SENTENTIA

USE OF THE TERMS PROTANDRY, PROTOGYNY, AND HERMAPHRODITISM IN MALACOLOGY

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ABSTRACT

The terms protrandry, protogyny, and hermaphroditism have distinct and precise meanings to theoretical ecologists, reproductive biologists, and evolutionary biologists. However, some malacologists have used these terms in other ways, causing the theoretical workers to misunderstand and misapply the reproductive patterns of mollusks. "Protandry" should be used to describe animals that change sex from male to female without reverting to male at a later time. Likewise, protogyny involves a single sex change, from female to male, and is rare in the Mollusca. Only evidence obtained from the study of individual animals can be accepted as proof that sex change occurs. Age- or size-specific sex ratio data are circumstantial evidence requiring further substantiation.

> If investigators will keep facts clearly separated from interpretation and use principally either photographs or camera lucida drawings for illustration instead of diagrams, some future biological theorist may be able to unify all the numerous and diverse contributions to the study of sex and sex inheritance.
>
> (Grave, 1942)

Forty years after Grave made a plea for clarity in the primary literature on sexuality in mollusks, theoretical biologists are indeed trying to unify the patterns of sexuality, not only to understand mechanisms of sex inheritance, but also to explain both the evolution and ecological importance of life histories in terms of natural selection. Ghiselin (1969, 1974) was among the first to do so using mollusks. Hypotheses have been constructed to explain protogyny and simultaneous hermaphroditism with reference to fish (Warner et al., 1975; Leigh et al., 1976; Fischer, 1981). Protandry has been analyzed theoretically for mollusks (Hoagland, 1978) and for shrimp (Carpenter, 1978; Charnov, 1979). Authors of synthetic analyses without taxonomic emphasis such as Charnov (1982), Charnov et al. (1976), Heath (1977), and Clark (1978) rely on papers in taxon-oriented journals to provide their data bases. Such authors seek ecological similarities among species that possess a particular type of sexuality.

Unfortunately, the definitions of the sexual categories differ between some taxonomic-oriented authors and the theorists. The result is confusion in the analysis of patterns in invertebrate sexuality. Many theoretical ecologists accept at face value the terms used in the original literature without detailed inspection of the data upon which the definitions are based. Moreover, researchers sometimes have not proven unequivocally the type of sexuality a mollusk possesses.

The intention of this communication is to define the terms protandry, protogyny, and hermaphroditism as they are understood by zoologists working on the evolutionary ecology of sex and life history. I will show why these restricted definitions are useful and indeed necessary in analyzing patterns of sexuality. I will then give examples of inappropriate use of the terms, and will suggest the kinds of data malacologists should use in determining the patterns of sexuality of their taxa.

DEFINITIONS

Hermaphroditism in its broadest sense is the production of eggs and sperm by the same individual. Several categories are recognized that differ in terms of their functional morphologies as well as their effect on genetics (degree of outbreeding) and sexual structure. *Simultaneous hermaphroditism* is the simultaneous release of eggs and sperm by one organism using the same gonad to produce both eggs and sperm. Simultaneous cross-fertilization or self-fertilization can occur in some simultaneous hermaphrodites (e.g., some land snails). However, more often, the eggs and sperm do not become mature and capable of fertilization exactly at the same time. In land snails, the male function

usually occurs first. Kraemer (1983) reported that in the freshwater clam *Corbicula*, eggs begin to ripen first, followed by sperm development; the products become fully mature simultaneously and self-fertilization is thought to be a possibility. In some other bivalves, sperm development begins prior to egg development, but there is much intraspecific variation in the timing of the development of sex products in bivalves. While Clark (1978) suggested in the term *opsiautogamy* for sequential egg and sperm ripening culminating in self-fertilization, I agree with Policansky (1982) that this term in unncessary. Policansky himself erected *sequential cosexual* to describe animals that have sequential egg and sperm ripening in the same season, whether self-fertilizing or not. I believe the main focus should be on the fact that such animals are still simultaneous hermaphrodites using the same organ to produce eggs and sperm within the same season. If we limit simultaneous hermaphroditism to those species that produce mature eggs and sperm exactly at the same time, we will have defined the term almost out of existence.

