

Hidden Impacts of Climate Change on Canada's Undersea Forests

Chapter 1: Warm Sea Water and High Kelp Density Magnify Bryozoan Abundance

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Chapter 2: Grazing by Kelp Crabs Amplifies Impacts of Bryozoans on Kelp

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Introduction

Warming ocean temperatures can impact individual organisms directly by affecting their environments and physiological states, and indirectly by altering relationships between species (Leonard 2000, Walther 2010, Harley 2011). Off the central coast of British Columbia (BC) in 2015, Coastal Guardian Watchmen (CGW) observed an expansive outbreak of a white encrusting animal on kelp. These observations coincided with what later became identified as a period of extreme ocean temperature anomalies, also known as “the blob”, a marine heat wave that emerged across the northeast Pacific Ocean (Bond et al. 2015). The white crust observed was a bryozoan of the genus *Membranipora*, an immobile epiphytic animal with planktonic larvae that settle and grow primarily on kelp and can also colonize other seaweeds and artificial substrates. The CGW reported that fronds of giant kelp (also known locally as flat kelp,

Macrocystis pyrifera) were so heavily encrusted by bryozoan in the summer of 2015 that they sank to the seafloor where they rapidly disintegrated. This observation concerned the Central Coast Indigenous Resource Alliance (CCIRA) and its four member Nations (Heiltsuk, Kitasoo/Xai'xais, Wuikinuxv, and Nuxalk) because giant kelp forests provide a critical source of food and habitat for culturally and economically important species, including northern abalone, sea urchins, and rockfish. Fronds of giant kelp are also collected and used by people as a substrate for herring spawn in a commercial spawn-on-kelp fishery, and kelp and other seaweeds are harvested for food social, and ceremonial (FSC) purposes. There is also an increasing interest in commercial seaweed harvest. Consequently, indirect effects of climate change, facilitated through potential temperature-induced outbreaks of encrusting bryozoan on kelp, could threaten future food security and livelihoods for BC's coastal First Nations.

Encrustation by the bryozoan *Membranipora* can negatively affect kelp by making it more susceptible to breakage and erosion (Krumhansl et al. 2011), limiting the ability of kelp to absorb nutrients (Hepburn et al. 2012), interfering with photosynthesis (Hurd et al. 2000), and inhibiting the release of reproductive spores (Saier & Chapman, 2004). On the east coast of Canada, where *Membranipora* is an invasive species, ocean warming enhanced the negative interaction between the bryozoan and native seaweeds, resulting in up to 98% loss of kelp biomass at some locations (Filbee-Dexter et al. 2016). However, the impact of this bryozoan on kelp has not been measured on the west coast of Canada, where it is a native species. We do not know how the timing and growth of bryozoan on kelp may change under future climate, which hinders the ability of coastal Nations to manage kelp harvests in ways that support resilient kelp forests. Understanding trends in bryozoan growth and sea surface temperature could, therefore, improve the capacity of coastal Nations to manage kelp harvests and related fisheries as ocean conditions continue to change.

Consistent with CGW observations made on BC's central coast, research in the Atlantic indicates that seawater temperature impacts the seasonal timing and amount of bryozoan on kelp (Saunders and Metaxas 2007, 2008; Saunders et al. 2010, Denley et al. 2019), and that flow and exposure to wave action can influence settlement (Pratt et al. 2022) and growth (Pratt 2008) of bryozoans on kelp. Also, research in southern California found that the density of giant kelp beds influenced the settlement and growth of *Membranipora* by filtering the bryozoan larvae out of the water column and altering local flow conditions (Arkema & Samhuri 2019). Finally, the

presence of epiphytes like bryozoans can influence the rate at which grazers feed on kelp (Wahl and Hay 1995). How crabs, snails, and other kelp canopy grazers respond to bryozoan encrustation could potentially enhance (O'Brien et al. 2013) or mitigate (Levin et al. 2002) negative impacts of bryozoan outbreaks on kelp, but these relationships have yet to be studied in BC.

To increase our understanding of future impacts of bryozoan growth on giant kelp off the coast of BC, this research addressed 4 questions:

- 1) How do environmental (seawater temperature, wave exposure) and biological (kelp density, grazer abundance) variables influence the amount of bryozoan on giant kelp over space and time?
- 2) Does bryozoan cover impact the size and density of giant kelp beds over time?
- 3) How will warming ocean temperatures associated with climate change affect the future impact of bryozoan on kelp and, consequently, the long-term viability of kelp harvests and related fisheries?
- 4) How do bryozoan cover, sea surface temperature and canopy grazers affect rates of kelp loss at the blade level?

The first three questions were examined using data from Nation-led field surveys at selected sites along the Central Coast and from additional surveys in Barkley Sound, Vancouver Island (Chapter 1). The fourth question was examined using data from field experiments conducted near the Bamfield Marine Sciences Centre (BMSC) in Barkley Sound (Chapter 2¹). As detailed below, the results of this research increase understanding of climate change impacts on kelp forest ecosystems and can inform adaptive management of kelp harvests and related fisheries under changing climatic conditions.

¹ Presented in greater detail in Meredith Fraser's MRM Thesis that accompanies this summary report.

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Methods

Nation-led field surveys of bryozoan & kelp

Surveys of bryozoan and kelp were conducted by Coastal Guardian Watchmen and Stewardship staff at 10 sites on BC's Central Coast. Six sites were surveyed in both 2020 and 2021, and 4 sites in 2021 only (Figure 1a). Additionally, 3 sites were surveyed in Barkley Sound on the west coast of Vancouver Island in 2020 and 2021 to examine regional differences in kelp and bryozoan dynamics (Figure 1b). Kelp beds selected for surveys consisted mostly of giant kelp (flat kelp, *Macrocystis pyrifera*). Seawater temperature ~1m below the surface was monitored at 8 sites on the Central Coast and all 3 sites in Barkley Sound from May/Jun to October, 2021 (Figure 1a,b). For sites and years when seawater temperature was not monitored directly, site-specific sea surface temperature (SST) was acquired using satellite data available from NOAA's "CoralTemp" dataset at a 5-km spatial resolution (NOAA Coral Reef Watch 2020). When site-specific seawater temperature was not required, for example, when comparing trends between years across all sites, we obtained daily SST from the British Columbia Light Station Sea-Surface Temperature and Salinity Data (Pacific) for the McInnes Island and Amphitrite Point light stations (<https://open.canada.ca/data/en/dataset/719955f2-bf8e-44f7-bc26-6bd623e82884>). These temperature data were most consistent with seasonal trends recorded by *in situ* data loggers deployed 1 meter below the surface (Figure A1.1). The degree of exposure to wave action was calculated for each site using a relative exposure index (REI) based on hourly wind data (frequency, speed, and direction) obtained from the Environment and Natural Resources Canada weather station in Bella Bella (<http://climate.wather.gc.ca>), coupled with site-specific fetch in all directions.

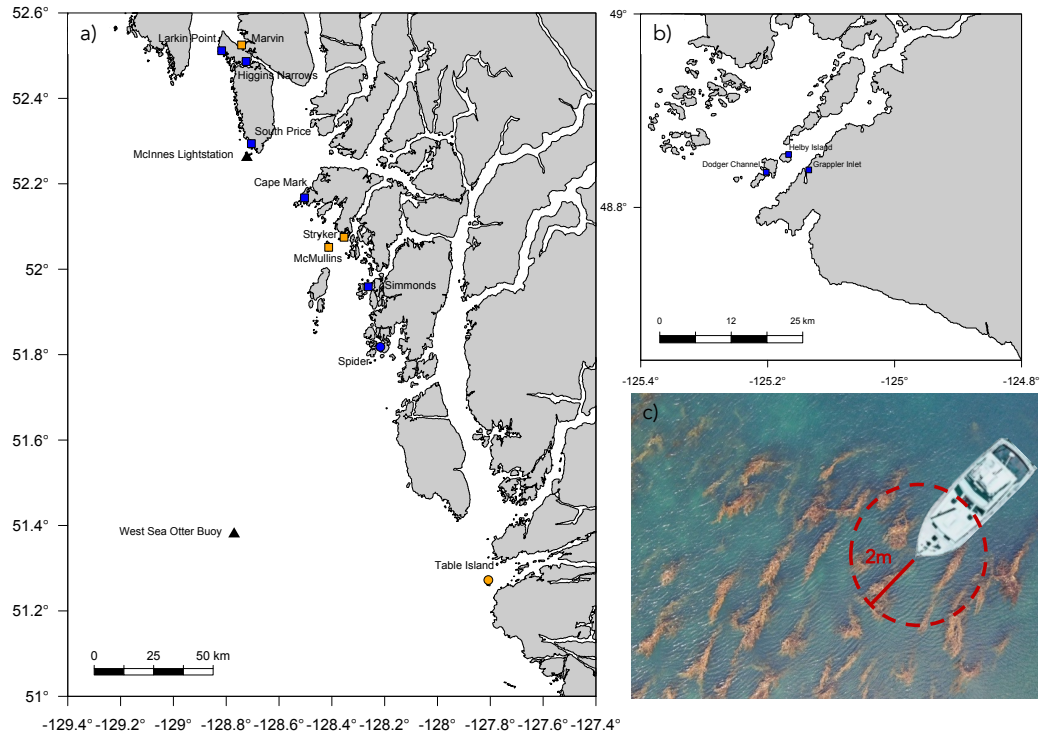


Figure 1. Maps of survey sites on the Central Coast (a) and Barkley Sound (b). Blue sites were surveyed in 2020 and 2021, orange sites were surveyed in 2021 only, square markers indicate sites where seawater temperature was monitored in 2021. Locations of the McInnes Island light station and the West Sea Otter MEDS buoy are also shown (black triangles). (c) 2-meter radius circle off the bow of the boat within which measurements of the health of the kelp bed were taken.

Surveys of selected kelp beds were conducted 2-3 times per year at each site to capture the anticipated seasonal timing of the annual growth and decline of bryozoan on kelp. The second year of surveys captured an anomalous warming event in the northeast Pacific Ocean ('heat dome') during which sea surface temperatures were approximately 3°C warmer than the previous 30-year baseline (average from 1991-2020) over ~2 weeks in late June to early July, 2021 (DFO 2022). The kelp bed at Table Island was surveyed only once in August 2021; we cannot be certain that we captured peak bryozoan cover on kelp at this site and data from Table Island have been excluded from site-specific analyses. However, these data provide an important baseline for comparison with potential future surveys and are described in a separate section of the Results.

Surveys were conducted by boat. Kelp beds were mapped by outlining the perimeter or linear extent of the bed using 5 GPS (location) points and recording the depth and distance from shore for each point. At each location point, kelp measurements were taken within a 2-meter

radius circle off the bow of the boat (Figure 1c). These measurements included kelp density, measured as the percent canopy coverage (< 20%, 20 – 40%, >40 – 60%, >60 – 80%, >80 – 100%), the percent of total kelp canopy cover encrusted with bryozoans (0%, >0 – 5%, >5 – 20%, >20 – 40%, >40 – 60%, >60 – 80%, >80 – 100%), and the types (snails, urchins, kelp crabs, hermit crabs) and total number of individuals of all grazer species pooled (<5, >5 – 15, >15 – 25, >25) in the kelp canopy. Five giant kelp blades were also collected and photographed at each location point to further document bryozoan cover (Appendix 2).

We analysed these data to determine the relative importance of environmental factors (seawater temperature, exposure to wave action) and biological drivers (kelp density, grazer abundance) influencing bryozoan growth on giant kelp over space and time. There were no observations with bryozoan cover of >80–100% and analyses included only 6 cover categories ranging from 0% to >60–80%. We also compared the density and size of kelp beds between survey years to determine whether bryozoan cover influenced the persistence of kelp from one year to the next. Finally, we compared trends in the seasonal timing and amount of bryozoan on kelp between survey years with different temperature regimes.

