

8

HERMAPHRODITISM AND GONOCHORISM

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Abstract

This chapter compares two sexual systems: hermaphroditism (each individual can produce gametes of either sex) and gonochorism (each individual produces gametes of only one of the two distinct sexes) in crustaceans. These two main sexual systems contain a variety of alternative modes of reproduction, which are of great interest from applied and theoretical perspectives. The chapter focuses on the description, prevalence, analysis, and interpretation of these sexual systems, centering on their evolutionary transitions. The ecological correlates of each reproductive system are also explored. In particular, the prevalence of “unusual” (non-gonochoristic) reproductive strategies has been identified under low population densities and in unpredictable/unstable environments, often linked to specific habitats or lifestyles (such as parasitism) and in colonizing species. Finally, population-level consequences of some sexual systems are considered, especially in terms of sex ratios. The chapter aims to provide a broad and extensive overview of the evolution, adaptation, ecological constraints, and implications of the various reproductive modes in this extraordinarily successful group of organisms.

INTRODUCTION

Historical Overview of the Study of Crustacean Reproduction

Crustaceans are a very large and extraordinarily diverse group of mainly aquatic organisms, which play important roles in many ecosystems and are economically important. Thus, it is not surprising that numerous studies focus on their reproductive biology. However, these reviews mainly target specific groups such as decapods (Sagi et al. 1997, Chiba 2007, Mente 2008, Asakura 2009), caridean

shrimp (Correa and Thiel 2003) and crayfish (Yazicioglu et al. 2016), or are more general reviews of mating strategies and behaviors (Subramoniam 2013, Dennenmoser and Thiel 2015), hormonal regulations (Ventura et al. 2011a), sex determination (Rigaud et al. 1997) and/or sexual systems (Bauer and Martin 1991, Subramoniam 2016), focusing more on proximate mechanisms than ultimate causes. Comprehensive reviews of crustacean reproduction, especially from an evolutionary perspective, are largely missing from the literature.

This gap in our knowledge is even more obvious when we consider the paucity of modern reviews of the evolution of hermaphroditism in the Crustacea (Charniaux-Cotton 1975, Juchault 1999), with the exception of a few taxa (e.g., branchiopods: Weeks et al. 2014, barnacles: Yamaguchi et al. 2012, Yusa et al. 2012, 2013) or specific systems (e.g., androdioecy: Weeks et al. 2006a, Weeks 2012). This is not unique to the Crustacea: the evolution of hermaphroditism has not been widely discussed in animals more generally (but see Ghiselin 1969, Jarne and Charlesworth 1993, Jarne 1995, Jarne and Auld 2006, Eppley and Jesson 2008, Schärer and Janicke 2009, Vega-Frutis et al. 2014, Meconcelli et al. 2015), even though more than 65,000 animal species are hermaphroditic (Jarne and Auld 2006).

Here, we review reproductive systems in crustaceans (see also Chapter 6 in this volume), with an emphasis on the various forms of hermaphroditism, including sequential and simultaneous hermaphroditism (male and female reproductive organs are present and function sequentially or at the same time), mixed sexual systems (such as androdioecy), and plastic strategies (population geographic variation in sexual systems in the same species; presence of non-sex-changing individuals in sequentially hermaphroditic populations, etc.). In particular, we list the known species that exhibit these hermaphroditic forms and consider the evolution of the numerous reproductive systems in crustaceans, documenting their taxonomic ranges and discussing their likely evolutionary transitions. We conclude by briefly discussing the environmental correlates of the various reproductive forms found among crustaceans.

OVERVIEW OF REPRODUCTION IN THE CRUSTACEA

Types of Reproductive Systems in the Crustacea

Few animal groups have as many reproductive systems as crustaceans (see Table 8.1 for definitions): asexual (parthenogenetic) lineages are common in freshwater ostracods (Butlin et al. 1998, Schön et al. 2000), in the brine shrimp *Artemia* (A in Fig. 8.1; Asem et al. 2016), in some terrestrial isopods (Bell 1982, no males have been found in *Armadillidium virgo* [Caruso and Bouchon 2011, D in Fig. 8.1]), and have been described in crayfish (Scholtz et al. 2003); cyclic parthenogenesis is often found in cladocerans (Hebert 1987, Decaestecker et al. 2009); separate sexes (functional males and functional females) are present in gonochoristic (dioecious) species as well as in sequential hermaphrodites (sex changers), where the same individual acts as one sex and successively as the alternate sex at different times of its life cycle; combined sexes (hermaphroditism) are found in systems where all individuals mature both male and female gonads at the same time (synchronous or simultaneous hermaphroditism), or in mixed sexual systems, where only some individuals are hermaphrodites but others are pure males (androdioecy; see Table 8.2). Coexistence of hermaphrodites and males can also occur following the development of female tissue in males (protandric simultaneous hermaphroditism), a mixed sexual system mainly found in the Infraorder Caridea (Bauer and Holt 1998, Bauer 2000). This amazing variety of modes of reproduction can thus be seen as a continuum (Ah-King and Nylin 2010, Kelly and Sanford 2010, Yusa et al. 2013).

Table 8.1. Definition of Sexual Systems Based on the Presence of Sexual Types

Sexual System	Population Composed of
Androdioecy	Males + hermaphrodites*
Gynodioecy	Females + hermaphrodites*
Gonochorism (Dioecy)	Males + females
Asexual (Parthenogenetic)	Females only
Cyclic Parthenogenesis	Asexual females most of the year followed by a single bout of sexual (male + female) reproduction at the end of the growing season
Simultaneous hermaphroditism	Hermaphrodites*
Sequential hermaphroditism	
i. Protandry	Male-first sex changers. Individuals reproduce as males initially and then switch to females, the second sex, also called secondary females in digynic populations (populations with two types of females) where some individuals are born directly as females (primary females). In some cases, some males might not change to females (and remain males through all their lives)
ii. Protogyny	Female-first sex changers. Individuals reproduce as females initially and then switch to males, the second sex, also called secondary males in diandric populations (populations with two types of males) where some individuals are born directly as males (primary males). In some cases, some females might not change to males (and remain females through all their lives)
Protandric simultaneous hermaphrodites	Males → Simultaneous hermaphrodites

* Simultaneous production of both male and female gametes

Sex-determining mechanisms also vary greatly in crustaceans (see Chapter 14 in this volume). Some isopod and amphipod females can produce offspring of exclusively one sex, a process known as monogeny (Bulnheim 1978, Juchault and Legrand 1986). Additionally, crustaceans can use both internal and external fertilization. When internal fertilization occurs, females can often be fertilized only during a brief period after molting, before their exoskeleton hardens again (Hartnoll 1969, Raviv et al. 2008). In this situation, males guard females until they are receptive (mate guarding; Jormalainen 1998). In some species, characterized by a terminal molt (after which the individual no longer grows), females can be fertilized even with a hard exoskeleton (Raviv et al. 2008). Given this variety and complexity of reproductive modes and systems, crustaceans are great model organisms to test theoretical predictions and perform applied studies on the ecology, reproductive behavior, sexual selection, and evolution of social and sexual systems of animals (Duffy and Thiel 2007, Dennenmoser and Thiel 2015, Chak et al. 2015).

Below, we describe the diversity of hermaphroditic reproductive systems in crustaceans. The vast bulk of crustaceans are gonochoristic (dioecious), and we do not specifically delineate those species in this chapter. We also refer readers to Chapter 9 of this volume for a complete discussion of asexual reproduction. Here instead, we first describe the various reproductive systems, and then present a brief discussion of their evolutionary transitions.

Sexual Reproduction

Gonochorism

Gonochorism or dieocy (separate sexes) is the most common sexual system in crustaceans (Juchault 1999, Correa and Thiel 2003, Subramoniam 2013). When genetically determined, separate sexes are fixed throughout the life cycle of individuals. Sexual development is regulated in malacostracan crustaceans by a hormone produced by the androgenic gland: the default sex is female (Ford 2008), and primary and secondary male characters are induced by the insulin-like androgenic gland hormone (Sagi et al. 1997, Chang and Sagi 2008, Ventura et al. 2011a, 2011b). In the presence of the hormone, testicular differentiation is initiated and the animal matures as a male; in its absence (i.e., in females), ovaries develop instead (Chang and Sagi 2008).

In many crustacean groups, sexual dimorphism allows the easy recognition of males from females, each sex characterized by a sex-specific phenotype. Males are usually larger than females and have larger chelipeds, or other weapons, in species where male-male competition is the rule, either in the form of direct aggressive interactions, mate guarding or territorial/burrow defense (see Chapter 10 in this volume). Larger females than males are found in penaeoidean shrimp, in many caridean shrimp (Bauer et al. 2014), and in other groups where high abundances allow for frequent contact between the sexes. In instances when one sex grows faster than the other, there has been interest in creating single-sex populations for aquaculture purposes (Ventura and Sagi 2012, see the successful manipulations of the giant freshwater prawn *Macrobrachium rosenbergii*; Ventura et al. 2012). Extreme sexual dimorphism is found in some dioecious barnacles (in particular in the order Pedunculata), where males are much smaller than females. Darwin (1851) called them “dwarf” males: they are attached directly to the “fertilization site” (on a female) and do not require the long (“groping”) penises that their hermaphroditic counterparts require for successful fertilization; multiple dwarf males can be attached to the same female (Yusa et al. 2012, Lin et al. 2015).

Even though there are two sexes, more than one male morphotype can be present, as found, for example, in the marine isopod *Paracerceis sculpta* where α -, β - and γ -males coexist in populations (Shuster and Wade 1991), the rock shrimp *Rhynchocinetes typus* where “typus,” “intermedius,” and “robustus” males are found (Correa et al. 2000), and *M. rosenbergii* where small, medium orange-clawed and large blue-clawed males (Ventura et al. 2011b) use different strategies to mate with females. When different male morphotypes are present, one type often phenotypically resembles a female (β -males, typus, and small, respectively, from the preceding examples), to allow them to enter unnoticed in the harem of the dominant males.

When secondary sexual characters are not evident, the localization of gonopores (or their absence in parthenogenetic crayfish; Vogt et al. 2004) can be used to differentiate males from females (and hermaphrodites, when both set of sexual gonopores are present), as well as the presence of an appendix masculina in males of many decapods, which regresses during sex change in protandrous species (Carpenter 1978, Bauer 1986a, Schatte and Saborowski 2006, Zupo et al. 2008). In some species (such as the brown shrimp *Crangon crangon*; G in Fig. 8.1) evidence of sex change can be inferred by comparing consecutive molts (Schatte and Saborowski 2006).

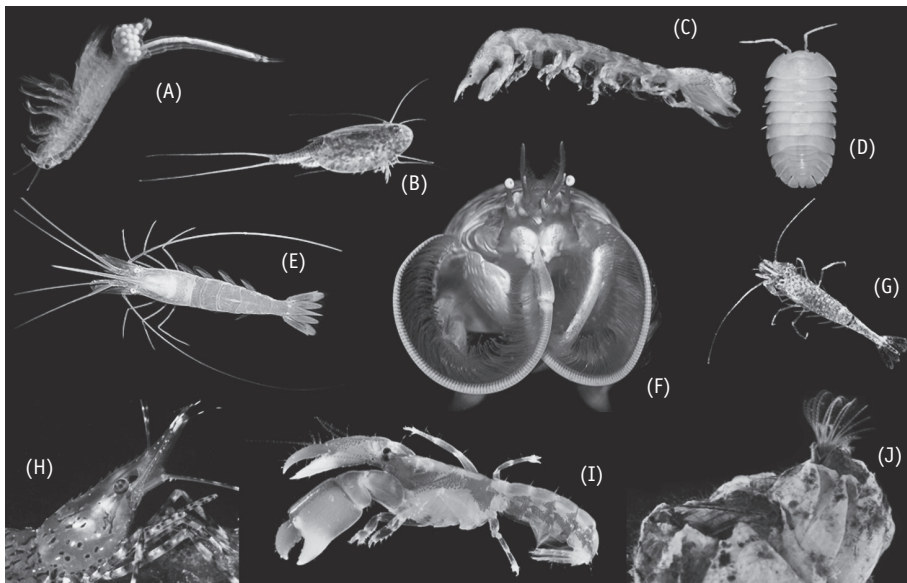


Fig. 8.1.

