UNIVERSIDAD AUTÓNOMA DE BAJA CALIFORNIA

FACULTAD DE CIENCIAS MARINAS
INSTITUTO DE INVESTIGACIONES OCEANOLÓGICAS

Invasiones simultáneas de macroalgas en un bosque de sargazo gigante
(*Macrocystis pyrifera*) cerca de su límite de distribución Sur
en el hemisferio Norte

T E S I S

QUE PARA CUBRIR PARCIALMENTE LOS REQUISITOS NECESARIOS PARA
OBTENER EL GRADO DE
MAESTRO EN CIENCIAS EN OCEANOGRAFÍA COSTERA

PRESENTA

LUCÍA MERCEDES RODRÍGUEZ BRAVO

ENSENADA, BAJA CALIFORNIA, MÉXICO. DICIEMBRE 2021

Resumen

Las especies invasoras están entre las mayores amenazas actuales a los ecosistemas costeros, moduladas por el cambio climático. Investigamos las dinámicas de una comunidad de macroalgas en Islas Todos Santos a lo largo de un año, cerca del límite de distribución de los bosques de sargazo gigante en el hemisferio norte. Las cuatro macroalgas más comunes en este sitio son el alga nativa *Macrocystis pyrifera*, y las no nativas *Sargassum muticum*, *Sargassum horneri* y *Undaria pinnatifida*. Describimos la densidad y biomasa, tanto anual como estacional, para cada una de estas especies. Hallamos que, a pesar de que el arrecife está dominado completamente por algas no nativas, la población de *M. pyrifera* en Islas Todos Santos retiene un potencial limitado para recuperarse. La comunidad de macroalgas que estudiamos mostró señales de uso complementario de los recursos, con máximos de biomasa y reclutamiento que variaron estacionalmente según la especie. Sin embargo, este ensamblaje fue documentado en un año con temperaturas favorables para *M. pyrifera*, lo cual posiblemente ayudó a su capacidad para reclutar y crecer. Dado que futuras olas de calor continuarán afectando desproporcionadamente a *M. pyrifera*, nuestros resultados sugieren que los esfuerzos para incrementar el número de juveniles de *M. pyrifera* podrían ser una técnica de restauración más efectiva que el manejo de estas algas no nativas. Nuestro trabajo resalta el valor de investigar la variabilidad de densidades, biomasa, y la relación con la temperatura de ensamblajes con múltiples macroalgas no nativas en un clima cambiante.

FACULTAD DE CIENCIAS MARINAS

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POSGRADO EN OCEANOGRAFÍA COSTERA

INVASIONES SIMULTÁNEAS DE MACROALGAS EN UN BOSQUE DE SARGAZO GIGANTE ((*MACROCYSTIS PYRIFERA*) CERCA DE SU LÍMITE DE DISTRIBUCIÓN SUR EN EL HEMISFERIO NORTE

T E S I S

QUE PARA CUBRIR PARCIALMENTE LOS REQUISITOS NECESARIOS PARA OBTENER EL GRADO DE

MAESTRA EN CIENCIAS EN OCEANOGRAFÍA COSTERA
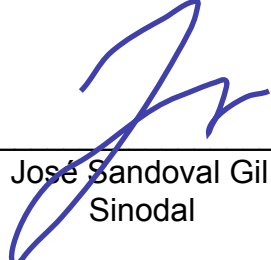
PRESENTA

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Abstract

Invasive species are among the foremost current threats to coastal ecosystems, with climate change modulating their success. We investigated the numeric abundance dynamics of a macroalgal assemblage near the southern distribution limit for kelp forests in the Northern hemisphere after an extreme marine heatwave. The four most common macroalgae at this site are the native *Macrocystis pyrifera*, and the non-natives *Sargassum muticum*, *Sargassum horneri* and *Undaria pinnatifida*. We described yearly and seasonal density and biomass for each of these species during the year. We found that despite a subcanopy entirely dominated by non-native algae, the *M. pyrifera* population at Isla Todos Santos retains a limited potential to recover. The macroalgal assemblage we studied showed signs of niche complementarity, with peaks in biomass and recruitment varying seasonally by species. However, we documented this assemblage in a year with favorable temperatures for *M. pyrifera*, which likely aided its capacity to recruit and grow. As marine heatwaves will continue to disproportionately impact *M. pyrifera*, our result suggests efforts to increase the number of *M. pyrifera* juveniles could be a more effective restoration technique than managing non-native macroalgae. Our work highlights the value of investigating the variability of density, biomass and the relationship with temperature of multiple macroalgal species in a changing climate.

Introduction

Invasive species and climate change are some of the foremost current threats to ecosystems (Early et al., 2016; Schaffelke et al., 2006), with climate change modulating the success of invasion by non-native species (Burgiel and Muir, 2010; Diez et al., 2012; McKnight et al., 2021; Rahel and Olden, 2008). Anthropogenic activity is increasingly facilitating the introduction of non-native species, as well as increasing atmospheric CO_2 levels, modifying nutrient cycles and altering ocean chemistry, increasing global temperatures, and altering climate and global ocean circulation patterns, with variable, complex effects in terrestrial and marine species assemblages (Burgiel and Muir, 2010; Harley et al., 2006; Pecl et al., 2017).

An invasive species is an established non-native species (does not need re-introduction to maintain its population over time) that can potentially cause harm to the environment, human health or the human economy (Boudouresque and Verlaque, 2002; Schaffelke et al., 2006). The specific consequences of invasion are variable, but include habitat modification, biotic homogenization encompassing extirpation of native species, facilitation of certain native species over others, alteration of trophic and evolutionary pathways, and partial or total loss of ecosystem services (Rodriguez, 2006; Schaffelke et al., 2006; Stephens et al., 2019; Wallentinus and Nyberg, 2007). Introduced macroalgae are especially capable of causing significant ecosystem change. They may alter food webs, modify ecosystem structure and function, and, under the right conditions, spread well

beyond their introduction point through highly efficient dispersal adaptations (Thresher and Kuris, 2004; Wallentinus and Nyberg, 2007).

As a consequence of climate change, extreme climatic events that have the potential to facilitate biological invasions such as heatwaves, storms, floods and droughts, are becoming more common (Castorani et al., 2018; Diez et al., 2012; Oliver et al., 2018; Straub et al., 2019). Extreme events may increase the dispersal of non-native species, favor non-natives with wider temperature tolerance or warmer affinities, and contribute to decreased biotic resistance of native communities through mechanisms such as mechanical removal, exposure to stressful conditions, and the proliferation of disease (Diez et al., 2012; Rahel and Olden, 2008). In parallel, the gradual increase of global temperature is influencing biodiversity redistributions across the globe, which can destabilize native species assemblages (Burrows et al., 2019; Pecl et al., 2017; Vergés et al., 2016). Taken together, this means that, in addition to potentially influencing the success rate of new invasions, climate change will continue to modify systems with established populations of invasive organisms, and may repeatedly foment conditions that put invasive species at a competitive advantage.

Temperate rocky reefs that harbor kelp forests are highly productive, economically and ecologically important subtidal coastal ecosystems, and are subject to the threat of species invasions (Beas-Luna et al., 2020, 2019, p.; Cavanaugh et al., 2019). Canopy and subcanopy forming macroalgae provide the majority of habitat structure, but competing invasive algae may displace them, resulting in dramatic effects on ecosystem structure

(Early et al., 2016; Wallentinus and Nyberg, 2007). High algal biomass provides habitat for commercially valuable species, services like storm surge protection for coastal areas, and economic opportunities linked to recreational use (Eger et al., 2021; Wu, 2017). Despite providing habitat and refuge to a great diversity of species, kelp canopies can also limit growth of understory species due to light deprivation (Britton-Simmons, 2006; Clark et al., 2004; Sánchez‑Barredo et al., 2020). Hence, invasive macroalgae may face difficulty thriving within a dense kelp forest.

Macrocystis pyrifera is the dominant foundational kelp species in a large portion of the subtidal forests in the Pacific Northwest, from Southern California, USA into the northern part of Baja California Sur (BCS) in the Mexican Pacific (Dayton 1985, Velasco et al 2018). The impacts of climate change have modified and will continue to modify *M. pyrifera* forests throughout their range, especially at the southern limit of the species distribution where they approach the edge of suitable conditions (Beas-Luna et al., 2020; Cavanaugh et al., 2019).

Climate change can alter the suitability of the environment in favor of non-native algae at the southern edge of *M. pyrifera'*s distribution. Adding to the native assemblage already being near its threshold for temperature tolerance, tropicalization and range expansions and contractions already put these systems in a state of "rearrangement". These rearrangement patterns may offer up the foothold needed by non-native species to become invasive (Cavole et al., 2016; Lonhart et al., 2019).

In the Mexican Pacific, Arafeh-Dalmau et al. (2019) describes the loss of fish and invertebrate species with northern distributions and cold water affinities and the increase in abundance of some species with warmer water affinities as a consequence of the 2014-2016 marine heatwave (MHW). This same event coincided with the expansion of invasive algal populations around three surveyed island systems in Baja California: Islas Todos Santos, Isla San Martín and Isla San Jerónimo (Arafeh-Dalmau et al. 2019).The Northernmost of these, Islas Todos Santos (ITS), is one of few sites in the Pacific Northwest outside of marinas hosting three high-profile invasive macroalgal species. *Sargassum muticum*, present at least since the 80s, has been joined in the last two decades by *Sargassum horneri* and *Undaria pinnatifida*, all of which now spatially co-occur with the native *M. pyrifera* (Aguilar-Rosas et al., 2007, 2004; Aguilar-Rosas and Aguilar-Rosas, 1985) (Appendix A). Although significant efforts have gone into studying these species and their invasive risk, studying this assemblage offers the unique opportunity to study the spatiotemporal interactions of a macroalgal assemblage largely, but not exclusively, composed of non-native players near the southern distribution limit of *M. pyrifera*.

This study aims to investigate the dominant macroalgal dynamics at a temperate subtidal rocky reef near the southern distribution limit for kelp forests in the Northern hemisphere in the face of multiple species introductions. First, we investigate the potential changes to this assemblage's structure and function, inside and outside a kelp canopy, considering the yearly density of individuals and biomass per area as abundance metrics. Second, we evaluate interspecific seasonal variation of dominance. Third, we relate

intraspecific seasonal abundance patterns to species phenology, and describe recruitment windows. Lastly, we examine the relationship between temperature and biomass for each species.

Methods

Study area

Islas Todos Santos (ITS; 31.809ºN, -116.800ºW) is a system of two islands located off the Northwest coast of the Baja California peninsula, 6.5 km Northwest of Punta Banda on Todos Santos Bay (Fig. 1). Historically, dense *M. pyrifera* forests have been present on both sides of the islands (Aguilar-Rosas et al., 1990; Paz-Lacavex et al., 2018). ITS is one of the longest studied sites on the Baja California coast, and some of the first records in the Mexican Pacific for the three invasive macroalgae in this study have been recorded here (Aguilar-Rosas et al., 2007, 2004, 1990; Aguilar-Rosas and Aguilar-Rosas, 1985).

