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

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Abstract

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 baseline macroalgal biodiversity data are lacking 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 low-cost and easily replicable survey protocol, in addition to publishing a

previously unpublished 1983-1984 historical dataset of the same area. Our datasets and our survey

protocol are freely available. Over 35 months we have recorded 61 taxa of macroalgae, including

the canopy forming kelp *Nereocystis luetkeana* and the introduced fucoid *Sargassum muticum*.

Surveying throughout the year at regular intervals has revealed large-scale seasonal shifts in

macroalgal community composition, the 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 et al. 2009; Lindstrom et al. 2021). However,

macroalgae remain understudied in comparison to other ecologically important groups (Harley et

al. 2012; Wernberg et al. 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 published 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 has been more limited, even though

these areas experience comparatively greater levels of anthropogenic stress, including pollution,

sedimentation, abiotic extremes, and invasive species (Blain et al. 2021; Ducrotoy 1999; Heery et

al. 2018; Todd et al. 2019; Vergés et al. 2020). 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 intertidal kelps in 1969 and 1970 but did not record other macroalgae

(Druehl and Hsiao 1977). A 1983-1984 monthly survey by David J. Garbary recorded intertidal

and subtidal macroalgal diversity and seasonality at multiple sites around metropolitan Vancouver,

but was unpublished.

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 taxonomic composition. Our goal was to establish a comprehensive baseline

dataset of: *(i)* Overall diversity of intertidal macroalgae at the site, *(ii)* Presence of any possible

introduced, invasive species, such as *Sargassum muticum* (Pawluk 2016; Salvaterra et al. 2013),

Mazzaella japonica (Pawluk 2016), or *Undaria pinnatifida* (Casas et al. 2004)*, (iii)* Spatial patterns

of macroalgal diversity across the intertidal gradient, and *(iv)* Intra and interannual shifts in

diversity and phenology of conspicuous algae. Alongside our data, we include and publish David

J. Garbary's 1983-1984 historical dataset, to which we compare our transect data to assess *(i)*

changes in diversity over time and *(ii)* differences in seasonal trends between historical and current

datasets.

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; Fig. 1A). 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). This site is a well-known local hotspot for intertidal biodiversity and has been extensively utilized by numerous research groups and educators from local institutions including the University of British Columbia and Simon Fraser University, as well as various non-academic stakeholders (e.g., Stanley Park Ecological Society). 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. 1B).

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. 1B). 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 tidal

height (Fig. 1C). 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%. Therefore,

our percent cover values were: 0, 1, 2, 3, 4, 5, 10, 15, …, 100.

Surveyor team size and composition varied by sampling visit and by season. In the winter,

when macroalgal diversity and abundance were relatively low and the transect distances relatively

short, the two co-first authors were generally able to survey all three transects on their own within

roughly two hours. In the summer, particularly from May to July, macroalgal diversity and

abundance were relatively high, which increased the time to survey each quadrat. During this time,

up to four additional surveyors (the two senior authors on this manuscript and the individuals listed

in the acknowledgements) assisted with each survey. To complete the surveys from May to July,

a minimum of three surveyors (1 per transect) were required. We provided a custom-made field

guide with photos and key morphological characteristics to help less experienced surveyors

identify the most common macroalgae at the site.

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 (e.g., crustose

coralline algae) 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 taxon

richness information despite requiring significantly less identification expertise (Bates et al. 2007).

A taxon list is available in Table 1. As a reference for future verification of taxonomic

identifications, 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 resulted in *Plocamium* sp. being excluded from the published dataset.

Quadrat tidal heights (Fig. 1) were measured on August 1st and 13th, 2023 with stadia poles

and a bubble level. The quadrat tidal 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 tidal heights

were measured, and thus inaccessible. The tidal height of these quadrats was extrapolated based

on known tide heights from previous surveys when these quadrats were accessible for surveying.

Quadrat tidal height measurements are indicated as real or extrapolated in the published 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 was 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 plyr package, 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).

Publication and analysis of 1983-1984 algal survey from nearby sites

A dataset from 1983-1984 collected by David J. Garbary has been used by many

researchers from BC as baseline data for the region, but these data were not publicly accessible

online. These data are monthly (or less frequent depending on the site) presence/absence surveys

of multiple sites around Metro Vancouver including both macro- and microalgae. These data

include dive surveys.

We updated the historical names in the dataset to reflect contemporary taxonomy, while

also retaining the original name assignment. The taxonomy of the dataset was updated using

AlgaeBase (Guiry and Guiry 2024) as a primary reference and Gabrielson and Lindstrom (2018)

as a secondary reference. Where there were discrepancies between the two references, the

reasoning provided in the footnotes of Gabrielson and Lindstrom (2018) was usually sufficient to

resolve the discrepancy. In cases where this was not possible, the taxonomy in AlgaeBase (Guiry

and Guiry 2024) was followed.

