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A review of reproduction in the seaweed genus *Fucus* (Ochrophyta, Fucales): Background for renewed consideration as a model organism

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The genus *Fucus* dominates the intertidal and shallow subtidal rocky reefs of the North Atlantic and also is commonly found in the intertidal of the North Pacific. It likely diversified 12.2-2.7 mya into two genetically distinct lineages: Lineage 1 with one species in the North Pacific and two in the North Atlantic; and Lineage 2 found only in the North Atlantic (one species recently introduced into the North Pacific). With 10 accepted species, *Fucus* spp. (and the Fucales) are unique among algae in having a diplontic life cycle, whereby the only haploid stage is the single-celled gamete. Further, *Fucus* spp. produce eight eggs in each oogonium; have hermaphroditic and dioecious species in each lineage; display sperm:egg ratios differing by more than one order of magnitude; have synchronized and predictable release of gametes; are capable of self- and/or cross- fertilization and asexual (fragmentation *via* adventitious branching) reproduction; readily hybridize in culture, as well as the field; and form ecads (free-living individuals with morphological variability linked to habitat) by hybridization or polyploidy. Consequently, the genus is an excellent model for a variety of studies in reproductive biology, employing laboratory and field manipulations as well as detailed genetic studies using the molecular 'omics'. We review here the relevant literature in order to fully understand and appreciate the unique opportunities that *Fucus* spp. provide as model organisms for future studies of reproduction.

KEYWORDS

***Fucus*, reproduction, review, diplontic life cycle, selfing, hybridization, fertilization, ecads**

Introduction

The brown algal genus *Fucus* (Ochrophyta, Fucales) is an important ecosystem engineer on sheltered and moderately exposed rocky shores of the North Pacific and the North Atlantic. As providers of an important foundational habitat, the species collectively provide shelter and food for a plethora of invertebrate and fish species, as well as a substrate for attachment of epibionts (Lüning, 1990; Chapman, 1995).

Fucus also is important as a food source for large land herbivores (both wild and domestic), as well as human cultures. For example, reindeer venture into the intertidal in high Arctic regions to forage on *Fucus* when snow cover is too deep and/or rain-on-snow icing makes it difficult to obtain their normal diet of lichens (Hansen et al., 2019). Elsewhere in northwestern Europe, seaweeds (including *Fucus* spp.) have been consumed by, and fed to, sheep, cattle, and pigs, both historically and presently (see references in Blanz et al., 2020). Sheep that escaped the annual round-up in Iceland and Norway often survived the harsh winters by foraging on intertidal *Fucus* (Landsborough, 1857). The feral and protected North Ronaldsay or Orkney sheep on North Ronaldsay (northernmost island of Orkney) have modified their gut biome, as a result of confinement to the intertidal by humans, to subsist almost entirely on seaweed, including *Fucus* (Balasse et al., 2005; Ruggeri, 2015). With respect to humans, *Fucus* spp. have been a food source, processed to a form of 'soda ash' for soap and glass making, used for centuries as fertilizer in maritime areas that could not support livestock for manure (Pereira & Cotas, 2019), and had/have a variety of traditional medicinal uses, albeit of suspect effectiveness (https://medlineplus.gov/druginfo/natural/726.html; but see Catarino et al., 2018).

Students and researchers began studying coastal intertidal regions as soon as marine laboratories were established along the shores of the North Atlantic, beginning in the mid-1800s (e.g., Station Biologique de Roscoff, 1859; Woods Hole, USA, 1871; Kristineberg Marine Research Station, 1877; Laboratory of the Marine Biological Association at Plymouth, 1885; Marine Biological Laboratory (USA), 1888; University of Oslo Drøebak, 1894) and a prominent subject for these early investigations was the readily available *Fucus*. However, perhaps the first published description of *Fucus* was over 300 years ago, in a 1711 paper by René-Antoine Réaumur that included detailed illustrations of what appears to be a combination of *Fucus vesiculosus* and *F. serratus* (Figure 1).

Coyer et al. (2006a) first proposed a North Pacific origin of *Fucus* based on a phylogeny derived from both a variable and conserved region of the mitochondrion that revealed: 1) sister-taxa to *Fucus* are found only in the North Pacific, and 2) high haplotype and nucleotide diversity in the variable mt region was present in the North Pacific, whereas only a single haplotype (shared with the North Pacific) was found in the North Atlantic. A later phylogenetic study using 13 protein-coding genes also supported a North Pacific origin of Fucales dating to 19.5-7 mya with divergence of the genus *Fucus* at 12.5-2.7 mya (Cánovas et al., 2011), agreeing with an earlier estimate of *Fucus* divergence at 2.3-5.5 mya using single-strand conformation polymorphisms (SSCP) of a mtDNA spacer region (Hoarau et al., 2007). However, the most recent *Fucus* phylogeny, with more extensive sampling throughout the Arctic and Subarctic and using 21 mtDNA-IGS haplotypes, placed the ancestor of the *F. distichus* complex (likely near the ancestral member of the genus) in the low Arctic/Subarctic (Laughinghouse et al., 2015). Sequence analysis of nuDNA and mtDA also revealed two distinct lineages within the genus, Lineage 1 with two accepted species and Lineage 2 with eight accepted species (see https://www.algaebase.org/search/genus/detail/?genus_id=71; Almeida et al., 2022).

Recent studies have illustrated the dynamic nature of speciation in *Fucus*. For example, microsatellite markers suggest that *F. radicans* diverged from *F. vesiculosus* the northern Baltic within the last 400 years (Pereyra et al., 2009). On the other hand, however, is extinction; the glacial relict populations of *F. virsoides* along the Slovenian coast declined significantly by 2010 and disappeared entirely by 2016 (Battelli, 2016).

Excellent reviews on the broad subjects of phylogeny (Cánovas et al., 2011); physiology (Chapman, 1995; Colvard et al., 2014; Colvard & Helmuth, 2017); gamete release and settlement/recruitment (Chapman, 1995; Brawley et al., 1999); and ecology (Chapman & Johnson, 1990; Chapman, 1995; Wahl et al., 2011) have been written and publications on various aspects of *Fucus* have increased dramatically, closely tracking key technological advancements (Figure 2). This review will address and update aspects of reproduction in *Fucus*.

General Characteristics

Sexual dimorphism (when reproductive) and the realization of dioecy and hermaphroditism in *Fucus* species were determined in the 1800s. Reproductive individuals produce numerous receptacles at the apical tips of branches, each of which contain many conceptacles. In dioecious species, all conceptacles on an individual contain either antheridia or oogonia (Figure 3); hermaphroditic species have conceptacles containing both antheridia and oogonia (see Engel et al., 2005). There are no monoecious species of *Fucus* (e.g., one individual with receptacles containing conceptacles with either antheridia or oogonia). *Fucus* spp. exhibit a diplontic life cycle with male heterogamy (XX/XY) (Heesch et al., 2021) and gametes are the only haploid cells. Sex of dioecious species often can be determined by eye in the field when reproductive: male

FIGURE 1
Illustration of *Fucus serratus* from Réaumur (1711). Note that one thallus appears to have receptacles and vesicles characteristic of *F. vesiculosus*, perhaps mistakenly interpreted as stemming from the same holdfast, when in fact, it may be two independent attachments, one on the other (see insert). Permission to reuse this image was confirmed by Service des Archives et du Patrimoine historique under the free use of public archive documents.

receptacles appear red/orange-colored because of carotenoids in eyespots for the negatively phototaxic sperm contained within antheridia of the conceptacles (Decaisne & Thuret, 1845), whereas female conceptacles are green or brown because of chloroplasts in the eggs (Whitaker, 1931). The egg begins dividing ~24 hrs after fertilization (Thuret, 1855).

All species of *Fucus* reproduce sexually, but sexual reproduction is difficult in brackish conditions. In *F. vesiculosus*, for example, the low salinity (<5 PSU) typical of the Baltic Sea: 1) drastically reduces the release of gametes; 2) diminishes longevity and motility of released gametes; 3) reduces fertilization rates; and 4) fosters polyspermy, which is lethal in *Fucus* and increases dramatically in brackish conditions (Brawley, 1991; Brawley, 1992; Serrão et al., 1996; Serrão et al., 1999a). Consequently, asexual reproduction (fragmentation *via* adventitious branching) is common among populations existing in marginal environments, including ecads (discussed below) and *F. radicans* in the Baltic (Tatarenkov et al., 2005; Pereyra et al., 2009; Johannesson et al., 2011). In the northern Baltic, *F. radicans* recruits both sexually and asexually, varying from complete sexual to >90% monoclonal with phenotypic variation significantly lower in monoclonal stands than in multi-clonal groups (Johannesson et al., 2012). Furthermore, a shift from sexual to asexual reproduction has occurred in a few

