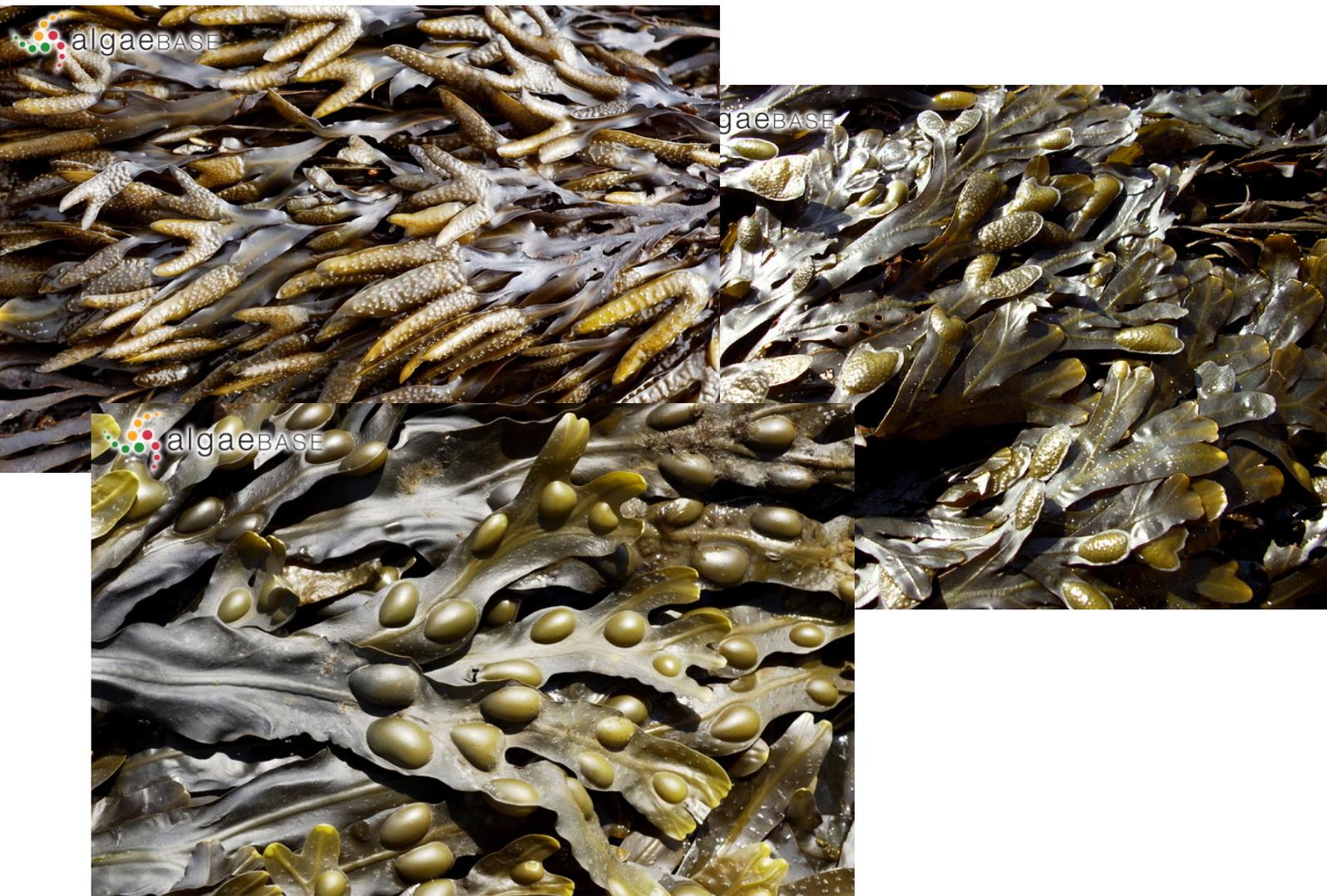


REPRODUCTION IN THE GENUS *FUCUS*

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Abstract

Fucus species (Phaeophyceae) inhabit intertidal rocky shores in temperate regions. It is a very important primary producer and an ecosystem engineer. The first event in the life history of *Fucus* is the production of gametes and, subsequently, zygotes by external fertilization, which is influenced by many environmental factors. What are the optimal conditions for *Fucus* species to spawn? I will elaborate on this and conclude that optimal conditions for the reproductive success of *Fucus* are to synchronously spawn during the afternoon (*Fucus* needs to be photosynthetically active) at low tide or slack high tide with calm water conditions (due to the water motion mechanism). Males and females should be in close proximity. Also the high quantity and longevity of gametes, the large egg cells (to increase the target area for sperm) and chemotaxis heighten the reproductive success. It depends on the species if lower temperatures are advantageous – for some species the reproductive success and dispersal is good, but the germling survival is very low at lower temperatures (i.e. during winter or early spring).

Pictures on the front page:

Left - *Fucus vesiculosus*, by unknown photographer (Algaebase - <http://www.algaebase.org/>).

Middle - *Fucus vesiculosus*, by unknown photographer (Algaebase - <http://www.algaebase.org/>).

Right - *Fucus spiralis*, by unknown photographer (Algaebase - <http://www.algaebase.org/>).

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Introduction

The genus *Fucus* belongs to the class Phaeophyceae (also known as brown algae) within the Division Heterokontophyta. There are many species and subspecies in the genus *Fucus* described, but not all are formally accepted as a taxonomic entity (see Algaebase - <http://www.algaebase.org/> - for an extended list of used names). Generally accepted and well known species are *Fucus vesiculosus*, *F. distichus*, *F. evanescens*, *F. gardneri*, *F. serratus* and *F. spiralis*. From these species also the evolutionary relationships (phylogeny) and the phylogeographical history are increasingly becoming clear (Coyer *et al.* 2003, 2006).

