Chapter 1

Reproduction and Larvae/Spore Types

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We describe the diversity of traits and adaptations that biofouling organisms have evolved to ensure reproductive success. Our chapter focuses on the processes of propagule production through sexual reproduction (fertilisation of gametes leading to a larval stage that may or may not disperse) or asexual reproduction (fragmentation of the embryo, larva or adult, or by production of diploid spores). We focus on key issues in broadcast spawning of gametes and fertilisation, adaptations to overcome Allee effects, and so-called ‘carry-over’ effects. In so doing we have not provided an exhaustive review of spore – or larval – types, but rather attempt to focus on areas that are currently at the forefront of research while highlighting avenues for further research.

1.1 Introduction

Concerns about biofouling organisms mostly focus on the rate and form of growth that allows organisms to spread and take up space on a surface. Yet isolated surfaces cannot be overgrown, and most unitary biofouling organisms like barnacles or polychaetes do not reproduce vegetatively. In these cases new biofouling must occur by way of some form of dispersive propagule – which for most animals and algae usually involves sexual reproduction (see Plate I A). This involves a cascade of processes, all of which need to happen successfully:

- Gametes (or spores) have to be produced and released at the right time.
- The sperm has to meet, fuse with and fertilise an egg.
- The resultant zygote or spore must be able to develop, perhaps feed, and disperse, whilst not getting eaten or diseased.
- The resulting competent larva/sporeling/germling must settle and recruit onto a surface.

In a biofouling context, understanding all the processes involved in this cascade is important because disruption to just one of them can provide a means to control the supply of potential recruits (see also Chapters 2 and 3). Clearly, this is a substantial research area that includes a wide range of organisms with diverse life histories. It is not our intent to review this topic comprehensively, but rather to provide an introduction to the main issues, emerging topics and key literature.
1.2 Some terminology

Most organisms which are important as biofoulers have a complex life cycle, involving at least one dispersive, usually microscopic, stage that does not look much like the adult sessile life form. A range of different, sometimes confusing, terminologies are used by zoologists and phycologists to refer to these propagules and the different processes that are employed to produce them. We define some of them here that we use below:

**Broadcast spawning**: Both male and female gametes are released and fertilisation occurs externally, in the sea (some authors also designate this as free spawning, but see below).

**Spermcast mating**: Male gametes are released and fertilise eggs retained by maternal individuals (also designated as free spawning egg brooders).

**Free spawning**: Considerable ambiguity has surrounded the definition of free spawning (e.g. [1]): Some authors have used this term to describe the release of sperm, independently of whether the eggs are released or retained (e.g. [2–4]), and others to describe the release of both sperm and eggs, i.e. identical to broadcasting (e.g. [5, 6]). We therefore restrict ourselves to using the terms ‘broadcasting’ and ‘spermcasting’, and avoid the ambiguous meaning of this term.

**Copulatory fertilisation**: Direct delivery of sperm to maternal individuals (by copulation or pseudo-copulation).

**Egg brooding**: Retention of eggs in the maternal individual until fertilisation.

**Embryo or larval brooding**: Retention of embryos following fertilisation up to a more advanced stage at which they are released, and which may still include a short pelagic phase or just direct settlement.

**Encapsulation**: Retention of embryos and/or larvae within protective benthic structures until they hatch, either as swimming larvae or as crawl-away juveniles.

**Larvae**: Potentially dispersive (multicellular) propagules produced by animals, most often by sexual reproduction. There is a huge range of different larval types and forms across different taxonomic groupings. One of the best overviews of the incredible diversity of larvae is the recent compendium edited by Young et al. [7]. More broadly, larvae are often classified according to whether they feed (planktotrophic) or do not feed (lecithotrophic) before they settle and metamorphose into a juvenile/adult form.

**Zygote**: The product of two gametes uniting to form a diploid cell. In animals, this develops into a larva. In algae, the zygote will settle and germinate into a diploid vegetative plant. A settling algal zygote will sometimes be called a *germling*.

