Janet L. Leonard *Editor*

Transitions Between Sexual Systems

Understanding the Mechanisms of, and Pathways Between, Dioecy, Hermaphroditism and Other Sexual Systems

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To my husband, Bruce Karsh, with all my love

Preface

The stimulus for this book came from Verena Penning of Springer Verlag, who approached me about doing a book related to the topic of a symposium "Phenotypic plasticity and the evolution of gender" which I had organized for the 2013 meeting of the Society for Integrative and Comparative Biology and which was published that year in *Integrative and Comparative Biology*. With her encouragement, I began thinking about whether there were new and unexplored areas in the field, which could be the basis for a useful and groundbreaking book, and I decided there was. The focus of this book is on taxonomic groups that demonstrate substantial diversity of sexual systems with the goal of understanding what selective pressures are associated with changes in sexual system and what evolutionary pathways and sex-determining mechanisms are involved in changes in sexual systems when they change. George Williams (1975), in his seminal book, *Sex and Evolution*, (a) pointed out that sexual systems are often extremely conservative, in defiance of the theory of the era, and (b) suggested that understanding what factors were important in determining sexual system or evolutionary changes in sexual system would best come from analysis of taxa characterized by lability or diversity in sexual system. This book, then, is an effort to follow Williams' suggestion by offering an array of chapters, each dedicated to a taxon (or group of taxa) which is variable in sexual system, with a goal of analyzing the selective pressures, evolutionary pathways, and/or sex-determination mechanisms that explain this diversity.

When one begins to review a field, one always finds that it is riddled with rabbit holes, many of them full of fascinating facts, discoveries, and ideas that enrich one's understanding of evolution and biology (and sometimes also the workings of scientists' minds), even though this material often proves completely irrelevant to the theme of the review. Occasionally, there is real treasure down one of these holes. It is probably fair to say that there are two types of scientists, those who enjoy rabbit holes and those who do not. I happen to enjoy them, perhaps too much, and consequently planning, participating in, and particularly reading the chapters of this book has been a great pleasure. I hope all the authors who have contributed to this book have had the same experience. It is also my fervent hope that readers of this book will find both an authoritative source for the topics in question and a rich source of rabbit holes to explore.

My thanks to Verena Penning, the whole staff of Springer Verlag, and especially the authors of the book's chapters who gave their time to making this book possible and have taught me so much and the many reviewers who have made the book better.

Santa Cruz, CA Janet L. Leonard

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Chapter 1
The Evolution of Sexual Systems in Animals

Janet L. Leonard

Abstract A sexual system is the pattern of gender allocation that characterizes a species. In both plants and animals, simultaneous hermaphroditism and dioecy are the most common and stable sexual systems. Other sexual systems, sequential hermaphroditism, environmental sex determination, gynodioecy, androdioecy, and trioecy, are less stable and less widely distributed. The boundaries between these sexual systems are not always clear, largely because phenotypic plasticity is an important and prevalent component of sexual reproduction. One can view sexual systems in the Metazoa as lying on a gradient of phenotypic plasticity from simultaneous hermaphroditism at the high end through sequential hermaphroditism and environmental sex determination to genetically determined dioecy, which has a minimum of phenotypic plasticity in sex allocation. The distribution of sexual systems across the Metazoa gave rise to Williams' Paradox, which states that the pattern is best explained by phylogeny rather than sex allocation theory. Today, sex allocation theory seems to explain transitions in sexual system in those taxa with labile sexual systems adequately. However, the stability of either dioecy or simultaneous hermaphroditism in many major taxa, such as phyla and classes, remains inexplicable. While in angiosperms the evolutionary pathways between dioecy and simultaneous hermaphroditism are fairly well understood, a plausible evolutionary sequence for transitions between dioecy and simultaneous hermaphroditism in animals has been lacking. Here, the proposal is made that it is useful to view transitions from simultaneous hermaphroditism to dioecy as the result of selection for decreasing phenotypic plasticity and *vice versa.* A scenario for evolutionary transitions between simultaneous hermaphroditism and dioecy, in animals, through intermediate stages of sequential hermaphroditism and environmental sex determination is proposed.

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1.1 Introduction

A sexual system is the pattern of gender allocation that exists in a species (Box 1.1). Dioecy, in which there are two types of individuals, males (individuals reproducing through sperm) and females (individuals that reproduce through eggs), and simultaneous hermaphroditism, in which all individuals are capable of reproducing through both sperm and eggs in a single breeding season, are the most common, widespread, and evolutionarily stable sexual systems in both multicellular plants and animals (Ghiselin 1974; Williams 1975; Maynard Smith 1978; Leonard 2013; Chaps. 2 and 3, etc.). However, there are many other systems such as sequential hermaphroditism, in which an individual reproduces through eggs during one part of its life and sperm during another; gynodioecy, in which populations are composed of a mixture of females and simultaneous hermaphrodites; androdioecy in which populations consist of males and hermaphrodites; and even some examples of trioecy, with populations consisting of males, females, and hermaphrodites (Ghiselin 1974; Leonard 2010, 2013) (see Box 1.1). Understanding the evolution of sexual systems from the standpoint of natural and sexual selection acting on individuals has been a focus of evolutionary ecology for over 40 years (Williams 1975, etc.), but important questions remain.

Box 1.1

A. Dioecy = gonochorism

Dioecy is a sexual system in which individuals reproduce in one sexual role (male or female), only, during their lifetime. It is characteristic of many large taxa (phyla and classes) in both plants and animals (insects, birds, mammals, reptiles, amphibian, vast majority of nematodes, gymnosperms, etc.). The sex of an individual can be determined by either genetic or environmental factors or a combination of the two.

B. Simultaneous hermaphroditism (SH)

1. Selfing simultaneous hermaphroditism: individuals produce both eggs and sperm and reproduce through self-fertilization exclusively. This sexual system has evolved many times but is not characteristic of any major taxon and may be short-lived, evolutionarily.
2. Outcrossing simultaneous hermaphroditism: individuals are capable of reproducing in both sexual roles (male and female) during a single reproductive season. Outcrossing simultaneous hermaphroditism, in which individuals can mate with another individual in both the male and female sexual role, is characteristic of many large taxa (phyla and classes) in both plants and animals. Some outcrossing simultaneous hermaphrodites are also capable of self-fertilization.

(continued)

Box 1.1 (continued)

C. Sequential hermaphroditism

Individuals reproduce in different sexual roles during different reproductive periods of their life histories. This may involve a single change in sex with increasing size/age, or it may involve more than one change from male to female or the reverse depending on environmental variables. Sequential hermaphroditism is not characteristic of phyla or classes but is characteristic of many families of teleost fishes and some families of caenogastropods and has evolved several times in polychaetes, gastropods, and some groups of shrimps. It is also found in angiosperms.

