



It's the Little Things: The Role of Microscopic Life Stages in Maintaining Kelp Populations

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Kelp forests are experiencing broad scale declines in abundance and shifts in latitudinal ranges in many areas of the world due to numerous environmental stressors, especially those associated with climate change. While the majority of studies on kelp ecology have focused exclusively on the macroscopic sporophyte life stage, a growing number of studies is showing quite convincingly that the microscopic zoospore and gametophyte life stages can be important to establishing spatial patterns in these marine forests, and in facilitating their recovery following deforestation. Unfortunately, their microscopic sizes have made them difficult to study in the field, leading to a 'black box' surrounding what we know about their ecologies. However, advances in experimental methodologies and a growing number of laboratories studying kelp microscopic life stages are revealing how they are affected by variability in environmental conditions, and are providing a clearer picture of how kelp forests might respond to a changing ocean climate. These studies have largely revealed that kelps can disperse over a wide range of distances, enhanced by the synchronous release and vertical transport of zoospores into shallower water, and by floating rafts of reproductive thalli. Settlement on the benthos is facilitated by both positive and negative chemotaxis, and by active selection of microhabitats that favor their growth and survival. Following settlement and subsequent germination, the haploid gametophytes can delay their development and form a bank of microscopic forms that persist during periods that are unfavorable for the large sporophyte populations, or they can develop and undergo sexual reproduction during which they respond to variability in environmental conditions. In particular, they are strongly affected by increases in irradiance (PAR, UVA + UVB) and temperature, decreases in nutrients and salinity, and by sedimentation and grazing. However, the manner in which they respond to these stressors varies among species and with their geographic distributions, which is integral to establishing biogeographic patterns in the large sporophyte populations. Given these factors are expected to change as the ocean climate changes, these species-specific responses have significant implications for future patterns of distribution and abundance of these iconic marine forests.

Keywords: climate change, gametophyte, kelp, microscopic, recruitment, sporophyte, zoospore

INTRODUCTION

Much has changed in our understanding of kelp microscopic life stages during the almost three decades since I first sterilized experimental reef patches in Carmel Bay, CA, USA to evaluate the role of a bank of microscopic life stages in the brown alga *Desmarestia ligulata* that delayed their reproduction during the winter and then produced sporophytes the following spring. Since then, the number of studies on the ecology and physiology of kelp microscopic life stages has grown tremendously, providing a much clearer picture of the role they play in kelp forest ecology and in the resiliency of these forests in the face of environmental variability. The reasons for this increase in studies are varied, but presumably include advances in or ability to study these stages in the field, a growing number of laboratories that are working on them, and an enhanced appreciation of the role these early life stages play in kelp forest ecology. While this has helped unlock the 'black box' surrounding what we know about kelp microscopic life stages, it remains unclear how they will be affected by climate change, and what this will mean for the biogeography and resiliency of kelp forests in the future. In this review, I discuss consequential discoveries surrounding these cryptic life stages and how they influence the biogeography of sporophyte populations that make up these iconic forests. I begin with a discussion of how kelps disperse over both long (100's to 1,000's of kilometers) and short (meters to 10's to meters) distances, and how this relates to their recovery following deforestation. I follow this with an examination of the potential for these microscopic life stages to delay their development and form a 'bank of microscopic forms' that allows them to survive during periods of unfavorable conditions. I then explore how variability in irradiance (PAR, UVA + UVB), temperature, nutrients, salinity, seawater pH, sedimentation, and grazing affects the survival, development, and reproduction of these microscopic life stages, and how this can determine biogeographic patterns of macroscopic sporophytes at both local and regional scales. I end with a discussion of the potential of using microscopic life stages in the conservation of kelp forests. For each of these topics, I discuss how these patterns may change under future ocean conditions as predicted by climate change.

KELP FORESTS IN A CHANGING CLIMATE

Anthropogenic activities have raised atmospheric carbon dioxide concentrations from a relatively stable 182–300 ppm over the past 800,000 years (Lüthi et al., 2008) to modern levels exceeding 400 ppm (Mauna Loa Observatory, NOAA). Future projections estimate that atmospheric CO₂ will surpass 1000 ppm by the year 2100 (IPCC, 2013). Ocean uptake of this excess CO₂ (Sabine et al., 2004) and the resulting atmospheric heat is causing the oceans to become more acidic (Doney et al., 2009), warmer (Levitus et al., 2005; Scheffer et al., 2006), and less productive (Gregg et al., 2005; Polovina et al., 2008). Further, as atmospheric and ocean temperatures continue to rise, glacial ablation and

enhanced precipitation are increasing freshwater discharge into coastal environments, which is lowering seawater salinities (Boyer et al., 2005; Dyurgerov and Meier, 2005; Arendt et al., 2009; Bieniek et al., 2014; Reisdorph and Mathis, 2014), altering circulation patterns and biogeochemical fluxes (Neal et al., 2010; O'Neel et al., 2015), and intensifying the effects of ocean acidification (Reisdorph and Mathis, 2014). These impacts are especially strong in mid to high latitudes (Miller et al., 2010; Doney et al., 2012) where the nearshore ecosystems are dominated by large forests of kelp (brown algae in the Order Laminariales) that provide food and habitat for numerous other organisms (Konar et al., 2015; Teagle et al., 2017; Metzger et al., 2019; Gabara et al., 2021), enhance primary production (Miller et al., 2011; Edwards et al., 2020; Spector and Edwards, 2020; Sullaway and Edwards, 2020), uptake and store inorganic carbon (Wilmers et al., 2012), alter seawater chemistry (Gonzales et al., 2017; Pfister et al., 2019; Corrano et al., 2020; Corrano et al., 2021), regulate nutrient fluxes (Jackson, 1977), and modulate hydrodynamic activity (Jackson and Winant, 1983; Hondolero and Edwards, 2017). As with other seaweeds (e.g. *Ulva*; Bews et al., 2021), kelps sequester heavy metals (Evans and Edwards, 2011) and nutrients (Kim et al., 2015) into their tissues, and can therefore be used for bioremediation of polluted waterways. They are also harvested for their nutritional and industrial properties (Borras-Chavez et al., 2012; Borras-Chavez et al., 2016). Consequently, a more detailed understanding how these forests are affected by climate change stressors will be fundamental to predicting patterns of their distribution and abundance, and how coastal ecosystems will function and be used in the future.

Kelp forests have been experiencing broad scale declines in distribution and abundance, and shifts in their latitudinal ranges in many areas of the world due to climate change (Connell and Russell, 2010; Wernberg et al., 2010; Filbee-Dexter et al., 2016; Krumhansl et al., 2016; Assis et al., 2017; Provost et al., 2017; Assis et al., 2018; Beas et al., 2020; Smale, 2020; Wernberg et al., 2019a). They are also subject to deforestation on local scales from a variety of factors, including large storm-driven waves (Ebeling et al., 1985; Seymour et al., 1989; Cavanaugh et al., 2011), El Niño Southern Oscillations (ENSOs) (Tegner and Dayton, 1987; Edwards, 2004; Edwards and Estes, 2006; Edwards, 2019), marine heat waves (Reed et al., 2016; Wernberg et al., 2016; Cavanaugh et al., 2019; Rodgers-Bennet and Catton, 2019; McPherson et al., 2021), sewage discharges and/or spills (Tegner et al., 1995; Connell et al., 2008; Foster and Schiel, 2010), and overgrazing by herbivorous urchins (Estes et al., 1998; Scheibling et al., 1999; Jeon et al., 2015). Indeed, modeling exercises suggest that populations of the kelp *Macrocystis pyrifera* have a 60% chance of being completely lost from many locations along the California coast, USA during any 20-year period (reviewed in Reed et al., 2006). Given several of these environmental stressors can occur simultaneously, it can be difficult to identify a single stressor responsible for driving kelp loss (Edwards, 2004; Wernberg et al., 2010). Evaluating how these forest recover from these losses can be even more difficult, but doing so will be necessary to predict how kelp forests will ultimately fare under a changing climate.

