



Exploring the Influence of Temperature on Aspects of the Reproductive Phenology of Temperate Seaweeds

Thibaut de Bettignies^{1,2*}, Thomas Wernberg^{1*} and C. Frederico D. Gurgel^{3,4,5}

¹ UWA Oceans Institute & School of Biological Sciences, University of Western Australia, Crawley, WA, Australia, ² UMS 2006 Patrimoine Naturel, Muséum National d'Histoire Naturelle, Paris, France, ³ The Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA, Australia, ⁴ Department of Environment, Water and Natural Resources, State Herbarium of South Australia, Adelaide, SA, Australia, ⁵ Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Florianópolis, Brazil

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*Correspondence:

Thibaut de Bettignies
thibaut.de-bettignies@mnhn.fr
Thomas Wernberg
thomas.wernberg@uwa.edu.au

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As plants on land, seaweeds are likely to be susceptible to temperature-mediated changes in phenology such as shifts in their reproductive timing. With this review, we aimed to investigate the importance of temperature on reproductive phenophase transitions (i.e., maturation and release of propagules) of temperate seaweeds while discussing how global warming might affect their reproductive phenology. A systematic literature search returned a total of 81 relevant papers, which were reviewed for evidence of environmental factors (including temperature) driving reproductive phenology. Only a few of studies reported effects of temperature on propagule release (spores and gametes). In contrast, reproductive maturation (both sporogenesis and gametogenesis) was found predominantly to be controlled by temperature. Our findings highlight the potential for phenological shifts in seaweeds in response to ocean warming. In contrast to the consistent advancement of spring events observed for terrestrial plants, there was evidence that warming can both advance and delay the timing of reproductive events for temperate seaweeds, especially the maturation of propagules. Because temperature was often found to act in combination with either day length or spectral composition, ocean warming might result in a mismatch between light and temperature requirements that could lead to reduced reproductive performance.

Keywords: temperate macroalgae, life cycle, phenophase, sporogenesis, gametogenesis, reproduction, warming, herbarium data

INTRODUCTION

Shifts in phenology—the seasonal timing of species' life-cycle events—has been one of the most pervasive biological responses to global warming over the past decades (Walther et al., 2002; Parmesan and Yohe, 2003; Menzel et al., 2006; Parmesan, 2006; Poloczanska et al., 2013). The advancement of spring events like earlier flowering (Parmesan and Yohe, 2003; Menzel et al., 2006), has been particularly well-documented on land through long-term studies of plants, such as cherry blossom in Japan drawing on data as early as the nineteenth century (Menzel and Dose, 2005). Differences among species in phenological responses to climate change are likely to have important

ecological consequences through asynchrony in interactions between trophic levels and mismatch between organism development and food availability (Edwards and Richardson, 2004; Visser and Both, 2005; Marshall et al., 2010; Thackeray et al., 2010).

Detecting impacts of climate change on species and ecosystems has been severely impeded by the lack of suitable baselines and time series against which to detect change, and these limitations have been particularly severe in marine ecosystems (Richardson and Poloczanska, 2008; Brown et al., 2011; Wernberg et al., 2012). However, globally, the seasonal timing of spring temperatures have been shifting 30–40% faster in the ocean than on land, seasonal isotherms moving forward at a rate of 1.5–2.5 days decade⁻¹ (Burrows et al., 2011). Given that many marine species are in close equilibrium with their thermal niches (Sunday et al., 2012) and that thermal variation across varying time scales in the marine environment is narrower than those observed in most terrestrial ecosystems (Pearson and Brawley, 1996; Miller-Rushing and Primack, 2008), it is reasonable to expect that phenological shifts in marine species will be similar or even more pronounced in response to climate warming, to what has already been observed on land.

The evidence for more pronounced phenological changes in the sea is increasing, with marine studies reporting some of the highest rates of advancement in spring phenology. For example, gonad development of the limpet *Patella depressa* has advanced by 10.2 days decade⁻¹ (Moore et al., 2011), blooms of dinoflagellates and development of meroplankton by 5.2 and 6.1 days decade⁻¹, respectively (Edwards and Richardson, 2004), and the onset of spawning in the bivalve *Macoma balthica* by 4.4 days decade⁻¹ (Philippart et al., 2003). A recent review of impacts of climate change in marine systems confirmed that average phenological shifts are greater in the ocean than land (Poloczanska et al., 2013).