**Spores**: Formally, a spore is defined as a unicellular reproductive unit produced by an (algal) sporophyte [8]. Algal biologists base their definitions of spores and gametes on whether a unicellular propagule settles and develops into a vegetative unit in its own right (a *spore*) or if it must first unite with another (gamete) to form a zygote which then settles and grows into a vegetative unit; unfortunately, the terms sometimes seem to be misapplied interchangeably. A spore can be produced mitotically (*mitospore*) or meiotically (*meiospore*), and be haploid or diploid, depending on the particular life history pattern of the alga in question – which is often exceedingly complex (see below). Perhaps further confusing zoologists, the prefix ‘zoo’ (*zoospore*) or the term ‘swarmer’ is sometimes used to indicate that a spore is motile.
1.3 Asexual production of propagules

Fragments of vegetatively produced (clonal) growth that break off from parental colonies can often function as dispersive propagules. Colonisation of new surfaces via these fragments can result from two processes: by successful settlement of the fragment, or by the release of larvae or gametes by the fragment. Settlement and re-establishment of fragments appears common among a range of groups including sponges, corals, ascidians, bryozoans and algae and can be a very important demographic process [9]. For example, an invading didemnid ascidian is presently causing major biofouling problems for mussel aquaculture in North America and, indeed, seems to be overgrowing and smothering virtually everything in its path [10]. The rope-like growth form of this and related species can result in lobe-shaped fragments being broken off naturally or as a result of human activities such as cleaning of mussel lines or scallop dredging. Thus, cleaning mussel lines of such ascidians may actually exacerbate biofouling because the new fragments which fall back into the water are capable of reattaching and growing if they lodge in an appropriate place [10].

The role of dispersive fragments as vehicles carrying gametes that are then shed in new locations is less well established, but in some cases gametes or larvae can develop and be released from surprisingly small fragments. For example, some sponges can release embryos from fragments only a few millimetres in diameter [11]. In general, the potential importance of rafting as a source of colonists and/or gametes has been largely overlooked until recently [12] and yet this could be a very important dispersal mechanism, particularly for large macroalgae [13, 14].

Several taxa produce asexual dispersive propagules. Amongst the more intriguing of these is the parthenogenetic production of larvae found in the *Lasaea* complex of clams in northeast Pacific. Most species of *Lasaea* produce outcrossed sexually derived larvae (see below), but a number of strictly asexual lineages produce larvae parthenogenetically and have apparently done so for a long period of evolutionary time [15]. These lineages do not self-fertilise in the usual sense; rather, the development of (diploid) eggs into parthenogenetic larvae is triggered by fertilisation with autosperm; the sperm then disintegrate within the egg cortex, rather than fusing with the egg ‘pronucleus’ [16]. Exclusively parthenogenetic reproductive strategies like this are rare amongst typical biofouling taxa, but facultative parthenogenesis, in which male and/or female gametes can develop into mature reproductive thalli if fertilisation does not take place, is recorded in a number of algae [17], including common biofoulers such as *Ulva* and *Codium* [18]. By providing reproductive assurance when population sizes are small and mate availability is low, facultative parthenogenesis may be an important form of reproduction in some taxa.

Much more commonly, organisms combine alternating periods of sexual and asexual reproduction. The most obvious and widespread examples of these are the various haploid–diploid life cycles of many macroalgae. For example, ‘diplohaplont’ life histories are common within the green and brown algae and involve the alternation of both haploid and diploid vegetative stages. The basic pattern is that meiotically derived (haploid) motile spores are produced by sporophytes and germinate into gametophytes. These in turn produce gametes mitotically, which then fuse (syngamy) to form a diploid zygote that germinates into the mature sporophyte, completing the cycle. There are, however, many variations on this theme and probably many more yet to be fully described [18–20]. For example, diploid sporophytes of the brown algae *Ectocarpus* can produce haploid zoospores via meiosis that will settle and grow into
haploid gametophytes or they can produce diploid zoospores by mitosis that will settle and grow into new diploid sporophytes [21]. Even more complex, the red algae (Rhodophyta) can incorporate a third life history phase, the carposporophyte, which is unique in that it is formed on the female gametophyte. In this context, sexual reproduction in red algae is more similar to brooding (spermcasting) animals than to the broadcast spawning strategies in other algal groups (see below). Algal life histories are exceedingly complex and we refer readers to other sources for much better overviews of these [3, 18–20]. Whether produced asexually or sexually, however, spores and gametes of algae are almost always unicellular (but see [22]).