D. Androdioecy

In androdioecy, breeding populations consist of a mixture of males and simultaneous hermaphrodites. Androdioecy is relatively rare in angiosperms but does occur and may offer an evolutionary path from dioecy to simultaneous hermaphroditism (Pannell 2002; Chap. 3; Delph 2009). In metazoan animals androdioecy has evolved many times but appears to be restricted taxonomically (Weeks 2012). The most common form of androdioecy in animals involves hermaphrodites that either self-fertilize or outcross with males but do not outcross with sperm (Weeks 2012). Another type of androdioecy, derived from hermaphroditic ancestors, does involve outcrossing by hermaphrodites. Some authors (Pannell 2002) restrict the term androdioecy to cases in which there is a genetic distinction between males and hermaphrodites as is usually the case in androdioecy derived from dioecious taxa (see Chaps. 3 and 4; Weeks et al. 2006).

E. Gynodioecy

In this sexual system, populations are made up of a mixture of females and simultaneous hermaphrodites. In angiosperms, it has evolved many times and it may represent part of a transition from simultaneous hermaphroditism to dioecy (see Charlesworth 1999; Delph 2009; Chap. 3). In animals it is extremely rare (review in Leonard 2010; Weeks 2012; see text). As with androdioecy, drawing a hard line between "true" gynodioecy with distinct, genetically determined morphs and cases of simultaneous hermaphroditism and a pure female state being developmental stages of the same individual is not always straightforward.

F. Trioecy

This sexual system involves populations consisting of a mixture of males, females, and simultaneous hermaphrodites. It is always very rare but has been found in both plants and animals, e.g., papaya and rhabditid nematodes. Trioecy may be either genetically or environmentally mediated (see text).

There are two major outstanding problems in understanding the evolution of sexual systems: (a) understanding the distribution of sexual systems among

Table 1.1 Sexual systems in the Plantae (Embryophyta)[a]

Phylum[a,b,c,d]			
	Class	Sexual system	Comments
			Spore plants
Anthocerophyta		Hermaphroditic[e]	Hornworts
Hepatophyta		Hermaphroditic[e]	Liverworts
Bryophyta		Hermaphroditic[e]	Mosses
Lycophyta			
	Lycopodiopsida	Hermaphroditic[e]	Clubmosses
	Isoetopsida	Hermaphroditic[e]	Spikemosses, quillworts
Monilophyta			
	Sphenopsida	Hermaphroditic[e]	Horsetails
	Filicopsida	Hermaphroditic[e]	Ferns
	Psilotopsida	Hermaphroditic[e]	Whisk ferns
			Seed plants
Gnetophyta		Dioecious	Vines, small trees, (Inc. *Ephedra*), and *Welwitschia*[d]
Coniferophyta		Dioecious or hermaphroditic	Conifers
Gingkophyta		Dioecious	One living species, *Ginkgo biloba*
Cycadophyta		Dioecious	
Magnoliophyta		Predominantly hermaphroditic, recurrent evolution of dioecy, gynodioecy, and occasionally androdioecy	Angiosperms

[a] Case and Jesson (Chap. 2)
[b] Lecointre and Le Guyader (2006)
[c] Margulis and Schwartz (1982)
[d] Wijesundara (2011)
[e] Sporophytes hermaphroditic as far as known; hence genets hermaphroditic, dioecious sporophytes theoretically possible but unknown (Chap. 2)

organisms and (b) identifying the evolutionary pathways from one sexual system to another. G.C. Williams (1975) pointed out that while the existing body of theory suggested that sexual systems should be sensitive to ecological factors (population density, encounter probability, length of reproductive lifetime, etc.), the distribution of sexual systems among organisms shows that this is often not the case. That is, for both plants and animals, the best predictor of sexual system in most taxa is not ecology but rather phylogeny, the phylum or class to which they belong (Williams' Paradox; see below and Leonard 1990, 2005, 2010, 2013). Table 1.1 shows the distribution of sexual systems across the Plantae, while Table 1.2 shows the distribution of sexual systems across the Metazoa. In both cases, whole phyla are characterized by dioecy, or hermaphroditism, while in both groups, a few taxa are

Table 1.2 Sexual systems in the Metazoa (Modified from Leonard 2013

Phylum		Mode(s) of sexuality	Comments
	Class		
Porifera		Usually hermaphrodites	No permanent gonads; not clear how often sperm and eggs ripen simultaneously versus sequentially; sessile
Placozoa		Yes	Very poorly known
Cnidaria		Either dioecious or hermaphroditic	Either pelagic or sessile
Ctenophora		Largely hermaphrodites	Pelagic
Platyhelminthes		Almost exclusively hermaphroditic	Free-living or parasitic; dioecy in parasitic family Schistosomatidae, sometimes in Didymozoidae[a]
Nemertea		Dioecious	Free-living
Rotifera		Dioecious	Free-living
Acanthocephala		Dioecious	Parasitic
Cycliophora		Dioecious; sessile female and dwarf male	Poorly known
Entoprocta		Protandric or simultaneous hermaphrodites	Sessile
Sipuncula		Dioecious except for one species	Tube-dwelling worms
Mollusca		Primitively dioecious	
	Solenogastres	Hermaphroditic	
	Caudofoveata	Dioecious	
	Polyplacophora	Mostly dioecious, one genus w/hermaphrodites[b]	Chitons
	Monoplacophora	Dioecious	
	Gastropoda[b]		
	Basal clades	Varied sexual systems	The basal clades include the Patellogastropoda, Vetigastropods, etc.
	Caenogastropoda	Largely dioecious; some sequential and simultaneous hermaphrodites[b]	
	Heterobranchia	Almost exclusively simultaneous hermaphrodites	
	Cephalopoda	Dioecious	
	Bivalvia	Largely dioecious; some hermaphrodites; various independent events	
	Scaphopoda	Dioecious	
Annelida			
	Polychaeta	Mostly dioecious	Both sedentary and errant families

(continued)

Table 1.2 (continued)

