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Protandrous Hermaphroditism

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Synonyms

Protandric hermaphroditism; Protandry

Definition

A reproductive system where individuals mature as males, but may reproduce as females later in life.

Introduction

In most animals, “males” and “females” are distinct classes of individuals that specialize in the production of sperm and eggs, respectively. However, a substantial minority of species are hermaphrodites, meaning that a single individual can produce both eggs and sperm, either simultaneously or at different stages of its life. “Protandrous” hermaphrodites begin their

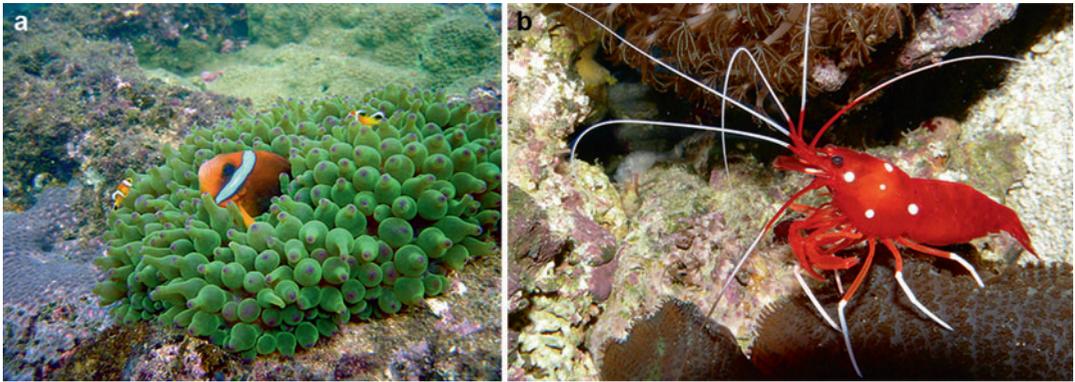
reproductive lives as males, but reproduce as females later in life.

Two examples help to illustrate (Fig. 1). Anemonefish live in small territorial groups, where reproduction and sex change are determined by a strict dominance hierarchy (Munday et al. 2006). The largest individual in the group is a breeding female, the second-largest is a breeding male, and all smaller individuals are nonbreeding males. If the female dies or is removed, then the largest male changes sex and takes her place. Protandrous hermaphroditism is also found in several species of “cleaner” shrimp that feed on the parasites and dead tissue of their fish clients. In shrimps of the genus *Lysmata*, individuals begin their reproductive lives as males, but can reproduce as both sexes later in life (Bauer 2006).

Terminology

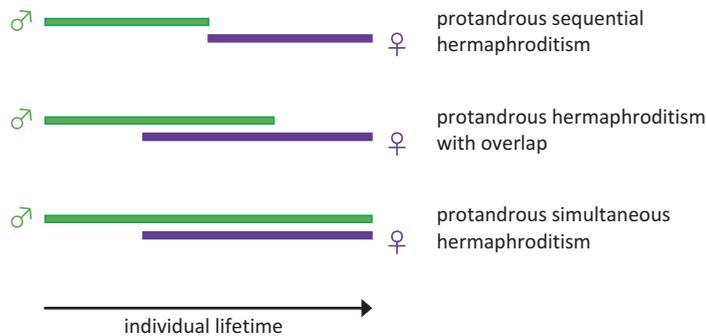
Protandrous hermaphroditism encompasses a continuum of life histories, distinguished by the degree of temporal overlap between male and female reproduction (Collin 2013; Fig. 2):

1. *Protandrous sequential hermaphroditism*:
Reproduce early as a pure male, and later as a pure female.
2. *Protandrous hermaphroditism with overlap*:
Reproduce early as a pure male, and later as a



Protandrous Hermaphroditism, Fig. 1 (a) An adult and juveniles of the Oman anemonefish *Amphiprion omanensis*, a protandrous sequential hermaphrodite, shown with the host anemone *Entacmaea quadricolor* (Photo taken from Simpson et al. (2014))