A critical step in the phenology of any organism is the recurring and seasonal transitions between the different phases of the life cycle (vegetative or reproductive) or phenophases (such as breaking leaf buds, open flowers, pollen release for plants). For seaweeds, the reproductive phenophase transitions include the maturation and release of propagules (spores and/or gametes). Like plants on land, most temperate seaweeds (marine macroalgae) are finely tuned to changes in their environment and often have distinct seasonal growth and reproductive cycles (Dring, 1988; Brawley and Johnson, 1992; Lüning, 1993; Pearson et al., 1998; Moring et al., 2013). Seaweeds comprise a group of phylogenetically unrelated, morphologically and physiologically diverse group of benthic autotrophic organisms that are found more diverse in temperate regions than in the tropics (mostly for the Rhodophyta and Phaeophyceae) (Kerswell, 2006; Keith, 2014). Forecasting how climate change and global temperature increases might affect the phenology of temperate seaweeds is difficult because many species have complex life cycles with an alternation between haploid and diploid phases (Figure 1) each of which could be controlled by an intricate interplay between endogenous cycles (e.g., circannual, circadian, or lunar) and a variety of environmental triggers. For example, in the kelp *Saccharina latissima* the growth cycle is under endogenous

circannual regulation (*Laminaria saccharina* in Makarov et al., 1999), the formation of sori (clusters of sporangia which contain spores) is induced by short-day cycles within a specific temperature range (Lüning, 1988) while gametogenesis in female gametophytes is a blue-light mediated response (Lüning, 1980). Consequently, it remains a substantial challenge to identify where in the seaweed life cycle, a temperature increase is likely to have an effect, and in which direction (advancement or delay in the phenology) the outcome might change.

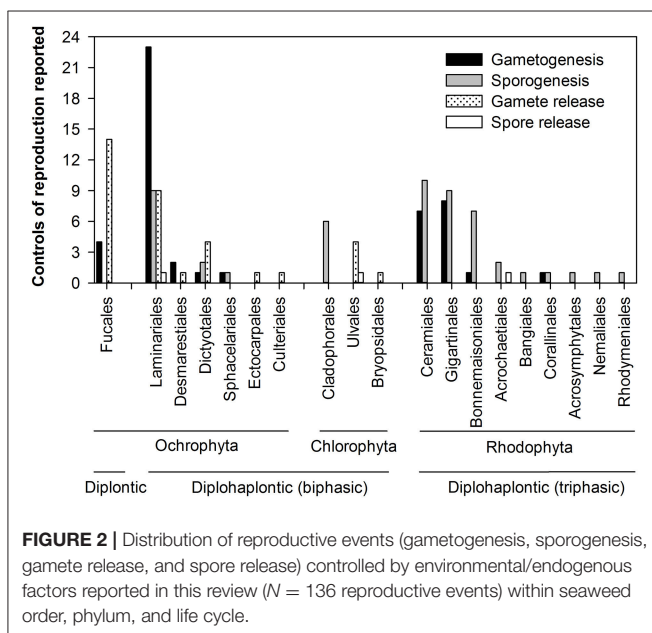
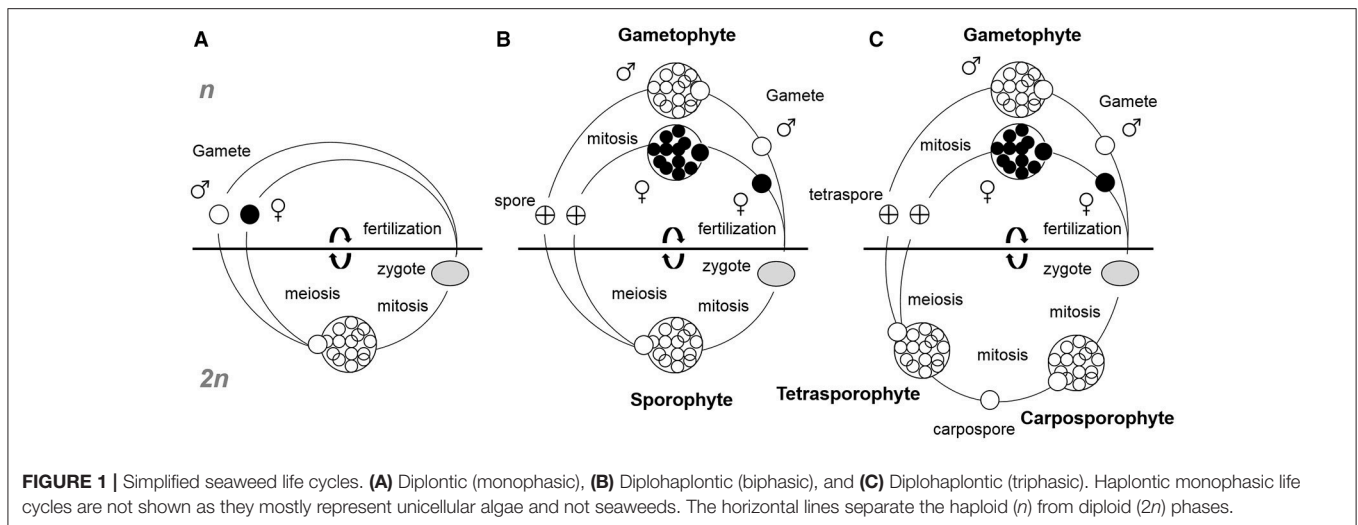
Seaweed life cycles can take one of three principal forms: haplontic monophasic (haploid thalli with zygotic meiosis), diplontic monophasic (diploid thalli with gametic meiosis, Figure 1A) or diplohaplontic biphasic or triphasic (different mode of alternation of generations between haploid and diploid generations, Figures 1B,C). The haplontic monophasic life cycle is most common for unicellular planktonic algae and less representative in seaweeds. The diplontic monophasic life cycle is characteristic of most fucoids brown algae (e.g., *Fucus*, *Sargassum*, *Cystoseira*), including the genus *Durvillea* and the green algal genus *Codium*. Diplohaplontic biphasic or triphasic life cycles are most common in seaweeds. Biphasic life cycles are well represented in the Laminariales and correspond to the alternation between macroscopic diploid sporophytes and microscopic haploid gametophytes. The more complex triphasic life cycles are common and restricted to the Rhodophyta and, in the majority of cases, encompass one haploid gametophyte phase and two diploid sporophyte phases. In this review, we deliberately discriminated propagule (here defined as spores and gametes) maturation from propagule release because it has been demonstrated that each process can be controlled by very different environmental factors, and therefore potentially exhibit different timing responses. For instance, *Fucus vesiculosus* in the northeast Atlantic initiates gametogenesis in response to short days (Bäck et al., 1991; Berger et al., 2001) whereas gamete release is a function of water movements and lunar or tidal cycles (Andersson et al., 1994; Serrão et al., 1996).