Phylum			
	Class	Mode(s) of sexuality	Comments
	Oligochaeta	Hermaphroditic	
	Hirudinea	Hermaphroditic	Predators and ectoparasites
	Echiura	Dioecious	Burrow-dwellers
	Pogonophora	Dioecious	Sessile tube-dwellers
Ectoprocta		Hermaphroditic	Sessile
Phoronida		Either dioecious or hermaphroditic	Sessile tube-dwellers
Brachiopoda		Dioecious, some hermaphrodites[c]	Sessile
Chaetognatha		Simultaneous hermaphrodites	Pelagic predators
Gastrotricha		Largely hermaphroditic	Interstitial
Priapulida		Dioecious	Sessile tube-dwellers or mobile predators
Loricifera		Dioecious	Interstitial
Kinorhyncha		Dioecious	Interstitial
Nematomorpha		Dioecious	Parasitic larvae; free-living adults
Nematoda		Dioecious or (rarely) androdioecious	Both parasites and free-living forms, dioecious
Onychophora		Dioecious	Terrestrial, tropical
Tardigrada		Dioecious	Aquatic
Euarthropoda			
	Chelicerformes	Dioecious	Pycnogonida, Merostomata, and Arachnida
	Remipedia	Hermaphroditic	Marine
	Cephalocarida	Hermaphroditic	Benthic, marine
	Maxillopoda	Dioecious or Hermaphroditic according to subclade	Copepods, ostracods, etc., dioecious; Cirripedia (barnacles; sessile, largely hermaphroditic)
	Branchiopoda	Largely dioecious, some hermaphroditic (notostracans) and androdioecious (chonchostracan) taxa	Largely freshwater; females often parthenogenetic
	Malacostraca	Mostly dioecious; some sequential and simultaneous hermaphrodites	Shrimps, crabs, and lobsters
	Hexapoda	Dioecious	Insects, 830,075 species
	Myriapoda	Dioecious	Centipedes, millipedes, etc.

(continued)

Table 1.2 (continued)

Phylum			
	Class	Mode(s) of sexuality	Comments
Mesozoa		Hermaphroditic and dioecious	Endoparasites; Rhombozoa are hermaphrodites which may self- or cross-fertilize; orthonectids dioecious
Echinodermata		Largely dioecious	Some hermaphrodites among the asteroids, holothuroids, and especially ophiuroids
Hemichordata		Dioecious	Sessile pterobranchs and free-living enteropneust worms
Chordata			
	Urochordata	Hermaphroditic	Sessile or pelagic in colonies
	Cephalochordata	Dioecious	"Amphioxus"
	Myxinoidea	Dioecious; some functional hermaphrodites	Hagfish; poorly known; highly female-biased sex ratios
	Petromyzontiformes	Dioecious	Lampreys; environmental sex determination
	Chondrichthyes	Dioecious	
	Actinopterygii	Largely dioecious; some sequential and simultaneous hermaphrodites among teleosts	Includes teleosts, sturgeons, gars, and bowfins
	Actiniata	Dioecious	Coelacanth; internal fertilization; live-bearing
	Dipnoi	Dioecious	Lungfishes
	Tetrapoda	Dioecious	Includes amphibians, reptiles, birds, and mammals

[a] Ghiselin (1974) and Anderson and Cribb (1994)
[b] Collin (2013)
[c] Kaulfuss et al. (2013)

more labile in their sexual system, such as the conifers among plants and the Cnidaria and annelids among animals. Assuming that taxa such as phyla and classes are, in general, evolutionarily older than orders and families, these patterns suggest that in many, if not most, cases, sexual systems are very old evolutionarily and therefore have been stable across hundreds of millions of years and a great variety of ecological conditions. For example, the class Hexapoda (insects) of the arthropods is believed to be about 400 million years old (Gaunt and Miles 2002) and is easily the most numerous class of animals in terms of numbers of species, but it is almost exclusively dioecious. In fact, if one includes the insects, the Metazoa are 95%

dioecious, whereas if one excludes the insects, the Metazoa are roughly 30% hermaphroditic (Jarne and Auld 2006). Similarly the phylum Platyhelminthes (13,780 species, Lecointre and Le Guyader 2006) is simultaneously hermaphroditic with very few exceptions (Ghiselin 1974). Sexual systems may be labile or conservative at any taxonomic level. Even in the cases in which the sexual system is labile within classes, sexual system may be quite conservative at the level of order or family [e.g., lysmatid shrimps (Chap. 10) or certain gastropods (Chap. 7)]. In other cases, species within a genus may vary in sexual system, as in the polychaete genus *Ophyrotrocha* (Chap. 5) or *Hydra* (Siebert and Juliano 2017) (see below).

Williams' Paradox (Williams 1975; Leonard 1990, 2013) states that theories of the advantages of hermaphroditism versus dioecy don't adequately explain the distribution of sexual system across the Metazoa. This observation gives rise to two questions: (a) What factors can explain this distribution? (b) Why are sexual systems so often very conservative? Comparative studies of groups that are relatively labile in sexual system may help in identifying the adaptive advantages of particular sexual systems as suggested by Williams (1975). This volume presents reviews of a variety of taxa that are labile in terms of sexual system, and, in general, the results show that sexual systems, in these labile groups, respond evolutionarily to the types of selective pressures that have been identified in theoretical and empirical studies over the last 50 years. The factors responsible for the extreme conservatism of sexual system in other taxa remain unclear at present.

The second major mystery of sexual system evolution concerns the evolutionary paths that lead from dioecy to simultaneous hermaphroditism or the reverse, in metazoan animals. Within angiosperms, there is a well-developed body of theoretical literature which predicts how dioecy evolves from simultaneous hermaphroditism. The usual path involves a situation in which a strong advantage to outcrossing for the producers of eggs favors the spread of genes for male sterility in a hermaphroditic population (Fig. 1.1). This results in a gynodioecious sexual system, and sexual selection favors hermaphrodites that emphasize pollen production at the expense of ovules, leading eventually to dioecy. In dioecious species, females may experience an advantage to some pollen production (perhaps for reproductive assurance) which can put males at a relative disadvantage. Then, selection for more male sex allocation in hermaphrodites in an androdioecious population will lead to stochastic loss of males and ultimately to a hermaphroditic sexual system (Fig. 1.1; Delph and Wolf 2005; Delph 2009; see also Pannell 2002; Wilson and Harder 2003). However, there is also evidence that monoecy, in which an individual plant has separate male and female flowers, may be a pathway from SH to dioecy in many angiosperms (see Chap. 3). In principle, the same arguments should be applicable to metazoans, but as Weeks (2012) pointed out in a very comprehensive review, in reality, neither gynodioecy nor androdioecy appears to be an evolutionary path between dioecy and hermaphroditism in animals [with the possible exception of barnacles (see Chap. 8; Yusa et al. 2013)]. As I have argued previously (Leonard 2013), it may be more useful to think of the evolution of sexual systems in animals as involving a continuum from more to less plasticity in sex allocation as one moves from simultaneous hermaphroditism, where sexual role may

