

REPRODUCTION AND SEX IN INVERTEBRATES

Alan N. Hodgson

Department of Zoology & Entomology, Rhodes University, Grahamstown 6140, South Africa

Keywords: Asexual reproduction, copulation, courtship, fertilization, genitalia, gonochorism, hermaphroditism, iteroparity, mate guarding, parthenogenesis, paternity assurance, semelparity, sexual conflict, spermatophores, spermatozoa

Contents

1. Introduction
 2. Asexual reproduction
 3. Sexual reproduction
 - 3.1. Sexuality
 - 3.2. Environment of Fertilization
 - 3.2.1. Broadcast Spawning and External Fertilization
 - 3.2.2 Spermcast Mating
 - 3.2.3. Internal Fertilization
 - 3.2.4. Sperm Heteromorphism and Paraspermatozoa.
 - 3.3. Copulatory Organs, Copulation and Sperm Transfer
 4. Mating behaviors of internal fertilizers: pre- and postcopulatory behaviors, selection and sexual conflict.
 5. Frequency of Reproduction (Iteroparity and Semelparity)
- Glossary
Bibliography
Biographical Sketch

Summary

Whilst asexual reproduction is common in many invertebrate taxa, and the sole means of producing the next generation in some, sexual reproduction is the predominant reproductive method. In the majority of sexually reproducing species the sexes are separate (gonochoristic), however, hermaphroditism occurs in many phyla and some are exclusively so. Sexual reproduction requires that haploid gametes are brought together and in species that inhabit aquatic environments this can occur either outside the body of the parents (external fertilization) or within the reproductive tract (internal fertilization). Terrestrial invertebrates only reproduce by internal fertilization. Whilst fertilization is left to chance in external fertilizers, a number of mechanisms have evolved to increase fertilization success, including producing large numbers of small gametes, gamete chemotaxis and recognition, parent aggregations, and synchronization of spawning. Internal fertilization has required the evolution of more complex reproductive systems and mechanisms of sperm transfer. The selection pressures of internal fertilization have resulted in gametes that are biochemically and morphologically complex (including the evolution of sperm heteromorphism), and tremendous diversity in all aspects of reproductive physiology and behavior, especially those aspects of pre- and post-copulation, as well as copulation itself. In terms of the

frequency of reproduction, invertebrates either reproduce once (semelparity) or several times (iteroparity) in a lifetime.

1. Introduction

Invertebrate is a term that can be used to embrace both multicellular animals that do not have a backbone as well as unicellular protists. For this reason invertebrate text books nearly always have at least one chapter on the Protista. For the purposes of this chapter, however, the author uses the term invertebrate to refer to multicellular invertebrates only. Most animal species are invertebrates, and they are therefore a very diverse assemblage of organisms grouped into about 30 phyla. Invertebrates are found in nearly all aquatic and terrestrial habitats from the poles to the tropics. They range in size from the microscopic, living between sand and soil grains (e.g. some round worms, Phylum Nematoda), to the gigantic e.g. the deep sea squid *Architeuthis* (Phylum Mollusca) which can be up to 16 m long. Body complexity is also highly variable, ranging from the very simple design of sponges (Phylum Porifera), in which cells are not organized into tissues, to the highly complex bodies of arthropods and mollusks.

The continued existence of any animal species relies on the ability of individuals, and populations, to reproduce successfully. Successful production of eggs that develop into juveniles is an important element for maximizing animal fitness. Although the reproductive biology of invertebrates is highly variable, far more than that of vertebrates, the next generation is either produced by asexual or sexual means, with the latter method being the most commonly used. Most species use one mechanism only, but some use a combination of asexual and sexual reproduction. In those species in which both methods are found, asexual reproduction enables growth or expansion into a particular niche whereas sexual reproduction is often the dispersal phase. In a life-cycle the generations may alternate between sexual and asexual reproduction, a phenomenon known as alternation of generations. This is found in animals such as jellyfish (Phylum Cnidaria) and tapeworms (Phylum Platyhelminthes).

To cover all facets of reproduction and sex in invertebrates is not possible here. In this chapter the author attempts to introduce the reader to some of the broader and fascinating aspects of the topic, which will hopefully stimulate further enquiry.

2. Asexual Reproduction

Asexual reproduction does not involve fertilization of eggs (ova), which means that union of the sperm and egg nucleus does not occur. Asexual reproduction occurs either by vegetative means (budding, fragmentation, fission) or by the production of unfertilized eggs (parthenogenesis).

