KELP GAMETOPHYTES IN CHANGING OCEANS

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Abstract   Kelp forests are ecologically diverse habitats that provide vast ecosystem goods and services, but are threatened by climate and anthropogenic stressors. Laminarian kelps have an alternating biphasic life cycle, and while there is a growing understanding of climate impacts on the macroscopic diploid sporophyte, impacts on the microscopic haploid gametophyte stage are just emerging. There exists a strong history of gametophyte literature on single species and environmental factors, but only recently studies have increasingly examined multiple climate stressors, species and populations. We synthesize studies on kelp gametophytes, building upon our understanding of their responses to environmental conditions and subsequent vulnerability in changing oceans. Kelp gametophytes have a broad tolerance to environmental conditions predicted to change with climate change, including temperature and irradiance, but large variation exists among species and populations. Key processes such as gametogenesis and early sporophyte development consistently appear more sensitive to environmental conditions than vegetative growth and may present bottlenecks to ongoing kelp persistence. Indirect effects of climate change negatively affect kelp gametophytes through competition, grazing and sedimentation. Modern genomic techniques are paving the way to transition research into field settings that include both sporophyte and gametophyte stages. Unravelling the response of gametophytes to changing environmental conditions is beginning to provide an understanding of overall kelp forest persistence and enables proactive conservation and management initiatives in changing oceans.

Keywords: Climate Change; Competition; Gametophytes; Grazing; Laminariales; Ocean Acidification; Resilience; Sedimentation; Temperature; Thermal Tolerance; UV Radiation

Introduction

Kelp forests, defined here as communities structured by macroalgae in the order Laminariales, are the dominant biogenic habitat of shallow temperate rocky reefs and underpin some of the most productive ecosystems globally (e.g. Kain 1979, Dayton 1985, Schiel & Foster 1986, Steneck et al. 2002, Graham et al. 2007, Smale et al. 2013, Wernberg et al. 2019a, Wernberg & Filbee-Dexter 2019).

Kelp forests provide habitat for many ecologically and economically important species (Bertocci et al. 2015) and are often the main primary producers in many temperate rocky reef systems (Mann 1973). They are the third most productive system globally (Filbee-Dexter & Wernberg 2018) and store and cycle large amounts of CO_2 (Krause-Jensen & Duarte 2016, Duarte 2017, Filbee-Dexter & Wernberg 2020). Through direct exploitation by harvesting (Buschmann et al. 2017) and indirect support of economically valuable industries such as fisheries and tourism, the value of kelp forests is estimated at \$US 684 billion annually worldwide (Eger et al. 2021).

Despite their importance, the cover of kelp forests is declining in many regions due to local anthropogenic impacts such as pollution, urban run-off and industrial effluents (Reed et al. 1994, Tegner et al. 1995, Coleman et al. 2008, Strain et al. 2014), overgrazing by urchins (Jones & Kain 1967, Chapman 1981, Johnson & Mann 1988, Keats et al. 1990, Filbee-Dexter & Scheibling 2014, Ling et al. 2015) and increased sedimentation (Foster & Schiel 2010, Alestra et al. 2014). Decline is also occurring due to global stressors such as ocean warming (Moy & Christie 2012, Vergés et al. 2014, Krumhansl et al. 2016, Filbee-Dexter et al. 2016, Filbee-Dexter & Wernberg 2018, Wernberg et al. 2019b, Berry et al. 2021, Coleman et al. 2022), marine heatwaves (Dayton et al. 1999, Wernberg et al. 2013, Arafeh-Dalmau et al. 2019, Smale et al. 2019) and increased frequency and intensity of storms (Dayton et al. 1992, Filbee-Dexter & Scheibling 2012, Davis et al. 2022). The decline of kelps can be due to direct impacts (Dayton et al. 1999, Smale & Wernberg 2013, Wernberg et al. 2016), or driven by indirect effects such as climate-induced range shifts of tropical grazers into temperate habitats (Johnson et al. 2011, Vergés et al. 2014, Wernberg et al. 2016) and suppressed recruitment due to algal turfs that thrive under urbanized or acidified conditions (Connell & Russell 2010, Connell et al. 2018, Filbee-Dexter & Wernberg 2018). These stressors on the marine environment have altered the ecological structure (Harley et al. 2012, Filbee-Dexter & Wernberg 2018, Vergés et al. 2019), adaptive capacity (Gurgel et al. 2020, Coleman et al. 2020a) and economic and social values derived from kelp forests (Bennett et al. 2016). In contrast to these general trends, localized increases in kelp cover have also occurred in some regions (Krumhansl et al. 2016, Krause-Jensen et al. 2020) and understanding what confers these positive responses is key for informing conservation, restoration and management of kelp forests globally (Coleman & Goold 2019, Layton et al. 2020b, Coleman et al. 2020b, Eger et al. 2020b).

Kelps are characterized by a haplo-diplontic life history with macroscopic diploid sporophytes alternating with microscopic haploid gametophytes. While we have a growing understanding of the functioning and resilience of kelp forests at their macroscopic sporophyte stage, our understanding of the microscopic gametophyte stage is considerably less (Schiel & Foster 2006). For example, a literature search using the keywords "gametophytes", "microscopic stages", "kelp" and "Laminariales" conducted on 5-12-2020 in Web of Science resulted in a final set of 192 papers (Figure 1), whereas a search on "sporophyte", "kelp" and "Laminariales" in the same search engine resulted in over 5000 publications. As such, several excellent reviews exist on the effects of climate change on the ecology and persistence of kelp forests (e.g. Steneck et al. 2002, Harley et al. 2012, Wernberg et al. 2019b), the reproductive biology of kelps (Santelices 1990, Amsler et al. 1992, Schiel & Foster 2006, Liu et al. 2017) and the potential of gametophytes to persist as a bank of microscopic forms (Hoffmann & Santelices 1991, Barrento et al. 2016, Wade et al. 2020, Schoenrock et al. 2020). Moreover, there are several reviews on the biology and ecology of individual kelp species that compare both gametophyte and sporophyte life stages (e.g. Kain 1979, Graham et al. 2007, Bartsch et al. 2008, Wernberg et al. 2019a) as well as a long history of gametophyte knowledge and studies that focus on aquaculture (Valero et al. 2017).

Despite this body of literature, studies on kelp gametophytes are largely biased towards single factor experiments on individual species, with multi-factor studies in the context of climate change only gaining traction in recent years (16% of the total number of studies identified above; Figure 1). Moreover, studies examining the impact of environmental factors predicted to be altered under
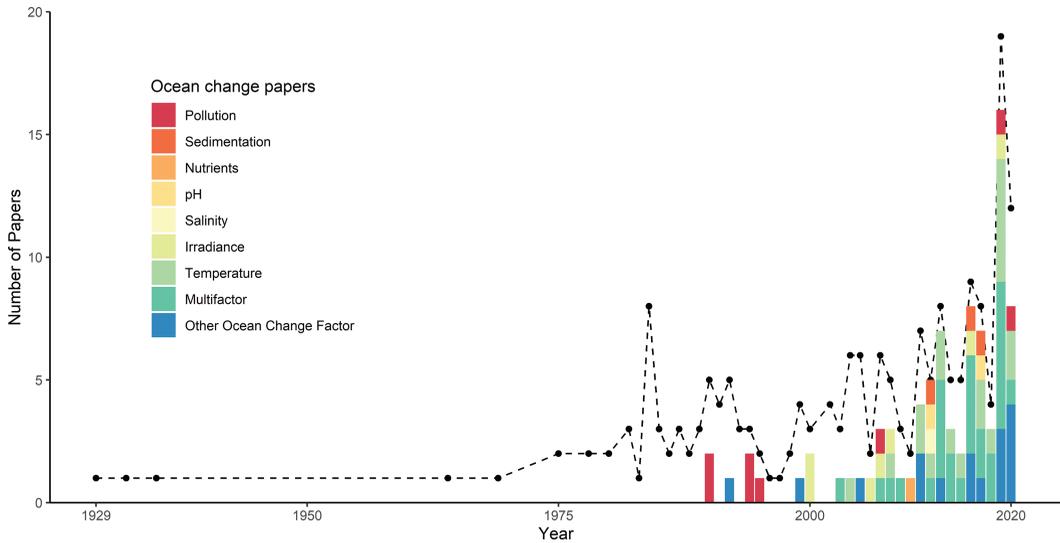
Figure 1 Database of papers collated through a Web of Science search with search terms "microscopic stages", "gametophytes", "kelp" and "Laminariales" on 5-12-2020. A total of 327 studies were found, which were then examined to concern solely laminarian kelps and gametophytes. The final database consisted of 192 papers and was sorted according to ocean change theme. The dotted line represents all papers throughout time, with the coloured bars representing the proportion of total papers that concern ocean change, sorted by theme.

anthropogenically driven climate change (e.g. marine heatwaves, acidification) on gametophytes account for less than half (45%) of papers and have only emerged in the past two decades with acceleration in the appearance of such studies in recent years (Figure 1).

This review presents a contemporary synthesis of how kelp gametophytes are influenced by variation in environmental conditions relevant to anthropogenic climatic change, indirect effects of climate change such as change of ecological interactions and other anthropogenic disturbances such as pollution and eutrophication (together termed ocean change hereafter) and the implications for kelp persistence. We build on earlier reviews to consider kelp gametophyte biology, ecology and physiology and integrate emerging studies on ocean change (Figure 1). We review the literature on kelp gametophytes across taxa and development stages to examine responses to environmental conditions (Figure 1) and highlight the implications for kelp persistence in changing oceans. Where possible, we compare differences in response to environmental conditions between gametophyte and sporophyte stages and summarize current knowledge on ecological interactions in the microenvironment that gametophytes inhabit. Finally, we identify knowledge gaps and key future research directions that will increase understanding of the role of gametophytes and provide pathways for conservation and management of kelp in a changing ocean.