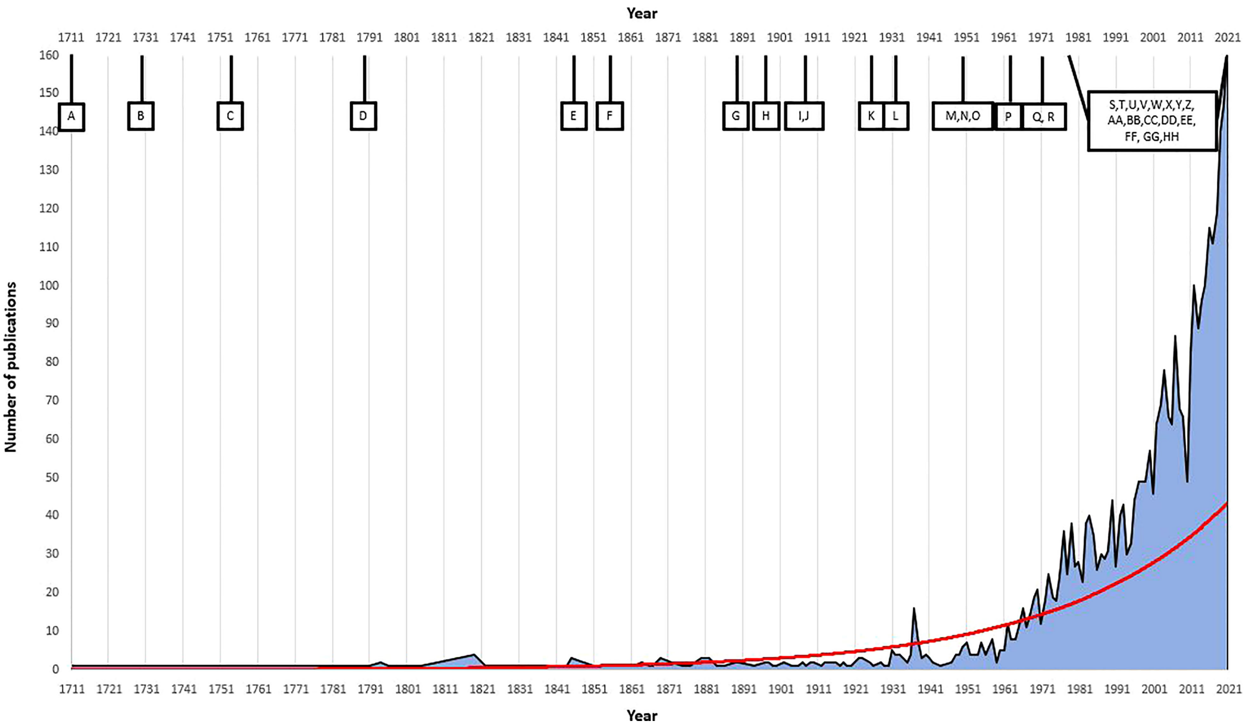

FIGURE 2
Correlation of number of *Fucus* publications and key advances in *Fucus* reproduction/research and general technological advancements over time. We used the software *Dimensions* (Digital Science; https://app.dimensions.ai/discover/publication) to search for *'Fucus'* in titles and abstracts of all journals and all dates. Red line is the exponential trendline based on the number of publications released. **(A)** 1711, first publication on *Fucus* reproduction (Réaumur 1711); **(B)** 1730, advancement in microscope technology (Tromp, 2015), **(C)** 1753, first taxonomic description of *Fucus* Linnaeus (Linneí and Salvius, 1753); **(D)** 1790-1900, early chemical, physiological and biological descriptions (Woodward, 1791; Stackhouse, 1801; Kniep, 1925); **(E)** 1845, initial research on life history, reproductive methods and taxonomy reassignment (Genus *Fucus*) (Decaisne & Thuret, 1845); **(F)** 1854, first description of fertilisation in *Fucus* and first cross-experiments (Thuret, 1855); **(G)** 1890, beginning of laboratory cultures (Campbell, 1889); **(H)** 1897, first cytological study of *Fucus* (Farmer & Williams, 1897); **(I)** 1909, first observation of fertalisation and total number of chromosomes (Yamanouchi, 1909); **(J)** 1909, early ecological studies (Baker, 1909; Baker, 1910); **(K)** 1925, first successful cross experiments (Kniep, 1925); **(L)** 1931, invention of the electron microscope (Freundlich, 1963); **(M)** 1950, first electron microscope image of *Fucus* (Manton & Clarke, 1950); **(N)** 1950, beginning of autocological research in *Fucus* (Knight & Parke, 1950; Burrows & Lodge, 1951); **(O)** 1951, natural hybridization experiment (Burrows & Lodge, 1951); **(P)** 1962, further studies on *Fucus* chromosome number (Evans, 1962); **(Q)** 1970, detailed experimentation on gamete release and gamete physiological structure and characteristics for *Fucus* (Pollock, 1970); **(R)** 1970-1995, in-depth research on individual, population and community ecology in *Fucus* (Chapman, 1995); **(S)** 1977, first generation sequencing (Heather & Chain, 2016); **(T)** 1979, detailed investigation on natural morphological variation and phenotic plasticity in *Fucus* (Scott & Hardy, 1994); **(U)** 1980, formal demographic analysis on *Fucus* species (Gunnill, 1980); **(V)** 1970-1990, development of PCR and microsatellites (Kaunitz, 2015; Saeed et al., 2016); **(W)** 1985, discovery of pheromonal gamete attraction in *Fucus* (Müller & Gassmann, 1985); **(X)** 1980-1991, comprehensive studies on egg production in *Fucus* (Vernet & Harper, 1980; Robertson, 1987; Ang, 1991); **(Y)** ~1990, detailed research in rates of reproduction, settlement, recruitment and population modelling in *Fucus* begun (Chapman, 1995); **(Z)** 1997-1999, rDNA and nrDNA sequencing of internal transcribed spacer region in *Fucus* and SSU and LSU sequences (Leclerc et al., 1998; Rousseau et al., 1997; Rousseau & de Reviers, 1999; Serrão et al., 1999a); **(AA)** 2002-2003, design of polymorphic microsatellite markers for *Fucus* (Coyer et al., 2002c; Engel et al., 2003); **(BB)** 2005, next generation sequencing begun (Heather & Chain, 2016); **(CC)** 2006, RNA extraction method designed for *Fucus* and tested with RT-PCR, RNA-labelling and Northern analysis methods (Pearson et al., 2006), **(DD)** 2006, complete mitochondrial genome for *F. vesiculosus* and mtDNA-based phylogeny showing the two *Fucus* lineages (Oudot-Le Secq et al., 2006; Coyer et al., 2006a); **(EE)** 2011, third generation sequencing (Heather and Chain, 2016); **(FF)** 2013, first investigation in sex-biased gene expression in *F. vesiculosus* (Martins et al., 2013); **(GG)** 2013-present, effects of climate change on *Fucus* distribution (Jueterbock et al., 2014; Rothäusler et al., 2018; Rugiu et al., 2018; Rothäusler et al., 2019); **(HH)** 2020-to present, complete annotated genome and transcriptome using illumina and nanopore platforms (https://phaeoexplorer.sb-roscoff.fr/home/).

absolute marginal populations of *F. vesiculosus* in the northern Baltic Sea (Tatarenkov et al., 2005).

It is important to realize that asexual reproduction does not necessarily reduce fitness, (Preston et al., 2022 and references therein). For example, *F. vesiculosus* in the Baltic Sea can exist in two forms: the most common being the epilithic form (attached, sexual and rarely asexual) and less commonly, the benthopleustophytic form (free-living and asexual) found on any substrate within the photic zone (Preston et al., 2022 and references therein). However, each form likely will respond differently to future environmental changes. Additionally, asexual reproduction may conserve existing genotypes by

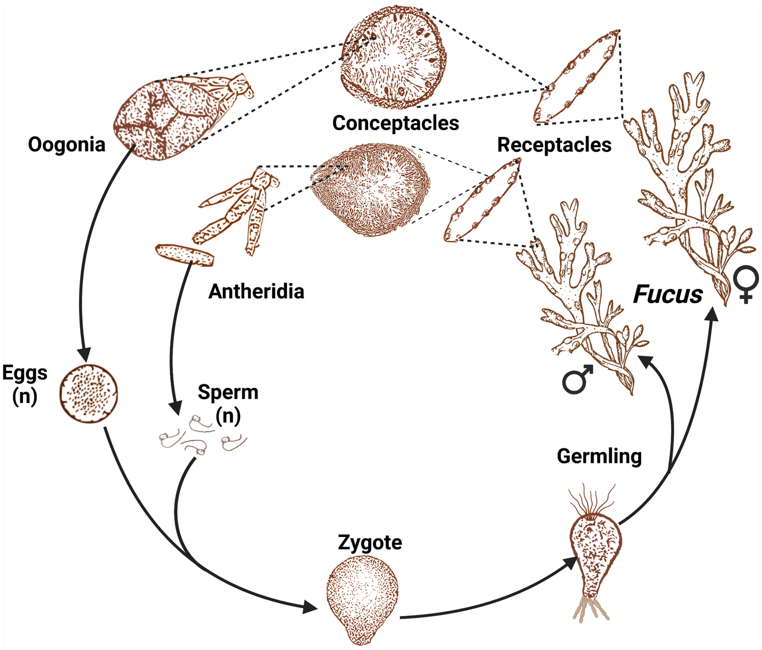

FIGURE 3
Dioecious life cycle of the genus *Fucus.* A representative illustration, not to scale, adapted from Müller (1991) footage, provided by Technische Informationsbibliothek (TIB) and created with BioRender.com. Receptacles of a hermaphroditic species contain both antheridia and oogonia, whereas in dioecious species (pictured), an individual is either male (all receptacles contain antheridia) or female (all receptacles contain oogonia).

preventing recombination of new genotypes, unlike selfing (see below) (Ardehed et al., 2015).

In *Fucus*, adventitious branches can form from both the thallus and holdfast, with regeneration most rapid from the midrib region of the thallus (Fulcher & McCully, 1969; Fulcher & McCully, 1971; McLachan et al., 1971; Van Alstyne, 1989). Branches can be induced by herbivory or in response to no obvious physical stimulus (Van Alstyne, 1989). The epidermal cells grow outward forming distinct 'embryos' instead of lateral branches, which are indistinguishable from early sexually produced embryos (Fulcher and McCully, 1969; McCook & Chapman, 1993).

