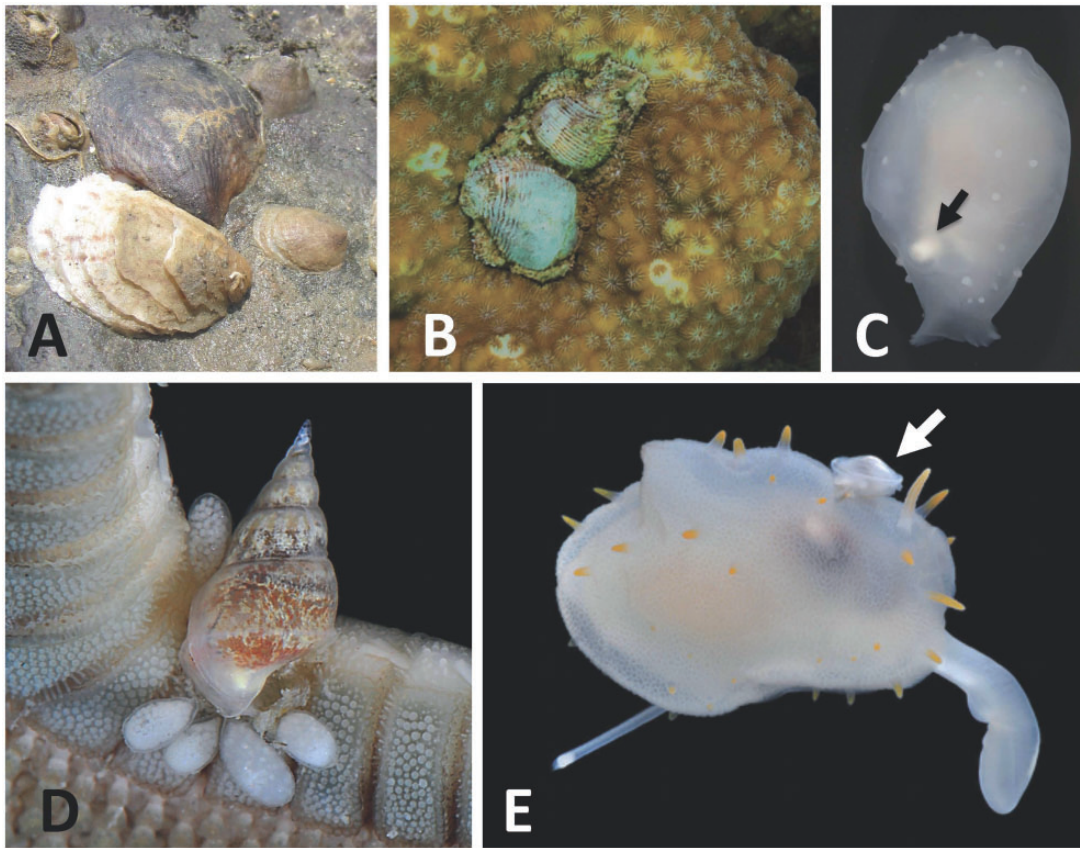


Fig. 3 Some of the taxa referred to in this paper. (A) *Crepidula cf. marginalis* (above) and *Crepidula lessoni* (below) live under rocks in the intertidal; (B) *Coralliophila abbreviata* from Bocas del Toro, Panama (photograph courtesy of Julia Schmidt-Petersen); (C) *Chlamydoconcha orcutti* from California (arrow indicates the internal male) (photograph courtesy of Greg Rouse); (D) *Parvioris* sp., a eulimid surrounded by egg capsules, attached to a starfish host (photograph courtesy of Arthur Anker); and (E) *Divariscintila* sp., a galeommatid with attached dwarf male (arrow) (photograph courtesy of Arthur Anker).

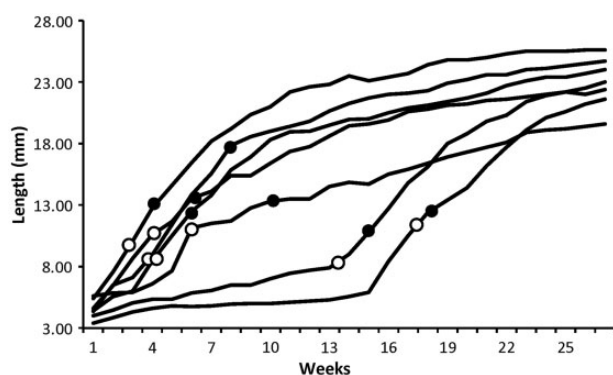


Fig. 4 The growth trajectories of several *Crepidula cf. marginalis*. Data represent a subset of typical growth trajectories from animals in the 2× food treatment in Mérot and Collin (2012b). The open circles represent the last date the animal was recorded as male and the dark circle indicates the first time it was reported as female. All animals were raised under the same, standardized conditions.

but it could also reflect genetic variation (as suggested by Coe 1944).