Animals too can alternate between sexual and clonal production, but the asexual propagules produced by animals are almost always multicellular. Colonial taxa such as corals, freshwater bryozoan and sponges are all well known for their ability to produce asexually derived larvae/propagules at various times, often depending on demographic or environmental conditions (e.g. [23–26]). For example, freshwater bryozoans produce desiccation-resistant asexual statoblasts during times of drying, which may be an important source for colonisation when conditions again become suitable [27]. Other animal life histories include an obligatory asexually produced stage (e.g. some hydroid medusae [28] – which in most species disperses freely and in all cases produces freely spawned gametes which unite to form a larval stage that then settles and metamorphoses to a juvenile). Similarly, some unitary animals produce asexual clones of themselves which can disperse short distances via crawling or drifting but at other times release gametes to produce sexually derived larvae capable of much wider dispersal. Anemones (anthozoans) are well known for this and can reproduce asexually using a variety of mechanisms including longitudinal (or even transverse) fission or through pedal laceration [29]. Equally, some tube-building serpulid and sabellid polychaetes bud off miniature versions of themselves from their posterior segments – a strategy which could lead to an obvious problem for the newly cloned individual trapped at the end of a tube behind its parent: how to get out? In at least some species of Filograna and Salmacina, adults build ‘escape hatches’ into the solid calcareous tubes as a way for budded-off children to escape and then start building their own tubes [30].

Finally, there are some truly strange life history strategies in which larvae produced are a combination of both sexual and asexual reproduction. Polyembryony is apparently used by all cyclostome bryozoans and involves the asexual clonal production (or twinning) of a sexually generated larva [5]. This strategy has been seen as something of a paradox in an evolutionary sense as it apparently combines the potential negative consequences of both fully outcrossed sexual reproduction and asexual reproduction [31]. One suggestion [32] is that polyembryony may provide a form of reproduction assurance when sperm are rare and/or quickly diluted in the sea [33] and there would not otherwise be enough sperm available to fertilise multiple eggs. Similar clonal splitting of sexually produced larvae is known in other free-living groups (e.g. echinoderms [34]), but this is an apparently rare strategy in sessile biofouling organisms. Even more bizarre are chimeric sponge larvae, which can be formed from the fusion of independently and sexually produced larvae [35]. In contrast to quite high relatedness often needed for fusion in adult sponges, allorecognition systems do not appear to be as well developed in the larvae of sponges such as Haliclona sp. Consequently, non-related larvae fuse quite readily to form larger larvae that swim and can still metamorphose and develop into adult sponges with a mosaic genetic identity. Perhaps because larger larvae may be more
successful competitors, fusion might give chimeric larvae size advantages during settling and recruitment (though see [36]). Larvae also behave in an aggregative way in the laboratory that would apparently increase the opportunities for fusion to happen, though if or how often this happens in natural field populations is unclear [35]. As an aside, genetically mosaic individuals (chimaeras) appear to be much more common than often appreciated, and examples are known across a wide range of colonial biofouling taxa such as sponges [37], ascidians [38, 39], hydroids [40] and red algae [41, 42]. Just how multiple and presumably interacting genotypes within a single demographic ‘individual’ influences allocation of resources to asexual or gametic reproduction and then affects sexual reproduction is a fascinating area for future research [43].

1.4 Sexual reproduction – mechanisms facilitating fertilisation

Sexual reproduction involves the union of haploid gametes, nominally a sperm from a male and an egg from a female, to form a diploid zygote (i.e. syngamy). Of course many organisms are hermaphroditic and so can act as a male (producing sperm) and female (producing eggs) either simultaneously or at different times, sequentially – first as a male (protandrous) or as a female first (protogynous). Thus, in many cases the terms male and female below refer to whether individuals are releasing sperm or eggs. In algae the situation can be even less distinct. Where gametes are isogamous (i.e. similar sized and functionally equivalent) but gametes from two different genetic individuals are required for fertilisation, gametes are referred to as +ve and –ve, indicating that complementary gametes are involved; the green alga Ulva is a well-known example where this occurs [20].

Where sexual reproduction takes place, there are three basic mechanisms which aquatic organisms use to get sperm and egg together:

1. There is some form of direct coupling during which males directly transfer sperm to the female and fertilisation takes place within the female (internal fertilisation).
2. Males release sperm freely into the water, allowing water movements to disperse the sperm to eggs which are retained/brooded within the female and fertilisation takes place internally (spermcasting).
3. Both sperm and eggs are released freely and fertilisation takes place externally, in the open water column (broadcasting).