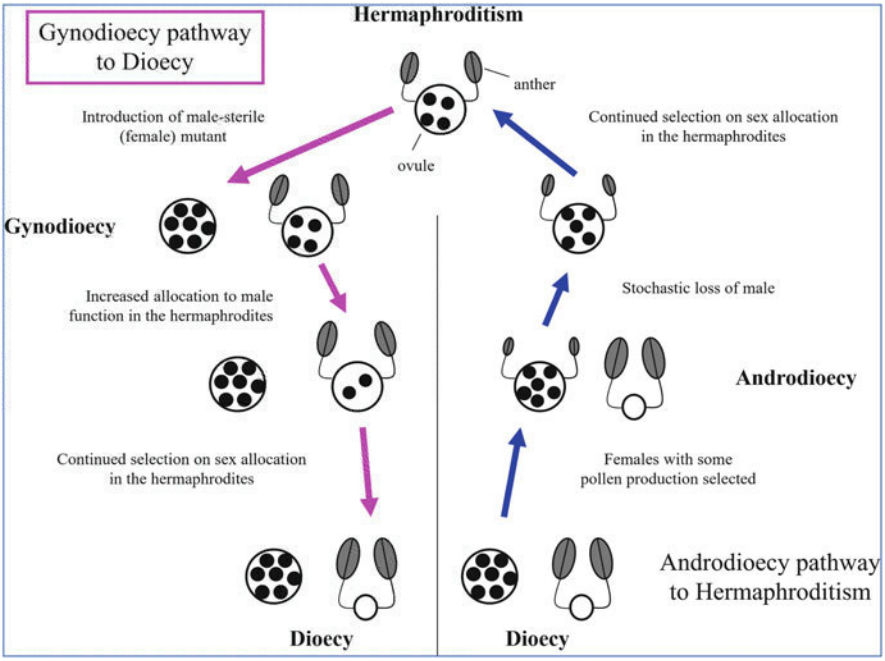

Fig. 1.1 A diagrammatic representation of the evolutionary pathways between dioecy and hermaphroditism in angiosperms (From Delph 2009). The hypothesized pathway from hermaphroditism through gynodioecy to dioecy is shown on the left in pink, and the pathway from dioecy to hermaphroditism through androdioecy is shown on the right in blue

be a purely behavioral choice, to dioecy with genetic sex determination, where sexual role is fixed at fertilization. Here I consider possible evolutionary paths between outcrossing simultaneous hermaphroditism (SH) and dioecy involving transitions through sequential hermaphroditism and/or environmental sex determination (Fig. 1.2). It remains to be seen to what extent these pathways actually are consistent with animal evolution.

1.2 Defining and Identifying Sexual Systems

Sexual systems can be defined in terms of the types of individuals that interact in a mating encounter. For example, Eppley and Jesson (2008) classified sequential hermaphrodites as dioecious for the purpose of their discussion of the evolution of sexual systems since mating interactions involve a functional male and a functional female. However, selection acts on the total reproductive success of individuals, which suggests that sexual systems should be defined in terms of the pattern of gender of genets (genotypic individuals), to use the botanical term. In both plants and animals, the two sexual systems that are strikingly stable evolutionarily, in that

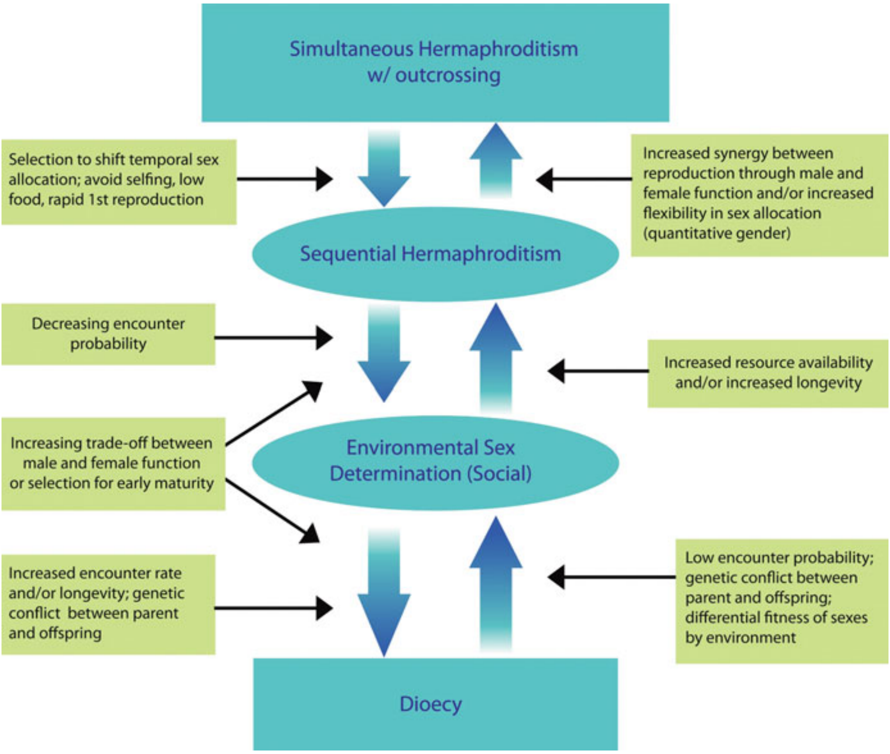

Fig. 1.2 A diagrammatic representation of hypothesized evolutionary pathways from simultaneous hermaphroditism with outcrossing to dioecy and back. The sexual systems are represented in blue with arrows indicating hypothesized directions of change in sexual system; the green boxes show suggested selective pressures that would promote the transition indicated by the black arrows. For the sake of clarity, dioecy, environmental sex determination, sequential hermaphroditism, and simultaneous hermaphroditism with outcrossing are depicted as discrete evolutionary states although in reality, there is a continuum between the sexual systems (see text)

they are conserved in whole phyla and classes, are dioecy (gonochorism) and simultaneous hermaphroditism with outcrossing in both roles. Other sexual systems tend to be both less common and less stable evolutionarily (see below).