Kelps exhibit heteromorphic life histories that alternate between microscopic and macroscopic life stages (North, 1994). Specifically, they follow a diplo-haplontic life history in which large diploid sporophytes release microscopic haploid zoospores from reproductive sori on either vegetative or specialized reproductive blades (i.e. sporophylls). These zoospores then disperse across a range of distances and settle on the benthos where they undergo gametogenesis and become either male or female haploid microscopic gametophytes. These gametophytes then produce sperm and eggs, which undergo syngamy to produce embryonic diploid sporophytes that grow in to the next generation of large sporophytes. Generally, the gametophytes need to be in close proximity (i.e. 1mm or closer) to each other to allow the sperm to swim to the eggs for sexual reproduction to occur (Reed et al., 1997). To aid this, female gametophytes release pheromones such as lamoxirene and desmarestene, which can be the main components in egg secretions and cause the male gametophytes to release sperm (Maier et al., 2001). The sperm then exhibit chemotaxis, allowing them to swim to and fertilize the eggs. Although lamoxirene has been identified as the most common pheromone produced in several European and North Pacific kelp species in the genera *Laminaria*, *Alaria*, *Undaria* and *Macrocystis*, some species such as *Laminaria digitata* may rely on desmarestene as a more potent chemoattractant (Maier et al., 2001). This suggests that while pheromone-induced sperm release and attraction is conserved among different kelp species, species-specific diversification of complex egg secretions and pheromone receptors can be observed at the chemoattraction level (Maier et al., 2001).

While most studies of kelp forest disturbance and recovery have focused on the large diploid sporophyte stage (e.g. Dayton et al., 1984; Ebeling et al., 1985; Seymour et al., 1989; Edwards, 2004; Edwards and Estes, 2006; Cavanaugh et al., 2011; Cavanaugh et al., 2019; Edwards, 2019), numerous studies have shown convincingly that the haploid microscopic life stages play a critical role in population recovery and in establishing spatial patterns in the larger sporophytes (e.g. Pierce and Cowling, 1991; Ladah et al., 1999; Swanson and Druehl, 2000; Ladah and Zertuche-González, 2007; Wernberg et al., 2019b; Beckley and Edwards, 2021). Given that these microscopic life stages could serve as population bottlenecks (*sensu* Underwood and Fairweather, 1989), it is important to understand how they respond to environmental variability. Unfortunately, their microscopic sizes and cryptic nature has made them difficult to study in the field (Hsiao and Druehl, 1973; Dayton, 1985; Edwards, 1999; Wernberg et al., 2019b), leading to a black box surrounding what we know about their ecologies and their roles in kelp forest resiliency. However, following Neushul's (1972) development of a subtidal microscope, advances in genetic analyses of the macroscopic sporophytes (e.g. Coyer et al., 1997; Swanson and Druehl, 2000; Macaya and Zuccarello, 2010; Carney et al., 2013), eDNA metabarcoding of biofilms on natural and biogenic substrates (e.g. Fox and Swanson, 2007; Rubechon et al., 2014; Peters et al., 2015; Akita et al., 2019; Akita et al., 2020a; Akita et al., 2020b), and in experimental field-based techniques that include the use of fluorescent markers

(e.g. Cole, 1964; Hsiao and Druehl, 1973; Edwards, 1999; Edwards, 2000), spectrophotometric evaluation of their photosynthetic pigments (e.g. Graham, 1999; Graham and Mitchell, 1999), the collection and laboratory culturing of natural (e.g. Silva, 1992) and outplanted (e.g. Hoffman and Santelices, 1991) substrates, and the sterilization of reef patches to remove the microscopic forms (e.g. Edwards, 1999; Edwards, 2000; Carney et al., 2013) have allowed for a more detailed study of them in the field. Perhaps more informative, however, is their examination in the laboratory under controlled conditions, which has provided an in-depth evaluation of their responses to environmental variability (reviewed in Veenhof et al., in press; Carney and Edwards, 2006; Schiel and Foster, 2015, this paper). As a consequence, the number of published studies on environmental effects on kelp microscopic stages has grown considerably over the past two decades (reviewed in Veenhof et al., in press), which has helped unlock the black box surrounding what we know about them.

ZOOSPORE DISPERSAL

A fundamental hurdle to understanding how kelp forests colonize newly available habitats is to discern how they disperse over long distances (Hoffman, 1987; Reed et al., 1988; Reed et al., 1992; Reed et al., 2000; Reed and Schroeter, 2004; Batista et al., 2018). For instance, some kelps that possess gas-filled portions of their thalli (e.g. in the genera *Macrocystis*, *Nereocystis*, *Eualaria*, *Egregia*, and *Pelagophycus*) may be able to disperse over distances of 100's to 1000's of kilometers or more when reproductive sporophytes are dislodged from the substrate and become floating rafts that are transported long distances *via* offshore currents (reviewed in Thiel, 2003). Such long-distance dispersal from detached macroalgae is believed to have allowed some algae to colonize oceanic islands (reviewed in Van den Hoek, 1987), and may be important in the face of climate change if it increases connectivity among disparate locations, or it opens new areas for colonization (Molinos et al., 2017; Batista et al., 2018). Indeed, floating rafts of *Macrocystis pyrifera* are commonly observed along the west coasts of North and South America (Dayton et al., 1984; Dayton, 1985; Hobday, 2000; Macaya et al., 2005; Hernández-Carmona et al., 2006; Rothäusler et al., 2009; Hinojosa et al., 2010; Macaya and Zuccarello, 2010), where they have been identified as important long distance dispersal vectors (Batista et al., 2018). Similarly, drifting *Nereocystis leutkeana* with reproductive sporophylls have been observed cast on the beach and floating near the coast of Shemya Island in the Aleutian Archipelago, which is approximately 1,170 kilometers to the west of the western range limit of the species at Unmak Island, Alaska (Miller and Estes, 1989). However, *Nereocystis leutkeana* has yet to establish large sporophytes to the west of Unmak Island, which may be due to constraints posed on its microscopic life stages (Miller and Estes, 1989; discussed below). *Nereocystis leutkeana* sporophytes have also been observed drifting along the coast of Oregon, USA where they have been identified as an

important vector for the colonization of associated flora and fauna (Kidder, 2006). In contrast, numerous kelp species do not possess gas-filled thalli, but at least some species (e.g. *Ecklonia radiata*) may exhibit long-distance dispersal *via* drifting thalli if they co-occur with other buoyant species such as *Sargassum* spp. (reviewed in Wernberg et al., 2019b). Still, others may possess gas-filled stipules in parts of their geographic ranges but not in others, as observed in *Eisenia arborea* (Matson and Edwards, 2006), though it is unknown if this allows for floatation after dislodgement.

Long distance dispersal from floating thalli may be important to the recovery of kelp forests following widespread deforestation. For example, *Macrocystis pyrifera* populations exhibited widespread losses over several hundred kilometers along Baja California, MEX during the 1997-98 ENSO (Ladah et al., 1999; Edwards, 2004; Edwards and Hernández-Carmona, 2005; Edwards and Estes, 2006; Lahad and Zertuche-González, 2007; Edwards, 2019). These forests recovered rapidly at some locations but took several years to recover at others (Edwards and Estes, 2006). However, it is unclear if recovery of these populations was facilitated by long distance dispersal of floating thalli. It is also unclear if long distance dispersal from floating thalli will be important to the recovery of the *Nereocystis leutkeana* populations that have been lost over large areas of the coast of northern California, USA following a marine heatwave and a strong ENSO (Rodgers-Bennet and Catton, 2019) or the *Eualaria fistulosa* populations that have been decimated by urchin grazing throughout most of the Aleutian Archipelago, USA (Estes et al., 1998; Konar et al., 2014; Metzger et al., 2019). Similar patterns of local and widespread kelp loss have been observed in Western Australia (Vanderklift and Wernberg, 2008), South Korea (Jeon et al., 2015), Maine, USA (Steneck et al., 2002), Nova Scotia, CAN (Scheibling et al., 1999), Spain (Voerman et al., 2013), Norway (Fagerli et al., 2013), British Columbia, CAN (Spindel et al., 2021), and central and southern California, USA (Ebeling et al., 1985; Pearse and Hines, 1979; Parnell, 2015) (also reviewed in Krumhansl et al., 2016). Long distance dispersal from floating thalli can be especially important in the face of climate change if changes in wind patterns, ocean heat balances, and/or freshwater inputs from glacial melting and river discharges alter ocean current patterns (e.g. Neal et al., 2010; Sun et al., 2012; Cetina-Heredia et al., 2015; O'Neel et al., 2015; Hays, 2017; Voosen, 2020) and thus influence kelp raft routes and/or speeds. Therefore, a better understanding of the role of long-distance dispersal from reproductive drifting thalli, which remains equivocal (discussed in Reed et al., 1992), and whether this will be altered by climate change is important if we are to evaluate how kelp populations will recover from these losses and persist in the future. Thus, more work in this area is sorely needed.