Despite the complexity and diversity of reproductive phenophase transitions found in temperate seaweeds (Figure 1) their need to be in tune with their environment to ensure evolutionary and ecological success implies a strong potential for temperature control over the phenophase transitions and for temperature-mediated phenological shifts. Here we review studies of the controls of phenophase transitions in temperate seaweeds. In doing so, we aimed to identify where temperature has been shown to affect different aspects of seaweed reproductive phenology to propose hypotheses about how global warming might affect seaweed reproductive phenology. Finally, we discuss the potential use of seaweed herbarium collections for detecting recent changes in seaweed phenology.

METHODS

Search Criteria

We searched for peer-reviewed studies of factors driving reproductive phenology in temperate seaweeds (25–65° latitude). Given the vast literature available on the controls of life cycle transitions in temperate seaweeds, we deliberately



focused our review only on temperate seaweeds to consider seaweeds thriving in *relatively similar* environmental conditions (see Wiencke and Clayton Margaret, 2009, for vegetative and reproductive phenology in polar seaweeds). Studies included both controlled laboratory experiments and detailed field observations. We searched available on-line data bases including the Web of Science, Current Contents, the UWA library collection, One Search and Google Scholar using different combinations of key words pertaining to seaweeds and their reproduction: “seaweed,” “macroalgae,” “temperate,” “reproduction,” “reproductive ecology,” “spore,” “zoospore,” “carpospore,” “tetraspore,” “gamete,” “phenology,” “seasonality,” “gametogenesis,” “sporogenesis,” “sporulation,” “tetrasporogenesis,” “control,” “trigger,” and “cue.” Additional papers were located by backtracking from the reference lists

in the initial search publications. Papers were included in our review only if they presented field and/or laboratory data to infer induction of reproduction by exogenous or endogenous factors. We excluded all published works that referred to sporadic field observations and conclusions made without clear demonstration or reporting (Appendix 1 in Supplementary Material).