The alternation of generations life cycle of kelp

Kelps are characterized by a haplo-diplontic life history with macroscopic diploid sporophytes alternating with microscopic haploid gametophytes (Figure 2). The haploid life stage begins following spore release from the mature adult sporophyte (as reviewed by Santelices 1990). Spores then develop a germ tube through which the first gametophyte cell grows (germination) and develops into male and female gametophytes that either undergo gametogenesis (i.e. production of gametes) or persist in a vegetative state, depending on environmental conditions (Harries 1932, Kain & Jones
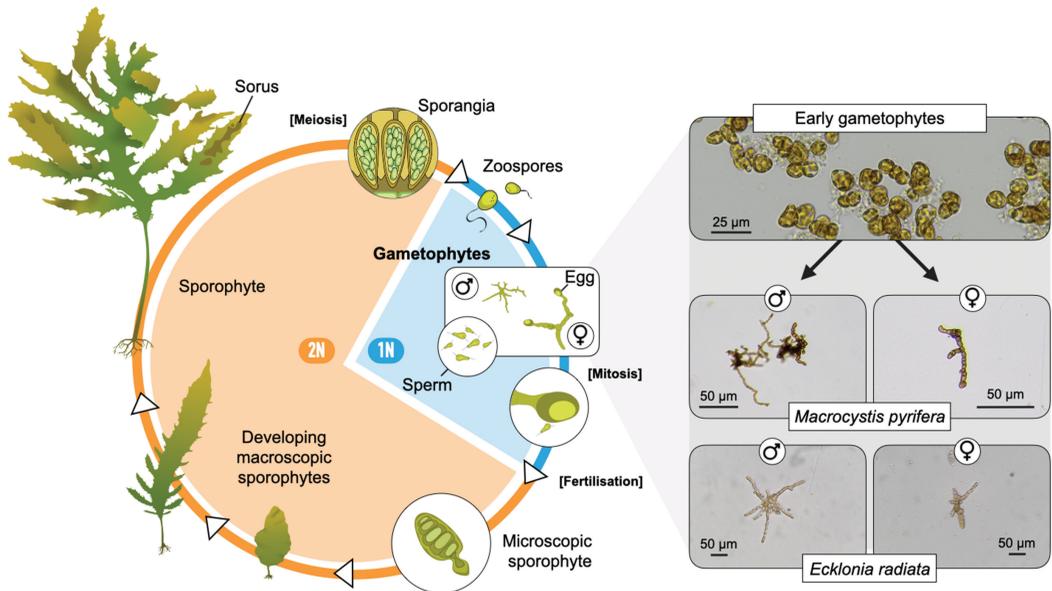
Figure 2 Haplo-diplontic life cycle of laminarian kelp. Diploid sporophytes produce spores by meiosis which develop into male and female haploid gametophytes. Fertilization can take place after the production of gametes, which results in recruitment of juvenile sporophytes.

1969, Lüning & Neushul 1978, tom Dieck 1993; Figure 2). Male gametes (sperm) are attracted to female gametes (oogonia) by pheromones released by females (Marner et al. 1984), resulting in fertilization and the subsequent development of a microscopic sporophyte and completion of the life cycle (Figure 2). While this review deals with factors influencing gametophytes rather than sporophytes, below we briefly summarise how environmental conditions and ocean change may alter sporophyte phenology as this has implications for the environment in which gametophytes grow.

Climate change has already facilitated shifts in phenology for many species (e.g. Scranton & Amarasekare 2017, Piao et al. 2019) including seaweeds (e.g. Tala et al. 2004, Coleman & Brawley 2005, Bartsch et al. 2013, de Bettignies et al. 2018), and because many aspects of sporophyte reproduction are tightly linked to environmental conditions (e.g. Lüning & tom Dieck 1989, Santelices 1990), sporophyte phenology is likely to change under predicted future climatic conditions. Reproductive phenology of kelp can be characterised as the production of sporangia in sori (fertility) and the timing of spore release and these processes, as well as the biology of spores generally, have been relatively well studied and reviewed (Santelices 1990, Amsler et al. 1992, Clayton 1992, Fletcher & Callow 1992, Schiel & Foster 2006, Liu et al. 2017, de Bettignies et al. 2018).

Kelp reproductive phenology can be strictly seasonal, or vary intra-annually depending on environmental conditions (Reed et al. 1996). Reproductive phenology may also be linked to sporophyte growth which is governed by circannual rhythms, or can be influenced directly by changing environmental factors such as temperature (tom Dieck 1991). Recent studies have shown that sori production may be the life-history phase with the narrowest environmental window (Bartsch et al. 2013, de Bettignies et al. 2018) highlighting the likely sensitivity of sporogenesis to changing environmental conditions. The dispersal of spores and their settlement are also important determinants of subsequent gametophyte development. Dispersal distance and settlement density are likely species-specific and vary seasonally (Reed et al. 1988, 1992) depending on several factors such as water motion and currents (Gaylord et al. 2002, 2006, Coleman et al. 2011). These factors can in turn be modified by kelp forest density (Graham 2003) and episodic events such as storms

(Reed et al. 1988). As spore dispersal is integral to population structure and connectivity (Graham 2003, Coleman et al. 2011, Oppliger et al. 2014), and is predicted to be altered under climate change (Coleman et al. 2017), research into reproductive phenology and its ties to environmental factors are at the base of the overall resilience of gametophytes to ocean change.

The impact of ocean change on gametophytes

Climate change and other anthropogenic stressors are fundamentally altering environmental conditions in the world's oceans and coastal waters. Ocean warming, acidification, increasing intensity and frequency of storms and extreme events in conjunction with increasing urbanisation and pollution presently threaten kelp forests globally (Filbee-Dexter & Wernberg 2018). This section reviews research on how environmental factors expected to change in future oceans (temperature, light, pH, sedimentation, nutrients, pollution and salinity) will impact the survival, growth and physiology of the gametophyte stage and its key developmental stage transitions (e.g. gametogenesis and sporophyte production; summarized in Figure 3). Where studies exist that specifically examine such environmental factors in an ocean change context, we highlight the response of gametophytes and implications for persistence in future oceans.

Effects of change in temperature on gametophytes

Temperature is among the most important drivers in the large-scale distribution of marine species, including kelps (Bartsch et al. 2012, Harley et al. 2012, Martínez et al. 2018, Smale 2020, Krause-Jensen et al. 2020). The impact of temperature on gametophytes is the most documented environmental factor, with 55% of papers identified in our search addressing impacts of temperature
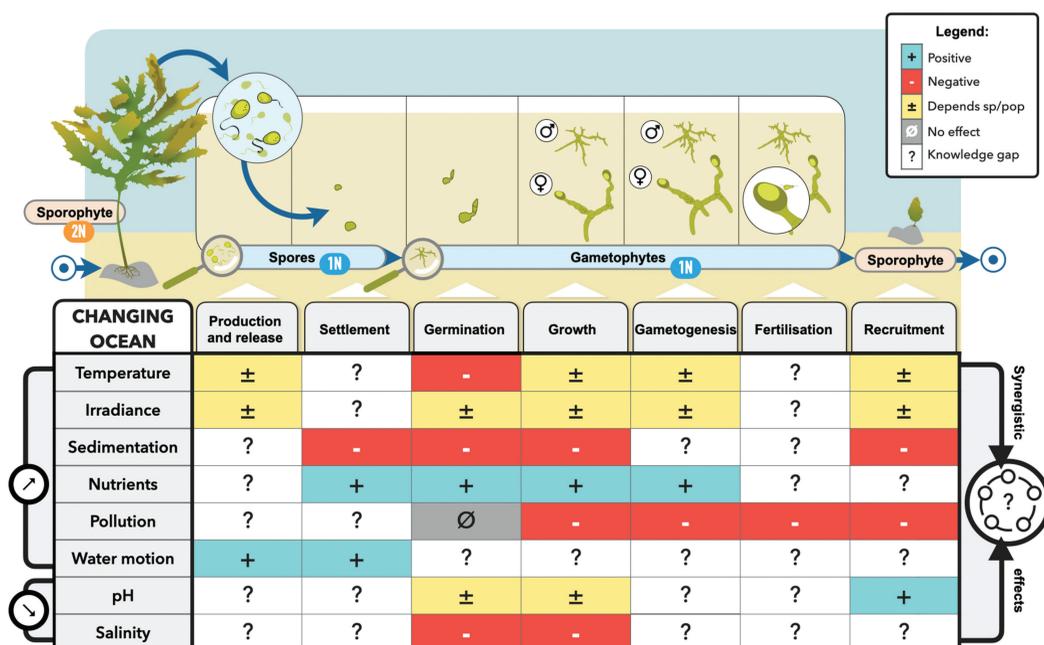
CHANGING OCEAN	Production and release	Settlement	Germination	Growth	Gametogenesis	Fertilisation	Recruitment
Temperature	±	?	-	±	±	?	±
Irradiance	±	?	±	±	±	?	±
Sedimentation	?	-	-	-	?	?	-
Nutrients	?	+	+	+	+	?	?
Pollution	?	?	Ø	-	-	-	-
Water motion	+	+	?	?	?	?	?
pH	?	?	±	±	?	?	+
Salinity	?	?	-	-	?	?	?

Legend:
+ Positive
- Negative
± Depends sp/pop
Ø No effect
? Knowledge gap

Figure 3 The ocean change factors influencing different microscopic life stages, including spores and juvenile gametophytes. Based on the available literature, variable, negative and positive impacts (up to a threshold) of ocean change factors are indicated in the table.

(Figure 1), and more than half (68%) of those papers specifically studying temperature in the context of ocean warming. Early research on gametophyte temperature tolerance was part of a larger effort to characterize the ecophysiology of kelps and identified a broad thermal range in which kelp gametophytes can survive (Ueda 1929, Kain & Jones 1964, Lüning & Neushul 1978, Novaczek 1984b, Bolton & Levitt 1985, tom Dieck 1993). Independent of location, most kelp gametophytes have a lower survival threshold of 0°C and their upper thermal limit ranges between 20°C and 30°C (tom Dieck 1993) which is hypothesised to have played an important evolutionary role in kelp dispersal across the equator for some species (Peters & Breeman 1992). Apparent differences in temperature tolerances between gametophytes and sporophytes, as well as the fact that many gametophytes exhibit higher temperature tolerances than conditions experienced by natural populations (e.g. Bolton & Lüning 1982), have led to the notion that gametophytes can persist even when environmental temperatures exceed the upper thermal thresholds of sporophytes (Ladah et al. 1999, Murua et al. 2013, Mohring et al. 2014, Komazawa et al. 2015, Park et al. 2017, Augyte et al. 2019, Rodriguez et al. 2019, Hollarsmith et al. 2020). This broad thermal tolerance of gametophytes relative to sporophytes is particularly important in the context of ocean warming (Ladah et al. 1999, Carney et al. 2013) and the predicted increase in extreme temperature anomalies such as marine heatwaves (Frölicher et al. 2018, Oliver et al. 2018, Smale et al. 2019).