On a local (i.e. reef) scale, kelp dispersal is predominantly carried out by microscopic zoospores that are passively transported *via* currents or wave orbitals (Dayton et al., 1984; Reed et al., 1988; Graham, 2003). While most studies suggest that the bulk of successful zoospore dispersal is generally limited to within a few meters of the parental sporophytes (Anderson and

North, 1966; Reed et al., 1988; Reed et al., 1992; Reed and Schroeter, 2004), reports based on modelling exercises (Gaylord et al., 2002; Gaylord et al., 2006), genetic analyses of the sporophytes they produce (Coyer et al., 1997; Carney et al., 2013; reviewed in Wernberg et al., 2019b), and the examination of glass microscope slides that had been placed at increasing distances from spore sources (e.g. Reed et al., 1988) have concluded that individual kelp zoospores can effectively disperse over distances of hundreds of meters to several kilometers. In the most extreme case, Amsler and Searles (1980) suggest that zoospores of *Macrocystis pyrifera* can disperse up to 35 km. Such long distance dispersal of individual zoospores can be facilitated through a variety of mechanisms, including the greater production and/or synchronous release of zoospores from specific locations within or near the edge of a forest (Reed et al., 1988; Amsler and Neushul, 1989a; Norton, 1992; Reed et al., 1997; Graham, 2003; Edwards and Konar, 2012), the vertical transport of zoospores into shallower portions of the water column where current velocities and dispersal potentials are greater (Amsler and Searles, 1980; Stevens et al., 2003; Cie and Edwards, 2011), and through processes that slow their sinking speeds (Hoffman and Camus, 1989; Gaylord et al., 2002; Raimondi et al., 2004). The latter may be aided by the fact that kelp zoospores possess large lipid reserves and are able to photosynthesize and swim while in the water column (Reed et al., 1992; Brzezinski et al., 1993). For example, the zoospores of *Macrocystis pyrifera* can swim for more than 120 hrs, though the majority of them likely stop swimming after about 48 hrs (Amsler, 1988; Amsler and Neushul, 1991; Reed et al., 1997). In contrast, the zoospores of *Ecklonia radiata* are able to swim for at least 24 hours but most appear to swim for only 1 or 2 hours (reviewed in Wernberg et al., 2019b), and few zoospores of *Laminaria hyperborea* likely swim for longer than 20 hours (Kain, 1964). However, swimming may affect their ability to settle, though this appears to vary among species. For example, *Macrocystis pyrifera* zoospores lose their ability to settle soon after they stop swimming, while *Pterygophora californica* zoospores appear to increase their ability to settle after they stop swimming (Reed et al., 1992). If the zoospores do not settle on the benthos, they can still form gametophytes, as observed in *Lessonia nigrescens* whose zoospores have been observed germinating after 4 days in the water column (Hoffman and Camus, 1989). It remains unclear, however, if these gametophytes can then settle on the substrate.

Even with the ability to swim for extended periods, kelp zoospores are likely too small ($\sim 3\text{--}7\ \mu\text{m}$) and their swimming speeds too slow ($\sim 0.0012\ \text{mm s}^{-1}$) to effectively disperse (Gaylord et al., 2002). Rather, swimming may simply allow the zoospores to find suitable substrates once in the boundary layer using chemotaxis (Amsler and Neushul, 1989b), or it may help move the zoospores vertically out of the boundary layer to prevent settlement, which can increase their time in the water column and thereby increase their current-driven dispersal potential (Amsler and Searles, 1980; Reed et al., 1988; Amsler et al., 1992; Reed et al., 1992). However, as zoospore dispersal distances increase, their density in the water column decreases

(Gaylord et al., 2002), resulting in diminishing settlement densities (Reed et al., 1997). This is important given the need for zoospores to be in close proximity so that the resulting male and female gametophytes are close to each other for successful sexual reproduction to occur (Dayton, 1985; Reed et al., 1997). On the other hand, increasing dispersal distances can also effectively reduce the density of related zoospores (i.e. siblings) settling next to each other, and thus decrease the negative effects associated with inbreeding (Raimondi et al., 2004; Carney et al., 2013). However, the negative effects of limited dispersal may be lessened if these species have already purged deleterious recessive alleles from their haploid stages, thereby allowing selfing to be an effective reproductive strategy as observed in *Postelsia palmaeformis* (Barner et al., 2010). Selfing may also allow species to more effectively colonize new habitats following long-distance dispersal given only a single individual needs to successfully establish there (Baker, 1955).

The transport of zoospores into shallower water can result in their being exposed to greater irradiances and higher planktonic grazer abundances, both of which reduce their survival and settlement competency (Cie and Edwards, 2008; Müller et al., 2009; VanMeter and Edwards, 2013). For example, VanMeter and Edwards (2013) exposed the swimming zoospores of *Macrocystis pyrifera* to mysids, which are small shrimp-like planktonic grazers that are abundant in southern California, USA kelp forests (Coyer, 1984; Turpen et al., 1994). They then used fluorescence microscopy to identify chlorophyll in the mysid guts and verified that they did in fact consume the zoospores, which in turn resulted in significant reductions in zoospore settlement relative to conditions without mysids. This is important given these mysids are more abundant in the shallower portions of the kelp canopies than near the benthos (Coyer, 1984; VanMeter and Edwards, 2013). This has obvious implications for the future if climate change alters the abundance of planktonic grazers in these forests, which may be expected given that changes in the distribution and phenology of zooplankton are occurring in numerous places in the world (e.g. Richardson, 2008; Johnson et al., 2011; Dam and Baumann, 2017). High irradiance (PAR, UVA+UVB) also negatively affects kelp zoospores, but these effects vary among kelp species (Swanson and Druehl, 2000; Wiencke et al., 2000; Roleda et al., 2005; Cie and Edwards, 2008; reviewed in Bischof et al., 2006). For example, Cie and Edwards (2008) exposed the swimming zoospores of *Macrocystis pyrifera* and *Pterygophora californica* to a range of irradiances between 75 and 1050 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR for periods of time between 1 and 12 hrs and found that while settlement of *Macrocystis pyrifera* was not significantly affected by exposure to high irradiance, settlement of *Pterygophora californica* was significantly reduced, and this effect strengthened with longer exposure times. Indeed, *Pterygophora californica* settlement completely ceased when its zoospores were exposed to irradiances of $\geq 575 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR for 12 hrs. Further, exposure to high irradiances resulted in delayed effects to the benthic microscopic life stages following settlement, as *Macrocystis pyrifera* zoospores did not produce viable gametophytes or embryonic sporophytes

following settlement when they were exposed to irradiance of 75 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR for 12 hrs, or to irradiances of 1025 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR for as little as 4 hrs. In contrast, *Pterygophora californica* zoospores produced gametophytes and embryonic sporophytes under all irradiances and exposure times tested, although the density of these decreased with increasing irradiance and exposure times. Interestingly, the negative effects of high irradiance often do not appear in the adult sporophytes (Edwards and Kim, 2010; Fejtek et al., 2011). Rather, this appears to be related to the light harvesting characters associated with photosystem II in the zoospores, which Graham (1999) found to be significantly different among even closely related kelp species. This difference is sufficient to discriminate among species of kelp zoospores using micro spectrophotometry (Graham, 1999; Graham and Mitchell, 1999). Regardless of their tolerances to high irradiances, shading from the kelp canopies can decrease irradiance within kelp forests and thus reduce these negative effects, as seen for *Alaria esculanta* along the coast of Kongsforden, Svalbard in the Arctic Ocean (Laeseke et al., 2019). Further, some kelps (e.g. *Nereocystis leutkeana*) may avoid exposing their zoospores to high irradiances by releasing them within a few hours just before or after sunrise (Amsler and Neushul, 1989a).

