EVOLUTIONARY PHYCOLOGY: TOWARDS A MACROALGAL SPECIES CONCEPTUAL FRAMEWORK

1   EVOLUTIONARY PHYCOLOGY: TOWARDS A MACROALGAL SPECIES

2   CONCEPTUAL FRAMEWORK[1]

3   Sophie J. McCoy[2], Stacy A. Krueger-Hadfield[3], Nova Mieszkowska[4,5]

4

5   [1] Date of Submission, Date of Acceptance

6   [2] Department of Biological Science, Florida State University, 319 Stadium Dr., Tallahassee, FL

7   32312, USA

8   e-mail: mccoy@bio.fsu.edu

9   phone: (850) 644-1549

10   fax: (850) 645-8447

11   [3] Department of Biology, University of Alabama at Birmingham, 1300 University Blvd,

12   Birmingham, AL 35294, USA

13   [4] Department of Environmental Sciences, University of Liverpool, L69 3GP, UK

14   [5] Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth,

15   Devon, PL1 2PB, UK

16

17   Running Title: Towards a macroalgal species concept

18   Abstract

19   Species concepts formalize evolutionary and ecological processes, but often conflict with one

20   another when considering the mechanisms that ultimately lead to species delimitation.

21   Evolutionary biologists are, however, recognizing that the conceptualization of a species is

22   separate and distinct from the delimitation of species. Indeed, if species are generally defined as

23   separately evolving metapopulation lineages, then characteristics, such as reproductive isolation

24   or monophyly, can be used as evidence of lineage separation and no longer conflict with the

25   conceptualization of a species. However, little of this discussion has addressed the formalization

26   of this evolutionary conceptual framework for macroalgal species. This may be due to the

27   complexity and variation found in macroalgal life cycles. While macroalgal mating system

28   variation and patterns of hybridization and introgression have been identified, complex algal life

29   cycles generate unique eco-evolutionary consequences. Moreover, the discovery of frequent

30   macroalgal cryptic speciation has not been accompanied by the study of the evolutionary ecology

31   of those lineages, and, thus, an understanding of the mechanisms underlying such rampant

32   speciation remain elusive. In this perspective, we aim to further the discussion and interest in

33   species concepts and speciation processes in macroalgae. We propose a conceptual framework to

34   enable phycological researchers and students alike to portray these processes in a manner

35   consistent with dialogue at the forefront of evolutionary biology. We define a macroalgal species

36   as an independently evolving metapopulation lineage, whereby we can test for reproductive

37   isolation or the occupation of distinct adaptive zones, among other mechanisms, as secondary

38   lines of supporting evidence.

39

40   Key words: Diversity, Macroalgal, Phycological, Seaweed, Speciation, Species Concept

41 **Introduction**

42 The resolving power of DNA sequences has enabled the identification of a myriad of

43 independently evolving lineages (Pante et al. 2015), and phycology has not escaped the ensuing

44 systematics revolution (Saunders 2005, Le Gall & Saunders 2010, Leliaert et al. 2014, Leliaert et

45 al. 2019). While discussion of species concepts in the scientific literature has increased since the

46 1960s, little of this discussion has revolved around species concepts, and specifically

47 incorporating evolutionary frameworks (e.g., De Queiroz 2007), for macroalgae (Fig. 1A).

48 Species and speciation are nevertheless two of the most basic elements of evolutionary biology

49 and there are important reasons why we need to pay careful attention to species

50 conceptualization and species delimitation in macroalgae. For higher plants, species have been

51 delimited through the lens of natural history and reproductive mode variation (Grant 1981), even

52 in the modern era of molecular barcoding and phylogenomics that have provided critical lines of

53 evidence for constructing phylogenetic relationships (e.g., Hörandl et al. 2009). Even when

54 taxonomic complexity is accounted for in plants, there are often conservation issues when plant

55 taxa do not fit neatly into a 'species'-based system (e.g., Hollingsworth 2003). Yet, for the

56 macroalgae, we do not possess the same intimate knowledge of mating system and reproductive

57 mode variation that botantists enjoy from a legacy of common garden experiments. Thus, we are

58 often blind as to macroalgal taxonomic complexity that can generate discordances among species

59 concepts as they may be applied to freshwater or marine taxa. Moreover, the profound variation

60 in life cycles exhibited across the red, green, and brown macroalgae suggests that delimiting

61 species may be challenging (Dudgeon et al. 2017) because some algal life cycles have unique

62 eco-evolutionary consequences (e.g., clonality results in an uncoupling of the life cycle,

63   reviewed by Krueger-Hadfield 2020). Thus, incorporating an explicit evolutionary framework

64   into our approach for conceptualizing an algal species should be of great importance to

65   phycologists, especially as we continue to identify new taxa using molecular tools and subdivide

66   existing morphological species into species complexes. Moreover, it will aid in a shift in

67   phycological thinking towards species as hypotheses (*sensu* Pante et al. 2015) and the

68   investigation of different mechanisms that lead to the separation of macroalgal lineages.

69

70   The existence of numerous macroalgal cryptic species are of particular concern in this context.

71   While some 'cryptic' species are the result of assigning the same name to morphologically

72   similar taxa throughout the world without the benefit of molecular tools, other cryptic species are

73   now regularly being found in the same habitats, such as the same intertidal zone or reef (e.g.,

74   Geoffroy et al. 2015, Montecinos et al. 2017, Gabrielson et al. 2018, Hughey et al. 2019). In the

75   latter case, species are indistinguishable by morphology and are often mistakenly assigned to the

76   same species name, confounding our understanding of their evolutionary ecology (Bickford et al.

77   2007). This limitation is critical, as our ability to differentiate between cryptic species may have

78   major implications for understanding the ecophysiology, local adaptation, population ecology,

79   evolutionary processes, and community ecology of these taxa (Mayr 1948). From an ecological

80   perspective, cryptic species render experimentation in nature difficult, when there are few

81   diagnostic, visual differences (e.g., Montecinos et al. 2017). Yet, species complexes figure into

82   the ecology of natural systems because life cycle variants, as well as ecotypes within species,

83   matter ecologically (e.g., De Jode et al. 2019). Therefore, before we can test important eco-

84   evolutionary hypotheses, such as how different cryptic species or their life cycle stages may

85   respond to climate change, we have to understand the processes by which variants within

86   species, and species themselves, diversify – which hinges on an evolutionary framework within

87   which to define speciation criteria. These considerations also fuel debates on the importance of

88   functional vs. genetic processes (Bortolus 2008). Thus, it is important to contextualize species

89   complexes with functional differences and similarities between genetic groups to gain an

90   understanding of the basis for speciation in these instances. While the overall study of cryptic

91   species has increased exponentially over the past 30 years, the study of the evolutionary ecology

92   of cryptic algal species has remained sparse (Fig. 1B). Here, we aim to further the discussion and

93   interest in species concepts and speciation processes in macroalgae.

94

95   A more formal conceptualization of a macroalgal species that can be separated from the

96   mechanisms that are generated through lineage divergence, that we in turn use as evidence of

97   delimitation (De Queiroz 2007), would facilitate communication and collaboration between

98   taxonomists, evolutionary biologists, ecologists, physiologists, and biogeographers. It is

99   necessary for synergy among these disciplines in order to generate a holistic approach to

100   understanding the mechanisms that underlie phycological biodiversity and ecophysiology. The

101   lack of explicit evolutionary frameworks in phycology poses a problem to our field as we seek a

102   holistic understanding of algal speciation. While the general tenants of our argument below apply

103   to both micro- and macroalgae, we focus here on freshwater and marine macroalgal taxa as a

104   starting point and more tractable taxa with which to understand the challenges associated with

105   macroalgal life cycle complexity and speciation. Future work should expand these ideas and

106   integrate microalgae into these frameworks. Below, we briefly review relevant aspects of

107   macroalgal biology that we need to consider when delimiting species, then outline the

108   evolutionary conceptual framework through which we should assess macroalgal species.

