

Hybridization of the marine seaweeds, *Fucus serratus* and *Fucus evanescens* (Heterokontophyta: Phaeophyceae) in a 100-year-old zone of secondary contact

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Historically, the intertidal seaweeds *Fucus serratus* (*Fs*) and *Fucus evanescens* (*Fe*) were sympatric only along the western coast of Norway. In the mid-1890s, *Fe* (monoecious) was accidentally introduced into the Oslofjord. Putative hybridization with the endemic *Fs* (dioecious) was observed in Oslofjord by 1977 and in the Kattegat and western Baltic Seas by 1998. At Blushøj, Denmark (Kattegat Sea) putative *Fs* × *Fe* hybrids were present only when densities of *Fe* and *Fs* exceeded 14 and 2 m⁻², respectively. All of the 58 putative hybrids that were collected in 1999 were dioecious and intermediate in morphology. Essentially all (57 out of 58) were reproductively mature, but the oogonia possessed fewer and more variably sized eggs than either parent. Examination of each parental species and putative hybrids with nuclear, mitochondrial and chloroplast molecular markers confirmed the occurrence of hybridization. Furthermore, all of the hybrids possessed *Fe*-type chloroplasts and mitochondria, indicating that only the *Fe* egg × *Fs* sperm pairing was successful in the field. The reciprocal cross of *Fs* egg × *Fe* sperm was absent in the field and significantly less successful in laboratory crossings. Asymmetrical hybridization has also been reported for several species of plants and animals.

Keywords: *Fucus*; hybridization; introduced species; seaweed

1. INTRODUCTION

Expanded levels of marine shipping and fishing have resulted in the introduction of non-native species to coastal habitats (Carlton 1996). With respect to marine macroalgae, most introductions result in the displacement of existing species, which in turn, often alter local community dynamics and trophic interactions. Several introductions of macroalgae and their negative consequences have been well studied: *Undaria pinnatifida* (Hay 1990; Floc'h *et al.* 1995); *Sargassum muticum* (Ambrose & Nelson 1982; Viejo 1997); *Codium fragile* subsp. *tomentosoides* (Carlton & Scanlon 1985); and *Caulerpa taxifolia* (Académie des Science-Paris 1997).

The potential of the exotic species to hybridize with endemic species is an often-overlooked aspect of species introductions. In some cases, hybridization leads to speciation and the new species significantly impacts local communities. For example, the estuarine cord grass *Spartina alterniflora* was accidentally introduced to the British Isles from eastern North America in the early 1800s, and in the new habitat, produced rare and sterile hybrids with the local species, *Spartina maritima* (Marchant 1967, 1968). As a result of chromosomal doubling in the sterile hybrid, a new species emerged (*Spartina anglica*) (Gray *et al.* 1991; Raybould *et al.* 1991), which subsequently induced major geomorphological changes in the tidal habitats and dis-

placed many native halophytes as it rapidly expanded its range (Ranwell 1964; Scholten & Rozema 1990).

Intra- and inter-generic hybridization have been documented for many species of red and brown algae, but virtually all studies have been based on laboratory cultures (Rueness 1978; Lewis 1996a). Hybridization has been verified with cytological or molecular markers for only two hybrids: chromosome counts for field-collected *Pelagophycus* × *Macrocystis* (Laminariales) hybrids (Lewis & Neushul 1995) and PCR detection of species-specific ITS1 nrDNA fragments for laboratory produced *Alaria* × *Lessoniopsis* (Laminariales) hybrids (Liptack & Druehl 2000). Unsurprisingly, there are no studies of hybrid zones in marine macroalgae.

Several species of *Fucus* (Fucales) dominate the intertidal and shallow subtidal biomass along northern European shorelines (Lüning 1990), where they exhibit a considerable degree of morphological variation both within and between populations. Putative *Fucus* hybrids have been reported from the field for *Fucus vesiculosus* × *Fucus spiralis*, *Fucus vesiculosus* × *Fucus serratus* and *Fucus ceranoides* × *Fucus spiralis* (Sauvageau 1909; Gard 1910; Stomps 1911; Burrows & Lodge 1953; Scott & Hardy 1994).

