Monthly macroalgal surveys reveal a diverse and dynamic community in an urban intertidal zone

Author information

Siobhan Schenk[1,2,5], sschenk@mail.ubc.ca, ORCID 0000-0003-0572-9303
Varoon P Supratya[1,2], varoonp@student.ubc.ca, ORCID 0000-0002-2891-0335
Patrick T Martone[2], pmartone@mail.ubc.ca, ORCID 0000-0002-6345-1023
Laura W Parfrey[2,3,4] lwparfrey@botany.ubc.ca, ORCID 0000-0001-6959-7616

1. Co-first
2. Biodiversity Research Center, Department of Botany, University of British Columbia, 6270 University Blvd, Vancouver, British Columbia V6T 1Z4, Canada
3. Biodiversity Research Center, Department of Zoology, University of British Columbia, 6270 University Blvd, Vancouver, British Columbia V6T 1Z4, Canada
4. Hakai Institute, PO Box 25039, Campbell River, British Columbia V9W 0B7, Canada
5. Corresponding author

Abstract

Historical baseline data are critical to measuring how communities shift in response to climate change and anthropogenic activity. Macroalgae are marine foundation species that are vulnerable to climate change, but there is a lack of baseline macroalgal biodiversity data for many areas of British Columbia, particularly at a high temporal resolution over years. This presents an obstacle for measuring how communities change in response to shifting average conditions as well as after extreme events, such as the 2021 heat dome. To increase baseline macroalgae biodiversity data in British Columbia, we established a monthly transect-based macroalgal survey in 2021 at an urban intertidal site with a survey protocol that is low cost and easy to replicate. Our datasets and our survey protocol are freely available. Over 35 months we have recorded 59 species of macroalgae, including the canopy forming kelp *Nereocystis luetkeana* and the non-native fucoid *Sargassum muticum*. Surveying throughout the year at regular intervals has revealed large-scale seasonal shifts in macroalgal community composition, timing of kelp recruitment, and a decrease in abundance of *Fucus distichus* in the upper intertidal zone over multiple years. Our publicly accessible data constitute the most comprehensive survey of intertidal macroalgal diversity in Burrard Inlet, illustrating how simple surveying methods can provide high resolution records of macroalgae biodiversity, particularly in easily accessible urban environments.

Key words

Macroalgae, Seaweed, Urban Ecology, Long-Term Survey, Biodiversity monitoring, Phenology, Monthly Sampling, British Columbia, Baseline data, Invasive species

Introduction

Marine macroalgae (seaweeds) are highly diverse and globally distributed foundation species. Macroalgae create habitat for other organisms (Steneck et al. 2002; Teagle et al. 2017), physically and chemically modify their surrounding environment (Pfister et al. 2019), and support higher trophic levels through primary production (Dayton 1985; Mann 1973). Macroalgae are also economically valuable, contributing 500 billion USD per year to the global economy, through ecosystem services, wild harvesting, and mariculture (Eger et al. 2023). Macroalgae are sensitive to changing environmental conditions, including those resulting from anthropogenic activity (Bindoff et al. 2019; Harley et al. 2012; Harley and Paine 2009). Rising average and extreme sea and air temperatures are the most pervasive anthropogenic impacts on the global biosphere (Lima and Wethey 2012; Parmesan and Yohe 2003; Poloczanska et al. 2013). However, pollution (Vergés et al. 2020), sediment runoff (Blain et al. 2021), eutrophication (Ducrotoy 1999), and invasive species (Salvaterra et al. 2013; Casas et al. 2004) are additional major sources of anthropogenic stress. These stressors all interact to affect macroalgal growth, reproduction, and survival (Breeman 1988; Davison and Pearson 1996; Harley et al. 2012; Helmuth et al. 2006), which in turn alters local intertidal range limits (Harley et al. 2012; Harley and Paine 2009; Helmuth et al. 2006), and global distribution (Andersen et al. 2013; Johnson et al. 2011; Steneck et al. 2002; Wernberg et al. 2010; Helmuth et al. 2006).

Shifts in macroalgal biodiversity brought on by climate change and other anthropogenic stressors are likely to have disproportionately large impacts on ecosystem function, such as reduced ecological facilitation (Halpern et al. 2007), habitat loss (Lilley and Schiel 2006), and trophic cascades (Rogers-Bennett and Catton 2019). Quantifying the effects of anthropogenic

stress on macroalgae requires documenting baseline diversity and long-term monitoring to track changes in macroalgal communities over time (Bates, Saunders, and Chopin 2009; Lindstrom et al. 2021). However, macroalgae remain understudied in comparison to other ecologically important groups (Harley et al. 2012; Wernberg, Smale, and Thomsen 2012), and comprehensive baselines are lacking in many regions (Bringloe and Saunders 2019; Mineur et al. 2015). The lack of macroalgal baseline data was apparent in British Columbia (BC) following the July 2021 heat dome, which subjected exposed intertidal organisms to temperatures of 43°C or higher in BC (White et al. 2023). With the available baseline data for intertidal invertebrates, heat dome mortality rates of over 70% could be estimated for mussels and barnacles (White et al. 2023), yet baseline data to make analogous assessments for local macroalgae were lacking despite anecdotally observed mass die-offs

In BC, macroalgal communities have often been surveyed along remote, relatively exposed coastlines. Notable macroalgal surveys have occurred on Calvert Island (Whalen et al. 2023), the West coast of Vancouver Island (Starko et al. 2019), Haida Gwaii (Levings and Stewart 2020), and the Gulf islands (Demes et al. 2012; Lindstrom 1973). In comparison, the published literature on macroalgal communities near urbanized regions is more limited, even though these areas experience comparatively greater levels of anthropogenic stress, including pollution, sedimentation, sedimentation, abiotic extremes, and invasive species (Vergés et al. 2020; Blain, Hansen, and Shears 2021; Ducrotoy 1999; Heery et al. 2018; Todd et al. 2019). A previous study in Howe Sound (Wonham et al. 2023), which has experienced extensive industrial activity, combined historical datasets and two sampling events from June to July in 2015. Another study in Burrard Inlet documented the diversity and phenology of kelps in 1969 and 1970 but did not record other macroalgae (Druehl and Hsiao 1977).

Addressing this knowledge gap, we initiated a macroalgal monitoring program in September 2021 at an intertidal site in Burrard Inlet, located in southern British Columbia. The highly urbanized character of Burrard Inlet was intended as a comparison to more isolated regions in BC to understand the impacts of intense anthropogenic stress on macroalgae. Furthermore, the accessibility of Burrard Inlet compared to more isolated study sites made it amenable to high-frequency year-round surveying, facilitating the detection of subtle phenological shifts and seasonal changes in species composition. Our goal was to establish a comprehensive baseline dataset of: *(i)* Overall diversity of intertidal macroalgae at the site, (ii) Abundance of any possible invasive species, such as *Sargassum muticum*, *Mazzaella japonica*, or *Undaria pinnatifida*, *(iii)* Spatial patterns of macroalgal diversity across the intertidal gradient, and *(iv)* Intra and interannual shifts in diversity and phenology of conspicuous algae.