Detached adventitious branches may reattach to the substratum *via* rhizoids and develop into apparently functional male and female thalli (asexual recruitment), which subsequently can form large clones with skewed sex ratios (Tatarenkov et al., 2005; Johannesson et al., 2011; Ardehed et al., 2015). For example, a large *F. radicans* female clone in the northern Baltic was distributed over 550 km and a large male clone over 100 km; both were likely to be a few thousand years old (Johannesson et al., 2011; Ardehed et al., 2015). Populations in more southerly Baltic locations, however, almost exclusively displayed sexual recruitment (Johannesson et al., 2011; Ardehed et al., 2015).

More recently, experiments with *F. radicans* demonstrated that temperature and light interactively resulted in the highest success of re-attachment of adventitious branches (Schagerström & Salo, 2019). Light level alone had no effects on success in cooler water temperature while success in high water temperature under low light levels was very low. Their results further suggested that rhizoid formation (re-attachment success) depends on the net primary production (metabolic balance) of the adventitious branches.

The notion that sexual reproduction in *Fucus* is impeded in areas of low salinity has been challenged by recent studies detailing a much more complex picture. Ardehed et al. (2016) found high levels of sexual reproduction in some *F. radicans* populations inhabiting the extreme low salinity (2-3 PSU) Gulf of Finland. Kinnby et al. (2019) showed that low salinity, temperature, and oxygen (i.e., high stress) were associated with high number of adventitious branches in *F. vesiculosus* and *F. radicans* populations within the Baltic, but outside the Baltic, high salinity, high phosphate, and low turbidity were positively correlated with adventitious branching. Kinnby et al. (2019) hypothesized that variation in patterns of adventitious branching between populations was due either to genetic differences arising from local adaptation unrelated to the physical factors that were measured or from stochastic effects

TABLE 1 Main reproductive period for *Fucus* spp. as recorded in different studies.

Lineage	Species	Mating type	Main sexual reproductive period	Location (GPS Coordinates)	Reference	Comment
1	*Fucus distichus*	H	(Summer)-Autumn	Maine, USA(42.98, -70.60)	Sideman & Mathieson (1983b)	“Dwarf form”
			Spring-Autumn-(Winter)	Maine, USA(42.98, -70.60)	Sideman & Mathieson (1983b)	subsp. *edentates*
			Spring or Autumn	Maine, USA(42.98, -70.60)	Sideman & Mathieson (1983a)	subsp. *evanescens*
			Autumn-Winter	British Columbia, Canada (49.26, -123.12)	Ang (1991)	Conceptacles fertile all year
			Spring	Nova Scotia, Canada(44.48, -66.08)	Edelstein & McLachlan, 1975	
			Autumn-Winter-(Spring)	Stavanger, Norway(58.99, 5.70)	Fredriksen (1985)	Small morphotype (subsp. *anceps*)
			Spring-(Summer)	Skagerrak, South-Norway (58.99, 9.75)	Steen & Rueness (2004)	Large morphotype (subsp. *evanescens*)
			Spring-(Summer)	Kiel Bight, Germany(54.44, 10.19)	Schueller & Peters (1994)	Large morphotype (subsp. *evanescens*)
			Winter-Spring	New Hampshire, USA(See reference)	Mathieson & Hehre (1982)	
			Winter-Spring	New Hampshire, USA(See reference)	Mathieson & Hehre (1982)	subsp. *edentatus*
			Spring-Summer	New Hampshire, USA(See reference)	Mathieson & Hehre (1982)	Large morphotype (subsp. *evanescens*)
			Spring-Summer	Southern Gulf of St. Lawrence, Canada(See reference)	Johnson et al. (2012)	subsp. *edentatus* and subsp. *evanescens*
			Spring	Orkney, UK(59.02, -2.99)	Perry & Hill (2015)	
			Spring-Summer	Avacha Bay, Russia(53.04, 158.60)	Kashutin et al. (2019)	subsp. *evanescens*
1	*Fucus serratus*	D	(Autumn)-Winter-Spring	Lofoten-Norway(68.15, 14.03)	Fredriksen (1990)	
			Autumn-Winter	Stavanger, Norway(58.99, 5.70)	Fredriksen (1990)	
			Autumn-Winter-Spring-(Summer)	Skagerrak, South-Norway (58.99, 9.75)	Steen & Rueness (2004)	
			(Autumn)-Winter	Oslofjord, South-Norway (59.30, 10.62)	Sundene (1953)	
			Autumn	Misterhult, Sweden(57.56, 16.73)	Malm et al. (2001)	
			Summer	Blekinge, Sweden(56.14, 15.39)	Malm et al. (2001)	
			Autumn-Winter	Isle of Man, UK(54.08, -4.76)	Knight & Parke (1950)	
			(Summer)-Autumn	Devon, UK(50.31, -4.089)	Knight & Parke (1950)	
			Summer	North Spain(See reference)	Arrontes (1993)	Conceptacles fertile all year
			Summer-(Autumn)	Southern Gulf of St. Lawrence, Canada(See reference)	Johnson et al. (2012)	
			Summer-Autumn	Isle of Man, UK(54.07, -4.60)	Williams (1996)	

(Continued)

TABLE 1 Continued

Lineage	Species	Mating type	Main sexual reproductive period	Location (GPS Coordinates)	Reference	Comment
			(Spring)-Summer-Autumn	UK(See reference)	d'Avack & Marshall (2015)	
2	*Fucus ceranoides*	D(H)	Spring-Summer	South Norway(See reference)	Lein (1984)	Hermaphroditic individuals probably are hybrids
			Not known	Iberian Peninsula(NA)	Gómez Garreta (2000)	Receptacles present all year, not necessarily fertile
2	*Fucus vesiculosus*	D	(Spring)-Summer-Autumn	Barsebäck, Sweden(55.77, 12.89)	Carlson (1991)	
			(Spring)-(Summer)	Hanko peninsula, Finland (59.88, 23.24)	Bäck et al. (1991)	
			(Spring)-Summer-(Autumn)	Lofoten-Norway(68.15, 14.03)	Fredriksen (1990)	
			(Spring)-Summer	Stavanger, Norway(58.99, 5.70)	Fredriksen (1990)	
			(Spring)-Summer	Skagerrak, South-Norway (58.99, 9.75)	Steen & Rueness (2004)	
			(Spring)-Summer-Autumn	Southeastern Sweden,(See reference)	Berger et al. (2001)	
			Spring-(Summer)	Isle of Man, UK(54.08, -4.76)	Knight & Parke (1950)	
			(Spring)-(Summer)	Devon, UK(50.31, -4.089)	Knight & Parke (1950)	
			Summer-Autumn-(Winter)	Ría de A Coruña, Spain(43.36, -8.35)	Viana et al. (2015)	Differences between sites
			Unknown	Iberian Peninsula(NA)	Gómez Garreta (2000)	Receptacles present all year, not necessarily fertile
			Spring	New Hampshire, USA(See paper)	Mathieson & Hehre (1982)	Conceptacles fertile all year
			Autumn	Blekinge, Sweden(56.14, 15.39)	Malm and Kautsky (2003)	
			Spring-(Summer)	Viana do Castelo, Portugal (41.67, -8.83)	Monteiro et al. (2012)	Conceptacles fertile all year
			Spring-(Summer)	Sines, Portugal(37.87, -8.82)	Ladah et al. (2003)	Conceptacles fertile all year
			Spring	Kiel Fjord, Germany(54.41, 10.19)	Wahl et al. (2010)	Conceptacles fertile all year
			Summer-Autumn	Waquoit Bay, USA(41.56, -70.52)	Yates & Peckol (1993)	
2	*Fucus radicans*	D/Veg	(Summer)	Öregrund, Sweden(60.33, 18.42)	Forslund & Kautsky (2012)	Main reproductive period first part of June
			(Summer)-(Autumn)	Saaremaa, Estonia(58.33, 23.08)	Schagerström (2013)	
			(Spring)-Summer	Gävle, Sweden(60.69, 17.24)	Schagerström & Kautsky (2016)	
2	*Fucus chalonii*	D	Summer	North Spain(NA)	Gómez Garreta (2000)	
2	*Fucus spiralis*	H	(Summer)-Autumn	Lofoten-Norway(68.15, 14.03)	Fredriksen (1990)	
			Summer (Autumn)	Stavanger, Norway(58.99, 5.70)	Fredriksen (1990)	
			Summer-(Autumn)	Skagerrak, South Norway (58.99, 9.75)	Steen & Rueness (2004)	

(Continued)