Results

Sea water temperature and kelp density drive bryozoan cover on giant kelp along the Central Coast

Of the environmental and biological variables we measured, the average sea water temperature over the month leading up to each survey and the density of the kelp bed were the main drivers of bryozoan cover on giant kelp (Figure 2, Table A1.1). Both warmer temperatures and higher kelp density were associated with higher bryozoan cover (Figure 3). This was consistent when analysing direct temperature measurements at fewer sites (n = 8: Cape Mark, McMullins, Simmonds, Stryker, Larkin Point, Marvin Island, Higgins Narrows, South Price) in 2021 and a combination of direct temperature measurements and sea surface temperature (SST) derived remotely from satellite data for all sites (n = 9) in 2020 & 2021 (Figures 2 & 3, Table A1.1). When all sites and both years were included in the analysis, wave exposure was also an important driver of the amount of bryozoan cover on kelp, with less bryozoan cover at more wave exposed sites (Figure 2 & 3, Table A1.1). The estimated effect of grazer abundance on

bryozoan cover was variable and uncertain, suggesting that, when all grazer species are pooled, grazers have little influence on bryozoan cover (Figure 2, Table A1.1, but see Chapter 2).

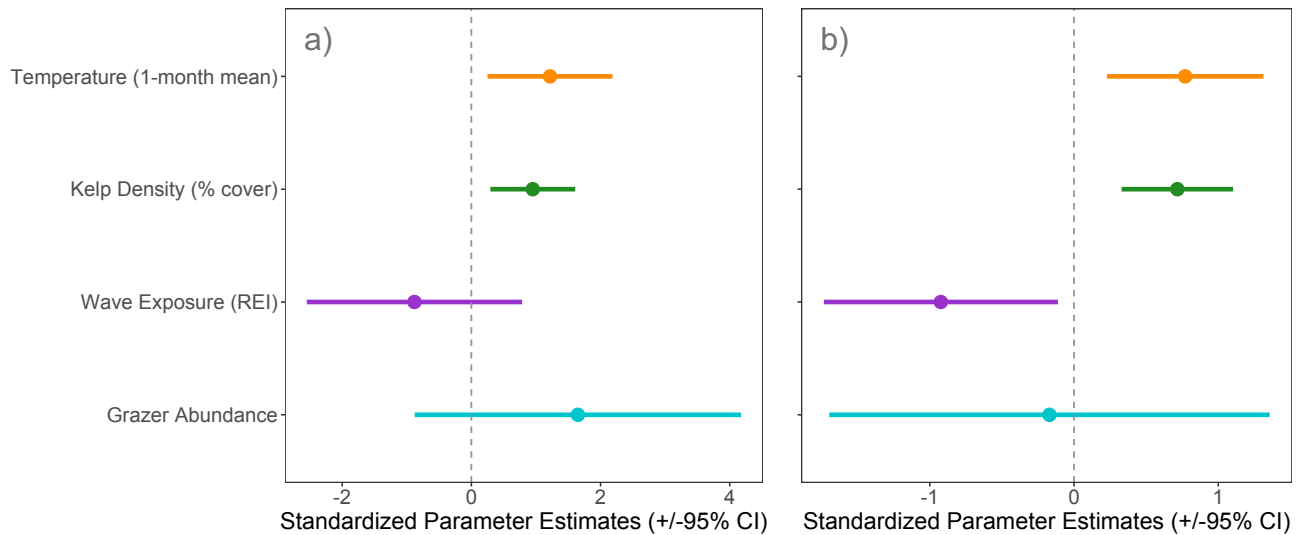


Figure 2. Relative importance of environmental and biological variables (parameters) driving percent cover of bryozoan on giant kelp measured during field surveys at a) 8 sites on the Central Coast for which direct measurements of seawater temperature were available from May 29 to October 15, 2021, and b) all sites surveyed on the Central Coast using both direct seawater temperature and satellite SST [sites surveyed from July 7 to November 11, 2020 ($n = 6$) and May 29 to October 15, 2021 ($n = 9$)]. Coloured dots and lines are the standardized parameter estimates and 95% confidence intervals, respectively. Dots to the right of the dashed zero line indicate a positive relationship with bryozoan cover, dots to the left of the dashed zero line indicate a negative relationship with bryozoan cover. The length of the confidence interval lines indicates the degree of uncertainty in our estimated effect of each variable on bryozoan cover. Confidence interval lines that do not overlap with the dashed zero lines are compelling evidence of an effect of that driver on bryozoan cover.

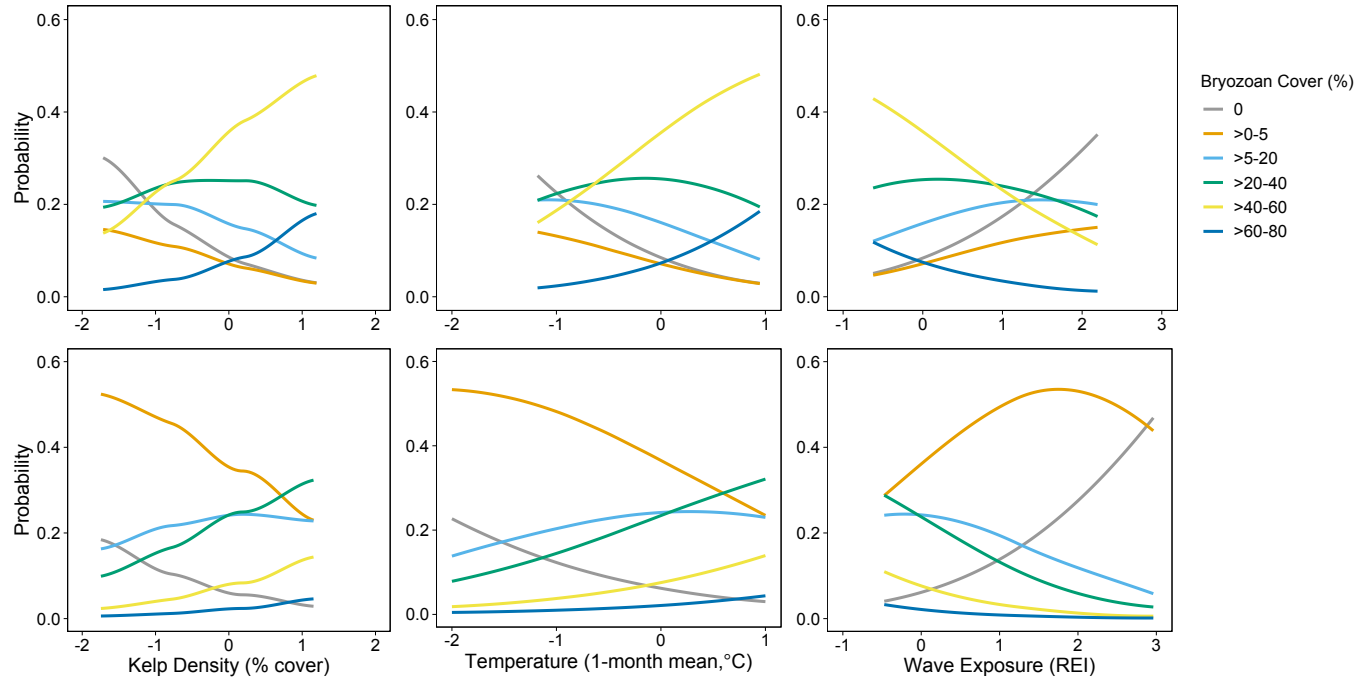


Figure 3. Predicted probabilities of observing each bryozoan cover (%) category on giant kelp as a function of informative environmental and biological variables selected using ordinal regression models (Table A1.1) based on surveys at 8 sites on the Central Coast for which direct measurements of seawater temperature were available from May 29 to October 15, 2021 (top panel) and all sites surveyed on the Central Coast using both direct seawater temperature and satellite SST [sites surveyed from July 7 to November 11, 2020 ($n = 6$) and May 29 to October 15, 2021 ($n = 9$)] (bottom panel). Environmental predictor variables are standardized by subtracting the mean and dividing by the standard deviation.

Kelp and bryozoan dynamics vary regionally along the coast of British Columbia

Preliminary analysis and personal communications with staff and researchers at Bamfield Marine Sciences Centre (BMSC) suggested that (a) in Barkley Sound the seasonal onset and maximum cover of bryozoan on giant kelp occurred earlier than on the Central Coast and (b) our first surveys in Barkley Sound in August 2020 and June 2021 missed the earlier period of maximum bryozoan cover in that area (Appendix 1: Figure A1.2; Tao Eastham, Tory Pritchard personal communications). This hindered our ability to identify drivers of bryozoan growth on kelp in this Barkley Sound. The earlier seasonal onset and maximum abundance of bryozoan on giant kelp in Barkley Sound may reflect warmer regional seawater temperatures relative to the Central Coast (Appendix 1: Figure A1.3).

Observed levels of bryozoan cover have minimal impacts on the size and density of giant kelp beds on the Central Coast over time

The size and density of individual kelp beds differed significantly among sites. However, in most cases, these variables remained stable for a given site over the 2-year survey period (Figures 4 & 5, Table A1.2). This was consistent among sites with both the highest (Higgins Narrows and Cape Mark) and lowest (Larkin Point and South Price) cover of bryozoan in 2020. The 3 exceptions for the Central Coast were (a) the kelp bed surveyed at Spider Island, which decreased in both size and density between 2020 and 2021 despite having only intermediate levels of bryozoan cover in 2020, (b) the kelp bed surveyed at Larkin Point, which increased in density but not size between 2020 and 2021, and (c) the kelp bed at Simmonds, which decreased in size but not density between 2020 and 2021 (Figures 4 & 5, Table A1.2). Changes in kelp density observed at Larkin Point and kelp bed size observed at Simmonds may reflect differences in the number and seasonal timing of surveys at these sites within each year. Only two surveys were conducted at Larkin Point in 2021, one in spring and one in summer, while in 2020 surveys were conducted at this site in spring, summer and fall. Similarly, although 3 surveys were conducted in both years at Simmonds, in 2020 kelp bed area was only measured during one of those surveys in the fall.

In contrast, all kelp beds surveyed in Barkley Sound decreased in size between 2020 and 2021 (Figures 4 & 5, Table A1.2), with the kelp bed at Helby Island also declining in density over that time (Figure 5, Table A1.2). However, because our surveys did not capture peak bryozoan cover on kelp in this region, we cannot determine whether observed declines in the size and density of kelp beds over time relate to high levels of bryozoan cover or other drivers of kelp decline in this region (e.g. Starko et al. 2019).

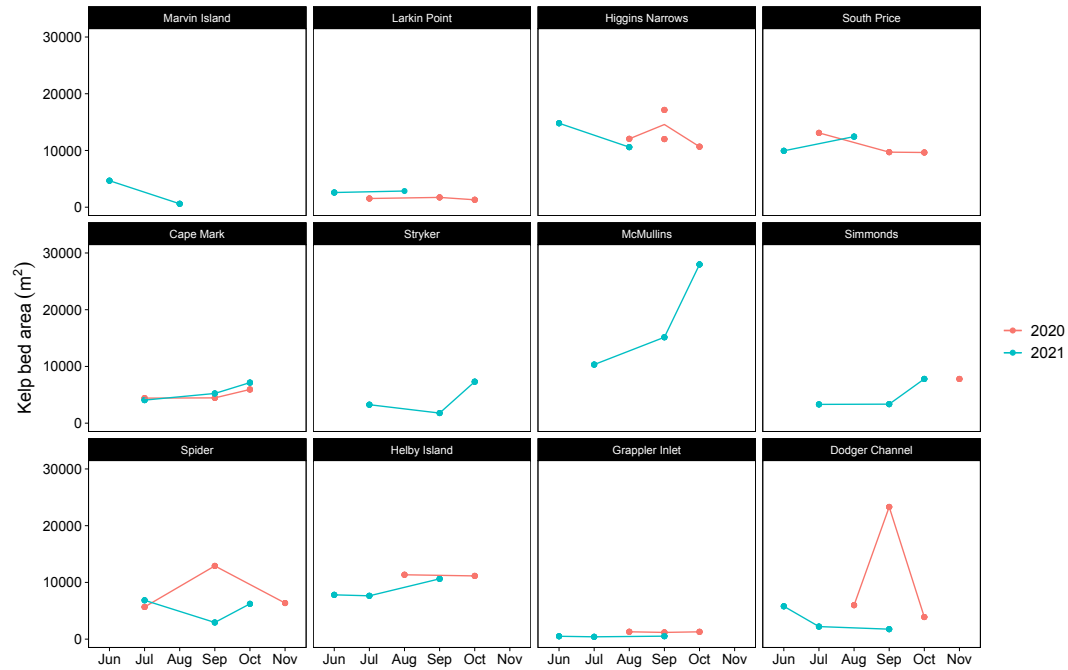


Figure 4. Kelp bed size (area, m²) at 9 sites surveyed 3 times from July 7 to November 11, 2020 and 12 sites surveyed 2-3 times from May 29 to October 15, 2021 on the Central Coast and in Barkley Sound.