For each seaweed (sometimes the same species at different latitudes), we extracted information on species identity, location, which factors were considered and the corresponding phenological event(s) (Figure 2). We considered tetrasporogenesis and sporogenesis as one event (sporogenesis), but we did not pool this with carposporogenesis because this maturation is very likely the direct consequence of fertilization of the carpogonium and the subsequent development of gonimoblast tissue. We then quantified the frequency of seaweed identifying temperature as a trigger or control for four reproductive events (gametogenesis, sporogenesis, gamete release, spore release), alone or in combination with other factors.

RESULTS AND DISCUSSION

Limitations in Seaweed Phenology Research

We found 81 papers totalling 136 reproductive events from 71 temperate seaweed species. Most studies on the influence of environmental/endogenous factors on reproductive phenology (hereafter “reproductive events”) were controlled laboratory experiments (Appendix 1 in Supplementary Material). A large part of the reproductive events studied (>40%) originated from northwestern Europe where such research has been particularly abundant (Germany, France, Ireland, and UK, Appendix 1 in Supplementary Material) and from North America (~28%, USA, Canada). This geographical bias limits our understanding of temperature as a driver of reproductive phenology to a narrow range of seaweed taxa and latitudes. In general, the research on seaweed reproductive phenology identified by our

selection criteria was most intensive between 1980 and 1995 then decreased for the most recent period (Appendix 1 in Supplementary Material). The strong geographical bias and the declining numbers of publications for phenological research in temperate seaweeds are worrying given the growing importance of phenological shifts in response to climate warming.

There was also a strong disparity in the seaweed taxa and reproductive events studied (Figure 2). Most research focused on five seaweed orders (~75%: Laminariales, Fucales, Ceramiales, Gigartinales, and Bonnemaisoniales) with ~30% of reproductive events (42 out of 136) studied on Laminariales (Figure 2, Appendix 1 in Supplementary Material). Limited information was found on spore release (3/136 studies) compared to the other phenophase transitions, which were studied at higher frequency: 51, 47, and 35 out of 136 studies for sporogenesis, gametogenesis and gamete release (Figure 2, Appendix 1 in Supplementary Material). Data reported from the Fucales were mostly on gamete release (>75%) whereas gametogenesis, sporogenesis, and gamete release were the focus for Laminariales (>95%) (Figure 2, Appendix 1 in Supplementary Material). Most reproductive events in Rhodophyta were spore (~66%) and gamete maturation (~32%). We found limited information for Chlorophyta with only 6 studies on sporogenesis and 5 and 1 on gamete and spore release, respectively (12/136; Figure 2, Appendix 1 in Supplementary Material).

Role of Temperature in Phenophase Transitions

Propagule Release

Only a few studies demonstrated exogenous control of spore release such as wave motion in *Alaria esculenta* and *Ulva lactuca* (Gordon and Brawley, 2004) or bacteria in *Acrochaetium* sp. (Weinberger et al., 2007) (Appendix 1 in Supplementary Material). Many papers mentioned periodicity of spore release linked with tidal movement, specific day time (light intensity) and wave action to both facilitate the mechanical scouring of reproductive tissue and spore dispersal, and synchronize spore release once matured (Hoffmann, 1987; Amsler and Neushul, 1989; de Bettignies et al., 2013). A certain level of seasonal synchrony in spore release might be required to deliver propagules under conditions favorable for survival and/or growth (e.g., substrate availability, optimum temperature, etc.) and to maximize subsequent fertilization success when needed and sporophyte recruitment. Such synchrony might depend on the timing and rate of spore maturation (sporogenesis). Seaweeds like *Undaria pinnatifida* (Laminariales) in California show pulses in recruitment coinciding with temperature drops, indicating that temperature might play a role in some species for spore maturation/release when variation in seawater temperature is severe and/or sudden (Thorner et al., 2004). Alternatively, these recruitment pulses could have been driven by nutrients, which are highly correlated with temperature in California (Edwards and Estes, 2006).