Fucus serratus (henceforth *Fs*) ranges from northern Portugal to the White Sea, Iceland, Nova Scotia, and into the Kattegat and southern Baltic Seas (Lüning 1990). The cold-water species *F. evanescens* (henceforth *Fe*) occurs off New England (USA), Greenland, Iceland and northwestern Norway (Powell 1957; Rice & Chapman 1985; Lüning & tom Dieck 1990). Thus, *Fs* and *Fe* are sympatric

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along portions of Iceland and the northwestern Norwegian coast.

Fe was accidentally introduced into the Oslofjord (eastern Norway) in the mid-1890s and then expanded south, appearing in the Skagerrak Sea in 1924, the central Kattegat Sea (west coast of Sweden) in 1933, and in the Kiel Bight (western Baltic) by 1992 (see Schueller & Peters 1994). Putative *Fs* and *Fe* hybrids reaching fertility in the field initially were reported in Oslofjord in 1977 (Lein 1984; Rice & Chapman 1985) and more recently at several locations in the Kattegat to western Baltic Seas from 1998 to 2000 (J. A. Coyer and A. F. Peters, unpublished data). Therefore, any hybridization between the native *Fs* and introduced *Fe* in the areas occurred within the last 100 years.

In the present study we use molecular markers to verify the occurrence of natural hybridization between *Fs* and *Fe*. Using field-collected specimens, we examined DNA polymorphism in *Fs*, *Fe* and putative *Fs* × *Fe* hybrids with five microsatellite loci (nuclear), as well as ITS1 (nuclear), rubisco (chloroplast) and *nad11* dehydrogenase (mitochondria) genes. We believe that our study is the first to apply microsatellite genotyping and single-strand conformation polymorphism (SSCP) towards verification of hybridization in field populations of marine macroalgae.

2. MATERIAL AND METHODS

The dioecious *Fs* is characterized by broad thalli with serrated margins and a distinct midrib, whereas the hermaphroditic *Fe* (all conceptacles on a single individual contain both antheridia and oogonia) have much narrower thalli with no serrations and an indistinct midrib (figure 1). The chromosome number for each species is 32 (or 34) (Lewis 1996b). Both species are perennial. In the Kiel Bight, *Fe* is reproductive during late winter and spring, whereas *Fs* is reproductive all year long (Schueller & Peters 1994). Eggs and sperm of the closely related *F. vesiculosus* typically disperse only 0.5 and 2 m, respectively, from the parents (Lifvergren 1996). Long-distance transport may occur, however, as detached individuals may drift to other areas.

Putative *Fs* × *Fe* hybrids were observed in April 1998, 1999 and 2000 at Blushøj, near Elsegårde, Denmark (56°10' N, 10°43' E). In April 2000, the spatial distributions of *Fs*, *Fe* and putative *Fs* × *Fe* hybrids were determined with 0.5 m² quadrats sequentially placed along three transects (19, 24, 26 m in length; 0.5 m in width) traversing the entire *Fucus* belt from 0 to ca. -2 m in depth. All post-recruit *Fucus* individuals (more than 10 cm in length) within the quadrats were collected, counted and weighed. Very few recruits were present. Tissue samples for DNA extraction were collected from 72 *Fs*, 70 *Fe* and 58 putative hybrids and processed as described in Coyer *et al.* (2002a).

Laboratory crosses for all combinations of male and female *Fs*, *Fe* and *Fs* × *Fe* hybrids were conducted as described in Coyer *et al.* (2002b). Negative (eggs only, no sperm added) and positive (conspecific crosses) controls were included for each cross. Mitotic divisions were present in all fertilized eggs, but not in negative controls, and parthenogenesis does not occur in *Fucus*. Reproductive success of the crosses was defined as development to four-week-old embryos.