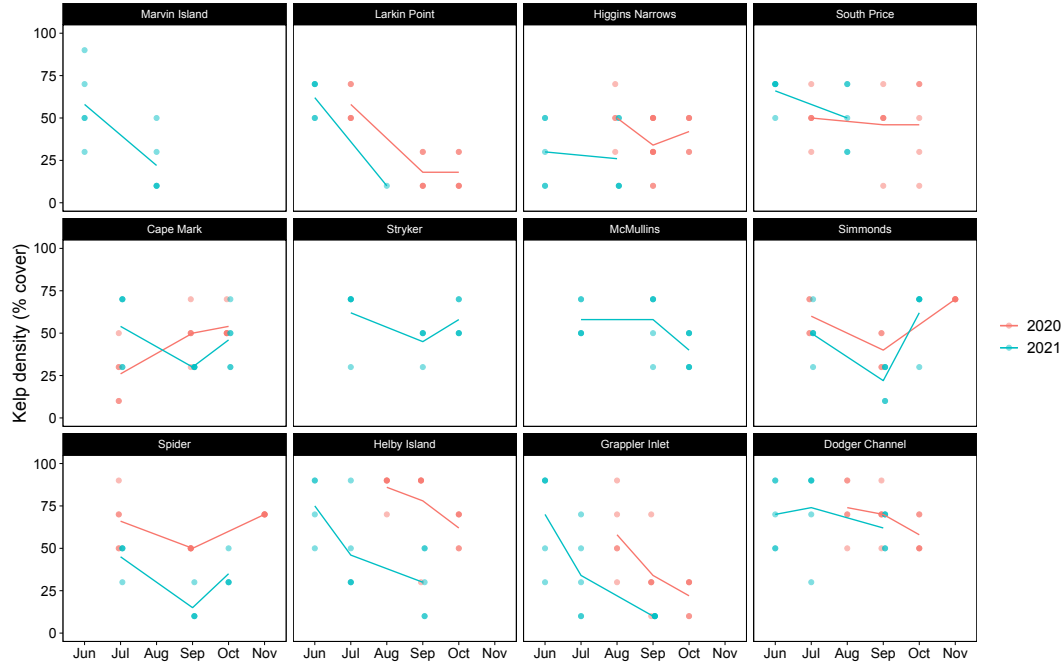


Figure 5. Kelp bed density (% canopy cover) at 9 sites surveyed 3 times from July 7 to November 11, 2020 and 12 sites surveyed 2-3 times from May 29 to October 15, 2021 on the Central Coast and in Barkley Sound.

Interannual temperature differences drive the seasonal timing but not the overall amount of bryozoan on kelp along the Central Coast

The average % cover of bryozoan on giant kelp from the spring to fall was consistent between survey years. However, the timing of maximum cover and of seasonal growth of bryozoan on kelp differed between years (Figure 6, Table A1.3). Peak bryozoan cover in 2020 occurred in early September to mid-October (day of year: ~250–300), with growth of bryozoan on kelp generally increasing over the season from June to November. In contrast, bryozoan cover on kelp in 2021 peaked in early July to mid-August (day of year: ~180–225) and began to decline later in the season. Shifts in the seasonal timing of bryozoan growth on kelp between years likely reflect interannual variation in temperature. Seawater temperature was more variable in 2021 compared to 2020 with substantially warmer temperatures in the spring and early summer, associated with the province-wide heat dome in late June to early July 2021, followed by a more rapid cooling in the fall (Figure 6, Table A1.3).



Figure 6. Bryozoan cover (with shaded 95% confidence intervals) on giant kelp over time (day of year) at 6 sites surveyed on the Central Coast from July 7 to November 11, 2020 and 9 sites surveyed from May 29 to October 15, 2021 in relation to daily averaged sea surface temperature from McInnes Island light station.

Current status of the Table Island kelp bed

The kelp bed at Table Island was surveyed on August 24, 2021. This bed consisted mostly of giant kelp at very low density (< 20% coverage, patchy and fragmented) that spanned an area of 6395 m². No bryozoan cover was observed on giant kelp at the time of the survey. Snails were present in the kelp canopy at patchy densities that ranged from less than 5 to greater than 25 per ~12.5m². Satellite sea surface temperature averaged over the month preceding the survey at this site was 14.9°C. This information provides an important baseline with which to compare potential future surveys of this site.

Bryozoan genera identified in field surveys

Two different bryozoan genera were identified during the field surveys, *Membranipora* and *Celleporella hyalina* (Figure A2.3). Unlike other bryozoans, *Membranipora* spp. have extremely rapid and indeterminate (continuous) growth and are the dominant competitors for space on kelp blades, often overgrowing other epiphytes, including the typically smaller colonies of *Celleporella hyalina* (observed in this study, Bernstein and Jung, 1979). The highest levels of bryozoan cover on kelp in our surveys were attributed to *Membranipora* spp., therefore, the discussion will focus on *Membranipora* spp. (hereon bryozoan).

Discussion

We found that denser kelp beds at warmer, less wave-exposed sites were most susceptible to greater bryozoan cover. Our findings corroborate the initial observations made by Coastal Guardian Watchmen during the 2014–2016 marine heat wave and are consistent with other research in the bryozoan's invasive (northeast coast of North America, Pratt et al. 2022) and native (Norway, Matsson et al. 2019) ranges, which found that seawater temperature is a significant driver of bryozoan cover on kelp. Bryozoan growth rates are greater at locally warmer sites during a given year (Saunders and Metaxas 2009a) or increase across sites during warmer years (Scheibling and Gagnon 2009). Warmer seawater temperatures have also been associated with earlier seasonal occurrence and peak abundance of bryozoan on kelp (Saunders and Metaxas 2008), possibly due to warmer temperature reducing development times of the bryozoan's planktonic larvae (O'Connor et al. 2007). Similarly, we observed earlier seasonal

occurrence of peak bryozoan cover on kelp in 2021 compared to 2020, in correlation with an anomalous warming event ('heat dome') in late June to early July 2021 (DFO 2022).

Although high bryozoan cover on kelp occurred earlier in 2021, bryozoan cover declined rapidly in the fall of that year compared to 2020, resulting in no difference in the average cover of bryozoan on kelp from spring to fall between years. Increasing cover from late spring into early winter, as we observed in 2020, is common of this bryozoan in its invaded habitat in Nova Scotia (Saunders and Metaxas 2009b, Denley et al. 2014). However, in the San Juan Archipelago, Washington, settlement and growth of bryozoan on kelp begins to decline in September (Harvell 1985), which is consistent with our observations from 2021. The decline in bryozoan cover on kelp in the fall of 2021 could reflect an advancement in the timing of the annual lifecycle of the bryozoan, in which settlement and growth of colonies on kelp is followed by reproduction and eventual senescence leading to mortality (Saunders and Metaxas 2009b, Denley and Metaxas 2016). Previous studies have shown that the timing of senescence in this bryozoan is related to colony age, regardless of temperature (Denley and Metaxas 2016). Thus, earlier seasonal occurrence of high bryozoan cover on kelp in 2021 may be followed by more rapid declines in cover as older colonies senesce.

Surprisingly, the importance of kelp density in driving spatial variation in bryozoan cover on kelp was similar to that of temperature, with higher bryozoan cover in more dense patches of kelp. Kelp density is also an important driver of spatial variation in bryozoan cover within kelp forests in southern California (Arkema and Samhouri 2019). There, bryozoan cover is lower on kelps in the interior of the forest than on those along the forest edge, and this spatial difference increases with increasing kelp density. Lower bryozoan cover towards the interior of denser kelp forests has been attributed to kelp filtering bryozoan larvae out of the water column and reducing local flow conditions, thereby limiting the rate at which both bryozoan larvae and suspended food particles consumed by bryozoans are delivered to the forest interior (Arkema and Samhouri 2019). Due to logistical constraints, our observations were made primarily along the perimeter or edge of kelp beds, which may explain why we detected an increase in bryozoan cover with kelp density in our study. Denser kelp canopies may act as better filters, trapping and retaining bryozoan larvae and contributing to increased settlement and cover of bryozoan along the perimeter of denser kelp beds. *M. pyrifera* can also create thermal microclimates (Molina-Montenegro et al. 2005). It is possible that limited flow within dense patches of kelp may lead to

localized warmer sea surface temperatures, which could facilitate increased growth of bryozoan colonies in denser kelp beds. While this does not appear to be the case in southern California (Arkema and Samhouri 2019), temperature modification by dense patches of kelp may play a larger role in determining spatial patterns in bryozoan cover in colder regions like BC's central coast. Additional bryozoan surveys along a linear cross-section of kelp beds could further examine the role of kelp density in driving variation in bryozoan cover within and among kelp beds.

Wave exposure was a significant driver bryozoan cover on kelp when the analysis included data for all 9 survey sites over both years. Kelp beds at sites that experienced higher levels of wave exposure had lower cover of bryozoan. Similar results have been shown experimentally over large spatial (100 km) and temporal (6 months) scales using cultured sugar kelp. Cover of bryozoan on cultured kelp decreased consistently from low, to intermediate, to high wave exposure sites along the west coast of Sweden (Visch et al. 2020). Wave action can inhibit planktonic larvae, like bryozoans', from settling on kelp by sweeping them off kelp blades before they can attach themselves to their surface (Koehl 2007). This mechanism likely contributed to lower bryozoan cover at more wave exposed sites in our study. In the Northwest Atlantic, wave exposure has been shown to negatively influence the abundance of bryozoan settlers but not the peak cover of adult bryozoan colonies on wild kelp (Pratt et al. 2022), suggesting that wave exposure can affect settlement of bryozoan recruits differently than growth of adult colonies. Up to a point, increased water flow associated with wave exposure can enhance feeding success, and consequently growth rates, of adult bryozoan colonies by increasing the rate at which colonies encounter and capture suspended food particles in the water column (Arkema 2009). However, beyond that point, higher flow rates can physically inhibit bryozoans from feeding (Arkema 2009). We observed a consistent decrease in the probability of detecting high levels of bryozoan cover with increasing wave exposure (Figure 3), suggesting that wave action on BC's exposed central coast exceeds threshold levels for enhanced colony growth rates and likely has an inhibitory effect. However, this is based on surveys conducted mainly along the outer edge of kelp beds. The effect of exposure on bryozoan cover may vary within a kelp bed due to the dampening of wave action in the interior of the bed by dense stands of kelp along the periphery.

Interestingly, we did not find evidence to suggest the abundance of grazers in the kelp canopy is an important driver of the amount of bryozoan cover on kelp. The uncertainty in the estimated impact of grazer abundance on bryozoan cover may be due in part to our survey method of assigning grazer abundance categories based on the total number of grazers pooled across all grazer species. Manipulative field experiments conducted concurrently with our field surveys suggest that impacts of grazers on rates of kelp loss and bryozoan cover are species-specific, with some grazers (kelp crabs) having large impacts while other species (snails) have negligible ones (see Chapter 2 of this report).