109

110   **Macroalgal biogeography**

111   Physiologically, macroalgae have limited dispersal compared with marine invertebrates or

112   terrestrial plants, which may be broadcast spawners or dispersed by wind or animals. Most

113   species of macroalgae rely on propagules, defined broadly to include vegetative or sexual

114   reproduction via spores or zygotes, that are either immotile or have limited locomotory

115   capabilities for their reproduction, proliferation, and dispersal (Santelices 1990). Generation time

116   and morphological structure of the propagule stage (Norton 1992), in addition to oceanographic

117   and bathymetric conditions (Breeman 1988, van den Hoek 1982 a,b, Gaylord et al. 2004),

118   determine the distance that propagules can travel from the parent population. In many cases,

119   these factors have led to an overall pattern of isolation-by-distance, where populations regularly

120   exchange migrants with nearby populations (Kimura & Weiss 1964, Brennan et al. 2014). Long-

121   distance dispersal is rare, but does occur, achieved primarily by rafting of detached, reproductive

122   thalli (Norton 1992, Valero et al. 2001, McKenzie & Bellgrove 2008, Fraser et al. 2009,

123   Buchanan & Zuccarello 2012, Provan et al. 2013, Bringloe & Saunders 2018).

124

125   Marine macroalgae are distributed along coastal latitudinal clines that correlate with a gradually

126   changing ecological niche space (s*ensu* Hutchinson 1957, Holt 2009). Temperature and

127   photoperiod are thus the primary abiotic factors controlling macroalgal biogeography (Dring

128   1984, Lüning 1990). Ranges track summer and winter isotherms (Mieszkowska & Sugden

129   2016), with range edges being set by temperatures exceeding lethal limits of the hardiest life

130   cycle stage or summer temperatures limiting growth or reproduction (Bartsch et al. 2012,

131   Breeman 1988, Hutchins 1947, van den Hoek 1982a). The limited long-distance dispersal of

132   macroalgae effectively reduces their colonization potential to a two-dimensional space that

133   cannot be divorced from concurrent changes in the Hutchinsonian niche.

134

135   The long evolutionary history of macroalgae and the multiple origins of macroalgal lineages

136   (Larkum & Vesk 2003) contribute to the ecophysiological versatility, genetic diversity, and

137   latitudinal ubiquity of this group, despite their limited dispersal ability. Patterns of macroalgal

138   diversity within range limits is an area with well-developed theory, but mixed observational

139   evidence. Overall, population sizes and individual fitness metrics decrease as environmental

140   conditions stray from species' optima near range edges (Zardi et al. 2015), consistent with

141   ecological and evolutionary theory (Castro et al. 2004, Hampe 2005, Viejo et al. 2010).

142   However, theory predicts a decline in genetic diversity among populations near range limits,

143   with local marginal populations acting as sink populations (Watkinson and Sutherland 1995).

144   Evidence from macroalgal studies is mixed (Zardi et al. 2015, Assis et al. 2013, Neiva et al.

145   2012, Krueger-Hadfield et al. 2013b), and populations reveal varying degrees of local adaptation

146   and ecotypic variation in response to environmental conditions (Breeman 1988, Pearson et al.

147   2009, Kolzenburg et al. 2019). Gene flow among macroalgal populations will become

148   increasingly disrupted in the face of increasing population fragmentation caused by pollution,

149   habitat modification, climate change, algal harvesting, trophic cascades, and other anthropogenic

150   stressors. Thus, it is important to consider patterns of population structure together with the rate

151   of external forcing as we draw conclusions about algal population genetic processes.

152

153   **Life cycle complexity**

154   The diversity of life cycles found across the macroalgae can be bewildering to the novice and

155   expert alike. Macroalgae can have diplontic (free-living diploid stage; e.g., *Fucus* or *Caulerpa*),

156   haplontic (free-living haploid stages; e.g., *Chara*), or haplodiplontic life cycles (free-living

157   haploid *and* diploid stages; e.g., *Dictyota, Ulva, Gracilaria*). The myriad of variations played

158   upon these three simplified life cycle types across the lineages of macroalgae is truly remarkable

159   (Bell 1994), but can complicate species delimitation when the natural history of the life cycle is

160   unknown. For example, while our understanding of the genetic advantages of diploidy and

161   haploidy are better understood (e.g., Valero et al.1992, Otto and Gerstein 2008), the only way

162   haplodiplontic life cycles can be evolutionarily stable states is when the haploid and diploid

163   stages in the life cycle occupy different niches (Hughes and Otto 1999; see reviews by Thornber

164   2006, Krueger-Hadfield 2020).

165

166   Species delimitation in taxa with biphasic life cycles, in which both the haploid and diploid

167   stages undergo substantial development and are free-living, could be more robust when using

168   both ploidy stages (but see below about coupling this information with mating systems under

169   *Mating system and reproductive mode considerations*). Indeed, for some taxa, heteromorphic

170   haploid gametophytes and diploid tetrasporophytes were classed in different genera before

171   laboratory based culture studies (e.g., *Gigartina* and *Petrocelis* that are now part of the reinstated

172   red algal genus *Mastocarpus*, Guiry et al. 1984). Yet, more recent work on the taxonomy of

173   *Mastocarpus* spp. in the Pacific has not included both life cycle stages, despite the necessary

174   alternation of genetics that is characteristic of the genus *Mastocarpus* (see Lindstrom 2008,

175   Lindstrom et al. 2001, and discussions by Dudgeon et al. 2017). Nevertheless, haplodiplontic

176   species experience evolutionary and ecological constraints because each ploidy stage is linked to

177   the other. Impacts on one stage may cascade through the species' entire life cycle (Thornber

178   2006, Krueger-Hadfield and Hoban 2016, Krueger-Hadfield 2020). As some species descriptions

179   rely on the heteromorphic or isomorphic alternation of generations, it is critical to assess patterns

180   of gene flow within these life cycles and include both ploidy stages in the gathering of evidence

181   about species delimitation. Understanding these patterns is a necessary component to forecasting

182   how species with complex life cycles will respond to climate change, though macroalgal life

183   cycles are often not included in these assessments (e.g., Pandori and Sorte 2019).

184

185   **Mating system and reproductive mode considerations**

186   Mating systems exert control over the very lines of evidence we gather to delimit species as they

187   partition the amount of genetic diversity within populations and the amount of genetic

188   differentiation among populations (Hamrick and Godt 1996), thus determining population

189   structure (Tibayrenc and Ayala 1991). Outcrossed mating systems typically result in genetically

190   diverse populations with higher potential for adaptation, while inbreeding (and self-fertilization,

191   its most extreme form) results in reductions in genetic diversity and effective population sizes,

192   potentially reducing adaptive potential (but see Pujol et al. 2009, as selfing can become

193   adaptive). Similarly, clonal (or asexual) populations, in which no recombination or fertilization

194   occurs, incur the same genetic consequences as inbred populations (Halkett et al. 2005). Mating

195   systems not only control, but are in turn controlled by standing genetic variability (e.g.,

196   inbreeding reduces genetic variation, reducing mating system variation, and reinforcing

197   inbreeding; Richards 1989), thereby shaping evolutionary trajectories by modulating the relative

198   importance of drift, migration, selection, and mutation.

199

200   The algal haplodiplontic life cycle has two critical implications that influence mating system for

201   species delimitation. The life history traits that affect mating systems are evolutionarily labile

202   and likely vary tremendously within and between macroalgal taxa, but data are woefully

203   inadequate, such as basic patterns of the relative rates of outcrossing versus inbreeding and

204   sexual versus asexual reproduction (Valero et al. 2001, Krueger-Hadfield 2020). First, in general,

205   dioecy, or separate sexes, is often used a proxy for outcrossing in higher plants and animals

206   (Krueger-Hadfield et al. 2015), but in haploid-diploid species, separate sexes do not prevent

207   cross-fertilization between male and female haploids that share the same diploid parent

208   (Klekowski 1969). Inbreeding results in smaller effective population sizes with lower genetic

209   diversity and reduced effective recombination, affecting species delimitation (Naciri & Linder

210   2015). While Olsen et al. (2020) recently included macroalgae in an assessment of inbreeding

211   rates in the sea, the distribution of taxa for which we have robust estimates of inbreeding, and

212   specifically using progeny arrays or paternity analyses is woefully inadequate (see also Krueger-

213   Hadfield 2020).

214

215   Second, many macroalgae are partially clonal, a reproductive system in which both clonal and

216   sexual (selfing, inbreeding, and/or outcrossing) reproduction occur (see Sosa et al. 1998, Valero

217   et al. 2001, van der Strate et al. 2002, Guillemin et al. 2008, Krueger-Hadfield et al. 2016, Pardo

218   et al. 2019). The balance between these two reproductive modes strongly influences the

219   ecological success of a species (Halkett et al. 2005, Silvertown 2008) and the ability to track

220   environmental change via phenotypic evolution (Orive et al. 2017). Yet, when asexual

221   reproduction occurs, one of the ploidy stages may be lost (Krueger-Hadfield et al. 2013a, 2016,

222   Dudgeon et al. 2017). Which ploidy stage is lost has important implications for the recovery of

223   the sexual life cycle (see Guillemin et al. 2008, Krueger-Hadfield et al. 2016) and for dispersal

224   potential (see Fierst et al. 2010, Krueger-Hadfield et al. 2013a, Dudgeon et al. 2017). As a

225   consequence, asexuality can facilitate range expansions resulting in different geographic patterns

226   and founder events that can complicate delimitation, particularly when the life cycle is not well

227   characterized (see, as examples, the patterns of geographic parthenogenesis in the red algal genus

228   *Mastocarpus* [Dudgeon et al. 2017] or the geographic separation between haploid and diploid

229   stages in ferns [Nitta et al. 2017]). The impacts of life cycle variation on haplodiplontic

230   systematics are largely unknown, but we need to expand our knowledge of the ecophysiology of

231   different life cycle stages (Krueger-Hadfield 2020).