Fucus inhabits intertidal rocky shores of temperate regions in which it dominates in biomass (van den Hoek *et al.* 1995). The genus is an important primary producer (van den Hoek *et al.* 1995) and supports a whole intertidal ecosystem. It is predated amongst others by the isopod *Idotea baltica* and secretes chemicals to reduce this predation (Jormalainen *et al.* 2005). Flat periwinkles prefer *Fucus* species as their diet as well (Watson & Norton 1987). The dense canopy of *Fucus* can offer protection from desiccation at low tide for critical life history stages of epiphytic algae (Rindi & Guiri 2004). Apart from epiflora, *Fucus* species are also inhabited by epifaunal species such as bryozoa (Boaden 1996), which in turn provide habitats for meiofauna, such as amphipods and other crustaceans (Boaden 1996; Frederiksen *et al.* 2005). Amphipods, juvenile cod (*Gadus morhua*) and other fishes seek shelter and protection in the dense canopies of *Fucus* (Duffy & Hay 1991; Borg *et al.* 1997). In this way, *Fucus* also functions as nursery area. A unique feature is the fact that the species *F. vesiculosus* is the only widely distributed large macroalga in the atidal and brackish Baltic Sea (Andersson *et al.* 1994).

The first event in the life history of *Fucus* is the production of gametes and, subsequently, zygotes by external fertilization (Ladah *et al.* 2008), like many other organisms living in the intertidal area (Yund 2000). External fertilization is influenced by many environmental factors, affecting the reproductive success. Furoid algae have therefore developed mechanisms to increase the probability of gamete encounters, such as synchronous spawning, release of gametes under optimal conditions for encounters, high quantity and longevity of gametes, morphological and physiological adaptations, and chemical cues for gamete location (Serrão *et al.* 1996; Brawley *et al.* 1999; Yund 2000; Coleman & Brawley 2005; Ladah *et al.* 2008).

In this thesis, I will elaborate on this topic and answer the following main and sub questions:

- **What are the optimal conditions for *Fucus* species to spawn?**
 - When does *Fucus* spawn?
 - How does tide influence fertilization success of *Fucus*?
 - How does water temperature influence reproductive success of *Fucus*?



The reproductive system

All members of the genus *Fucus* have the same oogamous diplont life cycle. This means that the life cycle of *Fucus* has only one vegetative phase, which is diploid. Meiosis takes place during the formation of the gametes (egg cells and spermatozoids). The egg cells and spermatozoids are therefore haploid. Some species are dioecious (*F. vesiculosus* and *F. serratus*) (Brawley 1992; van den Hoek *et al.* 1995; Serrão *et al.* 1996; Coyer *et al.* 2003) and other species are monoecious and hermaphroditic (*F. spiralis*, *F. distichus*, *F. evanescens* and *F. gardneri*) (Pearson & Brawley 1996; Brawley *et al.* 1999; Coyer *et al.* 2002; Ladah *et al.* 2008).

The life cycle of the genus *Fucus*, especially *F. vesiculosus*, has been well described (van den Hoek *et al.* 1995), hence I will use *F. vesiculosus* as an example for describing the reproductive system (Fig. 1). The reproductive structures of *F. vesiculosus* are at the tips of the thallus and are called receptacles. Each receptacle contains many conceptacles (van den Hoek *et al.* 1995; Pearson & Brawley 1996). In monoecious species oogonia and antheridia develop inside the same conceptacle, whereas there are separate male and female in dioecious species (Brawley *et al.* 1999). Monoecious species of the family Fucaceae can self fertilize and are therefore also hermaphroditic.

Oogonia (female gametangia) are formed in conceptacles of females. Every oogonium contains eight haploid egg cells. At maturity, the outer of three cell wall layers of the oogonium breaks apart and a package of eight eggs cells are released. These clusters are forced out of the conceptacle through secretion of mucilage. The other two gametangial membranes loosen and break down rapidly in contact with seawater, releasing the eight egg cells, which are negatively buoyant (van den Hoek *et al.* 1995; Pearson & Serrão 2006).

The biflagellated spermatozoids are formed in antheridia (male gametangia) which are located in the conceptacles of male individuals. The antheridium wall consists of two layers. When the spermatozoids are extruded from the conceptacle through secretion of mucilage, they are still contained within the inner wall of the antheridium. Once outside the package splits open and the spermatozoids are released (van den Hoek *et al.* 1995). The spermatozoids are negatively phototactic and swim to the egg cells, attracted by a chemical released by the egg cells, which is effective only at micrometre to millimetre distances (Serrão *et al.* 1996). In case of *F. vesiculosus* and two other *Fucus* species, this chemical is the pheromone fucoserratene (van den Hoek *et al.* 1995). As soon as one spermatozoid penetrates the egg cell, the fertilized egg cell surrounds itself with a wall to avoid polyspermy (fertilization one and the same egg cell by more than one spermatozoid) (van den Hoek *et al.* 1995), which is lethal to the embryo (Berndt *et al.* 2002). Zygotes sink rapidly (1 cm.min⁻¹) through



seawater (Kropf 1992). Because the nascent cell wall is sticky, zygotes adhere to almost any substratum they come into contact with (Kropf 1992). After attachment, the zygote grows into a new diploid gametophyte (van den Hoek *et al.* 1995).