On the east coast of Canada and in other parts of the world, outbreaks of this bryozoan (*Membranipora* sp.) have contributed to substantial loss of kelp (Saunders and Metaxas 2008, Scheibling and Gagnon 2009, Andersen et al. 2011, Witman and Lamb 2018). Encouragingly, we detected no change in the size or density of kelp beds in response to the levels of bryozoan cover observed in our 2-year surveys. These findings could be specific to *M. pyrifera*, the focal kelp species of our surveys. Loss and recovery of kelp beds following bryozoan outbreaks has only been quantified in the bryozoan's invaded habitat, where the dominant kelps are understory species that are slow growing (0.15 - 0.91 cm/d Simonson et al. 2015) compared to *M. pyrifera* (4–30 cm/d, Krumhansl et al. 2017). High productivity of *M. pyrifera* could mitigate biomass loss and facilitate recovery of kelp forests following years of high bryozoan cover. However, previous studies on the central coast have shown that recovery of *M. pyrifera* is sensitive to small variations in temperature of less than 1°C (Krumhansl et al. 2017), suggesting that if regional seawater temperatures continue to rise, the resilience of giant kelp to bryozoan outbreaks could decline. We also caution that the impact of bryozoan growth on loss and recovery of *M. pyrifera* could be more severe during extreme climatic events in the ocean, like marine heat waves, which did not occur during this 2-year study. Moreover, the effects of bryozoan outbreaks on slower growing understory kelps off the coast of BC requires further exploration.

Conclusions & Management Recommendations

The most important findings of this research were: 1) denser kelp beds at warmer, less wave exposed sites had higher levels of bryozoan cover, 2) the seasonal timing of high bryozoan cover on kelp was earlier in 2021, which coincided with anomalously warm sea surface temperatures early in the growing season (June). However, overall bryozoan cover on kelp from

May to October, was consistent across survey years, and 3) bryozoan cover during this study did not result in detectable changes in the size or density of kelp beds between one year and the next. Taken together, these results suggest that although warming ocean temperatures may not result in levels of bryozoan cover that impact the persistence of giant kelp beds in the near-future, anomalous warming events (e.g. ‘the blob’ of 2014-2016, ‘heat dome’ of 2021) may result in earlier seasonal timing of peak bryozoan cover overlapping with the optimal time for kelp harvest in June (Krumhansl et al. 2017). This problem may become more common as average ocean temperatures continue to rise and as extreme climatic events, like ‘the blob’ increase in occurrence and severity. Accordingly, our management recommendations that stem from this work include:

1. Harvest of kelp should be prioritized at cooler and more wave exposed sites that are more likely to yield healthier, higher quality kelp.
2. Management strategies should adapt to the strength and timing of ocean warming trends and anomalies that affect the earlier seasonal timing of bryozoan outbreaks. Kelp harvest amount and timing can be modified accordingly. Fortunately, the seasonal timing of peak cover of bryozoan on kelp is unlikely to shift as early as March/April, and therefore the risk to the SOK fishery may not be imminent.
3. Temperature is an important factor for predicting where and when high bryozoan cover on kelp will occur. Whenever possible, temperature monitoring and temperature-induced management actions (how much kelp is harvested, when it is harvested, and from where) should be included in adaptive management plans. If temperature data are not available directly, near-real-time satellite sea surface temperature (SST) anomaly data for the Northeast Pacific are available to view from https://github.com/BIO-RSG/Pacific_SST_NRT_Monitoring. These SST anomaly maps can guide expectations about the season timing of occurrence and peak cover of bryozoan on kelp in a given year.
4. Strategically thinning dense kelp beds to increase seawater flow and decrease seawater temperature within the bed may be a proactive management tool for reducing the amount

of bryozoan cover in a kelp bed. If done, this management action should be conducted as an experiment, where replicate treatments are monitored, and future management actions are updated based on the results. Since we did not explicitly test the mechanisms by which denser kelp beds resulted in higher bryozoan cover as part of this study, the benefits, risks, and potential consequences, of thinning dense kelp beds requires further experimental testing before being conducted at regional spatial scales.

Appendix 1: Additional Figures & Tables

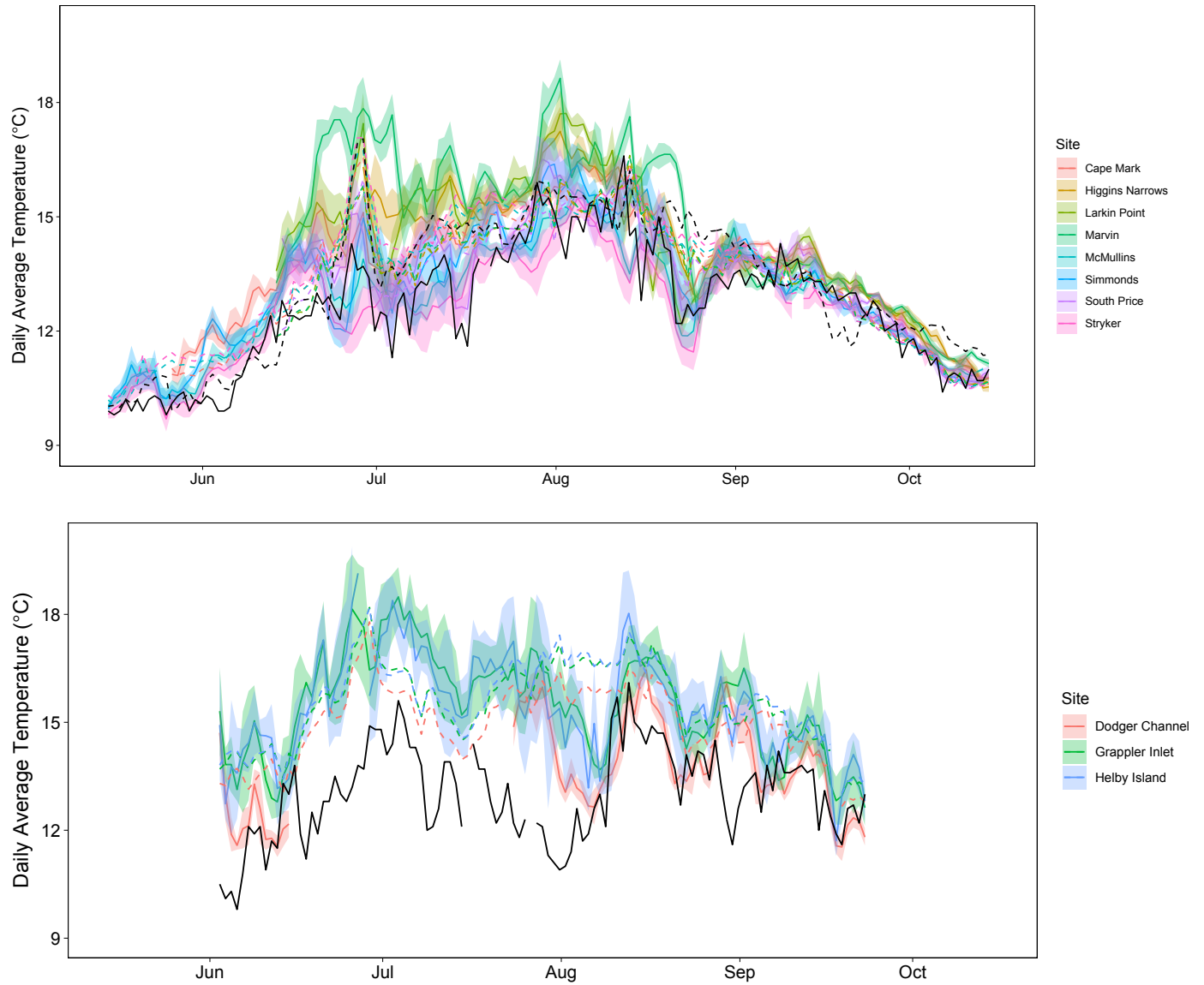


Figure A1.1. Comparison of available empirical and remote seawater temperature data. Coloured lines are study site-specific average daily temperature 1 meter below the surface (solid lines, mean \pm SD), and satellite sea surface temperature (dashed lines) at 8 sites surveyed on the Central Coast (top panel) and 3 sites surveyed in Barkley Sound (bottom panel) from May/Jun to October 2021. Black lines are empirical measurements of sea surface temperature recorded daily from the McInnes Island (Central Coast) and Amphitrite Point (Barkley Sound) light stations (solid line) and the West Sea Otter MEDS buoy (Central Coast, dotted line) over the same time period.

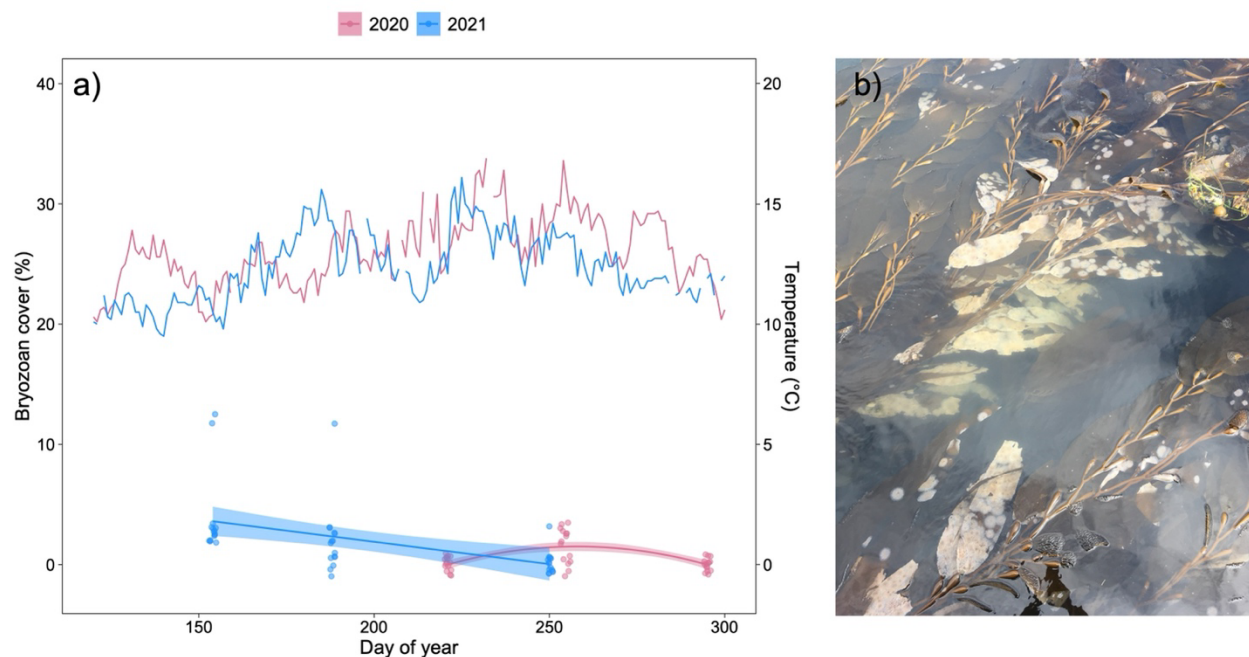


Figure A1.2. a) Bryozoan cover (with shaded 95% confidence intervals) on giant kelp over time (day of year) at 3 sites surveyed in Barkley Sound from August 8 to October 21, 2020 and from June 3 to September 7, 2021 in relation to daily averaged sea surface temperature from Amphitrite Point light station. b) Example of high bryozoan cover on giant kelp in Barkley Sound on June 14, 2021 (photo courtesy of Tory Pritchard)

