



# Local and regional variation in kelp loss and stability across coastal British Columbia

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**ABSTRACT:** Kelp forests are among the most abundant coastal marine habitats but are vulnerable to climate change. The Northeast Pacific has experienced recent large-scale changes in kelp abundance and distribution, but little is known about changes north of the British Columbia (BC) – Washington border. Here, we assessed whether and how floating canopy kelp (*Macrocystis pyrifera*, *Nereocystis luetkeana*) distributions have changed in recent decades along the extensive coast of BC. We assembled and analysed available kelp distributional data, comparing snapshots of kelp linear extent from 1.5–3 decades ago (1994–2007) to recently collected data (2017–2021) across 11 different subregions spanning the province. We then leveraged timeseries, where available ( $n = 7$  data sets), to contextualise patterns of change. In aggregate, the data suggest that kelp forests have declined considerably in some parts of the province, but with variable patterns of change across BC. In the warmest areas (southern BC), kelp persistence was negatively correlated with mean summer sea surface temperatures, which at times exceeded known thermal tolerances. In contrast, in northern subregions, top-down control by sea urchins and otters appeared to modulate kelp dynamics, with declines occurring in 2 subregions despite cool ocean temperatures. Timeseries data suggest that many declines occurred around the 2014–2016 marine heatwave, an event associated with sustained warming and altered trophic dynamics. Our results suggest that the extent of BC's kelp forests has declined in some places in recent decades, but that regional and local-scale factors influence their responses to environmental change.

**KEY WORDS:** Climate change · Extirpation · Kelp forest · Marine heatwaves · Sea star wasting disease · Trophic cascade · *Macrocystis* · *Nereocystis*

## 1. INTRODUCTION

Climate change and other anthropogenic stressors are causing large-scale changes in our ocean ecosys-

tems (Jackson et al. 2001, Brierley & Kingsford 2009, Mearns et al. 2010, Smale et al. 2019, Wernberg et al. 2024), at times driving rapid regime shifts to states of less desirable structure and function (Scheffer & Car-

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penter 2003). These shifts can result in the loss of habitat or productivity, which may have cascading effects on organisms that use those ecosystems (Folke et al. 2004, deYoung et al. 2008) and human communities that rely on them (e.g. Cesar et al. 2003, Pecl et al. 2017). The impacts of climate change and other human activities have driven widespread regime shifts across a range of coastal ecosystems, including coral reefs (e.g. Graham et al. 2015, Arif et al. 2022), seagrass meadows (e.g. Moksnes et al. 2018, Chefaoui et al. 2021) and seaweed communities (e.g. Filbee-Dexter & Scheibling 2014, Wernberg et al. 2016, Filbee-Dexter & Wernberg 2018). In temperate ecosystems, which often experience large seasonal and interannual fluxes in temperature and other climate-related variables, kelp forests are among the most abundant marine ecosystems (Jayathilake & Costello 2021, Starko et al. 2021) but are threatened in many regions (Pörtner et al. 2019, Wernberg et al. 2019). Kelp forests provide essential habitat for a wide range of ecologically and economically important species, including fishes, invertebrates and other seaweed species (Steneck et al. 2002, Teagle et al. 2017, Shaffer et al. 2020). Moreover, they are highly productive and therefore fuel the growth of higher trophic levels (Duggins et al. 1989, Pessarrodona et al. 2022). Thus, declines in kelp forest abundance and extent can have far-reaching consequences for nearshore ecosystems and beyond (Wernberg et al. 2019).