The negative effects of high irradiance on zoospores may be important in establishing patterns of depth distributions in the large sporophyte populations. For example, Swanson and Druehl (2000) measured zoospore tolerance to UV light in *Macrocystis pyrifera*, *Pterygophora californica*, *Saccharina groenlandica*, and *Hedophyllum sessile* within Barkley Sound, British Columbia and found that it correlated with sporophyte depth zonation patterns for each species. Likewise, Wiencke et al. (2000) found that when the zoospores from different species of kelp in Spain and Norway were exposed to similar levels of UV light, the zoospores from species occurring in deeper water exhibited lower germination rates than those obtained from species in shallower water. These negative effects, however, varied depending on the quality (wavelength) of light the zoospores experienced. Specifically, zoospores exhibited higher mortality when exposed to PAR+UVA+UVB than when exposed to PAR+UVA or PAR alone. Wiencke et al. (2000) also concluded that the loss of zoospore viability in species such as *Laminaria digitata* was primarily due to photo damage to the zoospores' DNA and photosystems. Similar findings from Helgoland, North Sea, have shown that zoospores obtained from deeper-water kelps such as *Laminaria hyperborea* are more strongly affected by UV light than the zoospores from shallower kelps such as *Laminaria digitata* and *Saccharina latissima* (Roleda et al., 2005), and that recovery of damaged photosystems was also related to their depth distributions, as *Laminaria digitata* exhibited greater recovery than either *Saccharina latissima* or *Laminaria hyperborea*. However, it should be noted that many kelp genera (e.g. *Nereocystis*, *Ecklonia*, *Eisenia*) do not fit obvious depth gradients, but rather span much of the water column and therefore may not be as reliant on zoospore tolerances to high irradiance. Regardless, the effects of irradiance can have important implications for the future if climate change results

in reduced productivity in coastal waters due to “coastal darkening” (Blain et al., 2021; Wollschläger et al., 2021) and/or greater losses of the kelp canopies due to increased storm activity (e.g. Seymour et al., 1989; Justic et al., 1997; Scavia et al., 2002; Behrenfeld et al., 2006; Byrnes et al., 2011; Bakun et al., 2015). Both of these can result in altered subtidal irradiances (Edwards, 1998; Clark et al., 2004; Foden et al., 2010) and thus altered patterns of zoospore production (Reed et al., 1988; Edwards and Konar, 2012). These impacts may be further exacerbated if increases in ocean acidification (OA) and/or ocean warming (OW) from climate change also negatively affect kelp zoospores. For example, Hoos (2015) showed that exposure to OA and OW resulted in mechanical and functional damage to the zoospores of *Egregia menziesii* that ultimately decreased their swimming speeds, settlement densities, adhesion abilities, and germination rates. Hoos (2015) concluded that these negative effects combined with reductions in habitat space for the macroscopic sporophytes will ultimately result in reductions in the abundance of future *Egregia* populations. Likewise, Shukla and Edwards (2017) found that exposing the zoospores of *Macrocystis pyrifera* to the individual effects of OA and OW resulted in decreased zoospore settlement and subsequent lower gametophyte production. Specifically, gametophyte production was four times greater when the swimming zoospores were exposed to 12°C than 15°C, and 25% greater when the zoospores were exposed to 400 μatm $p\text{CO}_2$ seawater than when they were exposed to 1500 μatm $p\text{CO}_2$ seawater. Given OA and OW are expected to increase in the future, this can have significant consequences on patterns of kelp abundance and distribution.

DO BANKS OF MICROSCOPIC LIFE STAGES FORM A ‘SEED BANK ANALOGUE’?

Once kelp zoospores have dispersed, they can settle on the benthos and germinate into male and female gametophytes. Settlement location appears to be non-random and selected for by the zoospores. For example, *Macrocystis pyrifera* and *Pterygophora californica* settlement is stimulated by nutrients, which may allow them to either choose or avoid microhabitats that favor or inhibit growth and reproduction in the resulting gametophytes (Amsler and Neushul, 1990). Further, selection of microhabitats may be aided by the zoospores actively swimming towards or away from microhabitats using chemotaxis (Amsler and Neushul, 1989b), and they can actively select surface depressions that facilitate survival once they are within the boundary layer (Amsler et al., 1992). Such surface depressions can then aggregate zoospore settlement, which will reduce the distance between gametophytes and enhance reproduction and sporophyte recruitment (Muth, 2012). Following settlement and germination, the resulting gametophytes can either undergo sexual reproduction and produce sporophytes, or they can delay reproduction and persist as a ‘bank of microscopic forms’ if environmental conditions are unfavorable to sporophyte growth and survival (Klinger, 1984; Chapman, 1986; Hoffman and Santelices, 1991; Blanchette, 1996; Ladah

et al., 1999; Carney and Edwards, 2006; Ladah and Zertuche-González, 2007; Carney and Edwards, 2010; Carney, 2011). More broadly, organisms that live in environments where conditions are temporally variable can reduce their metabolisms (Crowe, 1971; Pinter et al., 1984; Geiser, 2004; Heldmaier et al., 2004; Guidetti et al., 2011; Tøien et al., 2011; Careau et al., 2014; Dolinar and Edwards, 2021), or they can rely on alternate life stages that are either more tolerant of, or remain dormant during, periods of unfavorable conditions (Tauber and Tauber, 1978; Lubchenco and Cubit, 1980; Slocum, 1980; Hochachka and Guppy, 1987). These organisms can then emerge from dormancy and resume metabolic activity when conditions again become favorable for growth and survival (Hinton, 1968; Hollibaugh et al., 1981; Dolinar and Edwards, 2021). Indeed, the reliance on dormant life stages has been observed across a wide range of organisms, including terrestrial plants (Venable and Lawlor, 1980; Keeley, 1987; Leck et al., 1989), insects (Tauber and Tauber, 1978), microalgae (Hollibaugh et al., 1981), and marine crustaceans (Grice and Marcus, 1981; Maier, 1990). They have also been proposed for kelps and other marine macroalgae with similar diplo-haplontic life histories (Dayton, 1973; Dayton, 1985; Chapman, 1986; Hoffman and Santelices, 1991; Edwards, 2000; Kinlan et al., 2003; Carney and Edwards, 2006; Carney and Edwards, 2010; Carney, 2011; Carney et al., 2013; Ebbing et al., 2020; Schoenrock et al., 2021) where they have been shown to be important to sporophyte recruitment, especially when no sources of new zoospores are available (Dayton, 1973; Silva, 1992; Carney et al., 2005). For example, Silva (1992) collected biogenic substrates from deep water off Cordell Bank, California, USA and cultured them in the laboratory. He observed the recruitment of a *Nereocystis leutkeana* sporophyte on this substrate even though no apparent source of zoospores could be identified, and concluded that the sporophyte emerged from a vegetative gametophyte that had survived for several years. Likewise, Edwards (2000) sterilized the substrate in experimental plots on a rocky reef in Carmel Bay, California to remove all seaweed microscopic stages after all *Desmarestia ligulata* (a brown alga with a similar diplo-haplontic life history) sporophytes had disappeared from the reef due to natural senescence and winter storms, and found that this prevented new sporophyte recruitment in the following spring. In contrast, a dense recruitment of *Desmarestia* sporophytes was observed in adjacent non-sterilized plots. Lastly, Ladah and Zertuche-González (2007) suggest that microscopic life stages of *Macrocystis pyrifera* were able to survive the 1997-98 ENSO near their southern range limit in Baja California, MEX, perhaps in deeper water, and then promote kelp forest recovery following the ENSO.