Selected examples of non-gonochoristic species, to show the variety of reproductive modes in crustaceans. (A) The anostracan *Artemia parthenogenetica*, characterized by mixed sexual and asexual (parthenogenetic) populations. (B) The notostracan *Triops cancriformis* exemplifies “geographical hermaphroditism,” where populations can be gonochoristic, androdioecious, and hermaphroditic. (C) The free-living isopod *Cyathura carinata*, one of the few examples of protogynous (female-first sex changer) crustaceans. (D) The parthenogenetic cave-dwelling isopod *Armadillidium virgo*. (E) The protandric simultaneous hermaphrodite *Exhippolysmata oplophoroides*. (F) The protandrous (male-first sex changer) *Emerita analoga*. (G) The facultative protandrous *Crangon crangon*. (H) The protandrous *Pandalus danae*. (I) The simultaneous hermaphrodite *Allaxius cf picteti*, belonging to the family Axiidea, the only known example of simultaneously hermaphroditic decapods. (J) The simultaneous hermaphrodite *Amphibalanus improvisus*. See color version of this figure in the centerfold. Photos: (A and B) Jean-François Cart; (C) Hans Hillewaert; (D) Domenico Caruso; (E) J. Antonio Baeza; (F and I) Arthur Anker; (G) Asma Althomali; (H) Ann Dornfeld; (J) Ian Frank Smith.

Sequential Hermaphroditism

There are several forms of sequential hermaphroditism, which is defined as changing from one sex into another during some portion of the life cycle. Starting life as male and then changing to female is termed *protandry*, whereas starting life as female and changing to male is termed *protogyny* (Table 8.1; Warner 1975, Policansky 1982, Munday et al. 2006). It is hypothesized that sequential hermaphroditism is a response to size-specific difference in maximized fitness of each sex (size advantage model; Ghiselin 1969). In scenarios where the fitness of small males is not too different from the fitness of large males but small females are less fecund than large females, a male-first strategy (protandry) can allow successful production of sperm early in life with a later switch to females when the individuals are larger and can better afford higher egg production.

Protandry is very common among malacostracans (Table 8.3), especially in decapods, amphipods, and isopods. Outside these taxa, it has been described only in two parasitic species of barnacles: *Waginella* (formerly *Synagoga*) *sandersi* and *Gorgonolaureus muzikae* (Brook et al. 1994, Policansky 1982). Among decapods, the majority of described occurrences of protandrous sex change is found in the family Pandalidae (31 species; the genus *Pandalus* seems to be completely protandrous; Chiba 2007, H in Fig. 8.1), but also in the families Atyidae (six species), Crangonoidea

(five species), Campylonotidae (four species), Alpheidae, Hippidae (see *Emerita analoga*, F in Fig. 8.1), Hippolytidae and Merguinae (two species each) with individual occurrences in four more families (Table 8.3). In some cases (e.g., *C. crangon*; G in Fig. 8.1), protandry is facultative (Schatte and Saborowski 2006). Among amphipods, seven protandrous species have been recorded in the family Lysianassidae and one species, *Stegocephalus inflatus*, among stegocephalids (Johnson et al. 2001). Among parasitic isopods, 17 protandrous species have been described in the Cymothoidae (this family, comprising 386 species, is possibly all completely protandric; Brusca 1981) and two in the Bopyridae. Their parasitic lifestyle makes it particularly difficult to study their reproductive cycle (Smit et al. 2014). Among the ectoparasitic cymothoids, different sites are parasitized in fish hosts: gill chambers, buccal cavity and body surface (Fig. 8.2). While parasitic isopods are mainly protandrous, both protandry and protogyny are found among free-living aquatic isopods. Among terrestrial isopods (superfamily Oniscoidea), one species is recorded as protandrous and one as protandric simultaneous hermaphroditic (Johnson et al. 2001).

In systems where males compete for females, large males have higher reproductive success, and small individuals maximize their fitness as females (protogyny). Interestingly, protogyny is very common in fish but not in crustaceans: out of the 114 known sequentially hermaphroditic crustacean species, 93 are protandrous and only 21 are protogynous (Table 8.3). Protogynous species are distributed among free-living (non-parasitic) isopod species (Tsai et al. 1999), with four species in the family Anthuridae (C in Fig. 8.1) and four in the family Sphaeromatidae. Among the Tanaidacea there are seven protogynous species in the family Leptocheilidae, two in the family Nototanaidae, and one each in the families Paratanaidae, Kalliapseudidae, Tanaididae, and Apseudidae (e.g., Highsmith 1983, Brook et al. 1994). Protogyny is probably more common among the Tanaidacea than what is reported here (Dojiri and Sieg 1997, Larsen 2001). Protogynic tanaids often have polymorphic males: males that used to be females (“secondary males”; Table 8.2) are morphologically different from males developed directly from juveniles (“primary males”). Also, “tertiary males” (who developed from females who had two broods, and not just one) are different from the other males (Larsen

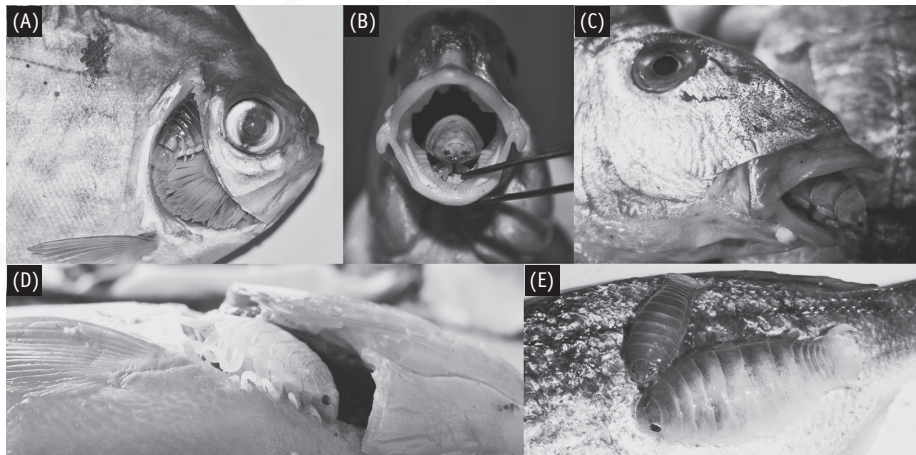


Fig. 8.2.

Ectoparasitic isopods in the family Cymothoidae (obligate parasites of fishes). (A) The gill chamber parasite *Anphira branchialis* on *Metynnus lipincottianus*. (B) *Ceratothoa italica* in the mouth of *Lithognathus mormyrus* and (C) escaping after realizing its host is dead. (D) *Braga patagonica* in the gills of *Pygocentrus nattereri*. (E) *Anilocra physodes* on *L. mormyrus*. See color version of this figure in the centerfold. Photos: (A and D) Charles Baillie; (B) Maria Sala-Bozano; (C and E) Stefano Mariani.

2001). Not all females change into males: this strategy seems to respond to a skewed sex ratio, due to higher mortality and a lack of feeding in males (Larsen 2001). In the tanaid *Leptocheilia africana*, once females molt into their male phase, they lose their functional mouth parts, do not feed anymore, and invest only in reproduction (Larsen and Froufe 2013). In *Leptocheilia dubia* males not only do not feed, but also are aggressive and fight for females (Highsmith 1983). Often protogyny is socially mediated (the dominant male prevents the other females from changing sex), which has been confirmed in tanaids (Highsmith 1983) and some isopods, even though this does not seem to be the case in *Gnorimosphaeroma oregonensis* (Brook et al. 1994).

A high level of plasticity is present in both protandric and protogynic sexual systems: not all individuals in all populations are sex changers. Some individuals can be born directly as the second sex (“primary males” in diandric protogynous species and “primary females” in digynic protandrous species; Tables 8.1 and 8.2) and thus do not change sex. Moreover, some species are facultatively sequentially hermaphroditic; i.e., not all individuals born as the first sex will change into the second sex, as is also seen in the tanaids, mentioned earlier, where the protogynous strategy depends on the population sex ratio (Larsen 2001). Both protandrous and protogynous hermaphrodites can be considered functionally dioecious, given that populations comprise males and females at any given time (Weeks 2012). However, the ability of individuals to be either sex at different times of their lives clearly differentiates these systems from strict dioecy. Interestingly, while protogyny is the most common system among fish, the majority of sex-changing crustaceans are protandric, as noted earlier. This difference is possibly related to the differing mating strategies employed by fish and crustaceans: while many fish have harem systems, where protogyny is advantageous (a female can greatly increase her fitness becoming the large dominant male; e.g., Munday et al. 2006), harems are not common in crustaceans. In harem crustacean species, like *P. sculpta* mentioned previously, alternative mating strategies are employed by males (Shuster and Wade 1991, Johnson et al 2001). Instead, in crustacean groups where protogyny is the norm, a change from female to male seems to be favored because of low abundance of males (see earlier discussion of tanaids), or large males might be favored during mate guarding, as hypothesized by Brook et al. (1994) in the isopod *G. oregonensis*. Bi-directional sex change (the ability of an individual to change sex multiple times, in either direction) is not confirmed in crustaceans, but is postulated in alpheid shrimps, *Arctostomus kominatoensis* and *A. dorsalis* (Nakashima 1987, Gherardi and Calloni 1993, Chiba 2007).

An unusual form of sequential hermaphroditism is termed “protandric simultaneous hermaphroditism” (Bauer 2000, 2006, Bauer and Newman 2004, Baeza et al. 2007). In this system, individuals develop first as males and then change into simultaneous hermaphrodites (Bauer 2000, Baeza 2009). This reproductive mode is typical of Lysmatidae (31 out of the 40 known species; Table 8.3; Lin and Zhang 2001, Bauer and Newman 2004, Bauer 2006, Baeza et al. 2007, E in Fig. 8.1) and possibly is found in Barbouriidae (four species) and Parastacidae (four species) and, unique among isopods, is reported in *Rhyscotus ortonedae* (formerly *Oniscoidea*). This sequential sexual change is also a response to differing reproductive values at different sizes: smaller males actually accrue more mates than larger males (Baeza 2007). When the shrimp attain a certain size, they then develop a female gonad but retain male functionality (Bauer 2000). Hermaphrodites do expend more effort in female gamete production, but still perform limited outcrossing as males (Baeza 2007). These shrimp have evolved from protandric sequential hermaphrodites (Baeza 2009, Baeza et al. 2009), so the retention of male function is a derived character in these species.

Interestingly, protandric simultaneous hermaphroditism is similar to androdioecy, in that at any one time the populations are mixtures of males and hermaphrodites. However, unlike other androdioecious crustaceans, wherein males are genetically distinct from hermaphrodites (Weeks et al. 2006a, Weeks 2012), in protandric simultaneous hermaphrodites, each individual

Table 8.2 Definition of Sexual Types

SEXUAL TYPES	
M	FIXED MALES found in gonochoristic and some androdioecious species. Males produce sperm or spermatophores. Primary and secondary male sexual characters (such as appendix masculina) are controlled by the androgenic gland
M	DWARF MALES characterized by extreme smaller size of males compared to conspecific females. Relatively common in dioecious barnacles, where they are found attached to the body of females
M	COMPLEMENTAL MALES found in androdioecious barnacles. The term was originally coined by Darwin (1851) to distinguish them from the miniature “dwarf” males in dioecious species
M	“RARE MALES” in parthenogenetic populations, composed mainly by females. They could be involved in “contagious parthenogenesis”
M	MALES (also SECONDARY MALES) in protogynous species (used to be females); sex-changers from female to male. They are the only males in monandric protogynous populations; they coexist with primary males in diandric populations
M'	PRIMARY MALES in diandric protogynous populations. Individual born male in a population where the majority of individuals are born female and change to male later in life
F	FIXED FEMALES found in gonochoristic species. Females produce eggs, which can be released or brooded attached to pleopods
F	FEMALES (also SECONDARY FEMALES) in protandrous species (used to be male); sex-changers from male to female. They are the only females in monogynic protandrous populations; they coexist with primary females in digynic populations
F'	PRIMARY FEMALES in digynic protandrous populations. Individuals born female in a population where the majority of individuals are born male and change to female later in life
H	SIMULTANEOUS OR SYNCHRONOUS HERMAPHRODITES able to produce male and female gametes at the same time
H	HERMAPHRODITES in protandrous simultaneous hermaphroditism (used to be males); sex-changers from males to hermaphrodites

will be both male and simultaneous hermaphrodite, depending on its age and size (Bauer 2000). In this way, the two reproductive modes are developmentally and ecologically different (Weeks 2012).