Vegetative methods – Species within a number of aquatic invertebrate phyla (e.g. Porifera [sponges], Cnidaria [e.g. corals, sea anemones], Ectoprocta [moss animals, in some text books referred to as the Bryozoa]) replicate by budding to produce individuals that can form a colony. In some instances the ‘individuals’ within the colony are interconnected (e.g. coral polyps). In others (e.g. solitary sea anemones, turbellarian flatworms [Phylum Platyhelminthes], some echinoderms) one part, or parts of the body

may become separated from the “adult” and develop into new individuals. For example some species of starfish (Phylum Echinodermata) can split in two, each section growing new arms to form two individuals. This is sometimes known as fragmentation. Freshwater turbellarian flatworms can undergo transverse fission or budding. During budding, zooids differentiate along the length of the parent’s body before fission separates them into new individuals (this form of asexual reproduction is called paratomy). Paratomy has also been observed in several families of polychaete worms (Phylum Annelida). The larvae of trematodes, an internal parasitic class of the Phylum Platyhelminthes, replicate to enormous numbers by asexual division (no meiosis). Such division is not confined to the larvae of internal parasites. The larvae of gall midges that feed on fungus also replicate asexually. The offspring produced by vegetative methods are therefore nearly always genetically identical to the parent. Unless some mutation occurs, there is no addition of genetic diversity to the population because replication is asexual, and therefore mixing of genes does not happen. The lack of genetic diversity may, however, not be disadvantageous as replication of one individual that may have a very successful genotype for a particular set of ecological conditions, can enable a population to rapidly increase in numbers. This can result in the exclusion of competitors, increase feeding efficiency, or reduce predation risks. Aphids, which are insects belonging to the Order Hemiptera, are a good example of invertebrates that show explosive population growth by asexual reproduction. Asexual replication during the larval stages of trematodes, increases the likelihood that a particular genotype will find a new host for adult development.

Parthenogenesis - Asexual reproduction can occur by parthenogenesis (virgin birth) in which unfertilized eggs develop into adults. Because offspring arise from gametes, parthenogenesis is thought to be a more advanced and recent form of asexual reproduction.

There are three main ‘forms’ of parthenogenesis. Arrhenotoky, whereby the offspring produced are haploid males, thelytoky or female producing, and amphitoky (producing either sex). In arrhenotoky wasps (Order Hymenoptera) the female determines whether or not an egg is fertilized by controlling sperm release. There are two main types of thelytoky. The first is apomixis, in which meiosis is suppressed and there is a single meiotic maturation. The offspring are identical to the parent and each other. The second is automixis, in which meiosis is normal and four haploid nuclei are produced from each gametocyte. Diploidy is restored by the fusion of two pronuclei. Thelytoky may also be obligate or cyclical. Obligate parthenogenesis has been described in relatively few species, about 1000 from a diverse range of invertebrate taxa. In such animals, sexual reproduction has never been recorded and males most probably do not exist; e.g. bdelloid rotifers (Phylum Rotifera). What is remarkable about bdelloid rotifers, however, is that although they do not engage in sex, genetic mixing occurs in these animals because they have the ability to incorporate fragments of the DNA of other organisms (bacteria, fungi, plants and possibly other rotifers) into their genome. This is known as horizontal gene transfer and possibly explains why these exclusively asexual animals have diversified into more than 360 species.

Cyclical parthenogenesis is known from a few groups only including monogonont rotifers, aphids and cladocerans (Crustacea) such as the water flea, *Daphnia*. Whilst

many generations may be produced asexually, at some stage in the life cycle, sexual reproduction occurs. In *Daphnia*, sexual reproduction may be triggered by high densities or environmental stress.

A remarkable form of parthenogenesis is that in which the participation of two sexes for successful reproduction is required. In a few species of nematode worms, mites, ticks and beetles, the unfertilized eggs cannot be laid unless the females have mated with a male, even though the male makes no genetic contribution to the offspring. This is known as gynogenesis (or in plants, pseudogamy - false marriage). An even more bizarre situation is found in the spider beetle *Ptinus clavipes* where males do not exist. To ensure successful production of offspring, the females of such species may also mate with the males of a closely related species (*P. pusillus*), but again gamete fusion does not occur.