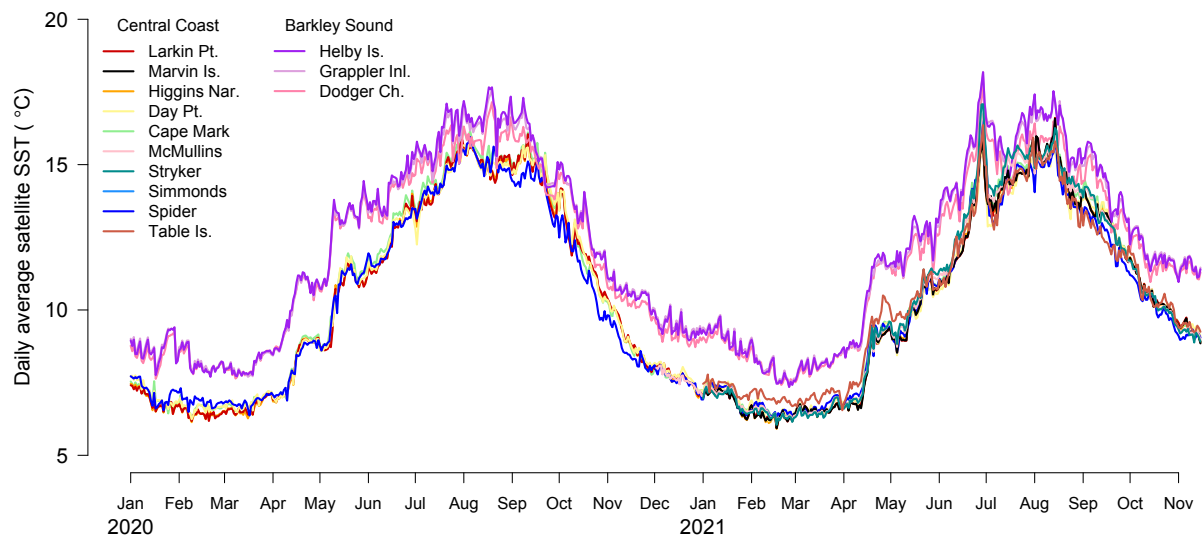


Figure A1.3. Daily average satellite sea surface temperature (SST) at 10 sites surveyed on the Central Coast and 3 sites surveyed in Barkley Sound from January 2020 to November 2021. Satellite SST for the 4 sites on the Central Coast that were only surveyed in 2021 (Marvin Island, McMullins, Stryker, and Table Island) is shown from January to November 2021 only.

Table A1.1. Results of ordinal regression models predicting the effects of environmental (average seawater temperature over the month preceding each survey, wave exposure) and biological (kelp density, grazer abundance) drivers on the amount (% cover) of bryozoan on giant kelp (6 cover categories: 0%, >0–5%, >5–20%, >20–40%, >40–60%, >60–80%) measured during field surveys at a) 8 sites on the Central Coast (Cape Mark, McMullins, Simmonds, Stryker, Larkin Point, Marvin Island, Higgins Narrows, South Price) for which direct measurements of seawater temperature were available from May/Jun to October 2021 (Figure 1a), and b) all sites surveyed on the Central Coast from July 7 to November 11, 2020 ($n = 6$) and May 29 to October 15, 2021 ($n = 9$) using both direct seawater temperature and satellite SST. Standardized parameter estimates and 95% confidence intervals are shown for the full models which include all predictor variables with separate intercepts for the random effect of site for a), and season (May & June = Spring, Jul & Aug = Summer, Sep to Nov = Fall) nested within site for b). Significant p -values shown in bold. *This table shows results depicted in Figures 2 & 3 of the main report.*

				Pseudo R ²
a) Bryozoan cover (%) ~ Kelp density + Seawater temperature + Wave exposure + Grazer abundance ($n = 69$)				0.36
Term	Estimate	95% CI	p	
Kelp density	0.9505	0.2940 – 1.607	0.0046	
Seawater temperature	1.218	0.2494 – 2.186	0.0137	
Wave exposure	-0.8815	-2.548 – 0.7853	0.2999	
Grazer abundance	1.649	-0.8778 – 4.175	0.2009	
b) Bryozoan cover (%) ~ Kelp density + Seawater temperature + Wave exposure + Grazer abundance ($n = 185$)				0.33
Term	Estimate	95% CI	p	
Kelp density	0.7163	0.3302 – 1.102	0.0003	
Seawater temperature	0.7709	0.2287 – 1.313	0.0053	
Wave exposure	-0.9230	-1.734 – -0.1116	0.0258	
Grazer abundance	-0.1704	-1.697 – 1.356	0.8268	

Table A1.2. Examining the effects of site (fixed factor, 9 levels) and year (fixed factor, 2 levels: 2020, 2021) on the size (m² area, square-root transformed) and density (% canopy cover) of kelp beds on the Central Coast and in Barkley Sound using 2-way ANOVA and likelihood ratio tests of beta regression models, respectively. Results of planned contrasts between years for each site are included with the direction of the mean difference indicated. Only significant differences in post hoc tests are shown ($\alpha = 0.05$). *This table shows results depicted in Figures 4 & 5 of the main report.*

Bed Area	MS	F _(df)	<i>p</i>	
Site	20609	104.9 ₍₈₎	<0.0001	
Year	6736	34.29 ₍₁₎	<0.0001	
Site x Year	1701	8.66 ₍₈₎	<0.0001	Spider, Simmonds, Helby, Grappler, Dodger: 2020 > 2021
Error	196			
Kelp Density		X ² _(df)	<i>p</i>	
Site		2168 ₍₈₎	0.0002	
Year		2222 ₍₁₎	<0.0001	
Site x Year		30.35 ₍₈₎	<0.0001	Larkin: 2020 < 2021 Spider: 2020 > 2021 Helby: 2020 > 2021

Table A1.3. Results of likelihood ratio tests for ordinal regression models examining differences in the seasonal timing (day-of-year, DOY: 1-365) and amount (% cover) of bryozoan on giant kelp (6 cover categories: 0%, >0–5%, >5–20%, >20–40%, >40–60%, >60–80%) between survey years (fixed factor, 2 levels: 2020, 2021) for the Central Coast. Kelp density did not differ between years ($t_{(187)} = 0.757$, $p = 0.450$) and there was no significant correlation between day-of-year and kelp density for either year (VIF <10, 2020: $r = 0.13$, $t_{(86)} = 1.17$, $p = 0.246$; 2021: $r = -0.19$, $t_{(99)} = -1.96$, $p = 0.053$). Therefore kelp density was not considered a confounding factor and was excluded in favour of simplified models to directly test our hypothesis that the seasonal dynamics of bryozoan cover on kelp differed between years. Models were constructed using a logit link function and with year as a scaled effect. Significant *p*-values shown in bold. Δ AICc compares reduced models where each corresponding model term has been dropped to the full model shown in bold. *This table shows results depicted in Figure 6 of the main report.*

Model	Δ AICc	LR stat (X ²) _(df)	<i>p</i>
Bryozoan Cover ~ DOY + Year + DOY:Year	0		
Dropped Term			
Year	9.1	0.7019 ₍₁₎	0.4021
DOY x Year	10.4	12.38 ₍₁₎	0.0004
DOY	14.2	5.837 ₍₁₎	0.0157

Appendix 2: Photographs of Bryozoan on Collected Giant Kelp Blades

In addition to visual measurements of the % coverage of kelp with bryozoan growing on it, bryozoan cover on kelp was also measured from photographs of giant kelp blades (~25 per site) collected during each survey using image analysis software (ImageJ). Bryozoan cover on individual kelp blades ranged from 0% to 100% and was averaged across all kelp blades ($n \sim 5$) collected from each location point at a given site during each survey. Bryozoan cover measured from photographs of kelp blades tended to underestimate visual measurements of bryozoan cover for surveys at all sites in both 2020 and 2021 (Figures A2.1, A2.2). This discrepancy between methods for measuring bryozoan cover may be due to a combination of logistical and biological challenges related to collecting and photographing giant kelp blades with bryozoan growing on them. Logistically, it was difficult to detect small colonies of bryozoan in the photographs even if they occurred at high densities resulting in high percent cover of bryozoan on kelp blades. During field surveys in 2020, Guardians found that holding collected kelp blades underwater when photographing them made small bryozoan colonies easier to detect in the photographs (Figure A2.3b). Accordingly, methods for photographing collected kelp blades were adapted in 2021 to include the option of photographing blades in plastic tote bins filled with seawater (Figure A2.3c-d). However, bryozoan cover measured from photographs of collected kelp blades still underestimated visual measurements for surveys at all sites in 2021 (Figure A2.2). This could reflect the biological consequences of high bryozoan cover on kelp blades. Heavy encrustation by bryozoans weighs down kelp blades and weakens kelp tissue causing blades to sink below the surface and become more prone to disintegrating during the collection process (Heiltsuk Guardian Doug Newman, personal communications; Figure A2.4). Consequently, it is difficult to collect intact giant kelp blades with high bryozoan cover to photograph. Additionally, the patchy distribution of bryozoan on kelp, ranging from 0 – 100% cover on blades within the same kelp bed, is better captured by visual measurements of the amount (%) of kelp with bryozoan growing on it at larger scales (2-meter radius circle off the bow of the boat) than by photographs of selected kelp blades.

For these reasons, we chose to use visual measurements of the percent cover of bryozoan on kelp in all analyses as a more accurate estimate of the amount of kelp within a kelp bed that had bryozoan growing on it. However, photographs of bryozoans on kelp blades were useful for identifying the species of bryozoan present. In addition to bryozoans of the genus *Membranipora*

(Figure A2.3a,d), *Celleporella hyalina*, a species that forms smaller colonies and grows more slowly than *Membranipora* spp., was also found at most sites (Figure A2.3b,c).

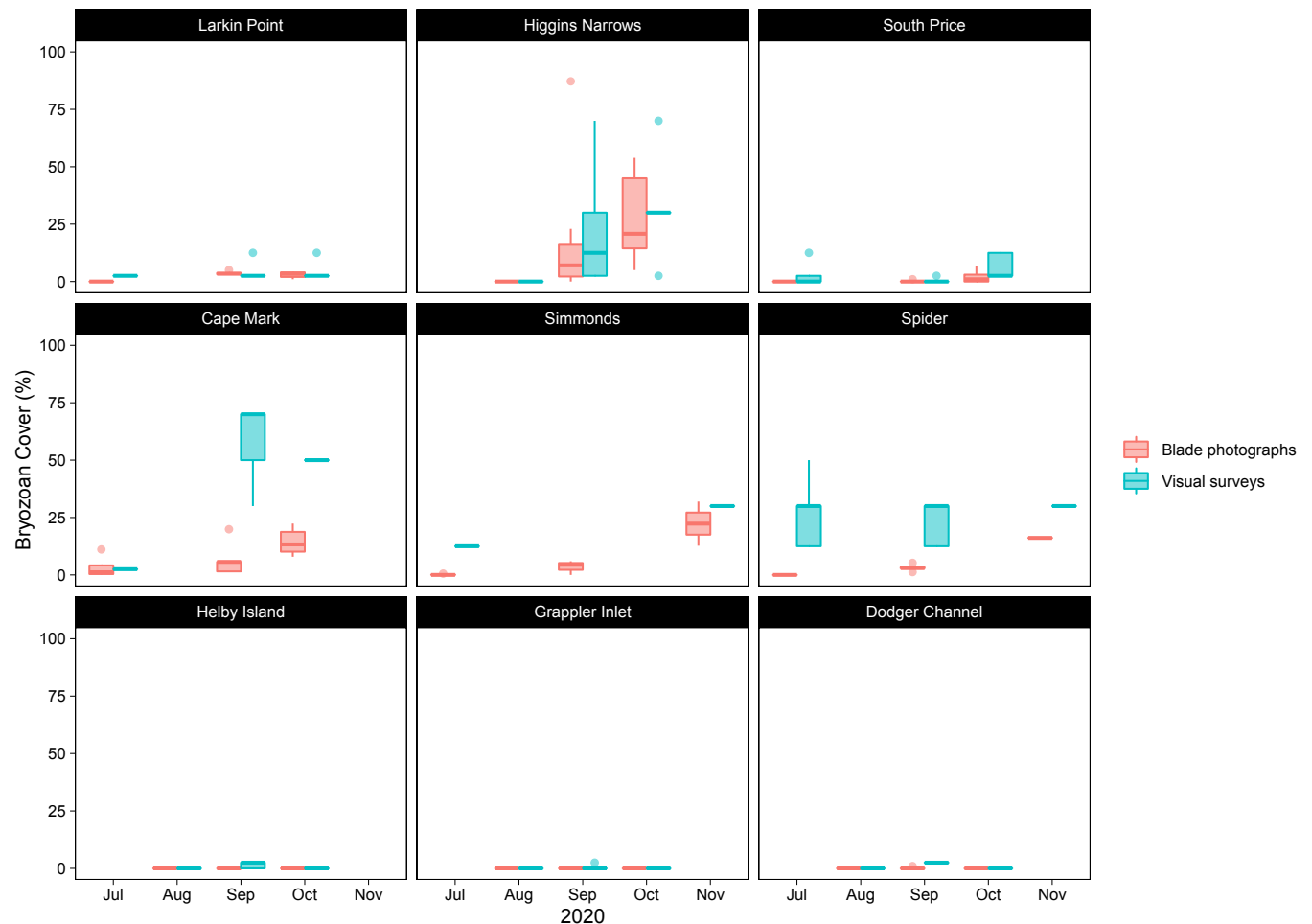


Figure A2.1. The amount of bryozoan cover (% , pooled across all visual measurements and photographs of collected kelp blades per site) measured on giant kelp during approximately monthly surveys of kelp beds at 9 sites in 2020 from visual measurements within a 2-meter radius circle off the bow of the boat (visual surveys, $n = 5$) and image analysis of photographs taken of collected giant kelp blades (blade photographs, $n \sim 25$).