Simultaneous or Synchronous Hermaphroditism

Pure simultaneous hermaphroditism (all mature individuals in a population able to produce male and female gametes at the same time) is considered to be rare in crustaceans (Michiels 1998), as it is almost completely absent in the Malacostraca, where it is present in just two families: Apseudidae in the Tanaidacea (Johnson et al. 2001, Kakui and Hiruta 2013, Table 8.3) and putatively in the Axiidae (Johnson et al. 2001, Chiba 2007, Poore and Collins 2009, Komai et al. 2010, I in Fig. 8.1) within the Decapoda (see later discussion). In other non-malacostracan orders, populations comprising entirely hermaphrodites have been reported in the Cephalocarida (Addis et al. 2012), in the cave-dwelling Remipedia (Neiber et al. 2011, Kubrakiewicz et al. 2012), in some spinicaudatan branchiopods (Scanabissi and Mondini 2002, Weeks et al. 2005, Weeks et al. 2014, Brantner

et al. 2013a), in notostracans (Macdonald et al. 2011, Mathers et al. 2013), and in the Cirripedia (Thoracica; Charnov 1987, Kelly and Sanford 2010, Yusa et al. 2012, J in Fig. 8.1). However, simultaneous hermaphrodites do often co-occur with males in androdioecious (in Branchiopoda and Cirripedia, see later discussion) and in protandric simultaneous hermaphroditic systems (e.g., caridean shrimp).

Simultaneous hermaphroditism has apparently evolved four separate times in the Spinicaudata (Weeks et al. 2014) and five times in the Notostraca (Mathers et al. 2013). In some branchiopods, gonochoristic, androdioecious, and hermaphroditic populations occur in the same species (“geographical hermaphroditism,” as in the case of the tadpole shrimp *Triops cancriformis*; Zierold et al. 2007; B in Fig. 8.1).

In the Cephalocarida self-fertilization is probable: the male and female functional gonads are separated, but the gonoducts join together and open in a single pair of hermaphroditic genital pores (Addis et al. 2012); the immotile, aflagellate sperm is also a sign of very low mating competition (Morrow 2004), which could be found in selfing hermaphrodites. Among the previously mentioned groups, aflagellate sperm is found in Branchiopoda and Cephalocarida, but not in Remipedia and Cirripedia (Morrow 2004), and internal fertilization or pseudocopulation (sperm is released in the mantle cavity of the other hermaphrodite; Barazandeh et al. 2013) or fertilization in a brood pouch/chamber (Weeks et al. 2002) is probable or confirmed in all of them (Morrow 2004). Hermaphroditic barnacles, on the other hand, seem to perform cross-fertilization among sessile mates, using groping penises, given their sessile condition (Charnov 1987). Only a few species are considered capable of self-fertilization, at least facultatively (Furman and Yule 1990), but for many of them this ability is not fully confirmed (Wrange et al. 2016). The assumption was partially due to the fact that isolated barnacles could produce fertilized eggs, but a recent paper has reported spermcast mating (the possibility for barnacles to capture sperm from the water; Barazandeh et al. 2013), and thus this assumption may not be valid.

Among Malacostraca, simultaneous hermaphroditism has been recorded only in two tanaid species: *Apseudes spectabilis* (Kakui and Hiruta 2013) and *A. sculptus* (former *A. hermaphroditicus*; Johnson et al. 2001). The first described instance of self-fertilization in malacostracans is for *Apseudes* sp. (Kakui and Hiruta 2013). The infraorder Axiidea is suggested to be hermaphroditic (see family Axiidae, formerly Calocarididae, in Table 8.3; I in Fig. 8.1), due to the presence of both gonopores in each individual (Johnson et al. 2001, Chiba 2007, Poore and Collins 2009, Komai et al. 2010), even though the internal reproductive system (i.e., the presence of an ovotestis; Davison 2006) has not been described. In other families, individual “intersexes” have been described (Dworschak 2002), but there are just a few specimens and the functionality of both gonopores has not been investigated.

Simultaneous hermaphroditism maximizes the number of females in a population and the chances of finding a mate under low densities (Clark 1978). These two benefits do not apply completely, though, if the eggs can be fertilized only after molting (Raviv et al. 2008). In this case, during the reproductive season simultaneous hermaphroditic individuals can act as females only for a limited period after their molt, while they can act as males most of the time (Baeza 2007). This would reduce the possibility of reciprocity of gamete transfer. Self-fertilizing hermaphrodites do not have this problem, but inbreeding depression instead may limit the fitness benefits of using this reproductive strategy (Weeks et al. 2006a). Molting as a physiological constraint to receptivity might explain why pure simultaneous hermaphroditism is so rare among crustaceans, and possibly instead promoted the evolution of protandric simultaneous hermaphroditism and androdioecy in this taxon.

Androdioecy

Branchiopod Crustaceans

Androdioecy has been described from two orders of branchiopod crustaceans (Table 8.3), which occupy ephemeral, aquatic habitats that experience a broad range of abiotic environmental conditions and population densities (Hamer and Martens 1998, Weeks et al. 2006b, Benvenuto et al. 2009, Calabrese et al. 2016). The ephemeral nature of populations combined with low population densities has been argued as the reason that androdioecy evolves from dioecy in animals (Pannell 2002), and it likely explains why androdioecy is so widespread in these two orders (Weeks 2012). The best studied of these branchiopods are spinicaudatan clam shrimp in the genus *Eulimnadia* (see later discussion) that have hermaphrodites and males (Fig. 8.3); the hermaphrodites can either self-fertilize or can mate with males, but they cannot outcross with other hermaphrodites. *Eulimnadia* is the most speciose androdioecious lineage of any known plant or animal, having upwards of 53 species (Reed et al. 2015). Although some *Eulimnadia* appear to be all-hermaphroditic (Weeks et al. 2005), androdioecy is thought to be the ancestral breeding system in this genus (Weeks et al. 2006c, Weeks et al. 2009b). Thus, these crustaceans are both the most speciose and the longest-lived (minimally 25 million years) clade of androdioecious animals (Weeks et al. 2006c, Weeks 2012).

Androdioecy has also been described in the notostracan tadpole shrimp: in four species of *Triops*, namely *T. newberryi* (Sassaman 1989), *T. cancriformis* (Zierold et al. 2007), *T. longicaudatus* (Sassaman et al. 1997), and *T. australiensis* sp. B (Mathers et al. 2013 supplementary material), and in two species of *Lepidurus* (*L. arcticus* and *L. apus*; Mathers et al. 2013 supplementary material). However, the details of the reproductive system and its ecological significance in these species have not been thoroughly investigated.

Androdioecious branchiopods produce a small amount of sperm in an otherwise female gonad (Zucker et al. 1997, Scanabissi and Mondini 2002, Weeks et al. 2005) and in most other respects resemble the females of closely related gonochoristic species (Weeks et al. 2008). Several clam shrimp species have been studied histologically (Zucker et al. 1997, Scanabissi and Mondini 2002, Weeks et al. 2005, Weeks et al. 2006d, Weeks et al. 2009a, Weeks et al. 2014, Brantner et al. 2013a, 2013b), and in the four separate derivations of hermaphroditism from dioecy, all clam shrimp were found to produce a small amount of sperm in different locations throughout the ovotestes (Weeks et al. 2014). In the Notostraca, fewer histological studies of hermaphrodites have been undertaken, but in the one species examined, ovotestes produce small amounts of sperm intermingled with egg production (Longhurst 1955). In all other respects, the hermaphrodites of both orders are indistinguishable from females (Sassaman 1995), which is consistent among animals that have derived hermaphroditism from dioecy (Weeks 2012).

Cirriped Crustaceans

Androdioecy has been established in 35 barnacle species, across nine families (Table 8.3). The males of the androdioecious barnacles (termed “complemental” males by Darwin, 1851, Table 8.2) settle on or in depressions in the shell plates of the hermaphrodites, or in some cases even crawl inside the mantle (Foster 1983). The mode of sex determination in these species is uncertain. Two hypotheses have been proposed: (1) all larvae are potentially hermaphroditic, but those that settle in niches on large hermaphrodites do not grow to a size where female tissues may develop (i.e., the substratum determines sex expression); or (2) the sexes are actually genetically fixed and will develop into each sexual type regardless of environmental conditions. Each of these ideas may be valid in different species, given that complemental males have arisen separately in at least seven instances in the Cirripedia (Foster 1983, Yusa et al. 2012).

Crisp (1983) and Charnov (1987) hypothesized that cirripedes stemmed from a hermaphroditic ancestor. However, this assessment was based purely on a historical perspective without a phylogenetic analysis, which has been later conducted by Høeg (1995), tracing mating system transitions on

Table 8.3. List of Non-Gonochoristic Species, Identified from Literature, with Description of Reproductive Mode

CLASS BRANCHIOPODA

Order	Family	Genus	Species	RepMode	Ref
Anostraca	Artemiidae	<i>Artemia</i>	<i>parthenogenetica</i>	M	1
Notostraca	Triopsidae	<i>Triops</i>	<i>cancriformis</i>	D, A, H	2
			<i>longicaudatus</i>	A	3
			<i>australiensis</i> sp.B	A	4
			<i>newberryi</i>	A	5
	<i>Lepidurus</i>	<i>Apus</i>		A	4
			<i>articus</i>	A	4
Spinicaudata	Limnadiidae	<i>Calalimnadia</i>	<i>malhei</i>	H	6
		<i>Cyzicus</i>	<i>gynecia</i>	H	7
	<i>Eulimnadia</i>		<i>africana</i>	A	8
			<i>agassizii</i>	H	9
			<i>antlei</i>	A	10
			<i>Azisi</i>	H	7
			<i>brasiliensis</i>	A	8
			<i>braueriana</i>	A	8
			<i>colombiensis</i>	A	8
			<i>cylindrova</i>	A	8
			<i>dahli</i>	A	11
			<i>diversa</i>	A	8
			<i>feriensis</i>	A	8
			<i>foliisimilis</i>	A	11
			<i>gibba</i>	A	7
			<i>graniticola</i>	A	12
			<i>gunturensis</i>	H	7
			<i>michaeli</i>	A	7
			<i>texana</i>	A, H	13
			<i>thompsoni</i>	A	9
	<i>Limnadia</i>		<i>lenticularis</i>	H	14

(Continued)

Table 8.3. (Continued.)

CLASS CEPHALOCARIDA		Genus	Species	RepMode	Ref
Order	Family				
Brachypoda	Hutchinsoniellidae	<i>Hutchinsoniella</i>	<i>macracantha</i>	SH	15
		<i>Lightiella</i>	<i>magdalena</i>	SH	15
CLASS MAXILLOPODA (THECOSTRACA) CIRRIPIEDIA					
Order	Family	Genus	Species	RepMode	Ref
Ibliformes	Iblidae	<i>Ibla</i>	<i>pygmaea</i>	A	16
			<i>quadrivalvis</i>	A	17
Laurida	Synagogidae	<i>Gorgonolaureus</i> <i>Waginella</i>	<i>muzikae</i>	PA	18
			<i>sandersi</i>	PA	18
Lepadiformes	Heteralepadidae	<i>Heteralepas</i>	<i>japonica</i>	SH	19
			<i>quadrata</i>	SH	19
			<i>vetula</i>	A	20
			<i>dannevigi</i>	SH	19
			<i>klepalae</i>	A	21
			<i>palinuri</i>	SH	19
			<i>xenophorae</i>	A	19
			<i>avis</i>	A	22
			<i>willeyi</i> (<i>tinkeri</i>)	A	23,24
			Lepadiformes	Lepadidae	<i>Conchoderma</i> <i>Lepas</i>
<i>hunteri</i>	SH	19			
<i>virgatum</i>	SH	19			
<i>anatifera</i>	SH	19			
<i>anserifera</i>	SH	19			
<i>australis</i>	SH	19			
<i>pectinata</i>	SH	19			
<i>testudinata</i>	SH	19			
<i>celata</i>	SH	19			
	Oxynaspididae	<i>Oxynaspis</i>			

	Poecilasmatidae	<i>Octolasmis</i>	<i>angulata</i>	SH	19
			<i>cor</i>	SH	19
			<i>lowei</i>	SH	19
		<i>Poecilasma</i>	<i>kaempferi</i>	SH	19
		<i>Temnaspis</i>	<i>amygdalum</i>	SH	19
Scalpelliformes	Calanticiidae	<i>Calantica</i>	<i>siemensi</i>	A	25
			<i>spmosa</i>	A	19
			<i>stuederi</i>	A	25
			<i>villosa</i>	A	19
			<i>septiophila</i>	SH	19
	Eolepadidae	<i>Ashinkaitelepas</i>	<i>longa</i>	SH	19
		<i>Leucolepas</i>	<i>rapanuii</i>	SH	19
		<i>Neolepas</i>	<i>zevinae</i>	SH	19
		<i>Vulcanolepas</i>	<i>osheai</i>	SH	19
		<i>Lithotrypa</i>	<i>valentiana</i>	SH	19
Pollicipedidae	<i>Capitulium</i>	<i>mitella</i>	SH	19	
	<i>Pollicipes</i>	<i>pollicipes</i>	SH	19	
		<i>polymerus</i>	SH	19	
		<i>sociabile</i>	SH	19	
Scalpellidae	<i>Arcoscalpellum</i>	<i>sp.</i>	A	19	
	<i>Aurivilliclepas</i>	<i>calycula</i>	A	26	
	<i>Euscalpellum</i>	<i>squamuliferum</i>	A	25	
	<i>Scalpellum</i>	<i>peronii</i>	A	27	
		<i>scalpellum</i>	A	27,28	
		<i>vulgare</i>	A	17	
	<i>Scillaelepas</i>		<i>arnaudii</i>	A	29
			<i>bocquetae</i>	A	30
			<i>falcate</i>	A	30
			<i>fosteri</i>	A	30
	<i>Smilium</i>		<i>hastatum</i>	A	25
			<i>peronii</i>	A	19
		<i>Trianguloscalpellum</i>	<i>balanoides</i>	SH	19

(Continued)

Table 8.3. (Continued.)