Methods

Survey site

In September 2021, we started conducting monthly intertidal vertical transect-based macroalgal biodiversity surveys near the Girl in a Wetsuit statue (GW) in Stanley Park, Vancouver, BC, Canada (49.3027, -123.1265; Figure 1). GW is located in the First Narrows region of Burrard Inlet, which is heavily urbanized and located near Downtown Vancouver and the Port of Vancouver, Canada's largest port (Cargo and Terminals 2015). While comparatively undeveloped, Stanley Park has also been subject to extensive shoreline modification, and experiences substantial foot, bicycle, vehicle, and equine traffic. Water flow in Burrard Inlet has been significantly impacted by development (Tsleil-Waututh Nation 2017). The First and Second

Narrows experience cooler and more saline surface waters than in the remainder of Burrard Inlet due to turbulent mixing as tidal flows pass through these constrictions (Davidson 1973). This difference in salinity is particularly evident in the spring, when the freshwater outflow from nearby major rivers is greatest, emptying directly into Burrard Inlet (Neilson-Welsh 1999). The side of Stanley Park where GW is located maintains salinities above 20 ppt, while nearby regions drop as low as 10 ppt (Ryan et al. 2019; Druehl and Hsiao 1977). The intertidal zone at GW consists of a near vertical seawall over a gently sloping beach of mixed cobble interspersed with occasional large boulders. The beach extends up to 95 m from the seawall when low tide reaches 0 m chart datum (Fig. 1).

Survey design

Our survey methodology was designed to be low cost and easy to replicate, while maximizing the chances of capturing changes in intertidal macroalgal communities over time, particularly distributional and phenological shifts that are expected to occur in response to climate change. The accessibility of GW permits a high-frequency monthly survey design that provides increased phenological resolution, which is critical because phenological shifts tend to be relatively subtle (measured in days to weeks) (Fitter and Fitter 2002; Rawal et al. 2015), and therefore require frequent monitoring to detect.

The monthly survey comprised three vertical transects, running perpendicularly to the shore from the seawall towards the water (Fig. 1). Vertical transects are a well-established survey design for ecological surveys in intertidal habitats and are well suited to capture range shifts along the intertidal gradient across intra- and interannual timescales (Druehl and Green 1982;

Miller and Ambrose 2000). The transect lines were replicated monthly using multiple photographically documented spatial reference points. On the seawall, these consisted of specific, conspicuous landmarks that are part of the seawall structure. Lower in the intertidal zone, the spatial reference points were very large boulders that are unlikely to move between survey events. The length of the transects varied between survey events because the accessible intertidal zone depends on tide height (Fig. 1). In general, we conduct each survey at the lowest tide of the month, though this has not always been possible.

Transect data collection protocol

Starting at the 0 m mark (at the seawall), 1 m^2 square quadrats were positioned every 5 m on the right-hand side of the transect (directions from the perspective of an observer looking down the shore towards the water) until the water's edge. The quadrats at 0 m were oriented vertically against the seawall, while all other quadrats were laid flat on the ground. After positioning the quadrat, a reference photo was taken and the percent cover of each macroalgal morphospecies attached to substrate within the quadrat was estimated as a metric of abundance. If the estimated percent cover was between 0% and 5%, percent cover was estimated to the nearest percent. If the estimated percent cover was over 5%, percent cover was estimated to the nearest 5%.

As in Bates et al. (2009), macroalgal morphospecies were identified in the field when possible. Macroalgae that were not identifiable in the field were brought to the University of British Columbia and identified to the lowest taxonomic level possible using a morphology-based taxonomic key (Gabrielson and Lindstrom 2018). Macroalgal specimens that were still

ambiguous, had an uncertain taxonomic status or that required genetic analysis to identify were assigned to a lumped morphogroup or identified to genus (see taxonomy notes in the supplemental methods). Genus-level taxonomic assignments retain most of the species richness information despite requiring significantly less identification expertise (Bates et al. 2007). A species list is available in Table S1. As a reference for future verification of species identities, a voucher collection of representative specimens for each macroalgal morphospecies was accessioned into the Beaty Biodiversity Museum Algae Collection (accession list on Borealis). Before uploading the macroalgal list to Borealis, macroalgae that were only recorded once across all quadrats and survey events and not verified in the lab were removed. Currently, this results in *Plocamium* sp. being excluded from the published dataset.

Quadrat heights relative to chart datum (Fig. 1) were measured on August 1st and 13th, 2023 with stadia poles and a bubble level. The quadrat heights were recorded from the lower corner of the quadrat, touching the transect (lower left quadrat corner). Four previously surveyed quadrats (transect 2, 45 m; transect 3, 95 m; transect 4, 85 m and 90 m) were underwater when quadrat heights were measured, and thus inaccessible. The height of these quadrats was extrapolated based on known tide heights from previous surveys when these quadrats were accessible for surveying. Quadrat height measurements are indicated as real or extrapolated in the dataset.

Kelp reproductive timing

Starting in April 2022, we opportunistically recorded the reproductive status of the four Laminariales (kelp) species present at GW. Reproductive status is recorded as a binary variable

indicating if any thalli with sori were observed anywhere at GW during the survey, as performed in Druehl and Hsiao (1977), providing rough reproductive phenology data for each kelp species. We did not conduct subtidal surveys, so we could not record reproductive status of subtidal kelps.

Data analysis

Data were analyzed in R 4.4.0 (R Core Team 2022). Measures of central tendency were calculated with the package plyr, version 1.8.9 (Wickham 2011). Plots were generated with ggplot2, version 3.5.0 (Wickham 2016) and formatted with ggpubr, version 0.6.0 (Kassambara 2022).

Results

Macroalgal biodiversity was high and seasonally dynamic in urban environments

In total, we identified 59 unique macroalgae over the entire survey duration (Table S1) These included 15 Brown algae (Phaeophyceae), 9 green algae (Chlorophyta), and 35 red algae (Rhodophyta). Across all years, we recorded the lowest mean macroalgal richness (± se) in September (6.0 ± 1.7), closely followed by October (6.7 ± 1.9). We recorded the highest mean macroalgal richness in May (34.0 ± 0.6), followed by June (30.3 ± 0.3). Red algae always had the greatest richness, followed by the brown, then green algae (Figure 2A). Species richness and seasonal trends were not significantly different between transects.

While the species richness in our overall dataset exhibited substantial variation across the year (Figure 2A), species richness also appeared to be negatively correlated with survey height in the intertidal, which was generally lower in the summer than in the winter. To control for the effect of tide height on taxonomic richness, we also confined our calculations to the lowest six quadrats that were regularly sampled year-round, which were between 0.7 and 0.9m chart datum (Figures 1C,2B). Between 0.7 and 0.9 m chart datum, seasonal changes in species richness were less pronounced for all major macroalgal groups than in the overall dataset, particularly for red and green algae. However, all major macroalgal groups still exhibited a springtime peak in richness, particularly for brown algae (Figure 2B), matching the kelp recruitment period.

Macroalgal cover varied seasonally.

The abundance of macroalgae also exhibited substantial seasonal variation (Figure 2C). Notably, we observed a striking annual shift from a brown algae dominated intertidal in the spring and early summer, to a green algae dominated intertidal zone in midsummer to fall, while overall macroalgal cover was low in winter (Figure 2D). This seasonal cycling was the result of a springtime period of kelp recruitment and growth. Starting in February, young kelp recruits could be found throughout the entire intertidal zone as high as the seawall, with kelps collectively reaching 50 to 100% cover in the lower intertidal by April to May (Figure 2D). Past May, kelps progressively died back to the subtidal following warm summer low tides, allowing for an increase in the abundance of heat- and desiccation tolerant green ulvoid algae (Figure 2E). Ulvoid algae persisted in high abundance into the later summer and early fall, and thereafter declined gradually into the winter. Despite being much more species-rich than the green and

brown algae combined (Figure 2B), average red algal cover was low and varied little over the year even when after survey height in the intertidal was controlled for (Figure 2C).

Individual macroalgal species also showed strong seasonal patterns in abundance, influencing broader macroalgal richness trends. For example, the brown algae *Melanosiphon intestinalis* and *Petalonia fascia* were recorded throughout the year but had a significantly higher cover (up to 10 times higher) from February to May. *Scytosiphon* sp., *Acrosiphonia arcta* and *A. coalita* were found across a large range of the intertidal zone at GW, but only between March and June.