The response of kelp gametophytes to change in temperature appears to be both species- and population-specific (Lüning & Neushul 1978, Bolton & Anderson 1987, Oppliger et al. 2012, Mohring et al. 2014, Lind & Konar 2017, Muth et al. 2019; Figure 3). Elevated temperature can negatively affect germination, particularly in colder adapted species (Lee & Brinkhuis 1988, Fredersdorf et al. 2009, Shukla & Edwards 2017, Gonzalez et al. 2018), but appears to have less impact on cosmopolitan species that occupy a broader thermal niche (Muth et al. 2019). In some instances, elevated temperatures have been found to positively influence germination (Izquierdo et al. 2002). The negative effects of increased temperature on kelps can have a cumulative impact on the transition from spore to gametophyte (Muth et al. 2019) and may depend on the temperature range over which they occur. The role of cumulative effects highlights the need for multi-factor, multi-species experiments across multiple life stages and over broad geographical ranges to fully understand the effect of changing oceans on all life-history stages (Muth et al. 2019).

Some general differences in requirements for gametogenesis are apparent between cold and warm temperate species. However, it is important to note that due to high variability in responses, these differences are not universal across locations, suggesting local adaptation. Laboratory studies have shown that species occurring in cold temperate waters (i.e. monthly means below 10°C in winter and below 15°C in summer) appear to have gametophytes that grow slower under decreased experimental temperatures and induce gametogenesis and sporophyte production at relatively low (5°C–18°C) temperatures (e.g. Lüning 1980, Lee & Brinkhuis 1988, Izquierdo et al. 2002, Nelson 2005, Martins et al. 2017, Augyte et al. 2019, Rodriguez et al. 2019). Species distributed in warm temperate (monthly means above 15°C in summer) waters generally appear to have higher thermal tolerance of the gametophyte stage, where gametophytes can survive experimental temperatures that are higher than the thermal maximum experienced by the source population and can undergo gametogenesis across a wide (10°C–25°C) temperature range (e.g. Novaczek 1984b, Deysher & Dean 1986b, Bolton & Anderson 1987, Thornber et al. 2004, Oppliger et al. 2012, Mabin et al. 2013, Hollarsmith et al. 2020). This indicates gametophytes may persist while conditions for sporophyte production are unfavourable and can become fertile and produce gametes when the environment matches their reproductive window, potentially acting as a seedbank (Hoffmann & Santelices 1991, Santelices et al. 2002). However, the reproductive window for gametophytes does not always match ideal environmental conditions for sporophyte growth, which demonstrates the importance of local environmental drivers and highlights the reproductive versatility that is often found among kelps (e.g. Muth et al. 2019, Liesner et al. 2020, Martins et al. 2020, Camus et al. 2021). Moreover, most studies have been done in laboratory settings and the ecological relevance of temperature tolerance

in gametophytes, as well as their ability to persist vegetatively for periods until their 'reproductive window' occurs, remains to be validated in natural settings (Deysher & Dean 1986a, Reed et al. 1997, McConnico & Foster 2005).

Another important factor that makes the study of temperature responses more complex is the within-species variation between geographically distinct populations and genotypes, particularly those growing along latitudinal thermal gradients. For instance, geographically distinct populations are often genetically differentiated due to a combination of isolation by distance, which is common among kelps (Valero et al. 2011, Durrant et al. 2014), and local adaptations (Wood et al. 2021, Vranken et al. 2021). Such differences can drive disparity in gametophyte thermal tolerance (Oppliger et al. 2012, Mohring et al. 2014) and fertility (Bolton & Levitt 1985, Camus et al. 2021) potentially due to selection and underlying genetic variation among individuals (Alsuwaiyan et al. 2021, Vranken et al. 2021). Populations that grow in cooler waters often produce more gametes and sporophytes at lower temperatures, whereas survival of gametophytes is higher with increased temperatures in warm-adapted populations within the same species (Bolton & Levitt 1985, Oppliger et al. 2012, Mabin et al. 2013, Mohring et al. 2014, Muth et al. 2019, Rodriguez et al. 2019, Hollarsmith et al. 2020, Camus et al. 2021). Gametophytes from populations at the warmer edge of their distribution can be more tolerant of high thermal stress (Oppliger et al. 2012, Muth et al. 2019, Hollarsmith et al. 2020), while populations with more narrow distributions often produce gametophytes that are more susceptible to temperature change (Lind & Konar 2017, Augyte et al. 2019, Choi et al. 2019, Gao et al. 2019). Even different individuals (genotypes) from within the same population can display very different responses and tolerance to temperature stress (Alsuwaiyan et al. 2021).

The temperature experienced by parent sporophytes can also impact gametophytes. Spores collected at different times from the same population can produce gametophytes with different thermal tolerances, with two laboratory studies showing that spring and summer spores produce relatively heat-tolerant gametophytes with higher growth rates (Mohring et al. 2013a, Murua et al. 2013). In turn, higher growth rates of gametophytes can enhance the production of sporophytes (e.g. Mabin et al. 2013, Martins et al. 2020). Conversely, *in situ* temperature during spore release and early growth of gametophytes has recently been confirmed to impact subsequent sporophytes in *Laminaria digitata,* which had higher growth rates across a range of temperatures when gameto-phytes were grown in cooler temperatures (Liesner et al. 2020). Based on these studies, it is likely that gametophyte growth and performance are highly dependent on temperature conditions experienced during spore production and increased temperatures in future oceans may severely affect kelp gametophytes (Martins et al. 2017, Muth et al. 2019) and subsequent sporophyte production (but see Layton & Johnson 2021). However, time lags between the production of spores and recruitment of sporophytes may indicate persistence of gametophytes (or microscopic sporophytes; Kinlan et al. 2003) in a dormant state until temperatures become suitable for recruitment (McConnico & Foster 2005). Similarly, different temperature optima for spore production and gametogenesis (Mabin et al. 2013, Mohring et al. 2013b) could indicate the persistence of gametophytes between pulses of spore release and recruitment.

Marine heatwaves, defined as discrete periods of anomalously warm water that exceed histori-cal norms of ocean temperature (Hobday et al. 2016) are superimposed on a background of ocean warming. Marine heatwaves are increasing in frequency and duration globally (Oliver et al. 2018) with devastating consequences for kelp forests (Dayton et al. 1999, Wernberg et al. 2013, Arafeh-Dalmau et al. 2019, Smale et al. 2019). Despite this, only 2% of studies examined the impact of heat-waves on gametophytes. Alsuwaiyan et al. (2021) simulated different types of marine heatwaves and found that all heatwaves negatively impacted *Ecklonia radiata* gametophyte performance and delayed gametogenesis and sporophyte recruitment. However, the response to heatwaves was also highly dependent on genotype, with some genotypes (from the same population) performing much better than others (Alsuwaiyan et al. 2021). Furthermore, heatwaves have been shown to decrease photosynthetic activity of gametophytes beyond a threshold of 20°C in some cold temperature

species (Delebecq et al. 2016), and indeed, a simulated marine heatwave caused high mortality (80%–100%) in juvenile sporophytes of *Macrocystis pyrifera* across different populations (Camus et al. 2021). Post-heatwave recovery may be possible, though population dependent, as gameto-phytes from warm-adapted populations of *L. digitata* had a higher recovery rate after simulated heatwave treatments (Martins et al. 2020).

Effects of change in light on gametophytes

Climate change is predicted to increase the frequency of storms (Coumou & Rahmstorf 2012, Collins et al. 2019) that may impact light provision to kelp forests and gametophytes in several ways. Storms can remove large proportions of the adult canopy and change light levels within kelp forests. Moreover, increases in storm events and run-off may change turbidity and light in nearshore coastal systems. This may affect gametophytes given that light availability is an important determinant of the distribution of kelp (Swanson & Druehl 2000, Roleda et al. 2005). In the total database of papers, 47% studied the influence of light on gametophytes, but less than half of those papers (46%) considered the impact of changes to light in the context of cli-mate change. Similar to the effects of temperature, the transition from one life stage to another is highly sensitive to light cues, but gametophytes can grow in a wide range of light condi-tions (Lüning & Neushul 1978, Lüning 1980, Novaczek 1984a, Bolton & Levitt 1985, Ebbing et al. 2020), and can even persist in darkness for extended periods (Kain & Jones 1969, tom Dieck 1993). Low light concurrent with adult canopy shading generally increases germination of spores once settlement has occurred (Augyte et al. 2019) and high light stress can decrease suc-cessful germination in *Lessonia, Pterygophora* and *Undaria* (Veliz et al. 2006, Cie & Edwards 2008, Morelissen et al. 2013), potentially affecting gametophyte density in open canopy patches created by storms.

Low light conditions generally induce growth in gametophytes (Kain & Jones 1964, Lüning & Neushul 1978, Bolton & Levitt 1985, Kinlan et al. 2003, Nelson 2005, Xu et al. 2015a, Augyte et al. 2019) and a change of light intensity and colour can be a cue for the onset of gametogenesis (Lüning & Dring 1975). The use of blue light to promote gameto-genesis (Lüning & Dring 1975) has been used for decades in aquaculture settings, whereas cultures are often grown in red light to suppress gametogenesis. To cue gametogenesis, some species require increased light (Deysher & Dean 1984, Novaczek 1984a, Nelson 2005, Choi et al. 2005, Morelissen et al. 2013, Tatsumi & Wright 2016), while others require decreased light (Izquierdo et al. 2002, Pang et al. 2008, Roleda 2016). The ability to induce gametogen-esis in high light conditions allows gametophytes to rapidly recruit when the canopy of adult kelps is removed after storms or other pulse disturbances (Dayton 1985, Schiel & Foster 1986), which has been documented among *Lessonia* and *Ecklonia* species growing in the southern hemisphere and the invasive *Undaria pinnatifida* (Novaczek 1984a, Nelson 2005, Choi et al. 2005, Morelissen et al. 2013, Tatsumi & Wright 2016). However, gametogenesis can also be prevented when irradiance is too high (Augyte et al. 2019) which may have implications for low latitude populations within western boundary currents where warm, nutrient poor and thus clearer waters are more frequently encroaching into temperate kelp habitats (Cetina-Heredia et al. 2014). Suppressed recruitment under light stress may have consequences for future kelp persistence, especially in view of competition with other algae that might be better adapted to changing light circumstances, such as invasive species (Morelissen et al. 2013) or in competi-tion for light with understory algae (Tatsumi & Wright 2016).