TABLE 1 Continued

Lineage	Species	Mating type	Main sexual reproductive period	Location (GPS Coordinates)	Reference	Comment
			Unknown	Iberian Peninsula(NA)	Gómez Garreta (2000)	Receptacles present all year, not necessarily fertile
			Summer-(Autumn)	New Hampshire, USA(43.05, -70.71)	Niemeck & Mathieson (1976)	
			Summer-(Autumn)	Isle of Man, UK(54.08, -4.77)	Subrahmanyan (1960)	
			Summer	Orkney, UK(59.02, -2.99)	Perry & Hill (2015)	
			Spring-(Summer)	Viana do Castelo, Portugal (41.67, -8.83)	Monteiro et al. (2012)	
			Spring-(Summer)	Sines, Portugal(37.87, -8.82)	Ladah et al. (2003)	
			(Spring)-Summer	North Wales(See reference)	Ferreira et al. (2015)	
			Autumn-Winter	Yerseke, Netherlands(51.51, 4.04)	Coelho et al. (2001)	
			Spring-Summer-Autumn-Winter	São Miguel Island, Portugal (37.73, -25.63)	Neto (2000)	Conceptacles fertile all year
2	*Fucus guiryi**	H	Spring-Summer	Tarifa, Spain(36.01, -5.57)	Sánchez de Pedro et al. (2019)	Fertile individuals all year, different between sites
			Spring-(Summer)	Viana do Castelo, Portugal (41.67, -8.83)	Monteiro et al. (2012)	
			(Spring)-Summer	Northern Portugal(See reference)	Zardi et al. (2015)	
			Autumn	Southern Portugal(See reference)	Zardi et al. (2015)	
2	*Fucus virsoides*	H	Spring-Summer-Autumn	Bay of Kotor, Montenegro (42.43, 18.64)	Mačič (2006)	
			Summer	Rovinj, Croatia(45.08, 13.62)	Zavodnik (1973)	
2	*Fucus cottonii*	Veg(D)	NA	Galway, Ireland(See reference)	Sjøtun et al. (2017)	Reproduces by fragmentation, however, some populations with receptacles have been found

D, dioecious; H, Hermaphroditic; Veg, vegetative. Spring=March-May, Summer=June-August, Autumn=September-November, Winter=December-February, '()'= covers less than half of the period, (See reference) = multiple sampling locations. *Now *F. limitaneus* and *F. macroguiryi* (see "Hybridization" in text). As the listed reproductive periods are rough estimates of optimal environmental conditions, population differences, and interactions with other environmental factors can shift and/or blur the identified ranges.

of population separation, and emphasized the need to identify additional environmental factors that may explain the predominance of asexual reproduction in the Baltic Sea. These studies clearly demonstrate that the recently formed postglacial Baltic Sea (8000 yrs; Björk, 1995), with steep gradients in physical characteristics from south to north (this and all further directional references are poleward), is a challenging and marginal environment for the closely related *F. radicans* and *F. vesiculosus* in terms of allocating resources to sexual or asexual reproduction.

Fucus spp. in Lineage 2 exhibit a general spring-summer reproduction period in most studies (Table 1), but in the low salinity Baltic Sea, *F. vesiculosus* displayed two peaks of reproduction: early summer (May-June) and late autumn (September-October) (Table 1; Berger et al., 2001). Summer-reproducing individuals initiated receptacle development and produced more, but smaller eggs in response to short-day laboratory conditions, whereas receptacle development was independent of daylight in autumn-reproducing individuals, suggesting the presence of two distinct genotypes (Berger et al., 2001). In southern Europe, mature oogonia are present all year in *F. vesiculosus* and *F. spiralis* (Table 1).

Maximum reproductive peaks for *F. serratus* on open coasts of the NE Atlantic occurred in both the spring and the autumn (March and September) and in the spring-autumn in the NW Atlantic, but in the Baltic Sea, mainland Swedish populations were reproductive in the autumn (October-November) and on the coast of Öland in the summer (June-July) (Malm et al., 2001). Fertilization success in *F. serratus* decreased markedly as salinity decreases, more so than for *F. vesiculosus*, but unlike *F. vesiculosus*, asexual reproduction was not observed in the Baltic (Malm et al., 2001). Non-overlapping reproductive periods also have been observed among *F. distichus* populations off the New England coast in the US (Sideman & Mathieson, 1983a; Sideman

& Mathieson, 1983b; Pearson & Brawley, 1996). In general, reproductive seasons vary within and among species of *Fucus* (Table 1) and clearly, continuation of non-overlapping reproductive periods within populations of a species could increase the probability of eventual speciation.

Gamete structure, release, and fertilization

Studies of reproductive structures in *Fucus* began soon after microscopes were developed. Decaisne & Thuret (1845) published one of the first microscopic descriptions of *Fucus* antheridia and 'spores', stating that the "transparent corpuscles (are) nearly pear-shaped, each one inclosing a single red globule; each one of these corpuscles is furnished with two very thin cilia, by means of which it moves with extreme vivacity". Conceptacles were described by Bower (1880), followed by descriptions of mitosis, meiosis, physiology of *Fucus* spermatozoids, conceptacle development, and egg development (e.g., Farmer & Williams, 1897; Farmer & Williams, 1898; Yamanouchi, 1909; Robbins, 1916; Roe, 1916; see also reviews by Whitaker, 1931; Fritsch, 1945). The first electron micrographs of *F. serratus* sperm revealed that the base of the anterior flagellum was enveloped by a flexible membrane of unknown function and the flagellum was covered with 'hairy' appendages; both were absent in the posterior flagellum. (Manton & Clarke, 1950). For further microscopic descriptions of gamete structure and fertilization in *Fucus*, see: Pollock, 1970; Brawley et al., 1976; Callow et al., 1978; Motomura, 1994. Recent advances in electron microscopy (high pressure freezing, microinjection of fluorescent dyes) examining ultrastructure, distribution, and *de novo* formation of plasmodesmata in *F. distichus* promise to advance studies of receptors and cell-to-cell communication (Nagasato et al., 2015).

In *Fucus*, there are eight eggs per conceptacle (Serrão et al., 1999b; Coyer et al., 2002b), however the number of eggs per receptacle can be species-specific; for example, *F. vesiculosus* produces 10x more eggs than *F. serratus* (Malm & Kautsky, 2003) and hermaphroditic species produce significantly fewer sperms/egg (40:1) than dioecious species (400:1) (Vernet & Harper, 1980). Additionally, sperm in the hermaphrodite *F. spiralis* are much smaller (0.7 1 < 0.46 µm, > 0.21) than in the dioecious *F. vesiculosus* and *F. serratus* (1.58 < 1.25 µm > 0.92), suggesting that the smaller hermaphroditic sperm have fewer energy reserves for swimming in search of eggs (Vernet & Harper, 1980). Experiments have indicated, however, that sperm numbers do not limit fertilization (Berndt et al., 2002). Egg volume varies widely among *Fucus* species, ranging from 235 x 10^3 μm^3 in *F. spiralis* to 68 x 10^3 and 181 x 10^3 μm^3 in *F. vesiculosus* and *F. serratus*, respectively (Vernet & Harper, 1980).

As soon as gametes were observed with the early microscopes, it was realized that *Fucus* provided a favorable system for the study of fertilization (Thuret, 1855); later observations revealed that *Fucus* sperm was attracted to the eggs (Robbins, 1916; see also references in Müller & Seferiadis, 1977). The extremely small amounts of attractant were below detection by instruments until the early 1970s when the pheromone fucoserratene was isolated and identified from eggs of *F. serratus* (Müller & Jaenicke, 1973). Maier and Müller (1986) reviewed extraction methods, identified sexual pheromones in several species of brown algae, including *Fucus*, and detailed how the passage of *Fucus* sperm through a critical concentration level induces a phobic return to the source of pheromone. Given the natural and complex chemical 'noise' that exists in the marine environment, it is perhaps not surprising that introduction of anthropomorphic pollution has the potential to increase the level of 'noise' and affect fertilization in *Fucus* (Steele, 1977).

To achieve maximum fertilization success in *Fucus*, gametes must be synchronously released from nearby individuals and under optimal environmental conditions. While mature oogonia were found all year in receptacles of *F. vesiculosus*, *F. spiralis* and *F. guiryi* (now *F. limitaneus*, Almeida et al., 2022) in a study from North-Portugal, release of eggs (measured as egg settlement) was mainly observed during late spring and summer, with very low settlement observed during the rest of the year (Monteiro et al., 2016). Andersson et al. (1994) measured egg release of *F. vesiculosus* from the Baltic Sea, and observed peaks that occurred in a semilunar pattern. In addition, the highest egg release took place during the evening, between 18:00 and 22:00. Serrão et al. (1996) demonstrated that photosynthesis was necessary for gamete release during calm conditions when extremely high levels of fertilization success, mostly >90%, were achieved (see also Pearson and Brawley, 1996, Pearson et al., 1998). Higher levels of fertilization success (100%) were noted for *F. vesiculosus* in calm conditions within a one-hour interval of a 6-7 hr high tide, 2-3 hrs after being covered by the rising tide (Berndt et al., 2002). Experiments demonstrated that release of gametes was correlated with depletion of dissolved inorganic carbon (DIC) in isolated tide pools during increased light conditions and that sensitivity of gamete release to high water motion was DIC dependent. Specifically, the boundary layer surrounding the receptacle becomes thicker in calm conditions and DIC becomes limiting to photosynthesis, acting as an initial signal on a pathway leading to gamete release (Pearson et al., 1998). In conclusion, gamete release in *Fucus* requires a sunny day, calm conditions, and high tide immersion (Brawley, 1990; Brawley, 1992; Pearson et al., 1998; Berndt et al., 2002; Monteiro et al., 2016).

Low-tide release of gametes, however, is possible under certain conditions. Berndt et al. (2002) documented gamete release in *F. vesiculosus* following several hours of submergence by a rising tide as photosynthesis is required to prepare receptacles for gamete release. They noted that release at low tide occurred after several days of stormy weather and postulated that the normal high tide release was subsequently inhibited and too many mature gametangia were present in the conceptacles leading to release at low tide.