Decreasing macroalgal cover in the upper intertidal zone

We recorded a large decline in macroalgal cover in the upper intertidal zone starting around in November 2022 (Figure 3A). Much of this decline was due to the decline of *Fucus distichus* (Figure 3B,C,D,E). *F. distichus* cover did not decline lower on the shore (Figure S1), showing that the decline in precent cover was confined to the seawall, rather than a site-wide phenomenon. Other macroalgae in the high intertidal, such *Mastocarpus* sp. gametophytes, showed no significant change in cover during the same time (Figure 3B). As a matter of fact, fleshy crustose algae (*Hildenbrandia* sp. and sporophytes of M*astocarpus* sp.) increased in abundance on the seawall during the *F. distichus* decline and generally throughout the duration of the survey (Figure 3B). In fact, fleshy crustose algae were absent from the seawall until March 2022, though they were recorded below 0.6 m chart datum since December 2021.

Kelp reproductive timing data

We observed all four kelp species present intertidally at GW having reproductive structures (sori patches) or sporophylls at least once throughout our monitoring program (Figure 4). Reproductive *Saccharina latissima* was found in all months except January, March, and June. *Nereocystis luetkeana* showed a clear trend in reproductive timing, with sori appearing between April and September. Reproductive *Costaria costata* and *Alaria marginata* were rarely observed reproducing intertidally, with three and one observed instance(s) respectively, all in 2024 (Figure 4).

Discussion

A lack of historical baseline data is a significant obstacle for quantifying changes in macroalgal communities in response to climate change and other anthropogenic stressors (Bates, Saunders, and Chopin 2009; Lindstrom et al. 2021). Our macroalgal monitoring program documented the diverse and dynamic intertidal macroalgal community at an urban intertidal site in BC, not only contributing to an improved understanding of the ecology of Burrard Inlet, but also serving as a baseline against which to track the impact of ongoing anthropogenic activity (Bindoff et al. 2019; Wonham, Gerstle, and Bates 2023; Poloczanska et al. 2013). Between September 2021 and July 2024, we recorded a total of 59 species of macroalgae and captured intra- and interannual trends in community composition, including seasonal shifts in dominant macroalgal taxa and a progressive multi-year decline of the foundational *F. distichus* in the upper intertidal zone. While it is likely that contemporary survey efforts have captured the majority of the species present at GW, the publicly available protocols and easy to update, public dataset we have established provide an opportunity to continue tracking macroalgal communities and

improve our understanding of the natural variation in biodiversity between years, and whether long-term directional trends in biodiversity are occurring.

The interannual changes we observed in *F. distichus* abundance in the high intertidal highlight the potential for even limited time-series data to capture change. Starting in November 2022, *F. distichus* cover on the seawall underwent a marked decline, and has not recovered as of July 2024. Declines of *F. distichus* have been documented in response to physical disturbance of the shoreline (Klinger and Fukuyama 2011) and marine heatwaves (Weitzman et al. 2021; Suryan et al. 2021; Whalen et al. 2023). However, the decline observed at GW did not appear to be associated with any specific trigger, beginning more than a year after the 2021 heat dome. Populations of *Fucus* spp. have been documented to undergo natural, cyclical changes in abundance over multi-year time periods (Little et al. 2017; Klinger and Fukuyama 2011), possibly due to biotic interactions (Little et al. 2017). It is possible that the changes in *F. distichus* abundance we observed represent a portion of a larger, cyclical pattern of variation. However, a longer period of surveying would likely be required to clearly distinguish a decline due to a discrete trigger from cyclical oscillations, as the latter may play out over decadal timeframes (Little et al. 2017; Klinger and Fukuyama 2011).

Beyond documenting the overall presence and spatial distribution of macroalgal taxa at GW, our high sampling frequency has also allowed us to capture seasonal dynamics of macroalgal diversity, providing a temporal baseline against which to compare any future shifts in seasonal phenology. One particularly striking seasonal dynamic at GW is the recruitment of young kelp sporophytes in spring, followed by their subsequent dieback and replacement with green ulvoid algae throughout the summer. The dieback of intertidal kelps at GW corresponds to a seasonal shift from cool temperatures and nighttime low-tides (October to March) to warmer

temperatures and daytime low tides (April to September) that expose the intertidal to increased thermal and desiccation stress (Druehl and Hsiao 1977). The concurrent increase of green algae (mainly ulvoids) to replace the kelps is consistent with their greater ability to tolerate these abiotic stressors (Thom and Albright 1990; Gao et al. 2017; Nelson, Nelson, and Tjoelker 2003; Gao et al. 2011). Intensifying thermal and desiccation stress due to ongoing climate change could accelerate the timing and/or reduce extent of intertidal kelp recruitment, or increase the overall predominance of ulvoid algae at GW. In fact, comparisons with historical data are available in the local area suggest that kelp zonation and phenology may already have shifted over the last several decades (Druehl and Hsiao 1977). For instance, while historical data shows that *C. costata* used to recruit as high as 1.3 m chart datum (Druehl and Hsiao 1977), we never encountered *C. costata* above 0.8 m chart datum. We also have observed only a single occurrence of intertidal *A. marginata* bearing sporophylls in three years of monthly surveying, whereas the historical data records reproductive intertidal *A. marginata* from April to September (Druehl and Hsiao 1977).

Sargassum muticum was the only invasive macroalga we detected at GW. This species may have been introduced to BC as early as 1902 (Pawluk 2016), and is known to be established and common throughout the province. At GW, *S. muticum* cover was generally low, at least in the intertidal zone. However, climate change may increase its competitive advantage over native species due to its wide thermal tolerance range compared to many native seaweeds (Atkinson et al. 2020; de la Hoz et al. 2019; Olabarria et al. 2013). We have not detected other macroalgal invasives at GW, such as the red alga *Mazzaella japonica* or the kelp *Undaria pinnatifida*. However, *M. japonica* has already been documented in the Strait of Georgia (Pawluk 2016; Saunders and Millar 2014), and environmental conditions in BC are suitable for the

establishment of *U. pinnatifida* (Silva et al. 2002; Zabin et al. 2009), which is established in Northern California (Félix-Loaiza et al. 2022). Regular biodiversity surveys near potential sites of introduction (e.g., major ports, such as the Port of Vancouver) could assist in the early detection of future species invasions.

Acknowledgements

Dr. B. Clarkston for her invaluable help to identify macroalgae and suggestions on how to improve the study and data usability. Volunteers who donated their time to help us collect these data. In particular: A. Choinski, A. Jackman, A. Simon, B. Clarkston, C. Wardrop, E. Evans, E. Jourdain, E. Menchions, E. Kohn, E. Porcher, G. Ainsworth-Cruickshank, MJ. Herrin, P. Lund, R. Burns, R. Perovich, R. Ogushi, V. Billy.

Competing interests

The authors declare there are no competing interests.

Author contributions

Conceptualization: SS, VPS
Data curation: SS
Formal analysis: SS
Funding acquisition: LWP, PTM
Investigation: VPS, SS, LWP
Methodology: SS, VPS, LWP, PTM
Project administration: SS, VPS, LWP
Software: SS
Resources: LWP, PTM

Supervision: LWP, PTM
Visualization: SS, VPS
Writing – original draft: VPS, SS
Writing – review & editing: VPS, SS, LWP, PTM

Funding

Natural Sciences and Engineering Research Council Discovery Grant to LWP and Canada Research Chair tier 2 to LWP. Natural Sciences and Engineering Research Council Discovery grant to PTM (RGPIN-2019-06240). Natural Sciences and Engineering Research Council (NSERC) Postraduate Scholarship – Doctoral (PGS-D) to VPS (#6564).