The numbers of eggs per oogonium and the sizes of eggs were quantified in one individual of each *Fe*, female *Fs* and female hybrid. Batches of oogonia were collected after release from the receptacles and the numbers of cells per oogonium were coun-

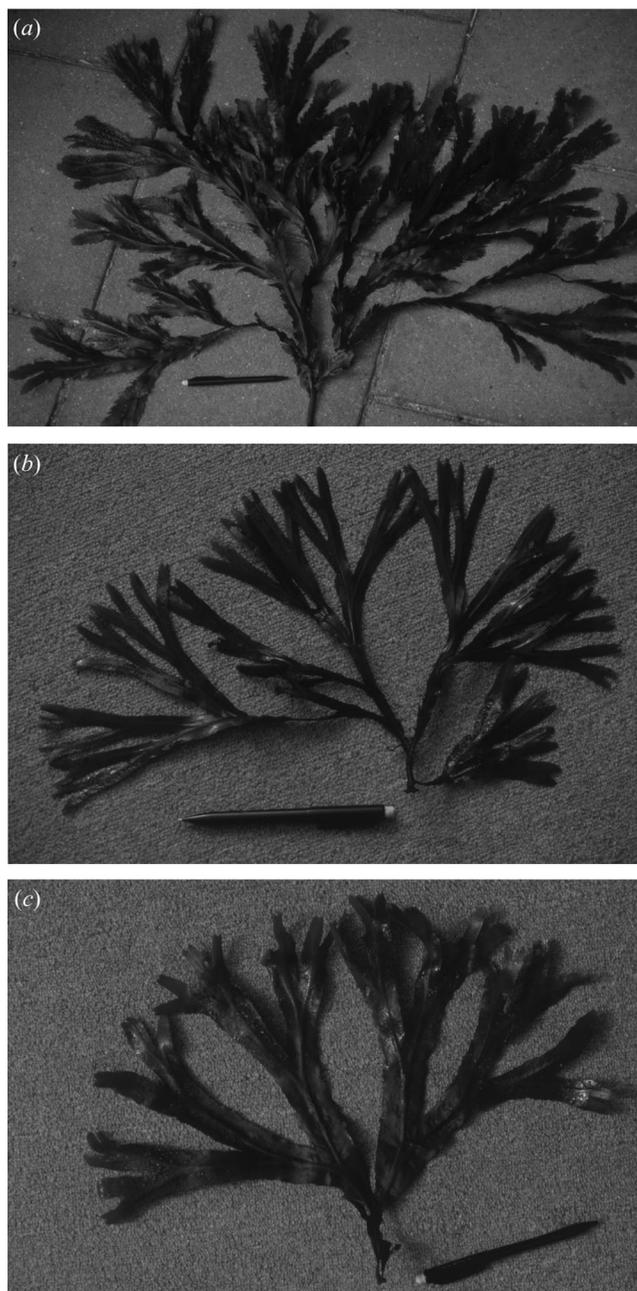


Figure 1. Photographs of (a) *Fs*, (b) *Fe* and (c) a *Fs* × *Fe* hybrid collected from Blushøj, Denmark in April 1999. The size of the pencil in each photograph is 14.5 cm.

ted. The egg diameters were measured with a light microscope at ×100 magnification after their release from the oogonia.

The sperm behaviour was observed at low magnification during the crossing experiments. The formation of sperm clouds concentrated around the eggs was interpreted as evidence for chemotaxis, that has been well studied in *Fucus* spp. (Müller & Seferiadis 1977). In addition, the detection of motile sperm in light microscopic preparations at ×400 or ×1000 magnification was taken as being evidence for the presence of competent sperm. Chemotaxis or sperm motility was not quantified.

DNA from fresh or dried tissue was extracted as described in Coyer *et al.* (2002a). The following five microsatellite loci were genotyped: *Fs*A198, *Fs*B113, *Fs*B128, *Fs*D39 and *Fs*F4 (Coyer *et al.* 2002a). ITS1 alleles and haplotypes of chloroplast (rubisco spacer) and mitochondria (*nad11*) were determined by SSCP analysis (Coyer *et al.* 2002b).