Perhaps for biophysical reasons [44], there appears to be no biological intermediary that facilitates the transfer sperm (or eggs) for fertilisation in aquatic systems; that is, there is no aquatic equivalent to the pollinator-mediated systems of terrestrial flowering plants [45].

Internal fertilisation is largely restricted to mobile animals, which are of little concern in biofouling (except perhaps as predators or grazers of biofoulers). The obvious exception to this pattern is barnacles, which fertilise internally by means of a famously long (relative to body size) penis. In the common European barnacles Semibalanus balanoides and Chthamalus montagui, penis length is up to 25 mm [46]; body size varies and is typically 8–12 mm. This constraint on fertilisation seems to drive larval settlement patterns: in a recent study, Kent et al. [46] found that larvae of S. balanoides, an obligate outcrosser, were far more likely to settle within one penis length of a conspecific than larvae of C. montagui, a facultatively selfing...
species. Although the issue has been discussed for a long time, the intriguing possibility that settlement distances in barnacles might be determined not only by penis length but also by capacity for selfing requires further investigation – not least because this will influence both mating system and reproductive success. A few studies have reported the capacity for selfing in barnacle species [47, 48], but we still know very little about the relative frequencies of selfing versus outcrossing in barnacles.

In contrast to internal fertilisation, spermcasting provides an obvious solution for transferring sperm in sessile taxa: where males cannot move to deliver sperm directly to females, they release it freely so that the sperm are advected to females. Spermcasting is used by many biofouling species, notably bryozoans, colonial ascidians and some species of red algae. Bishop and Pemberton [5] listed six generalisations concerning reproductive traits of spermcasters:

1. Sperm are relatively long lived once diluted in sea water.
2. Only very dilute sperm suspensions are needed to ensure fertilisation.
3. Sperm can be stored by the recipient.
4. There is extensive contact between allosperm and the somatic tissue of the recipient.
5. Gamete compatibility systems are often involved (although this is also true of many – perhaps all – other sexually reproducing taxa: see below).
6. Receipt of compatible sperm may trigger female investment.

The first three of these traits are adaptations that minimise sperm limitation effects (see below), whereas the last three allow for differential provisioning of larvae with maternal resources, depending on the genetic make-up of the fertilising sperm (see below). All of these generalisations are relevant to taxa such as bryozoans and colonial ascidians; however, not all spermcasting species show all of these adaptations. For example, in ostruid oysters, serpulid and spirorbid polychaetes, and some ascidians (e.g. Corella), fertilisation takes place within the mantle/atrial cavity, i.e. outside the body. In these cases the eggs are indeed retained by the mother, and it is probable that maternal control of water flow through the mantle/atrial cavity mediates fertilisation success, but it is not clear that sperm can be stored, or indeed that there is extensive contact between the sperm and the somatic tissue of the recipient. Moreover, eggs are fully provisioned before sperm are received and therefore there is no opportunity for sperm-induced maternal investment. This suggests that rather than spermcasting being a wholly distinct and separate category, it may rather lay at the end of a continuum of traits from broadcasting to ‘fully’ spermcasting. The processes that control sperm release, acquisition and fertilisation in spermcasters are very poorly understood, and this promises to be an exciting and productive research area.

For broadcast spawners, a key distinction is that there is little or no direct control over fertilisation: eggs and sperm are released into the water column where fertilisation occurs. Nonetheless, a series of adaptations have evolved to ensure fertilisation success in broadcast spawning species. These include several mechanisms to increase gamete concentration, such as spatial and/or temporal aggregation at spawning (simultaneous or ‘mass’ spawnings), gamete buoyancy and swimming behaviour, gamete longevity, chemical attraction of sperm to eggs and the retention of ‘sticky’ eggs, as well as adaptations to ensure that eggs are not fertilised by too many sperm (‘polyspermy’). We need to be careful to take variation in these traits into account when attempting to estimate the success of broadcast spawning: these traits vary widely not only between taxa, but also between populations, individuals, seasons and times of day, so that even comparisons within species can be difficult [49].
1.5 Demographic effects on fertilisation success – Allee effects

A critical requirement for sexual reproduction is the availability of a partner, and consequently sexual reproduction can be risky when the chance of finding a mate is low. Interestingly, reproductive rate scales with population density, whereas death rate often does not. The result is that below critical population densities, reproductive success is lower than the death rate, leading to extinction of that population (if rates do not change). This effect – the ‘Allee effect’ – is non-linear, and does not only apply to birth/death rates; it can result in reduced choice and/or lower quality of mates and correspondingly reduced or zero fitness [50].