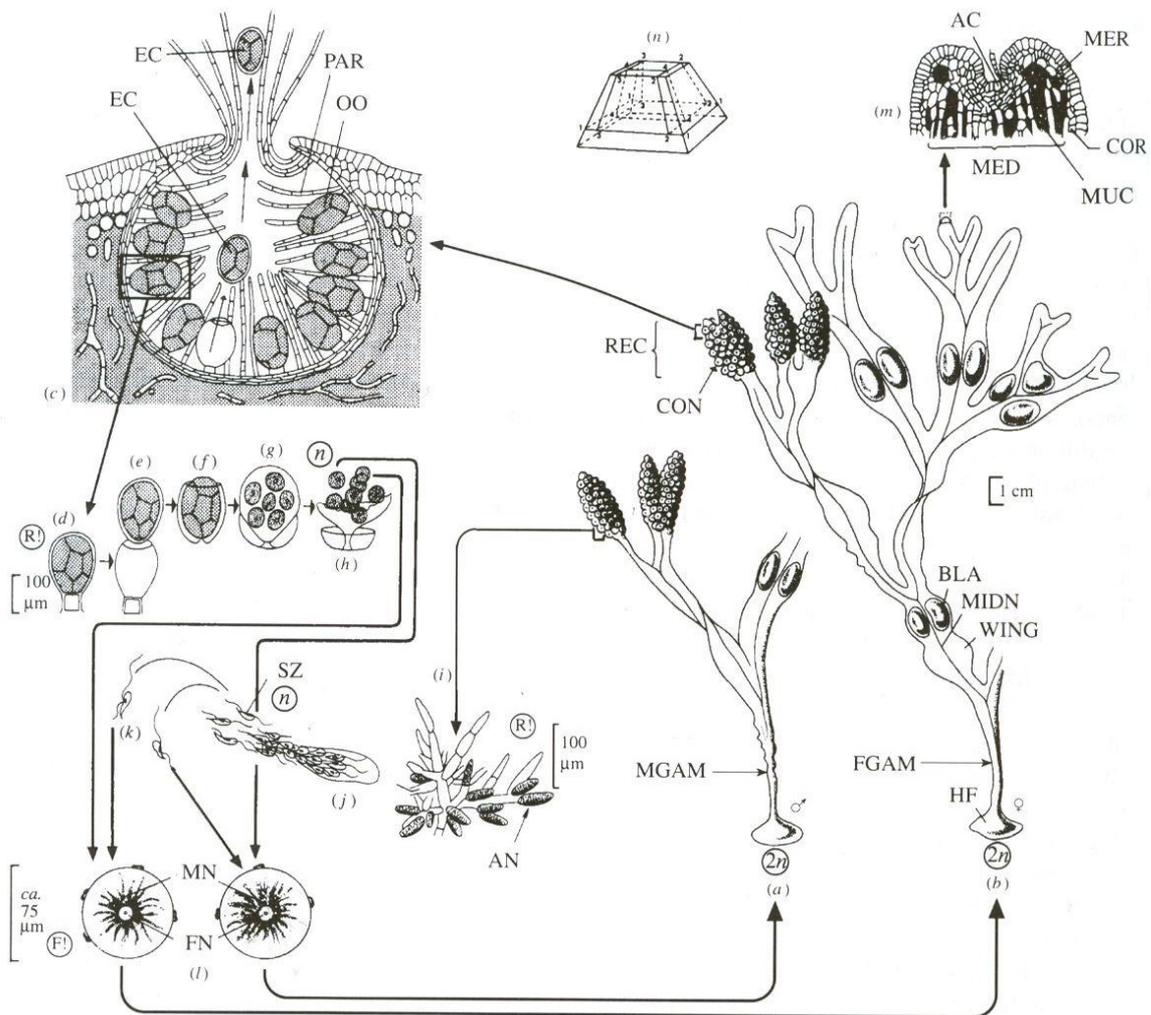


Fig. 1 Life cycle of *Fucus vesiculosus*. (a) Male gametophyte; (b) Female gametophyte; (c) Female conceptacle with oogonia; (d-h) Development of the oogonia and release of the egg cells; (i) Filaments bearing antheridia, which develop from the walls of male conceptacles; (j) Release of spermatozooids from an antheridium; (k) Spermatozooids; (l) Fertilization of egg cells. AN = antheridium; CON = conceptacle; EC = egg cell; F! = fertilization; FGAM = female gametophyte; FN = female nucleus; MGAM = male gametophyte; MN = male nucleus; MUC = mucilage; OO = oogonium; R! = reduction division (meiosis); REC = receptacle; SZ = spermatozoid; n = haploid; $2n$ = diploid. For further explanation of abbreviations, see van den Hoek *et al.* (1995).

Factors influencing the reproductive success of *Fucus*

The timing of synchronous gamete release, and therefore of synchronous maturation of receptacles, is very important for successful external fertilization and is dependent on a number of environmental factors. First I will elucidate on the time of spawning by *Fucus*, then on the tidal influence on the fertilization success of *Fucus* and lastly on how the water temperature influences reproductive success of *Fucus*.

Time of spawning

Photoperiod is the most commonly demonstrated factor initiating the reproduction in seaweeds (Brawley & Johnson 1992; Berger *et al.* 2001). Reproductive structures can be induced either by short-day (8h light: 16h darkness) or long-day (16h light: 8 h darkness) conditions. As Berger *et al.* (2001) showed, variation in seasonal timing can occur within one species, in their case *F. vesiculosus* in the Baltic Sea (Fig. 2). Their lab experiment showed no differences between autumn plants between short-day and long-day treatments as the plants initiated their receptacles simultaneously at the end of June. Nearly all tips developed receptacles, which had matured at the end of August. However, the summer plants did not initiate receptacles at the long-day treatment. Even in short-day conditions, a third of the summer plants remained vegetative. Summer plants of *F. vesiculosus* thus showed the