232

233   In ferns and lycophytes, eukaryotes with similar life cycle complexity as found in macroalgae, it

234   has been estimated that 10% of species do not reproduce sexually (Walker 1984). If an asexual

235   lineage is clearly distinct (often morphologically), then Gastony and Windham (1989) proposed

236   a 'genetic' species concept that is similar to the concept used for sexually reproducing

237   metapopulation (though it is important to note that models for eukaryotes as sexually

238   reproducing metapopulations is meaningless for asexual taxa, *sensu* Billiard et al. 2012).

239   However, for taxa in which the asexual lineage (which are often triploid) are indistinguishable

240   from their diploid progenitor, Gastony and Windham (1989) proposed to use the term variety.

241   Similarly, there are a whole host of terms employed by other vascular plant taxonomists that

242   could greatly facilitate how phycologists think about species delimitation (Grant 1981).

243

244   Bearing these differences between sexual (i.e., both inbreeding and outcrossing) and clonal

245   reproduction and their eco-evolutionary consequence in mind, species-level phylogenetic

246   analyses will require different evolutionary assumptions than those that are appropriate at

247   taxonomic levels of families and above. For example, phylogenetic studies often assume mating

248   systems have a negligible effect on genetic variation within and among species (Naciri & Linder

249   2015). However, mating systems exert strong influence on patterns of group variability. As a

250   result, evolutionary changes in mating systems are often associated with the development of

251   reproductive isolation and, subsequently, speciation. The frequency of selfing or asexuality can

252   further blur genetic breaks. Dandelions, for example, display taxonomic complexity driven in

253   part by strict asexuality bringing about complete reproductive isolation (Richards 1989).

254   Asexuals confound species delimitation through (i) sequence divergence, (ii) ploidy differences,

255   (iii) linkage of nuclear and organellar genes, (iv) lack of admixture, and (v) differences in

256   generation times between sexual and asexual lineages (Dudgeon et al. 2017). When partially

257   clonal taxa do undergo sexual reproduction, such as in the case of range expansions, they may

258   undergo selfing and/or inbreeding, further generating divergence among populations. Thus, for

259   organisms where detailed mating system data are lacking, species delimitation may be

260   confounded by viable alternative hypotheses when sexual and asexual life cycle variants are

261   analyzed together and treated methodologically as sexual (Dudgeon et al. 2017). Different

262   phylogenetic reconstructions may be retrieved depending on which specimens or loci are

263   sampled, especially among recently diverging species (Naciri & Linder 2015).

264

265   **A need for phylogenetic networks**

266   As previously discussed, botanical taxonomy developed from breeding studies in common

267   gardens. While there was a period in phycology during which these sorts of experiments were

268   undertaken to understand mating system variation through culturing experiments (e.g., Guiry et

269   al. 1984, Maggs 1988), the molecular revolution has sped up phylogenetic methodologies that

270   have far outstripped our basic natural history knowledge of macroalgal taxa. Nevertheless,

271   macroalgae exhibit tangled taxonomic characters, whereby characters may evolve independently

272   multiple times (e.g., holdfasts, bladders) or be gained then lost within a lineage, such as the

273   crustose morphology of *Crusticorallina* spp. (Hind et al. 2016). Molecular taxonomy may

274   alleviate the pressure to prioritize morphological characters, yet introduces complications of its

275   own. Hybridization is common across macroalgae (e.g., Coyer et al. 2002, 2011, Martins et al.

276   2019), a situation that is not easily represented in a phylogenetic context. Allopolyploidy, the

277   merger of two different species' genomes, has also been documented in macroalgal evolution

278   (e.g., Neiva et al. 2017, Sousa et al. 2019). Thus, we borrow some inferences from the plant

279   speciation literature, where interspecific hybridization has become recognized as an important

280   creative force in plant evolution - including in the evolutionary history of species which today

281 exhibit strong reproductive isolation (Cronn et al. 2004, Grant 1981). Hybridization may allow

282 the introgression of genes or variation that are later selected on to form true species (e.g., Fig.

283 2c), possibly leading to an acceleration of speciation due adaptive divergence and cementation of

284 barriers to gene flow during secondary contact, or alternatively impeding speciation altogether

285 (Abbott et al. 2013). Given how common this process seems to be in macroalgal evolution, the

286 ensuing reticulate phylogenies of many species thus require a phylogenetic network model,

287 rather than dichotomously branching trees (Grant 1981).

288

289 An open question remains about hybrid fitness in macroalgae, and the degree to which limited

290 gene exchange may occur between species. Evidence from a variety *Fucus* hybrids is mixed

291 (e.g., Billard et al. 2005, Coyer et al. 2002, 2007, 2011), while hybrid vigor has been

292 documented in *Laminaria* hybrids (Martins et al. 2019). Hybrids are certainly a common feature

293 of macroalgal communities, however their stability over time is not well understood. In part, this

294 is because evidence for past hybridization can be conflated with persistence of ancestral

295 polymorphisms ('gene trees' divergent from phylogenetic tress). When alleles are shared

296 between taxa in sympatry but not in allopatry, hybridization is ongoing (*sensu* Whittemore and

297 Schaal 1991).

298

299 Along with hybrid speciation, incomplete lineage sorting, wherein an ancestor confers some, but

300 not all unique traits to one evolutionary lineage and a different set of unique traits to another

301 lineage, leaves behind a confusing phylogenetic signature (Maddison 1997). Both hybridization

302   and incomplete lineage sorting are likely to occur among closely related species and populations

303   with incomplete reproductive isolation.

304

305   A genealogical species has been defined as "a basal, exclusive group of organisms, whose

306   members are all more closely related to each another than they are to any organisms outside the

307   group, and that contains no exclusive groups within it" (Shaw 1998). Exclusivity is further

308   specified as whether the genetic loci of organisms within the group have coalesced most recently

309   only with other organisms within the group (Baum and Shaw 1995), which has been applied as

310   showing reciprocal monophyly with respect to another genealogical species. This criterion

311   ignores situations of incomplete lineage sorting or genetic variability within an ancestral species.

312   Every allele sampled for analysis may be identical within a genetic species, with each allele

313   descended from a shared common ancestor within the group. Importantly, this does not imply

314   that all of these alleles originated from the same original ancestor, and alleles for different loci

315   may have descended from different individuals within the group (Hudson & Coyne 2002).

316   Further, newly speciated groups descendant from one portion of another species – for example,

317   resulting from island invasion or isolation of marginal populations – may lead to individuals

318   from the original population/species being more closely related to the new species than to

319   individuals within their own group, violating the exclusivity clause (Hudson & Coyne 2002).

320

321   Phylogenies are typically built using multiple genes, either as a consensus gene tree of

322   phylogenies built using each gene, or as a concatenated sequences tree, which uses a combined

323   'super-gene' alignment of concatenated gene sequences. While most multigene studies employ

324   concatenated sequences to build phylogenies, due to the increased effective sample size of this

325   technique, consensus gene trees account for differences in evolutionary rates or stochastic

326   differences in single gene polymorphisms, for example caused by incomplete lineage sorting

327   (reviewed in Gadagkar et al. 2005). As described above, the most recent common ancestor of

328   sampled individuals may fall within another species, when studying recently diverged groups. In

329   such cases, historical signals of species relationships are likely to be overwhelmed by stochastic

330   genetic processes if gene trees and species trees are assumed to be synonymous, leading to an

331   overestimation of speciation (Carstens & Knowles 2007). Further, varying degrees in a species'

332   ability or propensity to self-fertilize or to reproduce clonally will affect the distribution of these

333   stochastic differences between related lineages (see previous section).

334

335   **A species conceptual framework for macroalgae**

336   The only 'necessary property of species' is treating an entity as a separately evolving

337   metapopulation lineage (De Queiroz 2007). The unified concept of species advocated by De

338   Queiroz (2007) separates the issues of conceptualization and delimitation of species, whereby the

339   properties advocated by competing species concepts (see Table 1) are no longer at odds with one

340   another, but instead are used as evidence of lineage separation. More lines of evidence will

341   provide more corroboration of a given lineage. Most importantly, however, De Quieroz (2007)

342   states that the 'unified species concept shifts the emphasis away from traditional species criteria,

343   encouraging biologists to develop new methods of species delimitation that are not tied to those

344   properties' (e.g., reproductive isolation or monophyly). Our aim in this perspective is to build on

345   the existing methods used by phycologists, but shift our interpretation to one of a species

346   concept, followed by the interpretation of species delimitation in explicit evolutionary

347   frameworks.