We analyzed a subset of the historical dataset for comparisons with our contemporary

baseline data. We removed microalgae and endophytes, as our survey did not capture these. We

also restricted our comparisons to four sites around Stanley Park (Third Beach, Siwash Rock,

Brockton point, Coal Harbour), which were closest to our contemporary survey site. After these

data cleaning steps, we compared our macroalgal list to this 1983-1984 list. We analyzed the 1983-

1984 taxon richness following the same procedure as for our transect data.

Results

Macroalgal biodiversity was high and seasonally dynamic in urban environments

In total, we identified 61 macroalgal taxa over the entire survey duration (Table 1) These

included 15 brown algae (Phaeophyceae), 10 green algae (Chlorophyta), and 36 red algae

(Rhodophyta). Across all years, we recorded the lowest mean macroalgal richness ($\pm$ se) in

September (6.0 $\pm$ 1.7), closely followed by October (6.7 $\pm$ 1.9). We recorded the highest mean

macroalgal richness in May (34.0 $\pm$ 0.6), followed by June (30.3 $\pm$ 0.3). Red algae always had the

greatest richness, followed by the brown, then green algae (Fig. 2A). Taxon richness and seasonal

trends were not significantly different between transects when controlling for tidal height. Our

observed taxon richness was lower than in the 1983-1984 historical dataset; we re-encountered 12

out of 20 brown, 6 out of 12 green, and 30 out of 72 red algal taxa present in the historical dataset.

While the vast majority of taxa observed in our contemporary data were present in the historical

dataset, we documented 2 brown, 3 green, and 5 red algal taxa that had not been previously

recorded. Seasonal changes in diversity were similar between historical and contemporary

datasets.

The taxon richness observed in our overall dataset appears to be negatively correlated with

tidal height in the intertidal zone. We were able to access lower tide heights in the spring and early

summer compared to fall and winter, potentially biasing the results towards higher observed taxon

richness in spring and summer (Fig. 2A). To control for the effect of tide height on taxonomic

richness, we confined our calculations to the lowest six quadrats that were regularly sampled year-

round, which were between 0.7 and 0.9 m chart datum (Fig. 1C,2B). Between 0.7 and 0.9 m chart

datum, seasonal changes in taxon 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 (Fig. 2B),

matching the kelp recruitment period. In contrast to the seasonal dynamics we observed

intertidally, the 1983-1984 Garbary data, which included subtidal surveys unaffected by sampling

tidal height, displayed minimal seasonal variation in taxonomic richness.

Macroalgal cover varied seasonally.

The percent cover of macroalgae also exhibited substantial seasonal variation (Fig. 2C).

Notably, we observed a striking annual shift from a brown algae dominated intertidal zone 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 (Fig. 2C). This seasonal cycling was the result of a

springtime period of kelp recruitment and growth. Starting in February, young kelp recruits

(particularly *Saccharina latissima, Alaria marginata,* and *N. luetkeana*) could be found throughout

the entire intertidal zone as high as the seawall on all substrate types (boulders, cobble and shell

hash). By April to May, kelps collectively reached 50 to 100% cover in the lower intertidal zone

(Fig. 2C,D). Kelps then progressively died back to the subtidal following warm summer low tides.

The kelp dieback was followed by an increased abundance of heat- and desiccation tolerant green

ulvoid algae (Fig. 2C,E). Ulvoid algae persisted in high abundance into the later summer and early

fall, and thereafter declined gradually into the winter. Despite red algae being much more species-

rich than the green and brown algae combined (Fig. 2B), average red algal cover was low and

varied little over the year even after survey height in the intertidal zone was controlled for (Fig.

2C).

Individual macroalgal taxa 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 *Acrosiphonia*

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 (Fig. 1C, 3A). Much of this decline was due to the decline of *Fucus distichus*

(Fig. 3B,C,D,E). *F. distichus* cover did not decline lower on the shore (Fig. S1), showing that the

decline in percent cover was confined to the seawall, rather than a site-wide phenomenon. Other

macroalgae in the high intertidal zone, such as *Mastocarpus* sp. gametophytes (upright stage),

showed no significant change in cover during the same time (Fig. 3B). 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 (Fig. 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

301  We observed all four kelp species present intertidally at GW having sori or sporophylls at

302 least once throughout our monitoring program (Fig. 4). Reproductive *S. latissima* was found in all

303 months except January, March, and June. *N. luetkeana* showed a clear trend in reproductive timing,

304 with sori appearing between April and September. Reproductive *Costaria costata* and *A.*

305 *marginata* were rarely observed reproducing intertidally, with three and one observed instance(s)

306 respectively, all in 2024 (Fig. 4).

Discussion

309  A lack of baseline data is a significant obstacle for quantifying changes in macroalgal

310 communities in response to climate change and other anthropogenic stressors (Bates et al. 2009;

311 Lindstrom et al. 2021). Our macroalgal monitoring program documented the diverse and dynamic

312 intertidal macroalgal community at an urban intertidal site in BC following an extreme weather

313 event (2021 heat dome), not only contributing to an improved understanding of the ecology of

314 Burrard Inlet, but also serving as a baseline against which to track the future impact of ongoing

315 anthropogenic activity (Bindoff et al. 2019; Poloczanska et al. 2013; Wonham et al. 2023).