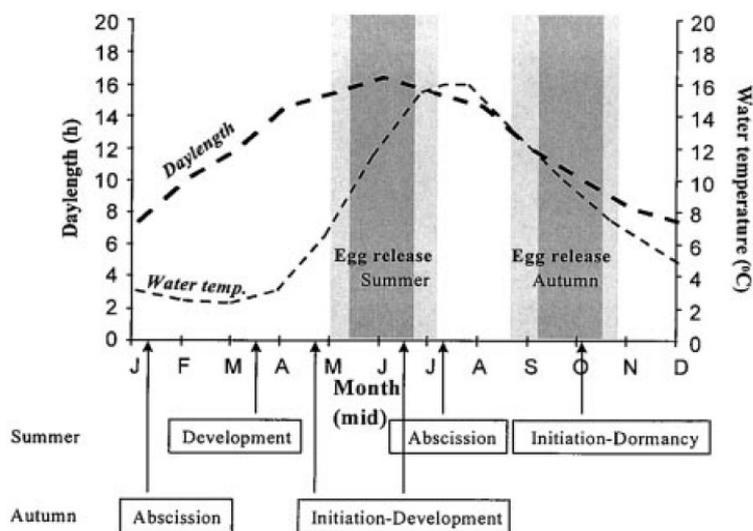


Fig. 2 “The two periods of egg release in *Fucus vesiculosus* on the south-eastern coast of Sweden, are shown together with daylength (h) and water temperature (°C). The yearly development, i.e. time for initiation, development and abscission of receptacles on summer-reproducing and autumn-reproducing *F. vesiculosus* in the Baltic Sea, is indicated with arrows. Data are based on both field and laboratory work.” From Berger *et al.* (2001).

characteristics of short-day plants by initiating receptacles under 12:12 h photoperiods (Berger *et al.* 2001). Reproduction is also seasonal in *F. distichus* and Baltic populations of *F. evanescens* (Pearson & Brawley 1996; Coyer *et al.* 2002). The onset of receptacle formation occurs in late autumn in response to short days. Gamete release occurs during the winter and early spring (Pearson & Brawley 1996). Not all species in the genus *Fucus* spawn seasonally; apparently *F. spiralis* spawns all year long in the Baltic (Coyer *et al.* 2002).

Gamete release in natural populations of *Fucus* occurs exclusively in the light (Pearson & Brawley 1996). Serrão *et al.* (1996) conducted an experiment to see if the process of spawning is driven by light. They used the receptacles of two furoid species, *Pelvetia fastigiata* and *F. vesiculosus*. They induced egg release in seawater (for *Fucus* Baltic seawater as the samples were collected in Askö, Sweden) with 0 (control), 1 and 10 μM 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU). DCMU specifically inhibits the photosystem II electron transport. They found that spawning is significantly reduced when DCMU is present (Fig. 3). Therefore, natural gamete release requires active photosynthesis. Serrão *et al.* (1996) concluded that “release may be stimulated by chemical changes

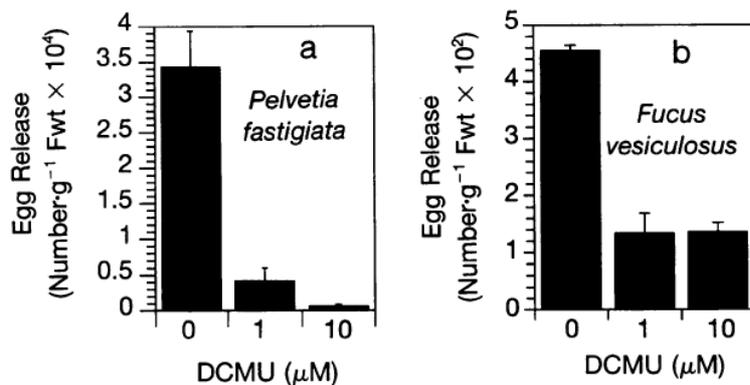


Fig. 3 Inhibitory effects of DCMU on egg release (mean \pm SE) under calm conditions in (a) *Pelvetia fastigiata* (six replicated per treatment) and (b) *Fucus vesiculosus* (four replicates per treatment). Significantly higher numbers of eggs were released in the controls than in the treatments. From Serrão *et al.* (1996).

occurring in the boundary layers surrounding the receptacles during photosynthesis under calm conditions, such as carbon limitation, increasingly alkaline pH or oxygen supersaturation”. They suggested that gamete release could be analogous to the guard cells of plants, where photosynthesis CO_2 supply is a signal for guard cell volume and stomatal opening.

Tidal phase

Spawning at low tide or at low water motion is advantageous but can have disadvantages as well. If there is no or little water motion, the antheridia with spermatozooids and oogonia containing egg cells are shed onto the surface of receptacles. Because oogonia, egg cells, antheridia and zygotes are negatively buoyant and the spermatozooids are negatively phototactic, they will settle directly below the point of release (Pearson & Brawley 1996). The absence of planktonic larval phase means that settlement is directly related to gamete release (Serrão *et al.* 1996). Thus there is no big dispersal of the zygotes when there is no or little water motion.

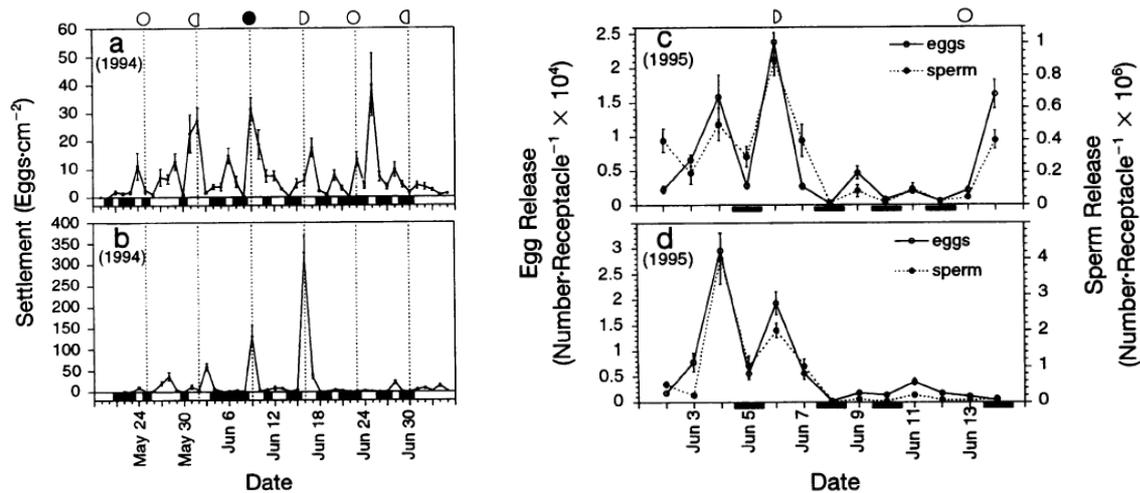


Fig. 4 Daily egg settlement (*a* and *b*) and gamete release (*c* and *d*) (mean \pm SE) for *Fucus vesiculosus* show that high release and settlement of eggs occurred only on calm days. Phases of the moon are shown above the graphs. Solid bars on the x axis represent days when currents caused movement of receptacles shortly prior to and during the natural time of high release in early evening. From Serrão *et al.* (1996).