On the other hand, time of day, tidal height, and wave exposure also influenced egg release and settlement patterns, which further differed according to mating type. Ladah et al. (2008) found that dioecious *F. vesiculosus* released more eggs later in the day and at a lower tide than the hermaphroditic *F. spiralis* which released few eggs throughout the day and at all tides. Thus, the importance of low tide or high tide in gamete release is equivocal.

Dispersal of released gametes is very limited. According to a model, small propagules released one meter from the substratum in turbulent water motion will be transported to the substratum within 2-25 seconds or during 1-6 waves (Denny & Shibata, 1989) and only a few meters laterally during this time frame. Furthermore, *Fucus* sperm are too short-lived to be effective agents of dispersal and are attracted to egg-produced pheromones at only µm to mm distances. Additionally, eggs are fertilized quickly after release, are subjected to lethal polyspermy, and the negatively buoyant zygotes secrete a sticky substance for rapid adherence to the substrate (Kropf, 1992; Serrão et al., 1996; Muhlin et al., 2008). Thus, viable *Fucus* gametes and zygotes are likely to disperse only a few meters from the parent (Arrontes, 1993; Serrão et al., 1997; Engel et al., 2005; Muhlin et al., 2008). Strong genetic structuring (isolation-by-distance) revealed by microsatellites among some populations of *F. serratus* implied limited dispersal due to salinity gradients (e.g., Coyer et al., 2003; Coyer et al., 2011a); whereas the lack of genetic structuring among nearby populations of *F. vesiculosus* may be due to high gene flow, inbreeding depression, microscopic forms persisting from previous generations, and/or inappropriateness of using neutral genetic markers to detect the presence of sub-populations (Zardi et al., 2013; Teixeira et al., 2016).

Additionally, long-distance dispersal *via* rafting of fertile *Fucus* that interbreed with attached individuals may increase connectivity among populations (Muhlin et al., 2008). For example, *F. vesiculosus* possesses air bladders on the vegetative thalli allowing rafting to distant locales when detached and free-floating (Coleman & Brawley, 2005; Tatarenkov et al., 2007; Muhlin et al., 2008; Rothäusler et al., 2015) or when attached to floating objects such as buoyant seaweed, natural wood, and anthropogenic debris (Thiel et al., 2011). Rafting may be particularly important in dispersal of hermaphroditic species as only one fertile individual is necessary for successful colonization *via* a stepping-stone dispersal over longer distances. Indeed, genetic analysis strongly infers the success of rafting for hermaphroditic *Fucus* species (Coleman & Brawley, 2005; Coyer et al., 2011b). Long-distance dispersal of clones *via* detached adventitious branches (asexual reproduction) also occurs. For example, Ardehed et al. (2015) found single thalli of *F. radicans* genetically assigned to clones from distant sites rather than from the population in which they were found and reported finding single and vital thalli 18 and 50 km from the nearest population. Such dispersal is important because in a new area, a unisexual population (=clone) may evolve into a bisexual population and initiate sexual reproduction (Ardehed et al., 2015).

Selfing

Simultaneous hermaphroditism can lead to self-fertilization (selfing), an important aspect of evolutionary biology. Hermaphroditism has been reported for 10 animal phyla and ~5% of animal species, a percentage that increases substantially if the highly specious insects are excluded (Jarne & Auld, 2006). In flowering plants, the transition from outcrossing to selfing occurs in many independent lineages (10-15% of seed plants) and may be a driver of speciation (Wright et al., 2013). Within the genus *Fucus*, *in vitro* fertilization experiments have demonstrated selfing in *F. spiralis* (Pollock, 1970; Vernet & Harper, 1980; Müller & Gassmann, 1985) and genetic investigations have supported selfing in *F. spiralis, F. guiryi*, and *F. distichus* (Billard et al., 2005; Coleman & Brawley, 2005; Engel et al., 2005; Coyer et al., 2007; Perrin et al., 2007; Billard et al., 2007; Coyer et al., 2011c; Almeida et al., 2017; Whitaker et al., 2017).

Selfing usually is considered to be deleterious (see Wells, 1979, and references therein). First, it increases the probability that recessive maladaptive genes will become homozygous and subsequently decrease adaptation and fitness (e.g., ‘dead end’ of Stebbins, 1974). Secondly, genetic recombination is limited and further reduces genetic potential to enhance survival and reproduction in a changing environment. Thirdly, effective population size may be reduced.

However, the notion of selfing being a ‘dead end’ over the long term is unclear and the evolutionary and ecological mechanisms need further investigation (Wright, et al., 2013). Some advantages to selfing exist (see Wells, 1979, and references therein). In angiosperms, for example, it is possible that environmental conditions will inhibit pollen dispersal, thereby leading to extinction unless selfing is employed. Additionally, when pollinators and/or mates are rare, or when sperm is limiting (or only self-sperm is available for fusion with eggs due to phrenological incompatibility; Engel et al., 2005) and outcrossing is uncertain, selfing offers reproductive assurance (see references in Vernet & Harper, 1980; Wright, et al., 2013, and Perrin et al., 2007). Selfing also allows transmission of a whole genome through both the male and female functions to the next generation (Fisher, 1941). Furthermore, selfing is a viable means of colonization requiring only one fertile individual and can be an advantage in a mixed population of two species that produce sterile hybrids. Prolonged selfing also can lead to purging of deleterious homozygotes and reduce inbreeding depression (Schoen, 2005; Igić et al., 2006) in unchanging environments. And finally, high-fitness selfed individuals with low rates of recombination at adaptive loci may facilitate colonization by locally-adapted genotypes (Eriksson and Rafajlović, 2021)

Selfing may be advantageous in the upper shore *F. spiralis* as the severe desiccation stress may maintain favorable co-adapted gene combinations by reducing recombination (shuffling of genetic material between male and female chromosomes during meiosis) (Stebbins, 1950; Engel et al., 2005). Additionally, selfing may be important in the closely related species *F. spiralis* and *F. macroguiryi* (formerly *F. guiryi* Almeida et al., 2022) that are sympatric along a vertical exposure gradient in the intertidal regions of northern Portugal and southern France. The two species are separated by a meter or so on the shore, and although extensive gene flow occurs between the species in sympatry (only *F. macroguiryi* is present in southern Iberia), experiments suggest that strong selection on physiological traits across the intertidal gradient maintains the distinct genetic and morphological species within their preferred vertical distribution (Zardi et al., 2011). The prevalence and importance of selfing (relative to outcrossing) in these species in sympatry remains to be determined.

The most recent common ancestor of *Fucus* probably occurred in the Atlantic/Arctic Ocean Basin, where subsequent diversification occurred after opening of the Bering Strait 5.5-5.4 mya (Cánovas et al., 2011). In this area, selfing may be an important and overlooked aspect underlying the diverse morphological forms exhibited by the hermaphroditic *F. distichus* complex throughout its range in the low- and sub-Arctic. Sequence analysis of a variable intergenic spacer and a conserved portion of the 23S subunit in the mitochondrion was unable to differentiate the several species/subspecies of *F. distichus* (e.g., *F. evanescens*, *F. gardneri*, *F. anceps*; Coyer et al., 2006a; Cánovas et al., 2011; Laughinghouse et al., 2015). Laughinghouse et al. (2015) found a distinct Arctic haplotype, clearly showing the ancestor of the *F. distichus* complex to be centered in the low Arctic/Subarctic and invoked glacial cycles in maintaining the various morphs.They postulated that during an interglacial period, the central Arctic becomes a mixing bowl, from which populations expand further into the northern regions of the Atlantic/Arctic. As ice advances southward during the following glacial period, these populations disperse south to widely separated suitable habitats and subsequently adapt to local conditions. During the next interglacial, the locally-adapted populations again expand to the central Arctic Ocean and admixture again occurs, thereby diluting the previously evolved local adaptations (Laughinghouse et al., 2015). The opportunity for differential importance of selfing may exist, with greater selfing occurring in the expanded populations during glacial advance than in the admixture during glacial retreat.

Mating system

The evolution of reproductive strategies has been extensively studied in plants as they exhibit a range of mating systems from hermaphroditism to monoecy to dioecy (Geber et al., 1999). In angiosperms, dioecy appears to be the derived state based on theoretical, empirical, and phylogenetic studies (Charlesworth, 2002; Charlesworth, 2006) and in *Fucus*, dioecy is thought to have evolved from ancestral hermaphroditism (Billard et al., 2005; Billard et al., 2007).

The hypothesis was supported by a recent study of ancestral states in the family Fucales. Using 13 protein-coding genes, Cánovas et al. (2011) established hermaphroditism as ancestral in the family (in accordance with plants), but switching from derived dioecy back to hermaphroditism in one species in each of the two *Fucus* lineages. The switch to the diploid sex-determination system from the haploid UV (*via* a hermaphroditic intermediate) occurred in several families of Fucales ~17.5 mya and the transition toward hermaphroditism within diploid lineages has occurred independently in several genera of the Fucaceae (Heesch et al., 2021).

It also may be significant that hermaphroditic species of *Fucus* frequently occupy exposed or higher shores, whereas dioecious species are found in the more frequently submerged lower or shallow subtidal regions (Vernet & Harper, 1980). Furthermore, multi-gene phylogenies of *Fucus* suggested that switching from dioecy to hermaphroditism has coincided with colonization of more extreme environments (Billard et al., 2010; Cánovas et al., 2011). Two hypotheses may explain the pattern. First, selfing may be favored among species in the higher shores because more frequent desiccation renders cross-fertilization more hazardous, and secondly, repeated exposure to the same physical conditions of the high shore does not 'penalize' the lack of recombination and genetic diversity in hermaphrodites, whereas evolving and high biological diversity/interactions in the more physically stable lower/submerged shores favors genetic diversity provided by dioecy and recombination (Vernet & Harper, 1980; Billard et al., 2010).