1.2.1 Dioecy (Gonochorism)

The definition of dioecy is that it is a sexual system in which individuals reproduce in one sexual role (male or female), only, during their lifetime. It is characteristic of many phyla and classes in both plants and animals (e.g., insects, birds, mammals, reptiles, amphibians, the vast majority of nematodes, three of the four phyla of gymnosperms, etc.). Therefore, dioecy is, evolutionarily, a very stable sexual system, as is outcrossing simultaneous hermaphroditism (see below; Williams 1975). Theoretical studies show that in many cases, dioecy is maintained even though sequential hermaphroditism ought to be the more adaptive sexual system (Kazancioğlu and Alonzo 2009), indicating that there are factors that stabilize dioecy as a sexual system.

1.2.1.1 Genetic Sex-Determining Mechanisms in Dioecy

A wealth of sex-determining mechanisms have been identified in dioecious organisms. In classical genetic sex determination (GSD), the sex of an individual is determined at fertilization and does not change. Mechanisms of GSD include specialized sex chromosomes, genes not localized on sex chromosomes, haplodiploidy, or other phenomena (see below) [for a review of early literature, see White (1948); for more recent work, see Beukeboom and Perrin (2014)]. In addition to the familiar XY and ZW sex chromosome systems identified in many taxa, there are much more exotic types of sex determination by sex chromosomes. Spiders have great diversity among families in the number and arrangement of sex chromosomes (Araujo et al. 2012). While therian mammals use a XY sex determination in which the SRY gene on the Y chromosome is a dominant determinant of male sex, platypus and echidna lack evidence of an SRY gene and have multiple X and Y chromosomes, and there is evidence for homology with the DMRT1 gene found on the Z chromosome of birds (Rens et al. 2007; Veyrunes et al. 2008). In birds, males are ZZ and females are ZW. Infection with a variety of organisms, such as the bacterium *Wolbachia* (Werren et al. 1986; review in Beukeboom and Perrin 2014), can also influence genetic sex determination. There is a unique genetic sex determination system in bivalves, called doubly uniparental inheritance (DUI), in which females inherit mitochondria from their mothers, whereas males inherit mitochondria from their fathers, and this determines sex (Chap. 6; review in Zouros 2013). Interestingly, in freshwater mussels, DUI is prevalent in the dioecious species which predominate in the group but is not found in the few hermaphroditic species of freshwater mussel (Breton et al. 2011). Collin (Chap. 7) discusses various genetic sex-determining mechanisms in caenogastropods. The sex of an individual can be determined by either genetic or environmental factors or a combination of the two (Eggers and Sinclair 2012; Ono and Harley 2013; Bachtrog et al. 2014; Kuijper and Pen 2014; see also Chaps. 6, 11, and 12). Recent work has shown that sex-determining mechanisms have evolved relatively quickly in many groups (see Chaps. 4, 6, 11, and 12; Beukeboom and Perrin 2014 for review). It has been suggested that maternal-offspring conflict can lead to rapid evolution of genetic sex-determining mechanisms, including sex chromosomes (Werren et al. 2002). Within angiosperms, dioecy has evolved many times (Bawa 1980) and may involve either genetic sex determination (including sex chromosomes) or environmental sex determination. The interaction of the two may be complex (Diggle et al. 2011).

1.2.1.2 Environmental Sex Determination

Environmental sex determination (ESD) and genetic sex determination (GSD) can interact (Holleley et al. 2015) (see below). For example, in flounder, XY individuals are males, and XX individuals are female unless masculinized by extreme temperatures or other stressors (Mankiewicz et al. 2013). One may, in fact, think of GSD and ESD as ends of a continuum rather than discrete phenomena (see Kraak and Pen 2002 for discussion). In classic ESD, the genotype is capable of becoming either male or female until sexual differentiation is triggered, before first reproduction, by a factor such as social environment, or environmental temperature (Bull and Vogt 1979; Korpelainen 1990; Mankiewicz et al. 2013; see Chap. 12), i.e., sex is phenotypically plastic during early development. The Charnov-Bull (1977) model of the evolution of sex determination argues that it is adaptive when the environment during development is variable and one sex fares better in one type of environment and the other sex does better in a different environment. The molecular pathways involved in ESD have been extensively studied in turtles (see Chap. 12). In teleosts, estrogen signaling pathways have been implicated in sexual differentiation with ESD (Chap. 11). In addition to social cues and temperature, other factors such as photoperiod (e.g., a gammarid amphipod; Bulnheim 1967), settling substrate, food availability, and growth rate may also be involved (see below and discussion for bivalves in Chap. 6). An experimental study in sea lamprey showed an increased skew to males in a cohort exposed to a low-productivity environment, whereas there was an increased percentage of females in a group of individuals placed into a high-productivity environment (Johnson et al. 2017). It was hypothesized that the relevant variable was larval growth rate. A similar phenomenon was observed in the laboratory in Midas cichlids in which the relative size of juveniles in a group was shown to determine sex, independent of genetic factors (Francis and Barlow 1993). In that case it was hypothesized that social interactions rather than growth rate *per se* were the determining factor in sex determination. These authors emphasized the connection between ESD in this dioecious species and the size-advantage hypothesis (SAH) for sequential hermaphroditism (Ghiselin 1969; Munday et al. 2006a; Warner 1975). The term “conditional sex expression” has been used to emphasize the close association between ESD and sequential hermaphroditism (Frank and Swingland 1988; see below).

In dioecious barnacles, sex may be genetically determined with even the larvae being dimorphic, or sex may be determined by the substrate of settlement with larvae settling on an uninfected host becoming female and larvae settling on a host previously infected by a barnacle becoming (dwarf) males (Yamaguchi et al. 2014). The probable duration of the substrate may also have an effect on sex determination in barnacles (Ewers-Saucedo et al. 2015). Sex is also apparently environmentally determined in other taxa with dwarf males, such as at least some species of the siboglinid genus *Osedax* (Rouse et al. 2008; Vrijenhoek et al. 2008; Miyamoto et al. 2013) and echiuran annelids of the families Bonellidae and Ikedidae (Baltzer 1926; Jaccarini et al. 1983; Berec et al. 2005; Goto et al. 2013). Although there is some evidence of a role for genetic sex determination in both *Osedax* and *Bonellia* (see discussion in Rouse et al. 2015), Berec et al. (2005) argue that once ESD with dwarf males has evolved, it should be resistant to invasion by genetic sex determination. [Reversed sexual size dimorphism in spiders has also resulted in dwarf males in some taxa, although spiders seem to have chromosomal sex determination (see Araujo et al. 2012).] In spore plants, over 50% of bryophyte species may be dioecious at the gametophyte stage (McDaniel et al. 2012; Perley and Jesson 2015) although the genet is presumed to be hermaphroditic in all cases (see Chap. 2). Similarly, ESD determines sex in ferns that are dioecious in the gametophyte stage, with the relevant cue being a pheromone associated with population density (Atallah and Banks 2015; Goodnoe et al. 2016).