(b) The fire shrimp *Lysmata debelius*, a protandrous simultaneous hermaphrodite (Photo by User:Haplochromis, CC BY-SA 3.0 (<http://creativecommons.org/licenses/by-sa/3.0/>), via Wikimedia Commons)



Protandrous Hermaphroditism, Fig. 2 Schematic showing different forms of protandrous hermaphroditism, distinguished by the degree of temporal overlap between

male function (green lines) and female function (purple lines) over an individual's lifetime (cf. Collin 2013)

pure female, with an intervening period of reproduction as both sexes.

3. *Protandrous simultaneous hermaphroditism*: Reproduce early as a pure male, and later as both sexes.

Still further along this continuum are species that reproduce as both sexes over their whole reproductive lifespans (i.e., life-long simultaneous hermaphrodites), but shift their relative allocation of resources from male to female reproduction over time (Leonard 2013). There are also species that start out as simultaneous hermaphrodites, but later reproduce as pure females. Neither

of these latter life histories is commonly referred to as “protandrous.”

Sex change is usually unidirectional. In a few taxa, however, the gonad degenerates between reproductive seasons, and sex is redetermined at the start of the next season (Collin 2013). Protandry may then occur within each reproductive season. A very small number of species exhibit flexible bidirectional sex change (Munday et al. 2006). These species are sometimes called “protandrous” if the initial sex is invariably male.

These definitions emphasize reproduction (i.e., functional sex) rather than morphological criteria, because the adaptive significance of protandry is

best understood by looking at reproductive success via each sex (Policansky 1982). The distinction matters because an individual may reproduce consistently as one sex (i.e., produce only one gamete type) and yet contain reproductive tissues typical of the other sex (Sadovy de Mitcheson and Liu 2008). Particular care should be taken in comparisons with the botanical literature, where “protandry” is often defined according to purely morphological criteria (Policansky 1982). In defining *when* an organism acts as a male or female, the timing of fertilization is the most useable criterion. For instance, in some species sperm mature earlier than eggs, even though both types of gamete are used in the same reproductive episode; these species should be classified as simultaneous hermaphrodites rather than sequential (Policansky 1982). This convention can lead to curious consequences when there is a long delay between the production and fertilization of gametes (e.g., due to storage of received sperm). For instance, a protandrous individual may act as a male (i.e., achieve fertilization) long after it ceases producing sperm.

Diagnosis and Detection

Protandrous hermaphroditism should ideally be diagnosed using (1) histological series of the gonads or other gametogenic tissues showing the stages of transition (e.g., from functioning testis to functioning ovary for protandrous sequential hermaphrodites), and/or (2) field or laboratory observations of sex change in individual animals, based on unambiguous behaviors such as spawning (Sadovy de Mitcheson and Liu 2008). External sex characteristics and behaviors are not always reliable indicators of functional sex. Even when assessing the gonads, care must be taken to distinguish functional tissues from immature, vestigial, or otherwise nonfunctional tissues that do not produce mature gametes (Sadovy de Mitcheson and Liu 2008).

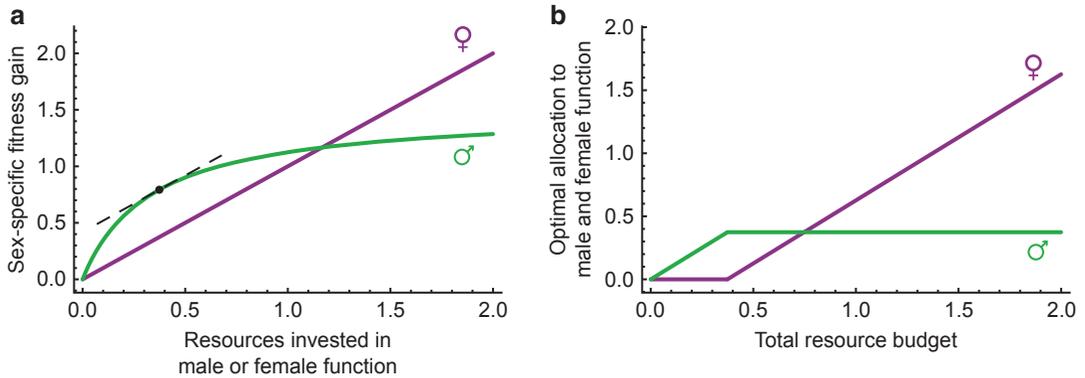
Differences in age or size distributions between males and females (or simultaneous hermaphrodites) can be suggestive of protandry, but should not be relied on as the only line of