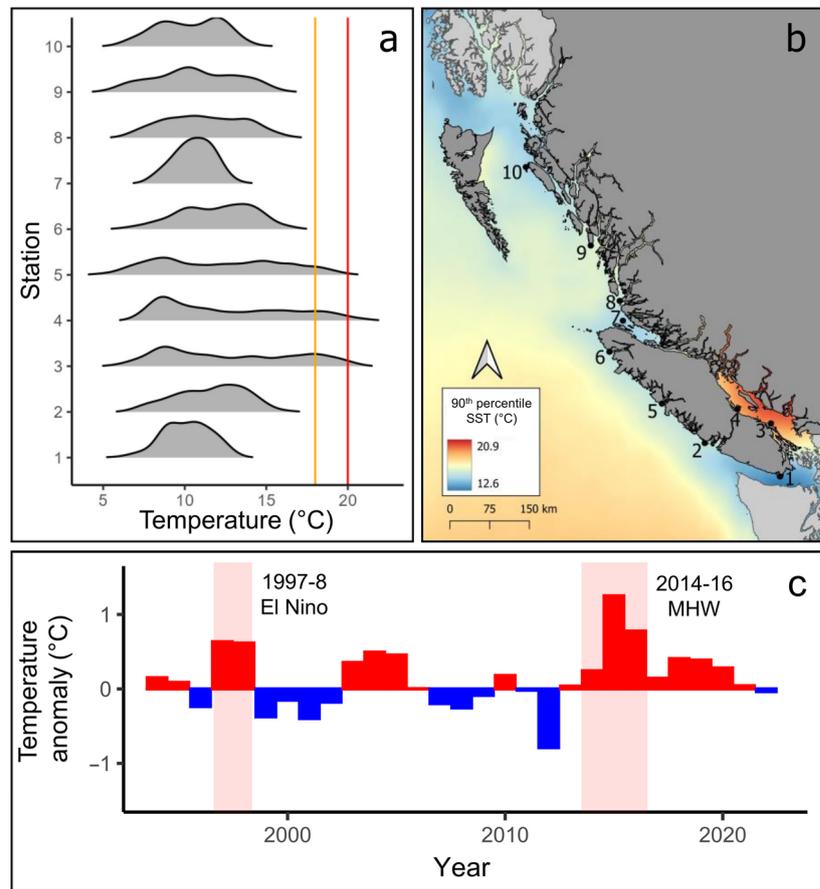
Evidence collected over the past 2 or more decades indicates that kelp forests are decreasing in abundance and extent across certain parts of the world due to combined effects of climate change and localized threats, including fishing, sewage run-off, invasive species and changes in freshwater outflow (Krumhansl et al. 2016, Filbee-Dexter & Wernberg 2018, Wernberg et al. 2019, Hollarsmith et al. 2022). In fact, the IPCC ranks kelp forests as the second most vulnerable coastal marine ecosystem to climate change (second only to coral reefs; Pörtner et al. 2019). However, the trajectories of kelp forests around the world have been highly variable, with some regions showing stability (e.g. Chile and the Falkland Islands: Mora-Soto et al. 2021; outer coasts of Oregon and Washington, USA: Pfister et al. 2018, Hamilton et al. 2020, Tolimeiri et al. 2022) or even increases in abundance (e.g. Gulf of Alaska: Hollarsmith et al. 2024; South Africa: Bolton et al. 2012), highlighting the variability in kelp forest trajectories at global, regional and local scales (Krumhansl et al. 2016, Wernberg et al. 2019, 2024). Where the collapse of kelp forest ecosystems has occurred, this has generally been associated with transitions to urchin barrens or commu-

nities formed by other (non-kelp) seaweeds (Wernberg et al. 2019, 2024), and there is evidence that transitions between these states can be challenging to reverse, often failing to return to the kelp forest state even after initial stressors are abated (Leinaas & Christie 1996, Hughes et al. 2005, Pearse 2006, Filbee-Dexter & Wernberg 2018, Feehan et al. 2019). In some areas, kelp forest losses have had profound ecological and economic consequences from the collapse and closure of fisheries to detrimental impacts on tourism-based industries (Rogers-Bennett & Catton 2019).