3. Sexual Reproduction (Amphimixis – In Which Genes from Two Individuals Mix)

The vast majority of invertebrates only reproduce sexually. Compared to asexual reproduction, sexual reproduction is regarded as being energetically more expensive. This is because energy is not only expended on gamete production, but in locating, courting and securing a mate, copulation, and providing nutritional resources (usually fat or protein) for the developing young. Many of these events, especially courtship and mating, are far from harmonious and there is often a great deal of antagonism between the sexes, a phenomenon known as sexual conflict. In addition, reproduction can compromise an animal's immunity, rendering it more susceptible to attack by pathogens and parasites. In many species, therefore, the cost of sexual reproduction is reduced longevity and fitness. This is perhaps why reproduction is usually the first activity to cease when animals are stressed or food is in short supply. Why sexual reproduction evolved, when asexual reproduction works for many species, is a topic of hot debate. Whilst there are many theories, sex brings about the advantage of variation through mixing of genes. This is because sexual reproduction involves the formation of haploid gametes (eggs and sperm) by meiosis within the gonads (testes in males; ovaries in females) and subsequent gamete fusion (syngamy) to produce a diploid zygote. The fusion of gametes that are vastly different in size (eggs are several orders of magnitude bigger than sperm) is known as anisogamy.

3.1. Sexuality

Two forms of sexuality exist in invertebrates, A) gonochorism (or dioecism) whereby the sexes are always separate, and B) hermaphroditism, whereby a genetic individual during its lifetime will have produced male and female gametes.

In many gonochoristic species it is very difficult to tell the males and females apart, unless the animals are dissected and the reproductive systems examined. This is particularly so of species that are broadcast spawners (see Section 3.2.1) and do not show any secondary sex characteristics e.g. bivalve mollusks such as mussels and clams, and polychaete worms. In some, however, the sexes may differ in size (sexual size dimorphism), often a result of sexual selection. This is taken to extremes in a number of

species in which males are significantly smaller (by at least 50%) than females, a phenomenon known as male dwarfism. Dwarf males are found in such diverse invertebrates as polychaete worms, echiuran worms, monogonont rotifers, parasitic copepods, dioecious barnacles (first described by Charles Darwin in his 1851 barnacle monograph who called the dwarf males 'little husbands'), bivalve mollusks (a few species that bore into hard substrata), the pelagic squid *Argonauta*, and spiders. In some (e.g. the siboglinid polychaete worm *Osedax* and the barnacles in which dwarfism occurs) the males, which mainly consist of reproductive organs, attach themselves to a female. Many of the dwarf males of nematode worms and flatworms are parasitic, living in the bodies of their hosts. This is also the case in the phylum Echiura, which are bottom dwelling marine worms that mainly feed on detritus. Dwarf males are best known from one family of these worms, the Bonellidae. The females produce small larvae, the sex of which is largely determined by environmental factors. In the absence of other adults of the same sex, the larvae will become females, but will develop into males if they encounter a female. Upon encountering an adult female the larva attaches to it using a muscular sucker. Most of the organ systems of the larva do not develop and after a few days the developing worm migrates through the gut of the female to live close to the oviduct where as a male it can fertilize the female's eggs.

Many gonochorists have a 1:1 sex ratio of males to females, but there are numerous exceptions to this. Whilst skewed sex ratios may be a result of environmental or genetic factors, in recent years microorganisms (especially bacteria) have been found to manipulate the sex of invertebrates, and is quite common in arthropods such as isopods, amphipods, mites and a variety of insects. Perhaps the most well known bacterium that manipulates invertebrate sex is *Wolbachia*. Microorganisms, such as *Wolbachia*, live inside the cells and are transmitted from the female to her offspring. Some bacteria cause feminization, in which males are converted to females during development. In others the bacteria cause death of males during embryogenesis or larval development, whilst in some wasps and mites, the bacteria induce parthenogenetic development.

There are a number of forms of hermaphroditism. Some invertebrate species are simultaneous hermaphrodites, producing both eggs and sperm at the same time, either in the same gonad (an ovotestis) or in a separate ovary and testis. An individual will have both male and female reproductive organs. In others sex change occurs with individuals beginning their sexual life as males, before becoming a functional female later (protandry), or more rarely functioning as a female, before switching to being a male (protogyny). Finally some species sequentially alternate between male and female phases, i.e. show sex reversal. An excellent example of a species with this type of hermaphroditism is the oyster *Crassostrea virginica* which first matures as a male, then becomes female, and thereafter may change sex every few years.