Although numerous studies have suggested the importance of delayed development in kelp microscopic life stages, it remains unclear which life stage (haploid gametophytes, diploid sporophytes, or both) undergoes this delay. While the haploid gametophytes have most often been suggested as the life stage that undergoes delayed development (Kain, 1964; Dayton, 1973; Hsiao and Druehl, 1973; Klinger, 1984; Dayton, 1985; Silva, 1992;

Blanchette, 1996; Edwards, 1999; Ladah et al., 1999; Edwards, 2000; Carney and Edwards, 2010; Ebbing et al., 2020), some studies have suggested that diploid embryonic sporophytes may serve as the stage that delays development (Kinlan et al., 2003; Ladah and Zertuche-González, 2007). This distinction is important given that both male and female gametophytes need to survive in close proximity to each other to undergo sexual reproduction once they resume development. However, delaying development as diploid embryonic sporophytes can allow for more rapid sporophyte recruitment when conditions become favorable because only one individual (the sporophyte) needs to survive the delay period, and because sporophyte recruitment is not slowed by the need to undergo sexual reproduction after their period of delay, as reproduction has already occurred. This, therefore may offer a competitive advantage by producing macroscopic sporophytes more quickly than in any competitors (Carney and Edwards, 2010; Carney, 2011). Diploid stages may also be better adapted to a broader range of environmental conditions than their haploid counterparts due to a greater array of possible gene combinations, which may serve as protection against the expression of deleterious mutations, and thus are often selected for in macroalgae (Perrot et al., 1991; reviewed in Thornber and Gaines, 2004). For example, Muth et al. (2021) found that the microscopic diploid sporophytes of *Lamniaria solidungula* in the Beaufort Sea were more tolerant to decreased salinities than the haploid gametophytes, while Matson and Edwards (2007) similarly showed that the large sporophytes of *Eisenia arborea* along the west coast of California, USA and Baja California, MEX were more tolerant to elevated temperatures than the microscopic haploid gametophytes. In contrast, haploid gametophytes have lower mutational loads (Crow and Kimura, 1965) and lower nutritional requirements because they have half the DNA content (Lewis, 1985; reviewed in Thornber and Gaines, 2004). Although studies identifying the life stage that makes up the bank of microscopic stages are few, the outplanting of glass slides containing the microscopic stages of *Nereocystis leutkeana* (Hsiao and Druehl, 1973) and *Desmarestia ligulata* (Edwards, 2000) that had been stained with calcofluor white and then later collected and examined using fluorescence microscopy has identified microscopic gametophytes as the life stage that forms the banks of microscopic stages in the field.

The process of delaying development in kelp gametophytes can be triggered when they do not receive adequate nutrients (Carney and Edwards, 2010), levels of iron (Lewis et al., 2013), or light (i.e. photosynthetically usable radiation; PUR) (Ebbing et al., 2020). In general, blue light has been shown to be important to proper algal development (e.g. Dring, 1988). More specifically, depriving kelp gametophytes of blue light can result in their failing to undergo sexual reproduction, and instead may allow them to persist for long periods of time. Indeed, haploid gametophytes can survive in a vegetative state in the laboratory for years and still produce sporophytes when returned to conditions that favor sexual reproduction (Yoneshigue-Valentin, 1990; Hoffman and Santelices, 1991; tom Dieck, 1993; see also reviews in tom Dieck, 1993; Carney

and Edwards, 2006; Barrento et al., 2016). Delaying reproduction, in turn, may be beneficial if it allows for more rapid sporophyte recruitment when favorable conditions return. For example, Carney (2011) found that delayed development in the microscopic gametophytes of *Macrocystis pyrifera*, *Pterygophora californica*, *Pelagophycus porra* and *Laminaria farlowii* resulted in more rapid sporophyte production compared with recently settled zoospores, perhaps conferring a competitive advantage for these sporophytes. Haploid gametophytes have consequently been characterized as 'seed bank analogues' (Edwards, 2000; Ladah and Zertuche-González, 2007) that are of mixed ages and different parentages, which can reduce inbreeding (Carney et al., 2013). However, unlike plant seeds, kelp gametophytes are haploid and consist of dioecious males and females that can exhibit different reproductive strategies. For example, Destombe and Oppliger (2010) note that the male gametophytes of *Laminaria digitata* grow and reproduce simultaneously, while females stop growing after reproduction, which they suggest enhances the reproductive success of the species. However, it is important to note that some studies that have placed boulders within kelp forests to collect zoospores for different periods of time suggest that kelp microscopic stages have little capacity for long-term survival in nature, at least in *Macrocystis pyrifera* and *Pterygophora californica*, and that sporophyte recruitment is largely driven by newly settled zoospores (Reed et al., 1997). This is similar to observations for some terrestrial plant seed banks when sources of new seeds are available (e.g. Alvarez-Buylla and Martínez-Ramos, 1990; reviewed in Cohen and Levin, 1987).

Unlike the seeds of terrestrial plants that remain truly dormant during stressful periods, the microscopic life stages of marine algae are physiologically active and highly sensitive to even small changes in environmental conditions (Graham, 1996; Matson and Edwards, 2007; Fredersdorf et al., 2009; Fejtek et al., 2011; Martins et al., 2017), especially regarding the interactive effects of climate change (Gaitán-Espitia et al., 2014; Shukla and Edwards, 2017). In particular, they are known to be sensitive to increases in temperature (Lüning, 1980; Ladah and Zertuche-González, 2007; Matson and Edwards, 2007; Martins et al., 2017; Lind and Konar, 2017; Shukla and Edwards, 2017; Small and Edwards, 2021), irradiance and UV (Graham, 1996; Edwards, 2000; Kinlan et al., 2003; Müller et al., 2008; Fredersdorf et al., 2009; Roldana, 2009; Fejtek et al., 2011; Ebbing et al., 2020; Silva et al., 2022), sedimentation (Devanny and Volse, 1978; Carney et al., 2005; Deiman et al., 2012; Zacher et al., 2016; Traiger and Konar, 2017), and grazing (Dean et al., 1984; Leonard, 1994; Henríquez et al., 2011; Zacher et al., 2016), and to decreases in salinity (Fredersdorf et al., 2009; Lind and Konar, 2017; Muth et al., 2021), nutrient availability (Hoffman et al., 1984; Hernández-Carmona et al., 2001; Kinlan et al., 2003; Muñoz et al., 2004; Carney and Edwards, 2010), and ocean pH (Olischläger et al., 2012; Shukla and Edwards, 2017). Temperature, in particular, has been shown to have both positive and negative effects on kelp gametophytes, and these effects can vary among different kelp life history states, as these microscopic stages of at least some kelp species

(e.g. *Hedophyllum nigripes* and *Laminaria digitata*) appear more tolerant to elevated temperatures than their macroscopic sporophytes are (Franke et al., 2021), but they are less tolerant in other species (e.g. *Pterygophora californica*) (Matson and Edwards, 2007). Further, the effect of temperature can be species-specific, which will likely affect the distribution and abundance of these forests in the future (e.g. Muth et al., 2019), and perhaps favor one species over another (e.g. Franke et al., 2021). For example, studies on *Macrocystis pyrifera* (Ladah and Zertuche-González, 2007; Shukla and Edwards, 2017), *Nereocystis leutkeana*, *Eualaria fistulosa*, *Saccharina latissima* (Lind and Konar, 2017), *Pterygophora californica* (Matson and Edwards, 2007) and *Laminaria* spp. (Lüning, 1980) have shown elevated temperatures that result from ocean warming or that occur along latitudinal gradients negatively affect growth and development in their gametophytes (Shukla and Edwards, 2017), while other studies on *Alaria esculenta* and *Laminaria digitata* (Silva et al., 1992) have shown elevated temperatures that arise due to seasonality positively affecting these stages. For the latter, it seems that cold temperatures in the winter in high latitude ecosystems may inhibit gametophyte development, but when temperatures warm to their summer levels, the gametophytes undergo sexual reproduction and produce sporophytes (Silva et al., 1992). This may have complex life history implications, as Martins et al. (2017) revealed that elevated temperatures cause *Laminaria digitata* gametophytes to delay their reproduction and thus grow larger, which may result in enhanced sporophyte recruitment in the autumn and spring. Further, elevated temperatures may cause complex changes in the way kelp gametophytes are affected by other abiotic and biotic stressors such as sedimentation and grazing, which can lead to shifts in community structure in the future, as suggested for *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* in the Arctic (Zacher et al., 2016).