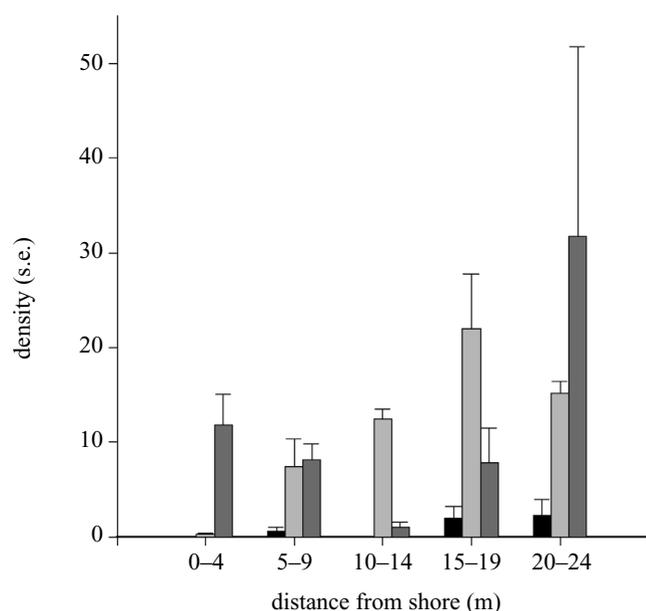


Figure 2. Density (+s.e.) of *Fs* (light grey bars), *Fe* (dark grey bars) and putative *Fs* × *Fe* hybrids (black bars) at Blushøj, Denmark. The means are derived from 0.5 m² quadrats along three transects in April 2000.

The ITS1 and five microsatellite loci were analysed as active elements in a factorial correspondence analysis (FCA) (GENETIX 4.02; Belkhir *et al.* 2001), a multivariate analysis that projects all individuals in a space defined by the components. In FCA (Benzécri 1973), each individual can be represented using each allele as an independent variable (She *et al.* 1987). Only individuals with complete genotypes were used and alleles present less than five times in the entire dataset were excluded from the analysis (Kotulas 1989).

3. RESULTS

Of the 58 putative hybrids collected at Blushøj in 2000, all were dioecious and all but one were reproductively mature. The receptacles of 30 randomly selected individuals revealed 16 females and 14 males. The average wet weights (s.d.) of the *Fucus* individuals collected at Blushøj were: *Fs*, 135.7 g (66.3); *Fe*, 51.9 g (32.0); putative hybrids, 57.2 g (28.1). *Fs* was distributed between the bimodal peaks of *Fe*, whereas putative *Fs* × *Fe* hybrids were present only when *Fe* and *Fs* formed mixed stands (figure 2). No putative hybrids were present if the densities of *Fe* and *Fs* were less than 14 and 2 m⁻², respectively.

Each oogonium of *Fs* and *Fe* contained eight eggs that were similar in size, as is the norm for *Fucus* (Fritch 1945). The egg diameter (*n*, mean, s.d.) in *Fe* (40, 98.7 µm, 7.7) was significantly (ANOVA, *p* < 0.0001) larger than in *Fs* (40, 70.3 µm, 4.7). The female *Fs* × *Fe* hybrids were different, as their oogonia contained variably sized (50, 78.7 µm, 25.7) and fewer eggs (*n* = 76, mean = 2.3, s.d. = 1.6) than the generic norm. Nevertheless, eggs released from the oogonia of hybrids chemotactically attracted sperm, as did eggs released from the oogonia of *Fe* and *Fs*. The antheridia and sperm of male *Fe*, *Fs* and *Fs* × *Fe* hybrids, were microscopically similar and all sperm

