Summer 2021

Epiphyte-host Dynamics Between Pyropia and Nereocystis in Central California

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DOI: <https://doi.org/10.31979/etd.yh6k-hnn4>
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EPIPHYTE-HOST DYNAMICS BETWEEN
PYROPIA AND *NEREOCYSTIS* IN CENTRAL CALIFORNIA

A Thesis

Presented to

The Faculty of the Department of Marine Science

Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Daniel J. Gossard

August 2021

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The Designated Thesis Committee Approves the Thesis Titled

EPIPHYTE-HOST DYNAMICS BETWEEN
PYROPIA AND *NEREOCYSTIS*
IN CENTRAL CALIFORNIA

by

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ABSTRACT

EPIPHYTE-HOST DYNAMICS BETWEEN *PYROPIA* AND *NEREOCYSTIS* IN CENTRAL CALIFORNIA

by Daniel J. Gossard

Macroalgal epiphytism is widespread, but many unique epiphyte-host interactions remain poorly understood. *Pyropia nereocystis* is an annual northeastern Pacific species that has evolved to primarily epiphytize the annual kelp *Nereocystis luetkeana*. I examined three aspects of *Pyropia-Nereocystis* epiphyte-host dynamics in the southern extent of the host's range: (1) temporal variation in epiphyte presence; (2) growth of gametophyte and sporophyte (conchocelis) stages using transplantation experiments; and (3) effects of epiphyte depth and host characteristics on the recruitment and biomass of the epiphyte. *Pyropia* exhibited a shift in presence on *Nereocystis* that differed interannually as a function of *Nereocystis* density and *Nereocystis* persistence. Greater clumping of unepiphytized *Nereocystis* and greater regularity of epiphytized *Nereocystis* were observed for multiple cohorts. *Pyropia* gametophytes grew similarly across transplanted depths, but *Pyropia* conchocelis exhibited greater growth with increased depth. Longer host apophyses were correlated with a deeper *Pyropia* recruitment and *Pyropia* biomass was positively correlated and thresholded by host characteristics. These results suggest regularity in epiphytism among *Nereocystis* populations in the central California region and spore limitation or host inhibition of *Pyropia* epiphytism at greater depths, despite a likely conchocelis presence at greater depths. Additionally, *Pyropia* may be regulated by variation in *Nereocystis* stipe characteristics relating to host apophyses, stipe surface area, and/or ecological effects experienced by individual *Nereocystis*.

ACKNOWLEDGEMENTS

For my mom, for my dad, and for Lynnsay who have all supported and encouraged me the whole way. For my advisor and committee whom I primarily attribute my scientific development. For my colleagues and BEERPIGs who know the struggle. For all my volunteers and dive teams. For all the staff and faculty at MLML. For my friends and family their support.

And especially for Rachell, whom I love dearly, whose love has been foundational for my perseverance, and to whom I dedicate this Thesis.

Thank you.

My journey through MLML and this work was made possible by funding provided by the California College of the Arts Science in Studio Grant, SJSU, the Simpkins Family Fund Scholarship, and mentoring at the COAST Scholars-in-Training program.

Additional thanks to work provided by Monterey Bay Seaweeds, CCWG, MLML Dive Ops, Olympia Oyster Restoration work, Seagrass: Catalina Rhodolith Assessment, Seagrass: Cow Burps, and the Bull Kelp Restoration Project.

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Introduction

Species interactions are fundamental ecological processes that comprise the framework of biological communities (Dayton, 1985; Menge & Sutherland, 1987; Menge, 1992; Wiens, 2011). Inexorably, these interactions are important drivers of population dynamics and evolutionary fitness of species; evolutionary adaptations that allow for the passage of genotypic advantages to subsequent generations further influence communities on evolutionary timescales (Barracough, 2015). Theories have described the importance of stochastic and deterministic forces on species interactions across generations, but ultimately a combination of these forces influences biological communities across spatiotemporal scales (see Chase & Meyers, 2011; Chamberlain et al., 2014). Flux within a community can occur through deterministic species interactions and can even result in the creation of new niches (e.g., tree canopies for ferns; Schneider et al., 2004). Epiphytism is one such example of a distinct niche rooted in interactions between species.

"Epiphyte" has dichotomously been defined as either (1) a plant that grows on something, or (2) an organism that grows on a plant (see Steel & Wilson, 2003), so inherently epiphytism requires the interaction between two species. When referring to organisms specifically within the kingdom Plantae, and for the definition of the term in the remainder of this study, the definition of epiphytism refers to a plant growing on another plant. For vascular plants, this niche is utilized based upon a deterministic evolutionary adaptation; a common synonym for epiphyte is "air plant," referring to the plant's capability to survive (at least one part of its lifecycle) without soil nutrient

absorption. The marine environment from which multicellular photoautotrophs ancestrally originated provides conditions that facilitate epiphytism as commonplace. Greater viscosity in the marine environment, relative to terrestrial environment, allows for diffusion of nutrients by marine photoautotrophs from the water column. Therefore, algae are not limited by the necessity of establishing more complex root systems (Hurd, 2000). Whereas the root system of vascular plants evolved to both anchor the plant and to act as a mechanism to absorb water and nutrients (Gray & Lawson, 1985), the primitive attachment system for algae (i.e., a holdfast) serves only that singular purpose of attachment, albeit the attachment process is more complex than simply growing over a surface (see Morrison et al., 2009).

The epiphytic niche for marine macroalgae is utilized by a wide range of species across all algal divisions (e.g., Harlin, 1973; Stewart, 1982; Correa & Martinez, 1996; Anderson & Martone, 2014). Since the marine aqueous environment provides a substrate-independent nutrient source, some marine epiphytes can be facultative epiphytes (i.e., recruit on other substrate besides algae), such as *Microcladia coulteri*, *Ectocarpus* spp., *Ulva* spp., and *Cryptopleura ruprechtiana* (Abbott & Hollenberg 1976; Kendrick & Hawkes 1988). Macroalgal epiphytes can also have highly specific hosts (obligatory or non-facultative), such as with *Coilodesme californica* on *Stephanocystis* (*Cystoseira*) *osmundacea* (Wynne, 1972), *Polysiphonia lanosa* on *Ascophyllum nodosum* (Levin & Mathieson, 1991), and *Sporocladopsis novae-zealandiae* on *Lessonia* spp. (Correa & Martinez, 1996). Like the development of anti-herbivory chemical compounds (see Hay & Fenical, 1988 for review), many algae have evolved allelopathy (e.g., Paul & Fenical,

2000) and other mechanisms such as tissue sloughing (see da Gama et al., 2014 for review) to prevent being overgrown by other organisms, including epiphytes.

Investigations testing hypotheses of non-facultative epiphyte-host relationships have discovered multiple mechanisms utilized by epiphytes to bypass host defenses, such as manipulation of the host's cell wall, utilization of microrugosity of the host, utilization of biochemical components provided by the host, and utilization of antibiotic production by the host (see Correa & Martinez, 1996). Gonzalez and Goff (1989) demonstrated that epiphyte specificity (i.e., a particular preference of host by an epiphyte) can even vary among conspecifics for epiphytes in the genus *Microcladia*. Generally, the mechanisms by which epiphytes interact with their hosts are still poorly understood, as are the ecological relationships between epiphytes and hosts.

Marine epiphytism has been most commonly associated with a negative relationship with the host, and the consequence of epiphyte presence can present itself in different ways. The obligate epiphyte *Soranthra ulvoidea*'s presence was found to increase the likelihood of detachment of its host *Odonthalia floccosa* in intertidal systems, manifesting a negative impact on its host (Anderson & Martone, 2014). The same drag amplification was speculated to be imposed by epiphytes on *Pterygophora californica* in seasonal or storm-related wave disturbance events in subtidal systems (Dayton, 1985). Additionally, Buschmann and Gomez (1993) found that the epiphyte *Ulva* spp. competitively depleted nutrients from and shaded its host *Gracilaria chilensis*. Commonly, through various mechanisms, epiphytism can deleteriously affect host persistence and growth.

Epiphyte-host interactions are not always clearly elucidated. The presence of epiphytes on the coral genus *Lobophora* increased competitive strength of the genus against sympatric corals, highlighting a positively facilitative epiphyte-host interaction (Eich et al., 2019). Another such example of a positive interaction is biotic anti-herbivory benefits provided by the epiphyte *Elachista fucicola* found in a study comparing grazing impacts on epiphytized and non-epiphytized *Fucus vesiculosus* (Karez et al., 2000). In some instances, however, commensal interactions between epiphytes and hosts cannot be discounted. Radiocarbon isotope tracing conducted on seagrasses and *Smithora naidum* found that carbon was transferred from the host by the epiphyte, yet the study did not demonstrate whether this transfer was deleterious to the seagrasses (Harlin, 1973). Similar nutrient transfer was also observed between eelgrass (*Zostera marina*) hosts and their epiphytic communities (Penhale & Thayer, 1980). Epiphyte-host relationships no doubt play a significant role in the evolutionary development and persistence of epiphyte populations.

Generally, facultative and non-facultative marine epiphytes adhere to principles of algal population dynamics that arose from foundational marine ecology. Population dynamics of algae can be controlled by biotic (e.g., Lubchenco & Menge, 1976; Dayton et al., 1984; Farrell, 1991; Edwards & Connell, 2012 for review) and abiotic factors (e.g., Dayton, 1971; Van Den Hoek, 1982; McConnico & Foster 2005; Gaylord et al., 2008; Pritchard et al., 2013; Tala & Chow, 2014). Sympatric epiphytes of *Ascophyllum nodosum* were shown to conform to vertical zonation patterns present among other algae in the intertidal (Longtin et al., 2009), where the upper zones favor stress tolerant algae

and lower zones favor competitively dominant algae (e.g., Doty 1946; Stephenson & Stephenson, 1972; Evans, 1947b; Dayton, 1971; Dayton, 1975; Dayton, 1985; Lubchenco, 1980). However, abiotic factors can also influence epiphyte-host relationships. For example, Levin and Mathieson (1991) observed that the epiphytism pattern of *Polysiphonia lanosa*, an obligate epiphyte on *A. nodosum*, varied based on wave exposure, where exposed sites contained higher abundances of the epiphyte. Recruitment location of the epiphyte along this gradient varied, where the epiphyte would recruit on the reproductive structures of the fucoid host in sheltered sites, whereas at exposed sites, the epiphyte primarily settled on injured tissue. The increased presence of the epiphyte at exposed sites appeared to be due to both increased host size at those sites as well as increased physical disturbance causing increased likelihood of injury to the host. Thus, the availability of substrata for epiphyte settlement increased in exposed sites, allowing for greater epiphyte biomass at those sites.

Epiphytes also play a role in successional dynamics within macroalgal communities. Epiphytes can amplify disturbances and dislodge hosts in the intertidal and subtidal (Anderson & Martone, 2014; Dayton et al., 1984). Opportunistic algae, which include many facultative epiphytes (Abbott and Hollenberg, 1976), can be characterized as ephemeral and capable of colonizing quickly after a disturbance (Lubchenco, 1978). Epiphytes on the stipes of understory kelp *Pterygophora californica* have been found to have greater recruitment when hosts are less dense (Reed, 1990), suggesting the ability to rapidly colonize post-disturbance when there is a greater amount of light. Alternatively, epiphytes on the stipes of *Laminaria hyperborea* have been shown to occupy a later

successional state than their hosts, where following a disturbance (trawling), the host fully recovered in density and size before its associated epiphyte community (Christie et al., 1998). On a broader latitudinal scale, generalized epiphyte abundance on kelp varied off the coast of south-western Australia. Epiphytes had a greater presence on *Ecklonia radiata* stipes when the canopy was present versus when it was removed, juxtaposing the epiphyte population dynamics on *Pterygophora* found by Reed (1990) (Bennett et al., 2015). They associated the increase in epiphyte presence with flow dampening associated with canopy presence, speculating that epiphytism was hindered by a scouring effect associated with greater flow rates.

Epiphyte-host populations naturally vary in persistence across both space and time. For example, Californian coralline turf systems acting as host substrate were shown to have no significant temporal differences in the percent coverage of epiphytes (Stewart, 1982). In contrast, epiphyte communities on the annual kelp *Nereocystis luetkeana* have been observed to vary temporally in composition following a generalized pattern of succession (Markham, 1969; Roland, 1980). Seagrass epiphytes, including *Smithora naiadum*, varied spatially among sites in biomass relative to abiotic factors such as nutrient supply, wave exposure, and depth (Borowitzka & Lethbridge, 1989). Epiphytism by *Microcladia coulteri* in British Columbia exhibited differences in among-species total thallus coverage for three different species that didn't mirror the abundance of those three species (Kendrick & Hawkes, 1988). Both distributional patterns and morphological differences along the coast of the Irish Sea for the subtidal epiphyte *Ectocarpus fasciculatus* significantly varied when epiphytism was quantified on *Laminaria digitata*

compared to *Himanthalia elongata* (Russell, 1988). These examples highlight some of the variability in population dynamics among epiphyte-host relationships.

In a general sense, algae have evolved varying reproductive strategies to cope with ecological variability. Alternating forms of different phenotypic/genotypic life stages, or heteromorphic, algal life histories, have been shown to enhance resilience of algal species when exposed to grazing and seasonal stressors in the intertidal (Slocum, 1980; Lubchenco & Cubitt, 1980). These life history stages can spatially or temporally vary in size or morphology to increase the likelihood of persistence in the face of heterogeneous perturbation (e.g., Edwards, 2000; Gaylord et al., 2008). Furthermore, seasonal wave stress leading to dislodgement of competitors in the intertidal frees up settlement space for algae that synchronize reproduction with seasonal cues (e.g., Farrell, 1991). Interspecific algal competition prior to seasonal disturbances and with minimal herbivory present favors competitively dominant algae (e.g., Lubchenco & Menge, 1976; see Edwards & Connell, 2012 for review), whereas a broad timing of algal spore release and settlement allow for opportunistic and competitively inferior species to persist in environments susceptible to disturbance (Dayton, 1971; Sousa, 1979a; Sousa 1979b).