Data availability

Detailed sampling protocols, sampling logs, and all data generated during this study are available in the Borealis Dataverse (https://doi.org/10.5683/SP3/IKGB6E), including an accession list of herbarium vouchers of representative macroalgal morphospecies. The dataset may be updated with more sampling timepoints if more sampling occurs past the publication date of this article. The physical herbarium vouchers are deposited at the Beaty Biodiversity Museum (University of British Columbia, Vancouver).

References

Andersen, Guri Sogn, Morten Foldager Pedersen, and Søren Laurentius Nielsen. 2013. "Temperature Acclimation and Heat Tolerance of Photosynthesis in Norwegian Saccharina Latissima (Laminariales, Phaeophyceae)." *Journal of Phycology* 49 (4): 689–700. https://doi.org/10.1111/jpy.12077.

Atkinson, James, Nathan G. King, Sophie B. Wilmes, and Pippa J. Moore. 2020. "Summer and Winter Marine Heatwaves Favor an Invasive Over Native Seaweeds." *Journal of Phycology* 56 (6): 1591–1600. https://doi.org/10.1111/jpy.13051.

Bates, Colin R., Gary W. Saunders, and Thierry Chopin. 2009. "Historical versus Contemporary Measures of Seaweed Biodiversity in the Bay of Fundy." *Botany* 87 (11): 1066–76. https://doi.org/10.1139/B09-067.

Bates, Colin R., Graham Scott, Michelle Tobin, and Ross Thompson. 2007. "Weighing the Costs and Benefits of Reduced Sampling Resolution in Biomonitoring Studies: Perspectives from the Temperate Rocky Intertidal." *Biological Conservation*, Forests in the Balance: Linking Tradition and Technology in Lanscape Mosaics, 137 (4): 617–25. https://doi.org/10.1016/j.biocon.2007.03.019.

Bindoff, Nathaniel L, William W L Cheung, James G Kairo, Javier Arístegui, Valeria A Guinder, Robert Hallberg, Nathalie Hilmi, et al. 2019. "Changing Ocean, Marine Ecosystems, and Dependent Communities." *Marine Ecosystems*.

Blain, Caitlin O., Sandra Christine Hansen, and Nick T. Shears. 2021. "Coastal Darkening Substantially Limits the Contribution of Kelp to Coastal Carbon Cycles." *Global Change Biology* 27 (21): 5547–63. https://doi.org/10.1111/gcb.15837.

Breeman, A. M. 1988. "Relative Importance of Temperature and Other Factors in Determining Geographic Boundaries of Seaweeds: Experimental and Phenological Evidence." *Helgoländer Meeresuntersuchungen* 42 (2): 199–241. https://doi.org/10.1007/BF02366043.

Bringloe, Trevor T., and Gary W. Saunders. 2019. "DNA Barcoding of the Marine Macroalgae from Nome, Alaska (Northern Bering Sea) Reveals Many Trans-Arctic Species." *Polar Biology* 42 (5): 851–64. https://doi.org/10.1007/s00300-019-02478-4.

"Cargo and Terminals." 2015. Port of Vancouver. March 18, 2015. https://www.portvancouver.com/cargo-terminals/.

Casas, Graciela, Ricardo Scrosati, and María Luz Piriz. 2004. "The Invasive Kelp Undaria Pinnatifida (Phaeophyceae, Laminariales) Reduces Native Seaweed Diversity in Nuevo Gulf (Patagonia, Argentina)." *Biological Invasions* 6 (4): 411–16. https://doi.org/10.1023/B:BINV.0000041555.29305.41.

Connell, Joseph H. 1961. “The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle Chthamalus Stellatus.” *Ecology* 42 (4): 710–23. https://doi.org/10.2307/1933500.

Davidson, Laurie Wayne. 1973. “On the Physical Oceanograhy of Burrard Inlet and Indian Arm, British Columbia.” University of British Columbia.

Davison, Ian R., and Gareth A. Pearson. 1996. “Stress Tolerance in Intertidal Seaweeds.” *Journal of Phycology* 32 (2): 197–211. https://doi.org/10.1111/j.0022-3646.1996.00197.x.

Dayton, P K. 1985. “Ecology of Kelp Communities.” *Annual Review of Ecology and Systematics* 16 (1): 215–45. https://doi.org/10.1146/annurev.es.16.110185.001243.

Demes, Kyle W., Rebecca L. Kordas, and Jennifer P. Jorve. 2012. “Ferry Wakes Increase Seaweed Richness and Abundance in a Sheltered Rocky Intertidal Habitat.” *Hydrobiologia* 693 (1): 1–11. https://doi.org/10.1007/s10750-012-1082-4.

Druehl, L. D., and S. I. C. Hsiao. 1977. “Intertidal Kelp Response to Seasonal Environmental Changes in a British Columbia Inlet.” *Journal of the Fisheries Research Board of Canada* 34 (8): 1207–11. https://doi.org/10.1139/f77-176.

Druehl, Ld, and Jm Green. 1982. “Vertical Distribution of Intertidal Seaweeds as Related to Patterns of Submersion and Emersion.” *Marine Ecology Progress Series* 9:163–70. https://doi.org/10.3354/meps009163.

Ducrotoy, Jean-paul. 1999. “Indications of Change in the Marine Flora of the North Sea in the 1990s.” *Marine Pollution Bulletin* 38 (8): 646–54. https://doi.org/10.1016/S0025-326X(98)00195-7.

Eger, Aaron M., Ezequiel M. Marzinelli, Rodrigo Beas-Luna, Caitlin O. Blain, Laura K. Blamey, Jarrett E. K. Byrnes, Paul E. Carnell, et al. 2023. “The Value of Ecosystem Services in Global Marine Kelp Forests.” *Nature Communications* 14 (1): 1894. https://doi.org/10.1038/s41467-023-37385-0.

Félix-Loaiza, Ana Carolina, Lucía Mercedes Rodríguez-Bravo, Rodrigo Beas-Luna, Julio Lorda, Eliot de La Cruz-González, and Luis Malpica-Cruz. 2022. “Marine Heatwaves Facilitate Invasive Algae Takeover as Foundational Kelp.” *Botanica Marina* 65 (5): 315–19. https://doi.org/10.1515/bot-2022-0037.

Fitter, A. H., and R. S. R. Fitter. 2002. “Rapid Changes in Flowering Time in British Plants.” *Science* 296 (5573): 1689–91. https://doi.org/10.1126/science.1071617.

Gabrielson, Paul W., and Sandra C. Lindstrom. 2018. *Keys to the Seaweeds and Seagrasses of Southeast Alaska, British Columbia, Washington, and Oregon*. PhycoID.

Gao, Guang, Anthony S. Clare, Craig Rose, and Gary S. Caldwell. 2017. “Eutrophication and Warming-Driven Green Tides (*Ulva Rigida*) Are Predicted to Increase under Future Climate Change Scenarios.” *Marine Pollution Bulletin* 114 (1): 439–47. https://doi.org/10.1016/j.marpolbul.2016.10.003.

Gao, Shan, Songdong Shen, Guangce Wang, Jianfeng Niu, Apeng Lin, and Guanghua Pan. 2011. “PSI-Driven Cyclic Electron Flow Allows Intertidal Macro-Algae Ulva Sp. (Chlorophyta) to Survive in Desiccated Conditions.” *Plant and Cell Physiology* 52 (5): 885–93. https://doi.org/10.1093/pcp/pcr038.

Halpern, Benjamin S., Brian R. Silliman, Julian D. Olden, John P. Bruno, and Mark D. Bertness. 2007. “Incorporating Positive Interactions in Aquatic Restoration and Conservation.” *Frontiers in Ecology and the Environment* 5 (3): 153–60. https://doi.org/10.1890/1540-9295(2007)5[153:IPIIAR]2.0.CO;2.