Kelp microscopic stages are sensitive to inter and intra specific competition due to differential settlement densities (Reed, 1990; Carney and Edwards, 2010), which can be modified by changes in ocean temperatures. For example, Zacher et al. (2019) found that ocean warming positively affected spore germination, gametogenesis and sporophyte formation in *Alaria esculenta* and *Laminaria digitata* in the Arctic, and that warming resulted in enhanced development in *Alaria esculenta* when co-cultured with *Laminaria digitata*, but this was not observed under colder (non-warming) conditions. Zacher et al. (2019) concluded that ocean warming could allow *Alaria esculenta* to gain a competitive advantage over *Laminaria digitata* and thereby alter community structure in Arctic the future. Given many of the factors associated with climate change are expected to change in the coming decades (Scavia et al., 2002; Boyer et al., 2005; Dyurgerov and Meier, 2005; Levitus et al., 2005; Behrenfeld et al., 2006; Arendt et al., 2009; Doney et al., 2009; Bieniek et al., 2014; Reisdorph and Mathis, 2014), it is likely that they, and more importantly their interactions, will be important to establishing and/or maintaining biogeographical patterns in the large sporophytes that make up the kelp forests. However, because the manner in which kelp microscopic stages

respond to these stressors varies among kelp species, climate change may drive shifts in species compositions in some locations (e.g. Deiman et al., 2012; Lind and Konar, 2017; Traiger and Konar, 2017; Silva et al., 2022). Such changes have already been seen for *Laminaria ochroleuca* and *Laminaria hyperborea*, with the more warm tolerant species *Laminaria ochroleuca* increasing in abundance and distribution along the rapidly warming Western English Channel (Smale et al., 2015). Likewise, Hondolero and Edwards (2017) note changes in the relative abundance of two kelp species, *Eualaria fistulosa* and *Nereocystis leutkeana*, in Kachemak Bay, Alaska, USA, with the more warm tolerant *Nereocystis leutkeana* increasing in abundance and *Eualaria fistulosa* decreasing in abundance. Indeed, some models predict that Northern hemisphere kelps will migrate northwards as these waters become more suitable for their growth and survival in the future (Assis et al., 2018; Smale, 2020). Therefore, a better understanding of how kelp benthic microscopic life stages are affected by environmental stressors and how this affects the way these stages interact with each other is key to better predicting how these ecosystems will be structured in the future.

The emergence of macroscopic sporophytes from the bank of microscopic forms (i.e. sporophyte recruitment) is strongly affected by complex interactions of numerous environmental factors. For example, recruitment of *Desmarestia ligulata* sporophytes occurs during a very narrow period in the spring when day lengths are increasing (Edwards, 1998). This is further supported by early work on *Saccharina japonica* by Tseng et al. (1959) and *Saccharina latissima* by Lüning (1980) who revealed that the light environment, including photoperiod, irradiance, and light color, is deterministic in the process of gametogenesis. Specifically, these gametophytes exhibit diel rhythms with day-night cycles synchronizing egg release and fertilization being largely limited to dark periods, and with egg release being inhibited by blue and UV light ($\lambda = 372, 413, 438, \text{ and } 481 \text{ nm}$). Response to changes in irradiance and light color may be important in the future if climate change results in increased water turbidity and thus coastal darkening (Wollschläger et al., 2021), which can affect gametogenesis and thereby alter sporophyte recruitment. Additionally, the process of sporophyte recruitment is generally negatively affected by high irradiance (Wernberg et al., 2019b; Ebbing et al., 2020; Paine et al., 2021; Silva et al., 2022) and elevated temperatures (Izquierdo et al., 2002; Morita et al., 2003; Mohring et al., 2014; Wernberg et al., 2019b; Franke et al., 2021; Paine et al., 2021; Silva et al., 2022), and positively influenced by increases in day length (Dring, 1988; Edwards, 2000; Nelson, 2005; Ratcliff et al., 2017) and elevated nutrient availability (Muñoz et al., 2004; Carney and Edwards, 2010; Carney, 2011; Ratcliff et al., 2017). Specifically, elevated seawater temperatures have been shown reduce gametophyte survival and/or sporophyte production in numerous species of kelp, including *Saccharina latissima* (Bolton and Lüning, 1982), *Pterygophora californica* (Matson and Edwards, 2007), *Macrocystis pyrifera* (Shukla and Edwards, 2017), *Ecklonia radiata* (Wernberg et al., 2019b), *Lessonia corrugata* (Paine et al., 2021), *Laminaria digitata* and

Hedophyllum nigripes (Franke et al., 2021), *Alaria esculanta* and *Laminaria digitata* (Silva et al., 2022), among others (e.g. Muth et al., 2019). However, the upper thermal tolerance of kelp gametophytes varies among species and with latitude (tom Dieck, 1993; Matson and Edwards, 2007; Muth et al., 2019; Zacher et al., 2019), and between male and female individuals (Franke et al., 2021). As noted earlier, these temperature tolerances may also be greater than those of the larger sporophytes, as seen in *Laminaria digitata* and *Hedophyllum nigripes* (Franke et al., 2021), or they may be less tolerant than the larger sporophytes, as seen in *Pterygophora californica* (Matson and Edwards, 2007). Likewise, OA has also been observed to negatively affect gametophyte survival and sporophyte production in some kelps, such as *Macrocystis pyrifera* (Gaitán-Espitia et al., 2014; Shukla and Edwards, 2017), but that increased CO₂ may ameliorate the negative physiological effects on zoospore germination and result in overall positive effects (Roleda et al., 2012). This again varies among species, as OA has also been observed to accelerate oogonium formation, but not affect sporophyte production in *Laminaria hyperborea* (Olischläger et al., 2012). Further, as with the macroscopic sporophytes (e.g. Brown et al., 2014), the combined effects of OW and OA appear equivocal, as they have been shown to have both positive (Shukla and Edwards, 2017) and negative (Gaitán-Espitia et al., 2014) effects on growth and development of *Macrocystis pyrifera* gametophytes, and they may affect the ability of these microscopic stages to delay their development (Gaitán-Espitia et al., 2014). When favorable levels of these conditions occur together, they can create “recruitment windows” during which conditions become ideal to support sporophyte production (Deysher and Dean, 1984; Deysher and Dean, 1986). Indeed, such recruitment windows have been observed in the spring along the west coast of North America when sporophyte recruitment is most abundant (Dayton et al., 1984; Edwards, 1998), but it remains unknown how climate change will affect sporophyte recruitment in the future (Harley et al., 2012). Certainly, this area can benefit greatly from additional studies.

MICROBE ASSOCIATIONS

To date, studies on multiple canopy-forming kelp species suggest they are associated with distinct microbial communities (Lemay et al., 2018; Lin et al., 2018; Minich et al., 2018; Weigel and Pfister, 2019; Ramirez-Puebla et al., 2020; Phelps et al., 2021). Studies from British Columbia, CAN on *Costaria costata*, *Alaria marginata*, *Pterygophora californica*, *Cymathoera triplicata*, *Laminaria setchellii*, *Nereocystis leutkreaana*, *Saccharina groenlandica*, *Saccharina latissima*, for example, have revealed that their microbiomes are distinct from the water column but are similar across different species of kelp, with annual versus perennial species supporting different microbial communities (Lemay et al., 2018). They have also been shown to vary among different parts of the kelp thalli that are of varied ages (Lemay et al., 2021). Further, kelp-associated microbiomes, which are

important to physiological functions (Lemay et al., 2021), can shift across depth gradients (Lin et al., 2018). OA has been shown to alter the microbial communities immediately surrounding some kelps (e.g. *Macrocystis pyrifera*) (Minich et al., 2018) and nearby benthic coralline algae (e.g. *Lithothamnion*) (Cavalcanti et al., 2018), and changes in these communities can have significant effects on the survival and development of kelp gametophytes (Morris et al., 2016). However, these effects appear to vary geographically, as Morris et al. (2016) found that the microbial communities found in seawater collected from Point Loma, San Diego, CA had detrimental effects on development in *Macrocystis pyrifera* gametophytes, while the microbial communities found in seawater collected from Catalina Island, which is 133 km to the northwest, had beneficial effects on these gametophytes. They attributed this variability to differences in how human populations affect the seawater microbial communities, as Point Loma lies immediately adjacent to the city of San Diego and is heavily impacted by a large human population, while Catalina Island lies approximately 40 km offshore and is more pristine. Therefore, the ultimate effects of climate change on kelp microscopic stages will likely involve complex synergies among multiple stressors, including OW, OA, irradiance, microbial communities, and human influences on the coastal environment. Further, if climate change reduces the frequency or duration of the recruitment windows, it can negatively affect how kelp microscopic stages emerge from their period of delayed development and thereby reduce patterns of sporophyte recruitment and slow recovery following deforestation in the future.