Animals that function first as one sex, then as another, repeatedly, possess *alternating sexuality*. Coe (1934a) used this term to describe certain bivalves. He reported that *Crassostrea virginica, Ostrea lurida*, and *O. gigas* alternate sex, while the gonad remains basically bisexual. In some species however, the first gonad may break down and cells differentiate as a new gonad of the opposite sex. Sometimes the individual functions as one sex for a whole season; other times it spawns as one sex and then the other in the same summer (reported for *Teredo navalis* by Coe, 1943). Usually the male gametes develop first (Coe, 1934b; 1936). Coe started confusion in the molluscan literature by calling animals that begin their life of alternating sexuality as males "protandric, with a rhythmical series of alternating sexual phases" (Coe, 1934a). However, protandry and alternating sexuality are mutually exclusive.

An ecological explanation of alternating sexuality is that sperm can be produced with less energy and developmental time than eggs, and are produced when the organism is energy-limited or short of certain particular nutrients required for egg production (Kennedy, 1983). However, this hypothesis has not been rigorously tested, and is not an attractive explanation for cases in which sex change occurs out of phase with nutrient availability. The sex ratio of populations with alternating sexuality is extremely labile. Herlin-Houtteville and Lubet (1975) reviewed the sexuality of bivalves, and emphasized that within a single genus, species that are simultaneous hermaphrodites and those with alternating sexuality have been reported. There may also be substantial error in the assignment of bivalves to sexual categories. But there is nonetheless a blurring of the distinction between simultaneous hermaphroditism and alternating sexuality. It becomes a matter of degree of separation of the ripening and release of male and female sex products.

Charnov (1979) and Policansky (1982) consider hermaphroditism to be simultaneous if male and female gametes are both produced in the same breeding season. While this definition separates the two terms, the separation does not reflect biological reality. In the Teredinidae and the oysters, animals often breed as males soon after breeding as females . . . . . is this the same breeding season? What of warm-water species that have no discrete breeding seasons but nevertheless alternate sexuality? *Crepidula* species change sex only once, but often do so within a breeding season; no one would call them simultaneous hermaphrodites for that one season. One alternative is to consider alternating sexuality to occur when the gap between male and female function is large enough that neither simultaneous cross-fertilization nor self-fertilization can occur. A further complication is that storage of viable sperm could lead some mollusks to self-fertilize even when they appear to have temporally-separate sexual functions. Detailed study of many marine hermaphrodites may show them actually to have alternating sexuality.

Sequential hermaphroditism is a general term for the temporally-separated function of an organism first as one sex, then as the other. Most authors restrict the term to protandry and protogyny (Charnov, 1979). Obviously, the term is not specific enough to be used without further information. So too with *sex change* and *sex reversal*, which are used synonymously and could refer to protandry, protogyny, or even alternating sexuality.

Protandry is the functioning of an organism first as male, then as female, with no further sex change. The two sexual phases are separated by a phase in which male primary and secondary sex characters disappear, and the animal re-differentiates as a female. In *Crepidula* for example, the penis is resorbed or reduced in size. There is some question as to whether, in most protandrous species, the gonad re-differentiates or whether the female gonad is an entirely separate structure. Protandry is most uniformly found in the marine gastropod family Calyptraeidae, though it is reported in many other molluscan families. *Protogyny* is the opposite of protandry; the organism first differentiates as a female, then re-differentiates as a male with no further change.

Protogyny has been attributed to mollusks rarely, and is not expected on theoretical grounds (Hoagland, 1978; Charnov, 1982). The basic ecological-evolutionary theory is that sex change from male to female is advantageous when a species can reproduce more with increase of size as a female, but size (or age) increase is not important to male fecundity. This is true of many mollusks in which brood size and fecundity are proportional to female size, but the ability for a male to successfully fertilize females may be even enhanced by small size (Hoagland, 1978). On the other hand, protogyny is common in fish in which the male defends a nest or a territory, and large size is important in his acquiring mates (Leigh et al., 1976; Charnov et al., 1976). In both protandry and protogyny, environmental factors often

control the timing of sex change, and the sex ratio of a population can be related to its density or age structure (Hoagland, 1978; Charnov, 1979).