348

349   As with all other taxa, macroalgal species are separately evolving metapopulation lineages. In

350   order to begin to build evidence for delimiting algal species, we discuss the utilization of the

351   following lines of evidence often used by phycologists. Phylogenetic species concepts comprise

352   the most appropriate starting point for the development of a macroalgal species conceptual

353   framework, as current taxonomic methods in phycology are based on molecular phylogenies

354   derived from the consensus of gene trees. We advocate for also using the properties outlined in

355   the traditional biological species concept in concert with molecular phylogenies, currently that

356   most often employed in phycology, as this will explicitly incorporate mating systems into species

357   delimitation. In Table 1 and in the text below, we outline existing species concepts, translating

358   them rather into lines of evidence for delimitation, that partially explain our understanding of

359   macroalgal speciation, and finally propose a species conceptual framework for macroalgae.

360

361   Multiple phylogenetic species concepts have been formally proposed in the literature, reflecting

362   the difficulty of fitting a continuum of relatedness into discrete categories (Coates et al. 2018).

363   Differences among phylogenetic approaches to species delineation involve (1) a specification of

364   paternal descent (sexual reproduction), (2) monophyly of a the most exclusive group, or (3)

365   greater relatedness of all group members to one another (Table 1; Cracraft 1989, de Queiroz and

366   Donoghue 1988, Baum and Donoghue 1995, Shaw 1998). Hudson and Coyne (2002) have

367   suggested that a proportion of reciprocally monophyletic loci must be specified as a metric for

368   consideration of a group as a species. Quantification of these definitions is appealing and

369   arguably necessary. Yet, such a definition blurs the biological significance of genealogical

370   speciation. By this definition (3) above, speciation could be transitory, allowing for

371   hybridization with sister taxa to create definable species. Simulations using a criterion of at least

372   50% monophyly and restricted to drift alone can reach speciation in under 200 generations for

373   small populations (Hudson & Coyne 2002), simultaneously making the role for selection unclear

374   and likelihood of local adaptation high, given the biogeography and natural history of

375   macroalgae.

376

377   Based on the robust field of speciation within ecology and evolutionary biology, it is critical to

378   maintain biological meaning in our definition of a macroalgal species. Thus, we must take in to

379   account niche partitioning among closely related species. The ecological species concept

380   essentially provides a stipulation that selection must have an axis on which to act during the

381   speciation process. We, thus, propose a macroalgal species conceptual framework that provisions

382   for inclusion of hybridization, life cycle complexity, and mating system variation where there

383   exists trait differentiation by combining critical aspects of the phylogenetic, biological, and

384   ecological species concepts, building on what Simpson (1961) called an evolutionary species. An

385   evolutionary species 'embraces a greater diversity of [mating] systems, and is consequently more

386   general' (Grant 1981). An evolutionary species is a population system which possesses the

387   following characteristics: (i) it is a lineage, in other words there is a sequence of ancestor-

388   descendant relationships among populations that exist in space and time, (ii) the lineage evolves

389   separately from other lineages (i.e., other species), (iii) it fits into its own ecological niche, and

390 (iv) it can change its evolutionary role over the course of its history (Simpson 1961). Importantly

391 for hybridization under the evolutionary species concept, the question becomes whether the two

392 species that hybridize lose their distinct eco-evolutionary roles. If they do not merge, then they

393 remain distinct species. Combining these elements, we define a **macroalgal species as a lineage**

394 **that evolves separately from other lineages (i.e., a basal group), and evidence supporting**

395 **these lineages can comprise but is not limited to the occupation of a distinct adaptive zone**

396 **(or zones for haplodiplontic taxa), monophyly, or reproductive isolation.** We encourage our

397 fellow phycologists to begin to think more outside the box for reconciling species

398 conceptualization and delimitation, especially for the latter in order to discover new, biologically

399 relevant methods with which to define macroalgal lineages.

400

401 Acknowledgements

405

406 References

407 Abbott, R., Albach, D., Ansell, S., Arntzen, J.W., Baird, S.J., Bierne, N., Boughman, J.,

408   Brelsford, A., Buerkle, C.A., Buggs, R. & Butlin, R.K. 2013. Hybridization and

409   speciation. *Journal of Evolutionary Biology*, 26(2), 229-246.

410 Arnaud-Haond, S., Duarte, C.M., Alberto, F. & Serrao, E.A. 2007. Standardizing methods to

411   address clonality in population studies. *Molecular ecology*, 16(24), 5115-5139.

412   Assis, J., N. Castilho Coelho, F. Alberto, M. Valero, P. Raimondi, D. Reed, & E. Alvares Serrao.

413   2013. High and distinct range-edge genetic diversity despite local bottlenecks. PLoS ONE 8:

414   e68646.

415   Balloux, F., Lehmann, L., & de Meeûs, T. 2003. The population genetics of clonal and partially

416   clonal diploids. *Genetics*, 164(4), 1635-1644.

417   Bartsch, I., Wiencke, C., & Laepple, T. 2012. Global seaweed biogeography under a changing

418   climate: the prospected effects of temperature. In *Seaweed biology* (pp. 383-406). Springer,

419   Berlin, Heidelberg.

420   Baum, D. A., & Donoghue, M. J. 1995. Choosing among alternative "phylogenetic" species

421   concepts. *Systematic Botany*, 560-573.

422   Baum, D., & K. L. Shaw. 1995. Genealogical perspectives on the species problem. Pp. 289–303

423   *in* P. C. Hoch and A. C. Stephenson, eds. Experimental and molecular approaches to plant

424   biosystematics. Missouri Botanical Garden, St. Louis, MO.

425   Bell, G. 1994. The comparative biology of the alternation of generations. In M.

426   Kirpatrick (Ed.), *Lectures on mathematics in life sciences: The evolution of haplo-diploid life*

427   *cycles* (pp. 1– 26). Providence, Rhode Island: American Mathematical Society.

428   Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Ingram, K.K. and Das,

429   I. 2007. Cryptic species as a window on diversity and conservation. *Trends in Ecology &*

430   *Evolution*, ø3), 148-155.

431   Billiard, S., López-villavicencio, M. Hood, M.E. & Giraud, T. 2012. Sex, outcrossing and

432   mating types: unsolved questions in fungi and beyond. *Journal of Evolutionary Biology*.

433   25:1020–38.

434   Billard, E., Serrão, E. A., Pearson, G. A., Engel, C. R., Destombe, C., & Valero, M. 2005.

435   Analysis of sexual phenotype and prezygotic fertility in natural populations of Fucus spiralis,

436   F. vesiculosus (Fucaceae, Phaeophyceae) and their putative hybrids. *European Journal of*

437   *Phycology*, 40(4), 397-407.

438   Bird, C. J., Sosa, P. A., & MacKay, R. M. 1994. Molecular evidence confirms the relationship of

439   *Petrocelis* in the western Atlantic to *Mastocarpus stellatus* (Rhodophyta,

440   Petrocelidaceae). *Phycologia*, 33(2), 134-137.

441   Bortolus, A. 2008. Error cascades in the biological sciences: the unwanted consequences of using

442   bad taxonomy in ecology. *AMBIO: A Journal of the Human Environment*, 37(2), 114-119.

443   Breeman, A.M. 1988. Relative importanve of temperature and other factors in determining

444   geographic boundaries of seaweeds: experimental and phenological evidence. *Helgolanderf*

445   *Meeresuntersuchungen* 42, 199-241.

446   Brennan, G., Kregting, L., Beatty, G. E., Cole, C., Elsäßer, B., Savidge, G., & Provan, J. 2014.

447   Understanding macroalgal dispersal in a complex hydrodynamic environment: a combined

448   population genetic and physical modelling approach. *Journal of the Royal Society*

449   *Interface*, *11*(95), 20140197.

450   Bringloe, T. T., & Saunders, G. W. 2018. Mitochondrial DNA sequence data reveal the origins

451   of postglacial marine macroalgal flora in the Northwest Atlantic. *Marine Ecology Progress*

452   *Series*, *589*, 45-58.

453   Buchanan, J., & Zuccarello, G. C. 2012. Decoupling of short-and long-distance dispersal

454   pathways in the endemic new zealand seaweed carpophyllum maschalocarpum

455   (Phaeophyceae, Fucales). *Journal of Phycology*, 48(3), 518-529.