CLASS MAXILLOPODA (THECOSTRACA) CIRRIPIEDIA cont.

Order	Family	Genus	Species	RepMode	Ref	
Sessilia	Archaeobalanidae	<i>Semibalanus</i>	<i>balanoides</i>	SH	31	
		<i>Amphibalanus</i>	<i>improvisus</i>	SH	3,2,33	
	Balanidae	<i>Balanus</i>	<i>calceolus</i>	A	34	
			<i>galeatus</i>	A	35	
	Bathylasmatidae	<i>Bathylasma</i>	<i>glandula</i>	SH	31	
			<i>masignotus</i>	A	34	
			<i>merrilli</i>	A	34	
			<i>azoricus</i>	SH	36	
	Bathylasmatidae	<i>Bathylasma</i>	<i>alcarum</i>	A	37	
			<i>corolliforme</i>	A	38	
	Catophragmidae	<i>Catomerus</i>	<i>polymerus</i>	SH	39	
	Chelonibidae	<i>Chelonibia</i>	<i>patula</i>	A	26	
			<i>testudinaria</i>	A	26,40	
	Pachylasmatidae	<i>Megalasma</i>	<i>striatum</i>	A	19	
			<i>warwickii</i>	A	19	
		<i>Octolasmis</i>	<i>unguisformis</i>	A	41	
			<i>trigonum</i>	A	42	
		<i>Tetrapachylasma</i>				

CLASS MALACOSTRACA					
Order	Family	Genus	Species	RepMode	Ref
Amphipoda	Caprellidae	<i>Paraprotella</i>	<i>teluksuang</i>	P	43
	Corophiidae	<i>Crassicorophium</i> (<i>Corophium</i>)	<i>bonelli</i>	P	43
	Crangonyctidae	<i>Stygobromus</i>	<i>albapinus</i> <i>pseudospinosus</i> <i>spinatus</i>	P P P	44 43 43
	Lysianassidae	<i>Acontiosoma</i>	<i>marionis</i> <i>tuberculata</i> <i>pungapunga</i>	PA PA PA	45+48 46 45+48
		<i>Amphorites</i> (<i>Stomacontion</i>)	<i>karta</i>	PA	47
		<i>Conicostoma</i>	<i>borius</i>	PA	48
		<i>Ocosingo</i>	<i>fenwicki</i>	PA	18
		<i>Scolopostoma</i>	<i>prionoplax</i>	PA	46+48
	Stegocephalidae	<i>Stegocephalus</i>	<i>inflatus</i>	PA	46
Decapoda	Alpheidae	<i>Arete</i>	<i>dorsalis</i> <i>indicus</i>	PA*** PA***	49S0 49S1
	Atyidae	<i>Atyoida</i>	<i>bisulcata</i> <i>serrata</i> <i>pilipes</i>	PA PA PA	49S2 49S2 49
		<i>Austratya</i>	<i>striolata</i>	PA	49
		<i>Caridina</i>	<i>richtersi</i>	PA	49S2
		<i>Paratya</i>	<i>curvirostris</i>	PA	45+49S3S4

(Continued)

Table 8.3. (Continued.)

Order	Family	Genus	Species	RepMode	Ref	
Decapoda cont.	Axiidae (Calocarididae)	Ambiaxiopsis	<i>altimanus</i>	SH?	55	
			<i>aberrans</i>	SH?	49	
			<i>flankinae</i>	SH?	49	
			<i>foveolatus</i>	SH?	49	
			<i>japonicus</i>	SH?	49	
			<i>propinquus</i>	SH?	56	
			<i>surugaensis</i>	SH?	49,57	
			<i>springeri</i>	SH?PA?	58	
			Bouvieraxius	<i>colpos</i>	PG?	
				<i>crossnieri</i>	SH?	49
		<i>formosus</i>		SH?	49	
		<i>laevis</i>		SH?	56	
		<i>laurentae</i>		SH?	49	
		Calastacus	<i>mexicanus</i>	SH?	59	
			<i>myalup</i>	SH?	49	
			<i>stiltrostris</i>	SH?	60	
			<i>felix</i>	SH?	49	
			<i>manningi</i>	SH?	49	
		Calaxiopsis	<i>mclaughlinae</i>	SH?	49	
			<i>serrata</i>	SH?	49	

Table 8.3. (Continued.)

Order	Family	Genus	Species	RepMode	Ref
Decapoda cont.	Crangonidae	<i>Argis</i>	<i>dentata</i>	PA	49:52:66
		<i>Crangon</i>	<i>crangon</i>	PA	52:49
	Hippidae	<i>Notocrangon</i>	<i>franciscorum</i>	PA	49
			<i>vulgaris</i>	PA	49
		<i>Emerita</i>	<i>antarcticus</i>	PA	49
			<i>analoga</i>	PA	48:52:67
	Hippolytidae	<i>Chorismus</i>	<i>asiatica</i>	PA	52
			<i>antarcticus</i>	PA	49
			<i>inermis</i>	PA?	49:62
	Lysmatidae	<i>Hippolyte</i>	<i>nohoci</i>	PSH?	68
		<i>Calliasmata</i>	<i>ensirostris</i>	PSH	68
			<i>ophioporoides</i>	PSH	62
		<i>Exhippolyasmata</i>	<i>amboinensis</i>	PSH	49:69
			<i>ankeri</i>	PSH	49:70
			<i>argentopunctata</i>	PSH	68
			<i>bahia</i>	PSH**	49:71
	Lysmata	<i>boggei</i>	<i>californica</i>	PSH	49:72
			<i>cf. acicula</i>	PSH	62
		<i>cf. anchisteus</i>	PSH	62	
		<i>cf. trisetacea</i>	PSH	70	
<i>Debelius</i>		PSH	49:70		
<i>galapaguensis</i>		PSH	70		

	<i>grabhami</i>	PSH	49:71
	<i>gracilirostris</i>	PSH	64
	Hochi	PSH	64:71
	<i>holthuisi</i>	PSH	73
	Lipkei	PSH	62
	<i>intermedia</i>	PSH**	64:71
	Moorei	PSH	62
	<i>nayaritensis</i>	PSH	74
	Nilita	PSH	49:66:71
	<i>pedersenii</i>	PSH	49:64:70
	Rafa	PSH	70
	<i>rnhibunae</i>	PSH	75
	<i>seticaudata</i>	PSH	49:66:71
	<i>ternatensis</i>	PSH	62
	Vittata	PSH	64
	<i>wurdemanni</i>	PSH**	49: 75
	<i>prima</i>	PSH	62:64:76
Merguinae	<i>oligodon</i>	PA	62; 64
	<i>rhizophorae</i>	PA	62; 64
	<i>coccinata</i>	PA?	49
	<i>dispar</i>	PA	48:49:77
	<i>gibba</i>	PA	49
	<i>glabra</i>	PA?	49
	<i>japonica</i>	PA	49

(Continued)

Table 8.3. (Continued.)

Order	Family	Genus	Species	RepMode	Ref
Decapoda cont.	Pandalidae cont.	<i>Pandalopsis</i> cont.	<i>lamelligera</i>	PA	49
			<i>cf. longirostris</i>	PA	49
			<i>montagui tridens</i>	PA	52
			<i>pacifica</i>	PA?	49
			<i>rubra</i>	PA	49
			<i>stenolepis</i>	PA	52
			<i>borealis</i>	PA	45:49,52:77
			<i>chani</i>	PA	49
			<i>curvatus</i>	PA	49
			<i>danae</i>	PA	45:49,52:77
			<i>eous</i>	PA	49
			<i>formosanus</i>	PA	49
			<i>goniurus</i>	PA	45:49,52:77
			<i>gracilis</i>	PA	49
			<i>gurneyi</i>	PA	49
			<i>hypsinotus</i>	PA	45:49,52:77
			<i>jordani</i>	PA	45:49,77
			<i>kessleri</i>	PA	52
			<i>latirostris (kessleri)</i>	PA	49,52:78
			<i>montagui</i>	PA	45:49,52:77
			<i>nipponensis</i>	PA	49
			<i>platyceros</i>	PA	45:49,77
			<i>prensor</i>	PA	49
<i>stenolepis</i>	PA	45:49,77			
<i>teraoi</i>	PA	49			
<i>tridens</i>	PA	49			

Parastacidae	<i>Parastacus</i>	<i>brasiliensis</i>	PSH?	49
		<i>nicoleti</i>	PSH	49
	<i>Samastacus</i>	<i>spinifrons</i>	PSH	4965
	<i>Virilastacus</i>	<i>rucaphuensis</i>	PSH	4965
Penaeidae	<i>Penaeus</i>	<i>kerathurus</i>	PA	52
Processidae	<i>Processa</i>	<i>edulis</i>	PA	49
Rhynchocinetidae	<i>Rhynchocinetes</i>	<i>uritai</i>	PA	79,80
Solenoceridae	<i>Solenocera</i>	<i>membranacea</i>	PA?	52
Thoridae	<i>Thor</i>	<i>amboinensis</i>	PA	81
		<i>manningi</i>	PA	45:49,62,66
		<i>carinata</i>	PG	45:52, 82
Anthuridae	<i>Cyathura</i>	<i>polita</i>	PG	52
		<i>profunda</i>	PG	45
		<i>tenuis</i>	PG	82
Armadillidiidae	<i>Armadillidium</i>	<i>virgo</i>	P	83
Bopyridae	<i>Munidion</i>	<i>pleurocondis</i>	PA	18
	<i>Orthione</i>	<i>griffenis</i>	PA	84
Cryptoniscidae	<i>Liriopsis</i>	<i>pygmaea</i>	PA	85

(Continued)

Table 8.3. (Continued.)

CLASSMALACOSTRACA cont.		Genus	Species	RepMode	Ref
Order Isopoda cont.	Family Cymothoidae	<i>Anilocra</i>	<i>frontalis</i> <i>pomacentri</i> <i>physodes</i> <i>branchialis</i> <i>patagonica</i> <i>oestroides</i> <i>excisa</i> <i>italica</i> <i>frontalis</i> <i>vulgaris</i> <i>audouinii</i>	PA PA PA PA PA PA PA PA PA PA PA	52 86 52 CB CB 87 92 88 89 93 52 90
		<i>Anphira</i> <i>Braga</i> <i>Ceratothoa</i> <i>Cymothoa</i>	<i>hemiramphi</i> <i>fushanensis</i> <i>puhi</i> <i>insularis</i> <i>epimerica</i> <i>acuminata (californica)</i> <i>elongata</i>	PA PA PA PA PA PA PA	45994 93 94 91 9395 52
		<i>Elthusa (Lironeca)</i> <i>Emetha</i> <i>Glossobius</i> <i>Ichthyoxenus</i> <i>Ichthyoxenus (Lironeca)</i> <i>Kuna</i> <i>Mothocya</i> <i>Nerocila</i> <i>Philoscia</i>	<i>balani</i> <i>floridiana</i> <i>aiasensis</i> <i>ortonadae</i> <i>parallelus</i> <i>insulare (luteum)</i> <i>naktongense</i> <i>oregonensis</i> <i>glynni</i>	PA P M, P PSH PA PG PG PG PG	96 83 83 52 94 97 45998 1945 45
		<i>Paraleptosphacroma</i> <i>Nagurus</i>	<i>cristatus</i> <i>modestus</i>	P P	83 83
		<i>Trichoniscus</i>	<i>pusillus (elisabethae)</i>	M	99,100

CLASS MALACOSTRACA cont.