One such example of the utilization of reproductive strategies to optimize resilience and opportunism is that of the red algal genus *Pyropia* (Bangiales). These algae are globally ubiquitous and contain numerous species that are both facultative and obligate epiphytes. *Pyropia* is a basal algal genus (121 million years ago; Xu et al., 2017) that is present on all seven continents and contains over 100 species (see Sutherland et al., 2011; Yang et al., 2020). The typical success of *Pyropia* and other bladed Bangiales can be

partially attributed to physiological adaptations allowing for the amelioration of thermal stress, UV radiation, desiccation, and photoinhibition (e.g., Smith et al. 1986, Blouin et al. 2011 for review, Brawley et al. 2017). Their success can also be attributed to their biphasic life history including a microscopic perennial diplontic conchocelis filament and an annual macroscopic haplontic gametophyte blade (Abbott and Hollenberg 1976, Sutherland et al. 2011).

The annual bladed-*Pyropia* gametophytes are saxicolous (settle on rocky substrate) or epiphytic with non-facultative or facultative substrate specificity (Abbott & Hollenberg, 1976; Sutherland et al., 2011). The phenotype of *Pyropia* gametophytes is simplistic and primitive, containing only two differentiated cell types: a specialized holdfast cell for attachment, and a vegetative parenchymatous cell that can develop into more specialized reproductive cells (Hawkes, 1978; Brawley et al., 2017). This annual gametophyte blade is present seasonally (in the winter-spring for most species) and can develop zygotosporangia and spermatangia on its blade if monoecious, or on respective male and female individuals if dioecious. Syngamy between spermatia released from spermatangia on blades and zygotosporangia result in the creation of diploid zygospores, which are non-motile and develop into microscopic euendolithic conchocelis phase (Drew, 1949). The ubiquitous and abundant *Pyropia* genus is an excellent example of adaptive radiation that utilizes nuanced life history traits to occupy various niches (i.e., seasonal differences in presence of annual gametophyte stage, monoecious versus dioecious gametophyte, subtidal versus intertidal gametophyte, facultative versus non-facultative epiphytism) to enable diversified persistence (see Wang et al., 2020).

The conchocelis is an excellent example of the successful incorporation of a biphasic diplohaplontic life history and is perhaps the basal evolutionary development that facilitated diversification within *Pyropia* and other red algae (Brawley et al., 2017). This microscopic stage has demonstrated the ability to actively bore into calcium carbonate, where it has been found within barnacle shells in the intertidal (Hawkes, 1978; Wang et al., 2020), in mid-range depths between 2m - 40m and in various shell bearing organisms (Clokier & Boney; 1980), and at the lower aphotic zone in deep sea corals in tropical regions (Tribollet et al., 2017). The lifespan of the conchocelis may persist beyond the feasibility of maintaining laboratory cultures (Waaland et al., 1990), implying that the perennial persistence of conchocelis sporophytes may provide an important asexual means of propagule dispersal over an extended period. Lavik (2016) examined *Porphyra* spp. in Norway and observed that free-living conchocelis developed conchosporangia, whereas conchocelis within scallop shells did not. These results suggest that conchocelis grow vegetatively within calcium carbonate substrate and develop reproductive conchosporangia at the boundaries of the substrate and the marine environment. After mitotically produced non-motile conchospores are released from the conchocelis, these spores settle on substrate and can recruit to form macroscopic haploid bladed gametophytes, completing the life cycle of *Pyropia*.

Several earlier studies of the microscopic conchocelis stage of *Pyropia* have isolated photoperiod response as a reproductive cue for numerous species within the genus (e.g., Ogata, 1960; Iwasaki, 1961). Experimental clearings throughout the year in central California reconciled these laboratory studies, finding that despite *Pyropia* being an

opportunistic genus, the recruitment of *Pyropia* gametophytes in central California is temporally limited to the photoperiod that induces conchospore dispersal (Romero 2009). Culture studies suggest that despite photoperiod being a determining characteristic of gametophyte recruitment, temporal differences in gametophyte recruitment likely exist for sympatric *Pyropia* species due to other abiotic variables such as temperature (e.g. Waaland et al., 1990). Maximal photon flux (photosynthetically active radiation; PAR) rates, total photon flux exposure, temperature differences, and other weather-related changes can be correlated with latitudinal and seasonal differences in photoperiod (Jassby et al., 1976).

Niche specialization within the bladed Bangiales is supported by the development of different stress tolerances between sympatric species along latitudinal and depth gradients. Tala and Chow (2014) found significant spatial (latitudinal) and temporal (seasonal) variation between bladed Bangiales reproduction, percent cover, and ecophysiology along the Chilean coast. Hong et al. (1998) showed that high intertidal *Pyropia* exhibited greater salinity tolerance and exposure recovery than low intertidal congeners. Smith et al. (1986) demonstrated a consequence of subtidal niche specialization: less desiccation tolerance for subtidal *Pyropia* when compared with sympatric intertidal *Pyropia*. Figueroa et al. (2003) further observed the loss of mycosporine-like amino acids used to inhibit photoinhibition by a subtidal *Pyropia* - compared with its high intertidal congeners. Coexistence of multiple *Pyropia* spp. in subtidal zones further supports niche specialization and persistence within habitats molded by additional biotic factors (Roughgarden et al., 1988). The bladed Bangiales that

inhabit subtidal habitats (e.g., *Pyropia thuretii*, *Porphyrella gardneri*, *Pyropia koreana*) are primarily epiphytic and have been studied far less frequently than their intertidal congeners (e.g., Hawkes, 1978; Sanchez et al., 2014; Nelson et al., 2014). *Pyropia* that grow subtidally exhibit "shade-adapted" productivity characteristics where they typically have adapted to optimally photosynthesize with less irradiance (Herbert & Waaland, 1988; Figueroa et al., 2003). Herbert and Waaland (1988) measured differences in photoinhibition, or the level in which excessive irradiance is physiologically detrimental, among sympatric subtidal and intertidal *Pyropia* and speculated that interspecific differences resulted from species-specific evolutionary adaptations in thylakoid membranes developed for each individual species. Aside from physiological differences, the consequences of evolving to fit the subtidal niche may also include differences in *Pyropia* population dynamics between species preferring each of the separate habitats.

An excellent example of the breadth of *Pyropia*'s adaptive radiation and niche diversification is the species *Pyropia nereocystis*. This species has a subtidal bladed gametophyte that was named for its primary occurrence on the bull kelp *Nereocystis luetkeana*, (order Laminariales) that persists off the northwestern Pacific coast (Abbott & Hollenberg, 1976). This epiphytism is not obligatory, as *Pyropia nereocystis* has been, albeit less frequently, observed to recruit on other Laminariales and in-vitro without a host (Blankinship & Keeler 1892; Abbott & Hollenberg 1976; Hawkes, 1978; Dickson & Waaland, 1985). The epiphyte-host relationship between these two species can be classified as facultative and primary due to the persistence of the epiphyte primarily being dependent on the presence of its host. Therefore, the distribution of *Pyropia*

nereocystis is primarily dependent on the distribution of its host *Nereocystis*, and ranges from the Aleutian Islands in Alaska to central California (Sutherland et al., 2011), although individuals have been identified on drift *Nereocystis* as far west as the Commander Islands in Russia (Selivanova & Zhigadlova, 2012) and as far south as southern California (Abbott & Hollenberg, 1976).

Pyropia nereocystis has been observed to occupy the same niche (a *Nereocystis* host) as its congener *Pyropia thuretii*. However, due to the recent genetic delineation and taxonomic revision of the bladed Bangiales (e.g., Sutherland et al., 2011; Milstein et al., 2013; Reddy et al., 2017; Meynard et al., 2019; Yang et al., 2020), arguments have been made that reject morphology as an identifying characteristic for bladed bangiales (Meynard et al., 2019). The primary distinguishing feature that demarcates the two *Pyropia* species, aside from genetic identification and a morphological identified of "ruffled" margins (Hawkes, 1978; Abbott & Hollenberg, 1976), lies within the difference that arises from gametogenesis: *Pyropia nereocystis* form evenly discolored marginal spermatangia that develop inward and *Pyropia thuretii* initially form spermatangia toward their apices that proceed proximally along their margins, mostly resulting in a streaked pattern (Hawkes, 1978). However, this cytological identification was also based on morphological characters, before considerable taxonomic revision was undertaken. Despite accounts of *Pyropia thuretii* being far less abundant on *Nereocystis* (e.g., Hawkes, 1978), and in an effort not to conflate identification to species, this study will hereafter refer to both *Pyropia nereocystis* and *Pyropia thuretii* as *Pyropia* in a more general sense pertaining to *Pyropia*'s epiphytism of *Nereocystis* (unless either species if

referenced specifically). Given the complexities relating to taxonomy with sympatric *Pyropia*, and seaweeds in general (see McCoy et al., 2020), this more general classification was deemed more appropriate.

Nereocystis has been classified as a facultative biennial kelp that primarily persists annually, but can persist as long as two years (Foreman, 1970). Thus, the availability of the host as substrate for the epiphyte *Pyropia* is ephemeral with certain time periods where few or no hosts are present in the environment. Multiple studies in central California have shown that the benthic recruitment of *Nereocystis* occurs primarily in the late spring and summer (e.g., Nicholson, 1970; Foreman, 1970), but individuals can recruit during the fall and winter, as well (Suskiewicz, 2010; Dobkowski, 2017).

Nereocystis express two growth forms: the first follows recruitment and encompasses vertical growth and stipe elongation to the surface creating a surface canopy expression in late spring (from here on called "canopy recruitment") and the second in which *Nereocystis* exhibit a growth transition from stipe elongation to blade elongation, thickening, and soral production (Duncan & Foreman, 1980). Increased summer photoperiod and irradiance levels allow for *Nereocystis* to store nitrogen and carbon in its thallus to utilize for growth and reproduction in the fall and winter (Wheeler et al., 1984).

Spatiotemporal heterogeneity may potentially influence the relationship between epiphyte *Pyropia* and host *Nereocystis*. Tautologically, *Pyropia*'s persistence and the overall epiphyte-host relationship may be influenced by *Nereocystis*'s persistence, recruitment, dispersal, and ecophysiological response to abiotic and biotic factors (Roland, 1980). *Nereocystis* populations within their biogeographical range are

influenced by habitat and associated environmental conditions (Foreman, 1970; Duncan, 1973; Supratya et al., 2020; Coleman & Martone, 2020). Additionally, populations can be spatiotemporally influenced by heterogeneous biotic factors, which may be temporally variable throughout *Nereocystis*'s life cycle (Foreman, 1984; Duggins et al., 2001; Carney et al., 2005; Dobkowski et al., 2019; see Rogers-Bennett & Catton, 2019). *Nereocystis* associated microbial communities, which have been demonstrated to vary geographically (Weigel & Pfister; 2019), may also influence the population dynamics and recruitment patterns of epiphytes. These factors may influence *Pyropia* and *Nereocystis* similarly or differently reflecting ecophysiological responses within their ranges to abiotic factors and species interactions independent of the epiphyte-host relationship. Woessner (1981) postulated that light intensities, which are heterogenous among central Californian *Nereocystis* forests, influence *Pyropia* development and abundance. Woessner's (1981) speculation could be expanded *de facto* to include latitudinal influences on irradiance and photoperiod. Furthermore, *Nereocystis* have a large depth range (intertidal down to greater than 25m; Foreman, 1970; Duncan, 1973) and therefore may provide spatially variable stipe substrate area for *Pyropia*, potentially influencing abundance and population dynamics.

The consequences of occupying the subtidal niche by *Pyropia* may have resulted in physiological alterations selected for within the habitat. Smith et al. (1986) showed that desiccation tolerance was all but absent in *Pyropia* taken from *Nereocystis* when compared with sympatric intertidal species. Furthermore, these subtidal *Pyropia* were shown to have lost photoinhibition resistance and shown to have adopted a shade-adapted

photosynthetic ecophysiology when compared with sympatric intertidal species (Bose et al., 1988; Herbert & Waaland, 1988, Herbert, 1990). In British Columbia, Hawkes (1978) observed these potential distributional ramifications when noting that the absence of *Pyropia* on the air-exposed sides of floating stipes. He observed that *Pyropia*'s vertical distribution along *Nereocystis* stipes was not uniform and that the majority of *Pyropia* biomass occurred within the top two meters (from the pneumatocyst) on host *Nereocystis* stipes. In contrast, two prior sources from California noted the majority of *Pyropia* biomass in central California occur between 3m - 5m (Abbott & Hollenberg, 1976) or between 5m - 9m depth (Hus, 1902). Roland (1980), in British Columbia, recorded vertical distributions similar to Hawkes' (1978) observations. These results suggest that between British Columbia and California, geographic variability may influence *Pyropia* abundance, if not simply vertical distribution. However, empirical data describing spatial variability in vertical distribution of *Pyropia* on *Nereocystis* stipes are scarce.

A non-facultative host-related growth component may regulate *Pyropia*'s recruitment and persistence along a vertical distribution on *Nereocystis* stipes. *Nereocystis* stipe elongation generally continues until the sporophyte extends within 2 m of the surface (Duncan & Foreman, 1980). Meristematic stipe tissue located toward the pneumatocyst (Nicholson, 1970) signifies older stipe tissue is retained at deeper depths toward the holdfast. The depth at which *Nereocystis* recruit, and thus the length of *Nereocystis* stipes, can be highly variable and range from the intertidal zone down to 25m (Foreman, 1970, Denny et al., 1997). Furthermore, currents or wave energy have been shown to result in stretching of stipes, and such elasticity mixed with differences in exposure

intensity likely results in various stipe lengths among populations (Koehl & Wainwright, 1977, Denny et al., 1997, Duggins et al., 2001). The relationship between wave forces and the stipe length to holdfast depth relationship [SL:HD] may restrict the abundance of *Pyropia* on stipes which have been stretched enough to expose greater proportions of the epiphytes to the air during lower tides (Hawkes, 1978). Additionally, the timing of *Pyropia* recruitment may influence its recruitment depth on *Nereocystis* stipes in regard to whether or not *Nereocystis* was still exhibiting stipe elongation during initial settlement of *Pyropia* conchospores.