We selected a rocky reef on the protected side of the canal that divides the islands as the study site. This reef hosts a small *M. pyrifera* stand at about 6 m depth. All three invasive algae are present throughout the islands. Still, this site hosts the maximum overlap of abundance of *S. muticum*, *S. horneri* and *U. pinnatifida* (pers. obs.), increasing the likelihood of interactions between the species.

Overall predominance

To characterize the algae community at ITS we conducted monthly scuba diving surveys from January to December 2020 (Appendix B1, table B1.1). We marked two locations approximately 50 m apart, inside and outside the kelp canopy. We used three 30 m transects distributed approximately at 90º of each other, with transects 1 and 3 running parallel to the edge of the canopy, and transect 2 running perpendicularly into or away from it, as illustrated in Fig. 2. Hereafter, each of these arrays of a permanent marker and three

transects will be called subsite "Canopy" and subsite "Outside". At each transect, we counted all macroalgal species (Appendix B1).

To calculate density, species counts were standardized into units of fronds m^{-2} for *Macrocystis pyrifera*, and units of individuals m^{-2} for the three invasive algae (Appendix B2). To estimate biomass (g m^{-2}) we used published size-weight relationships for *M. pyrifera*, *S. muticum* and *S. hormeri* (Marks et al., 2015; Reed et al., 2008). For *U. pinnatifida* we determined this relationship with algae collected during this study (Appendix B3).

To test for differences in dominance, we fit Generalized Linear Mixed Models (GLMM) with both density and biomass estimations of *M. pyrifera*, both non-native *Sargassum* species and *U. pinnatifida* as response variables. We used a negative binomial distribution (data was both non-Gaussian and overdispersed) and a log link function using the 'glmer.nb' function of the 'lme4' R package (Rstudio version 1.2.5033). To account for the repetition of transects over time, we assigned transect numbers within the fixed effect of 'Subsite' as a random effect. Alternative models were compared and discarded using the AIC criterion (Appendix B5, table B5.1). We corroborated all chosen levels were significant using ANOVAs (type 3 ANOVA or Wald chi-square test) for both models (p<0.05) (Appendix B5, table B5.2). All pairwise comparisons were based on these two models.

To determine if there was a difference in community dominance inside or outside the *M. pyrifera* canopy, we used Bonferroni corrected pairwise comparisons between subsites for each species, using both density and biomass.

Abundance changes across seasons between species

To evaluate seasonal changes in the macroalgal assemblage, we used Bonferroni corrected pairwise comparisons between species within each season. We use density and biomass metrics, and also corroborated if seasonal variation confirmed the overall dominance patterns.

Abundance changes across seasons within species

To test if the populations of the four species are stable throughout the year, we used Bonferroni corrected pairwise comparisons between seasons within each species to detect interspecific changes in density and biomass.

To characterize seasonal changes in species dominance by their respective life cycle stages, we characterized the phenology of each of the species. Phenology was divided into five categories: Recruit, Juvenile, Adult, Reproductive adult, and Senescent. We used density as our descriptive variable to develop a cumulative time series. We also computed the proportion of each life stage at each time we sampled.

Relationship with temperature

To assess if temperature dynamics during this year favored any of the four species, we integrated macroalgal biomass and temperature data using cross correlations. We used ONSET HOBO Pendant data loggers to record bottom temperature at the site (Appendix B4). We calculated a monthly value for mean temperature and temperature coefficient of variation (CV), and monthly mean biomass for each of the four species. We then ran time-lagged cross-correlations of mean temperature per species and CV per species. We only considered correlations with a negative lag time, since these described instances in which temperature values correlated with future biological values. Correlations assumed linear relationships. For each temperature variable/biomass combination, we visually checked linearity.

Results

We found a young *M. pyfiera* forest with a subcanopy entirely dominated by non-native algae. The most prevalent species were *S. horneri* (present in 92.3% of all transects surveyed), *U. pinnatifida* (84.6%), *M. pyrifera* (76.9%), and *S. muticum* (74.4%). Although we registered the presence of other subcanopy forming or otherwise noteworthy macroalgae, these were much more sparse. The most abundant were *Stephanocystis osmundacea* (65.4% prevalence, but very low density) and *Eisenia arborea* (48.7% prevalence) (Appendix C, table C1).

Overall predominance

The subtidal macroalgal community at ITS consisted of a *Macrocystis pyrifera* canopy with a mean yearly frond density of 0.75 fronds per m^2. *Sargassum horneri* presented the highest mean yearly density with 9.07 indivs. per m^2, while *Sargassum muticum* and *Undaria pinnatifida* presented yearly means of 2.07 and 0.98 indivs. per m^2 respectively. We did not find a difference between *M. pyrifera* and *U. pinnatifida* density (p=0.542). At the same time, *S. muticum* was about twice as dense as either *M. pyrifera* or *U. pinnatifida* (p<0.005), but was significantly less dense than *S. horneri*, which was over four times denser (p<0.005) (Table 1; Appendix C, table C2.1).

M. pyrifera registered the largest mean biomass of any species, almost four times larger than *S. horneri*. However, because of its variability, *M. pyrifera* and *S. horneri* had statistically similar total biomass (p=0.879). *S. muticum* and *U. pinnatifida* showed

significantly lower biomass in comparison with *S. horneri* (about a fourth) and *M. pyrifera* (over 12 times lower) (Appendix C, table C2.1). Our mean biomass estimations were highly variable (Table 1).

Additionally, *S. horneri* density and biomass were significantly lower inside the "canopy" subsite ($p<0.005$; Appendix C, table C2.2). Both the mean yearly density and the biomass were approximately double outside of the canopy than inside of it (Table 2). *Undaria pinnatifida* registered no difference between subsites, and *S. muticum* was denser in the canopy subsite but showed no difference in biomass between subsites (Table 2; Appendix C, table C2.2). *M. pyrifera* density and biomass were significantly higher inside the "canopy" subsite ($p<0.005$; Appendix C, table C2.2). The mean yearly density was about double, and the yearly mean biomass was 572.83 g m^{-2} inside of the canopy, while it was only 32.61 g m^{-2} outside (Table 2).

Abundance changes across seasons between species

We found seasonal changes in the macroalgal assemblage. Overall, the highest cumulative density of macroalgae was in late winter/early spring, while the highest biomass was during the fall (Fig.3). *S. horneri* presented the highest mean density in the fall (10.12 indivs. m^{-2}), winter (13.85 indivs. m^{-2}), and spring (10.39 indivs. m^{-2}) in comparison to the rest of the species. In the summer *S. horneri,* S. *muticum* and *U. pinnatifida* were equally dense (Table 3; Appendix C, table C2.3). For biomass we found a more dynamic pattern.

For example, in spring all species showed similar biomass, while in the fall, *M. pyrifera* showed the highest biomass (Table 3; Appendix C, table C2.3).

Abundance changes across seasons within species

Our results suggest the abundance of the four macroalgae changes across seasons driven by each species' life cycle (Appendix C, table C2.4). While all showed different seasonal patterns of abundance, *S. hormeri* and *S. muticum* presented similar biomass and life cycle dynamics, with the exception of recruitment times. We found *S. horneri* recruits all year long, but they were the most common life stage during early fall. *Sargassum muticum* early life stages were also present through the year but were most common in late summer. In contrast, we found the majority of *M. pyrifera* and *U. pinnatifida* recruits in early summer (Fig. 4).

Relationship with temperature

The mean water temperature at Islas Todos Santos was 16.6 ºC. We found the largest temperature variation (~12ºC) in late summer when we recorded both the maximum (24.2ºC) and minimum (12.3ºC) temperatures in the same month of August (Fig. 6). These temperatures align well with preferred ranges for all four algae studied. *Macrocystis pyrifera* temperature tolerance ranges from 9 to 26 ºC, although growth temperatures range between 14.5 and 18.5 ºC (Ladah and Zertuche-González, 2007; Zimmerman and Kremer, 1986). *Sargassum muticum* adults can survive between -1 and 30 ºC, but germlings don't

develop well below 10 ºC (Engelen et al., 2015; Norton, 1977). *Sargassum horneri* thrives

between 15 and 20 ºC but can withstand temperatures between 7 and 25 ºC(Choi et al.,

2008; Small and Edwards, 2021). *Undaria pinnatifida*'s tolerance range varies between

populations, with minimum tolerances between 0.1 and 15.5ºC and maximum tolerances

between 13.5 and 29.5 ºC. However, sporophytes generally senesce above 20ºC (James et

al., 2015).

We found a strong positive correlation (<|0.6|) between *M. pyrifera* biomass and the

coefficient of variation of the temperature with a 1-2 month lag, and a very strong positive

correlation (<|0.8|) with the mean temperature with no lag. We found strong negative

correlations between the coefficient of variation of the temperature and both species of

Sargassum with 0-1 month lag, and no relationship to mean temperature for either species.

For *U. pinnatifida* we found strong negative correlations for both temperature variables

(CV with a 4 month lag, mean temperature with a 2 month lag) (Appendix C, table C3.1).

Discussion

This study investigated the dominant macroalgal dynamics at a temperate subtidal rocky reef near the southern distribution limit for kelp forests in the Northern hemisphere in the presence of multiple non-native species. We found that the kelp forest at Islas Todos Santos is a great site to study the phenology of multiple macroalgal species to better understand how non-native introductions, in addition to environmental disturbance, change the structure, function and dynamics of a coastal ecosystem. We found that despite the establishment of three non-native species and an extreme marine heatwave and ENSO event in 2014-2016 that impacted *M. pyrifera* populations in much of the region (Beas-Luna et al., 2020; Cavanaugh et al., 2019), the kelp forest at ITS retains a limited potential to recover. Specifically, this macroalgal assemblage shows signs of complementary use of resources, with peaks in biomass and recruitment that vary by species over time. Thus, in this study we highlight the value of investigating the variability of density, biomass and the relationship with temperature of multiple macroalgal species in a changing climate.

Overall predominance

The subtidal macroalgal community at ITS could be currently considered a young, low density kelp forest (0.75 ± 1.60 fronds m$^2\pm$ SD, 1-74 fronds per adult individual). For comparison, a decade before, Beas-Luna and Ladah (2014) reported seasonal frond means at ITS of ~3.5 ± 0.5 fronds m$^2\pm$ SE in winter and ~5.5 ± 0.5 fronds m$^2\pm$ SE in spring, both

of which are much higher than our yearly mean, and even our densest season, fall, with

1.41 ± 2.43 fronds m^2± SD.