Serrão *et al.* (1996) conducted a field and experimental laboratory study to look at the environmental conditions of gamete release. In the field study, they followed daily egg settlement and gamete release in two Baltic populations of *F. vesiculosus*. Natural gamete release and settlement occurs close to all lunar phases (Fig. 4) under calm conditions. High water motion during late afternoon inhibits gamete

release (i.e. gamete release was low or absent) (Fig.

4). Male and female receptacles responded correspondingly to simulated turbulence in lab experiments, showing that a period of agitation near the time of natural gamete release inhibited egg release (Fig. 5). Figure 4 shows that the duration of the agitation period is unimportant, but the timing of the agitation on the receptacles is critical. *Fucus* responds quickly and very sensitively to hydrodynamic conditions. Agitated cultures released significantly more eggs and sperm after cessation of the agitation period than the cultures that not had been agitated. Other experiments showed that *F. distichus* has an endogenous rhythm of gamete development and release with a circatidal (or semilunar) periodicity, but that it has no diurnal periodicity of gamete release (Pearson *et al.* 1998).

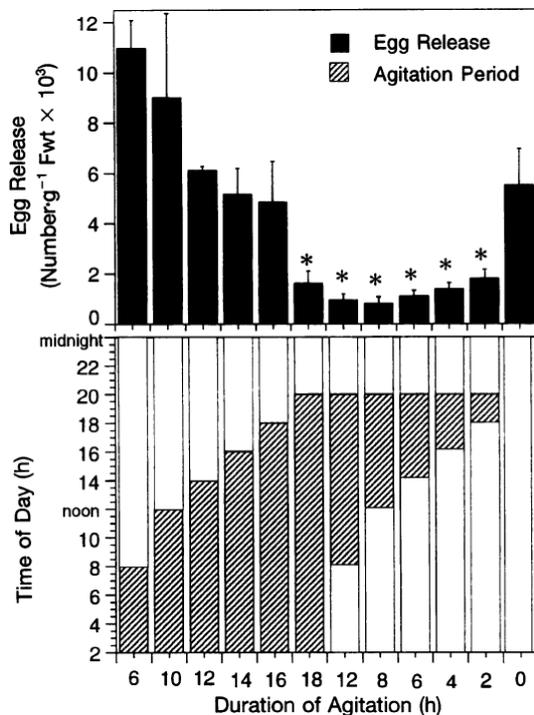


Fig. 5 Effect of time and duration of the period of agitations on the release of eggs (mean \pm SE) from Baltic *Fucus vesiculosus*. Asterisks indicate results that differ significantly from the control (calm). From Serrão *et al.* (1996).

Fucoid algae have a water motion mechanism which

restricts gamete release to calm periods (Serrão *et al.* 1996). Natural populations of *Fucus* spawn in periods of low water motion under high light and achieve high levels of fertilization success. These conditions are associated with low concentrations of dissolved inorganic carbon (DIC) in tide pools. At low water motion, carbon compounds (CO_2 , HCO_3^- , CO_3^{2-}) must diffuse across a thicker diffusive boundary layer around the receptacles. CO_2 diffuses 10^4 times slower in water than in air and HCO_3^- diffuses even more slowly (Kerby & Raven 1985). A reduction in bulk flow of medium across an algal thallus may have severe consequences as DIC depletion occurs in limited volumes of seawater. This probably results in photosynthetic carbon limitation in tide pools and photoinhibition is a likely consequence. Pearson *et al.* (1998) therefore hypothesized that inorganic carbon limitation under calm conditions may provide a signal resulting in gamete release. They showed that high concentrations of DIC (in their experiment, 20 mmol.L^{-1}) inhibited the gamete release of *F. distichus* significantly (Fig. 6). In another experiment with *F. vesiculosus* in which Pearson *et al.* (1998) looked at the effect of DIC and water motion on gamete release, they found that there was no evidence for a role for mechanosensing in controlling gamete release, because this was independent of water motion in DIC-free seawater (Fig. 7).

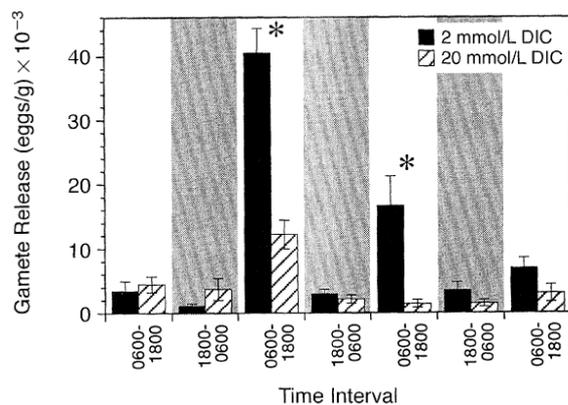


Fig. 6 The effect of DIC (dissolved inorganic carbon) on gamete release by receptacles of *Fucus distichus* under calm conditions. Grey bars show the dark part of the photoperiod (12:12 h). Significant inhibition of gamete release (eggs/gram fresh mass of receptacle) in the presence of 20 mmol.L^{-1} DIC in the light is noted with an asterisks. Values are means \pm SE (n = 5). From Pearson *et al.* (1998).