There are cases in which it is difficult to distinguish between dioecy and sequential hermaphroditism. In the polychaete *Grubea clavata*, Hauenschild (1953) demonstrated, in laboratory experiments, that initial sexual development resulted in either male or female worms and that male worms remained male throughout their lifetime, whereas after the initial egg-laying, a proportion of female worms regenerated the gonads as testes and then remained male throughout their lives. Other female individuals regenerated the gonads as ovaries after an initial egg-laying and laid eggs a second time. In the laboratory, the process repeated with a proportion of females changing to males after each egg-laying and remaining male, while other individuals regenerated ovaries and laid eggs again. Experimental interventions such as amputations, reduction in nutrition, and increased water temperature tended to increase the percentage of females becoming males, whereas only one (out of hundreds) of individuals, a very young male, was ever seen to change to female. Hauenschild concluded that young worms became female and remained female only under favorable conditions, whereas any loss of physical condition or deterioration of the environment led to a change to male. He reported similar phenomena in the related polychaete, *Exogone gemmifera*. Interestingly, in these polychaetes, maleness represents a type of "physiological sink" that individuals may fall into under unfavorable conditions or when the energy loss associated with egg-laying is sufficiently great (Hauenschild 1953; see also Franke 1986 for discussion of similar observations in other syllids). Breeding experiments indicated that while there was no obvious genetic sex determination (Hauenschild 1953), secondary males (those that started life as females) produce more daughters than do primary males (those who started reproduction as males) (Hauenschild 1959). Similar phenomena where sex depends on size and condition have been described in plants, but sex change can usually be in either direction (Heslop-Harrison 1957; Bierzychudek 1982, etc.; see below). In summary, there is neither a clear boundary between dioecy with genetic sex determination and dioecy with ESD nor a clear line between ESD and sequential hermaphroditism (see below).

1.2.2 Simultaneous Hermaphroditism

Simultaneous hermaphroditism (SH) is defined as a sexual system in which individuals reproduce through both sperm and eggs in the same breeding season, although not necessarily in the same sexual encounter. Simultaneous hermaphrodites may or may not be capable of self-fertilization. In fact, SH with, and without, outcrossing should, in principle, have rather different evolutionary consequences, and it is in taxa that show outcrossing that SH is stable across whole phyla and classes. It is important, therefore, to distinguish between species that have obligate selfing and species in which outcrossing occurs between simultaneous hermaphrodites. However, information as to the occurrence of selfing is often not available, and in some taxa such as the pulmonate gastropods, populations within a species may vary in the presence, absence, or frequency of selfing (Jarne and Charlesworth 1993; Jarne and Auld 2006; Baur 2010; Jarne et al. 2010). It is important to remember that the diversity found in nature will seldom be well captured by our terminology.

1.2.2.1 Obligately Selfing Simultaneous Hermaphroditism

In this sexual system, individuals produce both eggs and sperm and reproduce through self-fertilization exclusively. This sexual system has evolved many times in both plants and animals but is not characteristic of any major taxon and may be short-lived evolutionarily (see Darwin 1858; Weeks et al. 2006, 2009; Zierold et al. 2007; Denver et al. 2011; Weeks 2012; Chap. 4). Genetic analysis of progeny may be required to identify obligate selfing, which should lead to high levels of homozygosity. Obligately selfing individuals should show a reduced level of sperm production relative to outcrossing taxa since there will be no sperm competition and efficient mechanisms of fertilization. Reduced allocation to sperm has been demonstrated in populations of a freshwater mussel with high rates of selfing (Johnston et al. 1998), in a manner similar to that seen in angiosperms. Furthermore, in obligately selfing taxa, sperm and eggs should mature at approximately the same time, i.e., one would not expect a prolonged protandrous or protogynous period of development before maturation as in many simultaneous hermaphrodites. Also, the evidence suggests that obligately selfing hermaphroditic lineages are short-lived evolutionarily [for animals, see above (Zierold et al. 2007; Weeks et al. 2009; Chap. 4)]. Darwin (1858, p. 462) quoted a doctrine of Andrew Knight “that no plant self-fertilizes itself for a perpetuity of generations” and concluded “I am strongly inclined to believe that this is a law of nature throughout the vegetable and animal kingdoms.” Ghiselin (1974) dubbed this the Knight-Darwin law, and it still seems valid, although the question of how many generations constitute “a perpetuity” remains open. Modern genetic work supports this conclusion: there is evidence of a 20–40% reduction in genome size in androdioecious *Caenorhabditis* species of nematodes, in which most reproduction is through selfing, suggesting that self-fertilization may lead to a rapid and substantial loss of genetic variance

(Fierst et al. 2015) as has been shown in angiosperms (Wright et al. 2008). It seems probable that this loss of genes may be associated with the short-lived quality of obligately selfing species.

1.2.2.2 Outcrossing Simultaneous Hermaphroditism

Again, individuals are capable of reproducing in both sexual roles (male and female) during a single reproductive season. However, in outcrossing simultaneous hermaphroditism, individuals are capable of mating with another individual in both the male and female sexual role. This mating system is characteristic of many large taxa (phyla and classes) in both plants and animals: most angiosperms, the genets of all spore plants, as far as is known (see Chap. 2; Table 1.1), heterobranch gastropods, barnacles, platyhelminthes, urochordates, clitellate annelids, etc. (Table 1.2). Some outcrossing simultaneous hermaphrodites are also capable of self-fertilization [e.g., some cestodes (Milinski 2006), many pulmonates (Baur 2010; Jarne et al. 2010), the ctenophore *Mnemiopsis leidyi* (Sasson and Ryan 2016), many angiosperms, etc.]. Features of outcrossing SH that are not found in obligately selfing SH include sex allocation that varies with the physical and biological (particularly social) environment. That is, hermaphrodites that are mating with other hermaphrodites may vary their investment in sperm versus eggs according to their size, food availability, availability of mates, social status, etc. What has been termed adolescent protandry or protogyny, in which individuals first reproduce in one sexual role and then mature into SH, is often observed in outcrossing SH (e.g., Dunn 1975a, b; Bauer 2006; di Bona et al. 2014; Chaps. 5 and 10).