Dickson and Waaland (1985) were the only authors to date to publish results on successfully completing the life cycle *Pyropia nereocystis*. They determined that the conchosporangial induction period necessary for conchosporogenesis occurred across a wide range of temperatures (8°C-18°C) and that maturation and release of conchospores required consecutive winter and summer photoperiods. This photoperiod response hints at the mechanism for satisfying the specialized recruitment window on the annual *Nereocystis*. Dickson and Waaland (1985) explained their results using a seasonal model for photoperiod and temperature in Washington, USA, overlaying the respective phenologies of *Nereocystis* and *Pyropia*. The problem with applying these culturing results to a generalized model such as described by Dickson and Waaland (1985), is that the model did not take into consideration the temporal variability in recruitment of *Pyropia* or the spatiotemporal variability in photoperiod and temperatures along the geographical distribution of *Pyropia*. These differences in abiotic seasonal trends may imply spatiotemporal variability in recruitment of gametophytes across *Pyropia*

geographic distribution. Furthermore, Dickson and Waaland (1985) found that abiotic heterogeneity resulted in a range of reproductive output for *Conchocelis* and further abiotic heterogeneity may influence macroscopic *Pyropia* gametogenesis (Santelices 1990).

Despite past culture studies, site-specific surveys, and genetic work on *Pyropia* in the northern part of its range, information on population dynamics and spatial variability of *Pyropia* and its host *Nereocystis* at the southern edge of their range remain unclear. Furthermore, the evolutionarily unique epiphyte-host relationship between *Pyropia* and *Nereocystis* remains poorly understood. My study aimed to answer two broad questions regarding the epiphyte-host relationship between *Pyropia* and *Nereocystis* at the southern edge of the species' ranges: (1) How does *Pyropia* epiphytism vary spatially and temporally within the central California region? and (2) do host characteristics and environmental factors regulate the growth, distribution, and abundance of *Pyropia*?

Hypotheses

I addressed my first question by testing three separate hypotheses regarding epiphytism rate and synchronicity between *Pyropia* and *Nereocystis* populations. I hypothesized that: (H_{1a}) densities of epiphytized *Nereocystis* would be significantly greater than densities of unepiphytized individuals when both were present. Alternatively: (H_{1b}) densities of epiphytized *Nereocystis* would be significantly lesser than densities of unepiphytized *Nereocystis* when both were present or (H_{1c}) the epiphytism rate (densities of epiphytized versus unepiphytized *Nereocystis*) would shift over time, denoted by a significant interaction between epiphytism and time. Differences over time were not of interest for this hypothesis due to both epiphyte and host being annual species (i.e., changes over time were assumed to be significant). I attempted to characterize variability in epiphyte patchiness by comparing variability in non-epiphytized host densities with variability in epiphytized host densities.

My second hypothesis was that: (H_{2a}) variability (CV) for epiphytized *Nereocystis* would be significantly greater than non-epiphytized *Nereocystis* when both were present. Alternatively: (H_{2b}) variability (CV) for epiphytized *Nereocystis* would be significantly lesser than non-epiphytized individuals when both were present. Additionally: (H_{2c}) intraregional variability (CV) between epiphytized and non-epiphytized *Nereocystis* would shift over time, denoted by a significant interaction between variability in epiphytism presence and time. Due to the annual nature of *Nereocystis* to decrease in density over time (e.g., through senescence or detachment), this hypothesis tested for differences in the coefficient of variation (CV) for densities of epiphytized and non-

epiphytized *Nereocystis* while also accounting for differences in mean density between the two (CV; Hurlbert, 1990; Sokal & Rohlf, 1993; Gotelli & Ellison, 2004).

My third hypothesis was that: (H_{3a}) the phenologies *Pyropia* and *Nereocystis* would be asynchronous; the shortest time until intraregional maximum density for a cohort (i.e., 2018-2019) would be significantly greater for unepiphytized *Nereocystis* compared to the shortest time of maximum density of epiphytized *Nereocystis*.

For my second question, I hypothesized that since *Pyropia* was observed to occur in the upper few meters of *Nereocystis* stipes, (H₄) transplanted *Pyropia* would exhibit a deleterious ecophysiological growth response at deeper depths (less growth after 3 weeks) compared to shallower transplanted *Pyropia*. Hypothesis (H₄) was tested separately for both life phases of *Pyropia*.

Spatial variability may influence epiphyte-host population dynamics. Therefore, host morphology was compared at and after the time of initial *Pyropia* recruitment to test whether environmental heterogeneity influenced host populations. I hypothesized that at the time of initial *Pyropia* recruitment, host morphometrics among sites within the region (number of blades, maximum blade length, stipe biomass, blade biomass, and total biomass) would be significantly different (H_{5a}) in response to environmental heterogeneity. Furthermore, I predicted that environmental heterogeneity would influence *Pyropia* phenology and hypothesized (H_{6a}) there would be significantly different spatial and temporal variability in *Pyropia* gametogenesis.

Additionally, for my second question, I hypothesized that lowest *Pyropia* recruitment depth would be positively correlated with stipe length (H_{7a}) or be positively correlated

with more specific stipe morphometrics denoted by principal component analysis (PCA) (H_{7b}). I hypothesized that (H_{8a}) *Pyropia* biomass attached to the upper meter of the *Nereocystis* stipe would be a predictor of total biomass attached to that *Nereocystis*. Due to the susceptibility of *Pyropia* to desiccation, I hypothesized that the [SL:HD] would have a thresholding effect with larger ratios bounding the total biomass of epiphytized *Pyropia* (H_{9a}).

Lastly, I hypothesized that *Pyropia* biomass could either be substrate limited and be positively correlated with (H_{10a}) stipe surface area or have a positive correlation with (H_{10b}) more specific stipe morphometrics denoted by PCA.

Methods

Site Selection

Toward the southern end of *Nereocystis*'s range (Abbott & Hollenberg, 1976), I randomly selected five accessible sites between Carmel Pinnacles State Marine Reserve and Big Creek State Marine Reserve with the intention of generalizing to the region with no *a priori* influence of abiotic or biotic factors, excluding the presence of a *Nereocystis* bed at least 30 m x 50 m in size (Figure 1). Thus, spatial variability (site) was addressed as a random factor in subsequent analyses. A large number of site characteristics were anecdotally observed to be heterogeneous among sites and were assumed to comprise regional variability in algal population dynamics. Such characteristics included: heading from the bed toward the nearest shore location (i.e., shoreward position relative to predominant northwesterly swell), proximity to freshwater inputs, turbidity, range of bed depths, biological community composition (competitor and grazer community and abundances), swell intensity, seafloor geomorphology (rock type and rugosity), etc.

Spatial and Temporal Variability in Epiphyte-Host Distribution and Abundance

To test my phenological hypotheses (H_1 - H_3), I sampled populations of sporophyte canopy *Nereocystis* as a substrate and sampled the presence of *Pyropia* as an epiphyte within these populations. Comparisons were made among sites by sampling for canopy density of *Nereocystis* and presence/absence of epiphytized *Pyropia*, along with describing *Pyropia* biomass on *Nereocystis*, over time using a combination of surveys and collections. Sites were surveyed periodically between November 2017 and February

Figure 1

Nereocystis's Range and Study Sites

Note. *Nereocystis's* range is shown with a dotted line off the coast in the northeastern Pacific (bar = 1000 km) and the five sites that were sampled in this study are denoted by circles (bar = 10 km).

2019 (n = 9 sampling periods). Sites were sampled (n = 5 sites) by conducting 5 swath transects 1 m x 30 m per site per sampling period. Individual beds were sampled once approximately every 6-8 weeks (1 sampling period) with a maximum spread of each site being sampled within 2 weeks for each period. Regardless of seafloor depth, swath transects were conducted at a depth of 3 m below the surface (± 1 m due to wave orbit)

collecting *Nereocystis* counts and presence or absence of *Pyropia* on each *Nereocystis* encountered in the swath. *Pyropia* presence was determined by assessing each individual *Nereocystis* stipe to the maximum visual range (≥ 0.5 m below the diver) and by pulling each individual down and visually examining stipes for the presence of *Pyropia* (3m depth to the pneumatocyst). This method proved more easily navigable through *Nereocystis* beds than by conducting transects on the surface, and also allowed for deeper observation of *Nereocystis* stipes for *Pyropia* presence. Furthermore, this method allowed for the assumption that if *Pyropia* was not seen, it was not present on the *Nereocystis*, as *Pyropia* persists primarily on the upper two meters of the stipe (Hawkes, 1978).

Individual *Pyropia* from each site across multiple sampling periods were collected for genetic analysis in order to test for species identification (genetic identification of all individuals was practically infeasible due to both quantity of gametophytes and costs associated with genetic identification). Sixteen samples total were collected for genetic identification by randomly collecting them from all sites over the entirety of the study. Individual samples were dried in granulated silica gel prior to analysis. The sixteen samples were sent to the University of Rhode Island (Lane Lab) where they were ground, dissolved in a red algal buffer, had the *cox1* gene amplified using a M13LF2-M13Ri primer, and were sequenced to identify collected *Pyropia* to the species level (Robba et al. 2006). Due to limitations in total sample numbers for species identification, the inference of identification was to estimate the percentages of *Pyropia nereocystis* versus *Pyropia thuretii* rather than to infer the study pertained to just *Pyropia nereocystis* (the more abundant of the two on *Nereocystis*; Abbott & Hollenberg, 1976; Hawkes, 1978).

Ecophysiological Responses of Two *Pyropia* Life Stages to Depth

Ecophysiological growth response to depth was measured for *Pyropia* gametophytes (H₄) using transplants in April 2017. Three total *Pyropia* individuals (n = 3) at least 0.5 m in length were removed at the holdfast from separate *Nereocystis* individuals within 1 meter of hosts pneumatocystis. Three intercalary 3 cm x 5 cm rectangular punches of algal material were taken from within the margins of the *Pyropia* individuals and were randomly assigned to one of three different depths (6 m, 10 m, and 14 m below MLLW) to have three punches at each depth be from separate *Pyropia* replicates. Despite the interest in examining the effects of a treatment at a shallower depth, the shallowest depth treatment was required to be maintained at 6m depth to prevent mooring entanglement by passing boat traffic. Each punch was affixed within a 11.5 cm diameter x 14.5 cm tall cylindrical plastic Tupperware container using a plastic clothespin in order to exclude grazers and prevent blade damage. Each container was perforated with 2 cm diameter holes in the top and sides to maintain adequate water flow. Three polypropylene lines with subsurface buoys were deployed and moored at a depth of approximately 16 m in Stillwater Cove, CA. Samples were deployed along three polypropylene mooring lines at the depths of 6 m, 10 meters, and 14 m (Figure 2A). Depth treatments were selected based on historic reports of lower limits of *P. nereocystis* upon *N. leutkeana* stipes being between 6 and 10 meters (Hus, 1902; Abbott & Hollenberg, 1976; Hawkes, 1978). A deeper treatment was also used to investigate *P. nereocystis* growth responses at depths below its natural depth range. Depth treatments were standardized relative to MLLW. After three weeks, all *Pyropia* samples were collected and returned to the laboratory.

Pyropia gametophyte punches were photographed in order to determine area (cm^2 ; Figure 2B). Prior to photography, *Pyropia* samples were unfolded and laid flat on white tray aside a scale ruler. Photographs were converted to TIFFs and processed using Fiji (ImageJ) using scalebars within the photos to calculate the ending area of each punch.

Figure 2

Pyropia Gametophyte Transplant Experiment

Note. *Pyropia* punches were deployed for 3 weeks in (A) perforated Tupperware cages at three different depths between 6 m and 14 m depth. After collection, these punches were (B) photoanalyzed to determine change in area (cm^2). Photos credited to Daniel Gossard.

Growth responses at different depths for *Pyropia conchocelis* (H_4) were tested using laboratory cultured *Pyropia nereocystis* conchocelis transplanted to depth intervals in May 2019. *Pyropia* gametophytes (10 separate individuals from different *Nereocystis*) identified as *P. nereocystis* by zygotosporengia toward blade apices (Hawkes, 1978) were

collected from the Stillwater Cove, CA in March 2019 to be used for culturing conchocelis. These individuals were taken back to the laboratory, gently wiped with paper towels to remove epiphytes, and rinsed in a 1% iodine solution as a stressor to induce spore release and to reduce biofilm shedding into the subsequent spore solution (Muth et al., 2019). After rinsing again in autoclaved seawater, gametophytes were then stored layered between damp paper towels (with autoclaved seawater) in the dark at 10°C for 24 hours. After 24 hours, gametophytes were placed within 10°C autoclaved seawater to induce zygospore release. Zygospores were counted using a hemocytometer and diluted to approximately 20 zygospores per ml using three dilutions (diluted to 2000 zygospores per ml, diluted to 200 zygospores per ml, and diluted to 20 zygospores per ml).

Porous limestone tiles (25 mm length x 25 mm width x 5 mm depth) were used as settlement substrate for *Pyropia conchocelis*. Tiles were soaked in autoclaved seawater for 24 hours before exposing zygospores. After soaking, tiles were placed within small folded foil cups (25 mm length x 25 mm width x 20 mm depth) to maximize the likelihood of zygospores of landing on the tiles when the zygospore solution was added to the cups. After adding 5ml of autoclaved seawater to the cups in order to fully submerge the tiles, 10ml of zygospore solution (approximately 200 zygospores) was added to each cup and gently plunged to homogenize the water column within the cups. 30 tiles were seeded this way using zygospores from the same solution. All tiles were then placed in 10°C for 3 days in the dark to allow for undisturbed recruitment of conchocelis. After 3 days, all tiles were removed from their respective foil cups and

submerged gently within a large water bath tray filled with Provasoli Enriched autoclaved Seawater solution (Provasoli, 1968) and irradiated with approximately $25 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ photosynthetic photon flux density (PPFD) at a 16:8 photoperiod (light:dark).