Water temperature

Water temperature influences reproductive success as well as germling survival and growth. Apart from photoperiod, temperature has also been reported to induce the reproduction in *Fucus* (Brawley *et al.* 1999 and references therein). Processes in the cell slow down at lower temperatures - higher temperatures can speed up gamete maturation and release (Ladah *et al.* 2008). A number of studies were conducted to unravel the influence of low seawater temperatures on reproductive success and survival (Pearson & Brawley 1996; Steen & Rueness 2004; Coleman & Brawley 2005).

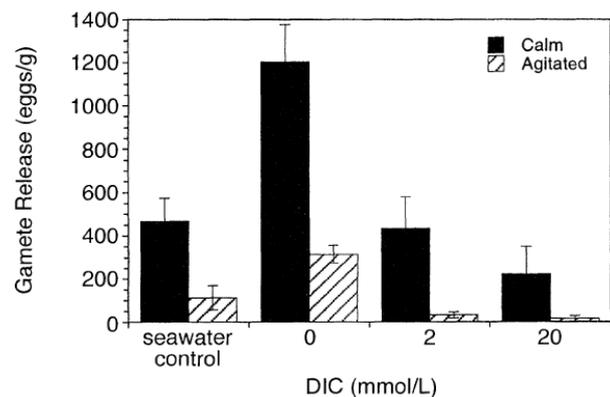


Fig. 7 The effect of DIC and water motion on gamete release by receptacles of *Fucus vesiculosus*. Values are means \pm SE (n = 4). From Pearson *et al.* (1998).

In Maine, USA, a population of *F. distichus* was studied by Coleman & Brawley (2005). Here *F. distichus* inhabits a very isolated rockpool habitat and spawns at low tide. They found that *F. distichus* may have evolved an adaptation to this isolated habitat: spawning during winter. This does not seem advantageous, as low temperatures slow the process of zygote adhesion. The zygotes are therefore longer exposed to high wave action, which reduces their survival. However, because the zygotes at 5°C do not adhere as fast as at 14°C (at which fucoid zygotes begin to secrete adhesive wall polymers at 4 h post-fertilization and adhere to surfaces by 6h post-fertilization; Kropf 1992) (see also Pearson & Brawley 1996), they can disperse up to five high tides (Fig. 8), which heightens the ability to disperse. *Fucus distichus* thus has a high dispersal potential and is therefore able to live in a very patchy habitat (Coleman & Brawley 2005).

The study conducted by Steen & Rueness (2004) looked at the survival and growth in six fucoid species at two different temperatures and nutrient levels. They collected six fucoid species from the Skaggerak and grew them in the laboratory at 7°C and 17°C, under high and low nutrient levels. Nutrient levels had less effect on survival and growth rate than temperature. The summer/autumn reproducing species *F. spiralis* and *Sargassum muticum* had low survival and growth of germlings at low temperature in comparison to the other fucoids (*F. vesiculosus*, *Ascophyllum nodosum*, *F. evanescens*, and *F. serratus*) which reproduce earlier in the year (Fig. 9). The temperature responses of germlings reflect the temperature range in these species' season of reproduction (Steen & Rueness 2004).

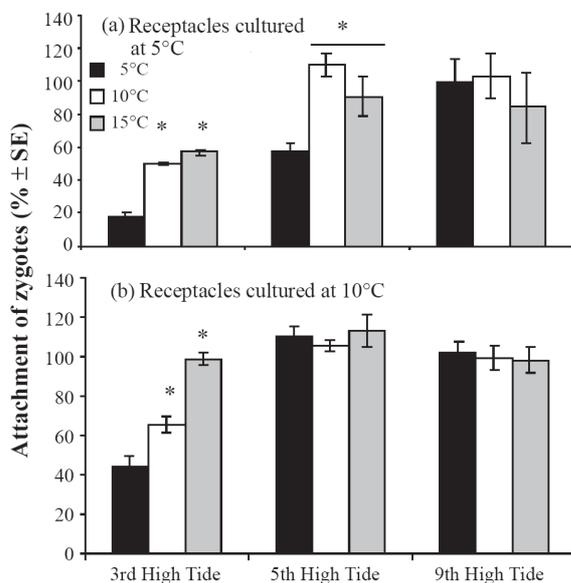


Fig. 8 Percentage attachment of zygotes from adults (receptacles) cultured and gametes released at (a) 5°C and (b) 10°C and cultured at 5, 10 and 15°C post-fertilization. There were $n = 3$ petri dishes per time per temperature and $n = 5$ random fields of view sampled per dish. * $p < 0.05$. Modified from Coleman & Brawley (2005).

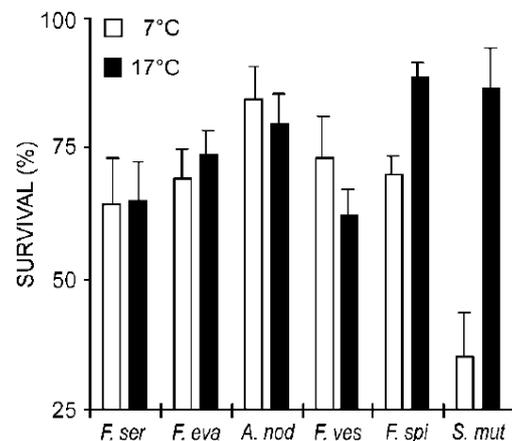


Fig. 9 The mean survival of fucoid germlings cultivated for 15 days at 7°C and 17°C with nutrient factor pooled. *F. ser* – *Fucus serratus*; *F. eva* – *F. evanescens*; *A. nod* – *Ascophyllum nodosum*; *F. ves* – *F. vesiculosus*; *F. spi* – *F. spiralis*; *S. mut* – *Sargassum muticum*. Error bars represent the upper 95% confidence limits. From Steen & Rueness (2004).