APPLICATIONS

From the preceding definitions, it is clear that there are functional and structural differences between one-time sex change, alternating sexuality, and simultaneous hermaphroditism. These differences affect the sex ratio, effective population size, and the degree of inbreeding of a population. If these three terms are defined as above, one can distinguish species that potentially self-fertilize from those that cannot; those with future labile sexuality from those that are fixed in sex once mature; those that change sex based on environmental factors from those whose hermaphroditism is continuous. Table 1 summarizes some ecological, genetic, and morphological differences between these three major types of sexuality.

The only certain way to distinguish among the types of hermaphroditism and sex change is to follow the lives of single individuals (Wright and Lindberg, 1979). Collecting mature sex products, observing functional change of external sex characters, or observing brooding provides conclusive evidence on functional sex change. Histological sectioning is sometimes ambiguous and more importantly it destroys the animal so that the temporal element unequivocally establishing the type of hermaphroditism is lost. Grave (1942), in sectioning the gonads of brooding females, was able to find maturing sperm. This is the best situation in which sectioning an individual can serve as positive evidence for sex change. Attribution of sex change is often based on circumstantial evidence, such as age and size. However, the presence of small males and large females is insufficient evidence for protandry (Wright and Lindberg, 1982). Subramoniam (1981) dissected numerous individuals of a mole crab and observed total sexual re-differentiation, which was conclusive as to sex change, but could not totally rule out alternating sexuality as opposed to protandry.

The greatest confusion on sexuality seems to be in the literature on marine bivalves, including oysters and Pholadacea. Workers have reported protandry, protogyny, alternating sexuality, and gonochorism all in the same species (Choquet, 1970, summary table p. 401). The genera *Bankia* and *Teredo* and some *Ostrea* species have been assumed to be protandrous. However, a re-examination of the literature (Coe, 1933, 1934a and b, 1936, 1941, 1943; Orton, 1927, 1933; Grave, 1942) shows that alternating sexuality (either in different breeding seasons or within the same season) is more accurate for most of these species studied so far. Asif (1979) correctly cautioned that size-sex data in tropical *Crassostrea* only suggest sex change; dwarf males and delayed female maturity could produce a pattern mimicking protandry. Yet Policansky (1982) quoted his work as demonstrating protandry. In general, the attribution of sexual types to mollusks quoted by Policansky should not be taken at face value, but should be checked against the original data and any recent work for confirmation, based on the definitions of sexual types and whether or not the data are sufficient to prove the case. One must also be careful not to attribute a mode of sexuality to all members of a genus or a family when only a few have been studied.

The freshwater bivalves are not without confusion as well. Evidence for some form of sequential hermaphroditism in species of *Corbicula* is circumstantial; at different times *C. fluminea* has been called both protandrous and protogynous (e.g., Morton, 1982, 1983). Nor have marine gastropods escaped the problem: Robertson (1981) used only size-sex data to state that *Epitonium albidum* is protandrous "with only one sex change." However, the greatest confusion in the use of "protandry" comes from entomologists, several of whom use the term for the case where males hatch before females (Fagerstrom and Wikland, 1982).

Table 1. Functional and structural differences between simultaneous hermaphroditism, one-time sex change, and alternating sexuality.

Character	Simultaneous Hermaphroditism	Protandry, Protogyny	Alternating Sexuality
Sex Ratio	Meaningless	Often density- or age-dependent	Often dependent on environmental conditions (food)
Self-fertilization	Possible	Rarely possible	Rarely possible
Labile sexuality	No	Not once mature	Yes
Effective population size vs. total population size	1:1	< 1	< 1
Gonad	Bisexual	Male or Female. New differentiation of gonadal material at sex change.	Bisexual; or newly differentiated at sex change.
Secondary sex characters	Usually lacking	Often well-developed animal externally recognizable as ♂, ♀, or re-differentiating (esp. in fish)	Usually lacking

Malacologists and other invertebrate zoologists should avoid calling an organism protandrous or protogynous unless the necessary evidence obtained from sufficient individuals is also reported. It will greatly aid research on sexuality if the major categories "simultaneous hermaphroditism", "protandry", "protogyny", and "alternating sexuality" are used in the same manner by researchers in different but inter-dependent disciplines.

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