The direct and indirect effects of ocean warming and marine heatwaves (MHWs) are among the biggest threats to kelp forests (Pörtner et al. 2019, Smale et al. 2019, Wernberg et al. 2019). MHWs are periods of unusually warm water that are becoming longer, more frequent and more intense as a result of climate change (Frölicher et al. 2018, Holbrook et al. 2020, Smith et al. 2023). These events threaten kelp forests both through the direct physiological effects of warm temperatures (especially if they exceed the thermal tolerance limits of a given kelp species) and through indirect effects associated with changes in trophic dynamics (Vergés et al. 2016, Rogers-Bennett & Catton 2019, Starko et al. 2022). In the Northeast Pacific, the period between 2014 and 2016 was characterised by a large-scale MHW known as 'The Blob' that drove rapid and persistent increases in summer sea surface temperature (SST) (Di Lorenzo & Mantua 2016, Tseng et al. 2017, Robinson et al. 2022). Kelp forests were negatively impacted both through physiological stress and die-back from extreme temperatures (Arafeh-Dalmau et al. 2019, Cavanaugh et al. 2019, Starko et al. 2019, 2022) and from the indirect impacts caused by the growing sea star wasting disease (SSWD) epidemic which was exacerbated by warm waters during this time period (Harvell et al. 2019, Rogers-Bennett & Catton 2019, Hamilton et al. 2021).

SSWD resulted in the functional extinction of the sunflower sea star *Pycnopodia helianthoides* across much of its distribution (Harvell et al. 2019, Hamilton et al. 2021), triggering trophic cascades that favoured sea urchins, the dominant herbivore of kelp forests (Schultz et al. 2016, Burt et al. 2018, Rogers-Bennett & Catton 2019, McPherson et al. 2021, Starko et al. 2022). The combined effects of warming and expanding urchin populations have driven kelp forest losses throughout the Northeast Pacific (Beas-Luna et al. 2020), with severe impacts observed in populations of both major floating canopy-forming kelp species: giant kelp *Macrocystis pyrifera* and bull kelp *Nereocystis luetkeana*. Additionally, while some kelp forests have recovered (Cavanaugh et al. 2023, Tolimieri et al. 2023), losses

Fig. 1. Sea surface temperature across space and time in coastal British Columbia (BC), Canada. (a) *In situ* temperature data measured at high tide in the summers (21 Jun to 20 Sep) of 2014 to 2017. Data are from Fisheries and Oceans Canada Lighthouse Stations (labelled 1–10) along the coast of BC. Plots indicate the relative density of all summer temperature measurements from 2014 to 2017. The orange line indicates 18°C and the red line indicates 20°C, which reflect known temperature thresholds for the kelp species investigated here (Muth et al. 2019, Supratya et al. 2020, Fernández et al. 2020). (b) Distribution of 90th percentile sea surface temperatures (SST) during the summers of 2014–2017 relative to the locations of lighthouse stations. (c) Annual temperature anomalies through time based on average of 4 stations that span the latitudinal range of BC (Stns 2, 4, 8, 10). MHW: marine heatwave



have continued or persisted in other areas (Finger et al. 2021, McPherson et al. 2021, Starko et al. 2022) as temperatures have remained warm (Chen et al. 2021, Starko et al. 2022, Mora-Soto et al. 2024; Fig. 1), and subsequent MHWs occurred in 2019–2020 (Chen et al. 2021, Whalen et al. 2023). Sunflower sea stars have also experienced limited recovery (Hamilton et al. 2021), allowing urchin populations to remain elevated (McPherson et al. 2021, Smith et al. 2021, Tolimieri et al. 2023).