Few studies have examined the effects of physical conditions on sex change in calyptraeids, independent of conspecific interactions. Extremely low concentrations of food result in the regression of any sexual characteristics and in low rates of growth in *Crepidula cf. marginalis* (Mérot and Collin 2012a). When food was increased to high levels, growth recovered rapidly but male function was not regained and the animals remain sexless until they reached the size at which the female system generally develops (Mérot and Collin 2012a). Medium food rations have a less severe effect but also result in a longer transitional period that is initiated earlier and completed later than in well-fed animals (Mérot and Collin 2012b). Similar results were reported for several North American species (Coe 1953). Taken together, these results suggest that the period of sex change involves less energy than does maintaining active reproduction. Desiccation stress has little

effect on sex change in *C. cf. marginalis* (Mérot and Collin 2012a), but substrate limitation in species living in soft-bottomed habitats may limit growth and induce sex change at smaller sizes (Collin 1995).

Case 2: Coral lovers (Coralliophilids)

Coralliophilids are specialized neogastropod predators on corals and other anthozoans. These snails copulate and brood their egg capsules in the mantle cavity. The most well-studied species live in small groups on host corals, and many species are sedentary or appear to move very little (Richter and Luque 2004). Recent histological analysis and experimental data show that several species previously thought to be dioecious are actually protandrous (Chen et al. 1998; Richter and Luque 2004) and that oocytes and spermatocytes were never observed developing simultaneously (Richter and Luque 2004). The presence of a residual penis in females had been interpreted as imposex in these species, and more detailed study of additional species is necessary to clarify the prevalence of protandry in the group (Richter and Luque 2004).

The sex ratios of protandrous coralliophilids in the field are not always significantly different from 1:1, and males and females can occur over 40–80% of the size range (Soong and Chen 1991; Richter and Luque 2004). Even when the size range of males and females appear similar, the sex ratio of the size classes differ and a statistical difference in the size distribution of the two sexes can be detected (Richter and Luque 2004). These distributions show that size at sex change varies within a population, and examination of opercula striae shows that the age at which sex change occurs also varies (Chen and Soong 2002).

Field observations indicate that sex change is influenced by association with conspecifics, and experimental data support these conclusions. Like calyptraeids, these snails occur in aggregations of varying sizes. In *Coralliophila meyendorffii* the size of the female in an aggregate is correlated with the size of the aggregation (Richter and Luque 2004). In the Indo-Pacific *Coralliophila violacea* a correlation between size of the smallest female and size of largest male in an aggregation indicates that the size at sex change is specific to each group of snails (Soong and Chen 1991). In the immobile coralliophilid *Qoyula monodonta* the probability that an individual is female increases with size regardless of social environment, while small animals are generally male if they are found in association with a female but are not sexually developed at the same size when they are found alone (Soong and Chen 2003). In an aquarium experiment with artificial groups of

C. meyendorffii sex change happens earlier in populations without females compared with those with females (Richter and Luque 2004). A field experiment using mark and recapture of *C. violacea* showed that none of the males paired with a female changed sex over the five months of the study, while almost half of the solitary males changed (Chen et al. 1998). These studies are all consistent with the idea that females repress sex change in smaller males. Finally, another mark and recapture experiment showed that the growth rates of *C. violacea* are higher for animals that changed sex than for those that did not (Chen and Soong 2002), similar to the pattern for calyptraeids.

The only environmental factor that has been examined with respect to sex change is the host coral on which these snails are found. The quality of the host on which these snails occur affects their growth rates, maximum size, and size at sex change (Chen et al. 2004). *Coralliophila violacea* from the Indo-Pacific and *Coralliophila abbreviata* (Fig. 3B) from the Caribbean can both occur on branching and massive corals. In *C. violacea* the animals grow and survive better on massive hosts and therefore change sex at a larger size than on branching hosts (Chen et al. 2004). Size at sex change increases with patch size on massive hosts, where females were significantly larger than males. On branching hosts, aggregations are smaller, male and female sizes are almost the same, and growth rates do not differ from those on massive hosts. *Coralliophila abbreviata* shows the opposite pattern, with the snails growing larger, consuming more, and changing sex at a larger size on the branching host. Like *C. violacea*, those on massive corals often occur in larger groups (Johnston and Miller 2007). The influence of the host's nutritional quality and the limitation of size of substrate in the branching corals could be fruitful areas of investigation.