Changes in sex allocation with size, age, social environment, and physical conditions occur frequently in outcrossing SH and have been termed “quantitative gender” (Lloyd 1982; Klinkhamer et al. 1997; Cadet et al. 2004). It has been suggested that in most cases of a size/age advantage of one sexual role over the other, shifting sex allocation with size/age can give the same adaptive advantage as an actual sex change. Klinkhamer and de Jong (2002) argued that there are two types of benefits of size: direct effects and budget effects. Budget effects are effects of size on reproductive success in one sexual role that are purely a product of the amount of resources available to invest. The fitness obtained for a given investment of resources will be the same for small and large individuals, but large individuals will have more resources to invest. In such cases a gradual change of sex allocation with size will be expected (Klinkhamer and deJong 2002). In contrast, direct effects are benefits to reproductive success in one sexual role that are associated with size *per se*; e.g., a taller wind-pollinated plant (or sessile broadcast-spawning invertebrate) will be able to disperse pollen/sperm over a wider area purely due to its height, thereby increasing its siring success. Therefore, in such species, large individuals should allocate resources preferentially to male function, becoming male; conversely since small plants will experience little siring success, they should become female. Similarly, in group-living fishes, if large individuals can dominate mating in a social group, large individuals should become male, making it profitable for small individuals to be female. If gain curves are linear, a sudden change of sex will be favored.

Also, in some species, individuals may act in only one sexual role although they have both testes and ovaries that are apparently functional (St. Mary 1993; Sadovy de Mitcheson and Liu 2008; di Bona et al. 2010; see also Chap. 5), indicating that histological and/or anatomical sex may not be a reliable guide to functional sex. In some cases, one of the types of gonads may not be fully functional [e.g., gobies (Cole and Hoese 2001) or spirochid trematodes (Anderson and Cribb 1994; Platt and Blair 1996)]. In bufonid toads, the testes of mature males are capped by Bidder's organ, which contains maturing oocytes (Farias et al. 2002), but there are apparently no reports of self-fertilization or functional hermaphroditism [personal communication, Marvalee H. Wake; but see Grafe and Linsenmair (1989)]. However, both sex change (see below) and hermaphroditism are easily induced experimentally (review in Wallace et al. 1999), so there would seem to be potential for selection to produce either sequential or simultaneous hermaphroditism. However, since amphibians are very susceptible to endocrine disrupters (e.g., Moresco et al. 2014), it is often hard to interpret reports of gonads with mixed gametes.

There are also cases intermediate between simultaneous and sequential hermaphroditism in which individuals change sex within a breeding season, sometimes repeatedly. For example, oysters of the genus *Ostrea*, which brood their zygotes, produce a clutch of eggs, then become male, and reproduce through sperm until the brood has hatched, when the gonad again becomes an ovary and produces eggs (Coe 1932; Chaparro and Thompson 1998; see also Chap. 6). Rapid alternation of sex within a breeding season has also been reported in a polychaete, *Ophryotrocha puerilis*, in which members of a pair change sexual role so that the larger individual is female, laying more eggs and growing more slowly. As the two individuals become more equal in size and changes become more frequent, the pair may ultimately both become simultaneous hermaphrodites (Berglund 1986). Such examples of alternating sex have traditionally been seen as sequential hermaphroditism, demonstrating the difficulty of fitting specific sexual systems into any overall scheme of definitions.

1.2.3 Sequential Hermaphroditism

In the classic definition of sequential hermaphroditism, individuals reproduce in distinct sexual roles during different breeding seasons of their life histories. This may involve a single change in sex, or it may involve more than one change from male to female or the reverse depending on environmental, physiological, or social variables (Leonard 2013). As stated above, this creates a gray area between simultaneous and sequential hermaphroditism (see also Klinkhamer et al. 1997; Cadet et al. 2004). Sequential hermaphroditism is not characteristic of phyla or classes but is characteristic of many families of teleost fishes (Erisman et al. 2013) and has evolved several times in polychaetes (Chap. 5), gastropods (see Collin 2013; Chap. 7), and some groups of shrimps (see Chap. 10). It is a relatively rare sexual system

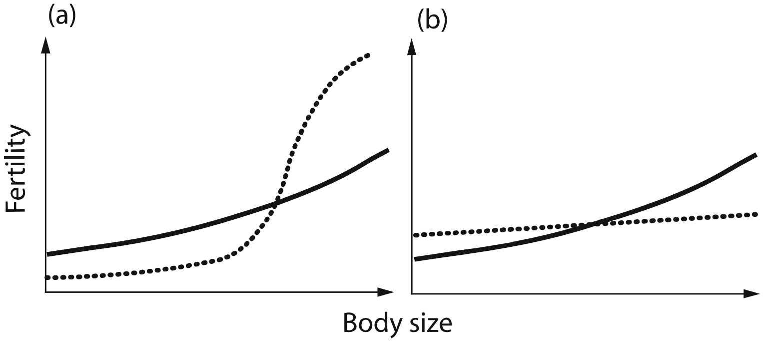

Fig. 1.3 The size-advantage model of sequential hermaphroditism (From Leonard 2013, based on Fig. 1 in Munday et al. 2006a). The offspring production expected for females (solid line) increases with body size if large females lay more eggs than small females. Expected male offspring production (dotted line) may or may not increase with body size, depending on whether large males have an advantage in securing mates. Sex change is favored when the size/age fertility curves of the two sexes cross. Protogyny (**a**) is predicted when the expected fertility of a male increases more rapidly with size/age than that of a female. Protandry (**b**) is predicted when the expected fertility of a female increases more rapidly with size than that of a male

(Kazancioğlu and Alonzo 2009; see also Ghiselin 1974; Policansky 1982, for review). Relatively little is known about the genetic correlates of sequential hermaphroditism. In the Pacific oyster *Crassostrea gigas*, in which populations show dioecy, protandric sequential hermaphroditism, and occasional simultaneous hermaphroditism, a genetic basis for sex change has been proposed with an interaction between a dominant male allele M and a protandric allele F, such that MF individuals are lifelong males and FF individuals are protandric sex changers (Guo et al. 1998; Zhang et al. 2014). Godwin and Roberts (Chap. 11) discuss the role of estrogen signaling pathways in sex change in teleosts. Although amphibians have chromosomal sex determination, as far as is known (Wallace et al. 1999), there is one report of protogynous sequential hermaphroditism in a laboratory population of a frog (Grafe and Linsenmair 1989). In angiosperms, sequential hermaphroditism is rarer, but it has evolved many times (Freeman et al. 1980; Charnov 1982) and involves very similar phenomena (Vega-Frutis et al. 2014). A large number of factors have been implicated as triggers for sex change in angiosperms, including light intensity, plant age, plant size, temperature, injury, disease, nutrients, etc. (Freeman et al. 1980).