A recent and detailed phylogenetic analysis of the low latitude hermaphroditic clade in the Iberian Peninsula and Northern Africa (*F. macroguiryi*, *F. spiralis*, *F. limitaneus)* by Almeida et al. (2022) suggested that the strong metapopulation structure within southern *F. vesiculosus* (dioecious) in restricted habitats favored parapatric speciation of an ancestral hermaphrodite lineage. A single ancestral hermaphrodite diversification event ~0.54 mya led to the *F. macroguiryi* and *F. limitaneus/F. spiralis* clades which differ in vertical ranges on rocky shores, with the morphologically and ecologically similar *F. limitaneus* and *F. spiralis* diverging more recently (~0.34 mya). Thus, the evolution of selfing lineages from outcrossing progenitors, a feature that is common among higher plants and some animals, has occurred several times in *Fucus* (Almeida et al., 2022).

Hybridization

Morphological variability within and between *Fucus* spp. is legendary (e.g., Sideman and Mathieson, 1985; Rice & Chapman, 1985; Rice et al., 1985; Munda & Kremer, 1997; Kalvas and Kautsky, 1998; Anderson & Scott, 1998). The ability to detect differences in DNA sequences, either indirectly or directly, has provided additional taxonomic characters with which to examine morphological differences and has proved to be especially important in unraveling some of the taxonomic confusion in *Fucus*, a genus consisting of 717 described names, of which 10 are currently accepted as species (https://www.algaebase.org/search/genus/detail/?genus_id=71).

Some species are more related than others. Using sequences of the internal transcribed region (ITS-1, 5.8S, ITS2) of nuclear ribosomal DNA, Serrão et al. (1999a) established the presence of two lineages (or clades) within the genus: Lineage 1 and Lineage 2 (see Table 1 for species within each Lineage), subsequently supported with the 23S subunit and intergenic spacer regions of mitochondria (Coyer et al., 2006a). Additionally, each Lineage contains hermaphroditic and dioecious species with reciprocal habitat specialist species: (*F. spiralis*=high intertidal; *F. serratus* low intertidal/subtidal and generalist species *F. vesiculosus* = high to low intertidal; *F. distichus* = high intertidal pools to low intertidal) (Coyer et al., 2006a). More recently, Cánovas et al. (2011) used 13 protein-coding genes to further clarify the two lineages and indicated that species in Lineage 1 are characterized by being northern in distribution, adapted to cold water and stress-receptible, whereas species in Lineage 2 are more southern in distribution and generally stress-tolerable. As discussed below, hybridization in *Fucus* occurs among species within a Lineage, rarely between, and always involves a parental species pair in which one parent is a hermaphrodite (e.g., *F. spiralis*, *F. distichus*) and the other is dioecious (e.g., *F. vesiculosus*, *F. serratus)* (Coyer et al., 2007).

A more complicated dynamic is evident in the low latitude hermaphroditic *F. spiralis* complex. Initially, two genetically and morphologically distinct entities, *F spiralis*-High and *F. spiralis*-Low, corresponded to *F. spiralis* var *spiralis* and *F. spiralis* var *platycarpus*, respectively, in addition to a third entity named *F. spiralis*-South (Billard et al., 2007; Billard et al., 2010; Coyer et al., 2011c). Using microsatellites in tandem with expressed sequence tags for partial sequencing of 14 protein-coding genes, *F. spiralis* var *platycarpus* (*F. spiralis*-Low) was synonymized with *F. spiralis*-South as *F. guiryi* (Zardi et al., 2011), a distinct entity in southern Iberia (allopatry), but as it was also distributed across *F. vesiculosus* and *F. spiralis* clades in Northern Portugal (sympatry), extensive hybridization and introgression is possible (Zardi et al., 2011).

A new study using a phylo-transcriptomic approach based on short read transcriptomic data (RNA-seq) of warm affinity Lineage 2 populations existing in sympatry (Britain, NW Iberia) and allopatry (SW Iberia, Morocco) further clarified the complex patterns of cryptic speciation (Almeida et al., 2022). Specifically, *F. spiralis*-Low diverged earlier than the others, necessitating removal of *F. spiralis*-Low from *F. guiryi* and designation as new species *F. macroguiryi* that is genetically, morphologically, and physiologically distinct from all others and is introgressed *F. guiryi* (Cánovas et al., 2011; Almeida et al., 2022). *F. guiryi* on the Canary Islands has thus reverted to the previously described *F. limitaneus* (Almeida et al., 2022).

Reports of field individuals with an intermediate morphology between two co-existing *Fucus* species have occurred several times in the past century (Gard, 1910; Gard, 1915; Powell, 1963; see also references in Scott & Hardy, 1994). Some viewed these forms as ecotypes, but others (e.g., McLachan et al., 1971; Scott & Hardy, 1994) stated strongly that hybridization most likely was the root of the considerable morphological variation in *Fucus*. At that time, verification of hybridization required difficult and labor-intensive crossing studies, although several attempts were made (Thuret, 1855; Williams, 1899; Sauvageau, 1909; Kniep, 1925; Burrows and Lodge, 1951; Burrows and Lodge, 1953; Bolwell et al., 1977; Scott & Hardy, 1994; Kim et al., 1997). Few zygotes resulting from the laboratory crosses between various species of *Fucus*, particularly between Lineage 1 and 2 species and *F. vesiculosus* x *Ascophyllum nodosum* (Kim et al., 1997), survived beyond a few days (e.g., Scott & Hardy, 1994).

The advent of genetic techniques made detection of hybridization much easier and more robust. For example, nuclear and cytoplasmic DNA reveal relatedness among individuals at the population level and above, whereas plastid DNA (mitochondria, chloroplasts) are maternally inherited. Microsatellites in particular have been invaluable for much more detailed studies of hybridization and introgression in many plants and animals, including the genus *Fucus*, as the bi-parentally inherited markers clearly delineate heterozygosity and parentage using both plastid and nuclear DNA.

The first molecular-based studies of hybridization in *Fucus* used the nuclear rDNA-ITS1 sequence, the *Rubiso* spacer in chloroplasts, and *nad*11gene in mitochondria; demonstrating that the plastids are maternally inherited in *Fucus* (Coyer et al., 2002a; Coyer et al., 2002b), although some ‘paternal leakage’ has been observed (Coyer et al., 2004; Hoarau et al., 2009). Results confirmed hybridization and introgression between Lineage 1 species *F. evanescens* (=*distichus*, see Coyer et al., 2007) and *F. serratus* in both field specimens and laboratory crosses, and further revealed that: 1) hybridization was asymmetrical, with the dioecious *F. serratus* contributing sperm and the hermaphroditic *F. evanescens* the eggs, and 2) hybridization was restricted to sympatric, rather than allopatric stands (Coyer et al., 2002a; Coyer et al., 2002b). Using 10 microsatellite loci of a mixed population consisting of native *F. serratus* and introduced *F. evanescens* in Denmark that had existed for 60-100 yrs, revealed: 1) nearly 13% of the individuals were F_1 hybrids (also asymmetrical as described above), 2) ca. 1.5% of genes were introgressed into each parental species, and 3) F_1 hybrids displayed lower survivorship (Coyer et al., 2007).

Several subsequent studies have employed microsatellites to examine hybridization and introgression in Lineage 2 *Fucus* spp. Engel et al. (2005) used five loci and found a higher proportion of genetically intermediate individuals (*F. vesiculosus* x *F. spiralis* hybrids) in two sympatric populations (12.5 and 14.2%) than in parapatric populations (5.6 and 9.0%). As for *F. serratus* x *F. distichus* (Coyer et al., 2002a), *F. spiralis* (hermaphroditic) eggs were fertilized by *F. vesiculosus* (dioecious) sperm (Billard et al., 2007). Hybridization was far more common in mixed populations, although did occur in separate distributions. In some cases, *F. spiralis* x *F. vesiculosus* F_1s were fertile (Billard et al., 2007; Billard et al., 2010). More recently, microsatellite analysis was combined with network analysis to reliably determine the occurrence of present-day hybridization between *F. spiralis* and *F. vesiculosus* (Moalic et al., 2011).

Hybridization also has been demonstrated among hermaphroditic species of Lineage 2. Short read transcriptomic data (RNA-seq) consistently indicated gene flow between *F. macroguiryi* and *F. limitaneus*, exceeding that between *F. macroguiryi* and *F. spiralis.* The pattern is best explained by assuming that *F. macroguiryi* was present further south than *F. spiralis* during glacial stages and farther from the ice limits, with extensive gene flow between *F. macroguiryi* and *F. limitaneus* in the south during relatively lengthy glacial periods contributing to the observed introgression signal (Almeida et al., 2022).

Clearly, hybrid fitness will determine the fate of a hybrid zone, and three scenarios are possible: 1) if there is no selection against the hybrids and introgression is extensive, all individuals become hybrids; 2) if introgressed individuals become established and/or are adapted for new habitats, new lineages can evolve; and 3) if hybrids are less fit, pre-zygotic isolating barriers can evolve to strengthen selection against formation of hybrids (=reinforcement), as less fit hybrids can be viewed as energetically expensive 'mistakes' (summarized in Hoarau et al., 2015). Two lines of evidence suggest that in *Fucus*, scenario 3 is most likely. First, *F. serratus* x *F. evanescens* hybrids have lower survivorship and reduced fertility than either parent (Coyer et al., 2007; Hoarau et al., 2015).