Case 3: True limpets (Patellogastropoda)

Protandrous sex change has evolved in several lineages of patellogastropods. Sex change is often inferred from size distributions of the two sexes (e.g., *Scutellastra flexuosa*; Lindberg 2007) and from the presence of indeterminate gonads or presence both of testes and ovaries in medium-sized individuals (e.g. *Patella vulgata* Bacci 1947; *Helcion pectunculus*: Gray 1997; *Patella kermadecensis*: Creese et al. 1990). Longitudinal studies of living animals have confirmed sex change in *Lottia gigantea* (Wright and Lindberg 1982), *Patella vulgata* (Le Quesne and Hawkins 2006), and *Patella ferruginea* (Espinosa et al. 2009). Since patellogastropods lack

copulatory structures, direct demonstration of sex change involves taking biopsies of the gonad of living animals, as it does in bivalves.

As is the case with calyptraeids and coralliophilids, the sex ratio and size at sex change vary naturally among sites (e.g., Branch and Odendaal 2003) and across seasons (McCarthy et al. 2008). In the South African limpet *Cymbula oculus*, larger limpets and a higher proportion of females occur at sites sheltered from waves compared with sites exposed to waves (Branch and Odendaal 2003). In many patellogastropods the large individuals are harvested by humans for food. This selective removal of large, presumably female, animals has been shown to affect the size at sex change. In the Mediterranean *Patella ferruginea*, size at sex change is larger at sites with higher densities of large animals (Rivera-Ingraham et al. 2011). Likewise, the Californian limpet, *Lottia gigantea*, is larger, shows later sex change, and has higher growth rates at sites that are protected from harvesting and have more large animals than do those with no protection (Fenberg and Roy 2012). *Cymbula oculus* are also larger and there are more females in areas protected from harvesting (Branch and Odendaal 2003).

Experimental manipulations show an effect of density on sex change, with low densities, good body condition, and few aggressive interactions resulting in earlier sex change. Protandrous limpets are generally large, territorial, show fidelity to the home site, and often are aggressive to conspecifics (Branch 1974; Lindberg 2007). Therefore, both aggressive interactions as well as the size and quality of the territory can affect body condition and probably sex ratio (Wright 1989). In *Patella depressa* experimentally increased density increases competition for food, decreases growth rate, and increases the number of males and non-reproductive individuals (Boaventura et al. 2003). Sex change has not been documented in *P. depressa*, but populations near the center of the range in Portugal show a size–sex distribution consistent with protandry (S. J. Hawkins and C. D. Borges, personal communication). Unfortunately, the design of this experiment in intraspecific competition could not be used to demonstrate whether sex change occurred (Boaventura et al. 2003), but protandry could explain the observed changes in sex ratio. Field manipulations of density show that *L. gigantea* have an increased probability of changing sex at lower densities, and that sex change occurs at smaller size at low densities (Wright 1989). The results from *P. depressa* support the suggestion that availability of food could mediate this effect (Wright 1989). There is also some

evidence that aggressive interactions, which occur more frequently at high densities, may inhibit sex change (Wright 1989).

It is unfortunate that so few experimental data are available on the effects of conspecific interactions on sex change in patellogastropods. Of the three systems reviewed here, they are the most behaviorally complex and constitute the group in which multiple parallel origins of protandry is most likely. Hopefully genomic and transcriptomic resources generated by the limpet genome project (Simakov et al. 2013) can be used to develop new, non-invasive methods for determining sex of individual limpets.

Are dwarf males a natural extension of protandry?

Dwarf males have been reported in several families both of gastropods and bivalves. These cases involve some of the most fascinating and poorly studied taxa. The term dwarf male has been used to refer to small males that are closely associated with females but do not differ much from normal free-living males, to highly modified parasites living on, or in, conspecific females. For example, in the Argentine oyster *Ostrea puelchana*, young individuals on hard substrates are usually male, but very small males with a different shell morphology are also found attached in a stereotypic position on the shells of females (Pascual et al. 1989). Experimental mortality of the host female releases the small males, which then grow quickly, attain a morphology similar to the free-living animals, and change to females. At the other end of the spectrum is the bivalve *Chlamydoconcha orcutti* (Fig. 3C) in which a morphologically simplified male lives in a cavity between the internalized shell and the reflected mantle of the larger animal. In this species the few large host individuals that have been dissected appear to be hermaphroditic with traces both of male and female gametogenesis in the gonad (Morton 1981). Dwarf males have also been reported in the shipworms *Zachsisia zenkewitschi*, *Xylophaga supplicata* and *Xyloredo* sp. (respectively, Yakovlev and Malakhov 1985; Haga and Kase 2013; Ockelmann and Dinesen 2011). In *Xylophaga supplicata* a deep-sea bivalve that lives associated with sunken wood often has tiny conspecifics attached to the shell near the hinge. These small animals, hardly larger than a larva, occur in several species and have been interpreted as evidence of external parental care of juveniles (reviewed by Haga and Kase 2013). Recent morphological examination has shown that these tiny animals are mature males and the larger host animals are protandrous, maturing as males at a significantly larger size than the attached dwarfs and