316 Between September 2021 and July 2024, we recorded a total of 61 taxa of macroalgae and captured

317 intra- and interannual trends in community composition, including seasonal shifts in dominant

318 macroalgal taxa and a progressive multi-year decline of the foundational *F. distichus* in the upper

319 intertidal zone. The publicly available protocols and easy to update, public dataset we have

320 established provide an opportunity to continue tracking macroalgal communities, helping to

improve our understanding of the natural variation and long-term directional trends in biodiversity

between years. As of the publication date of this manuscript, the surveys are ongoing and the online

data are updated accordingly.

The interannual changes we observed in *F. distichus* abundance in the high intertidal

zone 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

(Suryan et al. 2021; Weitzman et al. 2021; Whalen et al. 2023). However, the decline observed at

GW did not appear to be closely 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 (Klinger and Fukuyama 2011; Little

et al. 2017), 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 (Klinger and Fukuyama 2011; Little et al. 2017).

Compared to our contemporary baseline data, diversity was substantially higher in the

historical 1983-1984 dataset for red, green, and brown algae. However, the historical dataset also

included subtidal taxa observed during dive surveys covering a variety of substratum types,

while we only recorded attached algae in the predominantly cobbly intertidal zone. This likely

accounts for much of the greater taxon diversity observed in the historical data. For instance,

both co-first authors have observed *Opuntiella californica*, *Sarcodiotheca furcata*, and *Smithora*

naiadum (present in the historical data) as drift at GW, but have never observed it attached

intertidally. Most other algae present in only one or the other dataset were filamentous and/or

inconspicuous, and therefore may have simply been overlooked by historical or contemporary

surveyors. Overall macroalgal taxonomic richness at GW does not appear to have meaningfully

changed over the past 40 years.

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 observed at GW was the mass

recruitment of young kelp sporophytes in spring, followed by their subsequent dieback and

replacement with green ulvoid algae throughout the summer. The large range of tidal height and

substrates on which kelp sporophytes could be found indicate that spore settlement and

sporophyte recruitment may be relatively nonselective and not tied to specific substrates. While

other studies have suggested that kelp recruitment may be mediated by coralline algae (Barner et

al. 2016; Milligan and DeWreede 2000; Okamoto et al. 2013; Twist et al. 2024), they were

unlikely to have played a significant positive or negative role as a settlement cue at GW due to

the extreme rarity of crustose corallines at GW and absence of geniculate corallines, as well as

the fact that kelp recruitment occurred in much higher regions of the intertidal zone than there

were coralline crusts. The springtime peak in recruitment observed at GW is consistent with the

known population biology of all four kelp species involved: *S. latissima* (Andersen 2013;

Nielsen et al. 2014; Raymond 2020; Ulaski et al. 2020), *C. costata* (Maxell and Miller 1996), *A.*

marginata (McConnico and Foster 2005; Raymond 2020), *N. luetkeana* (Connell 1961;

Dobkowski et al. 2019; Maxell and Miller 1996; Ulaski et al. 2020). However, overall kelp cover

in this intertidal study peaked in May and declined thereafter, while previous subtidal studies

tended to document kelps persisting into the late summer and autumn (Helmuth et al. 2006). The

early 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) common across the Northeast Pacific that exposed the intertidal zone to

increased thermal and desiccation stress (Druehl and Hsiao 1977). The concurrent increase of

ulvoid green algae 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). Summer blooms of ephemeral ulvoid algae are common in the Salish Sea,

where they may overgrow other marine macrophytes and alter biodiversity (Nelson et al. 2008,

2003; Van Alstyne 2016). In Norway, *S. latissima* beds degraded by ocean warming have been

shown to seasonally alternate with low-growing turf algae in a similar fashion to the pattern

observed at GW, with increased kelp abundance in the spring and turf dominance in the summer

(Christie et al. 2019; Moy and Christie 2012).

Intensifying thermal and desiccation stress due to ongoing climate change could

accelerate the timing and/or reduce extent of intertidal kelp recruitment, which may be

accompanied by an increase in the overall predominance of ulvoid algae at GW. In fact,

comparisons with previously published historical data 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 *M. japonica* or the kelp *U. 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.

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Competing interests

415 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
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Data availability

Current study: 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).

Garbary 1983-1984 survey: The data and an overview of survey methods are available on

the Borealis Dataverse https://doi.org/10.5683/SP3/3X3L7O.

References

455   Andersen, G.S. 2013. Patterns of *Saccharina latissima* recruitment. PLoS One. **8(12):** e81092.
456   doi:10.1371/journal.pone.0081092.

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.

Table 1. Species list.