evidence. This is because (1) these patterns can equally be caused by sex differences in maturation or mortality, and (2) protandrous species may in any case show substantial overlap between the sexes, which may not be detected in low-powered studies (Charnov 1982; Sadovy de Mitcheson and Liu 2008).

These relatively stringent diagnostic requirements probably lead to under-detection of protandrous hermaphroditism (Policansky 1982; Collin 2013). In practice, separate sexes are usually assumed if no simultaneously hermaphroditic individuals are found; simultaneous hermaphroditism may similarly be diagnosed based on a small sample of individuals with both gonad types. Some species that are currently classified as separate-sexed may consequently be protandrous sequential hermaphrodites, whereas some supposedly simultaneous hermaphrodites may have an undiscovered protandrous phase (Leonard 2013).

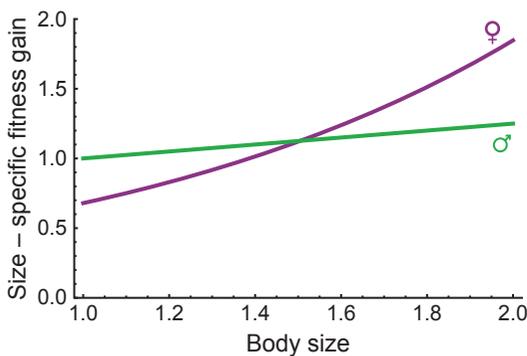
Occurrence

Protandrous hermaphroditism is rare but taxonomically widespread, occurring in a diverse range of animal phyla (Policansky 1982). In vertebrates, protandrous sequential hermaphroditism is known in the clownfish (subfamily Amphiprionina of the Pomacentridae), porgies (Sparidae), and flatheads (Platycephalidae), with isolated examples in several other fish families (Sadovy de Mitcheson and Liu 2008). All three forms of protandry are well-represented in the mollusks, including both gastropods (e.g., true limpets, Patellogastropoda; slipper limpets, Calyptraeidae) and bivalves (e.g., oysters, Ostridae; scallops, Pectinidae) (Collin 2013). Protandrous hermaphroditism is rare in crustaceans, but occurs in many decapod shrimp (Charnov 1982; Bauer 2006). Protandry is notably very rare in freshwater fish and entirely absent in land vertebrates and insects. Most protandrous species have close relatives that are separate-sexed or simultaneous hermaphrodites, indicating that protandry has evolved many times independently (Charnov 1982; Collin 2013).



Protandrous Hermaphroditism, Fig. 3 (a) Hypothetical relationship between gamete investment and the rate of fitness gain for male function (green) and female function (purple). For female function, fitness increases linearly with investment, whereas for male function, fitness increases steeply at first but then levels off. (b) The optimal investment of resources into male and female reproduction, shown as the total resources available to an individual varies, assuming the fitness gain curves from panel (a). If

the individual has a small resource budget, it is optimal to invest only in male function. As the resource level eventually increases, the marginal gains from female function eventually equal those from male function (marked as a black dot with dotted tangent line). After this point, all additional resources should be invested in female function. If access to resources increases with age, this selects for protandrous simultaneous hermaphroditism