After 30 days, each tile was inspected using epifluorescence microscopy for the presence of conchocelis recruits. Tiles were labeled using acrylic paint and sharpie and were examined under the microscope using a standardized positioning slide in conjunction with coordinates for each field of view (FOV). Three conchocelis were identified on each tile using a stratified random sampling method. After stratifying the tile into four evenly sized quadrants, three out of four quadrants were selected randomly on each tile and a random coordinate in each quadrant was selected at least two FOVs away from quadrant intersections. The nearest conchocelis to each randomly selected pair of coordinates, under the condition that it was at least one FOV distance from its nearest conchocelis neighbor, was identified and its coordinates were marked for re-examination after field deployment. Leica Acquire was used to capture photographs of each tracked conchocelis and Fiji (ImageJ) was used to calculate approximate areas of each conchocelis.

Fifteen tiles were randomly selected from the 30 seeded, randomized, and deployed along a polypropylene mooring line at depths stratified from 6m below MLLW to 20m below MLLW at Stillwater Cove, CA. To control for potential conchocelis recruitment from *Pyropia* zygospores released *in situ*, blank tiles were deployed alongside seeded tiles to be examined for recruitment after tile collection. One settled conchocelis treatment tile and one blank tile were attached using a stainless-steel nut and bolt to a

PVC Tee (Figure 3). Modules were deployed on April 23rd, 2019 (45 days after zygotospores were settled on tiles), using rigid shades constructed with PVC paper

Figure 3

Pyropia Sporophyte Transplant Experiment In-situ

Note. 25 mm² limestone tiles were utilized as substrates for zygospore seeding and monitoring change in growth and conchosporeogenesis (A); the conchosporeogenesis experiment (green arrow) was unsuccessful. Control tiles were used to monitor recruitment of conchocelis as a control for incidental recruitment on treatment tiles. Photo credited to Steve Lonhart.

around each PVC module to avoid exposing conchocelis to UV rays. Each module was attached using cable-ties at depths respective to randomized treatments assigned. Despite the interest in examining the effects of maintaining treatments at shallower depths, the shallowest depth treatment was required to be maintained at 6m depth to prevent mooring entanglement by passing boat traffic. Each depth treatment below was stratified at 1m intervals at a depth up to 20m. 39 days after deployment, modules were removed from the deployed mooring and secured within a cooler before being transported back to MLML for same-day processing.

Conchocelis tiles were photographed before deployment and after returning to MLML on June 1st, 2019 (Figure 4). The change in area for each conchocelis (μm^2 ; final

Figure 4

Epifluorescence Microscopy Imagery of Pyropia Sporophyte Transplant Experiment

Note. Epifluorescence microscopy images of *Pyropia* sporophyte conchocelis before deployment (A) and after recovery (B) were used to calculate change in area as a metric for growth. All tiles experienced conchocelis growth, and most tiles required stitching together of multiple fields of view to analyze the change in area. Photos credited to Daniel Gossard.

- initial area) was determined and used as the growth response for the experiment. Each conchocelis (3 per tile) was treated as a subsample and averaged to create a single replicate tile at any given depth along the depth gradient.

Influence of Host Morphology on Epiphyte Biomass

To test epiphyte regulation hypotheses (H_7 - H_{10}), collections of *Nereocystis* and all attached *Pyropia* ($n = 4$) were conducted from each of the 5 sites at all sampling periods. Collections were made after swath surveys by randomly selecting 4 *Nereocystis* thalli with *Pyropia* present when *Pyropia* was seasonally present (otherwise by just randomly selecting *Nereocystis*). Host thalli were dislodged at their holdfast and brought up to the surface by coiling the non-hollow portion of the stipes while ascending in the water column. Entire individual stipes coils were secured with a rubber coated gear tie and stored in labeled 200-liter contractor bags. Holdfast depth (seafloor depth) was recorded prior to collection, measured using analog or digital pressure gauges to the nearest 0.3 m (± 0.3 m).

Each *Nereocystis* was processed for morphometrics and *Pyropia* biomass within two hours or was otherwise kept shaded among other collected *Nereocystis* in a 4800-liter tank with flowing seawater for up to three days. A few *Nereocystis* begun deteriorating after three days and were discarded (assumedly due to poor water motion within the tank). Individual *Nereocystis* morphometrics were collected including: (1) diameters of the pneumatocyst and smallest diameter directly below the pneumaocyst (to the nearest 1 cm $\pm$ 0.1 cm); (2) largest and smallest diameters of the apophysis (to the nearest 1 cm $\pm$ 0.1 cm); (3) lengths of the pneumatocyst, lengths of the apophysis, non-hollow lengths,

and total stipe lengths (to the nearest 1 cm $\pm$ 1 cm); (4) blade wet weight, stipe wet weight, and total wet weight (to the nearest 1 kg $\pm$ 0.03 kg); and (5) number of blades,

Figure 5

Nereocystis Collection Parameters

B

$$\text{Stipe surface area} = 4\pi \times \left(\frac{(L1 \times D1a)^{1.6} + (L1 \times D1b)^{1.6} + (D1a \times D1b)^{1.6}}{3} \right)^{\frac{1}{1.6}} + \pi \times (D4 + D2) \times \sqrt{(D2 - D4)^2 + (L2)^2} + \pi \times (D3 + D2) \times \sqrt{(D3 - D2)^2 + (L3)^2} + \pi \times D3 \times L4$$

Note. *Nereocystis* stipe morphometrics, including four diameter and four length measurements (D1 – D4 and L1 – L4 respectively), were measured from each collected individual (A). These measurements were used for PCA and for the estimation of stipe surface area calculated by adding together the surface area of an ellipsoid (the pneumatocyst), the surface area of two truncated cones (the apophysis), and the surface area of a cylinder (the non-hollow lower stipe) (B).

maximum blade length (to the nearest 1 cm $\pm$ 0.5 cm) (Stekoll et al. 2006; Figure 5A; H₅, H₇₋₁₀). *Nereocystis* total stipe length was divided by the water column depth to obtain the stipe length:holdfast depth (SL:HD) for each individual *Nereocystis*. Diameters along each stipe were measured using precision calipers to an accuracy of 0.1 cm and lengths

were measured using a flexible measuring tape with an accuracy of 1 cm. Each stipe was examined for *Pyropia* closest to the *Nereocystis* holdfast and the distance between the pneumatocyst apex and that *Pyropia* was recorded as the lowest *Pyropia* recruit.

Biomass of *Pyropia* was collected in 1 m length bins along the stipe (H₇). The stipe was cut into 1 m length bins and all *Pyropia* were collected to a degree to maximize the biomass signal if excessively abundant (due to up to 1000s of individuals per *Nereocystis*), or otherwise entirely collected if rare within a bin (<50). Within each bin for the 2018-2019 *Pyropia* cohort, *Pyropia* individuals on each *Nereocystis* were subsampled and photographed for *post-hoc* determination of gametogenesis (H₉; Figure 6A, B). *Pyropia* wet weight biomass measurements were made on a calibrated scale with a 0.1 g accuracy. All, if not most, *Pyropia* (to a reasonable degree) from individual stipes were removed and material was oven-dried for 72 hours on individual foil sheets, appropriately sized for (and containing) varying *Pyropia* amounts per location (1 m bin along the *Nereocystis* stipe). Sheets were marked by location and pre-weighed and used as taring dishes to measure total dried biomass per individual among beds and over time. As none of the biomass on collected hosts were detectable (< 0.1 gDW) during the September 2018 sampling period (for the 2018-2019 cohort), and as biomass measurements were barely above or at the detectable limit on hosts during the November 2018 sampling period, these two periods were excluded from analyses.

Figure 6

Pyropia Gametophyte Collections

Note. *Pyropia* gametophytes in-situ (A) were laid flat for photoanalysis of zygotosporogenesis presence (B). Indicators of gametogenesis and zygotosporogenesis were observed among samples (green arrows). Photos credited to Shelby Penn (A) and Daniel Gossard (B).

All collections and sampling procedures were approved by California Department of Fish and Wildlife (CDFW) under permit SCP-13538.

Data Analysis

To test H₁, H₂, and H₃, *Nereocystis* count data for individuals with and without *Pyropia* present were transformed into densities ($\bar{x} \pm \text{SE}$, where $\bar{x}$ is the sampling mean and SE is the standard error from the mean) per m² to estimate population size at sites within regions. Densities and unbiased coefficients of variation ($(1 + \frac{1}{4n}) \times \frac{s}{\bar{x}}$, where n is # of samples at a specific site, s is standard deviation from the sampling mean at that site, and $\bar{x}$ is the sampling mean at that site) were used to test H₁ and H₂ by comparing each among sampling periods when *Pyropia* was present (ordinal fixed factor) and while attributing epiphytism presence as a factor (nominal fixed factor) using two-way analysis of variance (ANOVA). The assumptions of homoscedasticity and normality were assessed using a visual inspection of residuals, and transformations were made to the response variable if either assumption was violated.

To test H₃, the sampling period with maximum densities for *Nereocystis* with and without *Pyropia* present was identified for each site and the time at which that sampling date occurred (Day, Month, Year) was converted into Julian calendar days. Julian calendar days at which maximum densities occurred (n = 5 sites) were tested using a two-sample, one-tailed Wilcoxon Sign Rank Test to determine whether epiphytized *Nereocystis* maximum densities occurred significantly later than unepiphytized *Nereocystis* maximum densities (one-tailed due to *Pyropia* primarily requiring *Nereocystis* presence means that *Pyropia* maximum density cannot occur before *Nereocystis* maximum density).

A fixed factor one-way ANOVA was used to test whether *Pyropia* gametophyte growth response to depth (final area, cm²) significantly varied among depth treatments (H₄). One punch was removed from the data in the intermediate depth treatment (10 m) after determining that the punch underwent gametogenesis to the point at which it interfered with a measurement of the growth response (heavy perforation, fragmentation, and senescence). A *post hoc* Tukey HSD test was further used to determine significant differences among depth treatments. The assumption of homoscedasticity and normality were assessed using visual inspection of residuals.

Photographs of conchocelis recruits were photoanalyzed using Fiji (ImageJ) to calculate the growth response at the tile's depth (final - initial area; μm²; H₄). The response of the average conchocelis growth per tile was compared with the depth of each tile using a simple linear regression (n = 14) to assess whether a significant association with depth existed. Residuals were visually assessed for confirmation of independence and homoscedasticity. Unfortunately, four conchocelis were determined to have grown into adjacent conchocelis recruits on the tiles with denser recruitment and needed to be discarded (including one depth treatment).

Nereocystis morphometrics were used to test intraregional variability in host parameters at the time of *Pyropia* recruitment (H₅). Separate one-way ANOVAs, with site as a random factor, were used to test whether significant differences occurred in the number of *Nereocystis* blades per individual, total blade biomass per *Nereocystis*, total stipe biomass per individual, and total biomass per *Nereocystis* among sites at the time of

first recruitment within the region (denoted by the first sampling period in which any *Pyropia* was seen for the 2018-2019 cohort at any site).

Stratified haphazard (individuals taken in each of 1 m depth bins along host stipes) subsampling was used to select *Pyropia* individuals within 1 m bins along *Nereocystis* stipes to photograph for gametogenesis. Five to ten *Pyropia* individuals were subsampled in each bin (or less if there were less than five), but all subsamples were pooled when determining the presence of *Pyropia* gametogenesis among sites. A chi-square test of homogeneity was performed on two contingency tables, one constructed comparing the presence and absence of gametogenesis among sites for both the November 2018 and January 2019 sampling periods, and one between the two sampling periods while pooling all sites together (H_6). November 2018 and January 2019 were selected for comparison because they were the only time periods in which gametogenesis was present for the 2018-2019 *Pyropia* cohort (no gametogenesis present prior and complete absence of individuals by February 2019).

Nereocystis were measured from the apex of the pneumatocyst to the furthest distance down the stipe that individual *Pyropia* were observed to determine maximum *Pyropia* recruitment depth. This measurement was correlated with *Nereocystis* stipe morphometrics using Pearson's correlation analyses to test whether there were significant correlations between *Pyropia* maximum recruitment depth and *Nereocystis* stipe length ($H7a$) and *Nereocystis* [SL:HD] ($H7b$). Only *Nereocystis* on which the maximum depth of *Pyropia* were recorded were used in the analysis ($n = 35$). The morphometric variability among *Nereocystis* stipe hollow length, non-hollow length, pneumatocyst

diameter, sub-bulb diameter, and largest non-hollow diameter were rearranged as principal components 1-5 for *Nereocystis* with *Pyropia* present. Pearson's correlation was used to determine whether any principal component significantly correlated with deepest *Pyropia* recruitment depth after visual inspection of residuals.

PCA was conducted on *Nereocystis* stipe morphometrics for collected *Nereocystis*, also excluding those collected in September 2018 and November 2018, for *Nereocystis* containing *Nereocystis* with detectable biomass (≥ 0.1 gDW). Any *Pyropia* dry weight below 0.1 g was considered insignificant and counted as 0.01 gDW for descriptive purposes. Total dry weight (gDW) for each *Nereocystis* was calculated by summing each bin on that *Nereocystis*. *Pyropia* biomass collected during the September 2018 and November 2018 sampling periods were excluded due to not being developed to the point of inflating juvenile biomass contributions to the analysis. The predictive relationship between *Pyropia* biomass in the first meter bin and total dry weight on hosts was tested using a simple linear regression (H₈).

The [SL:HD] was calculated for each *Nereocystis* by dividing the measured field calculated holdfast depth (relative to MLLW) by the measured total stipe length (m). Thresholding of *Pyropia* biomass by *Nereocystis* [SL:HD] was tested using a logistic regression on *Pyropia* biomass after a binary transformation to above and below the median value for pooled May 2018, June 2018, and January 2019 sampling periods (H₉). An inverse prediction was used to determine the [SL:HD] at which 50% of individuals were above the median *Pyropia* biomass.