Chlorophyta	Phaeophyceae	Rhodophyta
Acrosiphonia arcta	Alaria marginata	Ahnfeltia fastigiata
Acrosiphonia coalita	Costaria costata	Antithamnionella spirographidis
Cladophora microcladioides	Desmarestia herbacea	Besa leptophylla
Cladophora pygmaea	Desmarestia ligulata	Bonnemaisonia californica
Rhizoclonium tortuosum	Desmarestia viridis	Callophyllis sp.
Rosenvingiella polyrhiza	Elachista fucicola	Campylaephora gardneri
Ulothrix palusalsa	Fucus distichus	Caulacanthus ustulatus
Ulothrix speciosa	Hincksia ovata	Ceramothamnion pacificum
ulvoid sp.	laminariales juvenile recruits	Chondracanthus exasperatus
Urospora penicilliformis	Melanosiphon intestinalis	Constantinea subulifera
	Nereocystis luetkeana	crustose coralline
	Petalonia fascia	Cryptosiphonia woodii
	Saccharina latissima	Cumathamnion decipiens
	Sargassum muticum	Gracilaria sp. or Gracilariopsis sp.
	Scytosiphon sp.	Grateloupia californica
		Hildenbrandia sp.
		Hollenbergia subulata
		Mastocarpus crust sp.
		Mastocarpus upright sp.
		Mazzaella splendens
		Neodilsea borealis
		Neoharaldiophyllum nottii
		Odonthalia floccosa
		Pikea pinnata
		Polyneura latissima
		Polysiphonia sp.
		Prionitis sternbergii
		Pterothamnion pectinatum
		Pterothamnion sp.
		Pyropia sp.
		Sarcodiotheca gaudichaudii
		Savoiea robusta
		Scagelia pylaisaei
		Schizymenia pacifica
		Sparlingia pertusa
		Wildemania sp.

Andersen, G.S., Pedersen, M.F., Nielsen, S.L. 2013. Temperature acclimation and heat tolerance of
photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). Phyc.
49: 689–700. doi:10.1111/jpy.12077.

Atkinson, J., King, N.G., Wilmes, S.B., Moore, P.J., 2020. Summer and winter marine heatwaves
favor an invasive over native seaweeds. J. Phyc. **56**: 1591–1600. doi:10.1111/jpy.13051.

Barner, A.K., Hacker, S.D., Menge, B.A., Nielsen, K.J., 2016. The complex net effect of reciprocal
interactions and recruitment facilitation maintains an intertidal kelp community. J Ecol **104**:
33–43. doi:10.1111/1365-2745.12495.

Bates, C.R., Saunders, G.W., Chopin, T., 2009. Historical versus contemporary measures of
seaweed biodiversity in the Bay of Fundy. Botany **87**: 1066–1076. doi:10.1139/B09-067.

Bates, C.R., Scott, G., Tobin, M., Thompson, R., 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**: 617–625. doi:10.1016/j.biocon.2007.03.019.

Bindoff, N.L., Cheung, W.W.L., Kairo, J.G., Arístegui, J., Guinder, V.A., Hallberg, R., Hilmi, N., Jiao,
M.S. Karim, L. Levin, S. O'Donoghue, S.R. Purca Cuicapusa, B. Rinkevich, T. Suga, A.
Tagliabue, and P. Williamson. 2019. Changing ocean, marine ecosystems, and dependent
communities. In: IPCC special report on the ocean and cryosphere in a changing climate
[H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K.
Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)].
Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 447-587.
doi:10.1017/9781009157964.007.

Blain, C.O., Hansen, S.C., Shears, N.T. 2021. Coastal darkening substantially limits the
contribution of kelp to coastal carbon cycles. Change Biol. **27:** 5547–5563.
doi: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. Helgolander
Meeresunters. **42:** 199–241. doi:10.1007/BF02366043.

Bringloe, T.T., Saunders, G.W. 2019. DNA barcoding of the marine macroalgae from Nome, Alaska
(Northern Bering Sea) reveals many trans-Arctic species. Polar Biol. **42:** 851–864.
doi:10.1007/s00300-019-02478-4

Cargo and terminals. 2015. Port of Vancouver. URL https://www.portvancouver.com/cargo-
terminals/ (accessed 1.19.24).

Casas, G., Scrosati, R., Luz Piriz, M. 2004. The invasive kelp *Undaria Pinnatifida* (Phaeophyceae,
Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biol.
Invasions. **6:** 411–416. doi:10.1023/B:BINV.0000041555.29305.41.

Christie, H., Andersen, G.S., Bekkby, T., Fagerli, C.W., Gitmark, J.K., Gundersen, H., Rinde, E. 2019.
Shifts between sugar kelp and turf algae in Norway: Regime shifts or fluctuations between
different opportunistic seaweed species? Front. Mar. Sci. **6:**
doi:10.3389/fmars.2019.00072.

Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution
of the barnacle *Chthamalus stellatus*. Ecology. **42:** 710–723. doi:10.2307/1933500.

Davidson, L.W. 1973. On the physical oceanograhy of Burrard Inlet and Indian Arm, British
Columbia. University of British Columbia.