Gamete release in the studied seaweeds was found to be triggered by various combinations of exogenous and endogenous factors such as lunar or tidal cycles (endogenous and exogenous),

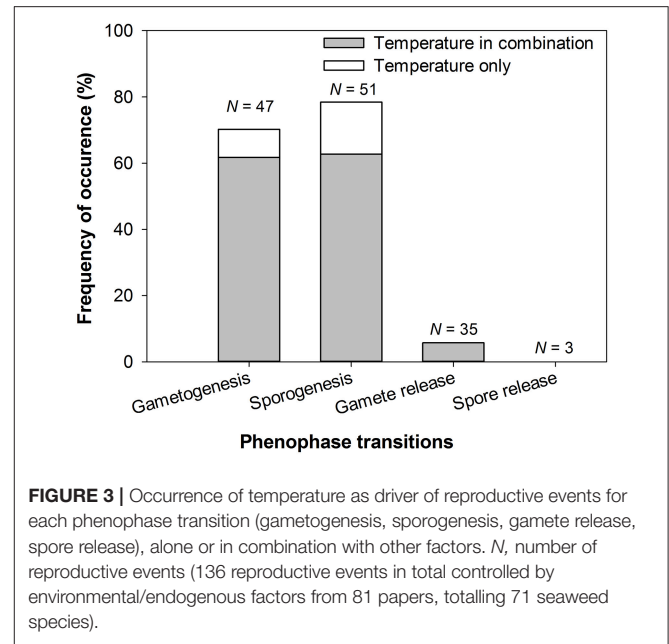


FIGURE 3 | Occurrence of temperature as driver of reproductive events for each phenophase transition (gametogenesis, sporogenesis, gamete release, spore release), alone or in combination with other factors. *N*, number of reproductive events (136 reproductive events in total controlled by environmental/endogenous factors from 81 papers, totalling 71 seaweed species).

irradiance threshold (day light), water movement (release during calm periods) and female pheromones (Page and Kingsbury, 1968; Müller et al., 1979; Brawley and Johnson, 1992; Andersson et al., 1994; Serrão et al., 1996; Berndt et al., 2002; Gordon and Brawley, 2004; Engelen et al., 2008; Lüning et al., 2008) (Appendix 1 in Supplementary Material). Temperature was only found to be a good predictor of gamete release for two seaweeds, *Ascophyllum nodosum* in Maine (USA) (Bacon and Vadas, 1991) and *Sargassum muticum* in California (USA) (Norton, 1981), both in combination with tidal parameters.

Propagule Maturation

Many studies reported propagule maturation to be a temperature-mediated process with both gametogenesis and sporogenesis under the influence of temperature in 70–75% of the seaweeds studied (Appendix 1 in Supplementary Material, Figure 3). Most studies on propagule maturations were found for seaweeds with an alternation of generations such as the Laminariales and only a few orders of Rhodophyta represented (mainly Ceramiales, Bonnemaisoniales and Gigartinales; see Figure 2, Appendix 1 in Supplementary Material). Interestingly, temperature was observed to have opposite effects on reproductive maturation rate and timing depending on the species considered (Appendix 1 in Supplementary Material, Table 1), presumably because the effects can be triggered either by cold or warm temperature.

For the majority of Laminariales studied, gametogenesis required low to medium temperature, relative to normal growth conditions, in combination with a specific spectral composition (Table 1, blue-light for most species of *Laminaria*) (Lüning and Neushul, 1978; Lüning, 1980). This suggests that an increase in seawater temperature might delay the formation and ultimately the release of gametes for many species of the Laminariales.

TABLE 1 | Factors associated with reproductive maturation (gametogenesis and sporogenesis) of temperate seaweeds studied found in combination with temperature for the three main phyla/life cycles studied (Chlorophyta, Ochrophyta, and Rhodophyta).

Phylum (Order)	Factors			
	Gametogenesis		Sporogenesis	
Ochrophyta / Chlorophyta				
(mainly Laminariales)	Light (s)	[11]	Light (s) x Nutrient	[1]
	Light (i)	[2]	Short days	[3]
Diplohaplontic -biphasic	Short days	[1]	Long days	[2]
	Long days	[1]	Temperature alone	[5]
	Long days x Nutrient	[1]		
	Temperature alone	[4]		
Rhodophyta				
Diplohaplontic -triphasic	Short days	[10]	Short days	[19]
	Long days	[3]	Long days	[5]
			Short days x Light (i)	[2]
			Temperature alone	[3]

Light (s) and Light (i) are respectively for spectral composition and irradiance level. Numbers in brackets indicate the number of reproductive events whose reproductive phenology is influenced by the corresponding factors.