The Allee effect is particularly relevant for invading species – in nearly all natural circumstances it does not just take two individuals to establish a species (Noah was seriously misguided!). Invading individuals need to be close enough to each other, spawn at the same time and be compatible for the inoculation to lead to successful reproduction. For this to occur, sufficient ‘propagule pressure’ (enough individuals recruiting and making it through to sexual reproduction) is needed to establish a novel population [51]. The potentially valuable corollary of this is that if we reduce population size below a critical level, we may be able to prevent (or at least limit) the number of sexually produced propagules and thus limit the recruitment of larvae/germlings to surfaces.

In the last 20 years there has been a lot of interest in the potential impacts of Allee effects in broadcast spawners. Specific attention has focused on Allee effects and sperm limitation – the condition in which a fraction of released eggs remain unfertilised because sperm concentrations are too low. Sperm limitation is probably common: gametes are relatively short-lived, and they disperse and dilute quickly (especially in strong flows). Consequently, despite many adaptations to increase likelihood of gamete contact (reviewed by Serrão and Havenhand [49]), gametes may often expire before ever having the chance to meet. Clearly, this could be a major constraint to reproduction, but how often does this actually happen?

Field experiments to measure fertilisation success suggest that sperm limitation could be important in many situations; however, there are many potential artefacts that limit our ability to measure fertilisation success experimentally. Yund and Meidel [52] have shown that the ‘broadcast’ spawning of urchins may actually involve the release of eggs in viscous fluids that retain them on the urchin surface, where they effectively ‘filter’ sperm from the passing water mass, thereby integrating sperm concentrations across a long period and elevating fertilisation rates over those expected from simultaneous unencumbered release of gametes. Similar release of eggs in mucus strings, and successful fertilisation within those strings, has been reported from the laboratory and field for the tunicate *Ciona intestinalis* [53]. Whether such adaptations are common among marine invertebrates is not known; relatively few species have been observed spawning in the field; however, the release of gametes in mucilage occurs commonly in algae, both at low tides (e.g. fucoids) and subtidally (e.g. rhodophytes). Indeed, it has been hypothesised that in red algae, the release of spermatia in mucus strings will greatly facilitate capture by the trichogyynes (spermatia are aflagellate and cannot swim), thereby enhancing fertilisation success (reviewed by Brawley and Johnson [18]). Even the briefest analysis shows that the potential benefits of this behaviour are considerable, and it is therefore surprising that this has not been reported more frequently (while noting the obvious caveat that absence of evidence is not evidence of absence). Indeed, there are very few observations of spawning in marine organisms in general, and data on the degree of spawning synchrony,
timing of spawning and correlations with environmental variables, and rates and variance in fertilisation success are all badly needed.

Notwithstanding these constraints, one generalisation that can be made is that the mating system (internal fertilisation, spermcasting, broadcasting) does seem to make a difference to fertilisation success. The very few data available suggest that internal fertilisers (such as barnacles) are not sperm-limited (although to our knowledge this has not been investigated and because sperm limitation would probably manifest as reduced reproductive frequency, this could have been overlooked and/or misinterpreted in previous studies). Similarly, spermcasters seem to be reasonably buffered against sperm limitation: genetic studies of ascidians and bryozoans show multiple paternity (in addition to reproductive assurance by selfing) and that reproductive success is largely independent of population density [4,5]. In contrast, for a great many species broadcasting remains a risky, though probably unavoidable, alternative.