Despite the growing evidence that MHWs and other extreme events have negatively impacted kelp forest ecosystems, the sheer extent and heterogeneity of these ecosystems makes it challenging to assess the scale of kelp deforestation. Kelp forests occupy more than one-third of the world's coastlines, an area 5 times that of coral reefs (Jayathilake & Costello 2021), and floating kelp forests occupy a range of  $>30^\circ$  latitude on the west coast of North America alone. Thus, widespread declines could have profound impacts on the availability of coastal habitat for associated species and the magnitude of nearshore productivity. This could have important implications for economically critical fisheries that rely on kelp habitats throughout

the Northeast Pacific, such as salmon and herring (Shaffer et al. 2019, 2020), and might also impact the extent to which coastal ecosystems cycle carbon at both global and regional scales (Krause-Jensen et al. 2018, Filbee-Dexter & Wernberg 2020).

To comprehensively assess the spatial scale and extent of kelp forest loss, we must work to incorporate historically understudied regions, including those that lack detailed multi-decadal timeseries, leveraging all available data to draw reliable inferences about how kelp forest distributions are changing. One region in which kelp forests have historically been understudied is the province of British Columbia (BC), Canada. Past glaciation has left BC's coast scarred with bays, fjords and channels that create inshore pockets of water that can experience highly variable oceanographic conditions. Indeed, some of these pockets warm up in the summer to temperatures comparable to near the southern limit of either kelp species (Starko et al. 2022). For example, waters in both the inner Salish Sea and the west coast of Vancouver Island have reached temperatures greater than  $20^\circ\text{C}$  in recent summers (Stns 3–5 in Fig. 1; Starko et

al. 2022). This is warmer than known growth optima for both canopy-forming kelp species (Fernández et al. 2020, Supratya et al. 2020), and crosses experimental thresholds of thermal tolerance (Lüning & Freshwater 1988, Muth et al. 2019, Supratya et al. 2020, Weigel et al. 2023), suggesting that in warm areas of BC, kelps are likely already threatened by intensifying warm-water events (i.e. MHWs). Indeed, recent fieldwork along focal stretches of the BC coast suggests that kelp forest declines have already occurred in some of these warm microclimates (Gendall 2022, Starko et al. 2019, 2022, Mora-Soto et al. 2024).

Kelp declines have also been documented elsewhere in BC in response to growing sea urchin populations (Schultz et al. 2016, Burt et al. 2018, Starko et al. 2022), suggesting that threats to kelp forests may be widespread across even cool parts of the province. Although refugial populations of *Pycnopodia* sea stars remain in BC, models comparing their current (2017–2020) and pre-epidemic (2009–2012) distributions indicate extreme declines in these predators across the entire province (Hamilton et al. 2021), suggesting that the ecological release of sea urchins associated with SSWD likely continues to cover most of the province. However, the impacts of SSWD on kelp forests likely depend on food chain length and structure. Specifically, when non-echinoderm urchin predators are present in addition to predatory sea stars, they potentially introduce functional redundancy, limiting the effects of sea star loss on the abundance of urchins and the subsequent effects on kelp forests (Burt et al. 2018, Eisaguirre et al. 2020). Given that sea otters, which prey heavily on urchins, are abundant in some parts of BC but not others (Nichol et al. 2020), the extent to which these threats are a concern across BC's nearly 26 000 km coastline (more than twice that of California, Oregon and Washington combined) remains largely unclear.

Here, we asked whether the extent of kelp forests in several parts of coastal BC has changed over the past 2–3 decades, in the context of recent environmental and biotic drivers, by assembling available data on kelp forest distributions. We focused on data of 2 types: (1) 'snapshot' data ( $n = 11$  subregions) from 2 timepoints spanning the period of interest, and (2) timeseries data ( $n = 7$  data sets) with higher temporal resolution (i.e. at least 3 years of data). Because many areas lack long-term monitoring programmes, we first present snapshot analyses with the intention of using these data of limited temporal coverage to offer a first pass approximation of how kelp forest linear extent (i.e. presence–absence along stretches of coastline) has changed over the past few decades, while