Sexuality can be linked to both invertebrate systematics and to environment. Thus some invertebrate taxa appear to be exclusively or predominantly gonochoristic (e.g. Nematoda; Sipunculida; Rotifera; Polychaeta of the Annelida; Chelicerata & Hexapoda of the Arthropoda; Cephalopoda & Bivalvia of the Molluska; Echinodermata), whereas other taxa are exclusively or predominantly hermaphroditic (e.g. Porifera, Ctenophora, Platyhelminthes, Opisthobranchia & Pulmonata of the Molluska; Clitellata of the Annelida; Ectoprocta). Hermaphroditism is particularly common in clonal and colonial

species. It is also clear that hermaphroditism has evolved independently many times, being the ancestral (plesiomorphic) sexual mode in some taxa, and the derived state (apomorphic) in others. Hermaphroditism, however, appears to occur more frequently in certain environments. For example, freshwater and terrestrial annelids and mollusks are hermaphrodites, whereas their marine relatives are nearly all gonochoristic. Hermaphroditism is also more common in deep-sea crustaceans when compared to those from shallow-waters. This therefore has raised the question as to whether there is a functional reason for hermaphroditism that can be explained by natural selection.

A number of theories/models have been proposed to try to explain the occurrence of hermaphroditism, the two most widely cited being the 'Low Density model' and 'Size Advantage model'.

- A The 'Low Density model' proposes that simultaneous hermaphroditism is of advantage in species that might find it difficult to locate a mate. This would occur in species that exist in low population densities, are very sluggish, sedentary or sessile. In such animals hermaphroditism would increase the probability (double the chance) that infrequent encounters between individuals will result in mating success. This model also suggests that if other individuals are not encountered then self-fertilization is possible, although many hermaphrodites have mechanisms to prevent or minimise this. This form of hermaphroditism is indeed common in sessile animals, but also in parasitic and deep-sea species, possibly because these ecological conditions do not result in frequent access to conspecifics.
- B The 'Size Advantage model' argues that sex change (sequential hermaphroditism) will be favored if there is an advantage to being a particular sex (i.e. being male or female) at a given size or age. Thus protogyny might be favored if male success is achieved by an increase in size. For example, large males might be able to control larger territories with its resources which would be of benefit. Protandry would be favored if female success (fecundity) increases with size (big females can produce more eggs or possibly be better equipped to defend their young). Differences in growth or mortality rates of sexes might also be a driving force of sequential hermaphroditism. Therefore if one sex has a higher growth rate it would be of advantage to be that sex first. On the other hand if one sex has a higher mortality, it is of advantage to be the other first.

In sequential hermaphrodites sex change can be genetically controlled, the change occurring at a specific size or age. In many species of shrimps (Sub-phylum Crustacea) and gastropods (Phylum Mollusca), however, sex change is under social or environmental control. Thus the sex of an individual can be influenced by density, sex ratio, and size relative to others in the social group. For example in flat oysters, males are attracted to the larger females during their larval stage. Once settled on a female, male growth is retarded by the females, and dwarf males may be older than free-living males of the same size. Similarly in slipper limpets (*Crepidula* spp.), which are gastropod mollusks that can form stacks, there is a large female at the bottom of a stack that influences the sex of the ones on top.

It has been argued that a disadvantage of simultaneous hermaphroditism is that

individuals must put energy into growing and maintaining two sets of reproductive organs. This may explain why fewer invertebrates are simultaneous hermaphrodites.

3.2. Environment of Fertilization

Successful sexual reproduction requires that male and female gametes are brought into close proximity to one another. This can occur in a number of ways.

-
-
-

TO ACCESS ALL THE 27 PAGES OF THIS CHAPTER,
Visit: <http://www.eolss.net/Eolss-sampleAllChapter.aspx>

Bibliography

Adiyodi, K.G. & Adiyodi, R.G. (eds.) (1983). *Reproductive Biology of Invertebrates*. Volume II. Spermatogenesis and sperm function. John Wiley & Sons. Chichester. [This volume contains chapters in which the sperm structures of most invertebrate phyla are described].

Arnqvist, G. and Rowe, L. (2005). *Sexual conflict*. Princeton University Press. [A detailed synthesis of this topic in which many invertebrate examples are used to explain how the evolutionary interests of males and females can be different.]

Barnes, R.S.K., Calow, P.P., Olive, P.J.W., Golding, D.W. and Spicer, J. (2001). *The Invertebrates: A synthesis*. 3rd Edition. Blackwell Publishing. [An invertebrate text that contains chapters devoted to invertebrate reproduction and development.]

Birkhead, T.R. (2000). *Promiscuity: An evolutionary history of sperm competition and sexual conflict*. London, U.K.: Faber and Faber. [An excellent popular science book that deals with many aspects of invertebrate reproduction.]

Birkhead, T.R. and Møller, A.P. (1998). *Sperm competition and sexual selection*, San Diego, US: Academic Press. [A collection of reviews by experts. Chapters 6 to 10 deal with some invertebrate groups. To get the most out of this book a good background in biology is needed.]