Secondly, reinforcement of pre-zygotic isolation appears to have evolved in older contact zones of *F. serratus* and *F. distichus*, but not in younger contact zones. Hoarau et al. (2015) examined hybridization and introgression of the two species in contact zones: 1) near Denmark where *F. distichus* was introduced ~150 yrs ago, 2) in Iceland where *F. serratus* was introduced ~150 yrs ago, and 3) northern Norway where the two species have co-existed since the end of the Last Glacial Maximum ~10,000 yrs ago. Both Danish and Icelandic populations revealed a high proportion of hybrids (13-24%) and several F_1 individuals, whereas the Norwegian populations displayed a low proportion of hybrids (2-3%) and an absence of F_1 individuals (Hoarau et al., 2015). Additionally, the success rate of interspecific laboratory crosses to one-week old embryos was significantly lower in the older contact zones of Norway than in the younger contact zones of Denmark and Iceland, again suggesting selection against hybridization and for pre-zygotic isolation (Hoarau et al., 2015).

Similarly, the introgression signal from *F. macroguiryi* (hermaphroditic) into *F. vesiculosus* (dioecious) in secondary contact has decayed, but is still detectable (Almeida et al., 2022). The decay may be due to steady reinforcement of species boundaries in the sympatric range, as observed for *F. distichus* and *F. serratus* in Norway (Hoarau et al., 2015), or a consequence of reduced contact time during range expansion (Almeida et al., 2022).

If gamete release in *Fucus* is delayed by environmental conditions such as high-water motion, mature gametes accumulate in the conceptacles. Several studies have demonstrated that when ripe receptacles are stored in the laboratory for several days before releasing gametes, species-specific barriers are diminished and hybrids can be produced (Bolwell et al., 1977; Edwards et al., 1997; Edwards, 1999). Additionally, fertilization success was significantly reduced when eggs were retained in the receptacles for ~ 3 weeks due to unfavorable environmental conditions for release (Serrão et al., 1999a).

Despite the wide occurrence of hybridization among *Fucus* spp., pre-zygotic mechanisms, such as asynchronous release of gametes, have evolved to significantly reduce hybridization. Monteiro et al. (2012, 2016) studied gamete release among four sympatric species of *Fucus* in northern Portugal. Dioecious *F. vesiculosus* and *F. serratus* released gametes during daytime neap tides, while hermaphroditic *F. guiryi* and *F. spiralis* released gametes during night-time high tides during the same phase of the semilunar cycle, effectively reducing the potential for hybridization with the dioecious *F. vesiculosus*. As the divergence between hermaphroditic and dioecious species may be > 1 mya (Cánovas et al., 2011), the shift in periods of gamete release is remarkably rapid.

Ecads

An especially interesting aspect of Fucales is the existence of ecads and the role of hybridization and polyploidy in their existence. Ecads are free-living individuals with morphological variability linked to habitat (Clements, 1905); in the case of *Fucus*, to the low-energy muddy shorelines of estuaries and high-intertidal salt marshes, and presumably arise from attached 'parental' species. Fucoid salt marsh ecads have been known for over 100 years for *F. vesiculosus* and *F. spiralis* in the North

Atlantic (Cotton, 1912; Baker & Bohling, 1916), and more recently *F. gardneri* (part of *F. distichus* complex; see Coyer et al., 2006a; Cánovas et al., 2011) in the North Pacific (Ruiz et al., 2000; Kucera & Saunders, 2008). Ecads also are known in the closely related fucoid *Ascophyllum nodosum* (Chock and Mathieson, 1976; Chock and Mathieson, 1979; Mathieson & Dawes, 2001; Mathieson et al., 2001). All fucoid ecads are characterized by the absence of a holdfast; a dwarf morphology; asexual reproduction; and curled, proliferating thalli (see also references in Wallace et al., 2004) and may be a major source of biomass and productivity in these habitats (Tyrrell et al., 2012; Tyrrell et al., 2015).

In one of the first uses of microsatellites to examine hybridization in *Fucus*, Wallace et al. (2004) concluded that: 1) the *muscoides*-like *Fucus* ecad in Maine (USA) salt marshes consisted mainly of *F. vesiculosus* x *F. spiralis* F_1 hybrids; 2) another ecad (*F. vesiculosus* ecad *volubilis*) may have arisen through introgression between fertile hybrids and *F. vesiculosus*; and 3) introgression had likely occurred between *F. vesiculosus* and *F. spiralis*. A later study using microsatellites and mtDNA analysis showed that *muscoides*-like *Fucus* ecads in Iceland were consistent with asymmetrical hybridization between the dioecious *F. vesiculosus* sperm and hermaphroditic *F. spiralis* eggs, whereas similar ecads in Ireland were the result of polyploidy (Coyer et al., 2006b).

Sjøtun et al. (2017) examined the complexity of *Fucus* ecads at three sites in western Ireland. In one location, a morphological cline existed with small *Fucus* individuals lacking bladders in the upper intertidal salt marshes ranging to *F. vesiculosus* in mid-intertidal; nuclear DNA content ranged from 1-1.8 pg, suggesting polyploidy in some individuals. At Locality 2, microsatellite analysis revealed salt marsh individuals were derived mainly from *F. vesiculosus*, whereas at Locality 3, salt marsh individuals were *F. vesiculosus* x *F. spiralis* hybrids with greatest affiliation to *F. spiralis*. DNA content of the small individuals from Locality 2 (ca. 4 pg) suggested they were octoploids, whereas the individuals from Locality 3 formed two groups based on DNA content: one with 3.9-4.6 pg and the other with 1.5-2.8 pg. Furthermore, DNA content of individuals in Locality 3 varied between 1.1-2.8 pg in *F. vesiculosus* and 2-3.5 pg in *F. spiralis*, demonstrating a somewhat stepwise increase in both species consistent with polyploidy. The authors hypothesized that the small salt marsh *Fucus* originated from genome size changes in the parents.

Neiva et al. (2012) used microsatellite loci to examine *Fucus* ecads from Oregon (US) in the North Pacific and Ireland and concluded that they were more related to *F. gardnerii*, and *F. spiralis*, respectively. Additionally, they suggested that fucoid ecads are evolutionarily independent populations stemming from hybrid or polyploid origins that confer a fitness advantage over their parental species in a marginal and/or stressful habitat.

An interesting ecad is *F. vesiculosus* growing on intertidal mussel beds in the Wadden Sea and along the North Sea coast, first described by Nienburg (1925, 1927) and later by others (Wohlenberg, 1937; Nienhuis, 1970; van den Hoek et al., 1979). The *F. vesiculosus* ecad lacks the species' characteristic gas bladders; reproduces vegetatively; and does not have a holdfast, being attached to the muddy substratum *via* the mussel's byssal threads (Albrecht & Reise, 1994). The association is mutual: the ecad prevents mussels from sinking into the mud, whereas the mussels anchor the ecads and allows steady growth (Nienburg, 1925; Nienburg, 1927). It is unknown if *F. spiralis* co-occurs on mussels, so derivation of the ecad by hybridization or polyploidy remains unknown.

Recently, a study of attached (epilithic) and free-living (benthopleustophytic) forms of *F. vesiculosus* in the Baltic Sea revealed the presence of polyploidy (likely through autopolyploidy) throughout the majority of populations regardless of form with important implications in population structure (Preston et al., 2022).There is no direct evidence of sexual reproduction in the free-living form, which probably originated asexually *via* detached pieces of thalli aggregating in sheltered locations (Preston et al., 2022), and presumably without a functioning holdfast. Thus, the free-living form is at least 'ecad like'. Although the free-living form was less genetically diverse than the attached, genetic diversity was still within expected limits for both forms and frequent asexual reproduction in the free-living form did not reduce the overall genetic variation in *F. vesiculosus*. Gene flow within and among the forms differed at various spatial scales, but the free-living populations were judged to be more unstable and at increased risk of local extinction (Preston et al., 2022).

Evolution of diplontic life cycle and sex-biased genes

In all orders of brown algae, sex is determined in the haploid stage of the gametophyte generation except for the Fucales, where sex is determined *via* haploid gametes during the diploid state (Coelho et al., 2019). Fucales also are of interest because of the relatively recent transition from haploid to diploid sex determination (Silberfeld et al., 2014), switching from ancestral hermaphroditism to dioecy and in some species, back to hermaphroditism (Billard et al., 2005; Billard et al., 2007; Cánovas et al., 2011). The switching of reproductive method coincides with a dramatic rise in sea levels ca. 75 mya and could have opened new ecological niches for Fucales (Heesch et al., 2021). It also is important to note that hermaphroditic lineages are better colonizers of marginal habitats via increased reproductive assurance and the maintenance of locally adaptive traits (Cánovas et al. 2011).

Genes that are differentially expressed in males and females (sex-biased genes) have been well documented across a wide number of animals, plants, and brown algae (see references in

Hatchett et al., 2021). A comparative transcriptomic study of vegetative and gender-specific reproductive tissue in *F. vesiculosus* revealed striking differences (Martins et al., 2013). For example, cell cycle and meiotic pathways were over-expressed in male (not female) reproductive tissue relative to vegetative tissue, as well as genetic information processing pathways associated with sperm production. Further, the number of sex-biased genes were ~3-fold higher in male relative to female tissue and the average expression level of male-biased genes was greater than female-biased genes. Candidate sex-biased genes in females were limited to those with likely roles in cell wall/matrix modification, whereas a variety of male-biased genes were related to development; signaling and signal perception; and potential flagella-localized proteins.