Day length is a factor less studied when measuring gametophyte performance, but appears to be as important as light intensity (Martins et al. 2017) and may influence kelps as they shift distribu-tion or their timing of reproduction with climate change. Cycles of day length are strongly corre-lated with seasonal changes in natural kelp populations, which are governed by circannual rhythms

(Lüning 1991, Lüning 1994), and can determine growth and gametogenesis in gametophytes (Deysher & Dean 1984, Mohring et al. 2013a, Martins et al. 2017). Increasing daylight hours has been found to promote both gametophyte growth and gametogenesis in several species (Mohring et al. 2013a, Martins et al. 2017, Choi et al. 2019), which is concurrent with summer/spring photoperiods. Under field conditions photoperiod, light intensity and temperature all increase concurrently meaning that teasing apart the individual influence of these factors is difficult. Some studies have tried to test the influence of these covarying factors. For instance, it has been shown for *M. pyrifera* that total irradiance received determines gametogenesis, irrespective of photoperiod and light intensity (Deysher & Dean 1986b). Conversely, short day lengths induce gametogenesis in *U. pinnatifida* rather than total light intensity (Choi et al. 2005), which allows recolonization after winter storms when day length is short, giving this species a potential competitive advantage over native perennial kelps (e.g. *L. digitata and Lessonia variegata*) where gametogenesis is induced under long day lengths (Nelson 2005, Martins et al. 2017).

UV radiation is recognized as a stressor throughout shallow coastal ecosystems and is expected to increase under climate change (Williamson et al. 2014, Barnes et al. 2019), which might alter the capacity of gametophytes to persist especially in places of high UV stress such as the Arctic (Müller et al. 2012). Both UVA and UVB radiation play a role in gametophyte development. Gametophytes are relatively more resilient to UV radiation than sporophytes, but exposure can still result in damage to the growing gametophyte (Müller et al. 2012). UVA is found to be less damaging than UVB to gametophyte growth, and in some cases even promotes germination (Tala et al. 2007, Müller et al. 2008). However, UVB can be severely damaging to gametophytes, with exposure resulting in up to 50% decreased germination (Huovinen et al. 2000) and the complete failure to recruit in some species (Tala et al. 2007, Roleda et al. 2007). Yet when the increase in UV radiation is gradual, some gametophytes have been found to survive and produce sporophytes (Tala et al. 2007). Some species can recover from the negative effects of UV radiation, and sporophyte recruitment has been observed when gametophytes are placed back under low light conditions (Roleda et al. 2007). This indicates that kelps can survive UV radiation as gametophytes, and recruitment can resume when conditions improve (Müller et al. 2012). The ability to cope with UV radiation and light stress is often observed in species growing in the intertidal and shallow subtidal waters (Augyte et al. 2019), and the ability to adapt to UV radiation could be a factor that determines the distribution of kelps in future oceans (Wood 1987, Tala et al. 2007, Müller et al. 2008, Fejtek et al. 2011).

A small number of studies have experimentally tested the interactive effects of light with other environmental factors and have shown that effects of light intensity and day length on growth and gametogenesis can interact with several other abiotic factors. Interactions of light and temperature often create a species-specific 'reproductive window' (Lüning & Neushul 1978, Lüning 1980, Deysher & Dean 1986b, Izquierdo et al. 2002, Müller et al. 2008, 2012, Martins et al. 2017, Augyte et al. 2019), and it is hypothesized that opposite regimes of light and temperature (i.e. low light, high temperature or high light, low temperature) induce fertility in gametophytes (Ebbing et al. 2021). This is important to consider in an ocean change context as the disparity between temperature and light might increase recruitment pulses, though this increased disparity may also alter the reproductive window with unknown ecological consequences. The influence of increased nutrient pulses can stimulate growth in light-limited gametophytes (Kinlan et al. 2003, Morelissen et al. 2013), which can be relevant for populations growing in upwelling sites and potentially beneficial to kelp species competing for light with understory algae. Day length, irradiance and ocean temperature covary over seasonal timescales, and gametophytes are likely to have evolved interactive responses to these variables. To obtain more accurate and comparable results in the future, it will be necessary to refine experimental methods to realistically reflect multi-stressor field conditions related to ocean change, as well as consider not only the quantity, but also the quality of light used in studies.

Effects of change in pH on gametophytes

The effect of lowered pH caused by increasing atmospheric CO_2 concentrations, known as ocean acidification, on marine organisms is a well-researched topic, but most studies have focused on negative effects on calcifying species (Hofmann et al. 2010, Connell et al. 2013). In contrast, fleshy algae such as kelps are expected to be largely unaffected by a decrease in ocean pH as their photosynthesis is saturated at current oceanic carbon concentrations (Hurd et al. 2019). When atmospheric CO_2 comes in contact with seawater it dissolves and subsequent reactions with water convert the majority of dissolved CO_2 into HCO_{3-} (bicarbonate) (Raven et al. 2005). Aqueous CO_2 requires less energy for most aquatic plants to take up into their cells as it can diffuse passively. Bicarbonate, in contrast, requires energy to take up using active carbon concentrating mechanisms (Hepburn et al. 2011). As many laminarian species are not able to downregulate their use of active carbon uptake, the added CO_2 for passive uptake may not pose a large benefit for kelps (Roleda & Hurd 2012).

Due to the active carbon uptake mechanisms of kelp, decreased pH can have either positive or neutral effects on growth and photosynthesis of sporophytes (Roleda & Hurd 2012), but few studies (5%) have researched the effect of lowered pH on gametophyte growth and gametogenesis (Figure 1). From these limited studies, however, it seems that an increase in CO_2 concentration can either increase growth (Roleda et al. 2012, Leal et al. 2016, 2017) or have no effect (Shukla & Edwards 2017, Gonzalez et al. 2018) on gametophytes. In contrast, germination can be decreased by a reduced pH consistent with future ocean acidification (Roleda et al. 2012, Xu et al. 2015a), although increased germination has also been observed (Leal et al. 2016). Differential responses to the interaction of ocean warming and ocean acidification suggest gametophytes' response to these dual stressors might be related to local environmental conditions. For example, *M. pyrifera* has been found to grow faster and larger under ocean warming and ocean acidification independently (Leal et al. 2016), while ocean warming and ocean acidification have been found to interact to impair growth and germination in the same species (Gaitán-Espitia et al. 2014, Shukla & Edwards 2017). This varying response to ocean warming and acidification within the same species might be the result of adaptation to local temperature and pH conditions. It has been shown that geographically and genetically separated populations of *M. pyrifera* can react differently to reduced pH, where populations more often exposed to low pH had a higher egg production in reduced pH compared to populations that do not experience pH fluctuations (Hollarsmith et al. 2020). In a study spanning populations of a broad latitudinal temperature range, Hollarsmith et al. (2020) showed high resistance of gametophytes to increased temperature and reduced pH concurrent with ENSO events and upwelling, but reproduction of gametophytes presented a bottleneck where fertility was most successful in varying populations when treatment pH and temperatures were concurrent with local temperatures and acidity. This increased fertility under environmental conditions matching that of the source population shows that gametophytes can be well adapted to their local environments, and an increase in extreme events such as marine heatwaves and increased ENSO events can constrain reproduction at the gametophyte stage (Hollarsmith et al. 2020). However, if such conditions are of short nature, gametophytes could persist in their resilient vegetative stage (Hollarsmith et al. 2020).

Gametophytes that survive acidification can be more resistant to a subsequent decrease in pH suggesting acclimation (Xu et al. 2015a). Indeed, kelp forests can themselves display large diel and seasonal fluctuations in pH driven by photosynthesis and respiration which can be larger than the projected reduction in ocean pH under climate change (Delille et al. 2009, Hofmann et al. 2011, Cornwall et al. 2013), which must be considered in laboratory studies to accurately predict the response of gametophytes to ocean acidification. The natural variation in pH often found in kelp forests may influence (and potentially increase) the tolerance of kelps, including gametophytes, to future acidification as they already experience reduced pH levels concurrent with projected ocean acidification (Hofmann et al. 2011). Interestingly,

due to high fluctuations in pH levels kelp farms are increasingly recognised as an efficient local buffer to decreased pH, as well as providing an environment that can facilitate adaptation for other marine organisms, suggesting that kelp farms may serve as local refugia from ocean acidification (Xiao et al. 2021).

Even if there are minimal direct effects of ocean acidification, kelps may be more likely to be indirectly affected under future acidified conditions. It has been suggested that kelp could become outcompeted by turf-forming algae, which are positively affected by the increased availability of CO_2 under ocean acidification (Connell et al. 2013, Provost et al. 2017, Connell et al. 2018). Through high turn-over rates (Copertino et al. 2005, Miller et al. 2009, Layton et al. 2019a) filamentous algal turfs can utilize the additional available carbon to increase growth rate and cover when temperatures rise (Connell & Russell 2010). It is thus possible that future ocean acidification could exacerbate declines in kelp forests associated with turf-forming algae (Filbee-Dexter & Wernberg 2018) by hindering the survival of gametophytes to reproduction and subsequent sporophyte recruitment (Connell et al. 2018, Layton et al. 2019a). The effect of turfing algae on gametophytes has not yet been studied, and so manipulative experiments of gametophytes in co-occurrence with turfs and under future ocean conditions are required to test these hypotheses.

Effects of change in nutrients, pollution and sedimentation on gametophytes

Climate change and other anthropogenic activities are also fundamentally changing levels of nutrients, pollution and sedimentation in coastal ecosystems (Brierley & Kingsford 2009). Ocean warming and changing ocean currents are decreasing nutrient availability for some temperate kelps (Behrenfeld et al. 2006, Keeling et al. 2010), while changes in storm frequency and terrestrial run-off may create local pulses of high nutrient loads and introduce pollution (Russell et al. 2009). Consequently, understanding the influence of nutrients, sediments and pollution on the survival and reproduction of gametophytes is essential for predicting future persistence of kelp.