Tanaidacea										
	Apsesuidae	<i>Apsedes</i>	<i>sculptus (hermaphroditicus)</i>	SH	82					
			<i>spectabilis</i>	SH	101					
			<i>holthuisi (sarsi)</i>	PG	102					
			<i>schubartii</i>	PG	103					
	Kalliapseudidae	<i>Monokalliapseudes (Kalliapseudes)</i>								
	Leptocheilidae	<i>Heterotanais</i>	<i>oerstedii</i>	PG	4552					
		<i>Leptocheilia</i>	<i>acrolophus</i>	PG	104					
			<i>africana</i>	PG	105					
			<i>dubia</i>	PG	1745					
			<i>forresti</i>	PG	45					
	Leptocheilidae cont.	<i>Leptocheilia</i>	<i>neapolitana</i>	PG	18					
		<i>Leptocheilia (Hargeria)</i>	<i>rapax</i>	PG	45					
	Nototanaidae	<i>Nototanais</i>	<i>dimorphus</i>	PG	106					
		<i>Nototanoides</i>	<i>trifurcatus</i>	PG	107					
	Paratanaidae	<i>Paratanais</i>	<i>maleficus</i>	PG	108					
	Tanaididae	<i>Sinelobus (Tanais)</i>	<i>standfordi</i>	PG	102					

CLASS OSTRACODA

Order

Podocopida

Family	Genus	Species	RepMode	Ref
Cyprididae	<i>Candellacypris</i>	<i>aragonica</i>	P	109
	<i>Eucypris</i>	<i>virens</i>	M	109110
	<i>Prionocypris</i>	<i>zenkeri</i>	P	109
Darwinulidae	<i>Alicenula</i>	<i>inversa</i>	P	109
	<i>Darwinula</i>	<i>stevensoni</i>	M	109
	<i>Microdarwinula</i>	<i>zimmeri</i>	P	109
	<i>Penthesilenula</i>	<i>brasiliensis</i>	P	109
		<i>kohanga</i>	P	109
	<i>Vestalenula</i>	<i>cornelia</i>	P	100
		<i>moloensis</i>	P	109
Limmocytheridae	<i>Limmocythere</i>	<i>inopinata</i>	P	100

(Continued)

Table 8.3. (Continued.)

CLASS REMIPEZIA					
Order	Family	Genus	Species	RepMode	Ref
Nectiopoda	Godzilliidae	<i>Godzillioognomus</i>	<i>frondosus</i>	SH*	iii
			<i>schrami</i>	SH*	iii
	Pleomothridae	<i>Godzillius</i>	<i>robustus</i>	SH*	iii
			<i>apletocheles</i>	SH*	iii
			<i>fragilis</i>	SH*	iii
	Speleonectidae	<i>Cryptocorynetes</i>	<i>elmorei</i>	SH*	iii
			<i>haptodiscus</i>	SH*	iii
			<i>longulus</i>	SH*	iii
			<i>entrichoma</i>	SH	iii
			<i>exleyi</i>	SH*	iii
		<i>Lasionectes (Kumonga)</i>	<i>atlantida</i>	SH*	iii
			<i>emersoni</i>	SH*	iii
		<i>Speleonectes</i>	<i>epilimnius</i>	SH*	iii
			<i>gironensis</i>	SH*	iii
		<i>kakuki</i>	SH*	iii	
<i>lucayensis</i>		SH*	iii		
<i>mimisi</i>		SH*	iii		
<i>ondinae</i>		SH*	iii		
<i>paraberjanimini</i>		SH*	iii		
<i>tulumensis</i>		SH*	iii		
<i>benjamini</i>	SH*	iii			
<i>tanumekes</i>	SH*	iii			

A: Androdioecious; D: Dioecious; SH: Simultaneous hermaphrodite; H: Hermaphroditic; PSH: Protandric simultaneous hermaphrodite; M: Mixed (asexual and sexual); PA: Protandry; PG: Protogyny; P: Parthenogenetic; * assumed; ** it is possible that some males "never switch to hermaphroditic"; *** (partial) — bidirectional; ? not confirmed.

¹Munoz et al. 2010, ²Zierold et al. 2007, ³Sassaman et al. 2007, ⁴Mathers et al. 2013, ⁵Sassaman et al. 2013, ⁶Weeks et al. 2006, ⁷Weeks et al. 2005, ⁸Sassaman 1988, ⁹Weeks et al. 2008, ¹⁰Rogers et al. 2010, ¹¹Sassaman and Weeks 1993, ¹²Scanabissi and Mondini 2002, ¹³Addis et al. 2012, ¹⁴Foster 1978, ¹⁵Darwin 1881, ¹⁶Brook et al. 1994, ¹⁷Newman 1996 as noted in Yusa et al. 2001, ¹⁸Kolbasov and Zevina 1999, ¹⁹Yusa et al. 2001, ²⁰Newman et al. 1969 as noted in Yusa et al. 2001, ²¹Hosie 2014, ²²Young 2003, ²³Crisp 1983, ²⁴Callan 1941, ²⁵Hoeg et al. 2016, ²⁶Jones and Lander 1995, ²⁷Newman 1980, ²⁸Hoch and Levinton 2012, ²⁹Furman and Yule 1990, ³⁰Wrangle et al. 2016, ³¹McLaughlin and Henry 1972, ³²Gomez 1975, ³³Dionisio et al. 1982, ³⁴Dayton et al. 1982, ³⁵Raimondi and Martin 1991, ³⁶Ewers-Saucedo et al. 2016, ³⁷Sawada et al. 2015, ³⁸Foster 1988, ³⁹Lim et al. 2015, ⁴⁰Taylor and Holsinger 2011, ⁴¹Allsop and West 2004, ⁴²Lowry and Stoddart 1986, ⁴³Lowry and Stoddart 2012, ⁴⁴Lowry and Stoddart 1983, ⁴⁵Nakashima 1987, ⁴⁶Chiba 2007, ⁴⁷Gherardi and Calloni 1993, ⁴⁸Policansky 1982, ⁴⁹Carpenter 1978, ⁵⁰Carpenter 1983, ⁵¹Komai 2011, ⁵²Komai et al. 2010, ⁵³Dworschak et al. 2012, ⁵⁴Kensley 2003, ⁵⁵Ngpe-Ho 2011, ⁵⁶Poore and Collins 2009, ⁵⁷Poore 2008, ⁵⁸Fiedler et al. 2010, ⁵⁹Omaga et al. 2012, ⁶⁰Baeza et al. 2013, ⁶¹Yazicioglu et al. 2016, ⁶²Bauer 1986b, ⁶³Barnes and Wenner 1968, ⁶⁴Baeza 2013, ⁶⁵Fiedler 1998, ⁶⁶Baeza et al. 2009, ⁶⁷Baeza 2008, ⁶⁸Bauer and Newman 2004, ⁶⁹Anker et al. 2009, ⁷⁰Baeza et al. 2007, ⁷¹Lin and Zhang 2001, ⁷²Murray et al. 2012, ⁷³Butler 1964, ⁷⁴Chiba et al. 2000, ⁷⁵Osawa et al. 2015, ⁷⁶Osawa et al. 2015, ⁷⁷Dworschak et al. 2012, ⁷⁸Bauer and Thiel 2011, ⁷⁹Baeza and Piantoni 2010, ⁸⁰Johnson et al. 2001, ⁸¹Caruso and Bouchon 2012, ⁸²Williams and Boyko 2012, ⁸³Adema and Huwae 1982, ⁸⁴Adlard and Lester 1995, ⁸⁵Madineo 2003, ⁸⁶Pawluk et al. 2015, ⁸⁷Aneesh et al. 2015, ⁸⁸Bakenhaer et al. 2006, ⁸⁹Bello et al. 1997, ⁹⁰Cook and Munguia 2015, ⁹¹Brusca 1978, ⁹²Tsai et al. 1999, ⁹³Brusca 1978, ⁹⁴Amott 2001, ⁹⁵Hiebert 2015, ⁹⁶Abe et al. 1982, ⁹⁷Bell 1982, ⁹⁸van der Kooij and Schwander 2014, ⁹⁹Kakui and Hiruta 2013, ¹⁰⁰Highsmith 1983, ¹⁰¹Pennafime and Soares-Gomes 2009, ¹⁰²Bird 2015, ¹⁰³Larsen and Froufe 2013, ¹⁰⁴Marinovic 1987, ¹⁰⁵Seg and Heard 1985, ¹⁰⁶Larsen 2001, ¹⁰⁷Schön et al. 2003, ¹⁰⁸Schmit et al. 2013a,b,c, ¹⁰⁹Neiber et al. 2011, ¹¹⁰Charles Baillet personal communication

the resulting tree. The analysis revealed that the two outgroup lineages were dioecious. Additionally, within the Cirripedia, the Acrothoracica and the Rhizocephala exhibit dioecy. The Thoracica is the most derived lineage and exhibits the first transition to hermaphroditism (Høeg 1995). The families within the Thoracica exhibit dioecy, hermaphroditism, and androdioecy, but the evolution of these sexual systems remains unclear. The Iblidae is the most basal family, diverging at the node where hermaphroditism is thought to have evolved. From this, it may be argued that complementary males in this family could have evolved from a dioecious ancestor. In the remaining families, it is more parsimonious that the complementary males evolved secondarily from hermaphrodites (Høeg 1995). Yusa et al. (2012) argue that androdioecy evolves from hermaphroditism and then dioecy is derived from androdioecy. To address the evolution of mating systems adequately in this group, a more robust phylogeny is required.

The barnacles described as androdioecious occur in various regions of the world, exhibit a variety of life histories, and are phylogenetically diverse (Yusa et al. 2012). Darwin (1851) first noted this mating system in *Scalpellum vulgare* and *Ibla quadrivalvis*. In the genus *Scalpellum*, two more species are known to have complementary males: *S. scalpellum* and *S. peronii*. Additionally, in the Scalpellidae, five species in the genus *Scillaelepas* are androdioecious (one now recorded as *Aurivillialepas*; Table 8.3). Within the genus *Ibla*, there is some confusion as to the number of androdioecious species (Table 8.3). Some of this confusion may stem from authors often using the terms “hermaphrodite” and “female” interchangeably, as well as “dwarf males” and “complementary males.” Within the order Sessilia, the families Balanidae and the Pachylasmatidae each contain four species with complementary males (Table 8.3). Two species of *Chelonibia* are androdioecious, *C. patula* and *C. testudinaria*, and both are commensal barnacles (Crisp 1983). *Koleolepas avis* and *K. tinkeri* (junior synonym of *K. willei*) are the only two species in the family Koleolepadidae that have been described as androdioecious (Hosie 2014). Other less-studied androdioecious barnacles include two species of *Bathylasma* (*B. alearum* and *B. corolliforme*) and two species of *Paralepas* (*P. xenophorae* and *P. klepalae*). Additionally, androdioecy has been described in four species of *Calantica*, two species of *Smilium* and *Octolasmis*, and one species each of *Heteralepas*, *Arcoscalpellum*, *Euscalpellum*, *Megalasma*, and *Tetrapachylasma* (Table 8.3).

EVOLUTION OF CRUSTACEAN REPRODUCTIVE SYSTEMS

Ancestral Crustacean Reproduction

There is growing consensus on the phylogenetic relationships among crustacean lineages (Jenner 2010; see Chapters 4 and 5 in Volume 8), but the reproductive mode of the first crustacean lineage (sometimes termed the “urcrustacean”; Hessler and Newman 1975) is unclear. Cisne (1982, p. 67) suggested that the first crustacean was free-living, marine, benthic and “probably” dioecious. However, others (Hessler and Newman 1975, Juchault 1999) suggested that the hermaphroditic Cephalocarida are representative of the ancestral crustacean. In this group, according to Cisne (1982, p. 69), hermaphroditism is likely derived as “an accommodation for reproduction at the low population densities at which cephalocarids seem to occur.” This again suggests a dioecious ancestry in Crustacea. Phylogenies based on morphological characters often place the Remipedia (especially the Nectiopoda) as the basal lineage (Wills 1997). Nectiopodans are hermaphroditic (Ito and Schram 1988). Molecular phylogenetic analyses have suggested that ostracods may be basal for crustaceans (Spears and Abele 1997, von Reumont et al. 2012). Ostracods are primarily dioecious, except for the derived cases of parthenogenesis (Cohen and Morin 1990). Thus, further research needs to be done to determine whether the ancestral crustacean reproduced via dioecy or hermaphroditism.

Although we do not know the reproductive mode of the “urcrustacean,” we do know that evolutionary transitions between various reproductive modes have occurred repeatedly within the Crustacea (e.g., Høeg 1995, Perez-Losada et al. 2012, Yusa et al. 2012, Mathers et al., 2013, Weeks et al. 2014). Below, we will discuss these transitions.