Nereocystis stipe lengths and stipe diameters at multiple section of the stipe were used to estimate stipe surface areas (H_{10b}). Stipe morphometrics were used to construct four stacked 3-d polygons simulating a *Nereocystis* stipe: a sphere representing the pneumatocyst, two stacked truncated cones representing the hollow portion below the pneumatocyst, and a cylinder representing the non-hollow portion of the pneumatocyst (Kain 1987). The sum areas of the four polygons equated to the estimated surface area of the *Nereocystis* (see Figure 5B for surface area formula). Pearson's correlation analysis was used to determine whether *Pyropia* gTDW was significantly correlated with *Nereocystis* host stipe length (H_{10a}) for *Nereocystis* that hosted a measurable quantity of *Pyropia* (≥ 0.1 gDW *Pyropia*) during the May 2018, June 2018, and January 2019 sampling periods. An additional Pearson's correlation analysis was used to determine whether *Pyropia* gTDW was significantly correlated with *Nereocystis* host stipe surface area (H_{10b}) for *Nereocystis* that hosted a measurable quantity of *Pyropia* during the same sampling periods. PCA was conducted on *Nereocystis* that were epiphytized with a measurable amount of *Pyropia* during the same sampling periods using the same stipe morphometrics used previously (H_{10c}). Pearson's correlation analysis was used to determine whether any principal component significantly correlated with *Pyropia* total biomass. Lastly, *Nereocystis* host productivity correlations with total *Pyropia* biomass were tested using an additional Pearson's correlation analysis during the same sampling periods. A fourth root transformation was performed on gDW of *Pyropia* to satisfy homoscedasticity for all correlation analyses.

All statistical analyses were performed using JMP 14 software.

Results:

How did *Pyropia* Epiphytism Vary Intraregionally?

Sampling between November 2017 and February 2019 within the region described the densities of two cohorts of epiphytized and non-epiphytized *Nereocystis*: one cohort was described starting shortly after *Pyropia* recruitment (2017-2018) and the other described through the entirety of the annual persistence of *Nereocystis*, and therefore also *Pyropia* (2018-2019; Figure 7; Table 1). The ratio of densities of epiphytized to

Figure 7

Intraregional Host Persistence is Interannually Different

Note. Density within the region was characterized by subsampling epiphytized and non-epiphytized *Nereocystis* at sites ($n = 5$ sites: 5 subsamples at each site) south of Monterey Bay. *Nereocystis* from the 2017-2018 cohort (epiphytized with *Pyropia*) overwintered to co-inhabit canopies within the region alongside the 2018-2019 cohort (dashed bar in the June 2018 sampling period represent overwintered, but not epiphytized by *Pyropia*), but all sites sampled within the region were devoid of the 2017-2018 *Nereocystis* cohort by February 2019.

Table 1*Pyropia-Nereocystis Epiphyte-host Recruitment and Persistence Dynamics*

Variable	First Observed Canopy Recruitment		Sampling Period of Maximum Density		Site Presence Overlapping with Consecutive Cohort?		Last Observed Sampling Period for Cohort ¹	
	<i>Nereocystis</i>	<i>Pyropia</i>	<i>Nereocystis</i>	<i>Pyropia</i> ²	<i>Nereocystis</i>	<i>Pyropia</i>	<i>Nereocystis</i>	<i>Pyropia</i>
2017-2018 Cohort								
Site 1	N/A ³	N/A ³	Nov 2017	Nov 2017	Yes	Yes	Jun 2018	Jun 2018
Site 2	N/A ³	N/A ³	Nov 2017	Nov 2017	No	No	Nov 2017	Nov 2017
Site 3	N/A ³	N/A ³	Nov 2017	Nov 2017	No	No	Feb 2018	Feb 2018
Site 4	N/A ³	N/A ³	Nov 2017	Feb 2018	No	No	Feb 2018	Feb 2018
Site 5	N/A ³	N/A ³	Nov 2017	Feb 2018	Yes	Yes	Jun 2018	Jun 2018
2017-2018 Cohort								
Site 1	Jun 2018	Sep 2018	Aug 2018	Nov 2018	No	No	Jan 2019	Jan 2019
Site 2	Jun 2018	Nov 2018	Aug 2018	Nov 2018	No	No	Nov 2018	Nov 2018
Site 3	Aug 2018	Sep 2018	Aug 2018	Nov 2018	No	No	Jan 2019	Jan 2019
Site 4	Jun 2018	Sep 2018	Aug 2018	Nov 2018	No	No	Jan 2019	Jan 2019
Site 5	Jun 2018	Sep 2018	Sept 2018	Nov 2018	No	No	Nov 2018	Nov 2018

Note. *Pyropia-Nereocystis* spatiotemporal epiphyte-host variability among sites in central California regarding recruitment timing, persistence, and maxima of epiphytized and non-epiphytized host densities.

¹ For measurable densities ($\geq 0.033 / \text{m}^2$)

² *Nereocystis* epiphytized by *Pyropia*

³ Sampling of the 2017-2018 cohorts started after canopy recruitment of *Nereocystis* and *Pyropia*

non-epiphytized *Nereocystis* were initially less than 1:1, but then moved to equal to or greater than 1:1 for the remainder of the cohorts' persistence (Figure 8). The 2017-2018 and the 2018-2018 *Nereocystis* cohorts overlapped in the June 2018 sampling period. The same characteristic was not observed for *Pyropia*, as all epiphytized *Nereocystis* (i.e., all the *Nereocystis* 2017-2018 cohort) fully senesced by the June 2018 sampling period before recruitment of 2017-2018

Figure 8

Epiphytized to Non-epiphytized Host Ratios Over Time

Note. Diminishment of epiphytized to non-epiphytized ratios occurred at the first sampling period when the 2018-2019 cohort of *Nereocystis* reached the canopy and a steady increase of epiphytized to non-epiphytized *Nereocystis* ratios occurred after initial recruitment of 2018-2019 *Pyropia*. No *Nereocystis* were present during the February 2019 sampling period.

Pyropia - first observed within the region during the September 2018 sampling period.

The same ratio shift from less than 1:1 epiphytized:non-epiphytized *Nereocystis* to greater than 1:1 occurred one sampling period earlier for the 2018-2019 cohorts (in November 2018) when compared to the 2017-2018 cohorts (in February 2018).

Additionally, strong wave forces and frequent storm events (pers. obs., Winter 2018-2019) were accompanied with a full removal of 2018-2019 *Nereocystis*, and thus

Pyropia, by the February 2019 sampling period. A significant interaction between epiphytism presence and sampling period (fixed factor two-way ANOVA: $F_{1,49} = 6.068$, $p = 0.0001$; excluding sampling period August 2018; Table 2) was driven by the shift in

the ratio between epiphytized and non-epiphytized densities as *Nereocystis* overall densities declined, suggesting a shift in epiphytism frequency over time. The two-way ANOVA did not meet the assumption of equal variances (Levene's Test: $F_{1,71} =$

Table 2

Two-way Fixed-factor (Pyropia Presence and Time) ANOVA Results for Epiphytized and Non-epiphytized Nereocystis Density During the Times Where Pyropia was Present.

Source	df	SS	MS	F	p
Sampling Period	6	0.503	0.0839	5.152	0.0004**
Epiphyte presence	1	0.367	0.367	22.538	0.0001**
Interaction	6	0.593	0.0988	6.068	0.0001**
Error	49	0.798	0.0163		
Total	62	2.261			

Note. The significant interaction between presence and sampling period was driven by differences in interannual host persistence and the recruitment lag between *Pyropia* and the *Nereocystis* canopy.

* $p < 0.05$, ** $p < 0.01$

26.91589, $p = 0.0001$), but ANOVAs are robust tools for statistical testing despite invalidated assumptions (Sokal & Rohlf, 1993). Temporal variability for *Pyropia* biomass among sites was mixed, but this was insufficiently described for the 2017-2018 cohort due to the absence of sampling until April 2018 (Figure 9). There was a conspicuous rapid onset of biomass between the November 2018 and January 2019 sampling periods for the 2018-2019 cohort.

To account for different population sizes of epiphytized versus non-epiphytized *Nereocystis* across all sampling periods, the coefficient of variation (CV) was calculated for each site and compared among sampling periods and for the presence of *Pyropia*.

Figure 9

Pyropia Biomass Can be Limited by *Nereocystis* Persistence

Note. *Pyropia* biomass (gDW; treating sites as replicates) per *Nereocystis* for the 2017-2018 cohort (for the February 2018 and April 2018 sampling periods) shows comparable quantities to the biomass from the 2018-2019 cohort collected on January 2019. The initiation of *Pyropia* biomass between November 2018 (the mean for all sites being 0.175 gDW) and January 2019 (the mean for all sites being 10.6 gDW) was the largest observable increase between consecutive sampling periods.

The CV response showed no significant interaction between *Pyropia* presence and sampling period (two-way fixed factor ANOVA: $F_{6,64} = 1.5043$, $p = 0.1956$), but was significantly different across sampling periods (two-way fixed factor ANOVA: $F_{6,64} = 2.3184$, $p = 0.0469$; Table 3) and was significantly greater for non-epiphytized versus epiphytized *Nereocystis* (two-way fixed factor ANOVA: $F_{1,64} = 12.8541$, $p = 0.0008$) (Figure 10A). *Pyropia* biomass CV was greater than the CV of epiphytized host densities, indicating that the regularity of the presence of *Pyropia* was greater than the regularity of

biomass (Figure 10B). However, the significance of this comparison could not be tested due to insufficient sample sizes for *Pyropia* biomass among sites.

Table 3

Two-way Fixed-factor (Pyropia Presence and Time) ANOVA Results for Sampling Coefficient of Variation for Nereocystis Epiphytized and Non-epiphytized Densities Across Time.

Source	df	SS	MS	F	p
Sampling Period	6	0.687	4.121	2.318	0.0469*
Epiphyte presence	1	3.808	3.808	12.85	0.0008**
Interaction	6	0.446	2.674	1.504	0.196
Error	51	15.11	0.2962		
Total	64	25.71			

* $p < 0.05$, ** $p < 0.01$

Genetic identification of biomass samples, all sixteen intraregional samples across time, were identified to species as *Pyropia nereocystis*.

The intraregional densities of epiphytized and non-epiphytized *Nereocystis* showed a temporal syncopation in recruitment onset between host and epiphyte (Figure 11). This syncopation was determined to be significant after testing the difference in Julian days until maximum density was reached for each site between *Nereocystis* and epiphytized *Nereocystis* (one-tailed, two-sample t-test: $df = 5$, $t = 2.989$, $p = 0.017$; Figure 11).

Noticeably, the amount of variability, expressed as standard error, was larger for *Nereocystis* maximum density onset time when compared to the epiphytized *Nereocystis* maximum density onset time. The onset of *Pyropia* epiphytism was accompanied by a decrease in host biomass metrics (Figure 12). After initial *Pyropia* recruitment for the 2018-2019 cohort, collected *Nereocystis* showed a significant decrease in blade biomass,

a significant decrease in the quantity of blades, a decrease in blade length, and a decrease in total biomass (Table 3).

Figure 10

Epiphytized Nereocystis Exhibited Greater Regularity Than Non-epiphytized Nereocystis

Note. Sampling regularity, indicated by CVs, was (A) significantly greater for non-epiphytized hosts compared to epiphytized individuals, significantly different over time, but there was no significant interaction between presence and time. *Pyropia* biomass CVs (B) were higher than the CVs of epiphytized host densities, however, were of insufficient sample size to analyze statistically.

Figure 11

Pyropia Epiphytized *Nereocystis* After *Nereocystis* Reached Maximum Canopy Density

Note. Comparisons between the initial occurrence of the greatest densities of epiphytized and non-epiphytized *Nereocystis* were conducted by converting the date at which those greatest densities occurred into Julian day and treating each site as a replicate ($n = 5$). Epiphytized *Nereocystis* maxima occurred significantly later than *Nereocystis* density maxima (one-tailed two-sample t-test: $df = 5$, $t = 2.989$, $p = 0.017$).

However, the primary substrate of *Pyropia*, the stipe of *Nereocystis*, did not change in biomass (Table 4), suggesting that *Nereocystis* stipe characteristics did not shift over time.

Figure 12

Host Nereocystis's Blades Diminished into Winter 2018-2019

Note. 2018-2019 (epiphytized) *Nereocystis* exhibited an overall decreasing trend in blade size and number after *Pyropia* recruited although the only significant decrease observed was for total *Nereocystis* blade biomass after a log transformation and the total number of blades.

Table 4*Temporal ANOVAs for Nereocystis Morphometrics After Pyropia Recruitment*

	df	SS	MS	F	p
Total Blade Weight (kg)					
Sampling Period	2	8.012	4.006	14.874	0.0007**
Error	11	2.963	0.269		
Total	13	10.975			
Stipe Weight (kg)					
Sampling Period	2	0.00476	0.00238	0.0102	0.9899
Error	11	2.576	0.234		
Total	13	2.581			
Total Thallus Weight (kg)					
Sampling Period	2	1.296	0.648	1.789	0.2124
Error	11	3.985	0.362		
Total	13	5.281			
Number of Blades					
Sampling Period	2	47.483	23.742	37.808	0.0001**
Error	11	6.9076	0.628		
Total	13	54.391			
Maximum Blade Length (cm)					
Sampling Period	2	29.432	14.716	1.986	0.1835
Error	11	81.517	7.411		
Total	13	110.949			

Note. The 2018-2019 (epiphytized) *Nereocystis* cohort exhibited an overall decreasing trend in blade size and number after *Pyropia* recruited although the only significant decrease observed was for total *Nereocystis* blade weight after a log transformation and the total number of blades. Epiphytized *Nereocystis* stipe weights did not change over time.

* $p < 0.05$, ** $p < 0.01$

Ecophysiological Patterns of *Pyropia*

Pyropia gametophyte blade growth did not vary relative to depth when transplanted to 3 depths between 6 m and 14 m below MLLW (one-way fixed factor ANOVA: $F_{2,5} = 1.0778$, $p = 0.4081$; Table 5). Both deeper treatments (10 m and 14 m) had greater mean growth when compared to the 6 m treatment (Figure 13).