The positive effect of nutrients on sporophyte growth has been well studied and nutrient (such as nitrate and phosphate) enrichment of culture media in a laboratory setting has a positive effect on growth rates of gametophytes and increases the proportion of gametophytes undergoing gametogenesis (Harries 1932, Carter 1935, Hoffmann & Santelices 1982, Hoffmann et al. 1984, Morelissen et al. 2013, Nielsen et al. 2016, Gao et al. 2019). However, it should be noted that nutrient addition in still cultures is necessary to mimic the replenishment of nutrients that occurs by water movement in natural settings, and it is unknown if the same effects are seen in the field. The addition of nutrients to cultures often has a positive effect on the later developmental stages of gametophytes (i.e. gametogenesis and fertilisation), as well as an increased positive impact on the growth rate of juvenile sporophytes (Harries 1932, Morelissen et al. 2013, but see Muth et al. 2019). In contrast, earlier stages (spores) do not require as many external nutrients due to lipid storage (Brzezinski et al. 1993). In field conditions, a lack of sporophyte recruitment under nutrient depletion suggests that gametogenesis is nutrient-limited in natural populations (Dayton et al. 1992), which is corroborated by increased recruitment and growth of sporophytes through nutrient addition in the field (Deysher & Dean 1986a). Some evidence exists that nutrient supply in the early stages of gametophyte development also affects the ability to recruit sporophytes. For example, *M. pyrifera* gametophytes failed to produce sporophytes in a laboratory setting after being exposed to low nutrient levels (Kinlan et al. 2003, Ladah & Zertuche-Gonzalez 2007), but showed increased production of sporophytes after a period of arrested development under low nutrient conditions (Carney & Edwards 2010). The observed difference is thought to be the result of the nutrient history in which the gametophytes were grown. Inducing spore release and germination in non-limiting conditions often results in poor performance when nutrient supply is subsequently lowered, whereas growing spores in limiting conditions from the point of spore release means gametophytes are capable of gametogenesis once nutrient limitations are lifted, often producing smaller sporophytes, but at a higher rate than gametophytes grown under continuously high nutrients (Muñoz et al. 2004, Carney & Edwards

2010, Lewis et al. 2013). Note that most of the nutrient addition studies discussed here were carried out in laboratories (and under still culture conditions), and results may vary in natural field conditions where nutrients are likely to be replenished through water motion and interact with multiple additional factors (e.g. temperature and light).

Species-specific responses to nutrients have been observed. For example, *Eisenia bicyclis* is known to require higher nutrient concentrations to induce gametogenesis than the more common *Ecklonia cava* (Choi et al. 2019). Similarly, variable effects of nutrient addition have been identified among geographically distinct populations of *M. pyrifera*, with different concentrations of nutrients required to induce gametogenesis (Lewis et al. 2013). Furthermore, nutrient enrichment interacts with increased light intensity (Morelissen et al. 2013), daylight cycles (Martins et al. 2017, Choi et al. 2019) and decreased temperature (Martins et al. 2017) to induce gametogenesis in other species. Increased gametogenesis in high nutrients and decreased temperature is concurrent with annual upwelling events; however, in future oceans warm, eutrophic waters can negatively impact gametophyte fertility (Martins et al. 2017). Even so, temperature seems more important than nutrient supply in determining the survival of gametophytes in future oceans (Muth et al. 2019). More recent multifactor experiments testing interactive effects of factors such as temperature, day length, sedimentation, nutrients, pH and salinity have demonstrated that such interactions affect stage transitions in gametophytes, which will be key for understanding kelp persistence in changing multi-stressor marine environments (e.g. Zacher et al. 2016, Martins et al. 2017, Muth et al. 2019, Rodriguez et al. 2019, Hollarsmith et al. 2020, Augyte et al. 2020; Figure 3).

Increasing urbanisation results in high wastewater output and pollution which can have a negative effect on kelp populations (Coleman et al. 2008, Connell et al. 2008, Jara-Yáñez et al. 2021). The negative effects of some pollutants can exceed that of future ocean warming and acidification (Leal et al. 2018). Copper is a well-researched metal pollutant that can negatively impact gametophyte development in several species (Garman et al. 1994a, Bidwell et al. 1998, Contreras et al. 2007, Leal et al. 2018). Copper and other metals, such as cadmium, zinc and arsenic, pollute nearshore waters via biofouling agents, wastewater from oil production and mining sites, and cadmium pollution has been observed near nuclear power plants (James et al. 1990, Reed et al. 1994, Garman et al. 1994a, Wang et al. 2019). Most studies demonstrate that these metals affect gametophyte development in successive life stages. For example, germination of spores is generally not affected, whereas gametophyte growth is increasingly negatively affected, and gametogenesis is completely inhibited in *E. radiata, Lessonia nigrescens, Lessonia spicata, M. pyrifera* and *U. pinnatifida* (Anderson et al. 1990, Bidwell et al. 1998, Contreras et al. 2007, Leal et al. 2018, Espinoza-González et al. 2021). The inhibition of gametogenesis naturally results in a loss of successive sporophyte populations. Importantly, although in high concentrations of metal pollutants (i.e. >10 mg/mL or higher) regeneration does not take place (Bidwell et al. 1998), in low concentrations (i.e. <100 μg/mL) the effects of metal pollution may be reversible (Wang et al. 2019) and long-term exposure can result in adaptation to high copper concentrations (Roncarati et al. 2015). Determining lethal thresholds and concentrations at which recovery or adaptation can be achieved for local kelp populations can inform conservation and restoration efforts through managing levels of pollution in urbanized coastal systems.

The mechanisms underlying the observed negative effects of pollutants, especially in gametogenesis, are still not fully resolved. It is likely, however, that pollutants interfere with cell division and DNA replication (Garman et al. 1994b) and possibly pheromone signalling between male and female gametophytes (Reed et al. 1994). Copper and other toxic metals may interfere with the cellular calcium pathway which makes membranes more permeable, perhaps interfering with adhesive qualities (Contreras et al. 2007, Leal et al. 2018). Alternatively, metal ions may potentially compete for space with ions in photosynthesis, interfere with signalling molecules necessary for cell determination and differentiation, and increase the number of reactive oxygen species in gametophyte cells, ultimately leading to cell degradation (Leal et al. 2018, Wang et al. 2020).

In addition to pollution, run-off from the land can increase sedimentation rates which negatively impact gametophyte germination, survival, reproduction and recruitment, likely due to the combined effects of decreased attachment surface (hard substrate) and interference with light and nutrient supply (Watanabe et al. 2016, Zacher et al. 2016, Traiger & Konar 2017) (Schiel et al. 2006, Layton et al. 2019b, 2020a, Watanabe et al. 2016, Zacher et al. 2016, Traiger & Konar 2017). Additionally, sedimentation rate can change the outcome of competition between gametophytes of different species. For example, *Nereocystis luetkeana* has a higher survival when settled first in the absence of sediment, but *Saccharina latissima* has a higher survival when settled first in the presence of sediment (Traiger & Konar 2017). Understanding multi-stressor scenarios caused by human disturbance such as pollution and increased sedimentation and their interactions with global climate stressors will be essential in assessing long-term health and resilience of kelp populations in urbanized environments (Russell et al. 2012, Zacher et al. 2016).

Effects of change in salinity on gametophytes

Salinity may decrease in some parts of future oceans, with influxes of fresh water more likely in Arctic areas due to glacial melt and nearshore areas experiencing greater run-off and freshwater input from storms (Collins et al. 2019). To date, gametophyte growth under varying salinities has been mostly assessed in Arctic and sub-Antarctic species, which are regions experiencing changes in salinity due to run-off from glacial melt. Indeed, while only 2% of studies researching change in environmental conditions on gametophytes focused on salinity (Figure 1), they were all on Arctic kelps. In all studies, a significant interaction of salinity with temperature was found, where higher temperatures interacted with lowered salinity to decrease germination and growth (Fredersdorf et al. 2009, Lind & Konar 2017, Rodriguez et al. 2019). However, temperatures needed to achieve these negative effects were often higher than these populations are expected to experience under near- to mid-term climate change (Fredersdorf et al. 2009). Additionally, populations of the same species living in different environments show maximum gametophyte growth and germination under varying salinities that match their local conditions, which indicates local adaptation to geographic change in salinity (Rodriguez et al. 2019). The inability to grow at very low salinity and high temperatures is thought to be the effect of decreased physiological functioning of cold-adapted species under higher temperatures (Fredersdorf et al. 2009). However, as some individuals were able to survive even under high temperatures and low salinities, gametophytes of these species may be resilient to reduced salinities (Lind & Konar 2017, Davis et al. 2022). Additionally, gametophytes can be more resilient to reduced salinities than sporophytes (Peteiro & Sanchez 2012), indicating microscopic stages can survive fluxes in salinity and be a source of population regrowth (Davis et al. 2022).

Sexual variation and sporophyte production in changing oceans

Factors affecting sex bias and reproductive strategies of gametophytes

The mode of reproduction and the rate and manner of sex determination can be influenced by environmental factors that are predicted to change in future oceans. While the development of gametophytes into males or females is genetically determined (Ouyang et al. 2009, Liu et al. 2009, Shan & Pang 2010, Lipinska et al. 2015, Zhang et al. 2019) environmental factors can influence sex ratios, most likely by post-germination mortality of either males or females (Oppliger et al. 2011). For example, increasing temperature has been found to increase the number of males in *M. pyrifera* (Rodriguez et al. 2019) and females in *L. variegata* (Nelson 2005). Variation in sex ratio is geographically dependent in some species, where more males of *M. pyrifera* are observed under high

temperatures in poleward populations (Rodriguez et al. 2019), but more females of *L. nigrescens* are found in lower latitude populations under temperature stress (Oppliger et al. 2011). High light intensity has been shown to skew the sex ratio to a higher proportion of females in *S. japonica* (Xu et al. 2015a). While some studies have shown an influence of environmental factors on sex ratios, others have found no effect and ascribed an observed skewed sex ratio to either a genetic influence or unmeasured environmental factors (Leal et al. 2016, Shukla & Edwards 2017, Gonzalez et al. 2018). There are no studies that examine gametophyte sex ratios under field conditions, though other temperate seaweeds can show a sex bias towards males in warm, low latitude populations (Wood et al. 2021) and male bias under warm temperatures is common among dioecious land plants (e.g. Munné-Bosch 2015, Petry et al. 2016). This suggests that skewed sex ratios in warming oceans could indeed hinder fertilisation and sporophyte production in kelps because the abundance and fertility of females will determine overall sporophyte recruitment. Indeed, gametogenesis in females (production of oogonia) has been shown to decrease, while antheridia production increased under experimental high temperature stress in several species (Müller et al. 2008, Choi et al. 2019, Martins et al. 2020, Hollarsmith et al. 2020). Decreased egg production by female gametophytes as observed in laboratory studies and subsequent recruitment failure under temperature stress may potentially explain why many kelp forests often fail to rapidly recover *in situ* following thermal stress such as heatwaves, while direct stress on adult sporophytes is most likely responsible for initial loss. For example, an increased number of oogonia has been observed in *M. pyrifera* in central populations, while the warmer marginal populations had a smaller number of oogonia and a lower fertility rate (Camus et al. 2021). Conversely, *E. radiata* increases egg production under temperature stress in warm edge populations (Bolton & Levitt 1985). There is clearly much versatility and compensatory mechanisms in reproductive strategies that allow kelp gametophytes to persist under a range of conditions (Bolton & Levitt 1985, Coleman & Veenhof 2021).