Reproductive Transitions

Transitions from Dioecy to Hermaphroditism

The evolution of hermaphroditism from separate sexes has not been widely debated, but it has been commonly assumed that an “intermediate” of androdioecy or gynodioecy (Table 8.1) may facilitate such a transition. Gynodioecy appears to be exceptionally rare in animals (Weeks 2012), but Pannell (1997, 2002) suggested that androdioecy might be a transitional strategy when evolving hermaphroditism from dioecy in a structured metapopulation in which “reproductive assurance” (i.e., the ability to self-fertilize when mates are rare) is strongly advantageous (e.g., in early colonizing species) but in which outcrossing is still advantageous when population size allows locating a suitable mate. Weeks and colleagues (Weeks et al. 2006a, Weeks et al. 2009b, Weeks 2012) proposed the “constraint” hypothesis for why androdioecy should be commonly derived from dioecy: if hermaphroditism is selectively favored in a previously dioecious species (e.g., for reproductive assurance), the constraint hypothesis suggests that the most likely hermaphrodite to evolve from a dioecious progenitor would be a female-biased hermaphrodite that allocates limited resources to sperm production but lacks the ability to mate with other hermaphrodites because of a lack of male secondary sexual characters (e.g., copulatory or mating structures; C in Fig. 8.3). Consequently,

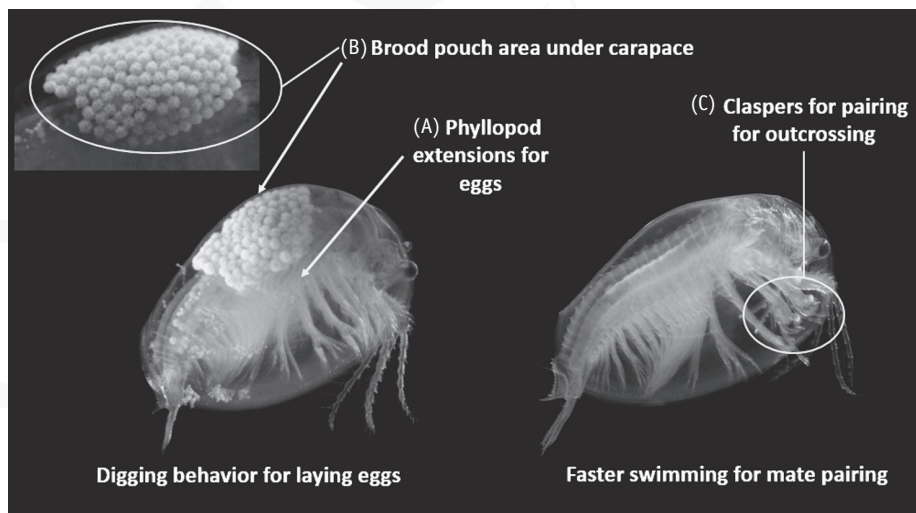


Fig. 8.3.

Hermaphrodite (left) and male (right) clam shrimp, *Eulimnadia texana*. In addition to the basic differences between male and female gametes, clam shrimp also have several secondary sexual differences. Clam shrimp females and hermaphrodites require extensions of the phyllopods (A) and a modified carapace to produce a brood chamber (B) to brood their eggs. Additionally, they need to dig holes in the sediment to bury their eggs. Males require specific mating behaviors (i.e., faster swimming) as well as clasping appendages (C) to pair for outcrossing. In clam shrimp, hermaphrodites have only the male characteristic of sperm production and none of the other secondary male characters, and thus cannot outcross with other hermaphrodites. See color version of this figure in the centerfold. Photos courtesy of Jean-François Cart.

these female-biased hermaphrodites can only self-fertilize. This hypothesis assumes that in dioecious species with many sex-specific traits, an evolutionary transition to effective expression of both sexes would be highly improbable (Weeks 2012), requiring the simultaneous acquisition of both primary (e.g., gamete production) and secondary sexual characters (Fig. 8.3). Therefore in sexually dimorphic, dioecious ancestors, androdioecy is more likely to evolve than gynodioecy because the number of evolutionary changes needed to produce a functional hermaphrodite from a male would be much higher.

Weeks (2012) tested these ideas and found that in 40 crustacean species, androdioecy had evolved from a dioecious ancestor in four genera: *Eulimnadia*, *Ibla*, *Lysmata*, and *Triops* (Fig. 8.4). Two of these are branchiopod crustaceans (*Eulimnadia* and *Triops*), one is a barnacle (*Ibla*), and one is a decapod (*Lysmata*). The latter two groups deserve special comment. As noted earlier, barnacles have complementary males that in some species are environmentally induced, becoming males when settling on larger hermaphrodites, but in other cases are genetically determined. The decapod *Lysmata* is a “simultaneous protandric hermaphrodite,” which means that the various *Lysmata* species are mixes of younger males that eventually develop into simultaneous hermaphrodites (Baeza 2007, 2009, Baeza et al. 2009). In both cases, the populations are mixes of males and hermaphrodites and thus could be considered androdioecious (Weeks 2012). As predicted earlier, there are no examples of crustaceans that have evolved gynodioecy from dioecy (Fig. 8.4).

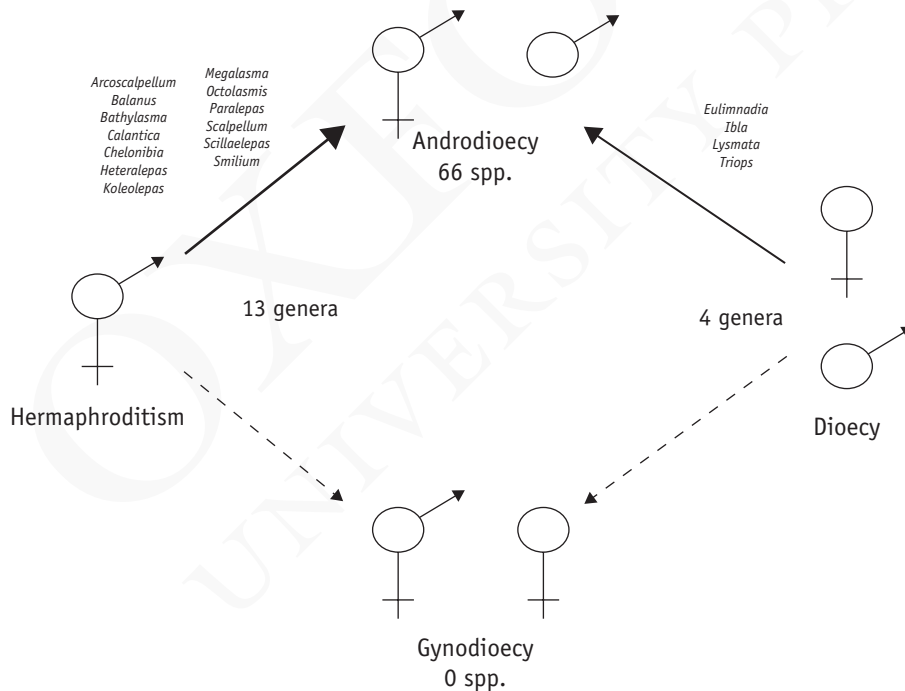


Fig. 8.4. Evolutionary transitions in reproductive systems from dioecy to hermaphroditism (or vice versa) through androdioecy (males and hermaphrodites) and gynodioecy (females and hermaphrodites). The thickness of the arrows represents the known occurrence of genera (listed in the figure). Dotted arrows represent a lack of known occurrences. The number of species for each intermediate reproductive type are noted below each type, and the identification of the various genera are shown above the respective arrows.

A good example of the constraint hypothesis (Weeks 2012) can be found in branchiopod crustaceans, especially the well-studied clam shrimp (Weeks et al. 2009b). Males produce amoeboid sperm that fertilize the females' eggs externally in a "brood chamber" (B in Fig. 8.3) on the dorsal surface of the female (Weeks et al. 2004). A hermaphrodite developed from a female would only need to produce sperm within the tubular gonad typifying clam shrimp (Scanabissi and Mondini 2000) to be capable of self-fertilization in the absence of males. On the other hand, a hermaphroditic clam shrimp developed from a male would need to gain the ability to produce yolk, shell the eggs, develop a brood chamber, gain the ability to store eggs in the brood chamber (i.e., by attaching them to extensions of the phyllopod appendages; A in Fig. 8.3), and develop the digging behavior needed to bury the eggs in the pond bottom (Zucker et al. 2002). Unless all of these phenotypes are controlled by the same regulatory pathway, it is highly unlikely that all of these evolutionary changes could occur simultaneously within an otherwise male genetic background. Thus one should expect the simplest pathway to produce a hermaphrodite would be the evolution of hermaphrodites from a female progenitor, which is what is observed in these clam shrimp (Zucker et al. 1997, Weeks et al. 2005, Weeks et al. 2006a, Weeks et al. 2009b). These patterns are mirrored in the branchiopod *Triops* as well (Zierold et al. 2007, Mathers et al. 2013).

Indeed, in all the androdioecious crustacean species derived from dioecious ancestors in which relative allocation patterns between male and female gametes have been reported, the hermaphrodites closely resemble females, with only minor amounts of reproductive effort devoted to sperm production (Weeks et al. 2006a, Chasnov 2010). As noted earlier, androdioecious branchiopod hermaphrodites resemble the females of closely related dioecious species (Weeks et al. 2008), and decapod shrimp in the genus *Lysmata* (Bauer 2006) also show female-biased allocation. As suggested earlier, these overall patterns can be explained by assuming a constraint on the development of a hermaphrodite that can competently perform as a male while simultaneously being competent as a female when there are numerous traits required to be competent in both male and female roles (Weeks 2012).

Transitions from Hermaphroditism to Dioecy

If the ancestral crustacean was hermaphroditic, then dioecy is a derived condition in all gonochoristic species. Juchault (1999) has an intriguing hypothesis for how such a transition occurred, suggesting that a cytoplasmic parasite (e.g., *Wolbachia*) infected hermaphrodites and inhibited male expression to increase the parasite's inheritance. This would create all-female invaders to otherwise hermaphroditic species. If this parasitic infection spread through the population, it would select for increased allocation to male function in the non-infected hermaphrodites. Over time, as the parasite spread, uninfected hermaphrodites would be selected to eventually lose female function to become strictly male. This would complete the transition from ancestral hermaphroditism to dioecy (Juchault 1999). We are unaware of any evidence that this has happened in any crustacean, but it is an intriguing idea.

More definitive results have been developed in the botanical literature where transitions from hermaphroditism to dioecy have been considered in detail. Such transitions have occurred dozens of times in flowering plants (Bawa 1980, Ashman 2002, Barrett 2010). Theoretical work suggests that dioecy does not evolve directly from hermaphroditism, but rather that either gynodioecy or androdioecy acts as an intermediate stage in the transition (Charlesworth and Charlesworth 1978). It is predicted that the intermediate breeding system of gynodioecy will be more common than androdioecy in plants (Lloyd 1975, Charlesworth and Charlesworth 1978), which is indeed observed (Pannell 2002).

In crustaceans, we find no transitions from hermaphroditism to gynodioecy and 13 generic transitions from hermaphroditism to androdioecy (33 total species; Fig. 8.4). Interestingly, each one of these transitions is a barnacle species evolving dwarf (or complementary) males from

hermaphroditic progenitors (Weeks 2012). In these androdioecious species, males are specifically serving a different purpose than the hermaphrodites, being a ready source of sperm to nearby, larger hermaphrodites (Yusa et al. 2012). Some have argued that these smaller males are following the same sequential reproductive maturity as the *Lysmata* noted earlier (i.e., maturing as males when small and then growing to simultaneous hermaphrodites; Callan 1941, Crisp 1983). If so, then this switch may indicate that barnacles are more fit as males when they are small because sperm are cheaper to produce than eggs, but then do better by switching to hermaphrodites when they are larger and can afford the higher cost of producing eggs, as argued by Charnov (1982). Others argue that the smaller males are a distinct morph to the larger hermaphrodites (Gomez 1975). In either case, the expression of the sexes is based on the different roles of hermaphrodites and males that correspond to different body sizes and population densities (Ghiselin 1969, Charnov 1982, Blanckenhorn 2000).