Davison, I.R., Pearson, G.A. 1996. Stress tolerance in intertidal seaweeds. J. Phyc. **32:** 197–211.
doi:10.1111/j.0022-3646.1996.00197.x.

Dayton, P.K. 1985. Ecology of kelp communities. Annu. Rev. of Ecol. Syst. **16:** 215–245.
doi:10.1146/annurev.es.16.110185.001243.

de la Hoz, C.F., Ramos, E., Puente, A., Juanes, J.A. 2019. Climate change induced range shifts in
seaweeds distributions in Europe. Res. **148:** 1–11. doi:10.1016/j.marenvres.2019.04.012
Demes, K.W., Kordas, R.L., Jorve, J.P. 2012. Ferry wakes increase seaweed richness and
abundance in a sheltered rocky intertidal habitat. Hydrobiologia. **693:** 1–11.
doi:10.1007/s10750-012-1082-4.
Dobkowski, K.A., Flanagan, K.D., Nordstrom, J.R. 2019. Factors influencing recruitment and
appearance of bull kelp, *Nereocystis luetkeana* (phylum Ochrophyta). J Phycol. **55:** 236–
244. doi:10.1111/jpy.12814.
Druehl, L., Green, J. 1982. Vertical distribution of intertidal seaweeds as related to patterns of
submersion and emersion. Mar. Ecol. Prog. Ser. **9:** 163–170. doi:10.3354/meps009163.
Druehl, L.D., Hsiao, S.I.C. 1977. Intertidal kelp response to seasonal environmental changes in a
British Columbia Inlet. J. Fish. Res. Bd. Can. **34:** 1207–1211. doi:10.1139/f77-176.
Ducrotoy, J. 1999. Indications of change in the marine flora of the North Sea in the 1990s. Mar.
Pollut. Bull. **38:** 646–654. doi:10.1016/S0025-326X(98)00195-7.
Eger, A.M., Marzinelli, E.M., Beas-Luna, R., Blain, C.O., Blamey, L.K., Byrnes, J.E.K., Carnell, P.E.,
Choi, C.G., Hessing-Lewis, M., Kim, K.Y., Kumagai, N.H., Lorda, J., Moore, P., Nakamura, Y.,
Pérez-Matus, A., Pontier, O., Smale, D., Steinberg, P.D., Vergés, A. 2023. The value of
ecosystem services in global marine kelp forests. Nat Commun. **14:** 1894.
doi:10.1038/s41467-023-37385-0.
Félix-Loaiza, A.C., Rodríguez-Bravo, L.M., Beas-Luna, R., Lorda, J., Cruz-González, E. de L.,
Malpica-Cruz, L., 2022. Marine heatwaves facilitate invasive algae takeover as foundational
kelp. Bot. Mar. **65:** 315–319. doi:10.1515/bot-2022-0037.
Fitter, A.H., Fitter, R.S.R. 2002. Rapid changes in flowering time in British plants. Science. **296:**
1689–1691. doi:10.1126/science.1071617.
Gabrielson, P.W., Lindstrom, S.C. 2018. Keys to the seaweeds and seagrasses of Southeast
Alaska, British Columbia, Washington, and Oregon. Sandra C Lindstrom, Department of
Botany, University of British Columbia. **Ed 2**. ISBN: 9780976381730.
Gao, G., Clare, A.S., Rose, C., Caldwell, G.S. 2017. Eutrophication and warming-driven green tides
(*Ulva rigida*) are predicted to increase under future climate change scenarios. Mar. Poll.
Bull. **114**: 439–447. doi:10.1016/j.marpolbul.2016.10.003.
Gao, S., Shen, S., Wang, G., Niu, J., Lin, A., Pan, G. 2011. PSI-driven cyclic electron flow allows
intertidal macro-algae *Ulva* sp. (Chlorophyta) to survive in desiccated conditions. Plant and
Cell Physiology. **52:** 885–893. doi:10.1093/pcp/pcr038.
Guiry, M.D., Guiry, G.M. 2024. AlgaeBase. World-wide electronic publication. Accessed 2024-11-
27. URL: https://www.algaebase.org/.
Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P., Bertness, M.D. 2007. Incorporating positive
interactions in aquatic restoration and conservation. Front. Ecol. Environ. **5:** 153–160.
doi:10.1890/1540-9295(2007)5[153:IPIIAR]2.0.CO;2.
Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A., Graham, M.H.
2012. Effects of climate change on global seaweed communities. J. Phyc. **48:** 1064–1078.
doi:10.1111/j.1529-8817.2012.01224.x.
Harley, C.D.G., Paine, R.T. 2009. Contingencies and compounded rare perturbations dictate
sudden distributional shifts during periods of gradual climate change. Proc. Natl. Acad. Sci.
U.S.A. **106:** 11172–11176. doi:10.1073/pnas.0904946106.
Heery, E.C., Hoeksema, B.W., Browne, N.K., Reimer, J.D., Ang, P.O., Huang, D., Friess, D.A., Chou,
L.M., Loke, L.H.L., Saksena-Taylor, P., Alsagoff, N., Yeemin, T., Sutthacheep, M., Vo, S.T.,
Bos, A.R., Gumanao, G.S., Syed Hussein, M.A., Waheed, Z., Lane, D.J.W., Johan, O.,
Kunzmann, A., Jompa, J., Suharsono, Taira, D., Bauman, A.G., Todd, P.A. 2018. Urban coral