Most *M. pyrifera* individuals in this study are fairly young; most of them were less

than a year old at the start of the surveys, after Félix-Loaiza et al. (in review) reported a

complete disappearance of the macroscopic form of the species in this reef in 2019. Despite

this, and the deliberate inclusion of a subsite with no initial *M. pyrifera* presence, *M.*

pyrifera is still one of the largest contributors to local biomass.

The subcanopy layer at ITS is completely dominated by non-native species, with a

large presence of both species of the *Sargassum* genera. However, neither population is as

dense as those recorded in some of the studies that have argued concern over the effects of

these species in kelp forests (Ambrose and Nelson, 1982; Kaplanis et al., 2016; Marks et

al., 2018; Miller and Engle, 2009). On the other hand, *U. pinnatifida* was much less

abundant than values reported in marinas or other heavily disturbed sites (James, 2017).

However, density assessments for populations sharing space with kelp canopies are sparse.

To our knowledge, there are currently no other density assessments for the Northeast

Pacific.

Our comparison inside and outside the kelp canopy suggested some interesting

trends. According to our data, *S. horneri* showed an inverse relationship to *M. pyrifera*.

The species was denser and achieved higher biomass on the subsite where *M. pyrifera* was

significantly less abundant. Also, *S. muticum* appeared to grow differently inside and

outside the kelp stand. While biomass remained the same, density was higher within the *M.*

pyrifera stand, which suggests a sparser but taller population of *S. muticum* where *S. horneri* was more abundant. This could suggest that the presence of multiple non-native macroalgae modifies each others' populations as well, in ways that could have repercussions for their impact on the native assemblage and ecosystems services.

Abundance changes across seasons between species

In line with the yearly assessment of dominance, *S. horneri* drives the highest density of algae m^{-2} overall in late winter/early spring, while biomass peaks in the early fall, mostly due to *M. pyrifera*. Seasonal variation, especially biomass, showed a mismatch of maximum values between dominant species at ITS. *Macrocystis pyrifera* biomass peaked in the fall, *U. pinnatifida* peaked in the summer and fell sharply afterwards, and both *Sargassum* species were highest in winter and early spring. Recent works have suggested that *S. horneri* is an opportunistic species that thrives in canopy-forming native spatiotemporal openings; a passenger rather than a driver of environmental change (Marks et al., 2020; Ryznar et al., 2021). Similar conclusions have been reached elsewhere for populations of *U. pinnatifida*, which seems to thrive mainly in human-made substrates and natural systems with little algal canopy, and may not be capable of having direct negative effects on kelp populations (South et al., 2017). Niche complementarity; the ability of these non-native species to occupy unused resources, appears to align with our results. This has important implications for kelp restoration efforts. If these non-native species are not directly competing with *M. pyrifera*, then it could prove more effective to foster native canopy recovery by increasing the number of young *M. pyrifera* sporophytes with

transplanting or mariculture efforts, rather than to spend resources in the control of these non-native species. This could be especially important after heatwaves, which disproportionately affect *M. pyrifera*, reducing mature adult populations and impairing the species' reproductive output.

Abundance changes across seasons within species

We found that the life cycle of each species had a major role driving the different patterns of abundance and function in this community. The young stand of *M. pyrifera* showed signs of growth during the year. Young life stages were associated with the summer, and biomass increased accordingly in the fall. Moreover, recruitment was present at both subsites, which suggests the small stand we studied is expanding. These recruits aren't likely to have come from this same population, since we recorded little evidence of sporophyll development in the adult sporophytes this year and there is a *M. pyrifera* population not far from the open ocean side of the canal. Still, this indicates that the presence of our non-native understory species may be hindering but isn't preventing *M. pyrifera* recruitment and regrowth.The pseudo-perennial *S. muticum* showed stable density through the year, in spite of a drop in biomass between spring and summer. A growth pulse in late summer culminated in peak winter biomass, however, we could not distinguish if this pulse was caused by recruitment of new individuals or regrowth of older holdfasts. The annual *S. horneri* showed a similar seasonal pattern to *S. muticum*, with a drop between spring and summer biomass, in this case matched by a drop in density, and peak winter biomass. *Sargassum horneri* showed recruitment throughout the year, peaking in winter, a

little later than *S. muticum* and also later than reports from Santa Catalina Island, which

have placed peak juvenile presence in the summer, but otherwise match our abundance and

phenology patterns (Marks et al., 2018). For the two *Sargassum* species, we failed to

capture reproductive adult and senescent life stages likely due to an interruption in

sampling during the month of April 2020. However, both populations plummeted between

March and late April samplings, which could imply reproduction and rapid senescence

happened in this time window as previously reported in Santa Catalina Island (Marks et al.

2018). The highly seasonal *U. pinnatifida* sporophytes showed a single large recruitment

pulse in late spring/early summer, and rapid population growth, reproduction and

senescence culminating in late fall. This single recruitment and growth pulse matches the

prediction made by James et al., (2015) based on sea surface temperatures for this area.

Again, the slight temporal differences in recruitment times for the four species point to the

sharing of spatiotemporal resources between species rather than direct competition. It is

noteworthy that *M. pyrifera* recruitment coincided with peak *U. pinnatifida* density and

biomass.

Relationship with temperature

Only *M. pyrifera* biomass showed a positive correlation to temperature, despite the

annual temperatures being within the range of tolerance for all four species studied. The

time-lagged correlation showed biomass of *M. pyrifera* increased about two months after

the coefficient of variation of the temperature increased. We also found a very strong

immediate positive correlation with the mean temperature. Inversely, time-lagged

correlation showed an immediate decrease in biomass for both *Sargassum* species with the increase of the coefficient of variation of the temperature. This is likely because the temperature variation is a signal of upwelling events coming in through the canal, which favor *M. pyrifera* growth but not any other alga. Contrary to *M. pyrifera*, *U. pinnatifida* showed strong negative correlations with both temperature variables. Biomass for this species increased 2 months after mean temperature decreased and 4 months after the decrease of the coefficient of variation of the temperature.

It is important to consider that we characterized the macroalgal structure on ITS during a year with few environmental disturbances. For the year 2020 the southern part of the California Current System followed suit in a 7-year trend of mild warming, but no large warm temperature anomalies were recorded close to the coast (Weber et al., 2021).

Conclusions

- The subtidal macroalgal community at Islas Todos Santos is currently a young, low density kelp forest. Still, *M. pyrifera* is one of the largest contributors to local biomass.

- The subcanopy layer at ITS is completely dominated by non-native species, with a large presence of both species of the *Sargassum* genera. However, neither population is as dense as those recorded in some of the studies that have argued concern over the effects of these species in kelp forests.

- We analyzed two subsites and found inverse relationships between *S. horneri* and *M. pyrifera* density and biomass.

- *Sargassum muticum* was denser where *M. pyrifera* was more abundant than where *S. horneri* dominated, but its biomass didn't differ, suggesting potentially interesting size distribution differences.

- Seasonal variation, especially biomass, showed a mismatch of maximum values between dominant species at ITS. *Macrocystis pyrifera* biomass peaked in the fall, *U. pinnatifida* peaked in the summer and fell sharply afterwards, and both *Sargassum* species were highest in winter and early spring.

- The life cycle of each species had a major role driving the different patterns of abundance in this community. Maximum presence of early life stages was staggered between the four species.

- The highly seasonal *U. pinnatifida* sporophytes showed a single large recruitment pulse in late spring/early summer, which matches predictions based on sea surface temperatures for this area.

- Temperatures throughout the year were within the range of tolerance for all four species studied. *M. pyrifera* showed positive time-lagged correlations with both mean temperature and its coefficient of variation, while *U. pinnatifida* showed negative correlations with both temperature variables.

Tables

Table 1. Mean yearly density (units of frequency m^{-2}) and biomass (g m^{-2}) ± SD of *M, pyrifera*, *S. horneri*, *S. muticum* and *U. pinnatifida*. Significant differences between species are denoted with lower-case letters in parentheses; species that are significantly different from one another don't share a letter (Bonferroni-corrected pairwise comparison, p<0.005).

	Mean density (units of freq. m^{-2})	**Mean biomass (g m^{-2})**
Macrocystis pyrifera	0.75 ± 1.60 (c)	302.72 ± 652.50 (a)
Sargassum horneri	9.07 ± 10.34 (a)	83.54 ± 120.42 (a)
Sargassum muticum	2.07 ± 3.05 (b)	24.30 ± 60.95 (b)
Undaria pinnatifida	0.98 ± 1.40 (c)	24.86 ± 29.28 (b)

Table 2. Mean yearly density (units of frequency m^{-2}) and biomass (g m^{-2}) ± SD of *M, pyrifera*, *S. horneri*, *S. muticum* and *U. pinnatifida* per subsite. Significant differences for the same species between subsites are denoted with an asterisk (*) (Bonferroni-corrected pairwise comparison, p<0.005).

	Mean density (units of freq. m^{-2})		**Mean biomass (g m^{-2})**	
	Canopy	**Outside**	**Canopy**	**Outside**
M. pyrifera	1.41 ± 2.05*	0.09 ± 0.29*	572.83 ± 836.13*	32.61 ± 117.71*
S. horneri	5.57 ± 9.38*	12.57 ± 10.17*	58.44 ± 109.76*	108.64 ± 126.66*
S. muticum	2.99 ± 3.95*	1.16 ± 1.27*	33.70 ± 82.31	14.89 ± 23.90
U. pinnatifida	0.70 ± 0.74	1.25 ± 1.80	26.38 ± 30.11	23.35 ± 28.75

Table 3. Mean seasonal density (units of frequency m^{-2}) and biomass (g m^{-2}) ± SD of *M, pyrifera*, *S. horneri*, *S. muticum* and *U. pinnatifida*. Significant differences between species are denoted with lower-case letters in parentheses; species that are significantly different don't share a letter (Bonferroni-corrected pairwise comparison, p<0.005).