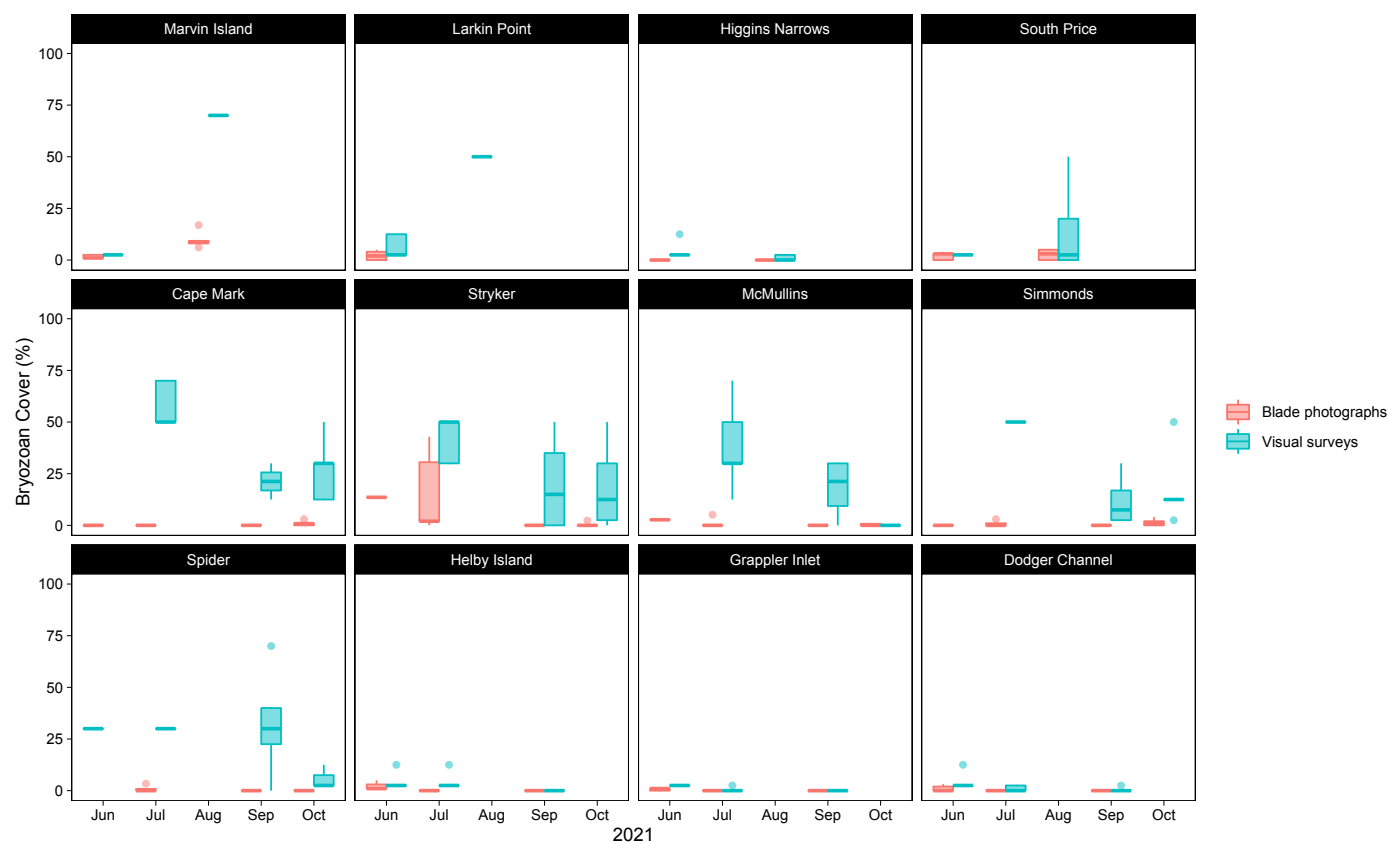


Figure A2.2. The amount of bryozoan cover (% , pooled across all visual measurements and photographs of collected kelp blades per site) measured on giant kelp during approximately monthly surveys of kelp beds at 12 sites in 2021 from visual measurements within a 2-meter radius circle off the bow of the boat (visual surveys, $n = 5$) and image analysis of photographs taken of collected giant kelp blades (blade photographs, $n \sim 25$).

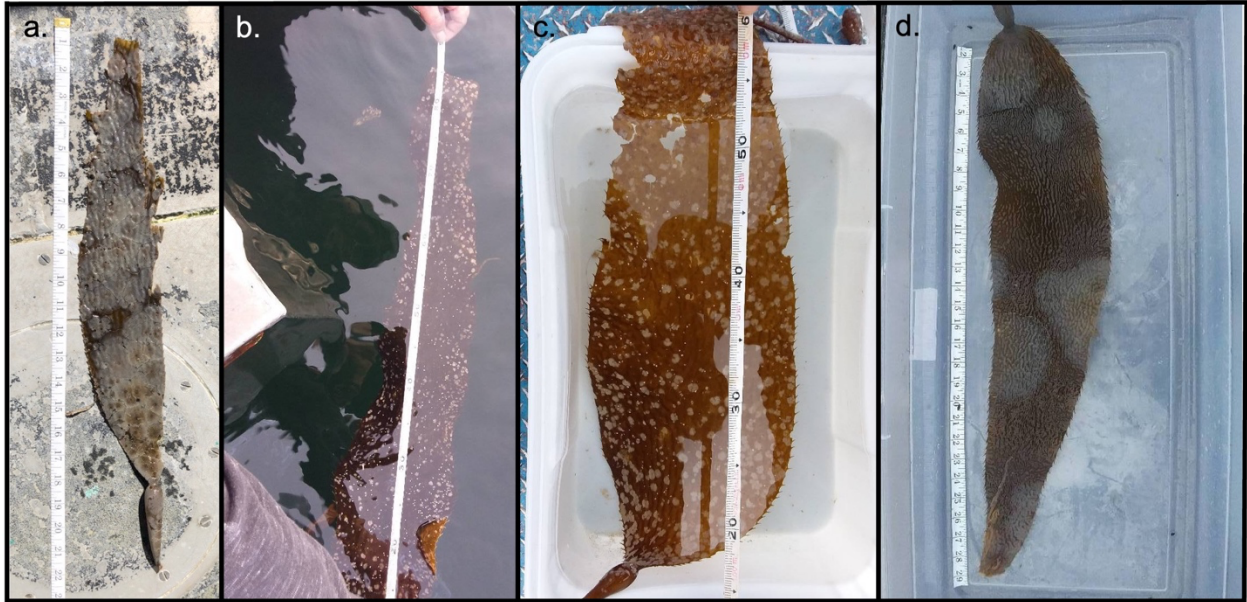


Figure A2.3. Example photographs of bryozoan on collected giant kelp blades. a) *Membranipora* spp. on a giant kelp blade during surveys in 2020, b) *Celleporella hyalina* on a giant kelp blade held underwater during surveys in 2020, c) *Celleporella hyalina* and d) *Membranipora* spp. on a giant kelp blade placed in a tote bin filled with seawater during surveys in 2021.

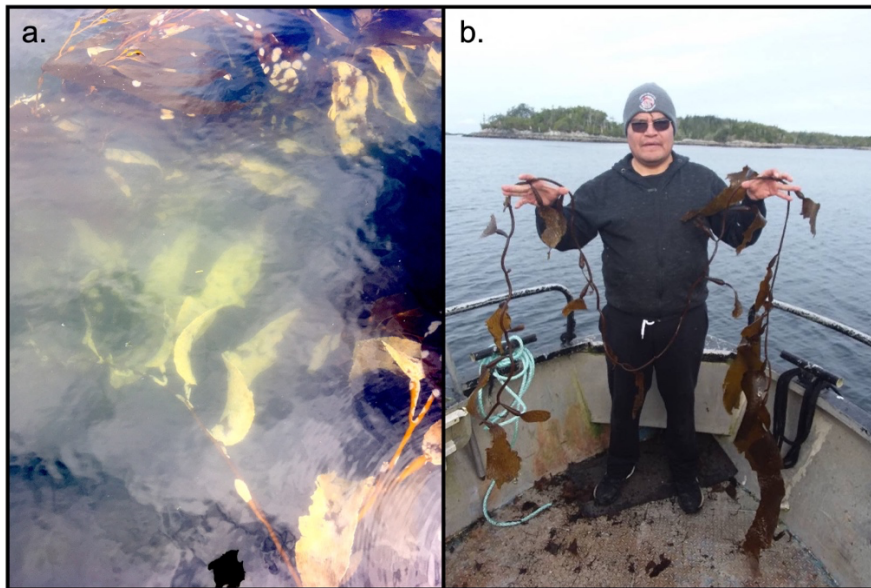


Figure A2.4. a) Giant kelp blades heavily encrusted with bryozoan that have sunk below the surface (photo: Tory Prichard). b) Heiltsuk Guardian Doug Newman holding up a giant kelp frond with blades that have disintegrated or melted during collection.

Chapter 2: Grazing by Kelp Crabs Amplifies Impacts of Bryozoans on Kelp

Background

Shifting relationships between grazers, epiphytes like bryozoans, and kelp are determined in part by the feeding mechanism and behavior of the grazer and can have impacts on kelp persistence and recovery (Steneck & Watling 1982). In the bryozoan's invaded habitat in the northwest Atlantic, *Lacuna* snails preferentially consumed non-encrusted kelp, acting synergistically with the bryozoan to reduce the structural integrity of kelp tissue and increase loss of kelp (Krumhansl et al. 2011; O'Brien et al. 2013, 2015). Thus, grazers have the potential to magnify the negative impacts of bryozoans on kelp. However, bryozoan cover may also reduce kelp loss due to grazing if it acts as a mechanical barrier to grazing (Durante and Chia, 1991).

To complement Nation-led surveys of bryozoan and kelp along the Central Coast, we conducted manipulative grazing experiments to assess whether the predominant grazers found in kelp canopies mitigate or exacerbate the impacts of bryozoan outbreaks on native kelp forest communities. We focused on the two dominant mesograzers observed in the kelp canopy, northern kelp crabs (*Pugettia producta*, hereafter kelp crabs) and dusky turban snails (*Tegula pulligo*, hereafter turban snails). Due to differences in feeding mechanisms between these two grazer species (Steneck & Watling 1982; Hiebert & Burgess 2015), we hypothesized that bryozoan-grazer interactions would be species-specific, but that rates of kelp loss would generally increase with increasing grazer biomass and sea surface temperature (Gillooly et al. 2001; Brown et al. 2004). We further hypothesized that increasing bryozoan cover would result in either increased or decreased rates kelp loss because bryozoans provide either enhanced nutritional value (Nestler and Harris 1994; Knip and Scheibling 2007) or a mechanical barrier to consumption (Durante and Chia, 1991), respectively.