456   Carstens, B. C., & Knowles, L. L. 2007. Estimating species phylogeny from gene-tree

457   probabilities despite incomplete lineage sorting: an example from *Melanoplus*

458   grasshoppers. *Systematic Biology*, 56(3), 400-411.

459   Castro, J., R. Zamora, J. A. Hódar, & J. M. Gómez. 2004. Seedling establishment of a boreal tree

460   species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a

461   marginal Mediterranean habitat. *Journal of Ecology,* 92, 266 – 277.

462   Coates, D.J., Byrne, M. & Moritz, C. 2018. Genetic diversity and conservation units: dealing

463   with the species-population continuum in the age of genomics. *Frontiers in Ecology and*

464   *Evolution*, 6, 165.

465   Coyer, J. A., G. Hoarau, J. F. Costa, B. Hogerdijk, E. A. Serrão, E. Billard, Myriam Valero, G.

466   A. Pearson, & J. L. Olsen. 2011. Evolution and diversification within the intertidal brown

467   macroalgae *Fucus spiralis/F. vesiculosus* species complex in the North Atlantic. *Molecular*

468   *Phylogenetics and Evolution*, 58(2), 283-296.

469   Coyer, J. A., Hoarau, G., Stam, W. T., & Olsen, J. L. 2007. Hybridization and introgression in a

470   mixed population of the intertidal seaweeds *Fucus evanescens* and *F. serratus*. *Journal of*

471   *Evolutionary Biology*, 20(6), 2322-2333.

472   Coyer, J. A., Peters, A. F., Hoarau, G., Stam, W. T., & Olsen, J. L. 2002. Hybridization of the

473   marine seaweeds, *Fucus serratus* and *Fucus evanescens* (Heterokontophyta: Phaeophyceae)

474   in a 100-year-old zone of secondary contact. *Proceedings of the Royal Society of London.*

475   *Series B: Biological Sciences*, 269(1502), 1829-1834.

476   Coyne, JA, and HA Orr. *Speciation*. Sinauer Associates Inc., Massachusetts, USA; 2004. 545 pp.

477   Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species

478   concepts for understanding patterns and processes of differentiation. *Speciation and its*

479   *Consequences*, 28, 59.

480   Cronn, R., & Wendel, J. F. 2004. Cryptic trysts, genomic mergers, and plant speciation. *New*

481   *Phytologist*, 161(1), 133-142.

482   De Jode, A., David, R., Haguenauer, A., Cahill, A.E., Erga, Z., Guillemain, D., Sartoretto, S.,

483   Rocher, C., Selva, M., Le Gall, L. & Feral, J.P. 2019. From seascape ecology to population

484   genomics and back. Spatial and ecological differentiation among cryptic species of the red

485   algae Lithophyllum stictiforme/L. cabiochiae, main bioconstructors of coralligenous

486   habitats. *Molecular Phylogenetics and Evolution*, 137: 104-113.

487   de Meeûs, T., Prugnolle, F. & Agnew, P. 2007. Asexual reproduction: Genetics and evolutionary

488   aspects. *Cell. Mol. Life Sci.* 64:1355–72.

489   De Queiroz, K., & Donoghue, M. J. 1988. Phylogenetic systematics and the species

490   problem. *Cladistics*, 4(4), 317-338.

491   De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic biology*, *56*(6), 879-

492   886.

493   Dring, M. J. 1988. Photocontrol of development in algae. *Annual Review of Plant Physiology*

494   *and Plant Molecular Biology*, 39(1), 157-174.

495   Dudgeon, S., Kübler, J. E., West, J. A., Kamiya, M., & Krueger-Hadfield, S. A. 2017. Asexuality

496   and the cryptic species problem. *Perspectives in Phycology*, 4, 47-59.

497   Fierst, J. L., Kübler, J. E., & Dudgeon, S. R. 2010. Spatial distribution and reproductive

498   phenology of sexual and asexual *Mastocarpus papillatus* (Rhodophyta). *Phycologia*, *49*(3),

499   274-282.

500   Fraser, C.I., Hay, C.H., Spencer, H.G., & Waters, J.M. 2009. Genetic and morphological

501   analyses of the southern bull kelp *Durvillaea antarctica* (Phaeophyceae: Durvillaeales) in

502   New Zealand reveal cryptic species. *J. Phycol*. 45, 436-443.

503   Gabrielson, P. W., Hughey, J. R., & Diaz-Pulido, G. 2018. Genomics reveals abundant

504   speciation in the coral reef building alga *Porolithon onkodes* (Corallinales,

505   Rhodophyta). *Journal of phycology*, *54*(4), 429-434.

506   Gadagkar, S. R., Rosenberg, M. S., & Kumar, S. 2005. Inferring species phylogenies from

507   multiple genes: concatenated sequence tree versus consensus gene tree. *Journal of

508   Experimental Zoology Part B: Molecular and Developmental Evolution*, 304(1), 64-74.

509   Gastony, G.J. & Windham, M.D. 1989. Species concepts in pteridophytes: the treatment and

510   definition of agamosporous species. *American Fern Journal,* 79: 65-77.

511   Gaylord, B., Reed, D.C., Washburn, L. & Raimondi, P.T. 2004. Physical–biological coupling in

512   spore dispersal of kelp forest macroalgae. *Journal of Marine Systems*, 49(1-4), 19-39.

513   Geoffroy, A., Mauger, S., De Jode, A., Le Gall, L., & Destombe, C. (2015). Molecular evidence

514   for the coexistence of two sibling species in *Pylaiella littoralis* (Ectocarpales, Phaeophyceae)

515   along the Brittany coast. *Journal of phycology*, *51*(3), 480-489.

516   Grant, V. 1981. Plant Speciation. 2nd ed. Columbia University Press: New York. 563 pp.

517   Guillemin, M.-L., Faugeron, S., Destombe, C., Viard, F., Correa, J.A. & Valero, M. 2008.

518   Genetic variation in wild and cultivated populations of the haploid– diploid red alga

519   *Gracilaria chilensis*: how farming practices favor asexual reproduction and heterozygosity.

520   *Evolution*. 62:1500–19.

521   Guiry, M.D., West, J.A. & Masuda, M. 1984. Reinstatement of the geneus Mastocarpus

522   Kuetzing (Rhodophyta). *Taxon*. 33, 53–63.

523   Halkett, F., Simon, J. & Balloux, F. 2005. Tackling the population genetics of clonal and

524   partially clonal organisms. *Trends in Ecology & Evolution*. 20, 194–201.

525   Hampe, A. 2005. Fecundity limits in *Frangula alnus* (Rhamnaceae) relict populations at the

526   species' southern range margin. *Oecologia* 143, 377–386.

527   Hamrick, J.L. & Godt, M.J.W. 1996. Effects of Life History Traits on Genetic Diversity in Plant

528   Species. *Philosophical Transactions: Biological Sciences*. 351, 1291–8.

529   Hind, K. R., Gabrielson, P. W., P. Jensen, C., & Martone, P. T. 2016. Crusticorallina gen. nov., a

530   nongeniculate genus in the subfamily Corallinoideae (Corallinales, Rhodophyta). *Journal of

531   Phycology*, 52(6), 929-941.

532   Hollingsworth, P. M. 2003. Taxonomic complexity, population genetics, and plant conservation

533   in Scotland. *Botanical Journal of Scotland*, *55*(1), 55-63.

534   Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and

535   evolutionary perspectives. *Proceedings of the National Academy of Sciences*, *106*

536   (Supplement 2), 19659-19665.

537   Hörandl, E., Greilhuber, J., Klímová, K., Paun, O., Temsch, E., Emadzade, K., & Hodálová, I.

538   2009. Reticulate evolution and taxonomic concepts in the *Ranunculus auricomus* complex

539   (Ranunculaceae): insights from analysis of morphological, karyological and molecular

540   data. *Taxon*, *58*(4), 1194-1216.

541   Hudson, R. R., & Coyne, J. A. 2002. Mathematical consequences of the genealogical species

542   concept. *Evolution*, 56(8), 1557-1565.

543   Hughes, J.S. & Otto, S.P. 1999. Ecology and the Evolution of Biphasic Life Cycles. *The*

544   *American Naturalist*. 154, 306–20.

545   Hughey, J. R., Maggs, C. A., Mineur, F., Jarvis, C., Miller, K. A., Shabaka, S. H., & Gabrielson,

546   P. W. 2019. Genetic analysis of the Linnaean *Ulva lactuca* (Ulvales, Chlorophyta) holotype

547   and related type specimens reveals name misapplications, unexpected origins, and new

548   synonymies. *Journal of phycology*, *55*(3), 503-508.