Spring		
	Mean density (freq. units m^{-2})	Mean biomass (g m^{-2})
Macrocystis pyrifera	0.23 ± 0.58 (b)	93.28 ± 237.29 (a)
Sargassum horneri	10.39 ± 10.24 (a)	171.61 ± 183.46 (a)
Sargassum muticum	1.19 ± 1.65 (b)	25.53 ± 32.42 (a)
Undaria pinnatifida	0.18 ± 0.10 (b)	30.55 ± 38.09 (a)
Summer		
	Mean density (freq. units m^{-2})	Mean biomass (g m^{-2})
Macrocystis pyrifera	0.65 ± 1.17 (b)	255.91 ± 475.00 (a)
Sargassum horneri	3.77 ± 5.03 (a)	20.41 ± 31.52 (bc)
Sargassum muticum	1.86 ± 4.00 (a)	7.12 ± 13.03 (c)
Undaria pinnatifida	2.06 ± 1.73 (a)	51.73 ± 25.02 (ab)
Fall		
	Mean density (freq. units m^{-2})	Mean biomass (g m^{-2})
Macrocystis pyrifera	1.41 ± 2.43 (b)	574.09 ± 993.39 (a)
Sargassum horneri	10.12 ± 11.61 (a)	43.39 ± 46.76 (b)
Sargassum muticum	2.15 ± 1.61 (b)	12.55 ± 10.06 (b)
Undaria pinnatifida	0.94 ± 1.17 (b)	6.14 ± 8.55 (b)
Winter		
	Mean density (freq. units m^{-2})	Mean biomass (g m-^{2})
Macrocystis pyrifera	0.35 ± 0.72 (c)	142.95 ± 294.23 (a)
Sargassum horneri	13.85 ± 11.53 (a)	162.55 ± 140.04 (a)
Sargassum muticum	2.85 ± 3.75 (b)	62.04 ± 116.87 (a)
Undaria pinnatifida	0.11 ± 0.15 (c)	10.23 ± 15.34 (b)

Figures
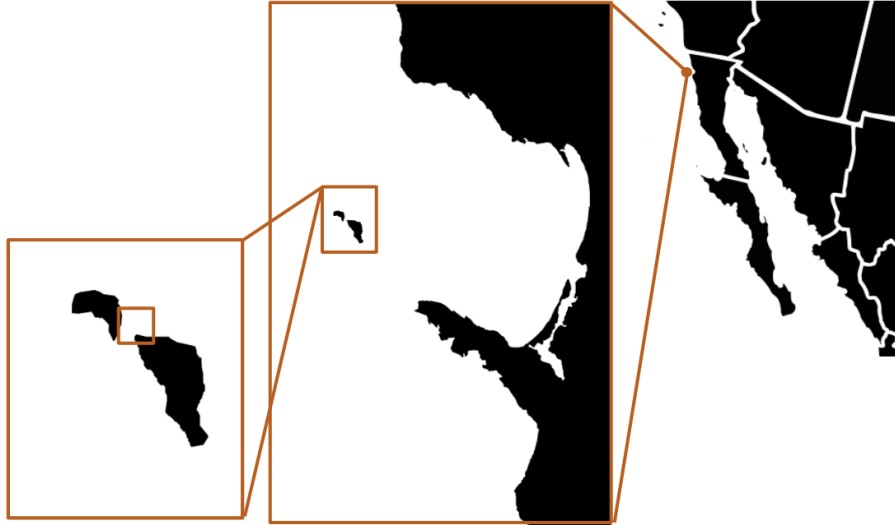
Fig. 1: Map of Islas Todos Santos within the Todos Santos Bay in Northern Baja California, México.
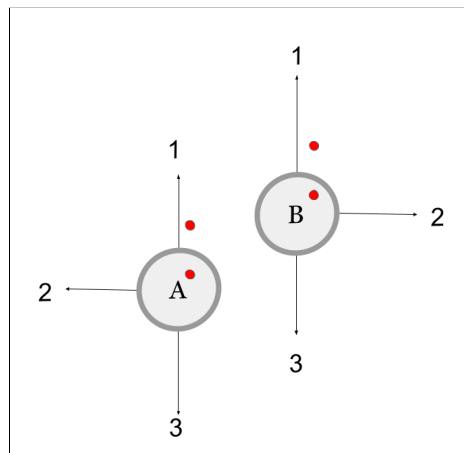
Fig. 2: Distribution of transect array deployed for every monitoring round (not to scale). Transects are marked 1-3, while permanent subsite markers are labeled "A" (Canopy), and "B" (Outside). The red dots represent temperature sensors.
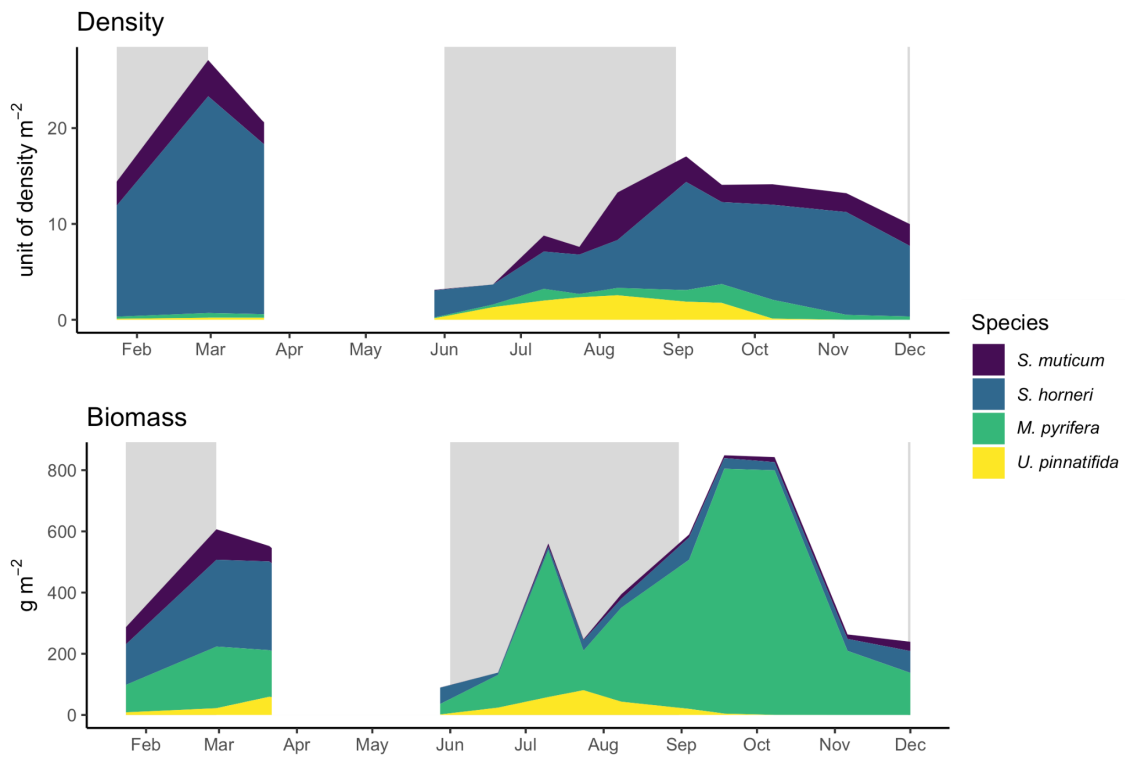
Fig. 3: Cumulative mean abundance of *Macrocystis pyrifera*, *Sargassum horneri Sargassum muticum* and *Undaria pinnatifida* per sampling during the year 2020. Abundance is expressed as density (above) and biomass (below). The gap in data constitutes a sampling break due to the COVID-19 emergency of 2020.
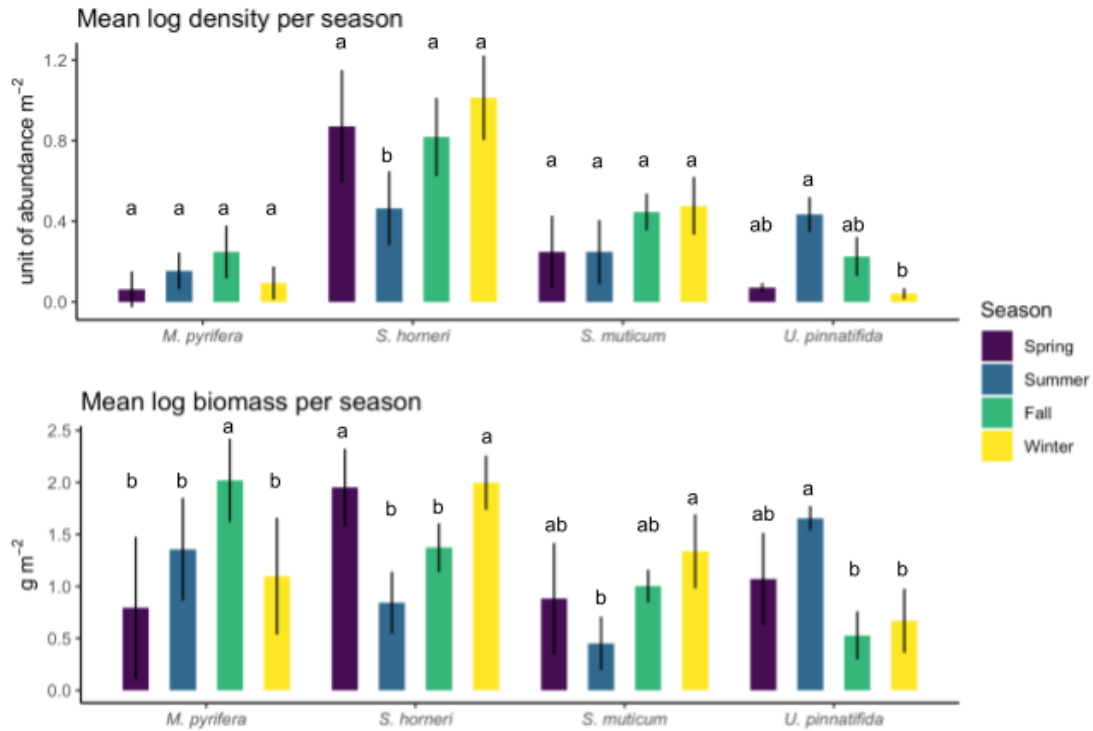
Fig. 4: Logarithmic mean seasonal abundance of *Macrocystis pyrifera*, *Sargassum horneri* *Sargassum muticum* and *Undaria pinnatifida* for the year 2020. Abundance is expressed as density (above) and biomass (below). Error bars represent confidence intervals.
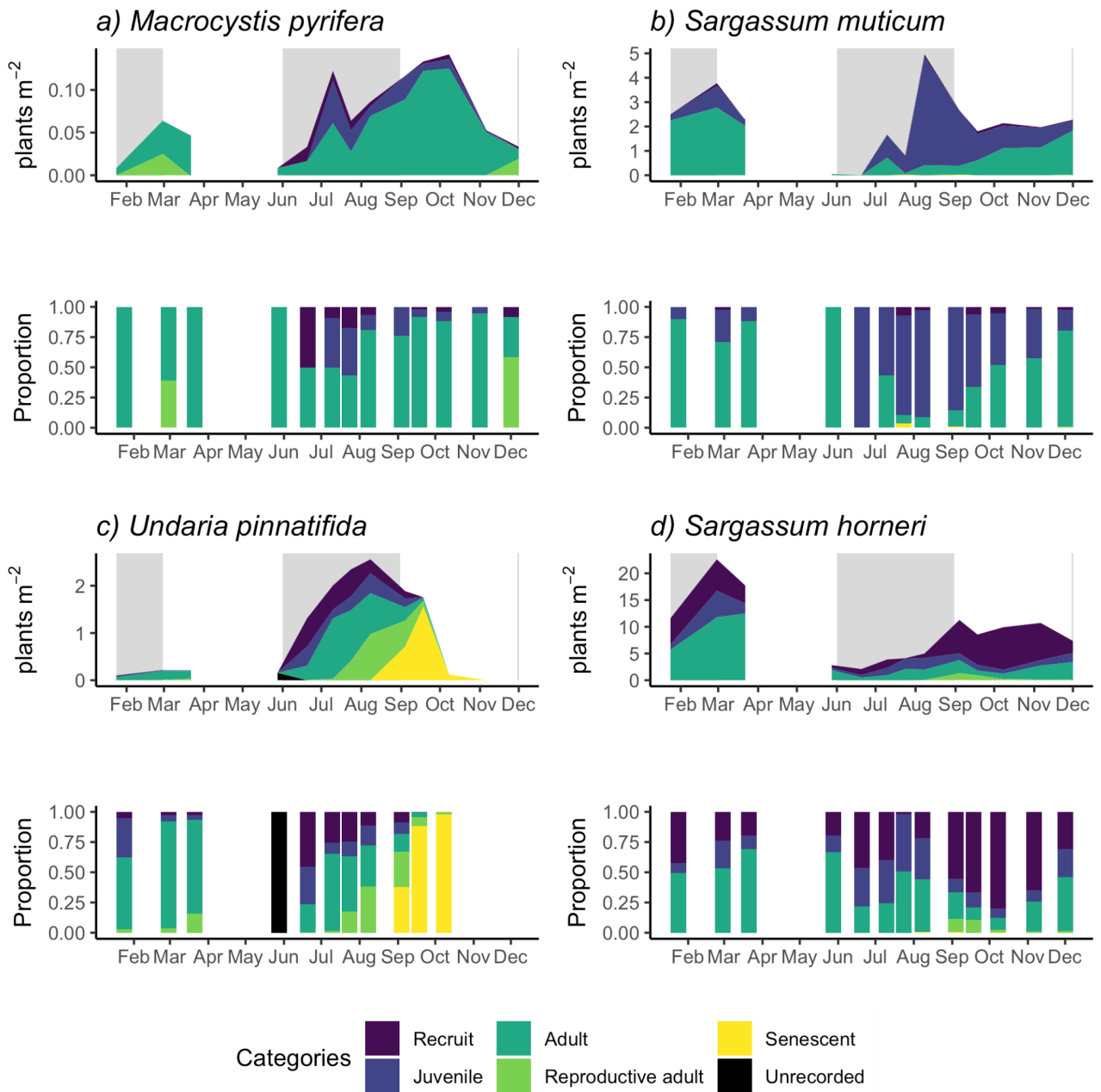
Fig. 5: Phenology of a) *Macrocystis pyrifera*, b) *Sargassum horneri*, c) *Undaria pinnatifida* and d) *Sargassum muticum* expressed as density (units of freq. m^{-2}) within each class (above) and relative proportion of the population belonging to each present class (below). Alternating gray and white background bands represent seasons, starting with winter (gray). The gap in spring data constitutes a sampling break due to the COVID-19 emergency of 2020.
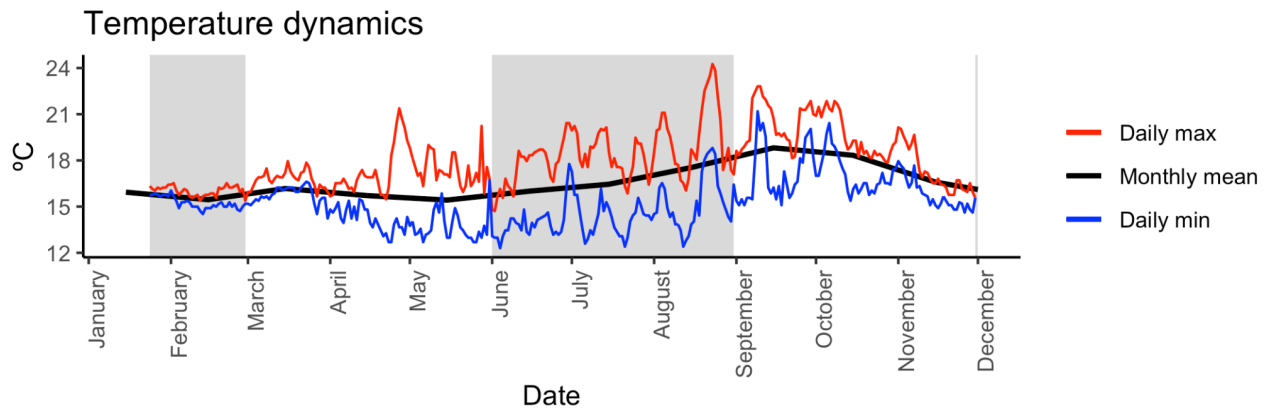
Fig. 6. Monthly mean (black), daily high (red) and daily low (blue) bottom temperature (ºC) registered. Alternating gray and white background bands represent seasons, starting with winter (gray).