Harley, Christopher D. G. 2003. “Abiotic Stress and Herbivory Interact to Set Range Limits across a Two-Dimensional Stress Gradient.” *Ecology* 84 (6): 1477–88.

Harley, Christopher D. G., Kathryn M. Anderson, Kyle W. Demes, Jennifer P. Jorve, Rebecca L. Kordas, Theraesa A. Coyle, and Michael H. Graham. 2012. “Effects of Climate Change on Global Seaweed Communities.” *Journal of Phycology* 48 (5): 1064–78. https://doi.org/10.1111/j.1529-8817.2012.01224.x.

Harley, Christopher D. G., and Robert T. Paine. 2009. “Contingencies and Compounded Rare Perturbations Dictate Sudden Distributional Shifts during Periods of Gradual Climate Change.” *Proceedings of the National Academy of Sciences* 106 (27): 11172–76. https://doi.org/10.1073/pnas.0904946106.

Heery, Eliza C., Bert W. Hoeksema, Nicola K. Browne, James D. Reimer, Put O. Ang, Danwei Huang, Daniel A. Friess, et al. 2018. “Urban Coral Reefs: Degradation and Resilience of Hard Coral Assemblages in Coastal Cities of East and Southeast Asia.” *Marine Pollution Bulletin* 135 (October):654–81. https://doi.org/10.1016/j.marpolbul.2018.07.041.

Helmuth, Brian, Bernardo R. Broitman, Carol A. Blanchette, Sarah Gilman, Patricia Halpin, Christopher D. G. Harley, Michael J. O’Donnell, Gretchen E. Hofmann, Bruce Menge, and Denise Strickland. 2006. “Mosaic Patterns of Thermal Stress in the Rocky Intertidal Zone: Implications for Climate Change.” *Ecological Monographs* 76 (4): 461–79. https://doi.org/10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2.

Hoz, Camino Fernández de la, Elvira Ramos, Araceli Puente, and José A. Juanes. 2019. “Climate Change Induced Range Shifts in Seaweeds Distributions in Europe.” *Marine Environmental Research* 148 (June):1–11. https://doi.org/10.1016/j.marenvres.2019.04.012.

Hughey, Jeffery, Paul Gabrielson, Christine Maggs, and Frederic Mineur. 2021. “Genomic Analysis of the Lectotype Specimens of European Ulva Rigida and Ulva Lacinulata (Ulvaceae, Chlorophyta) Reveals the Ongoing Misapplication of Names.” *European Journal of Phycology* 57 (June):1–11. https://doi.org/10.1080/09670262.2021.1914862.

Johnson, Craig R., Sam C. Banks, Neville S. Barrett, Fabienne Cazassus, Piers K. Dunstan, Graham J. Edgar, Stewart D. Frusher, et al. 2011. “Climate Change Cascades: Shifts in Oceanography, Species’ Ranges and Subtidal Marine Community Dynamics in Eastern Tasmania.” *Journal of Experimental Marine Biology and Ecology* 400 (1–2): 17–32. https://doi.org/10.1016/j.jembe.2011.02.032.

Kassambara, Alboukadel. 2022. *Ggpubr: “ggplot2” Based Publication Ready Plots*. https://CRAN.R-project.org/package=ggpubr.

Klinger, Terrie, and Allan K. Fukuyama. 2011. “Decadal-Scale Dynamics and Response to Pulse Disturbance in the Intertidal Rockweed Fucus Distichus (Phaeophyceae).” *Marine Ecology* 32 (3): 313–19. https://doi.org/10.1111/j.1439-0485.2011.00481.x.

Korpinen, S., V. Jormalainen, and T. Honkanen. 2007. “Effects of Nutrients, Herbivory, and Depth on the Macroalgal Community in the Rocky Sublittoral.” *Ecology* 88 (4): 839–52. https://doi.org/10.1890/05-0144.

Levings, Colin D, and Hannah L Stewart. 2020. “Research Priorities for Nearshore Algae in Coastal British Columbia Workshop and Gap Analysis – Final Report.” Fisheries and Oceans Canada.

Lilley, Stacie A., and David R. Schiel. 2006. “Community Effects Following the Deletion of a Habitat-Forming Alga from Rocky Marine Shores.” *Oecologia* 148 (4): 672–81. https://doi.org/10.1007/s00442-006-0411-6.

Lima, Fernando P., and David S. Wethey. 2012. “Three Decades of High-Resolution Coastal Sea Surface Temperatures Reveal More than Warming.” *Nature Communications* 3 (1): 704. https://doi.org/10.1038/ncomms1713.

Lindstrom, Sandra C. 1973. “Marine Benthic Algal Communities in the Flat Top Islands Area of Georgia Strait.” Univeristy of British Columbia.

Lindstrom, Sandra C., Jeffery R. Hughey, and Patrick T. Martone. 2011. “New, Resurrected and Redefined Species of Mastocarpus (Phyllophoraceae, Rhodophyta) from the Northeast Pacific.” *Phycologia* 50 (6): 661–83. https://doi.org/10.2216/10-38.1.

Lindstrom, Sandra C., Matthew A. Lemay, Samuel Starko, Katharine R. Hind, and Patrick T. Martone. 2021. “New and Interesting Seaweed Records from the Hakai Area of the

Central Coast of British Columbia, Canada: Chlorophyta." *Botanica Marina* 64 (5): 343–61. https://doi.org/10.1515/bot-2021-0038.

Little, Colin, Cynthia D. Trowbridge, Graham M. Pilling, Penny Stirling, David Morritt, and Gray A. Williams. 2017. "Long-Term Fluctuations in Intertidal Communities in an Irish Sea-Lough: Limpet-Fucoid Cycles." *Estuarine, Coastal and Shelf Science* 196 (September):70–82. https://doi.org/10.1016/j.ecss.2017.06.036.

Mann, K.H. 1973. "Seaweeds: Their Productivity and Strategy for Growth | Science." *Science* 182 (4116): 975–81.

Miller, Aw, and Rf Ambrose. 2000. "Sampling Patchy Distributions:Comparison of Sampling Designs in Rocky Intertidal Habitats." *Marine Ecology Progress Series* 196:1–14. https://doi.org/10.3354/meps196001.

Mineur, Frédéric, Francisco Arenas, Jorge Assis, Andrew J. Davies, Aschwin H. Engelen, Francisco Fernandes, Erik-jan Malta, et al. 2015. "European Seaweeds under Pressure: Consequences for Communities and Ecosystem Functioning." *Journal of Sea Research*, Protecting Marine Biodiversity to Preserve Ecosystem Functioning: a Tribute to Carlo Heip, 98 (April):91–108. https://doi.org/10.1016/j.seares.2014.11.004.

Neilson-Welsh, Laurie. 1999. "Saline Water Intrusion from the Fraser River Estuary: A Hydrogeological Investigation Using Field Chemical Data and a Density-Dependent Groundwater Flow Model." University of British Columbia.

Nelson, T. A., A. V. Nelson, and M. Tjoelker. 2003. "Seasonal and Spatial Patterns of 'Green Tides' (Ulvoid Algal Blooms) and Related Water Quality Parameters in the Coastal Waters of Washington State, USA" 46 (3): 263–75. https://doi.org/10.1515/BOT.2003.024.

Olabarria, Celia, Francisco Arenas, Rosa M. Viejo, Ignacio Gestoso, Fátima Vaz-Pinto, Mónica Incera, Marcos Rubal, Eva Cacabelos, Puri Veiga, and Cristina Sobrino. 2013. "Response of Macroalgal Assemblages from Rockpools to Climate Change: Effects of Persistent Increase in Temperature and CO2." *Oikos* 122 (7): 1065–79. https://doi.org/10.1111/j.1600-0706.2012.20825.x.

Parmesan, Camille, and Gary Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems." *Nature* 421 (6918): 37–42. https://doi.org/10.1038/nature01286.