It appears that the evolution of dioecy from hermaphroditism in crustaceans is quite different from that proposed for flowering plants. The transition from hermaphroditism to dioecy in flowering plants has been discussed in terms of avoidance of inbreeding (Lloyd 1975, Charlesworth and Charlesworth 1978) and is much more likely via the gynodioecious intermediate stage (Charlesworth 2006). However in crustaceans, the only known transitions from hermaphroditism are to androdioecy and not gynodioecy (Fig. 8.4), and these transitions are almost certainly not to avoid inbreeding depression, since barnacles are not inbreeding (Weeks 2012, Yusa et al. 2012). The groping penises of hermaphroditic barnacles are not likely to allow self-fertilization, as noted earlier. Instead, it appears that differential selective pressures on differently sized individuals drive sexual expression (i.e., differential sex allocation strategies with size; see Ghiselin 1969, Charnov 1982).

ECOLOGICAL CORRELATES OF REPRODUCTIVE SYSTEMS

Crustaceans have successfully colonized a wide variety of environments, including the most extreme, such as deserts, hydrothermal vents, and Antarctic lakes (Benvenuto et al. 2015), where population densities can be very low. Their success is due to their extraordinary adaptability, reflected by the tremendous diversity in morphology, physiology, ecology, behavior, and reproductive strategies that they display.

We have identified from the literature 334 species belonging to 67 families in 13 orders of five classes of crustaceans (Table 8.4), which are not gonochoristic (also, the list is not comprehensive for parthenogenetic species). Two classes, the Remipedia and Cephalocarida, seem to be completely characterized by simultaneous hermaphroditism (but data are scarce). These two classes have been commonly considered basal in the phylogenetic tree of crustaceans, although recent analyses group them together with Hexapoda as Allotriocarida (von Reumont et al. 2012; see Chapter 5 in Volume 8). They inhabit anchialine cave systems and marine benthic substrata, respectively, and their population densities are very low (Neiber et al. 2011). Thus, being able to simultaneously act as both sexes increases the chances to find a mating partner in these groups.

Another challenging habitat, where densities can fluctuate broadly, are ephemeral freshwater pools. In these environments, some spinicaudatan branchiopods are simultaneous hermaphrodites (six species), although the majority of non-gonochoristic species (which are also present) are androdioecious (15 species). Among the notostracan branchiopods, one species (*T. cancriformis*) presents androdioecious, hermaphroditic, and dioecious populations. In ephemeral environments, the ability to self-fertilize (in absence of males; see discussion of androdioecious populations) allows these species to colonize new pools with only a single individual (the self-fertile *E. texana* can produce offspring of different sexes: males and hermaphrodites; Weeks et al. 2006a).

Table 8.4. Number of Non-Gonochoristic Species, by Order and Family, with Description of Reproductive Mode

Order	Family	Total Number of Genera and Species	A	SH	PA	PG	PSH	P	M
Notostraca	Triopsidae	2, 15	6						
Spinicaudata	Limnadiidae	5, ~61	15	6					
Brachypoda	Hutchinsoniellidae	5, 13		2					
Ibliformes	Iblidae	2, 6	2						
Laurida	Synagogidae	8, 27			2				
Lepadiformes	Heteralepadidae	3, 39	3	4					
Lepadiformes	Koleolepadidae	1, 1	2						
Lepadiformes	Lepadidae	3, 12		8					
Lepadiformes	Oxynaspididae	1, 20		1					
Lepadiformes	Poecilasmatidae	8, 40		5					
Scapelliformes	Calanticidae	10, 44	4						
Scapelliformes	Eolepadidae	4, 7		5					
Scapelliformes	Lithotryidae	1, 3		1					
Scapelliformes	Pollicipedidae	2, 7		3					
Scapelliformes	Scapellidae	28, 268	12	2					
Sessilia	Archaeobalanidae	12, 121		1					
Sessilia	Balanidae	16, 94	4	3					
Sessilia	Bathylasmatidae	4, 20	2						
Sessilia	Catophragmidae	2, 2		1					
Sessilia	Chelonibiidae	1, 6	2						
Sessilia	Pachylasmatidae	7, 26	4						
Amphipoda	Caprellidae	88, 401							1
Amphipoda	Corophiidae	25, 149							1
Amphipoda	Crangonyctidae	9, 225							3
Amphipoda	Lysianassidae	78, 491			7				
Amphipoda	Stegocephalidae	25, 108			1				
Decapoda	Alpheidae	47, 659			2				
Decapoda	Atyidae	42, 468			6				
Decapoda	Axiidae (Calocarididae)	44, 112		33					
Decapoda	Barbouriidae	3, 8					4		
Decapoda	Cambaridae	12, 428						1	1
Decapoda	Campylonotidae	1, 5			4				
Decapoda	Crangonoidea				5				
Decapoda	Hippidae	3, 27			2				
Decapoda	Hippolytidae	37, 336			2				
Decapoda	Lysmatidae						31		
Decapoda	Merguiidae	1, 2			2				
Decapoda	Pandalidae	23, 188			31				

Order	Family	Total Number of Genera and Species	A	SH	PA	PG	PSH	P	M
Decapoda	Parastacidae	15, 165					4		
Decapoda	Penaeidae	32, 222			1				
Decapoda	Processidae	4, 68			1				
Decapoda	Rhynchocinetidae	2, 25			1				
Decapoda	Solenoceridae	9, 83			1				
Decapoda	Thoridae				2				
Isopoda	Anthuridae	25, 291				4			
Isopoda	Armadillidiidae	15, 315						1	
Isopoda	Bopyridae	158, 614			2				
Isopoda	Cryptoniscidae	8, 24			1				
Isopoda	Cymothoidae	43, 386			18				
Isopoda	Hemioniscidae	3, 10			1				
Isopoda	Philosciidae	114, 569						1	
Isopoda	Platyarthridae	9, 122						1	
Isopoda	Rhyscotidae	1, 23			1		1		
Isopoda	Sphaeromatidae	96, 706				4			
Isopoda	Trachelipodidae	21, 245						2	
Isopoda	Trichoniscidae	89, 519							1
Tanaidacea	Apeudidae	22, 167		2		1			
Tanaidacea	Kalliapseudidae	11, 41				1			
Tanaidacea	Leptochelidae	11, 61				7			
Tanaidacea	Nototanaidae	6, 10				2			
Tanaidacea	Paratanaidae	7, 34				1			
Tanaidacea	Tanaididae					1			
Podocopida	Cyprididae							2	1
Podocopida	Darwinulidae							6	1
Podocopida	Limnocytheridae							1	
Nectiopoda	Godzilliidae	3, 4		3					
Nectiopoda	Pleomothridae			2					
Nectiopoda	Speleonectidae	4, 16		17					
			56	99	93	21	40	20	4

A: Androdioecious; SH: Simultaneous hermaphrodite; PA: Protandry; PG: Protogyny; PSH: Protandric simultaneous hermaphrodite; P: Parthenogenetic; M: mixed. Total number of genera and species per family retrieved from Zhang (2011). Taxa in bold are possibly completely characterized by the same sexual system. For the order Anostraca, family Artemiidae please refer to Chapter 9, this volume.

A combination of simultaneous hermaphroditism and androdioecy is also found in the Cirripedia (34 hermaphroditic species belonging to 11 families; 37 androdioecious species belonging to nine families). Indeed, barnacles show a great variety of sexual systems, which might have evolved in response to their sessile lifestyle, densities (mating group sizes), and spatial limitations (Yusa et al. 2013, Sawada et al. 2015). Morphological constraints (small internal mantle cavity space to brood eggs) and energy allocation have also been considered to be linked to the evolution of a hermaphroditic lifestyle in this group (Hoch and Levinton 2012), favoring an almost completely female individual that can produce small amounts of sperm (with the male function that can be adjusted based on crowding and sperm competition).

Locating mates is also problematic in deep-sea habitats. Here, hermaphroditism is commonly reported for fishes (Warner 1984) and analogously we have found information for 33 simultaneous hermaphroditic species of deep-water axiid burrowing shrimps (class Decapoda; Table 8.4; I in Fig. 8.1). These species, and only two species in the family Apseudidae (class Tanaidacea, otherwise characterized by protogynous sequential hermaphroditism), are the only ones expressing simultaneous hermaphroditism, among the Malacostraca.

Simultaneous hermaphroditism increases the chances of successful fertilization, enhancing encounter rates with potential mates (any individual of the same species can be a potential mate, while gonochoristic species need to find a mate of the opposite sex). An even more extreme mechanism for reproductive assurance is self-fertilization, which can be advantageous when the density of conspecifics is extremely low and in early colonizing species (Baker 1955). This advantage might exceed the cost of inbreeding depression. Self-fertilization has been described in branchiopods and in one malacostracan species (*Apseudes* sp.; Kakui and Hiruta 2013); it is not excluded in the Cephalocarida (Addis et al. 2012), and might occur in some barnacles (still debated; Kelly and Sanford 2010, Barzandeh et al. 2013, Wrangle et al. 2016).

If simultaneous hermaphroditism augments fertilization success, sequential hermaphroditism (sex change) increases individual lifetime reproductive success (Warner 1975), as is the case in decapods (Charnov 1979, Charnov and Anderson 1989). Sequential hermaphroditism is often found among obligate parasites (Ghiselin 1969). The isopods belonging to the family Cymothoidae (obligate parasites of fishes; Fig. 8.2), Bopyridae, and Cryptoniscoidea (obligate parasites of crustaceans; Dreyer and Wägele 2001) are protandric sequential hermaphrodites. In the genus *Cymothoa* (which parasitizes the buccal cavity of fishes; B, C in Fig. 8.2), the first free-swimming male manca (post-larval juvenile) reaching a host will attach to the tongue of the fish, becoming a female, while the subsequent ones will remain males (Cook and Munguia 2013, Pawluk et al. 2015). Parasites face challenges similar to colonizing species and sessile organisms living at low densities; thus, sequential hermaphroditism will ensure the presence of the two sexes in the same host, as well as increasing individual lifetime reproductive success (larger females are highly fecund; Tsai et al. 1999). Among barnacles, in the infraorder Ascothoracida (parasites of coelenterates and echinoderms), two species, *W. sandersi* and *G. muzikae*, are protandrous (Policansky 1982, Brook et al. 1994), while the Rhizocephala (parasites of decapods) are dioecious (Høeg et al. 2016). Overall, protandry is favored to increase offspring production when there is little male competition and thus the second sex (female) is older, larger, and more fecund than the first sex, as well as being favored in parasitic species.

When male competition is high, larger males are more successful than smaller ones (but see Blanckenhorn 2000 for exceptions), thus individuals reproduce initially as females and then switch to males. As mentioned earlier, protogynous sex change is commonly found in harem fish (e.g., Munday et al. 2006), where it is often socially regulated (a condition-dependent strategy: females will not change to males in the presence of other males). Protogynous sex change does not appear to be socially regulated in the intertidal isopod *Gnorimosphaeroma oregonensis* (Brook et al. 1994),

but in this case, females can produce only one brood and males mate-guard females, so it is advantageous to produce a single clutch as a female and then keep reproducing as a male (with the additional advantage of larger size, to compete with other males). Socially mediated sex change also occurs in some parasitic protandric isopods (where females might release a pheromone to prevent other males from changing into female; Ravichandran et al. 2009) and in some protandric simultaneous crustaceans (Baeza and Bauer 2004).

Protandric simultaneous hermaphroditism (40 species described in 4 families) is less common than protandrous hermaphroditism (93 species belonging to 21 families), which may seem counterintuitive, given the possible advantage of maintaining male abilities (as a non-selfing hermaphrodite) when switching to the female phase. Initially, this unusual mating system was linked to a symbiotic lifestyle (expressed by socially monogamous species specialized as fish cleaners; Bauer 2000) characterized by limited mobility (for site fidelity to the cleaning station) and low population densities. In this condition, protandrous simultaneous hermaphroditism would have initially evolved and then been maintained in species occurring in denser aggregations (historical contingency hypothesis; Bauer 2000). However, recent phylogenetic analyses (Baeza 2013) do not support this hypothesis, leaving some questions about the evolution of this “puzzling” sexual system (Bauer 2000).

In general, most of the “unusual” reproductive strategies in crustaceans seem indeed beneficial when encounter rates with conspecifics are low and/or environments are unpredictable/unstable, which is commonly found in “colonizing,” parasitic, and symbiotic species (Baeza and Thiel 2007). The flexibility of crustacean reproductive systems allows them to be a very successful group in these challenging circumstances.