Table 5

Increased Depths Did Not Inhibit Pyropia Growth

	df	SS	MS	F	p
Depth	2	7099.723	3549.86	1.0778	0.4081
Error	5	16468.42	3293.68		
Total	7	23568.14			

Note. One-way fixed-factor (depth) ANOVA results for comparing ecophysiological growth response to transplantation indicated no significant differences among depths. * $p < 0.05$, ** $p < 0.01$

Figure 13

Pyropia Gametophytes Were Not Growth Restricted with Depth

Note. A three-week transplant of similar *Pyropia* punches to depths at and below the lower limit of recruitment showed no significant differences among growth responses among depths toward and below *Pyropia*'s observed lower depth limit. The mean growth response was least for the shallowest treatment.

The microscopic conchocelis stage, settled on limestone tiles, showed a positive linear growth correlation with depth (Figure 14; Pearson's correlation: $r = 0.72$, $df = 12$, $p = 0.0035$).

Figure 14

Conchocelis Grew More Quickly at Deeper Depths

Note. The 39-day experiment of transplanted conchocelis settled on limestone tiles across a range of depths showed a significantly increased growth response with depth.

What Regulates *Pyropia* Abundance?

Pyropia recruitment was first observed during the September 2018 and November 2018 sampling periods and therefore tests for significant differences in host morphometrics among sites were conducted on these dates. There were no significant differences in *Nereocystis* stipe weight, blade number, total blade weight, or total thallus weight in the September 2018 sampling period, but there was a significant difference in maximum blade length among sites (Table 6).

Table 6*Productivity Characteristics for Nereocystis in September*

	df	SS	MS	F	p
Total Blade Weight (kg)					
Sampling Period	4	102.30	25.57	2.481	0.096
Error	13	134.00	10.31		
Total	17	236.29			
Stipe Weight (kg)					
Sampling Period	4	36.14	9.04	2.209	0.125
Error	13	53.18	4.09		
Total	17	89.32			
Total Thallus Weight (kg)					
Sampling Period	4	238.86	59.72	2.804	0.070
Error	13	276.91	21.30		
Total	17	515.78			
Number of Blades					
Sampling Period	2	141695.69	35423.9	3.589	0.035*
Error	11	128322.75	9871		
Total	13	270018.44			
Maximum Blade Length (cm)					
Sampling Period	2	1669.194	417.30	1.192	0.360
Error	11	4549.750	349.98		
Total	13	6218.944			

Note. Random factor ANOVA results for *Nereocystis* morphometrics sampled in September 2018.

* $p < 0.05$, ** $p < 0.01$

Nereocystis in the November 2018 sampling period exhibited significant differences among sites in stipe weight, total thallus weight, and maximum blade length, while total blade weight and number of blades among sites were not significantly different (Table 7). Comparisons among sites for holdfast depths and [SL:HD] of collected *Nereocystis* for the 2018-2019 cohort indicated that despite differences in holdfast depths of collected individuals among sites (from the September 2018 sampling period through the January 2019 sampling period),

Table 7
Intraregional Nereocystis Morphometrics in November

	df	SS	MS	F	p
Total Blade Weight (kg)					
Sampling Period	4	42.41	10.60	1.633	0.218
Error	15	97.39	6.49		
Total	19	139.80			
Stipe Weight (kg)					
Sampling Period	4	124.19	31.05	8.242	0.001**
Error	15	56.51	3.77		
Total	19	180.70			
Total Thallus Weight (kg)					
Sampling Period	4	250.66	62.66	8.112	0.001**
Error	15	115.87	7.72		
Total	19	366.52			
Number of Blades					
Sampling Period	4	203271.63	50817.9	4.782	0.011*
Error	15	159407.93	10627.2		
Total	19	362679.56			
Maximum Blade Length (cm)					
Sampling Period	4	2177.20	544.30	1.112	0.387
Error	15	7337.75	489.18		
Total	19	9514.95			

Note. Random factor ANOVA results for *Nereocystis* morphometrics sampled in November 2018.

* $p < 0.05$, ** $p < 0.01$

differences in [SL:HD] arose only after the September 2018 sampling period (Figure 15; Table 8). In addition to differences among sites for *Nereocystis* morphometrics, significant differences were observed for gametogenesis for *Pyropia* among sites and between the last two sampling periods (Table 9). These significant differences suggest intraregional differences in environmental and/or biotic factors influenced both *Nereocystis* and *Pyropia*, supporting both H_{5a} and H_{6a}.

The second question was further addressed by testing hypotheses relating to the lower limit of *Pyropia* and testing hypotheses regarding the abundance of *Pyropia* on *Nereocystis* stipes.

Figure 15

Nereocystis Populations Likely Persisted Within Heterogeneous Environmental Conditions

Note. Whereas *Nereocystis* holdfast depths were significantly different among sites for the September 2018 – January 2019 sampling periods, *Nereocystis* [SL:HD] were significantly different among sites for the November 2018 and January 2019 sampling periods, but not for the September sampling period. The absence of data for site 2 in January 2019 is due to the complete removal of the *Nereocystis* canopy at that site before the date of sampling.

Table 8

Random Factor ANOVA Results for Holdfast Depth and [SL:HD] for the September 2018 Through January 2019 Sampling Periods

A. Holdfast Depth					
	df	SS	MS	F	p
September 2018					
Sampling Period	4	472.63	118.16	15.64	<0.0001**
Error	13	98.23	7.56		
Total	17	570.86			
November 2018					
Sampling Period	4	642.31	160.58	44.20	<0.0001**
Error	15	54.50	3.63		
Total	19	696.80			
January 2019					
Sampling Period	3	565.19	188.40	89.36	<0.0001**
Error	12	25.30	2.11		
Total	15	590.48			
B. [SL:HD]					
	df	SS	MS	F	p
September 2018					
Site	4	0.0157	0.004	0.296	0.875
Error	13	0.173	0.013		
Total	17	0.188			
November 2018					
Sampling Period	4	0.151	0.038	3.717	0.029*
Error	14	0.143	0.010		
Total	18	0.294			
January 2019					
Sampling Period	3	0.190	0.063	5.945	0.010*
Error	12	0.128	0.011		
Total	15	0.317			

Note. Despite the significant differences in holdfast depths among sites throughout the three periods, the differences among sites in [SL:HD] begun only after the initiation of fall/winter swells between the September 2018 and November 2018 sampling periods.

* $p < 0.05$, ** $p < 0.01$

Table 9*Zygotosporogenesis Differed Spatially and Temporally Within the Region.*

	No	Yes	Total	Frequency %
Gametogenesis by Site				
Site 1	98	2	100	2.0
Site 2	55	0	55	0
Site 3	266	2	268	0.75
Site 4	132	39	171	22.81
Site 5	128	32	160	20.0
Total	679	75	754	9.95
Gametogenesis by Date				
Nov 2018	358	3	361	0.83
Jan 2019	321	72	393	18.56
Total	674	75	749	9.95

Note. Contingency tables and associated Pearson's chi-squared tests indicated spatial differences in zygotosporogenesis for *Pyropia* within the region. Also, differences in zygotosporogenesis initiation between the November and January sampling periods for the 2018 cohort.

Regulation hypotheses relating to overall morphology of *Nereocystis* hosts were tested by first rearranging variability in morphological components (diameters of three locations on the stipe, hollow length, and non-hollow length) using principal component analysis (PCA) and testing correlations related to regulatory hypotheses. Separate PCAs were conducted for lower recruitment limit and biomass hypotheses regarding morphological correlations (Tables 10 and 11, respectively).

Table 10*Nereocystis Principal Components (Pyropia Lower Limit)*

Variable	PC1	PC2	PC3	PC4	PC5
Hollow Length	0.87	-0.03	-0.05	-0.32	-0.37
Non-hollow Length	0.76	-0.46	-0.26	-0.12	0.36
D ₁	0.63	0.42	-0.21	0.62	-0.02
D ₂	0.32	0.78	0.42	-0.28	0.20
D ₃	0.30	-0.45	0.80	0.25	-0.02

Note. Morphometric variability for epiphytized *Nereocystis* with measured *Pyropia* lower limits. Loadings calculated for each principal component were calculated using morphometric variables including hollow length, non-hollow length, and 3 diameters from *Nereocystis* with measured lower *Pyropia* lower recruitment limits (Eigenvalues - PC1: $\lambda = 1.92$, 38.41%; PC2: $\lambda = 1.19$, 23.88%; PC3: $\lambda = 0.94$, 18.79%; PC4: $\lambda = 0.64$, 12.85%; and PC5: $\lambda = 0.30$, 6.07%).

Table 11*Percentages of Sampled Nereocystis with Significant Pyropia Biomass by Site*

Site	Feb 2018	Apr 2018	Jun 2018	Aug 2018	Sep 2018	Nov 2018	Jan 2019	Feb 2019
Site 1	N/A	100	N/A	N/A	N/A	0	25	N/A
Site 2	100	100	N/A	N/A	0	50 ¹	N/A	N/A
Site 3	100	100	N/A	N/A	N/A	100 ¹	100	N/A
Site 4	100	100	N/A	N/A	N/A	100 ¹	50	N/A
Site 5	100	100	N/A	N/A	N/A	25 ¹	100	N/A

Note. Significant intraregional abundances of *Pyropia* (> 0.1 gDW) occurred after January. Percentages of *Nereocystis* with significant *Pyropia* abundances (≥ 0.1 gDW) for all sampling periods and at all sites exhibited a pattern of overall cohort biomass initiation and maintenance after November that persisted until *Nereocystis* were removed.

¹ Sites at this date had 50% or greater of the *Nereocystis* epiphytized by only 0.1 gDW *Pyropia*

Table 12*Nereocystis Principal Components (Pyropia Abundance)*

Variable	PC1	PC2	PC3	PC4	PC5
Hollow Length	0.63	0.53	-0.23	-0.48	-0.20
Non-hollow Length	0.91	-0.07	0.21	-0.13	0.33
D ₁	-0.15	0.45	0.88	0.00	-0.06
D ₂	-0.51	0.77	-0.31	0.05	0.24
D ₃	0.64	0.30	-0.01	0.70	-0.09

Note. Morphometric variability for epiphytized *Nereocystis* with significant (measurable) *Pyropia* abundance (gDW). Loadings calculated for each principal component were calculated using morphometric variables including hollow length, non-hollow length, and 3 diameters from *Nereocystis* with measured lower *Pyropia* lower recruitment limits (Eigenvalues - PC1: $\lambda = 1.92$, 38.32%; PC2: $\lambda = 1.16$, 23.28%; PC3: $\lambda = 0.97$, 19.32%; PC4: $\lambda = 0.73$, 14.65%; and PC5: $\lambda = 0.22$, 4.42%).

There was no observed relationship between host *Nereocystis* holdfast depth and the lowest *Pyropia* epiphytes observed (Pearson's correlation: $r = -0.0126$, $df = 34$, $p = 0.9418$; Figure 16), failing to support the hypothesis that light is the primary limiting factor for *Pyropia*'s lower limit. Stipe morphometrics, however, were shown to be correlated with increased *Pyropia* lower limits, as variability associated with longer hollow sections and shorter non-hollow sections (PC5; Table 10) were positively correlated with deeper lower limits (Pearson's correlation: $r = 0.4947$, $df = 34$, $p = 0.0022$; Figure 17). These results supported H_{7b} that lowest *Pyropia* recruitment is correlated with stipe morphometrics. *Pyropia* biomass (≥ 0.1 gDW) in the upper meter of host *Nereocystis* was a strong indicator of total *Pyropia* biomass on the whole stipe (Linear regression: $y = 2.45 * x$, $r^2 = 0.78$, $F_{1,15} = 71.74$, $p = 0.0001$; Figure 18), supporting hypothesis H_{8a}.

Figure 16

Nereocystis Recruitment Depth Did Not Mediate *Pyropia* Lower Limit

Note. After pooling samples across all sampling periods, no relationship was observed between the lowest *Pyropia* recruit observed on *Nereocystis* stipes and the depth of the hosts' holdfasts. This suggests that *Pyropia*'s lower depth limit is not restricted by the depth of the host.

Figure 17

Nereocystis Morphology Was Correlated with Pyropia Lower Limit

Note. The PC associated with greater hollowing length in host *Nereocystis* stipes relative to non-hollowing length (PC 5) was positively correlated with an increase in *Pyropia*'s recruitment depth limit. This hints at a relationship between hollowing and *Pyropia* recruitment (note the inverted y-axis), but also suggests that other factors likely also play a role in recruitment.

All epiphytized *Nereocystis* in the 2018-2019 cohort collected earlier than the January 2019 sampling period were epiphytized by less than 1.5 gDW (Table 11) and therefore, hypotheses testing for relationships between host morphometrics and *Pyropia* biomass only included the February 2018, April 2018, and January 2019 sampling periods.

Pyropia had a greater biomass on *Nereocystis* with a longer stipe length to holdfast depth ratio (i.e., when [SL:HD] was less than 1.05; Logistic regression: $n = 23$, $\text{ChiSq} = 3.70$, $p=0.0544$, inverse prediction of 50% at 1.0517 [SL:HD]; Figure 19). Significant positive correlations were found between *Pyropia* biomass and *Nereocystis* host surface area (Pearson's correlation: $r = 0.55$, $df = 21$, $p=0.0065$; Figure 20). *Pyropia* biomass and the

PC associated with longer and more cylindrical stipes (PC1; Table 12) were significantly positively correlated (Pearson's correlation: $r = 0.63$, $df = 21$, $p=0.0012$; Figure 21).

Figure 18

Pyropia Biomass Prediction

Note. For *Nereocystis* with significant biomass, *Pyropia* biomass attached to the upper meter of *Nereocystis* stipes is a strong indicator of total *Pyropia* biomass attached to the entire *Nereocystis* stipe. Due to half of samples being below 3 gDW (16 samples), all samples below 3 gDW were treated as subsamples and averaged to create a single data point.

All of these results indicated that *Pyropia* recruitment lower limit and abundance was influenced by host stipe morphology, *Pyropia* was more abundant on *Nereocystis* with larger surface area, and biomass was additionally thresholded below the regional median by a [SL:HD] greater than 1.05.