Pawluk, Kylee Ann. 2016. "Impacts and Interactions of Two Non-Indigenous Seaweeds Mazzaella Japonica (Mikami) Hommersand and Sargassum Muticum (Yendo) Fensholt in Baynes Sound, British Columbia." Thesis. https://dspace.library.uvic.ca/handle/1828/7264.

Pfister, Catherine A., Mark A. Altabet, and Brooke L. Weigel. 2019. "Kelp Beds and Their Local Effects on Seawater Chemistry, Productivity, and Microbial Communities." *Ecology* 100 (10): e02798. https://doi.org/10.1002/ecy.2798.

Poloczanska, Elvira S., Christopher J. Brown, William J. Sydeman, Wolfgang Kiessling, David S. Schoeman, Pippa J. Moore, Keith Brander, et al. 2013. "Global Imprint of Climate Change on Marine Life." *Nature Climate Change* 3 (10): 919–25. https://doi.org/10.1038/nclimate1958.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rawal, Deepa S., Sabine Kasel, Marie R. Keatley, and Craig R. Nitschke. 2015. "Herbarium Records Identify Sensitivity of Flowering Phenology of Eucalypts to Climate: Implications for Species Response to Climate Change." *Austral Ecology* 40 (2): 117–25. https://doi.org/10.1111/aec.12183.

Rogers-Bennett, L., and C. A. Catton. 2019. "Marine Heat Wave and Multiple Stressors Tip Bull Kelp Forest to Sea Urchin Barrens." *Scientific Reports* 9 (1): 15050. https://doi.org/10.1038/s41598-019-51114-y.

Ryan, Scott A., Gary Dana Wohlgeschaffen, Nusrat Jahan, Haibo Niu, Alice C. Ortmann, Trevor N. Brown, T. L. King, and Jason Clyburne. 2019. “State of Knowledge on Fate and Behaviour of Ship-Source Petroleum Product Spills.” Ottawa: Fisheries and Oceans Canada = Pêches et océans Canada.

Salvaterra, Tânia, Dannielle S. Green, Tasman P. Crowe, and Eoin J. O’Gorman. 2013. “Impacts of the Invasive Alga Sargassum Muticum on Ecosystem Functioning and Food Web Structure.” *Biological Invasions* 15 (11): 2563–76. https://doi.org/10.1007/s10530-013-0473-4.

Saunders, Gary, and Kyle Millar. 2014. “A DNA Barcode Survey of the Red Algal Genus Mazzaella in British Columbia Reveals Overlooked Diversity and New Distributional Records: Descriptions of M. Dewreedei Sp. Nov. and M. Macrocarpa Sp. Nov.” *Botany* 92 (March). https://doi.org/10.1139/cjb-2013-0283.

Silva, Paul, Rachel Woodfield, Andrew Cohen, Leslie Harris, and Jeffrey Goddard. 2002. “First Report of the Asian Kelp Undaria Pinnatifida in the Northeastern Pacific Ocean.” *Biological Invasions* 4 (September):333–38. https://doi.org/10.1023/A:1020991726710.

Starko, Samuel, Lauren A. Bailey, Elandra Creviston, Katelyn A. James, Alison Warren, Megan K. Brophy, Andreea Danasel, Megan P. Fass, James A. Townsend, and Christopher J. Neufeld. 2019. “Environmental Heterogeneity Mediates Scale-Dependent Declines in Kelp Diversity on Intertidal Rocky Shores.” *PLOS ONE* 14 (3): e0213191. https://doi.org/10.1371/journal.pone.0213191.

Steneck, Robert S., Michael H. Graham, Bruce J. Bourque, Debbie Corbett, Jon M. Erlandson, James A. Estes, and Mia J. Tegner. 2002. “Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future.” *Environmental Conservation* 29 (4): 436–59. https://doi.org/10.1017/S0376892902000322.

Suryan, Robert M., Mayumi L. Arimitsu, Heather A. Coletti, Russell R. Hopcroft, Mandy R. Lindeberg, Steven J. Barbeaux, Sonia D. Batten, et al. 2021. “Ecosystem Response Persists after a Prolonged Marine Heatwave.” *Scientific Reports* 11 (1): 6235. https://doi.org/10.1038/s41598-021-83818-5.

Teagle, Harry, Stephen J. Hawkins, Pippa J. Moore, and Dan A. Smale. 2017. “The Role of Kelp Species as Biogenic Habitat Formers in Coastal Marine Ecosystems.” *Journal of Experimental Marine Biology and Ecology*, Ecological responses to environmental change in marine systems, 492 (July):81–98. https://doi.org/10.1016/j.jembe.2017.01.017.

Thom, R. M., and R. G. Albright. 1990. “Dynamics of Benthic Vegetation Standing-Stock, Irradiance, and Water Properties in Central Puget Sound.” *Marine Biology* 104 (1): 129–41. https://doi.org/10.1007/BF01313166.

Todd, Peter A., Eliza C. Heery, Lynette H. L. Loke, Ruth H. Thurstan, D. Johan Kotze, and Christopher Swan. 2019. “Towards an Urban Marine Ecology: Characterizing the Drivers, Patterns and Processes of Marine Ecosystems in Coastal Cities.” *Oikos* 128 (9): 1215–42. https://doi.org/10.1111/oik.05946.

Tsleil-Waututh Nation. 2017. “Burrard Inlet Action Plan.” 2017 version. https://twnsacredtrust.ca/wp-content/uploads/2023/01/201711_Burrard_Inlet_Action-Plan_2017_Version_FINAL.pdf.

Vergés, Adriana, Alexandra H. Campbell, Georgina Wood, Lana Kajlich, Aaron M. Eger, Derrick Cruz, Madelaine Langley, et al. 2020. “Operation Crayweed: Ecological and Sociocultural Aspects of Restoring Sydney’s Underwater Forests.” *Ecological Management & Restoration* 21 (2): 74–85. https://doi.org/10.1111/emr.12413.

Weitzman, Benjamin, Brenda Konar, Katrin Iken, Heather Coletti, Daniel Monson, Robert Suryan, Thomas Dean, Dominic Hondolero, and Mandy Lindeberg. 2021. “Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of

Alaska." *Frontiers in Marine Science* 8. https://www.frontiersin.org/articles/10.3389/fmars.2021.556820.

Wernberg, Thomas, Dan A. Smale, and Mads S. Thomsen. 2012. "A Decade of Climate Change Experiments on Marine Organisms: Procedures, Patterns and Problems." *Global Change Biology* 18 (5): 1491–98. https://doi.org/10.1111/j.1365-2486.2012.02656.x.

Wernberg, Thomas, Mads S. Thomsen, Fernando Tuya, Gary A. Kendrick, Peter A. Staehr, and Benjamin D. Toohey. 2010. "Decreasing Resilience of Kelp Beds along a Latitudinal Temperature Gradient: Potential Implications for a Warmer Future." *Ecology Letters* 13 (6): 685–94. https://doi.org/10.1111/j.1461-0248.2010.01466.x.

Whalen, Matthew A., Samuel Starko, Sandra C. Lindstrom, and Patrick T. Martone. 2023. "Heatwave Restructures Marine Intertidal Communities across a Stress Gradient." *Ecology* 104 (5): e4027. https://doi.org/10.1002/ecy.4027.

White, Rachel H., Sam Anderson, James F. Booth, Ginni Braich, Christina Draeger, Cuiyi Fei, Christopher D. G. Harley, et al. 2023. "The Unprecedented Pacific Northwest Heatwave of June 2021." *Nature Communications* 14 (1): 727. https://doi.org/10.1038/s41467-023-36289-3.

Wickham, Hadley. 2011. "The Split-Apply-Combine Strategy for Data Analysis." *Journal of Statistical Software* 40 (1): 1–29.