Discussion and conclusion

There are both advantages and disadvantages to spawn at low tide for an external reproducers like *Fucus* spp. (for an overview, see Box 1). Because there is a minimal water volume, thus a low dilution factor, high gamete concentrations can be achieved when the incoming water reaches the algae (Ladah *et al.* 2008). Gamete release at low tide increases the reproductive assurance in this way (Pearson & Serrão 2006). This is highly advantageous for dioecious species (Ladah *et al.* 2008), but for hermaphroditic algae, this could mean that they are likely to become inbred (Brawley *et al.* 1999). Therefore Ladah *et al.* (2008) argued that dioecious species need to be more sensitive to wave exposure than hermaphroditic species. Furthermore, inbreeding might not necessarily be disadvantageous, as it can maintain adaptive gene complexes (Ladah *et al.* 2003, 2008). Gamete mixing for dioecious species is achieved because algae from different sexes often lie intermingled in dense wet stands, which maximizes gamete concentration from both sexes (Ladah *et al.* 2008). If not for these dense wet stands, dioecious species would be less likely to combine eggs and sperm from separate individuals (Brawley *et al.* 1999), which would lead to sperm limitation. Dioecy and hermaphroditism have evolved independently several times within the Fucaceae family (Fig. 10) (Ladah *et al.* 2003; Coyer *et al.* 2006).

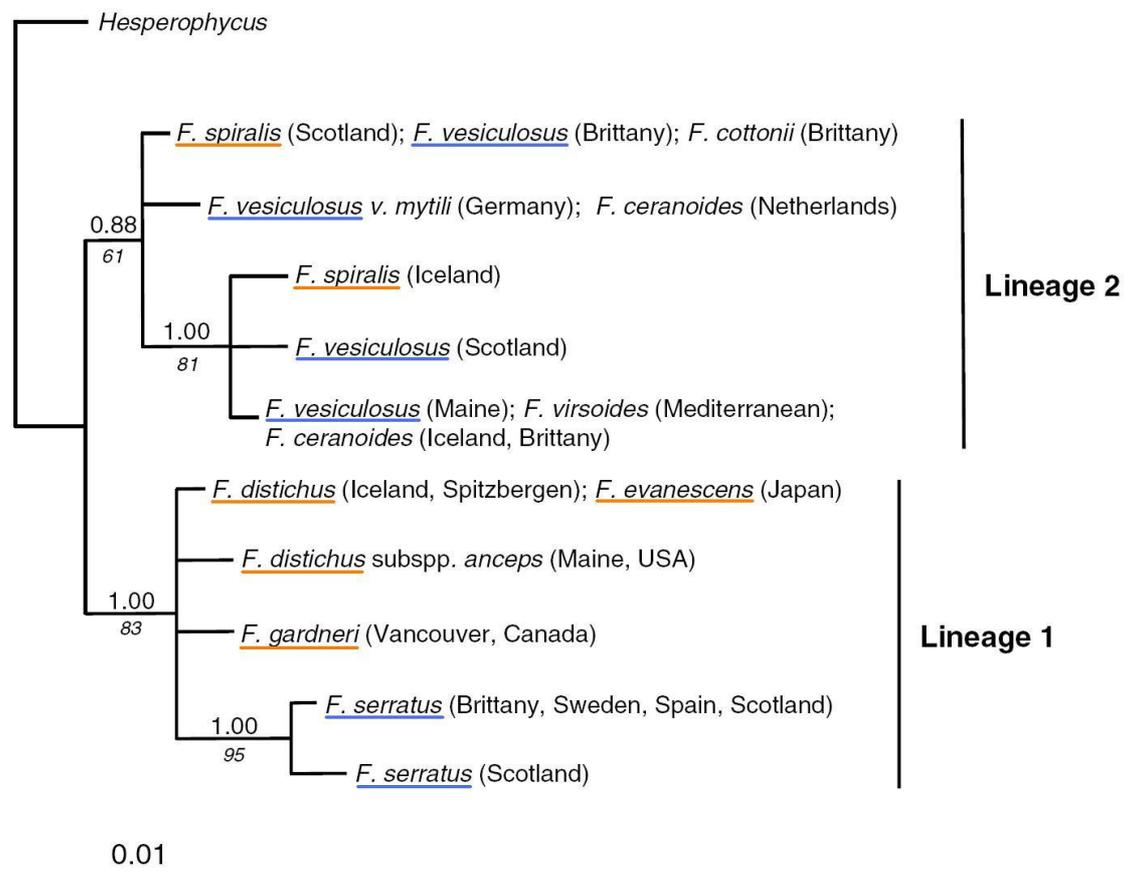


Fig. 10 Phylogenetic tree shows two lineages within the genus *Fucus*. Blue underscore means dioecy, orange underscore means hermaphroditism. Modified from Coyer *et al.* (2006).

The downside of gamete release during calm water conditions is limited dispersal and gene flow (Coyer *et al.* 2003). Also negatively buoyant eggs and negatively phototactic sperm are characteristics that suggest limited dispersal (Serrão *et al.* 1997; Coleman & Brawley 2005; Pearson & Serrão 2006). Another downside of spawning at low tide is that gametes are exposed to a greater range of temperatures and desiccation than when immersed (Ladah *et al.* 2008), reducing the survival of the gametes and thus reducing reproductive success. *Fucus distichus* has evolved an adaptation to its isolated habitat: spawning during winter. Zygotes do not adhere as fast in lower temperatures and can thus disperse one to several high tides before it settles permanently (Pearson & Brawley 1996; Coleman & Brawley 2005). Another furoid species, *Silvetia compressa*, spawns both at low and high tide and thus has both a great reproductive assurance (low tide release) and a long distance dispersal (high tide release) (Pearson & Serrão 2006). However, for none of the *Fucus* species this has been reported (Table 1). Spawning exclusively at high tide, both at high and low tide, or exclusively at low tide can dramatically affect recruitment processes and population structure (Brawley *et al.* 1999).