then apparently subsequently developing ovarian tissue. Of the six animals examined, the largest three included two females and one hermaphrodite (Haga and Kase 2013). Dwarf males have also been reported for the galeommatids *Montacuta* and *Ephippodonta* (Morton 1976), and *Peregrinamor ohshimai* (Lützen et al. 2001) among others (Fig. 3E). Species with dwarf males all occur in bivalve families in which protandry is common.

Similar bizarre lifestyles involving dwarf males occur in some gastropods but do not seem to be as common or widely distributed as in bivalves. Eulimids (Fig. 3D) show a range from *Thyca* species in which small males live near females (Elder 1979), to *Stilifer* in which small males and females both make galls in their host (Warén 1980), and to *Asterophila japonica* in which males and females both are shell-less endoparasites of starfish and the male is not much more than a sack of tissue 10% the body size of the female (Sasaki et al. 2007). There is some sparse evidence that the janthinid *Recluzia* cf. *jehennei* may also have dwarf or complemental males (Churchill et al. 2011).

The diversity of species with diminutive or dwarf males presents a fantastic opportunity for comparison with dwarf males in barnacles (Yusa et al. 2013, this issue). It has been inferred that the presence of the female represses development of the males. Could this be the typical repression of males evident in protandrous species taken to an extreme? Manipulative experiments are necessary to answer the fundamental questions: Do these dwarf males have the potential to grow and become large free-living hermaphrodites or females? If larvae settle alone do they bypass the male phase?

Conclusions

Sex allocation and sexual systems have been studied in more detail in molluscs than in most other groups of marine invertebrates. Despite this effort, the available information for any one group is patchy and rife with terminological inconsistencies. Reviews often run afoul of this (this article is probably no exception) and tentative conclusions of primary studies often are over-generalized to unstudied taxa or misinterpreted due to terminological inconsistencies. In-depth reviews of the primary literature inventorying what we really know about each clade of gastropods and bivalves will be vital for further progress in understanding macroevolutionary patterns and phylogenetic constraint in molluscan sexual systems. Targeting of species with unusual sexual systems for inclusion in phylogenetic analyses would be useful.

Detailed information and experimental data on molluscan sexual systems appears to be available for only a handful of well-studied families. For many families the sexual system has been inferred solely from anatomical data and the dynamics of sex allocation have yet to be investigated. Strategic choice of focal species to fill gaps in our knowledge or to target species in groups with known diversity could make significant contributions to our understanding, as would work on the genetic basis of sex determination, which is virtually unstudied in molluscs (but see Guo et al. 1998; Yusa 2007; Powell et al. 2010). In summary, the diversity of molluscan sexual systems offers a feast for researchers who wish to explore invertebrates' life histories. It is likely that a vast diversity of sexual systems, mating systems, and reproductive strategies still await discovery, and many aspects of the "well-known" systems still await investigation.

Acknowledgments

I thank Janet Leonard for organizing the symposium "Phenotypic plasticity and the evolution of gender roles" at the 2013 Society of Integrative and Comparative Biology (SICB) meeting, SICB for supporting the symposium, and Smithsonian Tropical Research Institute for supporting my research. I thank David R. Lindberg for discussion, an anonymous reviewer, and Greg Rouse, Julia Schmidt-Peterson and Arthur Anker for permission to use their photographs.

References

- Bacci G. 1947. Sex reversal in *Patella coerulea* L. and *Diodora gibberula* (Lam.). *Nature* 4055:94–5.
- Bauer G. 1987. Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *J Anim Ecol* 56:691–704.
- Baxter JM. 1983. Annual variation in soft-body dry weight, reproductive cycle and sex ratios in populations of *Patella vulgata* at adjacent sites in the Orkney Islands. *Mar Biol* 76:149–57.
- Boaventura D, Da Fonseca LC, Hawkins SJ. 2003. Size matters: competition within populations of the limpet *Patella depressa*. *J Anim Ecol* 72:435–46.
- Branch GM. 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 2. Reproductive cycles. *Trans R Soc S Afr* 41:111–60.
- Branch GM, Odendaal F. 2003. The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. *Biol Conserv* 114:255–69.
- Brante A, Fernández M, Viard F. 2011. Microsatellite evidence for sperm storage and multiple paternity in the marine gastropod *Crepidula coquimbensis*. *J Exp Mar Biol Ecol* 396:83–8.