reefs: Degradation and resilience of hard coral assemblages in coastal cities of East and
Southeast Asia. Mar. Poll. Bull. **135:** 654–681. doi:10.1016/j.marpolbul.2018.07.041.
Helmuth, B., Broitman, B.R., Blanchette, C.A., Gilman, S., Halpin, P., Harley, C.D.G., O'Donnell,
M.J., Hofmann, G.E., Menge, B., Strickland, D. 2006. Mosaic patterns of thermal stress in
the rocky intertidal zone: Implications for climate change. Ecol. Monogr. **76:** 461–479.
doi:10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2.
Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D.,
Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R.,
Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R.,
Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A.,
Swadling, K.M., Taw, N. 2011. Climate change cascades: Shifts in oceanography, species'
ranges and subtidal marine community dynamics in eastern Tasmania. J. Exp. Mar. Bio.
Ecol. **400:** 17–32. doi:10.1016/j.jembe.2011.02.032.
Kassambara, A., 2022. ggpubr: "ggplot2" Based Publication Ready Plots.
Klinger, T., Fukuyama, A.K. 2011. Decadal-scale dynamics and response to pulse disturbance in
the intertidal rockweed *Fucus distichus* (Phaeophyceae). Mar. Ecol. **32:** 313–319.
doi:10.1111/j.1439-0485.2011.00481.x.
Levings, C.D., Stewart, H.L. 2020. Research priorities for nearshore algae in coastal British
Columbia workshop and gap analysis – final report. Fisheries and Oceans Canada.
Lilley, S.A., Schiel, D.R. 2006. Community effects following the deletion of a habitat-forming alga
from rocky marine shores. Oecologia. **148:** 672–681. doi:10.1007/s00442-006-0411-6.
Lima, F.P., Wethey, D.S. 2012. Three decades of high-resolution coastal sea surface temperatures
reveal more than warming. Nat Commun. **3:** 704. doi:10.1038/ncomms1713.
Lindstrom, S.C. 1973. Marine Benthic Algal Communities in the Flat Top Islands Area of Georgia
Strait. Univeristy of British Columbia.
Lindstrom, S.C., Lemay, M.A., Starko, S., Hind, K.R., Martone, P.T. 2021. New and interesting
seaweed records from the Hakai area of the central coast of British Columbia, Canada:
Chlorophyta. Bot. Mar. **64:** 343–361. doi:10.1515/bot-2021-0038.
Little, C., Trowbridge, C.D., Pilling, G.M., Stirling, P., Morritt, D., Williams, G.A. 2017. Long-term
fluctuations in intertidal communities in an Irish sea-lough: Limpet-fucoid cycles. ESCA.
196: 70–82. doi:10.1016/j.ecss.2017.06.036.
Mann, K.H. 1973. Seaweeds: Their productivity and strategy for growth. Science. **182:** 975–981.
Maxell, B.A., Miller, K.A. 1996. Demographic studies of the annual kelps *Nereocystis luetkeana* and
Costaria costata (Laminariales, Phaeophyta) in Puget Sound, Washington. Bot. Mar. **39:**
479–490. doi:10.1515/botm.1996.39.1-6.479.
McConnico, L.A., Foster, M.S. 2005. Population biology of the intertidal kelp, *Alaria marginata*
Postels and Ruprecht: A non-fugitive annual. J. Exp. Mar. Bio. Ecol. **324:** 61–75.
doi:10.1016/j.jembe.2005.04.006.
Miller, A., Ambrose, R. 2000. Sampling patchy distributions:comparison of sampling designs in
rocky intertidal habitats. Mar. Ecol. Prog. Ser. **196:** 1–14. doi:10.3354/meps196001.
Milligan, K.L.D., DeWreede, R.E. 2000. Variations in holdfast attachment mechanics with
developmental stage, substratum-type, season, and wave-exposure for the intertidal kelp
species *Hedophyllum sessile* (C. Agardh) Setchell. J. Exp. Mar. Bio. Ecol. **254:** 189–209.
doi:10.1016/S0022-0981(00)00279-3.
Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E., Thibaut, T., Van
Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E.A., De Clerck, O. 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. J. Sea Res. **98:** 91–108.doi:10.1016/j.seares.2014.11.004.
Moy, F.E., Christie, H. 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral
algae along the south and west coast of Norway. Mar. Biol. Res. 8: 309–321.
doi:10.1080/17451000.2011.637561.
Neilson-Welsh, L. 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., Haberlin, K., Nelson, A.V., Ribarich, H., Hotchkiss, R., Alstyne, K.L.V., Buckingham, L.,
Simunds, D.J., Fredrickson, K. 2008. Ecological and physiological controls of species
composition in green macroalgal blooms. Ecology. **89:** 1287–1298. doi:10.1890/07-0494.1.
Nelson, T.A., Nelson, A.V., Tjoelker, M. 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:** 263–275. doi:10.1515/BOT.2003.024.
Nielsen, M.M., Krause-Jensen, D., Olesen, B., Thinggaard, R., Christensen, P.B., Bruhn, A. 2014.
growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay,
Denmark, and along the species' distribution range. Mar Biol. **161:** 2011–2022.
doi:10.1007/s00227-014-2482-y.
Okamoto, D.K., Stekoll, M.S., Eckert, G.L. 2013. Coexistence despite recruitment inhibition of kelps
by subtidal algal crusts. **493:** 103–112. doi:10.3354/meps10505.
Olabarria, C., Arenas, F., Viejo, R.M., Gestoso, I., Vaz-Pinto, F., Incera, M., Rubal, M., Cacabelos,
E., Veiga, P., Sobrino, C. 2013. Response of macroalgal assemblages from rockpools to
climate change: effects of persistent increase in temperature and CO2. Oikos. **122:** 1065–
1079. doi:10.1111/j.1600-0706.2012.20825.x.
Parmesan, C., Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across
natural systems. Nature. **421:** 37–42. doi:10.1038/nature01286.
Pawluk, K.A. 2016. Impacts and interactions of two non-indigenous seaweeds *Mazzaella japonica*
(Mikami) Hommersand and *Sargassum muticum* (Yendo) Fensholt in Baynes Sound, British
Columbia (Thesis).
Pfister, C.A., Altabet, M.A., Weigel, B.L. 2019. Kelp beds and their local effects on seawater
chemistry, productivity, and microbial communities. Ecology. **100:** e02798.
doi:10.1002/ecy.2798.
Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J.,
Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding,
J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A.,
Richardson, A.J. 2013. Global imprint of climate change on marine life. Nat. Clim. Change.
3: 919–925. doi:10.1038/nclimate1958.
R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for
Statistical Computing, Vienna, Austria.
Rawal, D.S., Kasel, S., Keatley, M.R., Nitschke, C.R. 2015. Herbarium records identify sensitivity of
flowering phenology of eucalypts to climate: Implications for species response to climate
change. Austral Ecol. **40:** 117–125. doi:10.1111/aec.12183.
Raymond, A.E.T. 2020. Life cycles of the kelps *Saccharina latissima* and *Alaria marginata*:
implications for mariculture and ecology in Alaska (Thesis).
Rogers-Bennett, L., Catton, C.A. 2019. Marine heat wave and multiple stressors tip bull kelp forest
to sea urchin barrens. Sci Rep. **9:** 15050. doi:10.1038/s41598-019-51114-y.