Protandrous Hermaphroditism, Fig. 4 Hypothetical relationship between body size and the rate of fitness gain for individuals of each sex. In the size advantage model, protandrous sequential hermaphroditism is adaptive if the female curve increases more steeply than the male curve, as shown here. The optimal timing of sex change occurs when the male and female curves cross

Mechanisms and Cues of Sex Change

Protandrous sex change is underpinned by a wide variety of mechanisms, consistent with its taxonomic diversity. Some taxa have clearly separated ovaries and testes, whereas others combine ovarian and testicular tissue inside a single organ, called an ovotestis (Policansky 1982). Germ

cells may specialize as one sex early in development or remain sexually bipotent for extended periods (Sadovy de Mitcheson and Liu 2008). In teleost fish, the endocrinal cues of sex change are highly species-specific, most likely reflecting the multiple independent origins of protandry, although gonadal steroids appear to play a key role in all studied species (Frisch 2004).

In protandrous sequential hermaphrodites, sex change is almost always sensitive to social cues such as the sex and size of nearby individuals (Munday et al. 2006; Leonard 2013). For instance, the largest individual in a pair or group may be female, while smaller individuals are male. Even when sex change is more gradual, it may respond to environmental or social indicators of the potential for reproduction via each sex (Charnov 1982; Leonard 2013).

Evolution and Adaptive Significance

To explain the evolution of protandrous hermaphroditism, theorists have explored how the potential for reproductive success changes with size (or sometimes age) for each sex. Two

kinds of size effects are commonly studied: (1) “budget” effects, in which the benefits of size are due simply to greater resource availability, and (2) “direct” effects, which are benefits of size per se (e.g., the dominance hierarchies of anemonefish) (Leonard 2013).

For protandrous simultaneous hermaphroditism, the most prevalent explanations rely on budget effects. For instance, suppose reproductive success is primarily determined by investment into gametes. If there is limited competition among the sperm of different individuals, then sperm production may bring diminishing fitness returns with increasing investment, while egg production shows more linear returns (Charnov 1982; see Fig. 3). Smaller individuals, with fewer resources at their disposal, should then invest only in sperm production, to make use of the higher initial returns. Larger individuals should invest more heavily in egg production, while continuing to produce a small amount of sperm (Fig. 3).

For protandrous sequential hermaphroditism, the most influential explanation is the size advantage model, which is based on direct effects of size on reproduction. It predicts that when reproductive success increases more rapidly with size in females than males, that individuals should begin their lives as females and then change sex (Warner 1975; Charnov 1982; see Fig. 4). Faster growth or lower mortality in males than females may similarly select for protandrous sequential hermaphroditism (Kazancıoğlu and Alonzo 2009). The model implicitly assumes that it is optimal to reproduce as only one sex at a time (i.e., no simultaneous hermaphroditism).

The size advantage model has been successful in predicting the direction and even the timing of sex change (e.g., Charnov 1982), but less effective at predicting its taxonomic distribution. Indeed, given the near-ubiquity of sex differences in growth, mortality and size-specific fecundity, many authors have questioned why sequential hermaphroditism is not more common (Warner 1975; Charnov 1982; Kazancıoğlu and Alonzo 2009; Leonard 2013). Sex change may be selected against if there are large costs associated with changing sex (e.g., due to the need to restructure

the reproductive organs or secondary sexual traits: Kazancıoğlu and Alonzo 2009). Evolutionary transitions from separate sexes to protandry may also face developmental or morphological constraints associated with combining two previously separate sex functions in a single individual (Charnov 1982). Even considering these factors, our ability to explain the distribution of protandrous hermaphroditism in any of its forms remains very limited (Leonard 2013).

Cross-References

- ▶ [Anisogamy](#)
- ▶ [Fecundity](#)
- ▶ [Gametes](#)
- ▶ [Gonads](#)
- ▶ [Gonochorism](#)
- ▶ [Hermaphrodite](#)
- ▶ [Ova](#)
- ▶ [Ovaries](#)
- ▶ [Protogynous Hermaphroditism](#)
- ▶ [Sperm Competition](#)

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