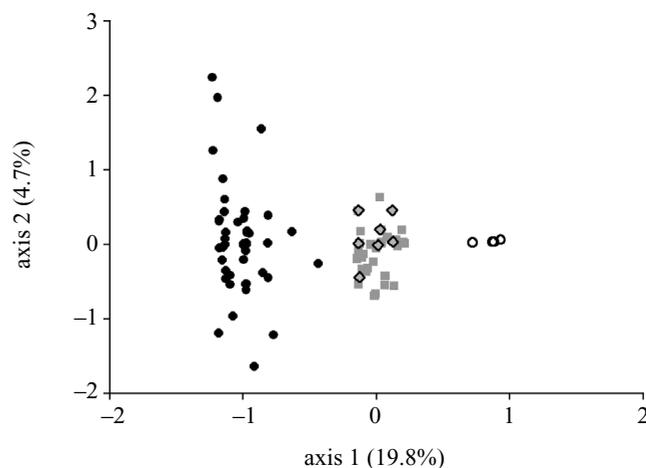


Figure 3. Two-dimensional FCA of all field individuals. The two dimensions depicted accounted for 24.5% of the variability. The laboratory crosses were included in the FCA as supplementary elements for visualization only and were not used to compute the factor axes. Black circles, *Fs*; white circles, *Fe*; stippled squares, field hybrids; stippled diamonds, laboratory hybrids.

displayed vigorous movement with chemotaxis towards the eggs.

Microsatellite and SSCP analysis confirmed that the 58 putative *Fs* × *Fe* hybrids collected at Blushøj in 2000 were true hybrids (figure 3, table 1). Additionally, all the field hybrids possessed *Fe*-type chloroplasts and mitochondria, indicating that only the *Fe* egg × *Fs* sperm pairing was successful in the field (table 1). In addition to being absent in the field, the reciprocal cross, *Fs* egg × *Fe* sperm, was significantly less successful in the laboratory crossings (figure 4).

4. DISCUSSION

A hybrid zone between *Fs* and *Fe* has existed for *ca.* 100 years in the Skagerrak, Kattegat and western Baltic Seas and therefore, represents the early stages of a secondary contact between previously allopatric populations of the two species. Furthermore, the barrier to gene exchange between *Fs* and *Fe* at Blushøj is asymmetrical, as only hybrids resulting from pairings of *Fe* eggs × *Fs* sperm were observed. Asymmetrical fertilization success among hybrids is a phenomenon that has been reported in several species of plants and animals (Kaneshiro 1976; Levin 1978; Arnold *et al.* 1996; Coyne & Orr 1998; Funk 1998; Tiffin *et al.* 2001).

Asymmetrical fertilization is usually attributable to sexual selection (Wilson 1979; Lyons *et al.* 1989; Arnold *et al.* 1996). More specifically, the asymmetrical mate choice hypothesis (Kaneshiro 1976) predicts that females of a newly evolved or derived taxon readily will accept males of the ancestral taxon because all of the male characteristics required by the females are present. Derived males, however, will be unable to fertilize females of an ancestral taxon because these males have 'lost' necessary stimuli in the mate recognition system. Thus, females from a derived taxon will mate with males from an ancestral taxon, but not vice versa. The hypothesis has been supported by laboratory and field studies of *Drosophila* and field studies of

Table 1. Genotypes (nuclear) and alleles (chloroplast, mitochondria) for *Fs*, *Fe* and *Fs* × *Fe* hybrids from the field (HF) and crossed in the laboratory (L). (Abbreviations: f, female; m, male.)

	nuclear (ITS1)				chloroplast (rubisco)		mitochondrial (<i>nad11</i>)	
	$\alpha\alpha$	$\alpha\beta$	$\beta\beta$	$\gamma\gamma$	A	B	1	2
<i>Fs</i>	0	0	71	1	0	72	0	72
HF	0	58	0	0	58	0	58	0
<i>Fe</i>	70	0	0	0	70	0	70	0
HF f × HF m (L)	0	1	1	0	2	0	2	0
HF f × <i>Fs</i> m (L)	0	1	2	0	3	0	3	0
HF f × <i>Fe</i> m (L)	0	4	0	0	4	0	4	0
<i>Fs</i> f × <i>Fe</i> m (L)	0	3	0	0	0	3	0	3
<i>Fe</i> f × <i>Fs</i> m (L)	0	4	0	0	4	0	4	0