1.6 Environmental factors affecting fertilisation

A wide range of environmental factors can directly or indirectly affect the processes that lead to larval/spore production. Salinity, dissolved gases, UV radiation, temperature and pH can all affect various chemical processes involved in sperm viability and motility, egg/zygote viability or the actual process of fertilisation itself [54]. Similarly, a range of physical processes can affect gametes and whether they get or stay together. Turbulence is critically important in determining not only rates of mixing of gametes, but also rates of dilution and dispersion – which may happen before gametes have had a chance to meet [54,55]. Gametes of some algae are positively phototactic leading them to move towards the surface, thereby concentrating them and thus increasing the likelihood of contact and fertilisation with other gametes [56–58]. There is also a plethora of ecotoxicological studies on the effects of various specific toxicants on sperm, eggs and developing zygotes/larvae. Again, toxicants can all potentially affect sperm and/or eggs and/or the developing zygote and/or the process of fertilisation itself [59] and, much less often investigated, multiple toxicants/physical stressors probably often do so in synergistic ways [60].

The impacts of environmental variables on fertilisation are less well investigated but can be critically important. For example, the membrane-based ‘fast’ blocks to polyspermy in most taxa involve Na\(^+\)/K\(^+\) ion channels that alter permeability of the membranes. In fucoid algae, these polyspermy blocks are efficient at preventing penetration by supernumerary sperm at typical marine salinities, but in the Baltic Sea and/or estuarine areas where salinities are lower, higher rates of polyspermy ensue, presumably because ion exchange and thus fast-electrical blocks work less well [61]. Equivalent data for marine invertebrates are lacking.

1.7 Links between fertilisation and subsequent larval attributes

For broadcast spawners, egg-size dependent fertilisation success can influence the average size and quality of larvae produced [62]. It has long been known that the cross-sectional area of an egg in part determines how easily an egg will be found by searching sperm [63,64]. Small eggs represent small targets for randomly swimming sperm, so when sperm are limited, smaller eggs are less likely to be found and are thus more likely to remain unfertilised. If egg size varies within a brood (which abundant evidence now indicates is the case, e.g. [65]), then
at low sperm concentrations, only the larger eggs will be fertilised. For the same reasons, when sperm are very abundant, larger eggs will be more likely to be fertilised by more than one sperm (before the polyspermy blocks can prevent further sperm penetration). In that situation only smaller eggs within a brood will be fertilised. This theoretical effect [66] has been demonstrated in the laboratory [62] and has been shown to have further ‘carry-over’ effects later in the life cycle (see below). The extent to which these processes operate in biofouling communities in the field is not known. Nor is it known whether such processes play any role at all in spermcasting and/or internally fertilising species (although the possibility to physically direct and manipulate sperm in such mating systems makes it unlikely that such ‘random’ processes play a large role).

Fertilisation success and subsequent zygote/larval development depends also on the genetic constitution of the egg and sperm. Firstly, sperm/egg binding proteins show considerable variation so that some genotypes will bind and fertilise more easily than others [67, 68]. This imposes yet another restriction on fertilisation success: even if sperm and egg meet, the likelihood that the sperm can penetrate and fertilise the egg may vary markedly. Consequently, we would predict that spawnings involving a greater number of individuals (more gamete genotypes in a mixture) would be more likely to generate a compatible match. A corollary of this is that such mass spawnings are also more likely to lead to high sperm concentrations, and hence polyspermy. The obvious trade-off between the risks of polyspermy and unfertilised eggs has been proposed to be one mechanism driving the evolution of variability in gamete recognition systems [67] in a manner analogous to the large versus small egg size trade-off discussed earlier. The mathematically self-evident benefits accruing from polyandrous spawnings have been demonstrated by Evans and Marshall [69], although they showed this at constant sperm concentrations (thereby excluding the increased risk of polyspermy that polyandrous spawnings imply).

Post-fertilisation compatibility issues will also limit the development of the zygote/larva. Perhaps the most obvious example is that of selfing versus outcrossing – an issue of particular relevance to clonal biofouling species. Many simultaneous hermaphrodites, such as the ascidian Ciona, have partial blocks to self-fertilisation. Yet these blocks can change with gamete age, and vary markedly between species [70–72]. In contrast, some species show no disadvantage from inbreeding (e.g. [73]), and indeed outbreeding depression may exist (e.g. [74]), although this is rare.

As a general note, selfing/inbreeding is probably more common than we tend to think. Alteration of algal life stages and ploidy levels, combined with limited dispersal of algal spores, almost inevitably leads to a large degree of inbreeding in many circumstances. Similarly, the universality of ‘blocks’ to selfing has been questioned, and several notionally ‘self-incompatible’ species have been shown to self, while other species known to be able to self have been shown to preferentially outcross – even at the gamete-recognition level [75]. Equivalent results relating to the probability of egg/larval provisioning have been shown for spermcasters [76, 77].