Hatchett et al. (2021) examined the evolution of sex-biased genes in vegetative and reproductive tissue of male and female *F. serratus* and *F. vesiculosus* with RNAseq and *de novo* reference transcriptome assembly. While very few genes were differentially expressed between male and female vegetative tissue (8-9% in each species), thousands of genes were differentially expressed in the reproductive tissues. A similar proportion of the genome displayed tissue-biased expression between receptacle and non-receptacle tissue, demonstrating that the majority of tissue- and sex-biased expression was allocated to the reproductive structures.

The authors also found that male-biased genes were highly conserved between the two species, with clustering of male reproductive samples by sex rather than by species. Furthermore, overexpression of male-biased genes was >3-fold the number of female-biased genes and conserved male-biased genes were enriched in functions related to gamete production, sperm competition, and flagellar proteins. The increase in male biased gene expression of the transcriptome also suggested that males may experience relaxed purification selection or stronger selection than females, a trait found in many other species of eukaryotes (Hatchett et al., 2021 and references therein). Female-biased genes were uniformly and highly expressed throughout the female and male tissues, thus sexual conflict over gene expression in *Fucus* may be resolved by down-regulating expression of pleiotropic female genes in male receptacles and restricting expression of male-biased genes to the male reproductive tissue resulting in an increase of male biased gene expression.

Climate change and *Fucus* reproduction

Several studies employing ecological niche modeling or other species distribution models (SDMs) comparing present-day vs. projected future distributions have been performed for *Fucus* under contrasting IPCC (Intergovernmental Panel on Climate Change) climate change scenarios (e.g., Nicastro et al., 2013; Assis et al., 2014; Jueterbock et al., 2014; Jueterbock et al., 2016). In general, all have demonstrated a northward shift into expanding suitable habitat and decline or extinction in the southern edge populations due to rising temperatures. For example, experiments with *F. serratus* confirmed that thermal extremes will regularly reach physiologically stressful levels in Brittany (France) and further south by the end of the 22nd century (Jueterbock et al., 2014).

On the other hand, expansion into northern habitats will require adaptations to cooler water and 24 hr light/dark months. Recent studies in *Fucus* species have focused on how climate change influences average seawater temperature, salinity and pCO_2 and how these changes affect reproductive success. Predicted future changes in seawater conditions for *F. radicans* in the Northern Baltic Sea, showed a high tolerance in photosynthesis and growth, but decreased survival and cessation of sexual reproduction (Rothäusler et al., 2018; Rugiu et al., 2018). In the southwest Baltic Sea (Kiel Fjord), *F. vesiculosus* was unaffected by elevated pCO_2 and/or warming, but matured earlier with a subsequent earlier gamete release (Graiff et al., 2017). Furthermore, southern edge populations of *F. vesiculosus* are exposed to higher sea and air temperatures (a proxy for climate change) have significantly lower biomass of reproductive tissue and smaller number of receptacles per individual (Ferreira et al., 2015).

Additionally, increased glacial melting may decrease salinity in some areas. For example, *F. vesiculosus* along the Finnish coast currently tolerates 5.8 PSU, but this is projected to reach 2.5 PSU by the end of the century (Meier et al., 2012). At 2.5 PSU egg release was reduced and at 3.5 PSU, sperm cells began to swell, drastically reducing reproductive success (Rothäusler et al., 2019). As discussed above, low salinities also increase the probability of lethal polyspermy (see 'General Characteristics, above).

Future directions

The continuing and rapid development of the 'omics' (genomics, transcriptomics, proteomics, metabolomics), as well as CRISPR/Cas9 techniques, provide invaluable tools to address even more questions in *Fucus* reproduction (as well as evolutionary history), especially with the future release of full genome data for several species (Table 2), and the ease of laboratory culturing and subsequent manipulation of gene lines. There also, however, remains the need for basic investigations in reproductive ecology, particularly among the lesser studied Lineage 1 species. Taking a larger view, investigating the various modes of reproduction (e.g., hermaphroditism, dioecy, hybridization, selfing, asexual reproduction, ecads) in *Fucus* may well lead to new insights in the study of reproduction in other organisms with a diplontic life cycle, consequently, *Fucus* can be a useful model organism. We offer below a small subset of questions to stimulate thoughts of future research.

TABLE 2 Current or soon to be available (SA) genomic data for *Fucus* spp.

Species	Sequencing type	Reference	Accession number	Size
Fucus distichus	Genome	Phaeoexplorer	SA	691.15 Mbp
	Transcriptome	Hatchett et al. (2021)	GJHE00000000	22.09 Mbp
	Mitogenome	Hughey & Gabrielson (2017)	NC_034672	36.40 Kbp
Fucus serratus	Genome	Phaeoexplorer	SA	1.15 Gbp
	Transcriptome	Hatchett et al. (2021)	GJHE00000000	30.59 Mbp
Fucus vesiculosus	Genome	Unpublished	ASM1484947v1	1.51 Gbp
	Transcriptome	Hatchett et al. (2021)	GJHE00000000	24.23 Mbp
	Mitogenome	Oudot-Le-Secq et al. (2006)	NC_007683	36.39 Kbp
	Chloroplast	le Corguillé et al. (2009)	NC_016735	124.986 Kbp
Fucus spiralis	Transcriptome	Hatchett et al. (2021)	GJHE00000000	24.63 Mbp
Fucus ceranoides	Transcriptome	Unpublished	HACY00000000	47.44 Mbp
Fucus virsoides	Transcriptome	Falace et al. (2018)	PRJNA524465	N/A

Phaeoexplorer: https://phaeoexplorer.sb-roscoff.fr/home/. Size of each assembly is represented by gigabase pairs, megabase pairs, kilobase pairs (Gbp, Mbp & Kbp, respectively). N/A, not available.

1. Why is Lineage 2 much more specious than Lineage 1 and how can whole genome analysis (and genome-wide markers such as SNPs) resolve the numerous and controversial number of species in Lineage 2? Although the genus evolved in, and radiated from, the central Arctic (Cánovas et al., 2011; Laughinghouse et al., 2015), far more species have emerged in the relatively younger North Atlantic than in the older North Pacific. Is it simply that there was less competition from other species of algae in the North Atlantic or did the diplontic life cycle of reproduction favor *Fucus* spp. in a younger habitat?
2. How/why is *F. vesiculosus* so successful in such diverse habitats (e.g., sheltered to moderately exposed, rocky shores to salt marshes, degree of immersion/emersion, brackish to marine salinity)? Comparative genomics/transcriptomics may reveal the presence/absence of genes, differential levels of gene expression, and/or an important role of epigenetics (heritable and reversible changes in transgenerational phenotypes without corresponding changes in DNA sequence) that may be unique to *F. vesiculosus*.
3. The existence of ecads leads to many ecological and genomic questions. For example, what are the longevity and growth patterns of ecads resulting from hybridization relative to those arising from polyploidy and how are both influenced by the local environment? From a genomic perspective: 1) what is the genetic basis for the hybridization or polyploidy dichotomy and is it reversible; 2) is the genome size divergence (e.g., Sjøtun et al., 2017) due to non-coding elements or gene duplication, 3) how do the mechanisms of inducement differ in dioecious (*F. vesiculosus*) and hermaphroditic species (*F. distichus*); and 4) is epigenetics a key factor or are different regions/genes in the genome important? Finally, is the *F. vesiculosus* ecad on mussels in the Wadden Sea a result of hybridization or polyploidy?
4. How does rate of selfing in hermaphroditic species vary with changing environments?
5. How does frequency of hybridization vary as a function of stochastic and dynamic environmental conditions (field and laboratory cultures)?
6. Detailed field studies of gamete release and fertilization success of Lineage 1 species are needed for comparison to the much more studied *F. spiralis* and *F. vesiculosus* in Lineage 2. For example, hermaphroditic *F. distichus* shares shore position with the dioecious *F. vesiculosus* and *F. serratus* is mostly subtidal with no equivalent in Lineage 1. How do aspects of reproduction in Lineage 1 vary as a function of tidal cycle, light, and water motion? Given the different shore positions, how do selfing rates and success differ when comparing *F. spiralis* and *F. distichus*?
7. What is the genetic basis for the morphological differences (particularly receptacles) among the various morphs of *F. distichus* (*F. anceps, F. evanescens, F. edentatus*, *F. gardneri*, etc.) and *F. vesiculosus* (with and without vesicles)? Is epigenetics present in *Fucus* spp.?
8. Does the metabolome (see Parrot et al., 2019) on *Fucus* fronds differ from that on receptacles and if so, why, and how do the differences influence gamete release?
9. What is the genomic/transcriptomic basis for non-overlapping reproductive seasons of *F. vesiculosus* observed in the Baltic Sea?
10. What is the genetic basis for reproductive isolation and the connection between prezygotic barriers to fertilization and within-species sexual selection?
11. How can whole genome sequencing identify sex chromosomes and molecules involved in sperm/egg receptors?

12. How will global changes (e.g., temperature, salinity, dissolved CO_2) affect aspects of *Fucus* reproduction (development time, gamete output/size/dispersal, fertilization, dispersal of fertilized eggs, etc.)?

Author contributions

WH: Original concept, drafting and editing of the manuscript, producing/providing figures, and tables. JC: Drafting and editing of the manuscript, design of figures. KS: Table and editing of the manuscript. AJ: Editing of the manuscript. GH: Editing of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1051838/full#supplementary-material

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