Population Consequences of Reproductive Systems

The type of reproductive mode influences sex ratios, mating success, and colonization events and thus has important ecological consequences at the population level. Sequentially hermaphroditic species experience skewed sex-ratios toward the first sex (male in protandry and female in protogyny), but sex ratios are even more variable due to the possibility that some individuals develop directly as the second sex (primary females in protandrous species and primary males in protogynous species; Table 8.2; Allsop and West 2004, Chiba 2007). Many species of the genus *Pandalus* are dyginic (with primary and secondary females), as is *Processa edulis*. More complex is the situation of *Thor manningi*, where not all males change sex; so secondary females coexist with sex-changing males, but also with primary females (shrimp born directly as the second sex) and males that will never change sex (Bauer 1986b). Primary and secondary males are also found in the protogynous tanaid *Leptochelia africana* (Larsen and Froufe 2013), the two alpheid species *Athanas indicus* and *A. kominatoensis*, and in the pandalid *Pandalus hipsinotus* (Correa and Thiel 2003). In all these cases, the reproductive value of an individual and its mating success depend on its sexual type and the frequency of other sexual types in the population.

Apart from primary and secondary males and different male morphotypes, “miniature males” are also present: complementary males in some androdieocius species and dwarf males in dioecious ones (Table 8.2), including barnacles (as mentioned earlier), epicaridean parasitic isopods, in the superfamilies Bopyroidea and Cryptoniscoidea (Dreyer and Wägele 2001, Asakura 2009), copepods (Vogt 2016), and anomurans (genus *Emerita*, where neotenous males maintain physical contact with females in turbulent surf waters; Asakura 2009). These tiny males, attached to females, can have a similar role as hermaphrodites, and they can be seen as an adaptation to low densities in challenging environments and during parasitism (Ghiselin 1969).

FUTURE DIRECTIONS AND CONCLUSIONS

Future Directions

The diversity of crustacean reproductive types offers excellent opportunities for carcinologists to explore the evolution and ecology of various sexual systems. A most productive start to these future studies would be to map reproductive modes onto a robust phylogeny of Crustacea to infer ancestral reproduction in these interesting animals. From such a mapping, we could determine which sexual systems evolved from which progenitors, and how frequently transitions occurred between various reproductive modes. Such a mapping could also reveal which systems are unlikely to lead to future changes (i.e., “evolutionary dead ends”). Adding comparisons to habitat types could also inform larger questions of reproductive evolution and evolutionary transitions between reproductive types.

Herein, we have concentrated primarily on various forms of hermaphroditic and mixed sexual systems (Table 8.4). Specific questions for these systems include the following: Are androdioecious species “transitional” stages between hermaphroditism and dioecy, or are they stable endpoints? More detailed phylogenetic analyses of androdioecy in the Notostraca that better resolve reproductive transitions as well as likely lineage ages for androdioecious taxa would be particularly revealing (Mathers et al. 2013). If androdioecy is determined to be long-lived in both the Notostraca and Spinicaudata, what ecological conditions select for androdioecy in these crustaceans? Correlations of reproductive system with habitat or other life-history traits in *Eulimnadia*, *Triops*, and *Lepidurus* could shed light on the conditions that select for androdioecy in these freshwater crustaceans.

A correlate of the preceding is whether there are any gynodioecious crustaceans, and if not, why not? Although gynodioecy is exceptionally rare in animals, it is likely that this mating system is simply under-reported (Weeks 2012). Hermaphroditic crustaceans are excellent systems to explore further for cases of gynodioecy, especially among the reproductively labile barnacles. In particular, self-compatible hermaphroditic barnacle lineages that experience inbreeding depression would be the most likely to evolve gynodioecy (Charlesworth and Charlesworth 1978), so that would be a fruitful area to explore.

Simultaneous and protogynous hermaphroditism are rare in crustaceans. Empirical tests, phylogenetic analyses, and theoretical models should be employed to gain a better understanding of the hypothesized physiological (e.g., molt) constraints for the former and possibly low presence of harem species in the latter. More research is needed in this field. Protandric simultaneous hermaphroditism appears to be limited to the family Lysmatidae and a minority of other crustacean species (Table 8.4).

We have listed 334 non-gonochoristic species, strictly limiting our list only to species where actual data are known about life-history traits and reproductive strategies. Some taxa seem to be completely characterized by the same sexual system, but we have preferred to be overly cautious in our analysis. Indeed, the paucity of detailed data on the mating and sexual system of many groups is a limiting factor to gather a better overview and a more detailed resolution on evolutionary processes. More studies should confirm what mating and sexual systems are found in crustacean groups to develop a more complete picture of the evolutionary transitions between dioecy, simultaneous hermaphroditism, and sequential (protandric and protogynous) hermaphroditism in crustaceans. Focused attention on reproductively labile taxa (e.g., the Branchiopoda, Ostracoda, and the barnacles) would allow a more complete picture of reproductively diverse crustaceans. The Isopoda are another large and heterogeneous group that should be explored (phylogenetically and ecologically), as they show a breadth of ecological niches (marine, freshwater, and terrestrial) and life-history strategies (free-living, commensal, and parasitic), as well as reproductive modes (Table 8.4), providing interesting comparative possibilities. Pairing such a broad phylogenetic comparison

among taxa with their corresponding ecological correlates would provide invaluable insights into the likely environmental pressures that selected for reproductive switches.

Finally, what are the applied implications of mating systems for conservation and management of commercially important stocks or endangered species?

Conclusions

Clearly, crustaceans exhibit a broad range of reproductive types (Tables 8.3 and 8.4), which reflects both the wide array of habitats in which they are found and their various ecological roles. The majority of crustaceans are gonochoric (dioecious), but as we have outlined in this chapter, there are numerous variations from the “standard” male + female reproductive mode. We have concentrated on delineating the variety of hermaphroditic reproductive modes, leaving the delineation of asexual reproduction to another chapter in this volume (see Chapter 9 in this volume). We have noted a lack of gynodioecy in Crustacea, which is mirrored throughout the Animalia (Weeks 2012). We have also noted the likely evolutionary transitions between these various reproductive systems and remarked on the known ecological correlates of many of these systems. Overall, comparative studies of crustacean reproductive modes in an ecological and evolutionary context are only in their infancy, with investigations of individual taxa (e.g., branchiopods, *Lysmata* decapods, barnacles) allowing glimpses into larger scale evolutionary patterns. However, much more research needs to be done to allow us to fit together the interesting information from these various taxa into a larger-scale view of crustacean reproductive evolution and what drives such evolution.

There are plenty of unanswered questions in reproductive evolution. Crustaceans are wonderful systems in which to delve into these questions.

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Fig. 8.1.

Selected examples of non-gonochoristic species, to show the variety of reproductive modes in crustaceans. (A) The anostracan *Artemia parthenogenetica*, characterized by mixed sexual and asexual (parthenogenetic) populations. (B) The notostracan *Triops cancrivorus* exemplifies "geographical hermaphroditism", where populations can be gonochoristic, androdioecious, and hermaphroditic. (C) The free-living isopod *Cyathura carinata*, one of the few examples of protogynous (female-first sex changer) crustaceans. (D) The parthenogenetic cave-dwelling isopod *Armadillidium virgo*. (E) The protandric simultaneous hermaphrodite *Emerita analoga*. (F) The simultaneous hermafroditous (male-first sex changer) *Emerita analoga*. (G) The facultative protandrous *Crangon crangon*. (H) The protandrous *Pandanus danac*. (I) The simultaneous hermaphrodite *Allaxius f. picteti*, belonging to the family Axiidae, the only known example of hermaphroditic decapods. (J) The simultaneous hermaphrodite *Amphibalanus improvisus*.

Photos: (A and B) Jean-François Cart; (C) Hans Hillewaert; (D) Domenico Caruso; (E) J. Antonio Baeza; (F and I) Arthur Anker; (G) Asma Althomali; (H) Ann Dornfeld; (J) Ian Frank Smith.



Fig. 8.2. Ectoparasitic isopods in the family Cymothoidae (obligate parasites of fishes). (A) The gill chamber parasite *Amphira branchialis* on *Metymnis lipincottianus*. (B) *Ceratothoa italica* in the mouth of *Lithognathus mormyrus* and (C) escaping after realizing its host is dead. (D) *Brage patagonica* in the gills of *Pygocentrus nattereri*. (E) *Anilocra physodes* on *L. mormyrus*. Photos: (A and D) Charles Baillie; (B) Maria Sala-Bozano; (C and E) Stefano Mariani.

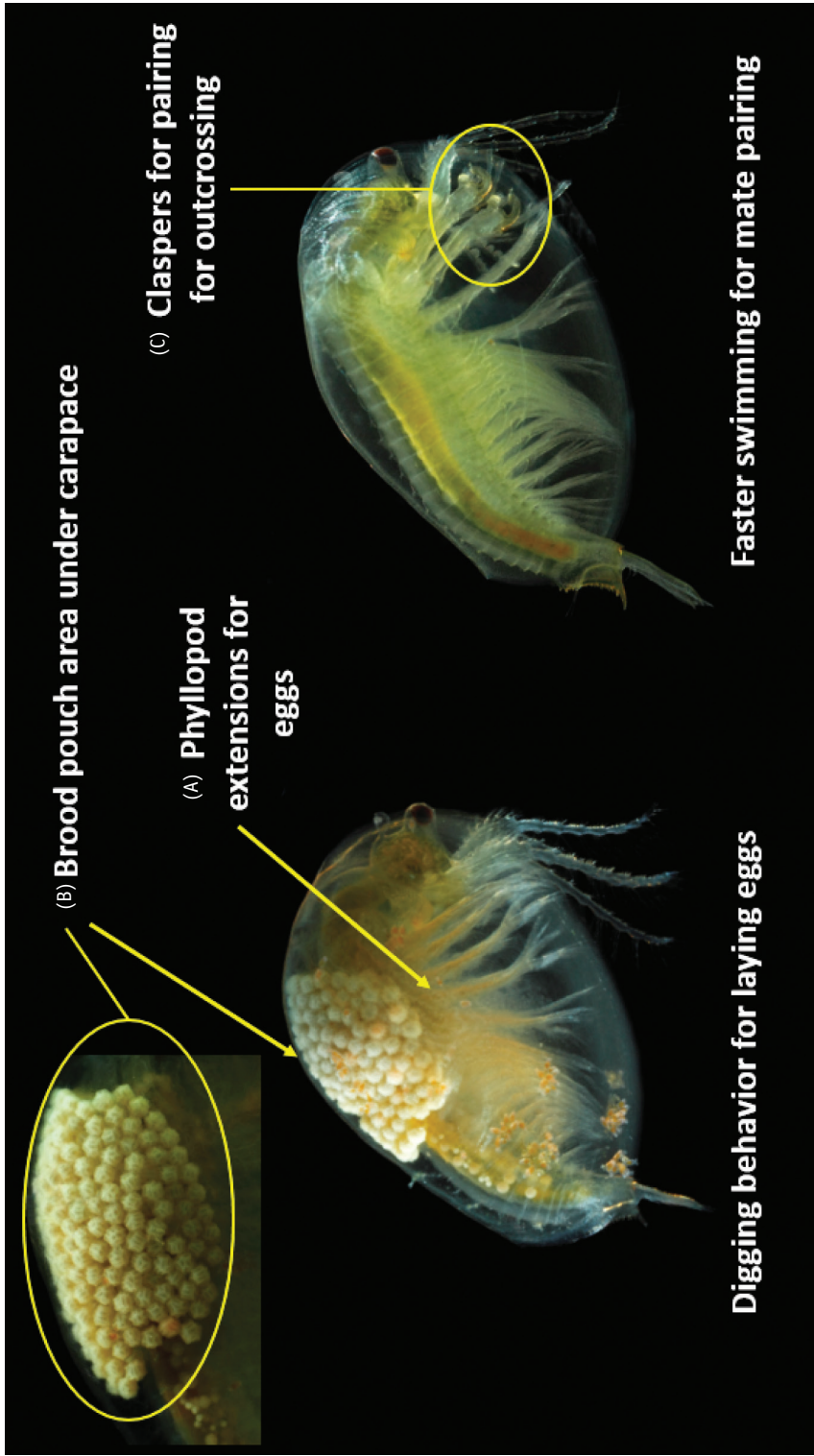


Fig. 8-3. Hermaphrodite (left) and male (right) clam shrimp, *Eulimnadia texana*. In addition to the basic differences between male and female gametes, clam shrimp also have several secondary sexual differences. Clam shrimp females and hermaphrodites require extensions of the phyllopods (A) and a modified carapace to produce a brood chamber (B) to brood their eggs. Additionally, they need to dig holes in the sediment to bury their eggs. Males require specific mating behaviors (i.e., faster swimming) as well as clasping appendages (C) to pair for outcrossing. In clam shrimp, hermaphrodites have only the male characteristic of sperm production and none of the other secondary male characters, and thus cannot outcross with other hermaphrodites. Photos courtesy of Jean-François Cart.