- Calvo M, Templado J. 2005. Reproduction and sex reversal of the solitary vermetid gastropod *Serpulorbis arenarius*. *Mar Biol* 146:963–73.
- Charnov EL. 1982. The theory of sex allocation. *Monographs in population biology* No. 18, 1–355.
- Chen MH, Soong K. 2002. Estimation of age in the sex-changing, coral-inhabiting snail *Coralliophila violacea* from the growth striae on opercula and a mark-recapture experiment. *Mar Biol* 140:337–42.
- Chen MH, Soong K, Tsai ML. 2004. Host effect on size structure and timing of sex change in the coral-inhabiting snail *Coralliophila violacea*. *Mar Biol* 144:287–93.
- Chen MH, Yang YW, Soong K. 1998. Preliminary observations on change of sex by the coral-inhabiting snails *Coralliophila violacea* (Lamarck) (Gastropoda: Coralliophilidae). *J Exp Mar Biol Ecol* 230:207–12.
- Churchill CK, Strong EE, Foighil DÓ. 2011. Hitchhiking juveniles in the rare neustonic gastropod *Recluzia cf. jehenei* (Janthinidae). *J Mollus Stud* 77:441–4.
- Coe WR. 1943. Sexual differentiation in mollusks. I. Pelecypods. *Q Rev Biol* 18:154–64.
- Coe WR. 1944. Sexual differentiation in mollusks. II. Gastropods, amphineurans, scaphopods, and cephalopods. *Q Rev Biol* 19:85–97.
- Coe WR. 1953. Influences of association, isolation, and nutrition on the sexuality of snails of the genus *Crepidula*. *J Exp Zool* 122:5–19.
- Collin R. 1995. Sex, size, and position: a test of models predicting the size at sex change in the protandrous gastropod *Crepidula fornicata*. *Am Nat* 146:815–31.
- Collin R. 2000. Development and anatomy of *Nitidiscala tincta* (Carpenter 1865) (Gastropoda: Epitoniidae). *Veliger* 43:302–12.
- Collin R. 2006. Sex ratio, life history invariants, and patterns of sex change in a family of protandrous gastropods. *Evolution* 60:735–45.
- Collin R, McLellan M, Gruber K, Bailey-Jourdain C. 2005. Effects of conspecific associations on size at sex change in three species of calyptraeid gastropods. *Mar Ecol Prog Ser* 293:89–97.
- Creese RG, Schiel DR, Kingsford MJ. 1990. Sex change in a giant endemic limpet, *Patella kermadecensis*, from the Kermadec Islands. *J Exp Mar Biol Ecol* 144:101–12.
- Cunha L, Gustavo MM, Amaral A, Rodrigues A. 2007. A case of simultaneous hermaphroditism in the Azorean endemic limpet *Patella candei gomesii* (Mollusca: Patellogastropoda), a gonochoristic species. *Invertebr Reprod Dev* 50:203–5.
- Dolgov LV. 1992. Sexual structure of a *Tridacna squamosa* population: relative advantages of sequential and simultaneous hermaphroditism. *J Mollus Stud* 58:21–7.
- Dupont L, Richard J, Paulet YM, Thouzeau G, Viard F. 2006. Gregariousness and protandry promote reproductive insurance in the invasive gastropod *Crepidula fornicata*: evidence from assignment of larval paternity. *Mol Ecol* 15:3009–21.
- Eernisse DJ. 1988. Reproductive patterns in six species of *Lepidochitona* (Mollusca: Polyplacophora) from the Pacific Coast of North America. *Biol Bull* 174:287–302.