549   Hutchins, L.W., 1947. The bases for temperature zonation in geographical distribution.

550   Ecological Monographs17(3), pp.325-335.

551   Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symp* 22:415–427.

552   Kimura, M. & Weiss, G.H. 1964 The stepping-stone model of population structure and the

553   decrease of genetics correlation with distance. *Genetics* 49, 561 – 576.

554   Klekowski Jr., E. J. 1969. Reproductive biology of the Pteridophyta. II. Theoretical

555   considerations. *Botanical Journal of the Linnean Society*, 62(3), 347-359.

556   Kolzenburg, R., Nicastro, K. R., McCoy, S. J., Ford, A. T., Zardi, G. I., & Ragazzola, F. 2019.

557   Understanding the margin squeeze: Differentiation in fitness-related traits between central and

558   trailing edge populations of *Corallina officinalis*. *Ecology and Evolution*, 9(10), 5787-5801.

559   Krueger-Hadfield, S. A., & Hoban, S. M. 2016. The importance of effective sampling for

560   exploring the population dynamics of haploid–diploid seaweeds. *Journal of Phycology*, 52(1),

561   1-9.

562   Krueger-Hadfield, S. A., Kübler, J. E., & Dudgeon, S. R. 2013. Reproductive effort of

563   *Mastocarpus papillatus* (Rhodophyta) along the California coast. *Journal of*

564   *Phycology*, 49(2), 271-281.

565   Krueger-Hadfield, S.A., Roze, D., Mauger, S. and Valero, M. 2013b. Intergametophytic selfing

566   and microgeographic genetic structure shape populations of the intertidal red seaweed

567   *Chondrus crispus*. *Molecular Ecology*, 22(12), 3242-3260.

568   Krueger-Hadfield, S. A., Roze, D., Correa, J. A., Destombe, C., & Valero, M. 2015. O father

569   where art thou? Paternity analyses in a natural population of the haploid–diploid seaweed

570   *Chondrus crispus*. *Heredity*, 114(2), 185-194.

571   Krueger-Hadfield, S.A. 2020. What's ploidy got to do with it? Understanding the evolutionary

572   ecology of macroalgal invasions necessitates incorporating life cycle complexity.

573   *Evolutionary Applications*, 13(3), 486-499

574   Krueger-Hadfield, S.A., Kollars, N.M., Byers, J.E., Greig, T.W., Hammann, M., Murray, D.C.,

575   Murren, C.J., Strand, A.E., Terada, R., Weinberger, F. and Sotka, E.E. 2016.

576   Invasion of novel habitats uncouples haplo-diplontic life cycles. *Molecular Ecology*. 25, 3801–

577   16.

578   Larkum, A. W. D. & Vesk, M. in *Photosynthesis in Algae* (eds. Larkum, A. W. D., Douglas, S.

579   E. & Raven, J. A.) 11–28 (Kluwer Academic Publishers, 2003).

580   Le Gall, L., & Saunders, G. W. 2010. DNA barcoding is a powerful tool to uncover algal

581   diversity: A case study of the Phyllophoraceae (Gigartinales, Rhodophyta) in the Canadian

582   flora. *Journal of Phycology*, 46(2), 374-389.

583   Leliaert, F., Vieira, C., Steen, F., De Clerck, O. 2019. Patterns and drivers of seaweed

584   biodiversity: speciation and dispersal of the red algal genus *Portieria* and brown algal order

585   *Dictyotales. European Journal of Phycology* 54 sup1, 37.

586   Lindstrom, S.C. 2008. Cryptic diversity and phylogenetic relationships within the *Mastocarpus*

587   *papillatus* species complex (Rhodophyta, Phyllophoraceae). *J. Phycol.* 44: 1300–1308.

588   Lindstrom, S.C., Hughey, J.R. & Martone, P.T. 2011. New, resurrected and redefined species of

589   *Mastocarpus* (Phyllophoraceae, Rhodophyta) from the northeast Pacific. *Phycologia* 50: 661–

590   683.

591   Lüning, K., 1990. Seaweeds: their environment, biogeography, and ecophysiology. John Wiley

592   & Sons, pp61.

593   Maddison, W. P. 1997. Gene trees in species trees. *Systematic Biology*, 46(3), 523-536.

594   Maggs, C. A. 1988. Intraspecific life history variability in the Florideophycidae (Rhodophyta).

595   *Botanica Marina* 31:465–490.

596   Martins, N., Pearson, G. A., Gouveia, L., Tavares, A. I., Serrão, E. A., & Bartsch, I. 2019.

597   Hybrid vigour for thermal tolerance in hybrids between the allopatric kelps *Laminaria*

598   *digitata* and *L. pallida* (Laminariales, Phaeophyceae) with contrasting thermal

599   affinities. *European Journal of Phycology*, 54(4), 548-561.

600   Mayr, E. 1948. The bearing of the new systematics on genetical problems the nature of species.

601   In *Advances in genetics* (Vol. 2, pp. 205-237). Academic Press.

602   Mayr, E. 1995. Species, classification, and evolution. *Biodiversity and Evolution*, 3, 12.

603   McKenzie, P.F., & Bellgrove, A. 2008 Dispersal of Hormosira banksii (Phaeophyceae) via

604   detached fragments: reproductive viability and longevity. *J. Phycol.* 44, 1108 – 1115.

605   Mieszkowska ,N. & Sugden, H. 2016. Climate-Driven Range Shifts Within Benthic Habitats

606   Across a Marine Biogeographic Transition Zone. *Adv. Ecol. Res.* 55*,* 325-369.

607   Montecinos, A. E., Guillemin, M. L., Couceiro, L., Peters, A. F., Stoeckel, S., & Valero, M.

608   2017. Hybridization between two cryptic filamentous brown seaweeds along the shore:

609   analysing pre-and postzygotic barriers in populations of individuals with varying ploidy

610   levels. *Molecular Ecology*, 26(13), 3497-3512.

611   Naciri, Y., & Linder, H. P. 2015. Species delimitation and relationships: the dance of the seven

612   veils. *Taxon*, 64(1), 3-16.

613   Neiva, J., G.A. Pearson, M. Valero, and E.A. Serrao. 2012. Drifting fronds and drifting alleles:

614   range dynamics, local dispersal and habitat isolation shape the population structure of the

615   estuarine seaweed *Fucus ceranoides*. *Journal of Biogeography,* 39, 1167–1178.

616   Neiva, J., Serrão, E.A., Anderson, L., Raimondi, P.T., Martins, N., Gouveia, L., Paulino, C.,

617   Coelho, N.C., Miller, K.A., Reed, D.C. and Ladah, L.B. 2017. Cryptic diversity, geographical

618   endemism and allopolyploidy in NE Pacific seaweeds. *BMC Evolutionary Biology*, 17(1), 30.

619   Nitta, J. H., Meyer, J. Y., Taputuarai, R., & Davis, C. C. 2017. Life cycle matters: DNA

620   barcoding reveals contrasting community structure between fern sporophytes and

621   gametophytes. *Ecological Monographs*, 87(2), 278-296.

622   Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, 27(3), 293-301.

623   Olsen, K.C., Ryan, W.H., Winn, A.A., Kosman, E.T., Moscoso, J.A., Krueger-Hadfield, S.A.,

624   Burgess, S.C., Carlon, D.B., Grosberg, R.K., Kalisz, S. and Levitan, D.R. 2020. Inbreeding

625   shapes the evolution of marine invertebrates. *Evolution* 74-5: 871–882.

626   Orive, M.E. 1993. Effective population size in organisms with complex life-histories.

627   *Theoretical Population Biology*. 44, 316–40.

628   Orive, M.E., Barfield, M., Fernandez, C. & Holt, R.D. 2017. Effects of Clonal Reproduction on

629   Evolutionary Lag and Evolutionary Rescue. *The American Naturalist*. 190, 469–90.

630   Otto, S.P., & Gerstein, A.C. 2008. The evolution of haploidy and diploidy. *Current Biology,* 18:

631   PR1121-R1124.

632   Pandori, L. L., & Sorte, C. J. 2019. The weakest link: sensitivity to climate extremes across life

633   stages of marine invertebrates. *Oikos*, *128*(5), 621-629.

634   Pante, E., Abdelkrim, J., Viricel, A., Gey, D., France, S. C., Boisselier, M. C., & Samadi, S.

635   2015. Use of RAD sequencing for delimiting species. *Heredity*, 114(5), 450.