Methods

We conducted field experiments in two kelp beds in Barkley Sound, BC, during August and October of 2020 (Figure 1A, B). Two different types of kelp were studied, stiff-stiped kelp (*Laminaria setchellii*) and giant kelp (*Macrocystis pyrifera*). Sites were selected to span a spatial gradient in summer sea surface temperature (SST) of 2°C (Figure 1B). We caged kelp blades

under the following grazer treatments: (1) kelp crab present (1 individual; Figure 1C); (2) turban snails present (varying number of individuals (1 – 20); Figure 1D); (3) control (no grazers present; Figure 1E). Cages were suspended at the surface within the kelp bed at each study site (Figure 1C-E). We measured sea surface temperature over the duration of our experiments using temperature loggers attached to the cages. We weighed and photographed kelp blades before and after the experiments to measure relative loss of kelp biomass (g) and change in bryozoan cover (cm^2) over time.

To examine effects of bryozoan cover and grazer species on rates of kelp loss, we caged blades of stiff-stiped kelp with varying levels of bryozoan cover (0 – 68 %) under all grazer treatments at both of our study sites for 4 days in October 2020. We used blades of stiff-stiped kelp because they were the only available species of kelp at the time with enough bryozoan cover for our experiment. However, both giant kelp and stiff-stiped kelp are brown algae that are readily consumed by grazers, therefore the effects of bryozoan cover and grazers on stiff-stiped kelp blades likely apply also to giant kelp blades. All grazer treatments captured a similar range of initial bryozoan cover on kelp blades. Seawater temperature did not differ significantly between our study sites during this experiment period.

To test the effects of temperature, grazer species and grazer biomass on rates of kelp loss, we caged blades of giant kelp with no bryozoan cover under all grazer treatments at both of our study sites for 7 days in August of 2020. We averaged temperature over the experimental period to determine the mean sea surface temperature (SST) at each site. Our two study sites differed by 2°C on average, effectively acting as one warm and one cool temperature treatment (site 1 “warm”: mean SST \pm SD = $17.77 \pm 1.08^\circ\text{C}$, site 2 “cool”: mean SST \pm SD = $15.53 \pm 0.69^\circ\text{C}$; see Figure 3B).

The August and October experiments were designed and analyzed separately to determine the relative effect of each unique driver, bryozoan cover and mean temperature, on grazer-mediated kelp loss over the experimental period. We also compared bryozoan cover on kelp blades before and after the two grazer species treatments to determine whether grazers had a detectable impact on the amount of bryozoan cover.

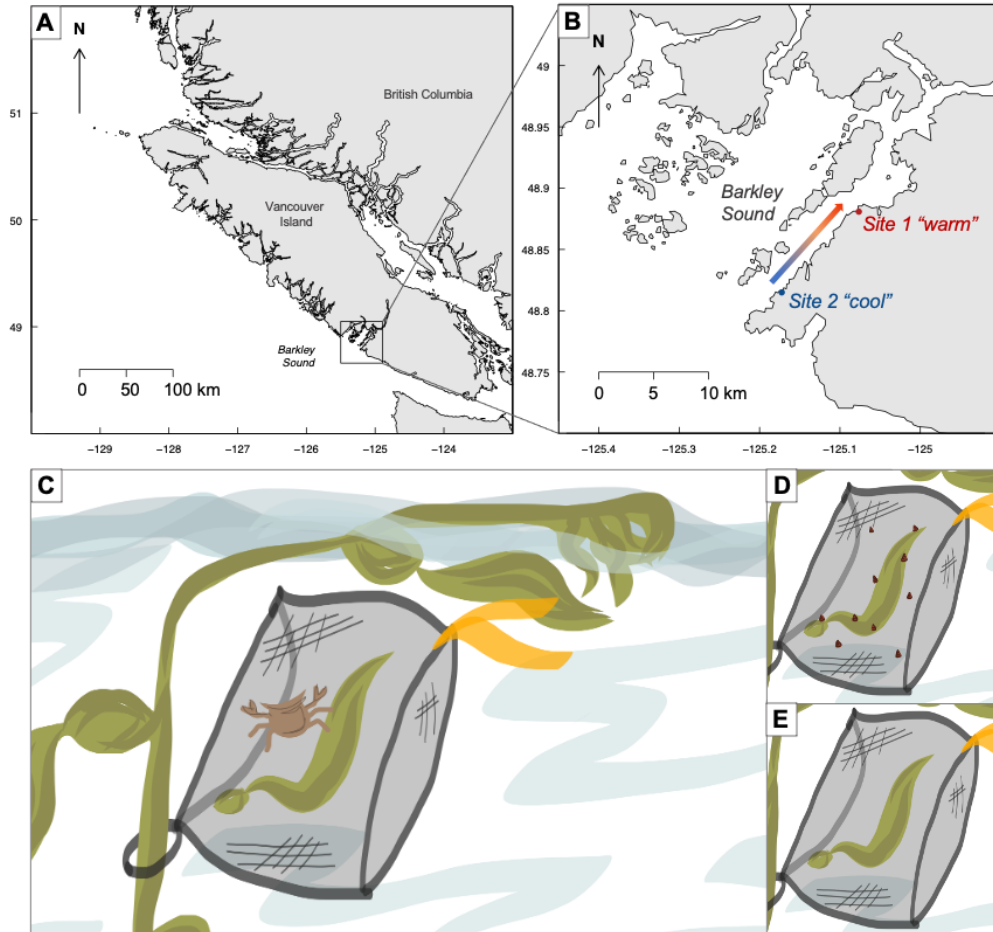


Figure 1. The relationships between bryozoan, grazers and kelp were explored in (A) Barkley Sound, on the west coast of Vancouver Island at (B) two sites spanning a gradient in summer sea surface temperatures of 2°C (shaded arrow: blue indicates cooler temperatures, red indicates warmer temperatures), through field experiments under grazer species treatments: (C) kelp crab present, (D) turban snails present, and (E) control (no grazers present).

Results

Bryozoan cover magnifies the effect of kelp crab grazers on kelp loss

The effect of bryozoan cover on rates of kelp loss depended on the species of grazer present. Relative rates of kelp loss increased with increasing bryozoan cover in the presence of kelp crabs but not of snails (Figure 2). Additionally, grazer species impacted bryozoan cover differently, with cover decreasing significantly in the presence of kelp crabs but not turban snails (see Figure A2 in Thesis).

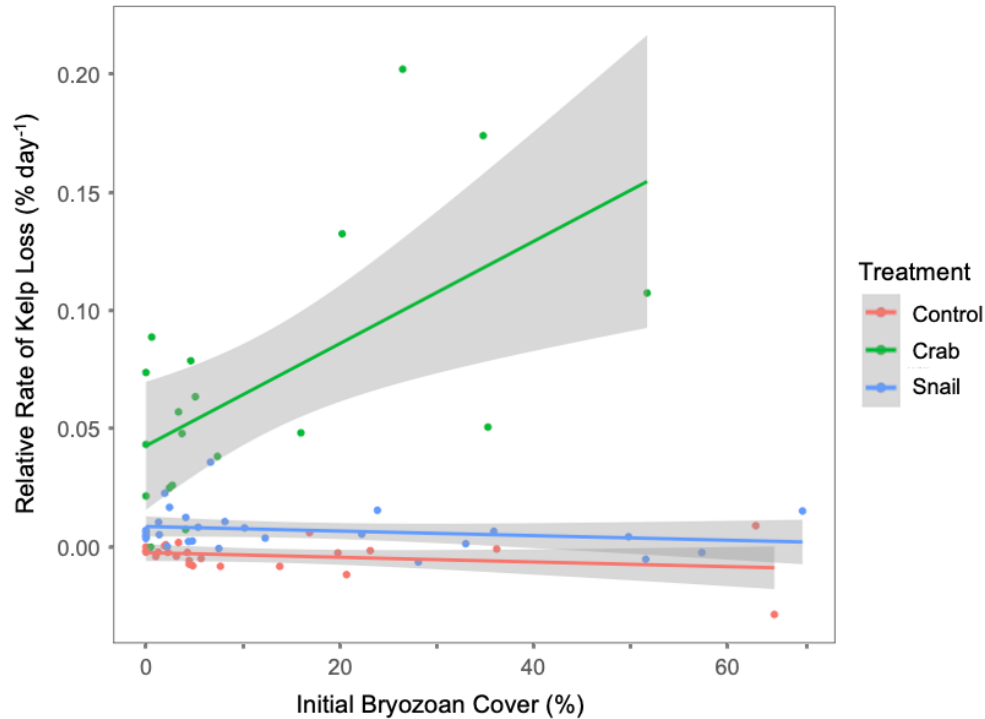


Figure 2. Interacting effects of bryozoan percent cover and grazer species on rates of kelp loss. Solid coloured lines correspond to each treatment group (Control, Crab, Snail), with 95% confidence intervals indicated by gray shading

Ocean temperature had a significant but weak effect on kelp loss

The rate of kelp loss increased significantly with increasing crab biomass, regardless of temperature (Figure 3A). However, the rate of kelp loss in the presence of kelp crabs was reduced at the site with warmer seawater temperature (Figure 3A). While statistically significant, uncertainty associated with the temperature effect was high, as indicated by the overlapping confidence intervals (Figure 3A). Under the snail treatment, neither mean seawater temperature, total snail biomass nor their interaction significantly affected rates of kelp loss. Importantly, no change in kelp biomass was observed in the control (no grazer) treatment, indicating that any observed kelp loss in our grazer treatments was likely the result of grazing behaviour.

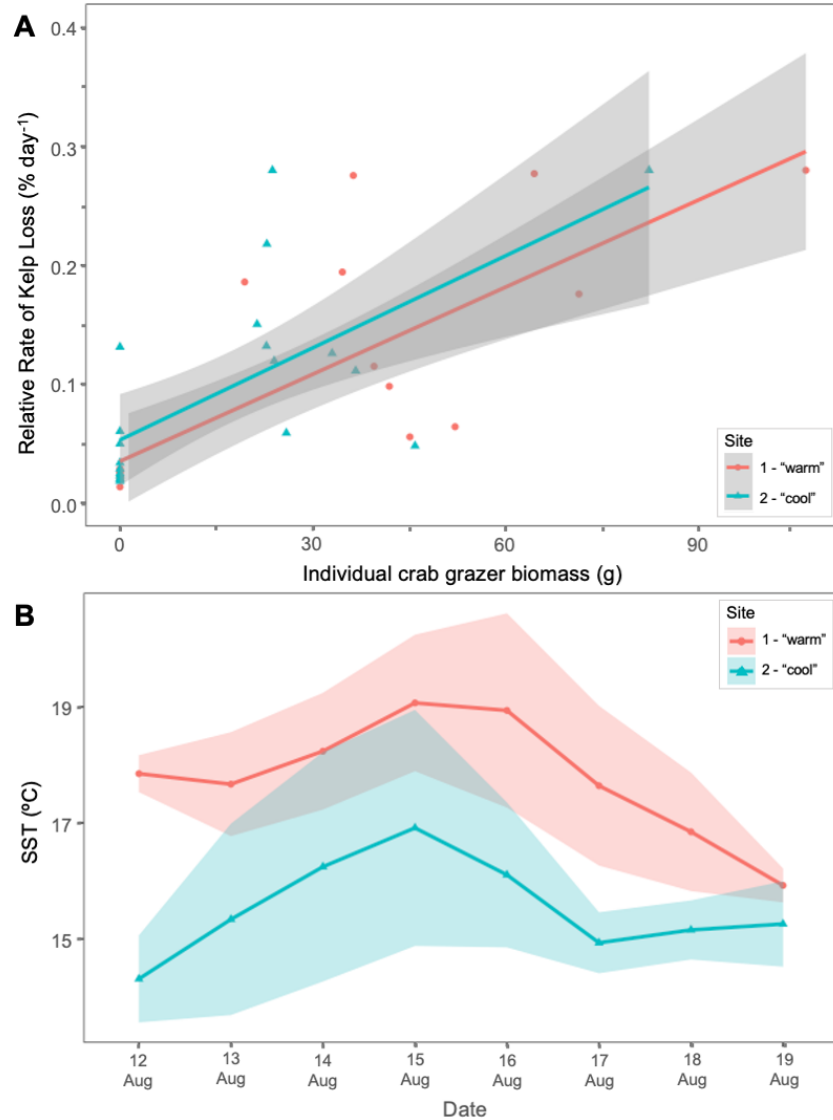


Figure 3. (A) Relative rate of kelp loss due to grazing by crabs as a function of individual crab biomass and site (as a proxy for mean sea surface temperature) with 95% confidence intervals indicated by gray shading. (B) Daily mean sea surface temperature (SST) (line) \pm SD (shaded ribbon) experienced at each experimental site in August.