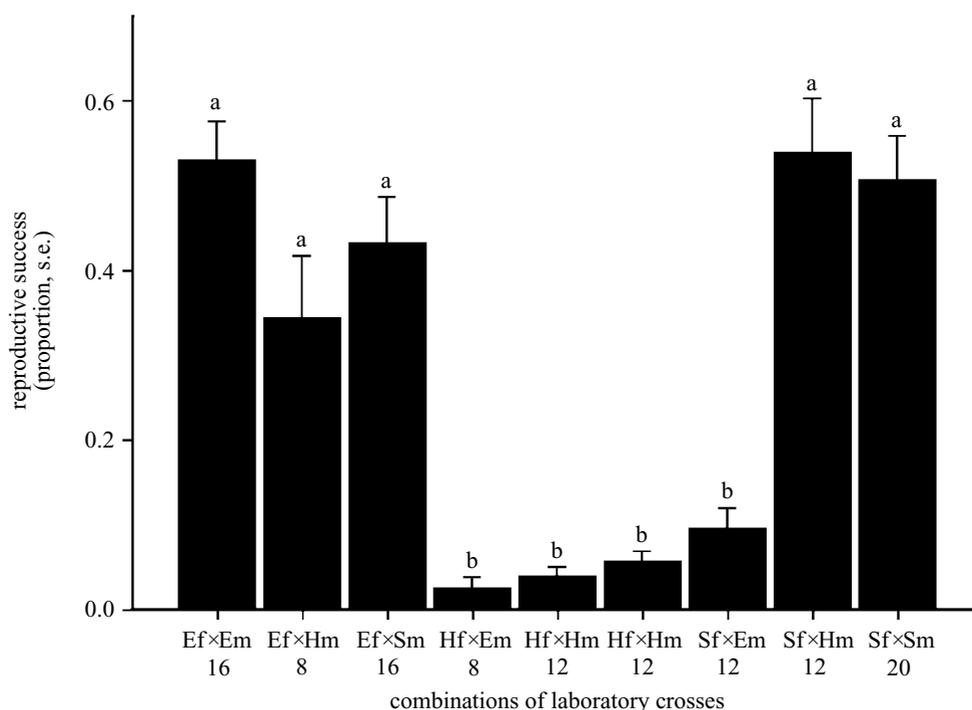


Figure 4. Reproductive success (the presence of four-week-old embryos) for all combinations of laboratory crosses between female and male *Fs* (Sf, Sm), *Fe* (Ef, Em) and *Fs* × *Fe* hybrids (Hf, Hm). The sample sizes are indicated below the bars; the crosses identified with the same letter (a or b) are not significantly different (proportion data arcsine-square-root transformed; one-factor ANOVA, Tukey–Kramer post-hoc test, $p < 0.05$).

sticklebacks (*Gasterosteus* spp.) (McPhail 1969; Ohta 1978; Powell 1978; Arita & Kaneshiro 1979). Although sexual selection is possible in plants (Wilson 1979; Lyons *et al.* 1989; Arnold 1994), the asymmetrical mate choice hypothesis has not been tested (Tiffin *et al.* 2001).

Asymmetrical hybridization in *Fucus* (passive mate choice) is analogous to the asymmetrical mate choice hypothesis of Kaneshiro (1976) (active and direct mate choice). A recent ITS-based phylogeny demonstrated that *Fs* is the ancestral *Fucus* (Serrão *et al.* 1999). Field hybrids at Blushøj consisted only of *Fe* egg (derived species) × *Fs* sperm (ancestral species); the reciprocal cross was not found and was significantly less successful in the laboratory (figure 4). The low success rate of a *Fs* egg–*Fe* sperm union may be due to events occurring after sperm

adhesion, as *Fs* eggs readily attracted *Fe* sperm in the laboratory, consistent with observations of others who noted extensive cross-specific attraction because all *Fucus* spp. eggs possess the same sperm-attracting pheromone (Müller & Seferiadis 1977; Maier & Müller 1986).

Alternatively, two other hypotheses may explain the asymmetry of hybrid success in *Fucus* from the field. First, an asynchronous release of *Fs* eggs and *Fe* sperm (the hermaphroditic species), relative to a synchronous release of *Fe* eggs and *Fs* sperm, may prevent *Fs* egg–*Fe* sperm hybrids. Second, the total number of *Fe* sperm in the field may be much less than *Fs* sperm, simply because *Fe* is a hermaphrodite and hermaphroditic species of *Fucus* produce significantly fewer sperms per egg (40 : 1) than do dioecious species (400 : 1) (Vernet & Harper 1980).