636   Pardo, C., Guillemin, M. L., Pena, V., Barbara, I., Valero, M., & Barreiro, R. 2019. Local coastal

637   configuration rather than latitudinal gradient shape clonal diversity and genetic structure of

638   *Phymatolithon calcareum* maerl beds in North European Atlantic. *Frontiers in Marine*

639   *Science*, *6*, 149.

640   Pearson, G. A., Lago-Leston, A., & Mota, C. 2009. Frayed at the edges: selective pressure and

641   adaptive response to abiotic stressors are mismatched in low diversity edge

642   populations. *Journal of Ecology*, 97(3), 450-462.

643   Provan, J., Glendinning, K., Kelly, R., & Maggs, C. A. 2013. Levels and patterns of population

644   genetic diversity in the red seaweed *Chondrus crispus* (Florideophyceae): a direct comparison

645   of single nucleotide polymorphisms and microsatellites. *Biological Journal of the Linnean*

646   *Society*, 108(2), 251-262.

647   Pujol, B., Zhou, S.-R., Vilas, J.S. & Pannell, J.R. 2009. Reduced inbreeding depression after

648   species range expansion. *PNAS*. 106, 15379–83.

649   Reusch, T.B.H., Boström, C., Stam, W.T. & Olsen, J.L. 1999. An ancient eelgrass clone in the

650   Baltic. *Marine Ecology Progress Series*. 183, 301–4.

651   Richards, A.J. 1989. *Plant Breeding Systems*. George Allen & Unwin. 544 pp.

652   Santelices, B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr.*

653   *Mar. Biol. Annual Rev.* 28, 177 – 276.

654   Saunders, G. W. 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal

655   holds promise for future applications. *Philosophical Transactions of the Royal Society B:*

656   *Biological Sciences*, 360(1462), 1879-1888.

657   Shaw, K. L. 1998. Species and the diversity of natural groups. Pp. 44–56 *in* D. J. Howard and S.

658   J. Berlocher, eds. Endless forms: species and speciation. Oxford Univ. Press, Oxford, U.K.

659   Silvertown, J. 2008. The Evolutionary Maintenance of Sexual Reproduction: Evidence from the

660   Ecological Distribution of Asexual Reproduction in Clonal Plants. *Int. J Plant Sci.* 169, 157–

661   68.

662   Simpson, G.G. 1961. Principles of Animal Taxonomy. NY.: Columbia University Press. 247 p.

663   Sosa P.A., Valero M., Batista F. & Gonzalez-Perez M.A. 1998. Genetic variation and genetic

664   structure of natural populations of *Gelidium* species: A re-evaluation of results. *Journal of*

665   *Applied Phycology,* **10:** 279-284.

666   Sousa, F., Neiva, J., Martins, N., Jacinto, R., Anderson, L., Raimondi, P.T., Serrão, E.A. &

667   Pearson, G.A. 2019. Increased evolutionary rates and conserved transcriptional response

668   following allopolyploidization in brown algae. *Evolution*, 73(1), 59-72.

669   Thornber, C. S. 2006. Functional properties of the isomorphic biphasic algal life

670   cycle. *Integrative and Comparative Biology*, 46(5), 605-614.

671   Tibayrenc, M. & Ayala, F.J. 1991. Towards a population genetics of microorganisms: The clonal

672   theory of parasitic protozoa. *Parasitology Today*. 7, 228–32.

673   Valero, M., Engel, C., Billot, C., Kloareg, B., & Destombe, C. 2001. Concept and issues of

674   population genetics in seaweeds. *Cahiers de Biologie Marine*, 42(1/2), 53-62.

675   Valero, M., Richerd, S., Perrot, V. & Destombe, C. 1992. Evolution of alternation of haploid and

676   diploid phases in life cycles. *TREE* 7:25–29.

677   van den Hoek, C. 1982a. Phytogeographic distribution groups of benthic marine algae in the

678   North Atlantic Ocean. A review of experimental evidence from life history studies.

679   *Helgoländer Meeresunterscuchungen,* 35, 153-214.

680   van den Hoek, C. 1982b. The distribution of benthic marine algae in relation to the temperature

681   regulation of their life histories. *Biological journal of the Linnean Society*, 18(2), 81-144.

682   Van der Strate, H. J., Van de Zande, L., Stam, W. T., & Olsen, J. L. 2002. The contribution of

683   haploids, diploids and clones to fine-scale population structure in the seaweed *Cladophoropsis*

684   *membranacea* (Chlorophyta). *Molecular Ecology*, 11(3), 329-345.

685   Van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon*, 233-239.

686   Viejo, R. M., B. Martínez, J. Arrontes, C. Astudillo, & L. Hernández. 2010. Reproductive

687   patterns in central and marginal populations of a large brown seaweed: drastic changes at the

688   southern range limit. *Ecography* 34, 75–84.

689   Walker, T.G. 1984. Chromosomes and their evolution in pteridophytes. Pp. 103-141. In

690   *Chromosomes in Evolution of Eukaryotic Groups*, Vol 2, ed. AK Sharma and A Sharma. Boca

691   Raton, FL: CRC Press.

692   Watkinson, A. R., & Sutherland, W. J. 1995. Sources, sinks and pseudo-sinks. *The Journal of*

693   *Animal Ecology*, 64, 126–130.

694   West, J. A., Polanshek, A. R., & Guiry, M. D. 1977. The life history in culture of *Petrocelis*

695   *cruenta* J. Agardh (Rhodophyta) from Ireland. *British Phycological Journal*, 12(1), 45-53.

696   Whittemore, A. T., & Schaal, B. A. 1991. Interspecific gene flow in sympatric oaks. *Proceedings*

697   *of the National Academy of Sciences*, 88(6), 2540-2544.

698   Zardi, G. I., K. R. Nicastro, E. A. Serrão, R. Jacinto, C. A. Monteiro, & G. A. Pearson. 2015.

699   Closer to the rear edge: Ecology and genetic diversity down the core-edge gradient of a

700   marine macroalga. *Ecosphere* 6, 1-25.

701   Table 1. Species concepts most relevant to macroalgal diversity and speciation. Modified from Coyne and Orr (2004). Note, the

702   macroalgal species conceptual framework provides an evolutionary lens with which to study macroalgae.

Basis of Concept	Name	Definition
Interbreeding	Biological Species Concept	Species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1995).
Evolutionary cohesion	Ecological Species Concept	A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976).
	Evolutionary Species Concept	A species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies (Simpson 1961).

|		
Evolutionary history	Phylogenetic Species Concept 1	A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a paternal pattern of ancestry and descent (Cracraft 1989).
	Phylogenetic Species Concept 2	A species is the smallest [exclusive] monophyletic group of common ancestry (de Queiroz and Donoghue 1988).
	Phylogenetic Species Concept 3	A species is a basal, exclusive group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group, and that contains no exclusive group within it (Baum and Donoghue 1995; Shaw 1998).
Combination	Macroalgal Species Conceptual Framework	A lineage that evolves separately from other lineages (i.e., a basal group) and evidence supporting these lineages can comprise but is not limited to the occupation of a distinct adaptive zone (or zones for haplodiplontic taxa), monophyly, or reproductive isolation.

704   Figure Legends

705   Figure 1. Number of papers returned from a Web of Science search in November 2019. Bars in

706   grey show all papers returned for the base search terms A) "species concept" and B) "cryptic

707   species" in the paper title. In blue, number of papers returned that contained the fragment

708   "alga," and in black, the number of papers returned containing the fragment "phyto" in addition

709   to the base search term. Numbers above bars give the total papers returned containing "alga" and

710   "phyto", respectively. No papers were returned containing the fragment "phyco" in addition to

711   the base search term in either case.