Furthermore, reproduction (mostly sporogenesis) was often resumed as soon as conditions returned to favorable for growth (longer days and increasing irradiance) (Lüning and tom Dieck, 1989), and therefore warming might also result in a narrowing of the reproductive window for many species.

For most of the Rhodophyta species (77%), both gametogenesis and sporogenesis (usually tetrasporogenesis) were controlled by a unique combination of temperature and day length resulting in a strict reproductive window (Dring, 1984; Molenaar et al., 1996; Molenaar and Breeman, 1997) (Table 1). This mechanism provides an accurate timing of the different reproductive phases and ensures the three modes of reproduction are well ordered through different temperature-day length combinations (van den Hoek, 1982; Kain, 1987). Temperate red seaweeds fail to reproduce, or their reproductive response is much lower outside the specific photoperiodic and temperature requirements (Molenaar et al., 1996) and this temperature-day length regulation of reproduction has been invoked to explain phylogeographic “reproductive boundaries” (Colijn and van den Hoek, 1971; Rietema and Breeman, 1982; van den Hoek, 1982; Yarish et al., 1984). This highlights that seaweed distribution is not only a function of temperature range for growth and survival, but also reproduction. Often the persistence of species outside of these reproductive boundaries is only possible through vegetative propagation or sporadic environmental conditions favorable for sexual reproduction such as *Asparagopsis armata* in northern Europe (Guiry and Dawes, 1992). If temperature increase is non-lethal and photoperiod requirements are met (day length and number of cycles), then it can either delay the timing of reproductive events for “short-day” species (induction under lower-than-average temperature) or advance it for “long-day” species (induction under higher-than-average temperature). This effect is likely to be amplified in seaweed species where critical day lengths are modified by temperature, indicating that

temperature can overcome photoperiod thresholds as the main driver of reproduction (Cunningham et al., 1993; Molenaar et al., 1996). Indeed shortening of the critical day length at lower temperatures for “short-day” species (Cunningham et al., 1993) and lengthening at higher temperature for “long-day” species (Molenaar et al., 1996) have been demonstrated. Collectively these findings (Table 1, Figure 3) stress the high potential for phenological shifts in temperate Rhodophyta under global warming, but the direction of shifts will depend on whether the seaweed is a “short-day” or “long-day” species.

In contrast to species from the Laminariales and some Rhodophyta species, we found insufficient information on temperature effects on gametogenesis in the Fucales (Appendix 1 in Supplementary Material). However, the commencement of receptacle development in spring for many Fucales, when light and seawater temperature start to increase (Terry and Moss, 1980; Bäck et al., 1991; Berger et al., 2001), suggest that temperature might play a role in this process. Recent findings (Kraufvelin et al., 2012) and previous work on gamete release (Norton, 1981; Bacon and Vadas, 1991) support this hypothesis, but more work is needed to understand the possible link between temperature, receptacle initiation and related factors such as day length. If the timing of reproduction is determined by temperature, it implies that warming could trigger earlier onset of receptacle initiation and subsequently earlier gamete release, which itself might not be under temperature-control.

Maturation of seaweed propagules requires time to complete, and consequently, cues indicative of seasonal changes are critical to deliver propagules when resources are optimal for their development. Both temperature and light parameters (particularly photoperiod) are reliable cues of seasonal change for the temperate seaweed species found in most studies (40–55° N, Appendix 1 in Supplementary Material) as indicated by their maximum seasonal variation across these latitudes (Appendix 2 in Supplementary Material). Temperature was often found in combination with different light characteristics such as day length, irradiance and spectral composition (Table 1, Figure 3). However, temperature and light changes indicative of season vary with latitude (Appendix 2 adapted from Wilczek et al., 2010) and their seasonal variations do not follow the same pattern with latitude (i.e., bell-shape curve of temperature vs. linear increase of seasonal variation in day length with increasing latitude, Appendix 2 in Supplementary Material). Consequently, their relative roles as seasonal cues for seaweed development might also vary with latitude. Temperate seaweeds of lower latitude (30–40° latitude) and tropical species might respond more to temperature variations than day length whereas seaweed reproductive development at higher latitude (50–65° latitude) and polar regions (65–90° latitude) might be more sensitive to light given their respective variations with latitude (Appendix 2 in Supplementary Material). More work at different latitudes is therefore needed to determine if the role of light and temperature variation (min/max, mean and or standard deviation of sea surface temperature) as triggers of reproductive phenology are consistent across latitudes.