Fewer *Fe* sperm relative to *Fs* sperm logically should result in smaller numbers of *Fe* sperm–*Fs* egg fertilizations. However, the asymmetry of hybridization success demonstrated by our laboratory crossings cannot be explained by either of these field-based hypotheses.

The ecological fate of *Fs* × *Fe* hybrids at Blushøj and elsewhere in the Skagerrak, Kattegat and Baltic Seas remains to be determined, but three possibilities exist. First, the hybrid population may consist only of F_1 individuals because F_2 s and backcrosses are less fit. This situation is an evolutionary dead-end for the hybrids and should lead to the reinforcement of pre-zygotic isolation mechanisms. Second, hybrid introgression (transfer of genes between parental species) may occur, leading to the transfer of adaptations or species mergers, both of which are well documented in animals and plants (Rieseberg 1998). Third, the hybrids may evolve into a new species.

It is highly likely that all field hybrids at Blushøj were F_1 individuals, rather than a mixture of later generation hybrids and backcrosses, and that the hybrids were less fit. Laboratory backcrosses produced individuals with ITS1 alleles from one or both parents, whereas the field hybrids only possessed an ITS1 allele from both parents (table 1). The striking absence of overlap between the *Fs*, *Fe* and *Fs* × *Fe* clouds in the FCA also indicates a lack of introgression due to backcrossing (figure 3). This was surprising because the fertility of hybrid eggs with hybrid or parental sperm (backcross) in the laboratory was very low, but the fertility of hybrid sperm was high (figure 4). The absence of F_2 individuals in the field may be a result of genetic incompatibilities (endogenous selection) expressed in F_2 individuals, as well as reduced viability in the habitat (exogenous selection).

Despite the apparent low fitness of *Fs* × *Fe* hybrids, the evolution of a new species may still occur. It is important to realize that limited fertility in present hybrid generations does not necessarily prohibit a progression to new evolutionary lineages (Arnold & Hodges 1995). For example, genotypic classes of hybrids have been documented, each of which can possess equivalent or higher levels of fitness relative to their parents (Arnold & Hodges 1995) and later hybrid generations can be as fit or more fit than either parent (Rieseberg 1998).

Fs × *Fe* hybrids were not found near Trømso, north-western Norway (Lein 1984), where *Fs* and *Fe* have been sympatric (= primary contact zone) for hundreds or perhaps thousands of years. How is it then, that in a 100-year-old zone of secondary contact, *Fs* × *Fe* hybrids have persisted for several years, attained a weight intermediate to both parents, and reached a high level of reproductive maturity? The answer may be that *Fs* populations in Europe exhibit significant genetic structure. In a study of 35 northern European populations of *Fs*, estimates of pairwise F_{ST} -values derived from seven microsatellite loci revealed significant differentiation (implying low gene flow) among all populations separated by ≥ 2 km (Coyer *et al.* 2003). For example, values between Bergen (western Norway) and each of 19 populations within the Skagerrak and Kattegat Seas, including Blushøj, ranged from 0.224 to 0.351. If *Fs* evolved barriers to hybridization with *Fe* along the northwestern coast of Norway (e.g. reinforcement of isolation in a primary zone of contact), the barriers are not likely to have spread to other *Fs* populations

because of limited gene flow. Thus, *Fe* individuals recently introduced to the Kattegat Sea would encounter no barrier to hybridization with local populations of *Fs*. Barriers to hybridization may be weak or non-existent in *Fe*, however, as the founding individuals probably came from an area of long-standing sympatry with *Fs*.

The discovery of *Fs* × *Fe* hybrids in a young zone of secondary contact provides a unique opportunity to understand the importance of hybridization in marine algae. Whether the hybrids eventually disappear because they are less fit or because isolation mechanisms have been reinforced, or evolve into a new species with the potential to compete with either or both parent species, remain to be determined. The *Fs* × *Fe* hybrids in the Skagerrak, Kattegat and Baltic Seas warrant further study by tracking all genotypes over multiple generations, and conducting detailed ecological and demographic investigations of hybrids and parents.

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