- Elder HY. 1979. Studies on the host parasite relationship between the parasitic prosobranch *Thyca crystallina* and the asteroid starfish *Linckia laevigata*. *J Zool* 187:369–91.
- Erismán B, Petersen CW, Hastings PA, Warner RR. 2013. Phylogenetic perspectives on the evolution of functional hermaphroditism in teleost fishes. *Integr Comp Biol* 53:736–54.
- Espinosa F, Rivera-Ingraham G, García-Gómez JC. 2009. Gonochorism or protandrous hermaphroditism? Evidence of sex change in the endangered limpet *Patella ferruginea*. *J Mar Biol Assoc Biodiv Rec* 2.
- Fenbergh PB, Roy K. 2012. Anthropogenic harvesting pressure and changes in life history: insights from a rocky intertidal limpet. *Am Nat* 180:200–10.
- Fox TH, Jespersen Å, Lützen J. 2007. Sperm transfer and reproductive biology in species of hermaphroditic bivalves (Galeommatoidae: Montacutidae). *J Morphol* 268:936–52.
- Ghiselin MT. 1969. The evolution of hermaphroditism among animals. *Q Rev Biol* 44:189–208.
- Goto R, Hamamura Y, Kato M. 2007. Obligate commensalism of *Curvemysella paula* (Bivalvia: Galeommatidae) with hermit crabs. *Mar Biol* 151:1615–22.
- Goto R, Hamamura Y, Kato M. 2011. Morphological and ecological adaptation of *Basterotia* bivalves (Galeommatoidae: Sportellidae) to symbiotic association with burrowing echinuran worms. *Zool Sci* 28:225–34.
- Graham A. 1954. Some observations on the reproductive tract of *Ianthina janthina* (L.). *J Mollus Stud* 31:1–6.
- Gray DR. 1997. Studies of the biology and ecology of the high shore South African limpet, *Helcion pectunculus* (Mollusca: Patellogastropoda) [dissertation]. Rhodes University.
- Gribben PE, Creese RG. 2003. Protandry in the New Zealand geoduck, *Panopea zelandica* (Mollusca, Bivalvia). *Invertebr Reprod Dev* 44:119–29.
- Gualart J, Calvo M, Acevedo I, Templado J. Forthcoming 2013. Two-way sex change in the endangered limpet *Patella ferruginea* (Mollusca, Gastropoda). *Invertebr Reprod Dev*.
- Guo X, Hedgecock D, Hershberger WK, Cooper K, Allen SK. 1998. Genetic determinants of protandric sex in the Pacific oyster, *Crassostrea gigas* Thunberg. *Evolution* 52:394–402.
- Haga T, Kase T. 2013. Progenetic dwarf males in the deep-sea wood-boring genus *Xylophaga* (Bivalvia: Pholadoidea). *J Mollus Stud* 79:90–4.
- Haszprunar G, Schaefer K. 1996. Anatomy and phylogenetic significance of *Micropilina arntzi* (Mollusca, Monoplacophora, Micropilinidae fam. nov.). *Acta Zool* 77:315–34.
- Heller J. 1993. Hermaphroditism in molluscs. *Biol J Linn Soc* 48:19–42.
- Hendler G, Franz DR. 1971. Population dynamics and life history of *Crepidula convexa* Say (Gastropoda: Prosobranchia) in Delaware Bay. *Biol Bull* 141:514–26.
- Hoagland KE. 1978. Protandry and the evolution of environmentally mediated sex change: a study of the Mollusca. *Malacologia* 17:365–91.
- Hoch JM, Cahill AE. 2012. Variation in size at sex-change among natural populations of the protandrous hermaphrodite, *Crepidula fornicata* (Gastropoda, Calyptraeidae). *Mar Biol* 159:1–9.
- Hoving HJT, Roeleveld MAC, Lipinski MR, Videler JJ. 2006. Nidamental glands in males of the oceanic squid

- Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae)—sex change or intersexuality? *J Zool* 269:341–8.
- Huys R, López-Gonzalez PJ, Roldan E, Luque AA. 2002. Brooding in cocculiniform limpets (Gastropoda) and familial distinctiveness of the Nucellicolidae (Copepoda): misconceptions reviewed from a chitonophilid perspective. *Biol J Linn Soc* 75:187–217.
- Jespersen Å, Lützen J. 2006. Reproduction and sperm structure in Galeommatidae (Bivalvia, Galeommatoidea). *Zoomorphology* 125:157–73.
- Johnston L, Miller MW. 2007. Variation in life-history traits of the corallivorous gastropod *Coralliophila abbreviata* on three coral hosts. *Mar Biol* 150:1215–25.
- Kano Y. 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zool Scripta* 37:1–21.
- Kocot KM, Cannon JT, Todt C, Citarella MR, Kohn AB, Meyer A, Santos SR, Schander C, Moroz LL, Lieb B, et al. 2011. Phylogenomics reveals deep molluscan relationships. *Nature* 477:452–6.
- Lamprell KL, Scheltema AM. 2001. Mollusca: Aplacophora, Polyplacophora, Scaphopoda, Cephalopoda. In: Wells A, Houston WWK, editors. *Zoological Catalogue of Australia*, Vol. 17. Melbourne: CSIRO Publishing.
- Lauren DJ. 1982. Oogenesis and protandry in the purple-hinge rock scallop, *Himnites giganteus*, in upper Puget Sound, Washington, USA. *Can J Zool* 60:2333–6.
- Laursen D. 1953. The Genus *Ianthina*: A Monograph. With 41 Fig. and Charts and 1 Pl.
- Le Quesne WJF, Hawkins SJ. 2006. Direct observations of protandrous sex change in the patellid limpet *Patella vulgata*. *J Mar Biol Assoc UK* 86:161–2.
- Lee JS, Park JS, Shin YK, Lee YG, Park JJ. Forthcoming 2012. Sequential hermaphroditism in Manila clam *Ruditapes philippinarum* (Bivalvia: Veneridae). *Invert Reprod Dev*.
- Leonard JL. 1991. Sexual conflict and the mating systems of simultaneously hermaphroditic gastropods. *Am Malacol Bull* 9:45–58.
- Leonard JL. 2010. The evolution of sexes, anisogamy, and sexual systems: natural vs. sexual selection. *The Evolution of Primary Sexual Characters in Animals*. New York, NY: Oxford University Press. p. 15–39.
- Leonard J. 2013. Williams' Paradox and the role of phenotypic plasticity in sexual systems. *Integr Comp Biol* 53:671–88.
- Lindberg DR. 2007. Reproduction, ecology, and evolution of the Indo-Pacific limpet *Scutellastra flexuosa*. *Bull Mar Sci* 81:219–34.
- Lützen J, Sakamoto H, Tagushi A, Takahashi T. 2001. Reproduction, dwarf males, sperm dimorphism, and life cycle in the commensal bivalve *Peregrinamor ohshimai* Shoji (Heterodonta: Galeommatoidea: Montacutidae). *Malacologia* 43:313–25.
- McCarthy M, Woosnam P, Culloty SC. 2008. Histological investigation of the reproductive cycles of the limpets *Patella vulgata* and *Patella ulyssiponensis*. *Mar Biol* 153:871–7.
- Mérot C, Collin R. 2012a. Effects of food availability on sex change in two species of *Crepidula* (Gastropoda: Calyptraeidae). *Mar Ecol Prog Ser* 449:173–81.
- Mérot C, Collin R. 2012b. Effects of stress on sex change in *Crepidula* cf. *marginalis* (Gastropoda: Calyptraeidae). *J Exp Mar Biol Ecol* 416–417:68–71.
- Morton B. 1976. Secondary brooding of temporary dwarf males in *Ephippodonta* (*Ephippodontina*) *oedipus* sp. nov. (Bivalvia: Leptonacea). *J Conchol* 29:31.
- Morton B. 1981. The biology and functional morphology of *Chlamydoconcha orcutti* with a discussion on the taxonomic status of the Chlamydoconchacea (Mollusca: Bivalvia). *J Zool* 195:81–121.
- Munday PL, Buston PM, Warner RR. 2006. Diversity and flexibility of sex-change strategies in animals. *Trend Ecol Evol* 21:89–95.
- Nakano T, Ozawa T. 2004. Phylogeny and historical biogeography of limpets of the order Patellogastropoda based on mitochondrial DNA sequences. *J Mollus Stud* 70:31–41.
- Nakano T, Ozawa T. 2007. Worldwide phylogeography of limpets of the order Patellogastropoda: molecular, morphological and palaeontological evidence. *J Mollus Stud* 73:79–99.
- Ockelmann KW, Dinesen GE. 2011. Life on wood—the carnivorous deep-sea mussel *Idas argenteus* (Bathymodiolinae, Mytilidae, Bivalvia). *Mar Biol Res* 7:71–84.
- Orton JH. 1909. On the occurrence of protandric hermaphroditism in the mollusc *Crepidula fornicata*. *Proc R Soc Lond B* 81:468–84.
- Orton JH. 1920. Sex-phenomena in the common limpet (*Patella vulgata*). *Nature* 104:373.
- Orton JH, Southward AJ, Dodd JM. 1956. Studies on the biology of limpets: II. The breeding of *Patella vulgata* L. in Britain. *J Mar Biol Assoc UK* 35:149–176.
- Pascual MS, Iribarne OO, Zampatti EA, Bocca AH. 1989. Female-male interaction in the breeding system of the puelche oyster *Ostrea puelchana* d'Orbigny. *J Exp Mar Biol Ecol* 132:209–19.
- Ponder WF, Lindberg DR. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zool J Linn Soc* 119:83–265.
- Policansky D. 1982. Sex change in plants and animals. *Ann Rev Ecol Syst* 13:471–95.
- Powell EN, Klinck JM, Hofmann EE. 2010. Generation time and the stability of sex-determining alleles in oyster populations as deduced using a gene-based population dynamics model. *J Theor Biol* 271:27–43.
- Proestou DA, Goldsmith MR, Twombly S. 2008. Patterns of male reproductive success in *Crepidula fornicata* provide new insight for sex allocation and optimal sex change. *Biol Bull* 214:194–202.
- Reid DG. 1986. *Mainwaringia* Nevill, 1885, a littorinid genus from Asiatic mangrove forests, and a case of protandrous hermaphroditism. *J Mollus Stud* 52:225–42.
- Richard J, Huet M, Thouzeau G, Paulet YM. 2006. Reproduction of the invasive slipper limpet, *Crepidula fornicata*, in the Bay of Brest, France. *Mar Biol* 149:789–801.
- Richter A, Luque AA. 2004. Sex change in two Mediterranean species of Coralliophilidae (Mollusca: Gastropoda: Neogastropoda). *J Mar Biol Assoc UK* 84:383–92.
- Rivera-Ingraham GA, Espinosa F, García-Gómez JC. 2011. Environmentally mediated sex change in the endangered limpet *Patella ferruginea* (Gastropoda: Patellidae). *J Mollus Stud* 77:226–31.