Figure 19

Nereocystis Thresholded *Pyropia* Biomass

Note. *Pyropia* biomass was thresholded by the [SL:HD] (Logistic regression: $n = 23$, $\text{ChiSq} = 3.70$, $p = 0.0544$) after a binomial *Pyropia* biomass transformation into ≥ 3.5 gDW and below 3.5 gDW (the median biomass of all samples). An inverse prediction determined 1.0517 to be the threshold at which 50% of samples were above or equal to 3.5 gDW and 50% were below 3.5 gDW.

Figure 20

Pyropia Biomass May Have Been Substrate Limited

Note. *Pyropia* biomass was positively correlated with *Nereocystis* surface area after a 4th root transformation to satisfy the assumption of homoscedasticity.

Figure 21

Nereocystis Likely Regulated Pyropia Biomass

Note. Greater *Pyropia* biomass was found on longer and more cylindrical *Nereocystis* stipes (PC1). *Pyropia* biomass was positively correlated with *Nereocystis* PC1 after a 4th root transformation to satisfy the assumption of homoscedasticity.

Discussion

This study advances the understanding of the relationship between *Pyropia* and its host *Nereocystis*. Adaptive radiation within the bladed-Bangiales resulted in a unique niche utilization by the gametophyte stage of this annual alga; *Pyropia* recruits almost exclusively on the stipe of another sympatric annual kelp species: *Nereocystis*. *Pyropia* epiphytism on *Nereocystis* stipes occurs throughout the range of the host *Nereocystis* and is primarily limited to the upper few meters in the water column (Hus, 1902; Abbott & Hollenberg, 1976; Hawkes, 1978), although in this study *Pyropia* was observed epiphytizing host *Nereocystis* at up to 12 m. However, like *Pyropia*'s settlement substrate

preference, natural variability and anomalous circumstances mar the understanding of this species. Within this narrow vertical distribution, individual *Pyropia* have been recorded to grow to the lengths of 10 m (longer than some of the *Nereocystis* measured in this study; Hawkes, 1978). There is evidence that the epiphyte-host relationship between *Pyropia* and *Nereocystis* is common and not exclusively obligative (Hawkes, 1978; Dickson & Waaland, 1985), but scientific investigation into the interactions between the two species has been lacking.

In the northeast Pacific, environmental factors change along a latitudinal gradient, and regional biotic characteristics can also be spatially and temporally heterogeneous (Hare & Mantua, 2000, Blanchette et al., 2008; Britton-Simmons et al., 2008; Carroll, 2009; Deser et al., 2010; Fiedler & Mantua, 2017; Gentemann et al., 2017). In central California, close to the southern limit of these species' ranges, this study comprised two fundamental components revolving around these epiphyte-host population dynamics. This study elucidated the spatial, temporal, and spatiotemporal dynamics of the epiphyte-host relationship within this region using a generalized selection of five accessible sites and sampling over a period greater than a year. This study also examined the relationship between these species by investigating and identifying significant relationships between host morphology and epiphyte biomass and recruitment depth.

Spatial, Temporal, and Spatiotemporal Variability in Epiphyte-Host Dynamics

Epiphyte-host population dynamics between the macroscopic phase of these two algae within central California varied regarding recruitment timing and dispersion of epiphytized versus non-epiphytized hosts. *Nereocystis* cohorts overlapped over the study

period, but the distinction between *Pyropia* cohorts was easily discernable for all sites due to comparably delayed recruitment period of *Pyropia* epiphytes and the limited temporal persistence of *Nereocystis* host cohorts. The absence of *Pyropia* from one or more sampling periods among sites, compared to no sampling period except for the last in which *Nereocystis* was entirely absent across all sites, suggests that persistence capabilities are more restricted for *Pyropia* compared to *Nereocystis*. Inherently, the term "annual" species implies temporal differences across the year (Maxell & Miller, 1996). However, the density patterns observed in this study, particularly the significant spatiotemporal shift from high densities of non-epiphytized hosts in spring and early summer to a late fall shift toward lower densities and more equal proportions of epiphytized to non-epiphytized hosts, magnifies the importance of the early winter temporal window in which *Pyropia* utilizes to complete its lifecycle. Furthermore, factors influencing the thinning of *Nereocystis* in that seasonal window, and spatial differences in the magnitude of these factors, likely play a role in a *Pyropia* cohort's magnitude of zygospore release (longer host persistence may lead to greater epiphyte spore release).

When population dynamics were examined in sampling periods where the two *Pyropia* cohorts sampled in this study were present, the density of epiphytized *Nereocystis* in central California expressed lower variability (CV) when compared to non-epiphytized *Nereocystis* among 5 sites within the region. The CVs serve as metrics to compare variability among populations of different sizes (Sokal & Rohlf, 1993; Gotelli & Ellison, 2004). *Nereocystis* expresses high spatial and temporal variability in population dynamics across their distribution (see Springer et al., 2007 for review). This high

variability makes the comparison of CV between epiphytized and non-epiphytized *Nereocystis* a useful metric to assess regularity in epiphytism. This metric was particularly useful to assess intraregional variability in epiphytism in this study because replication of transects within each site over time allowed for error components to be attributed within the region for each time period (Hurlbert, 1990). This suggests that epiphytism of *Nereocystis* is more regular within beds throughout the region than it is irregular. Furthermore, the regularity of epiphytized individuals suggests that the conchospore supply, allowing for the recruitment of *Pyropia* gametophytes, is ample. The persistence of non-epiphytized *Nereocystis*, however, denotes that conchospores (1) do not interact with every *Nereocystis* or (2) are not competent when interacting with some *Nereocystis* due to environmental or biotic (epiphyte-host interaction) factors. The perennation of conchocelis can be a source for recurring spore supply (Dickson & Waaland, 1985) even when a previous years' zygospore supply for alternation of generations was low. However, the potential for *Nereocystis* to not interact with conchospores (i.e., reject *Pyropia* recruitment or provide an unsuitable recruitment substrate) cannot be discounted. Further study could elucidate the percentage of *Nereocystis* that facilitate *Pyropia* recruitment by exposing a large number of *Nereocystis* directly with conchospores over a broad spatial scale.

The delay between the 2018-2019 epiphyte-host cohorts (≥ 2 months) between when *Nereocystis* was observed in the canopy and before *Pyropia* was observed in the region may be due to *Pyropia* having evolved a delay in conchospore dispersal (such as by environmental cues described by Dickson and Waaland [1985]) or due to epiphyte

prevention mechanisms by *Nereocystis*, such as with phlorotannins (e.g., McLachan & Craigie, 1966), tissue sloughing, or through the scouring effects associated with entanglement. This small window may have selected for *Pyropia* gametophytes that matured and sexually reproduced more quickly. Furthermore, speciation among congeneric *Pyropia* may have been facilitated due to the fact that sexual reproduction would need to occur: (1) among gametophytes within the same bed, or even among gametophytes on the same host; and (2) within the tiny window after *Pyropia*'s recruitment and before *Nereocystis*'s removal from the system. However, the low percentage of gametophytes in the region that were observed to have gone through sexual reproduction before complete host removal for the 2018-2019 cohorts (18.56%) suggests that a perenniating conchocelis phase may play a greater importance for years after which heavy storms minimize replenishment of conchocelis (e.g., the 2018-2019 *Pyropia* cohort). Regardless, the temporal window of opportunity for the persistence of *Pyropia* on *Nereocystis* highlights extreme specialization in synchrony for the annual epiphyte on its annual host and despite heterogeneity in persistence of its host.

Nereocystis seasonal thallus persistence can be variable in which populations can either disappear or overwinter (Foreman, 1970; Abbott & Hollenberg, 1976). These populations can be pre-programmed to decline through senescence, but can also be influenced by abiotic or biotic factors, such as wave forces or grazing, or a combination of the two (Denny et al., 1997; Duggins et al., 2001). Specific to *Nereocystis* in this study, sites were entirely absent of *Nereocystis* in the surface canopy before the 2017-2018 spring canopy recruitment (pers. obs.) while also entirely absent of *Nereocystis* at

the end of the 2018-2019 cohort. While the sites sampled in this study demonstrated the potential for fluctuating interannual persistence and removal, interspersed protected habitats within the region may have acted as refugia for the oldest and longest persisting *Nereocystis* and *Pyropia* individuals (pers. obs.). The significance of these refugia on the genotypic diversity of *Nereocystis* is uncertain, but in years in which heavy storms remove the vast majority of *Nereocystis* earlier in the winter (e.g., 2018-2019), a few individuals of both *Nereocystis* and *Pyropia* within these refugia may influence populations in substantial ways through prolonged propagule dispersal for both *Nereocystis* and *Pyropia* (Saunders, 2014). Given that the CV for epiphytized *Nereocystis* was less than that of non-epiphytized *Nereocystis*, a carefully planned spatial comparison of genotypic diversity between epiphyte and host could test whether persistent and/or sporadically patchy populations of *Nereocystis* are to the genotypic diversity of its epiphyte *Pyropia* (more specifically to the epiphyte *Pyropia nereocystis*). More broadly, further study needs to be conducted examining what drives interannual persistence of *Nereocystis* and *Pyropia* across the range of *Nereocystis*.

This study recorded intraregional heterogeneity of persistence for *Nereocystis*, and thus also *Pyropia*. Spatiotemporal differences in *Pyropia* epiphytism can be attributed to (1) host presence at a location; (2) differences in recruitment and persistence of the epiphyte both interannually and among sites; and (3) the interannual variability in host persistence. *Pyropia* biomass for the 2018-2019 cohort was observed to have a more delayed peak in gTDW when compared with the peak in densities of epiphytized *Nereocystis*. Considering the removal of all host substrate in early 2019, the biomass

potential of *Pyropia* at certain sites for the 2018-2019 cohort was likely not reached. The consequences of not reaching this potential may have been responsible differences in gametogenesis among sites. This emphasizes an important condition for the epiphyte-host relationship for this region: host removal can limit the epiphyte's localized dispersal before its biomass peak. The comparison between the 2017-2018 *Pyropia* cohort's biomass during the February 2018 sampling period and the 2018-2019 *Pyropia* cohort's biomass before the removal of *Nereocystis* may suggest a possible senescence phase for *Pyropia*. Herbert & Waaland (1988) and Figueroa et al., (2003) showed a lack of photoinhibition protection by *Pyropia*; individuals may be exposed to increasing PPFD if they persist into late spring/early summer. Senescence or outright mortality may result, and that combined with diminished recruitment after winter (Dickson & Waaland, 1985) could be responsible for an overall decrease in *Pyropia* biomass. The inadequate biomass sampling for the 2017-2018 *Pyropia* cohort and the removal of all 2018-2019 intraregional host *Nereocystis* by the February 2019 sampling period prevented an understanding of the potential *Pyropia*'s biomass peak (in addition to not describing intraregional peaks in *Pyropia* gametogenesis among populations) However, the large amount of variability *Pyropia* biomass among sites between the two years (and a low sample size) may suggest that the biomass peak is reached a few months after *Pyropia* recruits and then it's maintained as long as *Nereocystis* persists.

Factors Potentially Influencing *Pyropia*-*Nereocystis* Epiphyte-Host Dynamics

There was evidence of an effect of environmental and/or biotic heterogeneity (e.g., turbidity gradients, or competitor influences) or habitat differences (i.e., substrate depth)

on *Pyropia*'s substrate, such as the timing of *Nereocystis* canopy recruitment and the significantly different morphological characteristics of *Nereocystis* at the time of *Pyropia*'s earliest recruitment within the region. Environmental heterogeneity is further supported by intraregional differences in *Nereocystis* persistence within the region. The wide range of sporophyte recruitment depths is a testament to persistence capabilities of *Nereocystis* despite intraregional variability in depth-related abiotic and biotic factors (e.g., light or competitors varying with depth). Furthermore, the significant differences among site for *Nereocystis* holdfast depth and [SL:HD] suggest further environmental effects on *Pyropia*'s substrate. The halting of stipe elongation at the surface of the water column was previously shown by Nicholson (1970) and attributed to a physiological response to far red wavelengths of light by Duncan and Foreman (1980). Wave forces have been shown to contribute to variability in extension length (Koehl & Wainwright, 1977) and may have also contributed to [SL:HD] spatial heterogeneity. The [SL:HD] may have also been influenced by stipe entanglement among multiple individuals, a common occurrence (pers. obs.) before the stipe elongation phase ended. *Nereocystis*'s [SL:HD] deviation from the depth of the substrate (a 1:1 ratio) may have been due to other reasons such as a *Nereocystis* canopy interaction with delayed recruits (i.e., partial shading) or sporadic turbidity influences delaying termination of the stipe elongation phase of the individual (Duncan & Foreman, 1980). Regardless, as spatial heterogeneity impacts on algae are ubiquitous (see Hurd et al., 2014 for review), variable conditions experienced by host populations most likely also influenced *Pyropia* populations.

Intraregional differences in *Pyropia* gametogenesis for the 2018-2019 cohort support this conclusion.