Use of Herbarium Collections to Detect Phenological Shifts in Seaweeds

Detection of shifts in seaweed phenology in response to warming requires historical observations of timing of life cycle events such as reproduction, yet this information has rarely been collected systematically, particularly in the marine environment. However, like terrestrial botanists, phycologists have been preserving seaweeds in herbaria for at least two centuries (Coleman and Brawley, 2005; Wernberg et al., 2011). Because the reproductive organs are preserved in most herbarium specimens these collections are a promising source of historical information for detecting climate-related shifts in seaweed phenology and/or reduction of reproductively mature specimens (Primack et al., 2004; Miller-Rushing et al., 2006). The exploration of data contained in herbarium collections becomes highly relevant when and where no other source of baseline information exists and where sufficient numbers of exsiccatae for a same species have been preserved.

Some caution is however warranted when using herbarium collections because specimens were often primarily collected for taxonomic and/or biodiversity inventory purposes where reproductive organs have been important characteristics for identification. Collectors might thus have been biased to keep only reproductive specimens or species for which no reproductive structures are needed for accurate taxonomic identifications, such that the herbarium population could be non-representative of the overall population (Coleman and Brawley, 2005). Also, additional caution needs to be taken with herbarium data because temporal patterns might be confounded by sampling bias, spatial patterns, (e.g., more records and taxa are collected closer to major research centers than at any other location, and haphazard collections tend to occur closer to the summer during periods of good weather), and/or decadal variation of local temperatures. An analysis of the Dinard Herbarium in France demonstrated such bias with its algal collection reflecting changes in laboratory locations and differences in sampling strategies (exhaustive approach = few specimens for many taxa as possible vs. biocenotic approach = many specimen from different habitat for common taxa only) (Robuchon et al., 2016).

CONCLUSION

This review has highlighted the importance of temperature for reproductive maturation (both sporogenesis and gametogenesis) in temperate seaweeds. Although the literature is heavily biased toward mid to high latitudes in the northern Hemisphere and species from a limited number of seaweed orders, it is clear that different aspects of the reproductive phenology of temperate seaweeds are strongly linked to variation in temperature.

Contrary to the highly consistent unidirectional effect of warming, with the advance of spring events (e.g., earlier flowering), seen in most terrestrial plants (Primack et al., 2004; Menzel and Dose, 2005; Miller-Rushing and Primack, 2008),

there was evidence to suggest that warming can both advance and delay reproductive phenology of temperate seaweeds, depending on a diversity of temperature requirements for reproductive maturation and interactions with additional cues such as day length. In many temperate seaweeds, the reproductive maturation (~60%) was also associated with specific light characteristics (e.g., day length or spectral composition) in addition to favorable temperatures. Warming might then result in a mismatch between temperature and light requirements exacerbating negative effects on reproduction and potentially lead to reproductive failure. There is a clear need for a broader understanding of the interplay between temperature, other environmental drivers (e.g., day length) and seaweed reproduction. While this line of research is picking up again (Oppliger et al., 2012; Bogaert et al., 2016; Martins et al., 2017) further effort should be made to develop more integrative approach with interaction experiments in ecophysiological research (Oppliger et al., 2012; Martins et al., 2017) in combination with modeling if possible. Such results should be put then in perspective with underlying molecular mechanisms (Liu et al., 2017). So far, phenological shifts in response to ocean warming have not been detected for seaweeds. This is, however, likely to reflect a lack of studies based on appropriate baseline data. Detailed investigations of historical herbarium collections could reveal shifts that are either analogous or opposite to observations from terrestrial plants, or occurring in multiple more complex directions such as spring advancement, followed by a pronounced summer interruption (due to excessive warming), followed by a new reproductive spike in late summer and early autumn. Regardless, it is clear that our mechanistic understanding of how warming might influence the reproductive phenology of temperate seaweeds is limited by strong geographic and taxonomical biases, and that this is a research area ready for renewed effort.

AUTHOR CONTRIBUTIONS

TW and TdB conceived the study. TdB, TW, and CFDG designed the methodology. TdB collected and analyzed the data. TdB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00218/full#supplementary-material>

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