———. 2016. *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Wonham, Marjorie, Catherine Gerstle, and Colin Bates. 2023. "Combining Current and Historical Biodiversity Surveys Reveals Order of Magnitude Greater Richness in a British Columbia Marine Protected Area." *The Canadian Field-Naturalist* 136 (4): 348–60. https://doi.org/10.22621/cfn.v136i4.2903.

Zabin, Chela, Gail Ashton, Christopher Brown, and Gregory Ruiz. 2009. "Northern Range Expansion of the Asian Kelp Undaria Pinnatifida (Harvey) Suringar (Laminariales, Phaeophyceae) in Western North America." *Aquatic Invasions* 4 (3): 429–34. https://doi.org/10.3391/ai.2009.4.3.1.

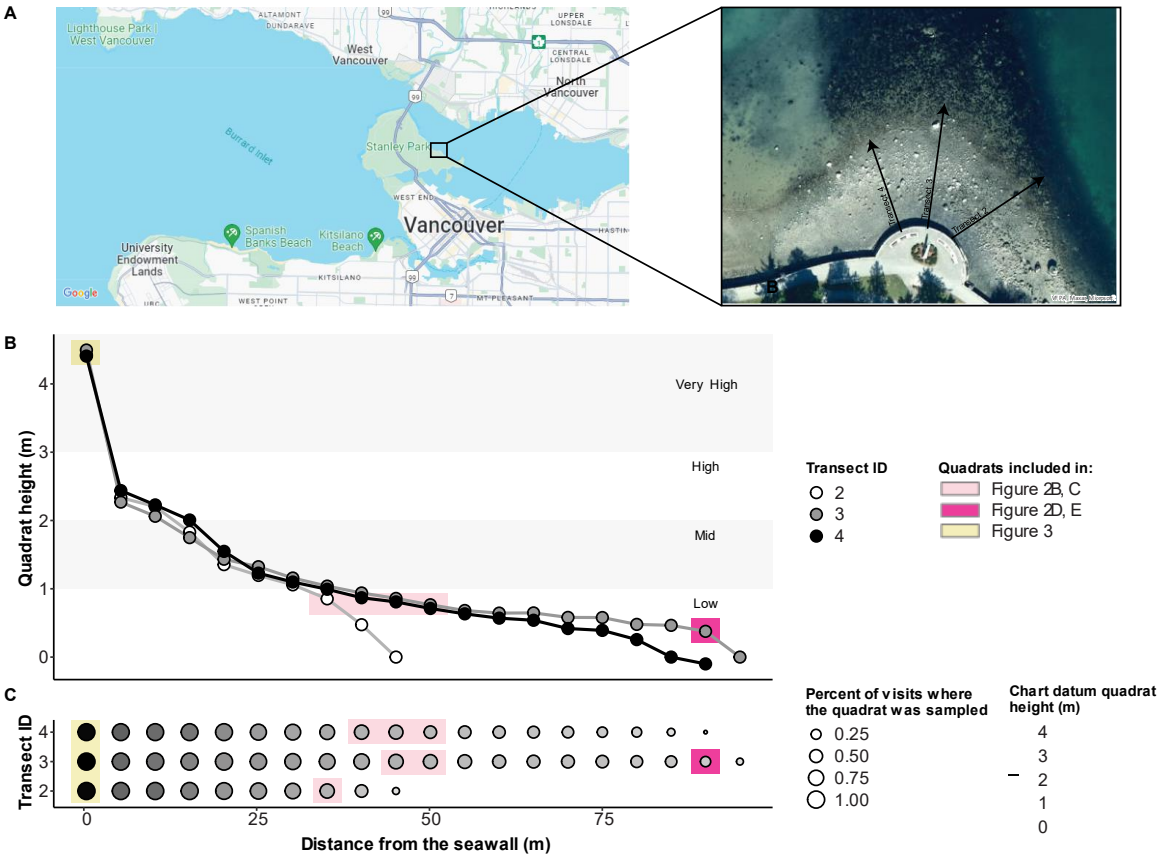

Figure 1. A) Map of local area with inset showing overhead photo and position of transects. **B)** The chart datum quadrat height and distance from the seawall along each of the three transects, showing the slope of the site. Rough delineations of intertidal zones based on shore height are indicated **C)** The frequency at which each quadrat was sampled as a percent of total sampling events (size) colored by chart datum quadrat height in metres. Note, the blue boxes in panels B and C indicate the six quadrats between 0.7 and 0.9 m chart datum height. The brown box in panels B and C show the quadrat at 90 m of transect 3.

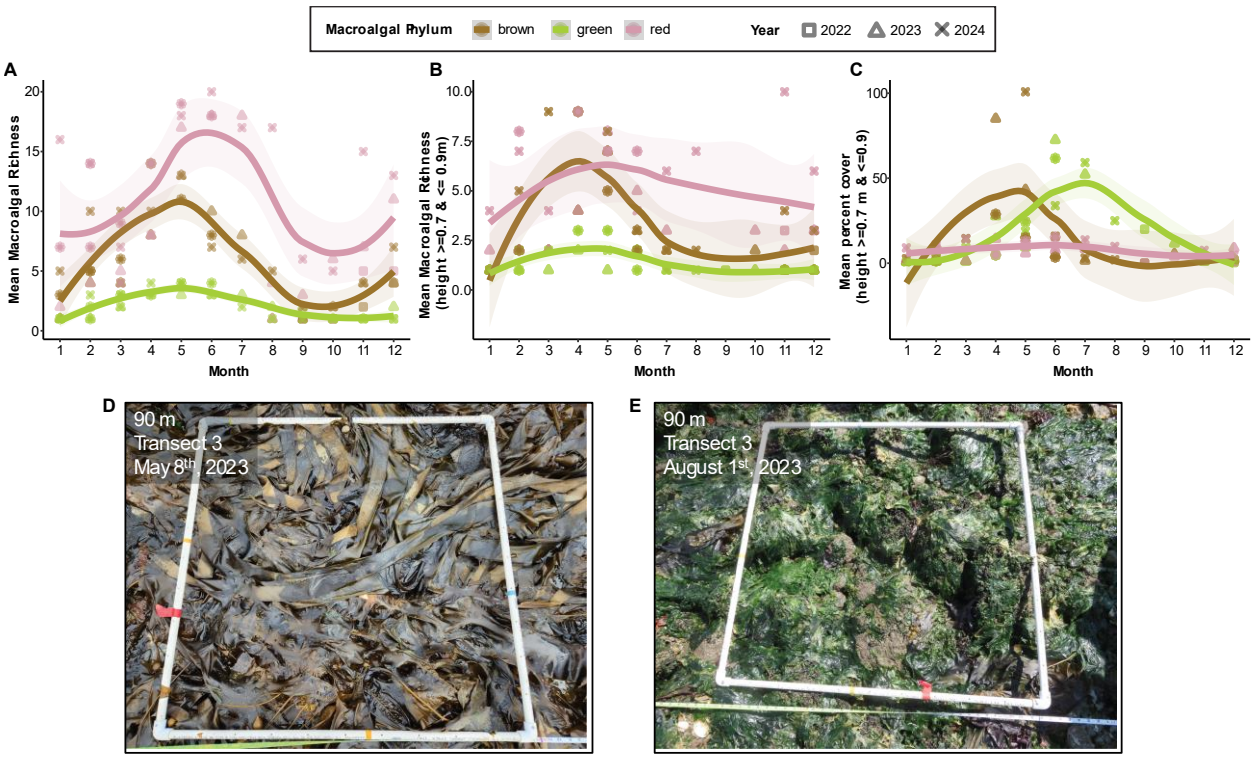

Figure 2. Line graphs showing the mean richness of each macroalgal group by across (A) the entire site or (B) between 0.7 and 0.9 m chart datum. (C) The mean macroalgal percent cover between 0.7 to 0.9 m chart datum. Transparent ribbons represent the standard error around the mean. Representative images from (D) May 2023 and (E) August 2023 of the change from high brown algal cover, dominated by kelps, to high green algal cover, dominated by ulvoid algae. Both images are from transect number 3, 90 m from the seawall (0 m chart datum height).