Ryan, S.A., Wohlgeschaffen, G.D., Jahan, N., Niu, H., Ortmann, A.C., Brown, T.N., King, T.L.,
Clyburne, J. 2019. State of knowledge on fate and behaviour of ship-source petroleum
product spills. Fisheries and Oceans Canada = Pêches et océans Canada, Ottawa.
Salvaterra, T., Green, D.S., Crowe, T.P., O'Gorman, E.J. 2013. Impacts of the invasive alga
Sargassum muticum on ecosystem functioning and food web structure. Biol. Invasions. **15:**
2563–2576. doi:10.1007/s10530-013-0473-4.
Saunders, G., Millar, K. 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:** doi:10.1139/cjb-2013-0283.
Silva, P., Woodfield, R., Cohen, A., Harris, L., Goddard, J. 2002. First Report of the Asian kelp
Undaria pinnatifida in the Northeastern Pacific Ocean. Biol. Invasions. **4:** 333–338.
doi:10.1023/A:1020991726710.
Starko, S., Bailey, L.A., Creviston, E., James, K.A., Warren, A., Brophy, M.K., Danasel, A., Fass, M.P.,
Townsend, J.A., Neufeld, C.J. 2019. Environmental heterogeneity mediates scale-
dependent declines in kelp diversity on intertidal rocky shores. PLoS One. **14:** e0213191.
doi:10.1371/journal.pone.0213191.
Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J.
2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Envir. Conserv.
29: 436–459. doi:10.1017/S0376892902000322.
Suryan, R.M., Arimitsu, M.L., Coletti, H.A., Hopcroft, R.R., Lindeberg, M.R., Barbeaux, S.J., Batten,
S.D., Burt, W.J., Bishop, M.A., Bodkin, J.L., Brenner, R., Campbell, R.W., Cushing, D.A.,
Danielson, S.L., Dorn, M.W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D.H., Hatch,
S.A., Haught, S., Holderied, K., Iken, K., Irons, D.B., Kettle, A.B., Kimmel, D.G., Konar, B.,
Kuletz, K.J., Laurel, B.J., Maniscalco, J.M., Matkin, C., McKinstry, C.A.E., Monson, D.H.,
Moran, J.R., Olsen, D., Palsson, W.A., Pegau, W.S., Piatt, J.F., Rogers, L.A., Rojek, N.A.,
Schaefer, A., Spies, I.B., Straley, J.M., Strom, S.L., Sweeney, K.L., Szymkowiak, M.,
Weitzman, B.P., Yasumiishi, E.M., Zador, S.G. 2021. Ecosystem response persists after a
prolonged marine heatwave. Sci Rep. **11:** 6235. doi:10.1038/s41598-021-83818-5.
Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A. 2017. The role of kelp species as biogenic habitat
formers in coastal marine ecosystems. J. Exp. Mar. Biol. Ecol. **492:** 81–98.
doi:10.1016/j.jembe.2017.01.017.
Thom, R.M., Albright, R.G. 1990. Dynamics of benthic vegetation standing-stock, irradiance, and
water properties in central Puget Sound. Mar. Biol. **104:** 129–141. doi:10.1007/BF01313166.
Todd, P.A., Heery, E.C., Loke, L.H.L., Thurstan, R.H., Kotze, D.J., Swan, C. 2019. Towards an urban
marine ecology: characterizing the drivers, patterns and processes of marine ecosystems
in coastal cities. Oikos. **128:** 1215–1242. doi:10.1111/oik.05946.
Tsleil-Waututh Nation, 2017. Burrard Inlet Action Plan (2017 version).
Twist, B.A., Mazel, F., Zaklan Duff, S., Lemay, M.A., Pearce, C.M., Martone, P.T. 2024. Kelp and sea
urchin settlement mediated by biotic interactions with benthic coralline algal species. J
Phyc. **60:** 363–379. doi:10.1111/jpy.13420.
Ulaski, B.P., Konar, B., Otis, E.O. 2020. Seaweed reproduction and harvest rebound in Southcentral
Alaska: Implications for wild stock management. ESCO. **43:** 2046–2062.
doi:10.1007/s12237-020-00740-1.
Van Alstyne, K.L. 2016. Seasonal changes in nutrient limitation and nitrate sources in the green
macroalga *Ulva lactuca* at sites with and without green tides in a northeastern Pacific
embayment. Marine Pollution Bulletin. 103: 186–194.
doi:10.1016/j.marpolbul.2015.12.020.