As well as physiological differences between male and female gametophytes, gene expression is shown to be sex-biased (Pearson et al. 2019). Higher gene expression activity was found in female gametophytes of *S. latissima* under increased experimental temperatures, indicating a higher sensitivity to heat stress (Monteiro et al. 2019). Functional expression patterns of female gametophytes are related to protein degradation and signalling, whereas male expression links more to cell division, growth and flagella production (Ouyang et al. 2009, Pearson et al. 2019). The occurrence of signalling molecules in females and cell division and growth expression in males is consistent with females producing pheromones, mainly lamoxirene (Marner et al. 1984) to attract male gametes (Müller et al. 1985, Maier & Müller 1986, Boland 1995, Gordon & Brawley 2004), and corroborates the male reproductive strategy of continuously producing reproductive cells (Destombe & Oppliger 2011).

Gametophytes can also produce sporophytes without fertilization through parthenogenesis and apomixis which are viable in culture conditions (Oppliger et al. 2007, Li et al. 2017), and this mode of reproduction has also been observed in warm-edge wild populations (Oppliger et al. 2014). It is interesting to speculate whether this reproductive mechanism is an adaptation to ensure persistence in marginal habitats where gametogenesis may fail. However, asexual reproduction potentially has negative consequences for the genetic diversity of wild populations (Oppliger et al. 2014) and reduced genetic diversity may compromise the persistence and adaptive capacity of kelps under climate and anthropogenic change (Wernberg et al. 2018). There is mixed evidence to support this idea. For example, studies have shown that reduced genetic diversity of gametophytes inhibited sporophyte production and growth (Raimondi et al. 2004) while others have shown no negative effect or only a slight disadvantage of gametophyte selfing and inbreeding on the subsequent sporophyte generation following thermal stress (Camus et al. 2021, Layton & Johnson 2021). Certainly, the ability to asexually reproduce is also hypothesized to benefit populations by fixing beneficial genes into a population (Coleman & Wernberg 2018, Müller et al. 2019). While it is still unclear what effect apomixis may have on natural populations and how this influences climate change resilience, the

use of apomixis in maintaining stock cultures of gametophytes to preserve declining wild populations is currently being explored (Müller et al. 2019).

Gametophytes can also be selfed if males and females from the same parent plant fertilise, or inbred if related individuals mate, potentially leading to inbreeding depression. Inbreeding can be enhanced where genetic diversity is limited, such as in warm, marginal populations (Wernberg et al. 2018), highly fragmented populations (Reynes et al. 2021) or where there have been population bottlenecks following stress-induced mortality (Gurgel et al. 2020). Despite this, a recent study by Camus et al. (2021) found that the degree of selfing and inbreeding in gametophytes did not affect the resilience of the F1 sporophyte generation to a marine heatwave. Even though fertility decreased with inbreeding, female gametophytes may be able to detect the degree of kinship in potential mates and increase fecundity (i.e. production of eggs) accordingly (Camus et al. 2021). Interestingly, this kinship effect was less pronounced in warm-edge populations which may represent an adaptation to having fewer available mates in marginal populations (Camus et al. 2021). These results suggest that the underlying mechanisms of fertilization in gametophytes begs much further research, and their flexibility in mating strategies can prove an important avenue for climate change resilience (Coleman & Veenhof 2021), which is especially relevant in warm-edge populations.

Transition from gametophyte to sporophyte: comparing performance

Comparison of the relative performance of both gametophyte and sporophyte stages can hint at how changing oceans may impact kelp persistence as the transition between these stages is a key bottleneck in the kelp life history. Our review identified that 30% of studies compare both gametophytes and sporophytes that grow beyond their microscopic stages. Overall, photosynthetic rates of gametophytes are less affected by changing light, temperature and salinity than the sporophyte generation (Gerard 1990, Fredersdorf et al. 2009, Borlongan et al. 2019), although some studies have recorded similar optimum temperatures for photosynthesis for both life stages (Watanabe et al. 2014, Borlongan et al. 2018). This indicates that gametophytes may have a greater ability to grow and persist under a wider range of environmental conditions. Gametophytes are also repeatedly defined as shade adapted (Lüning & Neushul 1978), with low light requirements to achieve net photosynthesis and displaying a lower light saturation point than the sporophyte generation (Fain & Murray 1982, Altamirano et al. 2003, Xu et al. 2015b, Roleda 2016, Borlongan et al. 2018, Borlongan et al. 2019, Gao et al. 2019). This reflects the circumstances under which gametophytes grow in the field, as they will usually grow under the shade of the adult canopy and/or understory algae (Schiel & Foster 2006).

The juvenile sporophyte can be more sensitive to light stress and photodamage than the gametophyte stage in several species (Kinlan et al. 2003, Altamirano et al. 2004, Roleda et al. 2007, Augyte et al. 2019). Lower sensitivity to light may allow gametophytes to survive under a range of conditions in the field and initiate gametogenesis in response to environmental conditions that are also favourable for juvenile sporophyte growth (Izquierdo et al. 2002). The adverse effects of photodamage can also be enhanced under low temperatures, which is an effect that can be more pronounced in the sporophyte generation (Borlongan et al. 2019). Gametophytes are capable of controlling photodamage by upregulating accessory pigments (Delebecq et al. 2016) and the capability of gametophytes to recover from UV damage will be of increasing relevance in safeguarding future kelp populations as increased storms (Coumou & Rahmstorf 2012, Collins et al. 2019) will create a patchier distribution (Layton et al. 2019b) which will lead to local increases in UV radiation.

There is recent interest in uncovering which genes are expressed under stressful conditions in both gametophytes and sporophytes, particularly as a line of defence against ocean change (Henkel & Hofmann 2008, Martins et al. 2019). Differential expression patterns between sporophyte and gametophyte generations indicate different cellular pathways between these life-history phases (Crepineau et al. 2000, Shan et al. 2015). For instance, gametophytes of *L. digitata* and *S. japonica*

show a higher expression of metabolic genes in comparison with sporophytes (Crepineau et al. 2000, Liu et al. 2019). Gametophytes are more thermally tolerant than sporophytes in some species and are thus presumed to have a metabolic pathway in place to attenuate heat stress, such as heat shock proteins (Henkel & Hofmann 2008). These proteins have, however, not been found until recently, partly because only two kelps have their genomes sequenced (*S. japonica*; Ye et al. 2015, *U. pinnatifida*; Shan et al. 2020) and information on transcriptomics is still in its early stages (Shan et al. 2020). Heat shock proteins have been identified in *U. pinnatifida* gametophytes, which use them to attenuate thermal stress, as well as differential expression patterns between sporophytes and gametophytes under thermal stress (Henkel & Hofmann 2008, Shan et al. 2015). This differential expression was also observed in *S. japonica*, where the sporophyte stress response included expression of proteins pertaining to cell cycle control and cytoskeleton adaption, and the gametophyte heat stress response pertained to metabolism and coenzyme transport (Liu et al. 2019). Similarly, genome-wide sequencing has recently shown that loci under selection in populations of kelp sporophytes can show balancing selection suggesting that gametophytes and sporophytes may be under selection for different environmental conditions (Vranken et al. 2021).

Ecological interactions of gametophytes in changing oceans

Climate mediated ecological interactions such as competition and grazing are well documented drivers of change in the sporophyte generation of kelp (e.g. Tegner & Dayton 2000, Steneck et al. 2002, Vergés et al. 2014, Wernberg et al. 2016, Filbee-Dexter & Wernberg 2018), but are less understood in the gametophyte stage. This is particularly relevant to address given that climate and anthropogenic change will impact the gametophytes themselves as well as their grazers and competitors, which can interact to either exacerbate or diminish the effects of climate change.

Interspecific interactions: competition & symbiosis

Interspecific competition between gametophytes within and among species forms an integral part of their overall survival. While gametophytes possess inherent mechanisms to combat competition such as chemical deterrents (Amsler et al. 1992) and can potentially trigger premature gamete release of competitors (Maier et al. 2001), other factors influencing interspecific competition may change in future oceans. For example, the outcome of interspecific competition can be determined by initial settlement density (Reed 1990), which may change as spore release is tied to factors predicted to change in future oceans, such as water motion and temperature (see previous sections). Increased disturbance will also create a patchier distribution in kelp forests (Layton et al. 2020a), and annual kelps and other opportunistic species that colonize rapidly can potentially be competitors of perennial kelps (Reed & Foster 1984, Pereira et al. 2011). For example, gametophytes of *Saccorhiza polyschides* perform relatively better under increased temperature stress than the perennial kelp *Laminaria ochroleuca*, necessitated by the increased reliance of annual populations on the persistence of the gametophyte stage (Pereira et al. 2011). In competition with the perennial *S. latissima,* the annual kelp *N. luetkeana* exhibits better survival success when settled first, whereas *S. latissima* is better able to cope with increased sedimentation, which is often detrimental to kelp sporophyte production (Traiger & Konar 2017; Figure 4). The relative advantage of *N. luetkeana* over *S. latissima* depending on timing of spore settlement indicates the importance of reproductive phenology noted earlier in this review.