### 1.8 Hatching and development

One of the most obvious differences between brooders and broadcasters is the location of embryonic development. Brooders (a category that includes all spermcasters, and some – though certainly not all – internal fertilisers) generally retain the embryos until they have hatched...
as larvae and are capable of independent swimming and feeding. In many mobile internal fertilisers, encapsulation of eggs/embryos in benthic masses is an important alternative ‘brooding-like’ strategy [78]; however, this is not relevant for most biofoulers.

The developing embryos of broadcasters, in contrast, are exposed to the environment throughout their embryonic development, and only when they reach the larval stage can they begin to swim, feed and benefit from defensive behaviours. Staver and Strathmann [79] have shown that early development rates of such ‘unprotected’ embryos are significantly faster than those of encapsulated or brooded embryos, suggesting strong selective pressures to minimise early development times. The defensive capacities of larvae (as distinct from embryos) have been known for a long time [80, 81]; see review by Morgan [82]. Nonetheless, larval mortality rates can be extremely high, and are often ten times those of benthic encapsulated embryos [82]. The large numbers of eggs typically released by broadcasters help to overcome this mortality.

1.9 Mobility and survival of larvae/spores

The mobility of larvae and spores is generally very limited, but nonetheless plays a major role in their dispersal. Most propagules are ciliated, flagellated or swim by muscular movement of appendages [83]. This topic has been reviewed extensively by Chia et al. [83] and Young [84], and is typically cited for highlighting the gross disparities between larval swimming speeds (<cm s \(^{-1}\)) and near-shore currents (often >m s \(^{-1}\)). Nonetheless, recent work has shown the capacity of slow-swimming bivalve larvae to significantly influence their distribution in ocean currents (e.g. [85]) and to settle in rapid flows (reviewed by Koehl [86]).

The fate of larvae and spores during the dispersive phase – especially the impacts upon them of nutritional/light regimes that influence their energy reserves, and hence their ability to endure prolonged dispersal and searching for suitable settlement sites – is almost wholly unknown. The difficulties of tracing microscopic larvae in open water masses are obvious and despite several significant advances in technology that aid such measurement (e.g. [87, 88]), this still remains a very poorly understood – yet vital – component of the life history.

1.10 Carry-over effects

One aspect of larval/spore experience that has been investigated closely is so-called ‘carry-over’ effects. These are effects of processes that happen during one life stage but which are expressed in later life stages [89]. Perhaps the most obvious aspect of this is the respective survival and settlement probabilities of larvae that have received plentiful, versus scant, provisioning over the larval period. However, carry-over effects can be far more subtle. There is increasing evidence that events during egg provisioning, fertilisation and embryonic and larval development can have profound influences on settlement and post-settlement success [89–92]. These events may have positive and/or negative impacts, raising again the importance of Fu-Shiang Chia’s exhortation that larvae should not be studied in isolation, but in terms of the whole life cycle [93]. To our knowledge, equivalent investigations have not been undertaken with algal spores and gametes; however, it is to be expected that similar results will be found.
If this turns out to be important, then a possible focus for future biofouling control methods is to develop strategies that influence the quality of the very earliest life stages of biofouling organisms so that gamete viability, fertilisation success and/or successful spore/larval development are compromised.

1.11 Conclusions

- Biofouling organisms utilise a wide variety of mechanisms to produce dispersive propagules; both sexual and asexual reproduction is common.
- With the obvious exception of barnacles, sexual reproduction in biofouling organisms nearly always involves the release of sperm (only) or broadcast spawning both eggs and sperm.
- There are many apparent adaptations to overcome potential Allee effects in biofouling organisms. Selection is likely for spawning behaviours that increase gamete encounter rates during suitable environmental conditions and on gametic traits themselves that would increase the likelihood of successful fertilisation. Similarly, the ability to self or reproduce parthenogenetically in some organisms may allow for reproductive assurance when population sizes are low.
- Larval/germling traits can be affected by processes before, during and after fertilisation. Such effects may be carried over through metamorphosis and have impacts on later life history stages.

References

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