It has been debated whether sperm limitation affects the reproductive success of external fertilizers a lot (Yund 2000; Berndt *et al.* 2002). Yund (2000) concluded that sperm limitation probably does not occur. The water motion mechanism of *Fucus* prevents it from spawning at high water motion (Serrão *et al.* 1996; Pearson *et al.* 1998), thereby reducing the occurrence of sperm limitation. In natural furoid species studied to date, fertilization success is very high, ranging from 75 to 100% with most values above 90% (Pearson & Brawley 1996; Serrão *et al.* 1996; Brawley 1992, 1999; Berndt *et al.* 2002; Ladah *et al.* 2003), except for *F. vesiculosus* in the Baltic Sea near the northern limit of its distribution (Serrão *et al.* 1999). Fertilization success decreases with increasing water motion (Coyer *et al.* 2003). I think sperm limitation is limited due to the water motion mechanism and therefore does not occur very commonly in the genus *Fucus*.

Germling survival is not as high as fertilization success, ranging from 60 to 85% for different *Fucus* species (Steen & Rueness 2004). However, in a study after the effect of density on *F. vesiculosus*, a lot of macrorecruitment was found (Creed *et al.* 1996). It has not become clear whether fertilization or germination is the limiting factor in the reproductive success of *Fucus*.

Box 1 Advantages and disadvantages of spawning at low and high tide for *Fucus*.

Advantages of spawning at low tide:

- Gamete mixing for dioecious species is achieved because algae from different sexes often lie intermingled in dense wet stands, which could maximize gamete concentration from both sexes (Ladah *et al.* 2008)
- High concentrations would be mixed in minimal water volume (i.e., low dilution) as incoming tide reaches *Fucus* (Ladah *et al.* 2008)
- Hermaphroditic species: gamete release at low tide may increase reproductive assurance if sufficient seawater is present for the gametangia to break down and fertilizations to occur (Pearson & Serrão 2006)

Disadvantages of spawning at low tide:

- Dioecious species are less likely to combine eggs and sperm from separate individuals (Brawley *et al.* 1999)
- Hermaphroditic species most likely become inbred (Brawley *et al.* 1999)
- Eggs are exposed to a greater range of temperatures and desiccation than when immersed (Ladah *et al.* 2008)

Advantages of spawning at high tide/high water motion:

- Some water motion: better mixing of gametes (Serrão *et al.* 1996)
- Hermaphrodite species: wave-induced water motion may prevent extensive inbreeding (Brawley *et al.* 1999)
- Longer distance dispersal at high-tide release (Coleman & Brawley 2005)

Disadvantages of spawning at high tide/high water motion:

- Rapid dilution of gametes and sperm due to water motion (Serrão *et al.* 1996)
- Damage to zygotes (Serrão *et al.* 1996)

Summing up, optimal conditions for the reproductive success of *Fucus* spp. are to synchronously spawn during the afternoon (when *Fucus* is photosynthetically active) at low tide or slack high tide with calm water conditions. These factors are crucial for all *Fucus* species. Further, males and females should be in close proximity. Also the high quantity and longevity of gametes, the large egg cells (to increase the target area for sperm) and chemotaxis heighten the reproductive success. It depends on the species if lower temperatures are advantageous – for some species the reproductive success and dispersal is good, but the germling survival is very low at lower temperatures (i.e. during winter or early spring).

Table 1. Overview of mentioned *Fucus* species and their reproductive system, tidal zone, spawning season and tide.

Species	Reproductive system	Tidal zone	When spawn year	When spawn tide
<i>Fucus distichus</i> L.	Hermaphrodite (Coyer <i>et al.</i> 2006); monoecious (Pearson & Brawley 1996)	High intertidal pools to low intertidal (Coyer <i>et al.</i> 2006); not exposed to air normally (Brawley <i>et al.</i> 1999)	Winter and early spring (Pearson & Brawley 1996)	Low tide (Coleman & Brawley 2005)
<i>Fucus evanescens</i> C. Ag.	Hermaphroditic (Coyer <i>et al.</i> 2002)	Low to midintertidal zone (Brawley <i>et al.</i> 1999); low inter-tidal and subtidal (Steen & Rueness 2004)	Baltic: late winter/ spring (Coyer <i>et al.</i> 2002); Skaggerak: March-June (Steen & Rueness 2004)	Low tide (Brawley <i>et al.</i> 1999)
<i>Fucus gardneri</i> P.C. Silva	Monoecious (Brawley <i>et al.</i> 1999)	Lower to midintertidal zone (Brawley <i>et al.</i> 1999)		Low tide (Brawley <i>et al.</i> 1999)
<i>Fucus serratus</i> L.	Dioecious (Coyer <i>et al.</i> 2003)	Low intertidal/subtidal (Steen & Rueness 2004; Coyer <i>et al.</i> 2006)	Baltic: October-November or June-July (Berger <i>et al.</i> 2001); Skaggerak: September-June (Steen & Rueness 2004)	
<i>Fucus spiralis</i> L.	Hermaphrodite (Ladah <i>et al.</i> 2008)	High intertidal (Steen & Rueness 2004; Coyer <i>et al.</i> 2006)	Baltic: all year long (Coyer <i>et al.</i> 2002); Skaggerak: June-September (Steen & Rueness 2004)	
<i>Fucus vesiculosus</i> L.	Dioecious (Serrão <i>et al.</i> 1996)	High to low intertidal (mid intertidal, Skaggerak), with constant submergence in the Baltic, and marine to brackish salinities (Steen & Rueness 2004; Coyer <i>et al.</i> 2006)	Baltic: May-June and September-November (Berger <i>et al.</i> 2001); Skaggerak: May-July (Steen & Rueness 2004)	Low tide (Berndt <i>et al.</i> 2002; Ladah <i>et al.</i> 2008)

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