The size-advantage hypothesis (SAH), first developed by Ghiselin (1969), states that sequential hermaphroditism will be adaptive when reproductive success (or more precisely, reproductive value; Warner 1988) increases more steeply with increasing size for one sex than the other (Fig. 1.3). In the well-known cases of protogyny in group-living fishes, individuals mature first as females, and then individuals that are able to grow large and socially dominant change sex to become male and defend spawning sites and/or harems (Fig. 1.3a; Warner 1984a, 1988; Munday et al. 2006a). This may occur even though individuals incur substantial costs in deferred current reproduction and growth, because of the substantial increase in reproductive value associated with being a dominant male (Warner 1984b). In labroids of the genus *Symphodus*, sex change is associated with the ability of large males to dominate mating, whereas in species with substantial paternal care, sex change does not occur (Warner and Lejeune 1985). In protandry, which is the common form of sequential hermaphroditism in many fish and invertebrates, individuals mature first as males, producing sperm and growing until they reach a point at which their reproductive value would be higher as a female, since they have attained a body size where they can produce more eggs than they could find to fertilize as males (Fig. 1.3b). Forty years of empirical and theoretical research have demonstrated that other factors can also explain sequential hermaphroditism (Munday et al. 2006a; Collin 2013). For example, both differential mortality and differential growth rate may be sufficient to provide an adaptive advantage for sex change (through an effect on reproductive value) even though size *per se* may not have a differential effect on reproductive success for the two sexual roles (Iwasa 1991). Levels of sperm competition (Muη̃oz and Warner 2004) and nutritional status (Yamaguchi et al. 2013) have also been shown to be important in determining whether an individual's reproductive value will be enhanced by sex change at a particular size in fishes. Thus, the decision of an individual to change sex may depend on a variety of proximate cues that reflect the environment of the individual and social group. An alternative hypothesis that size at sex change is usually invariant for a species (Charnov and Skúladóttir 2000; Allsop and West 2003) seems inconsistent with the evidence in most cases [(Buston et al. 2004; Cipriani and Collin 2005); see discussion in (Munday et al. 2006a)].

One well-studied system in angiosperms that is very consistent with the size-advantage hypothesis, which has been so important in animals [(Ghiselin 1969, 1974; Munday et al. 2006a); see below], is a perennial forest herb, the Jack-in-the Pulpit (*Arisaema triphyllum*). In this species, sex is associated with size: small individuals are immature, larger individuals are male, and the largest individuals are female (Policansky 1981; Bierzychudek 1982). Both genetic and environmental factors may influence the actual size at which individuals change sex in a given population (Viti et al. 2003). Therefore, *A. triphyllum* is a protandrous sex changer; i.e., it matures first as a male, producing pollen, and then, at a later time and larger size, becomes female, receiving pollen and producing seeds. Protogyny is the opposite pattern in which an individual first matures as a female and then becomes male. {N.B.: The terms protogyny and protandry are, unfortunately, used rather loosely in the literature. For example, many authors refer to protandry in heterobranch gastropods, by which they mean that in many species of this simultaneously hermaphroditic clade, sperm will mature before eggs in an individual, even though copulation may be reciprocal and the allosperm stored until the recipient matures eggs [e.g., the pteropod *Limacina* has been described as having copulation that is simultaneously reciprocal between mature males (Lalli and Wells 1978)]. In molluscs, this usage dates back at least to Pelseneer (1895) and is unlikely to be eradicated in the foreseeable future. Similar issues arise in other taxa.}

While sequential hermaphroditism has been dealt with, theoretically, as a discrete phenomenon [the SAH does not consider changing sex allocation in hermaphrodites (Henshaw 2018)], in the empirical data, the boundaries between sequential hermaphroditism and simultaneous hermaphroditism, on the one hand, and dioecy, on the other, are unclear. There are instances in which individuals may change sex more than once in their lives in both plants (Heslop-Harrison 1957; Freeman et al. 1980) and animals. In some plants, individuals may change sex each season depending on their current physical size, nutritional condition, or environment (Heslop-Harrison 1957). Some fish may change from female to male and back to female, or the reverse, if they lose a mate (Nakashima et al. 1996; Sadovy de Mitcheson and Liu 2008; Kuwamura et al. 2011; Sawada et al. 2017). Transcriptome analysis indicates that sex steroid pathways, including the aromatase gene, are involved in sex change in an anemone fish with bidirectional sex change (Casas et al. 2016). As discussed above, *Ostrea* oysters start reproduction as females, but the gonad converts to a testis when larvae are being brooded in the brood chamber, and once the larvae are released, the testis converts back to an ovary (Coe 1932; Chaparro and Thompson 1998), and there is a polychaete in which a pair of individuals alternate changing sex until the size difference and interval between sex changes become very short and the pair both become simultaneous hermaphrodites (Berglund 1986). In some mushroom stony corals, individuals may change sex between each spawning episode, correlated with consecutive full moons (Loya and Sakai 2008), although not all do. In one sabellid polychaete, *Bispira brunnea*, protandrous sequential hermaphroditism has been invoked to explain a pattern of populations consisting of males, females, and apparently functional simultaneous hermaphrodites, although we usually think of the transition from male to female in sequential hermaphrodites as being too rapid to involve a functional simultaneously hermaphroditic intermediate (Davila-Jimenez et al. 2017). Another possible explanation would be trioecy (see below). As is often the case, the species is not sufficiently well understood to allow us to distinguish between the hypotheses, although sequential hermaphroditism is well known in polychaetes (Chap. 5), whereas trioecy is not. More typically in sequential hermaphroditism, [e.g., the bivalve *Arca noae* (Bello et al. 2013)] during the intermediate phase with both types of gonads present, they are nonfunctional. In these cases, the line between simultaneous and sequential hermaphroditism is hard to draw.

The line between dioecy and sequential hermaphroditism is also rather fuzzy in many cases. In angiosperms, individuals of “dioecious” species may change sex in response to a variety of environmental variables (Heslop-Harrison 1957), indicating an overlap between dioecy with environmental sex determination (ESD) and sequential hermaphroditism. For example, shade is associated with maleness in a dioecious orchid, with females located in sunny spots, and if part of a female inflorescence is shaded, experimentally, it will become male (Zimmerman 1991). In animals, this has been less studied, but in cases such as the bluehead wrasse, which is the classic example of a protogynous sex changer, it has been found that whether individuals begin life as a female or develop directly into a male without a female stage depends on the social environment in which they are reared (Munday et al. 2006b). That is, the social environment determines whether an individual becomes a protogynous sex