Bishop, J.D.D. and Pemberton, A.J. (2006). The third way: spermcast mating in sessile marine invertebrates. *Integrative and Comparative Biology* 46, 398-406. [A very good review of this mechanism of fertilization in aquatic marine invertebrates.]

Chase, R., and Blanchard, K.C. (2006). The snail's love dart delivers mucus to increase paternity. *Proceedings of the Royal Society of London, Series B* 273, 1471-1475. [Recent findings on the reproductive role of calcium darts in land snails.]

Eberhard, W.G. (1985). *Sexual selection and animal genitalia*. Harvard University Press. [A comprehensive review of this topic.]

Gillott, G. (2003). Male accessory gland secretions: modulators of female reproductive physiology and behavior. *Annual Review of Entomology*, 48 163-184. [A comprehensive review of the reproductive role chemicals produced by male insects.]

Hodgson, A.N. (1999). Paraspermatozoa, in *Encyclopaedia of Reproduction* (Knobil, E. and Neill, J.D. eds), pp. 656-668. Academic Press. [A brief review of heteromorphic sperm in invertebrates].

Holman, L. and Snook, R. (2008). A sterile sperm caste protects brother fertile sperm from female-

mediated death in *Drosophila pseudoobscura*. *Current Biology*, doi:10.1016/j.cub.2008.01.048. [Recent research presenting new information on the potential role of non-fertilizing sperm in insects.]

Hosken, D.J. and Stockley, P. (2004). Sexual selection and genital evolution. *Trends in Ecology and Evolution* 19 87-93. [This article examines the role of sexual selection driving the evolution of genital morphology.]

Jamieson, B.G.M., Ausi , J. and Justine, J-L. (eds) (1995). *Advances in Spermatozoal Phylogeny and Taxonomy*. M moires du Mus um National d'Histoire Naturelle 166, 564pp. [Several chapters in this volume present detailed information on the structure of invertebrate spermatozoa.]

Karlsson, B. (1998). Nuptial gifts, resource budgets, and reproductive output in a polyandrous butterfly. *Ecology* 79, 2931-2940. [An informative article synthesising information on nuptial gifts in Lepidoptera.]

Koene, J. M. and Schulenburg, H. (2005). Shooting darts: co-evolution and counter-adaptation in hermaphroditic snails. *BMC Evolutionary Biology* 5, 25. [This article looks at dart shooting in snails and presents information on the reason for dart shooting and dart structure.]

Levitan, D.R. (1995). The ecology of fertilization success in free-spawning invertebrates, in *Ecology of marine invertebrate larvae* (McEdward, L., ed.). pp. 123-156 CRC Press, Boca Raton. [This article examines many aspects of the fertilization biology of broadcast spawners.]

Michiels, N.K. and Newman, L.J. (1998). Sex and violence in hermaphrodites. *Nature* 391, 647. [An account of hypodermic insemination in free-living flatworms. For many this article was the one that brought this mechanism of fertilization to the attention of many zoologists.]

Prenter, J., MacNeil, C. and Elwood, R.W. (2006). Sexual cannibalism and mate choice. *Animal Behaviour* 71, 481-490. [A review of the occurrence and hypotheses for this type of behavior in invertebrates, especially spiders.]

Ravi Ram, K. and Wolfner, M.F. (2007). Seminal influences: *Drosophila* Acps and the molecular interplay between males and females during reproduction. *Integrative and Comparative Biology* 47, 427-445. [Reviews the known functions of male accessory gland proteins and how they affect female reproduction.]

Simmons, L.W. (2001). *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press. [The book deals with many aspects of the reproductive biology of insects.]

Swanson, W.J. (2003). Sex peptide and the sperm effect in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences* 100 (17), 9643-9644. [A short review of how accessory gland proteins can affect female fruit flies. A good background in biology is helpful for understanding some of the article.]

Vacquier, V.D. (1998). Evolution of gamete recognition proteins. *Science* 281, 1995-1998. [An ideal introduction to explaining the role of proteins in gamete interactions.]

Vollrath, F. (1998). Dwarf males. *Trends in Ecology and Evolution* 13, 159-163. [This article reviews the occurrence of male dwarfism in a number of taxa.]

Biographical Sketch

Alan Hodgson is a Full Professor in zoology at Rhodes University. Whilst having a general interest in mollusks and in the reproductive biology of marine invertebrates, he has a special interest in invertebrate gamete formation, structure and function. He has used such studies to explore fertilization mechanisms and systematic and phylogenetic relationships of a variety of invertebrate taxa.