Vergés, A., Campbell, A.H., Wood, G., Kajlich, L., Eger, A.M., Cruz, D., Langley, M., Bolton, D.,
Coleman, M.A., Turpin, J., Crawford, M., Coombes, N., Camilleri, A., Steinberg, P.D.,
Marzinelli, E.M. 2020. Operation Crayweed: Ecological and sociocultural aspects of
restoring Sydney's underwater forests. Ecol. Manag. Restor. **21:** 74–85.
doi:10.1111/emr.12413.
Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D.,
Lindeberg, M. 2021. Changes in Rocky Intertidal Community Structure During a Marine
Heatwave in the Northern Gulf of Alaska. Front. Mar. Sci. **8:** 2296-7745. doi:
10.3389/fmars.2021.556820.
Wernberg, T., Smale, D.A., Thomsen, M.S. 2012. A decade of climate change experiments on
marine organisms: procedures, patterns and problems. Glob. Chang. Biol. **18:** 1491–1498.
doi:10.1111/j.1365-2486.2012.02656.x.
Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Staehr, P.A., Toohey, B.D. 2010. Decreasing
resilience of kelp beds along a latitudinal temperature gradient: potential implications for a
warmer future. Ecol. Lett. **13:** 685–694. doi:10.1111/j.1461-0248.2010.01466.x.
Whalen, M.A., Starko, S., Lindstrom, S.C., Martone, P.T. 2023. Heatwave restructures marine
intertidal communities across a stress gradient. Ecology. **104:** e4027.
doi:10.1002/ecy.4027.
White, R.H., Anderson, S., Booth, J.F., Braich, G., Draeger, C., Fei, C., Harley, C.D.G., Henderson,
S.B., Jakob, M., Lau, C.-A., Mareshet Admasu, L., Narinesingh, V., Rodell, C., Roocroft, E.,
Weinberger, K.R., West, G. 2023. The unprecedented Pacific Northwest heatwave of June
2021. Nat. Com. **14:** 727. doi:10.1038/s41467-023-36289-3.
Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
Wickham, H. 2011. The Split-Apply-Combine Strategy for Data Analysis. J. Stat. Softw. **40:** 1–29.
Wonham, M., Gerstle, C., Bates, C. 2023. Combining current and historical biodiversity surveys
reveals order of magnitude greater richness in a British Columbia marine protected area.
Can. Field. Nat. **136:** 348–360. doi:10.22621/cfn.v136i4.2903.
Zabin, C., Ashton, G., Brown, C., Ruiz, G. 2009. Northern range expansion of the Asian kelp *Undaria*
pinnatifida (Harvey) Suringar (Laminariales, Phaeophyceae) in western North America. AI. **4:**
429–434. doi:10.3391/ai.2009.4.3.1.
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