The use of novel genetic techniques such as nested PCR with species-specific primers has allowed the occurrence of gametophytes of different kelp species, and potential interactions, to be quantified *in situ*. For example, the dominant canopy forming species *N. luetkeana* had a more widespread occurrence of their microscopic stages than *Hedophyllum sessile* (Fox & Swanson 2007) which may indicate that the gametophyte generation of *N. luetkeana* has some competitive
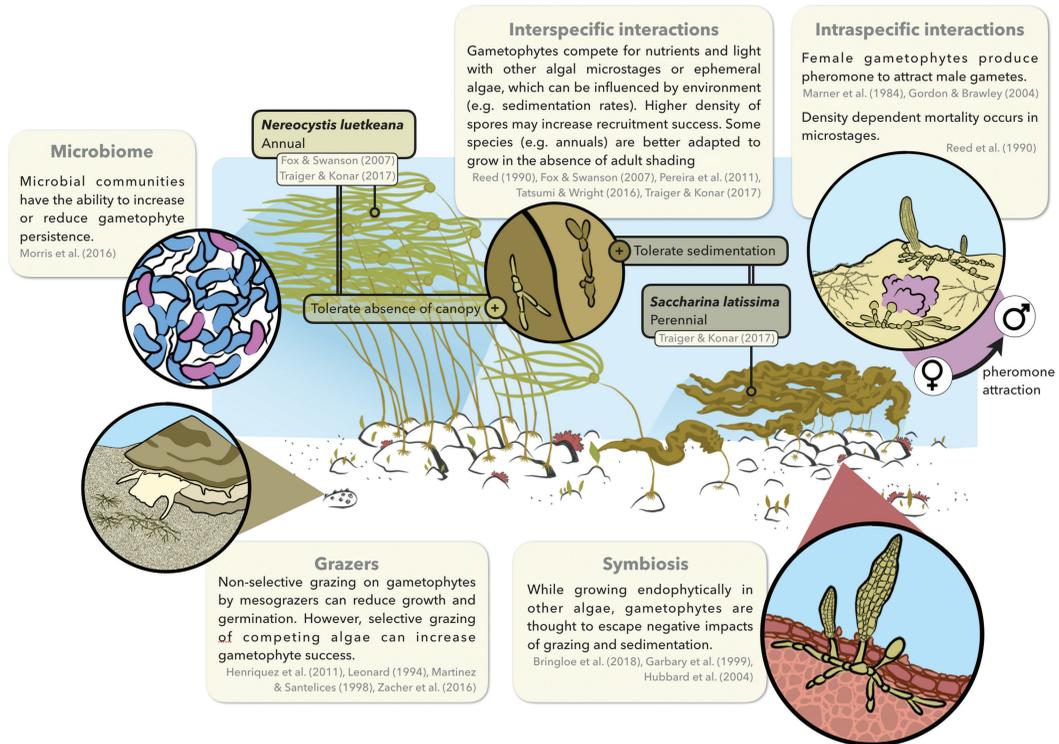
Figure 4 Examples of interactions that take place on a microscale inside and outside of the sporophyte canopy. Studies on these subjects are few, and the field conditions in which gametophytes live and survive are an important future avenue of research.

advantage over *H. sessile* relating to dispersal potential or colonization of substrates. However, even when spore dispersal and presence of microscopic forms are high, recruitment might not take place. A recent study shows kelp recruitment in post-disturbance patches may be limited due to competition with faster-growing turfing algae for light (Layton et al. 2020a). Indeed, areas composed mostly of small understory algae are devoid of kelp gametophytes (Akita et al. 2019) and the species composition of microscopic stages can be very different from the sporophyte distribution in that same area (Robuchon et al. 2014). This disparity in distribution between gametophytes and sporophytes could be due to a seasonal effect, but can also be an indication that kelp gametophytes are losing in competition for space with understory and turf-forming algae, in which light requirements of germinating gametophytes might play a role (Tatsumi & Wright 2016).

Understanding interspecific competition and ecological interactions on microscales may benefit from the development of metabarcoding for detecting the presence of gametophytes and other species within the environment (e.g. Fox & Swanson 2007, Robuchon et al. 2014). Co-culturing different species of gametophytes or other taxa will also aid in determining the effects of competition, but to date, only a few studies have attempted this (e.g. Reed 1990, Traiger & Konar 2017). Further convergence of several avenues of research (e.g. co-culturing, *in situ* use of metabarcoding, multifactorial mesocosm ecological experiments) may help understand ecological interactions among species, as well as 'winners and losers' in a changing ocean within the microenvironment that gametophytes occupy.

Gametophytes can also live as endo- or epiphytes on red algae (Garbary et al. 1999, Hubbard et al. 2004, Bringloe et al. 2018) and other kelp (Lane & Saunders 2005; Figure 4), but the significance of this in natural settings is unknown. This symbiosis is hypothesized to attenuate the negative

effects of sedimentation and grazing by growing inside the protective layer of other algal cell walls. For example, oogonia have been found protruding from red algal cell walls, which indicates that gametophytes are reproductive when living epiphytically (Garbary et al. 1999). As sedimentation and grazing are primary drivers of kelp loss (Strain et al. 2014, Ling et al. 2015), living epiphytically may prove advantageous in future oceans, though this needs to be corroborated in field settings.

Interactions of kelp gametophytes with microbes

Beneficial relationships between kelp sporophytes and associated microbes (termed the holobiont) are well established (Egan et al. 2013, Marzinelli et al. 2015, Pfister et al. 2019) and microbes may play a role in sporophyte resilience to ocean change (e.g. Qiu et al. 2019), but research establishing the role of microbes on gametophytes is still in its infancy. Microbial communities obtained from urbanised nearshore waters negatively affected *M. pyrifera* gametophyte abundance and size, whereas microbes from more pristine environments enhanced growth when present in intermediate abundance (Morris et al. 2016; Figure 4). A positive association with bacteria has also been shown when associated microbiota negate the toxic effects of polluting metals (Wang et al. 2020), but negative effects may occur when fast growing filamentous bacteria compete for space with gametophytes in polluted environments (Reed et al. 1994). Evidently, interactions with microbes may either increase or decrease the resilience of gametophytes to ocean change factors such as pollution and urbanization, and through their manipulation might prove a functional method of increasing resilience (Egan et al. 2013).

Effects of grazing on gametophytes

Increased grazing by herbivores on adult sporophytes is recognized as a pressing threat to kelp forest persistence under climate change (Santelices & Ojeda 1984, Vergés et al. 2014, Ling et al. 2015) due to either increases in rates of herbivory from co-occurring grazers (Provost et al. 2017, Rich et al. 2018, Miranda et al. 2019) or climate-driven poleward extensions of herbivores into temperate systems (Vergés et al. 2014, Ling et al. 2015, Vergés et al. 2016). Less is known, however, about how grazing affects the gametophyte stage. It has been shown in laboratory settings that grazing by echinoderms and gastropods can negatively affect gametophyte growth and recruitment (Leonard 1994, Martinez & Santelices 1998, Zacher et al. 2016, Veenhof et al. 2022; Figure 4) and it is hypothesized that amphipods, urchins and fish can also graze on gametophytes (Dayton et al. 1984, Amsler et al. 1992, Sala & Graham 2002, Franco et al. 2017). Although grazing is seen as a negative impact on successful kelp recruitment, herbivores can enhance gametophyte survival and subsequent sporophyte recruitment if herbivores graze selectively on competing understory algae (Henriquez et al. 2011, Zacher et al. 2016). In a multifactor design, Zacher et al. (2016) showed a species-specific response where temperature, sedimentation and grazing pressure can either decrease or stimulate gametophyte growth of *Alaria esculenta*, *L. digitata* and *S. latissima*. Specifically, the direction of singular effects was similar for all species, where increased temperature benefited germination and grazing increased sporophyte density, but sedimentation decreased recruitment of sporophytes. However, the interactive effects between grazing and abiotic factors were species-specific and could reinforce the positive effects of increased temperature and decreased disturbance of sedimentation (Zacher et al. 2016). As these are all factors that are influenced by ocean change, their study showed that climate change may alter kelp composition in a complex and hard to predict manner.

Grazing by herbivores appears to have a greater direct negative impact on gametophytes than on juvenile sporophytes (Martinez & Santelices 1998), but can have an indirect positive influence on gametophyte survival through removal of sediment (Zacher et al. 2016) and competing algae (Henriquez et al. 2011) as well as enhancing fertilization and sporophyte recruitment following grazer ingestion (Veenhof et al. 2022). Sustained urchin barrens indicate recruitment of adult

sporophytes is prevented by grazing; however, there is an indication that algal diversity is still present on a microscale (Akita et al. 2019, Coleman & Kennelly 2019, Shum et al. 2019). Additionally, spores of *L. nigrescens* can survive digestion by sea urchins, and other seaweed species can be recruited from fertile material after digestion by molluscs (Santelices et al. 1983, Santelices & Correa 1985, Veenhof et al. 2022). The sparse amount of research on grazer and gametophyte interactions makes these conclusions preliminary, but the complexity of interactions between herbivores and microscopic stages of kelps and the paucity of knowledge of the biotic microenvironment gametophytes inhabit will mean that filling this knowledge gap will be central in understanding kelp persistence under increasing ocean change.

Future opportunities & knowledge gaps

Climate change is one of the most pressing issues faced by marine ecosystems globally (Henson et al. 2017). Predicted increases in temperature, acidification, UV radiation and non-climate related human impacts will affect ocean physics and chemistry (Collins et al. 2019), which in turn affects species physiology, distributions and interactions (Harley et al. 2012, Field et al. 2014). Negative impacts on kelp forests such as loss of biodiversity and change in ecological structure are already apparent (e.g. Wernberg et al. 2013, Filbee-Dexter et al. 2016, Berry et al. 2021) and climate projections suggest further loss in the future (e.g. Assis et al. 2017, Davis et al. 2021b). The response of gametophytes to environmental factors predicted to change in future oceans gives both concern and hope for the long-term persistence of kelp forests.

This review has revealed that gametophytes appear to be relatively tolerant to a wide range of ocean temperatures and light (Müller et al. 2012, Mabin et al. 2013, Hollarsmith et al. 2020), albeit with responses dependent on location (Oppliger et al. 2012, Mohring et al. 2014, Muth et al. 2019, Martins et al. 2020) and thermal history (Liesner et al. 2020). Temperature increases may have the largest impacts on gametophytes of temperate and warm adapted kelps (e.g. Gonzalez et al. 2018, Augyte et al. 2019, Hollarsmith et al. 2020), and could partly underpin recruitment failure and large sporophyte declines in populations around the world (Muth et al. 2019, Wernberg et al. 2019b), particularly at warm range edges (Vergés et al. 2016, Smale et al. 2019). Summer temperatures and/or temperature anomalies such as marine heatwaves are increasingly exceeding the temperature thresholds for stage transitions in gametophytes in the south-east Pacific Ocean (Shukla & Edwards 2017, Gonzalez et al. 2018, Muth et al. 2019) and the North Sea (Müller et al. 2008, Bartsch et al. 2013). As future kelp persistence and distribution may largely be driven by thermal tolerance (Martínez et al. 2018), understanding thermal plasticity in the gametophyte stage should be a prime direction of future research. Some advances have been made in understanding the genetic basis for thermal tolerance (Liu et al. 2019), how these genetic patterns manifest under naturally occurring temperature gradients in the field (Vranken et al. 2021) as well as the potential for adaptive capacity of gametophytes under increased heat stress (Mabin et al. 2019, Vranken et al. 2021), but more research is required to demonstrate causation and link these patterns to conditions characteristic of field settings (but see Liesner et al. 2020). Efforts to map and preserve thermal and adaptive genetic variation more generally will also inform the capacity of gametophytes to face the challenge ocean warming poses (Wade et al. 2020, Coleman et al. 2020b, Wood et al. 2021).