- Sasaki T, Muro K, Komatsu M. 2007. Anatomy and ecology of the shell-less endoparasitic gastropod *Asterophila japonica* Randall and Heath, 1912 (Mollusca: Eulimidae). *Zool Sci* 24:700–13.
- Siddiqui G, Ahmed M. 2002. Gametogenic patterns of the larviparous oyster *Ostrea nomades* from Karachi, Pakistan (Northern Arabian Sea). *Aquacult Res* 33:1049–58.
- Simakov O, Marletaz F, Cho SJ, Edsinger-Gonzales E, Havlak P, Hellsten U, Kuo DH, Larsson T, Lv J, Arendt D, et al. 2013. Insights into bilaterian evolution from three spiralian genomes. *Nature* 493:526–31.
- Smith SA, Wilson NG, Goetz FE, Feehery C, Andrade SC, Rouse GW, Giribet G, Dunn CW. 2011. Resolving the evolutionary relationships of molluscs with phylogenomic tools. *Nature* 480:364–7.
- Soong K, Chen JL. 1991. Population structure and sex-change in the coral-inhabiting snail *Coralliophila violacea* at Hsiao-Liuchiu, Taiwan. *Mar Biol* 111:81–6.
- Soong K, Chen MH. 2003. Sex expression of an immobile coral-inhabiting snail, *Quoyula monodonta*. *Mar Biol* 143:351–8.
- Strathmann RR. 1978. Progressive vacating of adaptive types during the Phanerozoic. *Evolution* 32:907–14.
- Tsubaki R, Kato M. 2012. Host specificity and population dynamics of a sponge-endosymbiotic bivalve. *Zool Sci* 29:585–92.
- Warén A. 1980. Revision of the genera *Thyca*, *Stilifer*, *Scalenostoma*, *Mucronalia* and *Echineulima* (Mollusca, Prosobranchia, Eulimidae). *Zool Script* 9:187–210.
- Warner RR, Fitch DL, Standish JD. 1996. Social control of sex change in the shelf limpet, *Crepidula norrisiarum*: size-specific responses to local group composition. *J Exp Mar Biol Ecol* 204:155–67.
- Wright WG. 1988. Sex change in the Mollusca. *Trends Ecol Evol* 3:137–40.
- Wright WG. 1989. Intraspecific density mediates sex-change in the territorial patellacean limpet *Lottia gigantea*. *Mar Biol* 100:353–64.
- Wright WG, Lindberg DR. 1982. Direct observation of sex change in the patellacean limpet *Lottia gigantea*. *J Mar Biol Assoc UK* 62:737–8.
- Yakovlev Y, Malakov VV. 1985. The anatomy of dwarf males of *Zachsia zenkewitschi* (Bivalvia: Teredinidae). *Asian Mar Biol* 2:47–56.
- Yusa Y. 2007. Causes of variation in sex ratio and modes of sex determination in the Mollusca—an overview. *Am Malacol Bull* 23:89–98.
- Yusa Y, Takamura M, Sawada K, Yamaguchi S. 2013. Diverse, continuous, and plastic sexual systems in barnacles. *Integr Comp Biol* 53:701–12.