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Appendix

Appendix A: Background

<u>*Macrocystis pyrifera* forests</u>

      Macrocystis pyrifera (Linnaeus) C. Agardh, 1820 (Laminariales), commonly referred to as giant kelp, is a brown alga and the world's largest benthic organism. The life cycle of *M. pyrifera* consists of a heteromorphic alternation of generations between a microscopic haploid gametophyte and a macroscopic, perennial diploid sporophyte (Dayton, 1985). It takes approximately six to nine months for a settled spore to mature into a canopy-forming sporophyte, which can live for more than 6-8 years (Dayton et al., 1984). A *M. pyrifera* sporophyte consists of a bundle of fronds that arise from a basal system of stipes and a common holdfast. Each rope-like frond possesses multiple blades attached by small gas bladders.

      Macrocystis pyrifera, as a foundation species and ecosystem engineer, has been subject to extensive scientific interest (as reviewed in (Graham et al., 2007) and references therein). For the northeastern Pacific, its historic range extends between Point Año Nuevo in Santa Cruz, CA, USA and Punta Hipólito, BCS, Mexico (Edwards and Estes, 2006). *M. pyrifera* forests are highly dynamic systems; population collapse and subsequent recovery happen repeatedly at varying scales (Dayton and Tegner, 1984), however, climate change, especially marine heatwaves, and other anthropogenic stressors are putting stress on the ability of these systems to recover after disturbances (Smale et al., 2019; Steneck et al., 2002). As a clear example, (Beas-Luna et al., 2020) estimated the southern edge of *M.*

*pyrifera'*s distribution in the northeastern Pacific is moving poleward at a rate of 1.6 km per year based on the last ten years.

<u>Invasive macroalgae</u>

Additional to climate change related stressors, some kelp forests in the northeastern Pacific now host populations of *Sargassum muticum* (Yendo) Fensholt, 1955 (Fucales), *Sargassum horneri* (Turner) C. Agardh, 1820 (Fucales) and *Undaria pinnatifida* (Harvey) Suringar, 1873 (Laminariales), all non-native macroalgae with invasive potential.

Sargassum muticum

Sargassum muticum is a monoecious, pseudo perennial fucoid alga native to northeast Asia (Yendo, 1907). Each year, individuals die back to their holdfast, seasonally regrowing multiple thalli from a single stem. Main branches produce multiple lateral branches with small leaflike structures and spherical air vesicles. When fertile, *S. muticum* bears hermaphroditic receptacles. Gametes are expelled in pulses, and fertilized eggs remain attached for several days until propagules are released as germlings with a developing rhizoid (Deysher and Norton, 1981).

This alga is considered invasive in many places around the world, and currently exhibits a circumglobal distribution, with established non native populations on the Pacific coast of North America and much of the North Eastern Atlantic (as reviewed in Engelen et al., 2015). The colonization of the northeastern Pacific by *S. muticum* predates the appearance of *S. horneri* and *U. pinnatifida* by several decades. First introduced in British Columbia in the 1940s, likely in association with oyster cultures (Cheang et al., 2010;

Scagel, 1956), this alga rapidly expanded its range southward, arriving in Baja California in the early 1970s, Bahía Tortugas by 1988, and Guadalupe island in BCS by 1993 (Aguilar-Rosas and Aguilar-Rosas, 1993, 1985; Espinoza, 1990; Nienhuis, 1982).

Sargassum muticum has been present on Islas Todos Santos (Baja California) since at least 1984 (Aguilar-Rosas and Aguilar-Rosas, 1985). At ITS the species vertical range spans from intertidal habitats to a maximum depth of 20 m (Aguilar-Rosas et al., 1990). Since its introduction, it has become a conspicuous and abundant part of intertidal and shallow subtidal communities.

The circumglobal success of *S. muticum* as an invasive macroalga is attributed largely to characteristics that make it opportunistic. Although it requires clear rocky substrate to grow, small populations expand quickly once established, sexually reproducing to produce germlings. Over long distances, floating vegetative branches don't decay in the water column, and because they can self fertilize, they are likely the conduits for the expansion of *S. muticum* between faraway points (Deysher and Norton, 1981). Early on in the history of its appearance in the northeastern Pacific *S. muticum* was demonstrated to be capable of modifying macroalgal assemblages with varying degrees of impact. For example, after the disappearance of *M. pyrifera* in many parts of the Californias during the 1976 El Niño event, *S. muticum* took over in areas, apparently inhibiting recruitment of *M. pyrifera* (Ambrose and Nelson, 1982). This was also observed in Catalina Island after the 1982-1984 El Niño (Schiel and Foster, 2019), however, *M. pyrifera* eventually recovered in both cases, with *S. muticum* maintaining presence in open areas with a much lower density

(Schiel and Foster, 2019). More recently, due to its long history in the area, *S. muticum* is sometimes described as a naturalized alga, already fully "equilibrated" and established into these ecosystems (Kaplanis et al., 2016; Miller and Engle, 2009). Indeed in the North coast of Spain, where *S. muticum* has also been present since the 1980s, (Fernández, 2020) described a boom-bust cycle over a period of seventeen years, with moderate effects on macroalgal assemblages during the expansion period, and minimal effects afterward. Most strong negative effects of *S. muticum* on native algae have been recorded in intertidal zones, while it appears that subtidal effects, especially when a thick surface canopy is present, are weaker (Schiel and Foster, 2019).

Sargassum horneri

Sargassum horneri (Turner) C. Agardh (originally identified as *S. filicinum*) is native to warmer parts of Korea and Japan (Lee and Yoo, 1992; Tseng et al., 1985; Yoshida, 1983). Recent molecular studies merged *Sargassum filicinum,* which is monoecious, with *Sargassum horneri*, a diecious species with a wider spread in eastern Asia (Tseng et al., 1985; Uwai et al., 2009). As such, I refer to our local invasive population as *S. horneri*.