THE IMPORTANCE OF MICROSCOPIC STAGES TO KELP BIOGEOGRAPHY

As noted earlier, the individual and combined effects of variability in temperature, irradiance, salinity, large-scale climatic events, and climate change can have profound effects on patterns of kelp biogeography (Buschmann et al., 2004; Graham et al., 2007; Schiel and Foster, 2015; Smale, 2020; Muth et al., 2021). Thermal temperature tolerances, in particular, have a strong influence on establishing patterns among latitudes (Van den Hoek, 1982) and appear to be driving shifts in the geographic distributions of some species (discussed above). However, within latitudes, different kelp species exhibit distinct geographic range limits due to their species-specific requirements for, and/or tolerances of, temperature, nutrient, and light conditions (tom Dieck, 1993; Oppliger et al., 2012; Muth et al., 2019). While some of this occurs through impacts to the macroscopic sporophytes, environmental constraints on the microscopic stages can also be integral in establishing biogeographic patterns in kelp populations (tom Dieck, 1993; Matson and Edwards, 2007; Oppliger et al., 2012; Wernberg et al., 2019b; Muth et al., 2021). Further, while the macroscopic sporophytes of at least

some kelp species, such as *Macrocystis pyrifera* (Kopczak et al., 1991), *Saccharina latissima* (Gerard, 1988; Gerard, 1990), *Eisenia arborea* (Roberson and Coyer, 2004), *Laminaria digitata* (Liesner et al., 2020), and *Ecklonia radiata* (Bennett et al., 2015) exhibit ecotypic adaptation to local conditions that may allow them to persist where other ecotypes cannot, it is unclear if the microscopic stages do as well (Bolton and Lüning, 1982). However, studies on *Saccharina latissima* in Long Island, New York, USA (Gerard, 1990) and *Ecklonia radiata* from New Zealand (Novaczek, 1984) suggest that the microscopic gametophytes of at least some species do exhibit ecotypic adaptation to local conditions. The importance of this, however, largely remains within the black box of uncertainty surrounding kelp microscopic stages.

Regardless of whether kelp microscopic stages exhibit ecotypic adaptation to local conditions, there is strong evidence that they can be integral in establishing biogeographic ranges in the forest-forming large sporophytes (tom Dieck, 1993; Muth et al., 2019). For example, Matson and Edwards (2007) note that *Pterygophora californica* and *Eisenia arborea* both occur along the west coast of North America and have similar northern ranges near Vancouver Island, British Columbia, CAN. However, their southern ranges differ, with *Pterygophora californica*'s southern range ending at Bahía Rosario, Baja California, MEX, and *Eisenia arborea*'s range extending approximately 550 km farther south to Bahía Magdalena, Baja California Sur, MEX. Matson and Edwards (2007) found that while the adult sporophytes of both species are tolerant of the warmer waters observed in the south, the microscopic gametophytes exhibit very different responses to these temperatures. Specifically, in laboratory experiments, *Eisenia arborea* gametophytes survived and produced embryonic sporophytes under both 12° and 18°C, which are characteristic of bottom temperatures observed in Bahía Rosario and Bahía Magdalena, respectively, but the gametophytes of *Pterygophora californica* produced embryonic sporophytes only under the cooler temperatures. In fact, the gametophytes of *Pterygophora californica* all died when grown under 18°C. This is similar to the findings of Small and Edwards (2021) who found that expansion of the southern and northern biogeographic range limits of the invasive brown alga *Sargassum hornerni* along the California, USA coast were largely set by low tolerance of its microscopic germlings to both high and low temperatures, respectively, as the germlings did not fully develop under temperatures that are outside the species current range. Although *Sargassum horneri* is not a kelp and does not exhibit a diplo-haplontic life cycle, but rather is in the order Fucales and exhibits a diplontic (animal-like) lifecycle, it provides further experimental evidence that the geographic ranges of habitat-forming seaweeds can be set by abiotic influences on their microscopic life stages.

On a longitudinal gradient, Miller and Estes (1989) observed that the western range limit of *Nereocystis leutkeana* in the Aleutian Islands was set at Unmak Island, just to the east of the Samalga Pass. While they did not determine the factors that set this range limit, they did hypothesize that it was likely due, at least in part, to the ability of its microscopic stages to reproduce

under the lower light conditions that are established by the heavier cloud and fog cover to the west. In suggesting this, they note that there was an abundance of drifting reproductive sporophytes west of the Samalga Pass (discussed earlier). They also note that *Nereocystis leutkeana*'s microscopic life stages do not develop properly under low light conditions (Vadas, 1972), and that the western Aleutians are generally foggy and characterized by low irradiance in the summer when *Nereocystis leutkeana* recruitment occurs (Armstrong, 1977). This again may help explain why no *Nereocystis leutkeana* sporophytes have been observed farther to the west on Shemya Island even though drifting reproductive sporophytes have likely provided spores there. Lastly, Muth et al. (2019) examined the effect of ocean temperature on 12 species of kelp from the eastern Pacific Ocean and found that sporophyte production was always observed at 12°C, but sporophyte failure was common at a warmer temperature of 18°C. Muth et al. (2019) conclude that warming ocean temperatures will likely cause recruitment failure of some species, especially those near the warmer edge of their ranges, and thus affect kelp resiliency in the future. A major exception to this has been observed in two species of *Undaria* (*Undaria pinnatifida* and *Undaria undarioides*), which both exhibited optimal temperatures for gametophyte growth to be 20°C along the coast of Japan (Morita et al., 2003). However, the optimal temperature for gametophyte maturation was 10 – 15°C for *Undaria pinnatifida* and 20–21°C for *Undaria undarioides*, and this difference is believed to be a major factor determining the distribution of these two species along the coast of Japan (Morita et al., 2003). In contrast, Henkel et al. (2008) studied gametophytes of *Undaria pinnatifida* that were obtained from different locations along the California coast, USA and found that they exhibited very broad thermal tolerances, remaining metabolically active in temperatures up to 31°C, which exceeded normal environmental conditions. Further, Watanabe et al. (2014) found that gametophytes of *Undaria pinnatifida* collected from Kagoshima Bay, Japan could not survive temperatures of 28°C, and that temperatures above 20°C affected gametophyte performance. Watanabe et al. (2014) concluded that the species could become locally extinct along the coast of Japan if temperatures continue to rise with climate change.

THE IMPORTANCE OF KELP MICROSCOPIC STAGES TO PATTERNS OF DEPTH ZONATION

Kelps occur from the intertidal to depths of more than 30 m (Schiel and Foster, 2015), with some reports of their existence to more than 200m (Žuljević et al., 2016). While some of the depth patterns in kelps can be attributed to irradiance effects on their swimming zoospores, much can also be attributed to effects on its benthic microscopic life stages, as discussed above. For example, populations of *Macrocystis pyrifera* appear to be excluded from the intertidal and very shallow subtidal along much of the