712

713   Figure 2. Consider four groups A, B, C, D; A and B share several morphological characteristics

714   and another set is common to B and C and another set to C and D. Different systems of

715   classification will occur based on what characters are given priority by different researchers,

716   such that one system may yield A) A-B and C-D, and another B) A-C and B-D. In C), consider

717   the possibility that a fifth species, E, may have hybridized with the lineage of group A to

718   generate a lineage that was then selected upon to yield groups B, C, and D.
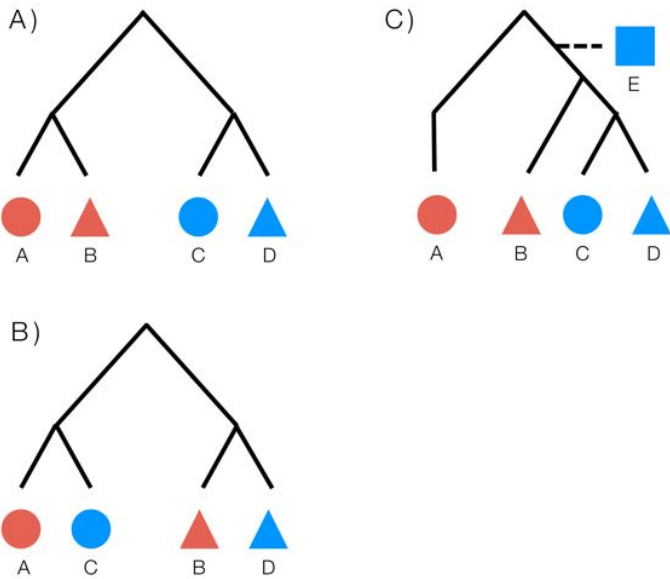
719

720   Figures

721   Figure 1.
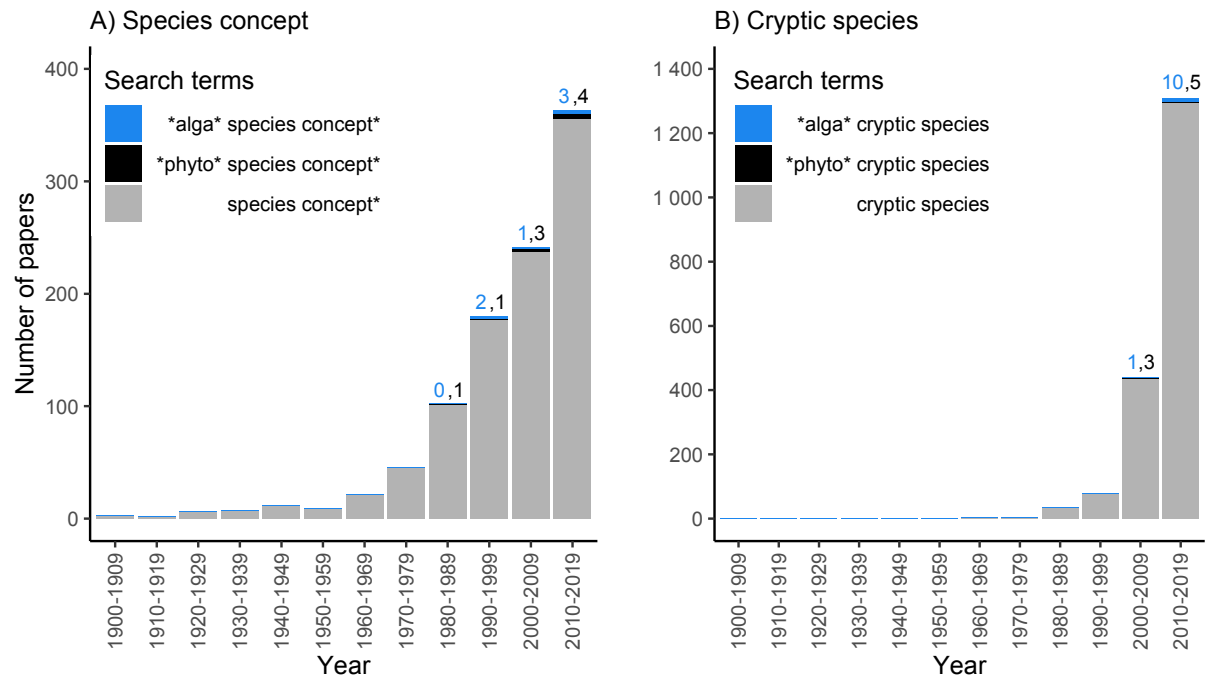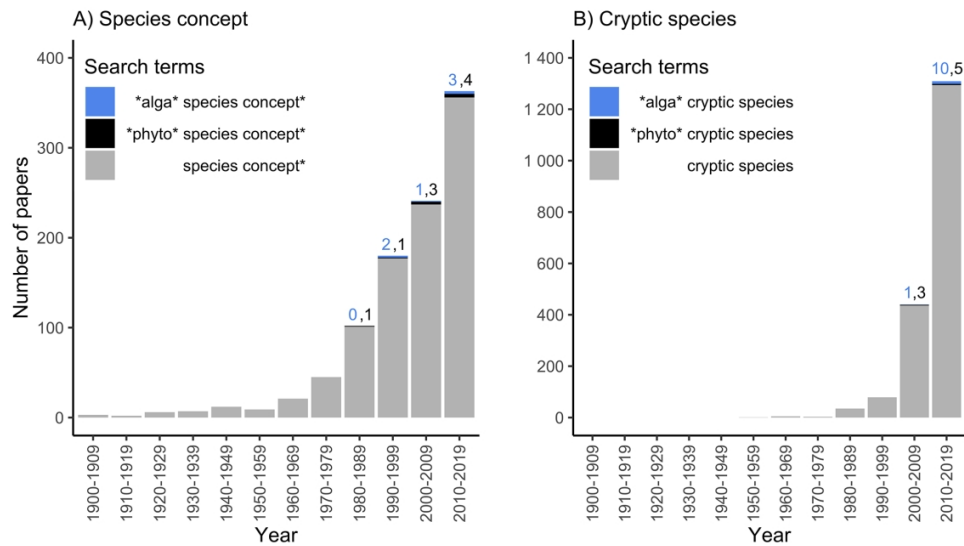

722

723   Figure 2.

724

Figure 1. Number of papers returned from a Web of Science search in November 2019. Bars in grey show all papers returned for the base search terms A) "species concept" and B) "cryptic species" in the paper title. In blue, number of papers returned that contained the fragment "alga," and in black, the number of papers returned containing the fragment "phyto" in addition to the base search term. Numbers above bars give the total papers returned containing "alga" and "phyto", respectively. No papers were returned containing the fragment "phyco" in addition to the base search term in either case.
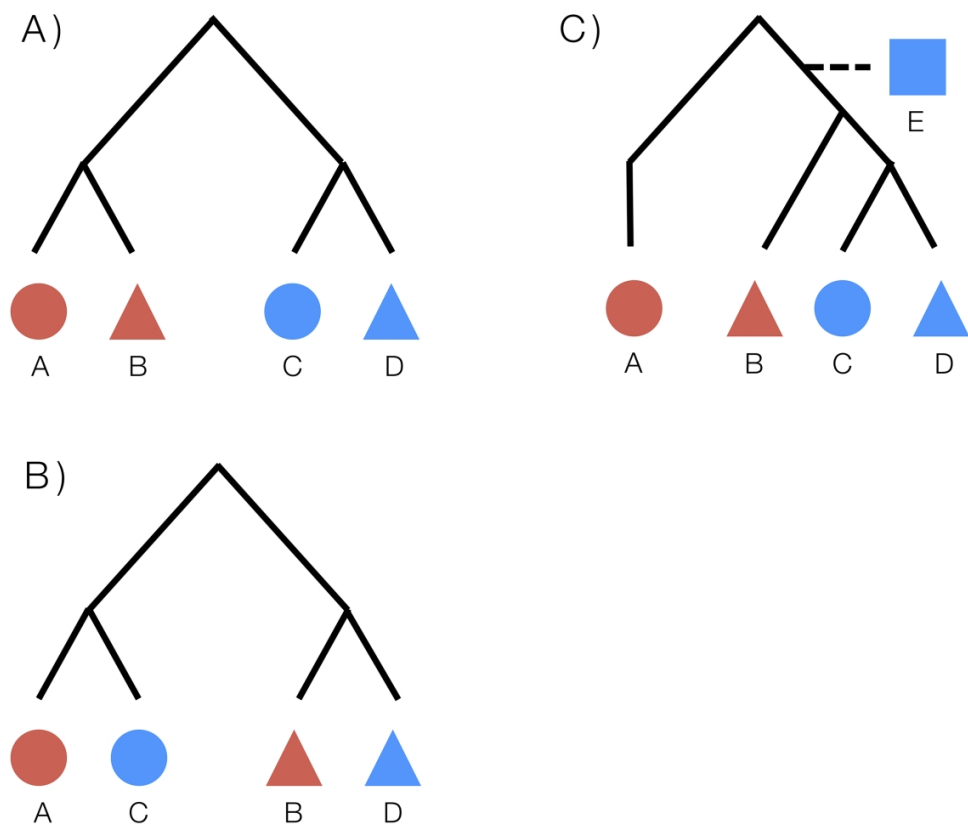
186x106mm (300 x 300 DPI)

Figure 2. Consider four groups A, B, C, D; A and B share several morphological characteristics and another set is common to B and C and another set to C and D. Different systems of classification will occur based on what characters are given priority by different researchers, such that one system may yield A) A-B and C-D, and another B) A-C and B-D. In C), consider the possibility that a fifth species, E, may have hybridized with the lineage of group A to generate a lineage that was then selected upon to yield groups B, C, and D.

219x192mm (300 x 300 DPI)