S. horneri in the northeastern Pacific is a monoecious fucoid with a diplontic life cycle similar to that of *S. muticum*. However, while *S.muticum* is pseudo perennial, *S. horneri* is annual. Individuals start as embryos, which develop into fern-like algas with a common holdfast. A single erect frond then grows up to several meters in length, bearing many vegetative blades with ellipsoid gas bladders (Marks et al., 2015; Yoshida, 1983). Reproductive receptacles form, fertilization occurs when sperm penetrates the eggs in the

conceptacles on the surface of the receptacles, after which embryos are released and settle to the benthos. After reproduction, the parent plant senesces.

While *S. muticum* has a long history outside of its native range, *S. horneri* is a relatively new invasive species, and has only been introduced to the Pacific coast of North America. First identified as *Sargassum filicinum* (Harvey, 1860), the initial introduced population was discovered in Long Beach Harbor, California, in 2003, expanding to Santa Catalina Island by 2006 (Miller et al., 2007). Since then, it has rapidly colonized areas of the Pacific coast of North America, expanding faster southwards than northwards, possibly due to facilitation by currents, but also suggesting it may be better suited for warmer conditions (Marks et al., 2015). In 2005, drifting *S. horneri* individuals were found in Todos Santos Bay, and well-established populations were found by 2006 (Aguilar-Rosas et al., 2007). By 2009, *S. horneri* had spread as far south as Isla Natividad, BCS (Riosmena-Rodríguez et al., 2012). By 2013 its northern distributional limit reached Santa Barbara, CA (Marks et al., 2015). In its introduced range, *S. horneri* has been observed from the intertidal to a depth of 30 m in Southern California and at least 8 m in Baja California, with peak density at around 5-10 m (Marks et al., 2018; Riosmena-Rodríguez et al., 2012).

The initial mode of introduction of *S. horneri* is thought to be a consequence of maritime trade or other vessel-related activities, either by hull fouling or ballast water transport. Its presence in many marinas and other heavily frequented areas suggest recreational boating may be the cause of secondary introductions (Marks et al., 2015;

Miller and Engle, 2009). As with *S. muticum*, expansion across the Northwest Pacific has been driven by a combination of prolific sexual reproduction at the local level and the capacity of floating individuals to become reproductive and seed downcurrent areas at larger spatial scales (Marks et al., 2018, 2015; Miller and Engle, 2009).

Besides being exceptionally well-suited for long-distance dispersal and colonization, *S. horneri* possesses many of the other traits that have made *S. muticum* a successful invasive species: It is rapid-growing, highly fecund, and capable of self fertilizing (Marks et al., 2015). It has also been subject to considerable attention because of its rapid expansion (Kaplanis et al., 2016; Marks et al., 2015). It took 14 years for *S. muticum* to expand its range between Ensenada, BC and Isla Natividad, BCS. In comparison, *S. horneri* appeared at Isla Natividad just 4 years after appearing for the first time in Ensenada (Riosmena-Rodríguez et al., 2012). However, while *S. muticum*'s range eventually reached as far south as Punta abreojos (Aguilar-Rosas and Aguilar-Rosas, 1985), as of 2020 *S. horneri* still has not been recorded south of Isla Natividad.

The biomass of *S. horneri* appears to be strongly seasonal in Southern California: Juveniles are most prevalent in the summer, plants grow rapidly during the winter and peak in biomass, then reproduce and subsequently senescence in spring (Marks et al., 2018). Its dominance however, is rather patchy: while in some areas it has become very dense, it remains rare in others (Caselle et al., 2018; Marks et al., 2015). A study of two intertidal populations in Todos Santos Bay, Baja California, adds an interesting consideration: while a site with more solid substrate but high *S. horneri* density and biomass showed only

marginal impacts on other algal species, a site with cobble substrate and much lower *S. horneri* density and biomass did show an impact on the native macroalgal assemblage (Cruz-Trejo et al., 2015).

    Undaria pinnatifida

    Undaria pinnatifida (Harvey) Suringar is native to southeastern Russia, Japan, Northern China and Korea. Like *M. pyrifera*, *U. pinnatifida* is a brown alga of the order laminariales. Its life cycle consists of a heteromorphic alternation of generations between microscopic haploid gametophytes and macroscopic diploid sporophytes. An *U. pinnatifida* "individual" or "plant" in the context of this research refers to a macroscopic sporophyte of this species. *U. pinnatifida* sporophytes consist of a single frond, comprising a holdfast, stipe or stem, and blade.

    Unlike *M. pyrifera* sporophytes, *U. pinnatifida* is annual, and sporophytes rapidly senesce after reproduction. In its native range, *U. pinnatifida* is a winter annual, the presence of sporophytes is typically reduced in the summer by high water temperatures (Saito, 1975). However, the morphological plasticity of its sporophytes enables it to tolerate a wide variety of environmental conditions (James, 2017). In its introduced range, if conditions are suitable, some populations recruit multiple times a year, which allows them to maintain a year-round presence (Castric-Fey et al., 1999; James et al., 2015). This is more likely to occur at temperatures below 15 ºC (Thornber et al., 2004). Also contributing to its success as an introduced species, *U. pinnatifida* gametophytes can remain dormant for

years until suitable conditions occur (James, 2017; Thornber et al., 2004), making it nearly impossible for an established population to be eradicated.

The global history of invasion of *U. pinnatifida* is not as long as that of *S. muticum*; the first established population outside of its range was detected in the 70s (Boudouresque et al., 1985), yet it is also circumgobally introduced. This species has a few other distinctions: one, its status as invasive rather than non-native is still debated, since its effects on ecosystems are varied, and some populations appear to have an additive rather than substitutive effect on local species (James, 2017; Raffo et al., 2009; Schaffelke et al., 2005; South et al., 2017), and two, it is widely cultivated as a valuable resource, with several populations introduced purposefully for economic purposes. Because of these multiple vectors of introduction, populations worldwide have a high genetic diversity (Voisin et al., 2005). To date, and excluding the northeastern Pacific, it is present outside its native range in the Mediterranean Sea, England, Atlantic Europe, New Zealand, Tasmania, Australia, and Argentina (Aguilar-Rosas et al., 2004; James et al., 2015; Silva et al., 2002). However, it is most common as an introduced species in marinas and other human-made structures. Its occurrence as part of the understory in giant kelp forests is more limited, currently only documented in Australia, New Zealand and Santa Catalina Island, in addition to this study's site.

In the northeast Pacific, *U. pinnatifida* was first detected in March 2000 in Los Angeles Harbor (Silva et al., 2002). Although subsequently additional specimens were reported in piers and shallow water as far as Monterey bay, the first established population in a kelp forest was encountered and described in 2001 in Santa Catalina Island, CA (Miller et al., 2007). In the Pacific coast of Mexico, *U. pinnatifida* was first reported at Islas Todos Santos in September 2003, where it now occurs with a distribution that spans from the intertidal to 40m depth (Aguilar-Rosas et al., 2014, 2004). The introduction of *U. pinnatifida* to Islas Todos Santos differs from those of both *Sargassum* species in one important way: It may have been intentional. While both *Sargassum* species appeared in the Mexican Pacific as a result of their expansion from points of accidental introduction further North, Aguilar-Rosas et al., (2014) suggests that *U. pinnatifida* may have been introduced deliberately into ITS as feed for abalone farming. Although intended to be confined to ITS due to its lack of floating structures, the current distribution for the species spans several other points in Todos Santos bay, notably including the intertidal zone adjacent to the closest marina to the islands (Aguilar-Rosas et al., 2014).

Appendix B: Methods

B1: Data collection

To assess the macroalgal community structure and phenology of the macroalgae, the following parameters were quantified:

Species density and size structure

All canopy-forming macroalgae present within 1 meter of each side of a transect were counted, for a total area of 60 m² per transect, with special attention to *Macrocystis pyrifera* and *Undaria pinnatifida* (Table B1.1). For both *Sargassum muticum* and *S. horneri*, highly abundant species, quadrats were used to count a subset of organisms. For most sampling dates, quadrats measuring 1 m² were deployed every 5 m within each transect, alternating sides, and all individuals of both *Sargassum* species contained within the quadrats were counted, for a total of 6 quadrants per transect, or 6 m² surveyed. On exceptional dates, both *Sargassum* species were surveyed in variable areas due to lower densities or field constraints (Table B1.2).

Size structure was also obtained for the four species from the individuals counted. For *M. pyrifera* sporophytes, individuals less than 1 m in height were measured, while the number of fronds 1 meter above the holdfast was recorded for larger individuals. For *U. pinnatifida* sporophytes, density grew too high to allow for full measurement and reproductive status evaluation of all individuals between June and September 2020. When the abundance per transect was higher than ~50 individuals, only the first ten individuals every 10 m were measured (for a total of ~30 measurements per transect). For both *Sargassum* species, all individuals per area surveyed >10 cm were measured, with individuals smaller than 10 cm counted and classified as recruits.

Phenology

To keep terms comparable, all measured individuals of the four algae were classified into recruit, juvenile, adult, reproductive adult, and senescent life stages. For *M. pyrifera* sporophytes and both *Sargassum* species, recruits, juveniles, and adults were classified based on size. Reproductive adults were classified on the basis of presence of reproductive structures, and senescent individuals were classified as post-reproductive adults with extensive tissue damage. For *U. pinnatifida* sporophytes, recruits were classified based on size, while juveniles, adults, and reproductive adults were classified based on the presence and degree of maturity of the sporophyll (Miller and Engle, 2009). As above, senescent individuals were identified as post-reproductive adults with extensive tissue damage. Table B1.3 details the specific characteristics per species used for this categorization.

Physical parameters

Four ONSET HOBO Pendant Temperature/Light Data Loggers were maintained at the site for the duration of the experiment. Each subsite had two loggers affixed to structures at the sea floor, near the start of the semi-permanent transects. Loggers were initially deployed in January 2020 and swapped approximately every two months for the rest of the year. All loggers were set to record temperature (ºC) and light (lux) measurements every 5 minutes.

Table B1.1: Sampling for the year 2020, with legend detailing any deviation from standard sampling. Sampling in quadrats is <u>underlined</u>.