California, USA coast due to hydrodynamic forces that act on its large sporophytes (Graham, 1997) and to high irradiances that negatively affect its microscopic stages (Graham, 1996). Specifically, Graham (1996) examined the effect of high irradiance on the benthic microscopic stages of *Macrocystis pyrifera* and found that the species' shallow water limit was set, at least in part, by the inability of its microscopic stages to tolerate high irradiance. While he did not identify the life stage that was responsible, this is in agreement with earlier work by Lüning and Neushul (1978) who found that exposing the gametophytes of *Macrocystis pyrifera* and *Pterygophora californica* to irradiances exceeding $900 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR, which would be expected in very shallow water, for as little as 1 to 4 minutes killed them. However, these irradiances are likely far higher than those that induce photoinhibition in these gametophytes over longer time periods. For instance, Fain and Murray (1982) found that photosynthesis in *Macrocystis pyrifera* gametophytes is light saturated at $70 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR, and then begins to decline at $140 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR. However, this too varies among kelp species, with some deeper water species being far more sensitive to high light. For example, Fejtek et al. (2011) exposed the microscopic gametophytes of *Macrocystis pyrifera* and *Pelagophycus porra* to light levels of $18\text{--}20 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR, which are characteristic of levels observed near the benthos within the shallower (10–15 m) *Macrocystis pyrifera* forest in Point Loma, California, and found that while *Macrocystis pyrifera* gametophytes survived and grew well, 100% of the *Pelagophycus porra* gametophytes died within 24 hrs. In contrast, exposure of the gametophytes of both species to irradiances of $2\text{--}4 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR, which are characteristic of the levels observed near the benthos within the deeper (25–35 m) *Pelagophycus porra* forest just offshore of the *Macrocystis pyrifera* forest resulted in high survival and healthy photosystems in both species. Examination of these gametophytes using PAM fluorometry indicated that *Pelagophycus porra* gametophytes were not able to acclimate to the higher irradiances found within the *Macrocystis pyrifera* forest. This suggests that, like *Macrocystis pyrifera*, the shallow depth distribution of *Pelagophycus porra* is set by the low tolerance of its microscopic stages to high light (Fejtek et al., 2011). Conversely, Vadas (1972) found that gametophytes of *Nereocystis leutkeana* did not mature when grown at irradiances at or below $4 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR (161 lux) and concluded that the species' deep water depth limit was set by low light conditions. This may be related to the fact that *Nereocystis leutkeana* produces its spores in sori near the surface of the water column where irradiances are high, or due to the fact that *Nereocystis leutkeana* occurs in much shallower water than *Pelagophycus porra*. Whether light sensitivity of the microscopic stages is important to setting the distributional limits of even deeper water kelps, such as *Pleurophyucus gardneri*, which grows to greater than 30 m off the central California coast Spalding et al. (2003), *Agarum cribrosum*, which grows to 40 m off the Gulf of Maine (Vadas and Steneck, 1988), or *Laminaria rodriguezii*, which grows to >70 m in the Mediterranean Sea, and possibly to 260 m depth in the Adriatic Sea (reviewed in Žuljević et al., 2016), is unknown but certainly worth investigating.

MICROSCOPIC STAGES EMBEDDED IN COMMUNITIES

Kelp gametophytes occur in variety of microhabitats, including within and on the surface of other algae (Garbary et al., 1999; Hubbard et al., 2004), and on the shells of gastropods (Henríquez et al., 2011). For example, Garbary et al. (1999) observed kelp gametophytes living endophytically in the cell walls of 17 different species of red algae in the San Juan Islands. While they did not identify the gametophyte species, they note that these were within sites that were dominated by several kelps species, namely *Alaria marginata*, *Costaria costata*, *Laminaria groenlandica*, *Nereocystis leutkeana*, and *Agarum fimbriatum*. These gametophytes, of which there were hundreds per host individual, exhibited oogonia on raised stocks that extended above the surface of their host. However, these gametophytes may not grow and develop as fast as those on the surface of their host (Hubbard et al., 2004), and not all kelp species (e.g. *Nereocystis leutkeana*) became endophytic, thus reflecting possible host specificity. Similarly, *Desmarestia* sp. gametophytes were first discovered in nature embedded in the tissues of the sea pen *Ptilosarcus gurneyi* by Dube and Ball (1971), which when cultured in the laboratory produced sporophytes. Whether this is due to selective settlement (discussed earlier) or simply a result of random settlement of the zoospores, is unclear, but selection of microhabitats that may offer some protection from benthic grazers has been observed (e.g. Amsler et al., 1992). Indeed, kelp gametophytes are susceptible to grazing by urchins (Dean et al., 1984; Dean et al., 1988), sea stars (Leonard, 1994), and gastropods (Henríquez et al., 2011; Zacher et al., 2016). For example, Henríquez et al. (2011) found that successful recruitment of *Macrocystis pyrifera* sporophytes along parts of the Chilean coast was linked to the capacity of its gametophytes to colonize secondary substrates, such as those created by the shells of slipper limpets (*Crepidatella fecunda*), which offered protection from other grazing gastropods. Further, Dean et al. (1988) showed that whit urchins (*Lytechinus anamesus*) grazed on kelp gametophytes more intensely than other brown algae that compete with the kelps in a southern California kelp forest (e.g. *Stephanocystis osmundacea*), and therefore may result in exclusion of the kelps and altered community composition. However, climate change may lead to complex ways in which grazers affect kelp microscopic stages. For example, Zacher et al. (2016) found that grazing on the microscopic stages of *Alaria esculanta*, *Laminaria digitata*, and *Saccharina latissima* by limpets was altered under elevated temperatures and levels of sedimentation in a species-specific way, and that this will be important to shaping Arctic kelp communities as the ocean climate changes. This may have significant consequences in the future if climate change also leads to changes in benthic algal compositions, such as the replacement of kelp forests by turf algal communities, which may further alter grazer activities and abundances (Filbee-Dexter and Wernberg, 2018; Zarco-Perello et al., 2021). To better resolve this will require a more detailed examination of available microhabitats in relation to zoospore

settlement rates, which may benefit from further advances in eDNA metabarcoding techniques.

MICROSCOPIC STAGES AS A TOOL FOR CONSERVATION AND RESTORATION

As noted earlier in this review, kelps have been experiencing broad scale declines worldwide due to a variety of stressors. This has raised concern about the proper functioning of ecosystems and opened new lines of research into ways to restore them. In particular, research focused on enhancing the abundance and survival of kelp microscopic stages in the field may provide meaningful solutions to kelp restoration efforts (e.g. Carney et al., 2005). Further, it may be possible to identify genetic strains of kelp gametophytes (i.e. ecotypes) that are more resistant to climate change stressors (e.g. Martins et al., 2019) or that maintain genetic diversity of local populations (Barrento et al., 2016), and then delay their development in the laboratory for extended periods so that they can be used as seed stock to replenish kelp populations in areas where they have been lost. This will require more research into how they respond to environmental conditions, what induces them to delay their development, and what causes them to resume development. One promising approach in particular, is the use of “Green Gravel” (small rocks that are inoculated with kelp microscopic stages and then cultured in the laboratory until the kelps are 2–3 cm tall) (Fredriksen et al., 2020). This is now being widely applied along the coast of northern California to help restore the *Nereocystis leutkeana* populations that have been lost in recent years. It is equivocal, however, whether it is necessary to culture these in the laboratory until the kelps are macroscopic or if the green gravel can be released when the kelps are still microscopic (reviewed in Morris et al., 2020). The latter may reduce costs associated with culturing, energy requirements, and person power, and thus should be considered. This will undoubtedly benefit from further studies that provide a deeper understanding of how these microscopic stages survive, develop and reproduce. Although much has been learned about the ecology of kelp microscopic stages during the last few decades, it is clear that a better understanding of how these cryptic life stages survive and reproduce under different environmental conditions, and how this varies among species is essential if we are to conserve these iconic marine forests in the future.

CONCLUDING REMARKS

Kelp forest have been under threat worldwide from numerous environmental factors, including storms, coastal development, urchin grazing, marine heat waves, ENSOs, and climate change. To date, most of the research on how these stressors affect kelps has focused on the large sporophyte life stage that forms these

iconic forests. This information has unfortunately not been well integrated into the full life cycle of kelps in nature, which has limited our understanding of the processes by which these forests persist and how they will respond to climate shifts and deforestation in the future. Unlocking this black box surrounding these cryptic life stages will shed light on how their biogeographic ranges and local abundances may change in the future. Indeed, advances in experimental methodologies and a growing body of work on kelp microscopic life stages are demonstrating rather convincingly that these early life stages are instrumental to kelp persistence in a variable ocean. In particular, predicted increases in ocean warming, ocean acidification, large-scale climatic events (e.g., ENSO), storm frequencies, irradiance, and UV radiation, and decreases in salinity, ocean pH, and nutrient availability will likely alter patterns of kelp zoospore dispersal and settlement, gametophyte survival and viability, and sporophyte production. The manner in which these stressors affect kelp microscopic stages, however, will likely vary among kelp species, and with interactions among multiple stressors, leading to complex changes in kelp abundances and geographic distributions. An increased understanding of the ecology and physiology of these cryptic life stages, and of the possibility of maintaining seed stocks of resistant genotypes or using Green Gravel may help guide the conservation of our iconic kelp forest in the future. Regardless, one thing is clear; as alluded to in the title of this paper, which mirrors my first conference talk on the subject, it really is ‘the little things’ that matter, and a better understanding of them is fundamental to a complete understanding of kelp forest ecology.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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