The conchocelis phase of *Pyropia* may provide heteromorphic benefits to population dynamics as were previously mentioned (i.e., an overwintering perennating conchocelis). However, little is understood about its spatial distribution, ecophysiological relationship with reproduction, and population dynamics relating to its lithic substrate. Although ecophysiological differences have been observed between conchocelis and gametophyte stages of *Pyropia* (e.g., Wang et al., 2019). It is possible that the conchocelis phase of *Pyropia nereocystis* exhibits similar niche differentiation and zonation preferences similar to the differentiation observed among gametophytes of sympatric *Pyropia* species (e.g., Tala & Chow, 2014). Bioerosion, such as described by Schneider and Torunski (2008) using the example of the effects of grazing gastropods' radulas, may allow for exposure of vegetative conchocelis to the marine environment and removal of competitors for light, providing an explanation conchosporangial development in regions where conchocelis is easily overgrown by epilithic algae (e.g., the shallow subtidal or low intertidal zone). Whereas this study could not demonstrate the effect of depth on conchosporogenesis among conchocelis maintained at different depths, the positive relationship observed between growth and depth for *Pyropia* conchocelis on limestone tiles suggests that abiotic and/or biotic factors may influence distributional patterns for *Pyropia* conchocelis. The ecophysiological relationship between *Pyropia* and its environment may extend to variability in reproductive cues along a distributional gradient, where certain thresholds can act as boundaries for either depth related or

latitudinal range distributions, such as between gametophyte stages of kelp species (Matson & Edwards, 2007). Multiple reports of positively buoyant conchospores (Mathieson, 1975; Levine & Sahoo, 2010; Andersen, 2012) suggest a retention of propagules toward the top of the water column where they can either aggregate in the intertidal proximal to where they were released or be transported longshore. Since there is evidence that conchospores are positively buoyant (Mathieson, 1975; Levine & Sahoo, 2010; Andersen, 2012), it is reasonable that a mixture of positive buoyancy and physical wave forces may allow for conchospore transport to suitable recruitment locations within *Nereocystis* canopies, despite those conchospores having originated at depths with insufficient conditions for gametophyte recruitment (i.e., lack of *Nereocystis* substrate). This positive buoyancy is the likely cause of primary *Pyropia* gametophyte recruitment residing on upper *Nereocystis* stipes, as transplanted gametophytes showed no ecophysiological growth ramifications after being transplanted deeper, yet this needs to be tested by exposing *Nereocystis* stipes with conchospores along a depth gradient and monitoring recruitment. Increased depth distribution due to decreased light requirements could act synergistically with positive conchospore buoyancy potentially resulting in greater dispersal distances; populations of *Pyropia* may be connectively open due to their conchospores, but population connectivity may be impacted by conchospore competency limitations after initial dispersal (maximum viable time between conchospore release and settlement). All of these potential influences of population dynamics of *Pyropia* may be further complicated due to variability in calcium carbonate settlement substrate affecting distribution and abundance of conchocelis. Several experiments come to mind testing

these variables, such as examining genetic connectivity among *Nereocystis* and *Pyropia* on small and large scales across their geographic range and exploring competency of suspended conchospores over time.

In addition to the observed effects of intraregional heterogeneity on *Pyropia* (i.e., variable recruitment timing and gametogenesis), this study identified two *Pyropia* gametophyte metrics that were correlated with *Nereocystis* stipe characteristics: (1) *Pyropia* deepest recruitment depth on the stipes of *Nereocystis*; and (2) *Pyropia* biomass (gDW). These relationships suggest that *Nereocystis* plays a regulatory role on *Pyropia*. Evidence of *Nereocystis*'s regulatory effect manifested separately for the two phenological components of *Pyropia*, suggesting a level of independence between recruitment depth and growth for *Pyropia*. Explaining the mechanisms by which these regulatory effects take place, however, is limited to speculation.

There was no relationship between stipe length of *Nereocystis* and the *Pyropia* lower depth limit, suggesting that the depth in which *Pyropia*'s host holdfast is situated is not a limiting factor in *Pyropia*'s lower limit. However, despite the lack of pattern associated with stipe length, it is important to note that the lower limit was observed to be close to the 1:1 [LL:HD] (*Pyropia* lower limit:*Nereocystis* holdfast depth) on some hosts, where *Pyropia* had recruited on hosts' stipes close to the host holdfasts for shallower individuals. Although the incidence rate was low, four individuals showed this deeper distribution, suggesting that the reportedly buoyant conchospore supply can establish competency close to holdfasts. This established competency may be due to a well-mixed water column or due to conchospores generated from conchocelis proximal to holdfasts.

More generally, the positive relationship between stipe characteristics (PC [5]: *Nereocystis* with longer and thinner hollowed stipe portions and shorter non-hollow portions having greater *Pyropia* lower limits) and *Pyropia*'s lowest epiphytized depth was determined significant. This relationship suggests a link between apophysis morphology and recruitment of *Pyropia* that may be direct or indirect. The lack of characteristics described by this PC may have been responsible for the lack of competency for settled conchospores, regardless of light availability (i.e., availability of light at deeper depths along the stipe). Apophysis (and pneumatocyst) formation is due to the production of air due to the splitting of medullary tissue at meristematic regions (Dromgoole, 1981a), and consequent damage may result in provision of secondary metabolites to the environment around *Nereocystis* (see Knoblauch et al., 2016b). Alternatively, an untested factor may have both caused morphological differentiation described in the PC while also allowing for recruitment of *Pyropia* (e.g., microbial community on *Nereocystis* stipes; Dethier et al. 2014, Weigel & Pfister, 2019). Importantly, the facilitation of *Pyropia* recruitment depth by *Nereocystis*, as well as the observation of *Pyropia* recruits below 10 m, suggests that conchospore supply can be provided down to deeper depths and that regulation of the lower limit was directly or indirectly associated with *Nereocystis* hollowing.

The biomass of *Pyropia* attached to the upper meter of the stipe was a strong indicator of the total biomass of *Pyropia* attached to the entire *Nereocystis*. The prediction model in this study indicated that approximately half of the total *Pyropia* biomass is in the upper 1 m of the stipe. This concurs with Hawkes' (1978) conclusions that the majority of *Pyropia* biomass is attached to the upper 2 m of the stipe. However,

whereas Hawkes (1978) sampled negligible biomass occurred below 3 m, this study revealed individual *Nereocystis* with significant *Pyropia* biomass (>0.1 gDW) up to 6 m depth. *Pyropia* biomass accumulation on *Nereocystis* exhibited patterns suggestive of host regulation. There was a threshold relationship observed between *Nereocystis* [SL:HD] and *Pyropia* biomass, indicative of a maximum [SL:HD] above which *Pyropia* abundances drop off. At a ratio of greater than approximately 1.1:1, *Pyropia* biomass was limited in biomass to values below 3.5g per host, whereas below that SL:HD ratio *Pyropia* biomass was not limited and reached values as high as 77.5 gDW per host. This relationship was unclear due to sampling limitations, but likely was caused by one of two reasons: (1) *Pyropia* biomass was limited in the upper region of the stipe on *Nereocystis* that are longer than the depth of the water column and therefore are exposed to air more readily regardless of tidal cycles, and/or (2) *Pyropia* biomass was limited in the upper region of stipes that are entangled and thus experience routine conspecific scouring effects. Smith et al. (1986) demonstrated that exclusively subtidal species of *Pyropia* cannot physiologically tolerate desiccation stress and individuals succumb to mortality with moderate air exposure. An epiphytized stipe floating on the surface and exposed to cyclical physical oceanographic forces (e.g., tidal flux, differing wave direction) may expose enough of the stipe to enough air over a given time period long enough to prevent considerable *Pyropia* biomass accumulation on those stipes. The second hypothesis was first suggested by Woessner (1981) who noted that clumped *Nereocystis* contained less *Pyropia* biomass in the field. His reasoning for this was a scouring effect caused by physical forces imposed on entangled *Nereocystis* stipes limiting recruitments of *Pyropia*.

Without further study, the precise reasoning for this relationship between *Pyropia* biomass and *Nereocystis* SL:HD is unclear, but is likely caused by abiotic forces imposed on the optimal recruitment locations on the stipe (i.e., the apophysis).

Additionally, *Pyropia* biomass accumulation was shown to be correlated with different parameters, supporting the explanation that multiple host-related factors may play a role in *Pyropia* phenology. The correlation between *Nereocystis* surface area and *Pyropia* biomass suggests that *Pyropia* is substrate-limited. This substrate limitation is likely compounded by both the relationship between *Pyropia* biomass and *Nereocystis* density (total number of individuals to be epiphytized), in addition to the relationship between surface area on individual *Nereocystis* and *Pyropia* biomass on that individual host. The observed relationship between stipe characteristics denoted by the principal component (PC) as thinner and longer individuals with more cylindrical apophyses (increased lower apophysis diameter). This relationship can be indicative of two potentially beneficial qualities this *Nereocystis* morphology provides to *Pyropia*. This morphology may result in longer persistence of *Nereocystis* leading to potentially larger *Pyropia* epiphytes. An alternative less likely explanation may be that apophysis morphology is a response to physical forces stretching the stipe (Koehl & Wainwright, 1977) or a response to physical forces influencing the tearing process of medullary stipe tissue during apophysis creation and elongation (Nicholson, 1970). Though *Nereocystis* are likely to experience similar wave forces within a site, interaction with conspecifics (entanglement; Koehl & Wainwright, 1977), or within site morphological consequences

of heterogeneity of blade number (i.e., different drag forces; Nicholson, 1970; Denny et al., 1997) relating to wave forces could have resulted in differentiation within a site.

The regulatory relationship between *Nereocystis* and the abundance of *Pyropia* may have been attenuated by the early comprehensive removal of *Nereocystis* in the region. Alternatively, the relationship observed in this study have been overstated due to this early removal (or may have even been absent if *Nereocystis* hosts from the 2018-2019 cohort were to persist later into 2019). Each of the aforementioned effects of greater persistence of hosts may be indicative of population-scale importance; the former scenario would suggest greater importance in individual epiphyte-host relationships, while the latter scenario would suggest greater importance in the early establishment of *Pyropia* biomass likely associated with greater fitness. The correlative relationships described only existed within a subset of epiphytized individuals; epiphytized *Nereocystis* without significant biomass comprised a large proportion until the January 2019 sampling period. Furthermore, variability in *Pyropia* abundance may have also been due to pre- or post-recruitment responses to differing abiotic or biotic factors within the region. Factors influencing the specific *Nereocystis* morphology favoring *Pyropia* among individuals may have colinearly facilitated *Pyropia* growth, and further study is needed to isolate environmental and host-related factors on *Pyropia* growth. Further study utilizing transplanted *Pyropia* conchospores and measuring ecophysiological responses for *Pyropia* across a variety of environmental factors is recommended. Additionally, biotic effects on *Pyropia* gametophytes need further study, as bite marks at some sites and not

others suggest grazers or consumers of associated invertebrates may have played a role in limiting or delaying biomass accumulation of *Pyropia*.

Future Studies

There are several avenues for testing hypotheses to further elucidate the relationship between *Nereocystis* and epiphytized *Pyropia*. The physiological importance of the *Nereocystis* apophysis on recruitment and biomass accumulation of epiphytic *Pyropia* can be further investigated. Translocation within *Nereocystis* stipes (Nicholson & Briggs, 1972) and associated DOM emission into the surrounding water column may be an excellent starting point. Stipe composition has been shown to be variable over time (Wheeler et al., 1984) and may also reveal specific parameters that differ between epiphytized and non-epiphytized *Nereocystis*. Other epiphytes absorbing nutrients from a host (Harlin, 1973) could suggest a pathway for investigation, where examining whether radioactive carbon isotopes originating in hosts are transferred to epiphytes, or the intensity of transfer suggesting a level of dependence. Further study with placing *Pyropia* conchospores at various locations along a depth gradient along *Nereocystis* stipes could be used to decouple physiological parameters with environmental variability to better parameterize *Pyropia*'s physiological dependence on *Nereocystis*. Usage of innovative tagging methods such as used by Nicholson (1970) to examine self-thinning and persistence of *Nereocystis* is a promising direction for identifying morphometrics among individuals that may support persistence (as were modelled by Denny et al., 1997; see Demes & Pruitt, 2019). Whether *Nereocystis* morphology selects for host persistence and thus allows for *Pyropia* biomass accumulation, or whether the *Nereocystis* themselves are

providing resources to *Pyropia* for growth remains to be seen. However, the correlations mentioned are indicative of an advantage provided to *Pyropia* by *Nereocystis*.

Addressing The Potential For Two Epiphytic *Pyropia* Species

Lastly, to prevent conflation between *Pyropia nereocystis* and *Pyropia thuretii*, genetic analysis was performed on some samples collected across time and space throughout the study period. The fifteen samples were all identified as *P. nereocystis*, which was expected, given the paucity of *P. thuretii* identified in the area by Hawkes (1978). Furthermore, some individuals sent for genetic identification possessed "ruffled margins" that Hawkes (1978) among others (i.e., Hus, 1902) identified as a defining characteristic for *P. thuretii*, further highlighting the necessity for genetic identification for parsing the genus. Given that the defining characteristics based on gametogenesis differences were not present throughout the whole study period and given the small sample size that was genetically identified, it is conservative to assume that *P. thuretii* were present within samples. However, due to the 100% identification of *P. nereocystis*, and prior (albeit also lacking genetic identification; Hawkes, 1978) accounts of *P. thuretii* being sparse within the region, it is likely that the majority if not the vast majority of *Pyropia* abundance was *Pyropia nereocystis*.

Conclusions

While much remains to be tested regarding epiphyte-host population dynamics between *Pyropia* and *Nereocystis*, this study identified patterns that suggest populations of *Nereocystis* have a multifaceted regulatory relationship with *Pyropia* in the presence of dynamic environmental heterogeneity at the southern extent of both species' range. The maxima of epiphytized *Nereocystis* occurred significantly later than unepiphytized *Nereocystis*'s population canopy density maxima within the region, exemplifying *Pyropia*'s occupation of a multigenerational spatiotemporal niche on *Nereocystis*. The correlation between *Pyropia*'s lower limit and *Nereocystis* morphology, thresholding of *Pyropia*'s abundance by *Nereocystis* [SL:HD], correlation between *Pyropia*'s abundance and *Nereocystis* substrate availability, and correlation between *Pyropia*'s abundance and *Nereocystis* morphology suggest a multifaceted regulatory relationship between *Nereocystis* and *Pyropia*. This regulatory relationship is further affected by environmental parameters that can heterogeneously determine host persistence within the region, while also likely influencing epiphyte ecophysiology. The variability associated with *Nereocystis* stipes' morphological parameters (PCs) that correlated with *Pyropia* recruitment depth and *Pyropia* abundance was different, suggesting differences in the relationship between *Nereocystis* stipes and each epiphyte metric. Further study is needed to determine the strength of causality behind this multifaceted relationship imposed by *Nereocystis* and further study is needed to clarify the role *Pyropia*'s conchocelis plays in *Pyropia*'s biogeography.

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