2020	*Macrocystis pyrifera*	*Sargassum muticum*	*Sargassum horneri*	*Undaria pinnatifida*
Winter				
Jan 24	✓	<u>✓</u>	<u>✓</u>	✓
Feb 29	✓	<u>***</u>	<u>***</u>	✓
Spring				
Mar 21	✓	<u>*</u>	<u>*</u>	✓
May 28	✓	<u>*</u>	<u>*</u>	X
Summer				
Jun 20	✓	<u>**</u>	<u>**</u>	✓
Jul 10	✓	<u>*</u>	<u>*</u>	✓*
Jul 24	✓	<u>✓</u>	<u>✓</u>	✓*
Aug 8	✓	<u>**</u>	<u>**</u>	✓*
Fall				
Sep 4	✓	<u>✓</u>	<u>✓</u>	✓*
Sep 18	✓	<u>✓</u>	<u>✓</u>	✓*
Oct 8	✓	<u>✓</u>	<u>✓</u>	✓
Nov 6	✓	<u>✓</u>	<u>✓</u>	-
Winter				
Dec 12	✓	<u>✓</u>	<u>✓</u>	-

Transects:

✓   standard sampling

✓*   subset measured and classified

-     zero individuals recorded

X   no size or classification data recorded

<u>Quadrats:</u>

<u>✓</u>   full quadrats (standard sampling)

<u>*</u>   half quadrats

<u>**</u>   mixed quadrats: larger total area than half quadrats

<u>***</u> mixed quadrats: smaller total area than half quadrats

Table B1.2. Parameters defining phenology for four species of macroalgae

	Recruit	Juvenile	Adult	Reproductive adult	Senescent
Macrocystis pyrifera	≤ 20 cm	20-100 cm	> 100 cm	Presence of sporophyll laminae (regardless of maturity)	Post-reproductive, extensive tissue damage
Sargassum muticum	≤ 5 cm	6-20 cm	> 20 cm	Presence of receptacles (regardless of maturity)	Evidence of decaying receptacles and extensive tissue damage
Sargassum horneri	≤ 5 cm	6-20 cm	> 20 cm	Presence of receptacles (regardless of maturity)	Evidence of decaying receptacles and extensive tissue damage
Undaria pinnatifida	<20 cm, no lobes or trace of a sporophyll	Blade with midrib but no sporophyll at all	Partially formed sporophyll	Sporophyll present all around the thallus	Decaying sporophyll, non existent blade

B2: Data post-processing-Density

<u>*Macrocystis pyrifera*</u>

　　　Macrocystis pyrifera density permitted full transect assessments. We evaluated *M. pyrifera* density in number of fronds, rather than number of individual sporophytes, as it is a better metric for a young *M. pyrifera* stand such as this one. For statistical analyses, we calculated density (in fronds m^{-2}) per transect as our base unit.

<u>*Sargassum muticum/Sargassum horneri*</u>

As previously described, *Sargassum muticum* and *S. horneri* were largely quantified using quadrats. In all cases, the total area surveyed per transect was used to calculate density (in individuals m^{-2}) per transect as our base unit.

Undaria pinnatifida

Undaria pinnatifida was counted in full for every transect. For statistical analyses, we calculated density per transect (sporophytes m^{-2}) and used this as our base unit.

B3: Data post-processing-Biomass and phenology

Macrocystis pyrifera

We calculated *Macrocystis pyrifera* biomass following the method described in (Reed et al., 2008). In this paper, the following equations were used to calculate the length of *M. pyrifera* fronds, using the number of fronds 1 m above the holdfast (N_{1m}), the number of fronds at the surface (N_{srfc}), water depth from the holdfast to the surface (D) and the length of the canopy portion at the longest frond (*MAX*):

$$subsurface\ length\ =\ (N_{1m} - N_{srfc})[1\ +\ 0.5(D\ - \quad (1)$$

$$water\ column\ length\ =\ (N_{srfc})(D) \qquad\qquad (2)$$

$$canopy\ length\ =\ (N_{srfc})(0.5MAX) \qquad\qquad (3)$$

For analyses presented here, we assumed fronds for all adult sporophytes reached until just below the surface, therefore all counted fronds were transformed into meters using only equation (1). This assumes that $N_{1m}=N_{srfc}$, and D=6m, our mean site depth.

We converted calculated frond length data to biomass (wet g m^{-2}) using the ratio of wet mass to frond length given in Reed et al. (2008) for subsurface canopy (0.117 kg m^{-1}), which we converted to g m^{-2} to match all other biomass data.

We assigned phenological categories of *M. pyrifera* per individual sporophyte, following the rationale detailed in Table B1.2. We didn't require any extrapolation.

Sargassum muticum/Sargassum horneri

For *Sargassum horneri,* we calculated biomass following the size-to-damp-biomass relationships in (Marks et al., 2018):

$$\text{Recruit: biomass(g)} = 0.0179*\text{size(cm)}^{1.7633} \tag{1}$$

$$\text{Immature: biomass(g)} = 0.0992*\text{size(cm)}^{1.2711} \tag{2}$$

$$\text{Fertile-unripe: biomass(g)} = 0.0496*\text{size(cm)}^{1.4817} \tag{3}$$

$$\text{Fertile-ripe: biomass(g)} = 0.0147*\text{size(cm)}^{1.7641} \tag{4}$$

Because, unlike our length measurements, (Marks et al., 2018) measured diameter as the size indicator for recruits to develop the above written equations, we used the relationship given for immature individuals (2) for organisms classified as recruits, juveniles, and adults. For organisms classified as reproductive adults and senescent we used the relationship for fertile-unripe individuals (3). As the two species are closely related and are morphologically similar, we applied the same conversion to both *Sargassum horneri* and *S. muticum*.

We assigned phenology categories to all *Sargassum* counted and measured within the quadrats. Beyond the density adjustment, no extrapolation was required.

Undaria pinnatifida

For *Undaria pinnatifida, d*ensity forbade measuring and describing all present sporophylls. We extrapolated *U. pinnatifida* sizes and frequency of each life stage from a subset of measured and described individuals in each transect. We assigned the proportion of each size/reproductive status combination measured to the rest of the individuals counted within each transect section. We rounded proportions to correspond to full individuals. Additionally, during transects conducted on May 24, 2020, *U. pinnatifida* individuals were counted, but no additional life stage information was taken. For phenology estimates, these individuals were all categorized as "Unrecorded", and for size estimates, this data point was linearly interpolated to the nearest 5 cm approximation of the average size of all individuals recorded in the two adjacent timepoints (n=549, average size = 37.7±32.9 cm, interpolated size=40 cm).

We derived a size to biomass relationship from the measurements and damp weight of 80 *U. pinnatifida* individuals collected in April 2021 in the Bay of Ensenada. Although we initially attempted to fit the data according to phenological categories, the best weight:length relationship fit was achieved with a single power function derived from all individuals collected (R^2=0.67) of the following form:

$$\text{Biomass(g)} = 0.0036 * \text{size(cm)}^{2.4821}$$

B4: Data post-processing-Temperature

Although four HOBO loggers were deployed at all times, mechanical failures, and therefore data gaps, were not uncommon. As a basis for all statistical analyses, temperature measurements were averaged per day over all available data, without distinction between loggers. When more than one logger was functional on the same day, data were visually assessed previous to averaging to ensure reasonable consistency between loggers.

B5: Statistical models

Table B5.1: Description and AIC for tested GLMM models (a)Dependent variable=density, b) Dependent variable=biomass). The chosen model is **bolded**.

a)

AIC	DF	Fixed effects	Random effect
1357.050	3	None-null model	Transect number
1356.465	3	None-null model	Transect number within Sub_sites
1181.483	18	Two way interaction between Season and Species	Transect number
1118.825	**22**	**Two way interactions between Sub_site and Species, and between Season and Species**	**Transect number within Sub_sites**
1123.224	34	Three-way interaction between Sub_site, Season and Species	Transect number within Sub_sites

b)

AIC	DF	Fixed effects	Random effect
2975.718	3	None-null model	Transect number
2955.895	3	None-null model	Transect number within Sub_sites
2857.165	18	Two way interaction between Season and Species	Transect number
2783.113	**22**	**Two way interactions between Sub_site and Species, and between Season and Species**	**Transect number within Sub_sites**
2791.294	34	Three-way interaction between Sub_site, Season and Species	Transect number within Sub_sites

Table B5.2: ANOVA table (Type III Wald chi-square test) on the fixed effects of the Density GLMM (a) and Biomass GLMM (b). Significance set at Pr(>Chisq) ≤ 0.05.

a)

Source	DF	Chi-square	Pr(>Chisq)
Season	3	11.526	0.009
Species	3	34.883	<0.001
Sub site	1	21.356	<0.001
Season x Species	9	64.223	<0.001
Sub site x Species	3	61.036	<0.001

b)

Source	DF	Chi-square	Pr(>Chisq)
Season	3	31.002	<0.001
Species	3	8.575	0.036
Sub site	1	97.829	<0.001
Season x Species	9	115.850	<0.001
Sub site x Species	3	95.996	<0.001

Appendix C: Results

C1: General results

Table C1: Prevalence of each macroalga species registered in the 78 total transects sampled at ITS during the year 2020. Species that were present in a majority of the transects are underlined.

Species	Num. of transects (/78)	Percent prevalence (%)
Sargassum horneri	72	92.3
Undaria pinnatifida	66	84.6
Macrocystis pyrifera	60	76.9
Sargassum muticum	58	74.4
Stephanocystis osmundacea	51	65.4
Eisenia arborea	38	48.7
Laminaria spp	29	37.2
Egregia menziesii	3	3.8
Codium fragile	1	1.3

C2: Pairwise comparisons

Table C2.1: Multiple pairwise comparisons with Bonferroni-corrected p-values (significance level = p value≤ 0.05) of 'Species' level averaged over 'Subsite' and 'Season' levels on the Density GLMM (a) and Biomass GLMM (b). Results are given on the log scale.

a)

Contrast	Estimate	Std. Error	z value	p value
Macrocystis pyrifera - Sargassum horneri	-3.463	0.353	-9.822	<0.001
Macrocystis pyrifera - Sargassum muticum	-1.980	0.364	-5.438	<0.001
Macrocystis pyrifera - Undaria pinnatifida	-0.566	0.434	-1.303	1.000
Sargassum horneri - Sargassum muticum	1.483	0.179	8.286	<0.001
Sargassum horneri - Undaria pinnatifida	2.898	0.296	9.792	<0.001
Sargassum muticum - Undaria pinnatifida	1.415	0.309	4.578	<0.001

b)

Contrast	Estimate	Std. Error	z value	p value
Macrocystis pyrifera - Sargassum horneri	0.179	0.240	0.745	1.000
Macrocystis pyrifera - Sargassum muticum	1.395	0.241	5.793	<0.001
Macrocystis pyrifera - Undaria pinnatifida	1.459	0.241	6.047	<0.001
Sargassum horneri - Sargassum muticum	1.217	0.240	5.063	<0.001
Sargassum horneri - Undaria pinnatifida	1.281	0.241	5.319	<0.001
Sargassum muticum - Undaria pinnatifida	0.064	0.242	0.264	1.000

Table C2.2: Multiple pairwise comparisons with Bonferroni-corrected p-values (significance level = p value ≤ 0.05) of Species-Subsite interactions averaged over the Season level on the Density GLMM (a) and Biomass GLMM (b). Only comparisons that share the same 'Species' level are shown. Results are given on the log scale.

a)

Contrast	Estimate	Std. Error	z value	p value
Macrocystis pyrifera: Canopy - Outside	2.799	0.606	4.621	<0.001
Sargassum muticum: Canopy - Outside	0.942	0.281	3.353	0.022
Sargassum horneri: Canopy - Outside	-1.111	0.251	-4.436	<0.001
Undaria pinnatifida: Canopy - Outside	-0.492	0.350	-1.405	1.000

b)