Discussion

This study illustrates how indirect effects of climate change on northeast Pacific kelp forests, in particular increasing bryozoan outbreaks, can be magnified by species interactions in the ecosystem. Specifically, rates of kelp loss increased with greater bryozoan cover when kelp crab grazers were present (Figure 2). In addition, bryozoan cover decreased significantly in the presence of kelp crabs (See Figure A2 in Thesis). There are two mechanisms that could explain

the observed impact of kelp crabs: (1) kelp crabs preferentially consume bryozoan covered kelp (Nestler and Harris 1994, Levin et al. 2002, Knip and Scheibling 2007); and (2) the bryozoan cover softens kelp tissue making it easier to consume and/or more likely to disintegrate during grazing leading to incidental loss (Krumhansl et al. 2011). Bryozoans may provide nutritional benefits to grazers if they are physically able to consume them, causing some grazers to target bryozoan-covered kelp (e.g., green sea urchins, Levin et al. 2002). For other grazers, bryozoan cover can act as a mechanical barrier that inhibits their consumption of kelp (e.g., *Tegula* snails, Durante and Chia 1991). Further choice experiments will be needed to determine if there is any preferential consumption by kelp crabs.

Regardless of the specific mechanisms, our results reveal that the rates of kelp loss depend on the species of grazer present. In this case, turban snails did not have any detectable effect on bryozoan cover or rates of kelp loss (see Table 1C, Figure A2 in Thesis), and therefore have weaker grazing effects at the scale of a kelp blade compared to kelp crabs. This was consistent under both temperature treatments and across the range of snail densities we investigated (1-20 snails per kelp blade), which approximated densities observed in field surveys. The observed species-specific impacts to kelp loss may be best explained by differences in species' feeding mechanisms and anatomy (Steneck and Watling 1982), as well as body size (Gillooly et al. 2001, Brown et al. 2004).

Generally, warmer temperatures increase metabolic rates and therefore are expected to increase grazing rates (O'Connor 2009; Carreira et al. 2020; Gilson et al. 2021). However, we found that warmer ocean temperatures (+ 2°C) were weakly associated with lower rates of kelp loss in the presence of kelp crab grazers (Figure 3A; see Table 1B, C in Thesis), which is inconsistent with prior studies (Brown et al. 2014, Gilson et al. 2021, O'Connor 2009). The weak response of kelp crabs, or lack of response in the case of snails, may be because these organisms are accustomed to the 2°C temperature difference (15 to 17°C) they experienced during our experiments, given that such fluctuations are within the natural temperature range experienced by organisms in this temperate region across the depth range they inhabit or over a tidal cycle (Pawlowicz 2017; see Figure 3B for daily mean SST and variation during the experimental period in August 2020).

While warmer ocean temperatures during our experiments did not directly increase rates of kelp loss through grazing, there is strong evidence that increasing ocean temperatures are

expected to result in increased cover of bryozoan on kelp (Chapter 1). Given that we detected increased rates of kelp loss with greater bryozoan cover when kelp crab grazers were present, increased bryozoan cover may indirectly amplify kelp loss through grazing by kelp crabs. We therefore suggest that at the scale of a kelp blade, kelp crabs can exacerbate the impacts of climate induced bryozoan outbreaks, however, this relationship does not apply to all grazers (e.g., snails, Figure 4).

It is possible that the effects of kelp crabs will have greater or differential impacts beyond those revealed by these experiments. For example, beyond the level of the kelp blade, kelp crabs could have a net positive effect on kelp forests by effectively “pruning” bryozoan-covered kelp. Depending on the extent of cover, this may indirectly facilitate the growth of new fronds and of other kelp individuals by redirecting of energy towards new growth and reproduction and allowing more sunlight to reach the seafloor (Kimura and Foster 1984, Dayton et al. 1984, Krumhansl et al. 2017). This has been seen in other cases on the Central Coast where moderate reduction of canopy cover of giant kelp and feather boa kelp (*Egregia menziesii*) through harvest led to increased growth and recovery (Krumhansl et al. 2017, Kobluk et al. 2021). Larger-scale studies and continued monitoring with grazer species-specific counts are needed to understand the combined impacts of bryozoan encrustation, warming ocean temperatures and canopy grazer interactions at broader ecological scales of kelp beds and kelp seascapes.

Overall, this work provides locally relevant insights into key species interactions that can affect rates of kelp blade loss. This has implications for predicting kelp availability and, consequently, viability to support cultural and commercial uses of kelp by the Central Coast Nations (Figure 4). The results of this study reveal that kelp crab grazers can influence rates of kelp blade loss, especially when experienced in combination with increasing bryozoan cover (Figure 4). These findings emphasize how grazers can amplify the indirect effects of climate change and are therefore key considerations when predicting changes to marine ecosystems in the face of ongoing warming of temperate oceans.

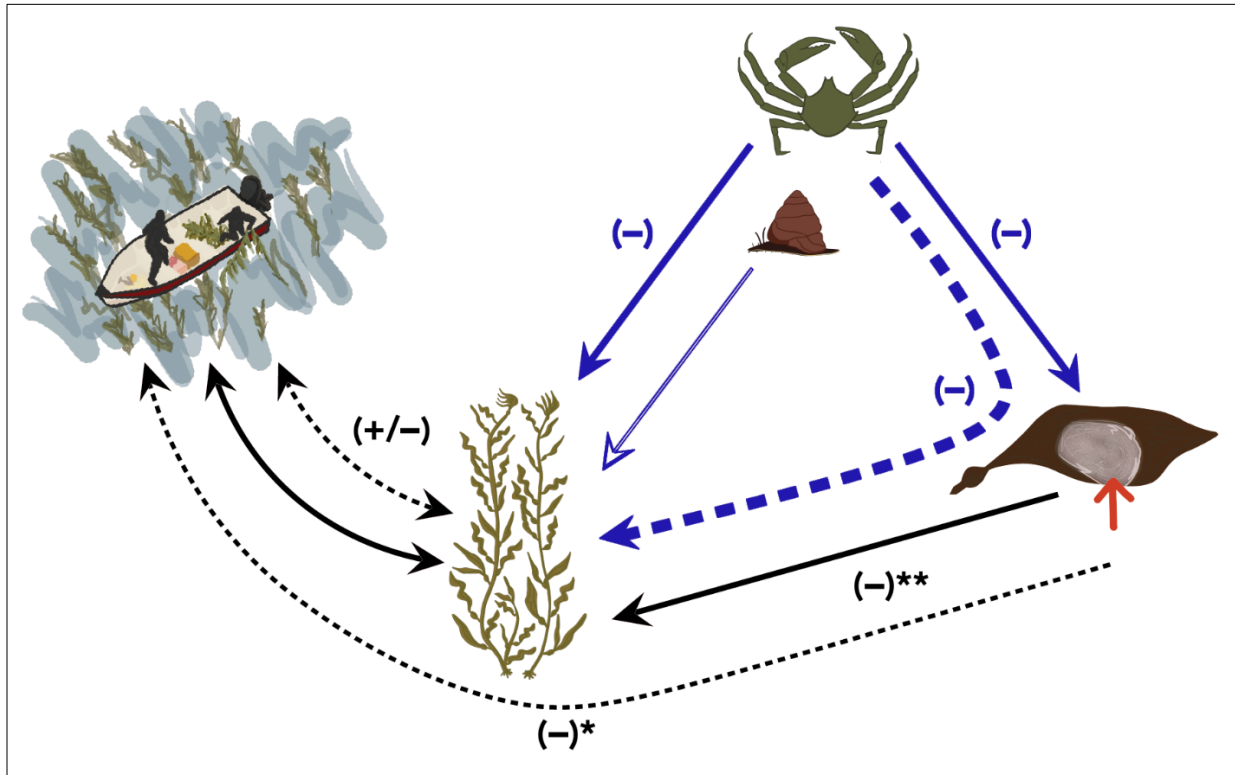


Figure 2. Conceptual model of interactions tested by this study (blue arrows) or hypothesized (black arrows). Species-interactions (kelp crabs and turban snails) with kelp and bryozoan on kelp (red arrow) are, in part, determined by grazer size and feeding mode. Bryozoan cover has a direct negative effect on kelp quality (**Chapter 1) and therefore an indirect effect on people and kelp harvests (*as shared by Central Coast First Nations during the initial workshop). Direct (solid lines) and indirect (dashed lines) interactions vary in relative strength (strong = thick lines, weak = thin lines) and direction (+ positive, - negative).

Conclusions

Bryozoan cover can increase rates of kelp blade loss due to grazing, but this relationship does not apply to all grazer species. To understand how specific grazer species may affect loss and recovery of kelp beds in response to bryozoan outbreaks will require further investigation beyond the scale of a single kelp blade, including field surveys of bryozoan and kelp that quantify species-specific grazer abundances (rather than total number of grazers pooled across species). Overall, our experimental observations of an interaction between bryozoan cover and kelp crab grazers elevate the importance of ecosystem-based approaches to management. Continued consideration of the many species within kelp forest systems and their interactive effects can contribute to a holistic planning approach in response to climate change.

Acknowledgments

First and foremost, we would like to thank the Coastal Guardian Watchmen past, present and future for their critical ongoing observations that initiated this research. Specifically, we would like to thank Doug Newman, Max Johnson Jr., Jeff Brown, Carl Wilson, Walter Campbell (Heiltsuk Guardians), Sandie Hankewich, Ernie Mason (Kitasoo/Xai'xais Fisheries), Bo O'wadi, and Adam Nelson (Wuikinuxv Guardians), as well as Christina Service (KXIRA) and Tristan Blaine (CCIRA) for conducting field surveys and providing continued guidance and support throughout this project. We would like to thank CCIRA, the Stewardship Directors and Staff of its member Nations: the Heiltsuk, Kitasoo/Xai'xais, Wuikinuxv, and Nuxalk Nations, for guidance, support and input on this research. We are especially grateful to Mike Reid, Sandie Hankewich, and Desiree Lawson, as well as Michael Vegh (Heiltsuk Nation) for sharing their insight and perspectives and providing feedback on this work. We would also like to thank the team at Bamfield Marine Sciences Centre (BMSC), especially Tao Eastham, Siobhan Gray, Tory Pritchard and Tom Campbell, for assisting in field surveys and facilitating manipulative experiments. In addition, thank you to members of SFU's Coastal Marine Ecology Lab Heather Earle and Kelsey Miller for their assistance conducting the manipulative experiments out of BMSC. Finally, we would like to thank the Pacific Institute for Climate Solutions (PICS), the Marine Environmental Observation, Prediction and Response Network (MEOPAR) and Simon Fraser University for providing the funding and in-kind support needed to complete this project.

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