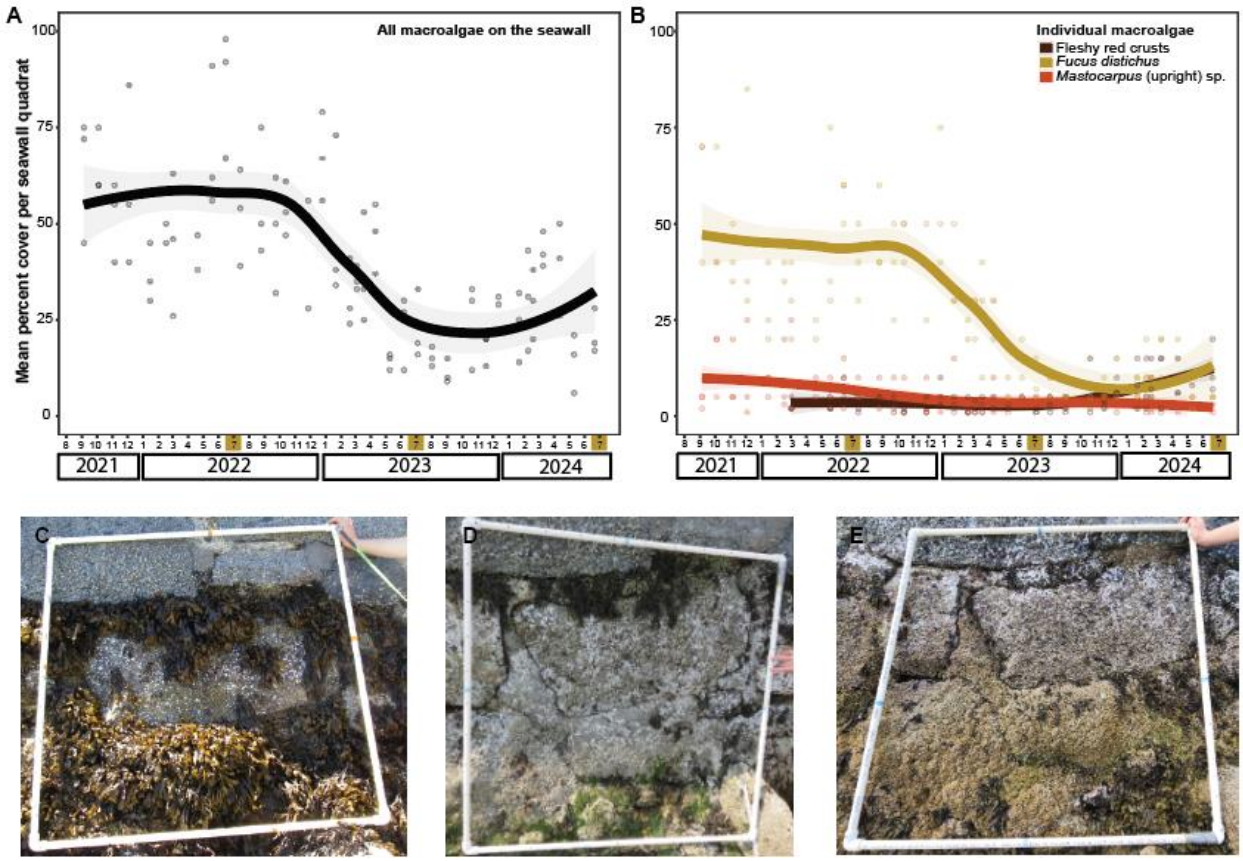

Figure 3. Plot of the percent macroalgal cover per quadrat on the seawall of (A) all macroalgae and (B) selected macroalgal species. Points show the individual transect values and the lines represent the mean of all three transects. Ribbons show the standard error around the mean. (C,D,E) Photos from the seawall quadrat from transect 3 in July C) 2022, D) 2023, and E) 2024. Brown squares on the x-axis of panels A and B correspond to the dates shown in photos C to E.

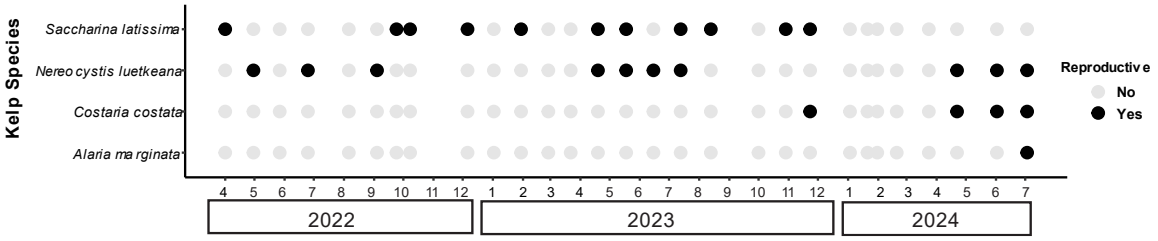

Figure 4. Plot showing if any reproductive kelp by species were observed by sampling visit.

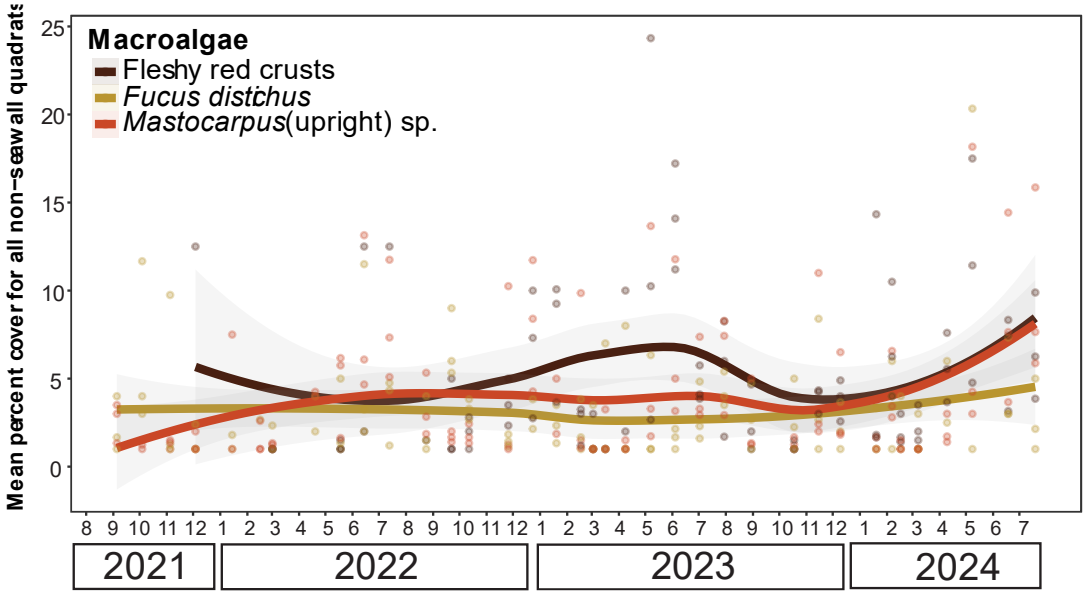

Figure S1. Plot of the percent macroalgal cover per quadrat across all quadrats sampled per sampling visit excluding seawall quadrats (Figure 2B). Points show the individual transect values and the lines represent the mean of all three transects. Ribbons show the standard error around the mean.