Even though gametophytes can be resilient to a variety of temperature and light regimes, their phase changes (i.e. gametogenesis, recruitment of sporophytes) are tightly linked to specific environmental cues which may be disrupted and alter population dynamics in the future (de Bettignies et al. 2018, Capdevila et al. 2019, Muth et al. 2019). The reproductive phenology of many kelps is likely to change with changes in seasonal temperatures and duration, and this may result in gametophytes growing under different environmental conditions than in the past (Martins et al. 2017). Kelp life cycles respond to circannual rhythms (tom Dieck 1991, Lüning 1991), with irradiance and temperature providing important cues in the onset of gametogenesis (Lüning 1980, Roleda 2016).

This might cause a mismatch between environment (e.g. optimum temperature for growth of gametophytes) and the developmental transition from gametophytes to sporophytes (de Bettignies et al. 2018), as optimum conditions for growth can differ from those measured for survival (Mohring et al. 2013a) or fertility (Bolton & Levitt 1985, Martins et al. 2017). In addition, thermal conditions during early stages can have repercussions on performance in successive life stages (Liesner et al. 2020). However, the ability of gametophytes to remain in a dormant state when conditions are unfavourable for weeks to several months (Hoffmann & Santelices 1991, Barradas et al. 2011, Carney et al. 2013; Figure 5) could mitigate this problem, and potentially facilitate a shift in growing season and persistence through harsh conditions.

The potential of kelp gametophytes to temporarily persist through harsh conditions as a microscopic seedbank (Hoffmann & Santelices 1991, Santelices et al. 2002, Carney et al. 2013, Schoenrock et al. 2020) is a current and relevant topic of discussion (Schoenrock et al. 2020; Figure 5). In laboratories, gametophyte cultures can be preserved for decades (e.g. tom Dieck 1993). In field studies, however, tracking gametophyte growth and recruitment on out-planted microscope slides indicates recruitment occurs over a short period, suggesting multiple short 'reproductive windows' rather than long-term persistence of a bank of microscopic forms (Deysher & Dean 1986a, Reed et al. 1994, 1997). Field-based experiments have also tracked the regrowth of kelp beds following canopy removal as an indication of the persistence of microscopic gametophytes in the field in a dormant form (Barradas et al. 2011, Hewitt et al. 2005, McConnico & Foster 2005) or in the form of microscopic sporophytes (Kinlan et al. 2003), and found recruitment with no apparent source of spores, indicating the presence of dormant microscopic stages (Schoenrock et al. 2020). Additionally, several studies using genetic markers have established a widespread presence of gametophytes in the field (i.e. Bringloe et al. 2018, Fox & Swanson 2007, Robuchon et al. 2014) and genetic parentage analyses of recruits suggest that a bank of gametophytes of mixed age and origin may exist (Carney et al. 2013). The benefits of a bank of microscopic forms with a mixed genetic make-up may lie in the ability to preserve genetic variability that supports the adaptive capability to changing conditions (Carney et al. 2013,
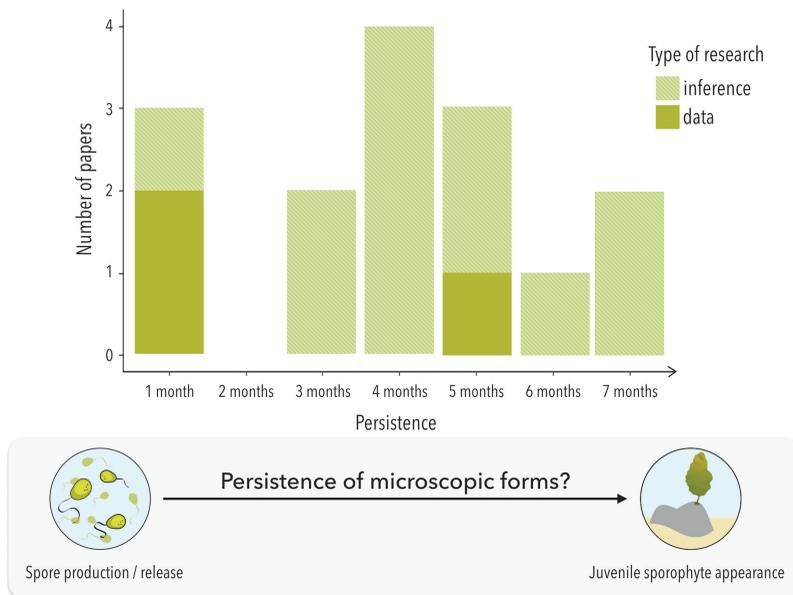

Figure 5 A collation of studies that research the possibility of microscopic forms of kelps persisting for different periods. Studies are categorized by whether the study was based on data from gametophytes tracked in the field ("Data"), or by tracking recruitment after canopy removal ("Inference").

Coleman & Goold 2019, Coleman & Wernberg 2020, Wade et al. 2020). Persisting through harsher conditions and recruiting when environmental conditions are suitable may indeed be of great benefit for overall kelp forest health and recovery.

The existence of banks of microscopic forms would be unlikely to present a pathway for persistence through extreme events, such as marine heatwaves, that exceed the physiological thresholds of gametophytes. Indeed, failure of kelp to recover following loss of sporophytes after extreme events (e.g. Wernberg et al. 2013, Filbee-Dexter et al. 2016, Arafeh-Dalmau et al. 2019) suggests that gametophytes cannot survive, or their stage transitions are hindered, during such extreme conditions, and recovery may be dependent on dispersal of spores from surviving sporophyte populations. Indeed, refugia from grazing pressure in cryptic habitats (Zarco-Perello et al. 2021) and temperature and reduced salinity in deep kelp forests (Davis et al. 2021a, 2022) are potential sources of replenishment. Field studies suggest that the majority of sporophytes that recruit in natural populations are thought to have originated from recently settled spores (Reed et al. 1997). Certainly, there is little empirical evidence that gametophytes persist vegetatively for more than ~7 months (Figure 5). Whether and for how long gametophytes can persist as a dormant bank of microscopic forms through warming or other impacts remains a critical knowledge gap that needs to be filled to determine the future of kelp forests, by developing creative solutions to link field research with understanding from laboratory studies.

The development of germplasm or culture banks may help secure the future of kelps and their adaptive capacity (Wade et al. 2020). Germplasm banks hold the potential to preserve threatened or lost genetic and adaptive diversity and facilitate reseeding and restorative initiatives (Coleman et al. 2020b, Wade et al. 2020). Indeed, algal culture libraries that were established decades ago are still used for current experiments (e.g. Martins et al. 2019) and are commercially available (e.g. https://ku-macc.nbrp.jp/strain/list). Building on these historical culture collections, *M. pyrifera* gametophytes have been successfully preserved in germplasm banks for up to 5 years, representing genetically distinct gametophyte cultures to preserve naturally occurring genetic diversity (Barrento et al. 2016). Indeed, loss of kelp populations is already being addressed through restoration (Bekkby et al. 2020, Coleman et al. 2020b, Eger et al. 2020a,b, Layton et al. 2020b, Vergés et al. 2020) and the existence of algal culture collections can play a role in this process (Filbee-Dexter et al. 2022). Recently, gametophytes have been harnessed to develop a novel kelp restoration tool, "green gravel", whereby gravel is seeded with gametophytes in the laboratory before being out-planted into the field as juvenile sporophytes and gametophytes (Fredriksen et al. 2020). This method is now being applied globally (www.greengravel.org). Successful restoration of kelp forests has been achieved in the past by out-planting juvenile sporophytes (Wilson & North 1983, Hernández-Carmona et al. 2000, Eger et al. 2020a), but green gravel overcomes the challenges of such techniques by eliminating the need to employ divers or use engineered structures and allows control over what genotypes are seeded (Fredriksen et al. 2020). This technique provides an ideal platform to 'future-proof' kelp forests via utilising culture banks to seed gravel and restore reefs with either enhanced genetic diversity or specific adaptive traits (Coleman et al. 2020b, Coleman & Wernberg 2021) or primed individuals with increased thermal tolerance (Jueterbock et al. 2021).

Ecological interactions are also set to change in future oceans and their role in the gametophyte stage remains a critical knowledge gap. Specifically, competition of kelp gametophytes with species that perform better under higher sedimentation rates, nutrients and acidification such as turfing algae warrants more research, as this form of competition will likely become increasingly apparent under future climates (Tatsumi & Wright 2016, Filbee-Dexter & Wernberg 2018, O'Brien & Scheibling 2018). Similarly, elucidating the role of positive interactions among kelp and other algal species, such as the role of microbiomes, may present novel pathways for enhancing resilience in a restoration context (Eger et al. 2020a).

The application of novel genomic techniques has great potential to advance the understanding of the persistence of gametophytes in changing oceans. Specifically, genomics should be used to

identify the presence of gametophytes in the field (e.g. Robuchon et al. 2014, Bringloe et al. 2018, Akita et al. 2019, Shum et al. 2019, Nagasato et al. 2020, Schoenrock et al. 2020) and link presence to changing environmental conditions, including persistence through extreme events. The differences in the response of gametophytes versus sporophytes to environmental change can be understood through examining patterns of selection through genomic data (Vranken et al. 2021) as well as transcriptomics (Liu et al. 2019). Further linking loci to annotated kelp genomes may provide insights into the functions that mediate such patterns (Vranken et al. 2021) and more investment into sequencing kelp genomes is needed. Identification of genes and variants that perform better under future climatic conditions could even pave the way for the development of climate-resilient transgenic gametophytes through genetic engineering or synthetic biology (Coleman & Goold 2019, Coleman et al. 2020b) transforming the way we conserve and manage kelp in future oceans.

Clearly, gametophytes are an essential part of kelp forest persistence and research investigating their responses to climate and anthropogenic impacts is beginning to reveal their role in predicted future ocean ecosystems. The ability of gametophytes to persist in a dormant state through harsh environmental conditions may be facilitated by their broader tolerance to environmental stress relative to sporophytes, but where, when and for how long this may occur remain overarching knowledge gaps. With present kelp loss in many parts of the world, it is apparent that proactive interventions are required to reverse and prevent ongoing degradation of kelp forests (Coleman et al. 2020b). Through their relative tolerance to a wide range of conditions, experimental and genetic tractability, and capability to be cultured and stored, gametophytes may hold the key to designing and implementing proactive management and conservation strategies to secure the future of kelp forests.

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