Contrast	Estimate	Std. Error	z value	p value
Macrocystis pyrifera: Canopy - Outside	3.477	0.352	9.891	<0.001
Sargassum muticum: Canopy - Outside	0.664	0.332	1.999	1.000
Sargassum horneri: Canopy - Outside	-1.308	0.350	-3.733	0.005
Undaria pinnatifida: Canopy - Outside	0.362	0.341	1.061	1.000

Table C2.3: Multiple pairwise comparisons with Bonferroni-corrected p-values (significance level = p value≤ 0.05) of Species-Season interactions averaged over the Subsite level on the Density GLMM (a) and Biomass GLMM (b). Only comparisons that share the same 'Season' level are shown. Results are given on the log scale.

a)

Contrast	Estimate	Std. Error	z value	p value
Spring				
Macrocystis pyrifera - Sargassum horneri	-4.679	0.773	-6.050	<0.001
Macrocystis pyrifera - Sargassum muticum	-2.347	0.815	-2.881	0.475
Macrocystis pyrifera - Undaria pinnatifida	-0.544	1.022	-0.532	1.000
Sargassum horneri - Sargassum muticum	2.332	0.450	5.183	<0.001
Sargassum horneri - Undaria pinnatifida	4.135	0.764	5.413	<0.001
Sargassum muticum - Undaria pinnatifida	1.804	0.806	2.238	1.000
Summer				
Macrocystis pyrifera - Sargassum horneri	-2.235	0.464	-4.817	<0.001
Macrocystis pyrifera - Sargassum muticum	-1.735	0.475	-3.653	0.031
Macrocystis pyrifera - Undaria pinnatifida	-1.869	0.470	-3.977	0.008
Sargassum horneri - Sargassum muticum	0.501	0.318	1.577	1.000
Sargassum horneri - Undaria pinnatifida	0.366	0.307	1.193	1.000
Sargassum muticum - Undaria pinnatifida	-0.134	0.325	-0.413	1.000
Fall				
Macrocystis pyrifera - Sargassum horneri	-2.405	0.395	-6.067	<0.001
Macrocystis pyrifera - Sargassum muticum	-1.061	0.417	-2.545	1.000
Macrocystis pyrifera - Undaria pinnatifida	-0.282	0.444	-0.635	1.000
Sargassum horneri - Sargassum muticum	1.344	0.296	4.541	<0.001
Sargassum horneri - Undaria pinnatifida	2.123	0.332	6.396	<0.001
Sargassum muticum - Undaria pinnatifida	0.780	0.356	2.193	1.000
Winter				
Macrocystis pyrifera - Sargassum horneri	-4.534	0.577	-7.865	<0.001
Macrocystis pyrifera - Sargassum muticum	-2.778	0.591	-4.701	<0.001
Macrocystis pyrifera - Undaria pinnatifida	0.431	0.922	0.468	1.000
Sargassum horneri - Sargassum muticum	1.756	0.328	5.362	<0.001
Sargassum horneri - Undaria pinnatifida	4.965	0.780	6.369	<0.001

Sargassum muticum - Undaria pinnatifida	3.209	0.790	4.063	0.006

b)

Contrast	Estimate	Std. Error	z value	p value
Spring				
Macrocystis_pyrifera - Sargassum_horneri	-1.996	0.595	-3.353	0.096
Macrocystis_pyrifera - Sargassum_muticum	0.027	0.545	-3.503	1.000
Macrocystis_pyrifera - Undaria_pinnatifida	-0.089	0.594	-0.150	1.000
Sargassum_horneri - Sargassum_muticum	2.023	0.591	3.422	0.075
Sargassum_horneri - Undaria_pinnatifida	1.907	0.592	3.221	0.154
Sargassum_muticum - Undaria_pinnatifida	-0.116	0.590	-0.197	1.000
Summer				
Macrocystis_pyrifera - Sargassum_horneri	1.522	0.430	3.541	0.048
Macrocystis_pyrifera - Sargassum_muticum	2.171	0.428	5.071	<0.001
Macrocystis_pyrifera - Undaria_pinnatifida	0.144	0.424	0.341	1.000
Sargassum_horneri - Sargassum_muticum	0.649	0.429	1.512	1.000
Sargassum_horneri - Undaria_pinnatifida	-1.377	0.425	-3.241	0.143
Sargassum_muticum - Undaria_pinnatifida	-2.026	0.423	-4.788	<0.001
Fall				
Macrocystis_pyrifera - Sargassum_horneri	2.366	0.422	5.604	<0.001
Macrocystis_pyrifera - Sargassum_muticum	3.408	0.424	8.031	<0.001
Macrocystis_pyrifera - Undaria_pinnatifida	4.038	0.428	9.429	<0.001
Sargassum_horneri - Sargassum_muticum	1.041	0.418	2.489	1.000
Sargassum_horneri - Undaria_pinnatifida	1.672	0.422	3.958	0.009
Sargassum_muticum - Undaria_pinnatifida	0.630	0.424	1.485	1.000
Winter				
Macrocystis_pyrifera - Sargassum_horneri	-1.177	0.484	-2.430	1.000
Macrocystis_pyrifera - Sargassum_muticum	-0.024	0.480	-0.050	1.000
Macrocystis_pyrifera - Undaria_pinnatifida	1.744	0.488	3.576	0.042
Sargassum_horneri - Sargassum_muticum	1.153	0.483	2.388	1.000
Sargassum_horneri - Undaria_pinnatifida	2.921	0.490	5.958	<0.001

| Sargassum_muticum - Undaria_pinnatifida | 1.768 | 0.486 | 3.637 | 0.033 |

Table C2.4: Multiple pairwise comparisons with Bonferroni-corrected p-values of Species-Season
interactions averaged over the Subsite level on the Density GLMM (a) and Biomass GLMM (b). Only comparisons that share the same 'Species' level are shown.

a)

Contrast	Estimate	Std. Error	z value	p value
Macrocystis pyrifera				
Spring - Summer	-1.046	0.759	-1.378	1.000
Spring - Fall	-1.865	0.737	-2.530	1.000
Spring - Winter	-0.431	0.830	-0.520	1.000
Summer - Fall	-0.819	0.436	-1.880	1.000
Summer - Winter	0.615	0.579	1.060	1.000
Fall - Winter	1.434	0.550	2.605	1.000
Sargassum horneri				
Spring - Summer	1.398	0.342	4.083	0.005
Spring - Fall	0.409	0.327	1.252	1.000
Spring - Winter	-0.286	0.331	-0.864	1.000
Summer - Fall	-0.988	0.275	-3.592	0.039
Summer - Winter	-1.684	0.305	-5.518	<0.001
Fall - Winter	-0.695	0.289	-2.410	1.000
Sargassum muticum				
Spring - Summer	-0.433	0.432	-1.003	1.000
Spring - Fall	-0.579	0.428	-1.351	1.000
Spring - Winter	-0.862	0.440	-1.959	1.000
Summer - Fall	-0.146	0.322	-0.452	1.000
Summer - Winter	-0.429	0.337	-1.273	1.000
Fall - Winter	-0.283	0.332	-0.852	1.000
Undaria pinnatifida				
Spring - Summer	-2.371	0.751	-3.156	0.192

Spring - Fall	-1.603	0.767	-2.089	1.000
Spring - Winter	0.544	1.038	0.524	1.000
Summer - Fall	0.768	0.351	2.186	1.000
Summer - Winter	2.915	0.782	3.727	0.023
Fall - Winter	2.147	0.797	2.692	0.852

b)

Contrast	Estimate	Std. Error	z value	p value
Macrocystis pyrifera				
Spring - Summer	-0.865	0.512	-1.689	1.000
Spring - Fall	-2.593	0.527	-4.921	<0.001
Spring - Winter	-0.731	0.544	-1.344	1.000
Summer - Fall	-1.728	0.443	-3.900	0.012
Summer - Winter	0.134	0.459	0.292	1.000
Fall - Winter	1.863	0.453	4.110	0.005
Sargassum horneri				
Spring - Summer	2.653	0.531	5.000	<0.001
Spring - Fall	1.769	0.517	3.421	0.075
Spring - Winter	0.088	0.532	0.166	1.000
Summer - Fall	-0.884	0.419	-2.110	1.000
Summer - Winter	-2.565	0.472	-5.436	<0.001
Fall - Winter	-1.681	0.457	-3.674	0.029
Sargassum muticum				
Spring - Summer	1.278	0.513	2.490	1.000
Spring - Fall	0.787	0.512	1.537	1.000
Spring - Winter	-0.782	0.538	-1.454	1.000
Summer - Fall	-0.491	0.425	-1.156	1.000
Summer - Winter	-2.060	0.455	-4.527	<0.001
Fall - Winter	-1.569	0.449	-3.492	0.058
Undaria pinnatifida				
Spring - Summer	-0.632	0.517	-1.222	1.000
Spring - Fall	1.534	0.518	2.963	0.365

Spring - Winter	1.102	0.539	2.046	1.000
Summer - Fall	2.165	0.422	5.135	<0.001
Summer - Winter	1.734	0.464	3.736	0.023
Fall - Winter	-0.432	0.464	-0.930	1.000

C3: Cross correlations

Table C3.1: Correlation coefficients of time-lagged linear relationships between (a) mean monthly temperature (°C), (b) monthly coefficient of variation of the temperature (%) , and mean monthly biomass of *M. pyrifera*, *S. muticum*, *S. horneri* and *U. pinnatifida* (g m^{-2}). Correlations of ± 0.6 are considered significant. Highest significant correlation per species is <u>underlined</u>.

a)

	Lag (months)							
	-7	**-6**	**-5**	**-4**	**-3**	**-2**	**-1**	**0**
M. pyrifera	-0.253	-0.199	-0.296	-0.305	-0.137	0.157	0.687	<u>0.909</u>
S. muticum	0.078	0.137	0.165	0.236	0.239	0.089	-0.23	-0.387
S. horneri	0.131	0.167	0.219	0.211	0.149	-0.118	-0.399	-0.410
U. pinnatifida	0.241	0.164	-0.039	-0.306	-0.333	<u>-0.627</u>	-0.580	-0.070

b)

	Lag (months)							
	-7	**-6**	**-5**	**-4**	**-3**	**-2**	**-1**	**0**
M. pyrifera	-0.497	-0.468	-0.176	0.197	0.414	<u>0.740</u>	0.615	0.290
S. muticum	0.173	0.163	0.166	0.201	0.155	-0.110	-0.613	<u>-0.776</u>
S. horneri	0.176	0.166	0.137	0.131	0.026	-0.420	<u>-0.725</u>	-0.721
U. pinnatifida	0.221	-0.106	-0.517	<u>-0.619</u>	-0.339	-0.247	-0.028	0.221