acknowledging limitations associated with sampling dynamic populations at only 2 timepoints. These data are primarily derived from very high-resolution oblique shoreline photography, but for 1 subregion were derived from high-resolution (<3 m) satellite imagery. For each subregion ( $n = 11$ ), 1 sampling point from 1.5–3 decades ago (1994–2007) and a second sampling point from the last few years (2017–2021) are included. We then used available timeseries data ( $n = 7$  data sets) near or within snapshot subregions to put patterns of change observed in the snapshot analyses into a more robust temporal context and determine the likely timing of any changes in kelp forest extent or abundance. For presentation, and to account for spatial variation in the timing of imagery (see Section 2), we grouped both data types into 3 geographic regions (Southern, Central and Northern; Tables 1 & 2). Overall, we asked 4 questions: (1) Have kelp forests experienced more losses (i.e. local-scale extirpations) than gains (i.e. local expansions) across the areas of BC for which data are available? (2) How extensive have changes in kelp extent been? (3) Is there evidence that local environmental conditions (e.g. temperature) have mediated the impacts of environmental change on kelp forest distributions (for example, with warmer areas more likely to experience kelp declines)? and (4) Have areas with sea otters been more likely to persist or even expand through recent perturbations due to top-down control on urchin populations? Overall, this assessment aims to offer a first approximation of how kelp forests have changed in several parts of BC over recent decades with the goal of informing whether floating kelp forests (*Macrocystis* and *Nereocystis*) are of conservation concern in parts of BC.

## 2. MATERIALS AND METHODS

### 2.1. Study design

We selected study areas based primarily on data availability, and with the goals of capturing a range of SSTs as well as regions with and without sea otters. We began with analyses of 2 timepoints (hereafter, 'snapshot analyses'; Table 1) to offer an approximation of changes in kelp distributions from before and after the onset of recent heatwaves and the decline in *Pycnopodia* populations. Because both warming and losses of *Pycnopodia* began in late 2013 or early 2014 in BC (Di Lorenzo & Mantua 2016, Hamilton et al. 2021), we used data from 1 year between 1994 and 2007 as 'early' data (Timepoint 1) and from 1 year

Table 1. Study regions used to assess changes in canopy kelp distribution from 'snapshot' analyses. Asterisks (\*) indicate subregions (i–xi) that were also included in timeseries analyses. Sample size indicates the number of shoreline segments per subregion. For region, S: Southern; C: Central; N: Northern. For kelp species present, MP: *Macrocystis pyrifera*; NL: *Nereocystis luetkeana*; † indicates which species is more common when both are present. For otter status: +: increasing populations; –: otter populations not present

Sub-region	Subregion name	Region	Latitude	Longitude	Timepoint 1	Timepoint 2	Sample size	Otter status	Kelp species present
i	Valdes and Gabriola Islands	S	49.0 to 49.2	–123.6 to –123.8	29 July 2004	7 August 2021	50	–	NL
ii*	Mayne and Saturna Islands	S	48.8 to 48.9	–123.0 to –123.4	29 July 2004	7 August 2021	98	–	NL
iii*	Cowichan Bay	S	48.7 to 48.8	–123.5 to –123.7	24 September 2004	27 July 2017	97	–	NL
iv	Juan de Fuca Entrance	S	48.5 to 48.6	–124.3 to –124.7	13–14 August 2007	9 August 2021	117	–	NL
v	West Coast Trail	S	48.6 to 48.8	–125.2 to –125.3	14 August 2007	8–9 August 2021	140	–	MP, NL†
vi*	Barkley Sound	S	48.8 to 48.9	–125.0 to –125.2	14 August 2007	8 August 2021	290	–	MP†, NL
vii	Nootka Sound	C	49.4 to 49.6	–126.5 to –126.8	26 June 1994	24 July 2021	74	+	MP†, NL
viii	Quatsino Sound	C	50.3 to 50.5	–127.5 to –128.2	17 May 1999	17 June 2018	61	+	MP†, NL
ix*	South Central Coast*	N	51.8 to 52.2	–128.2 to –128.6	21 July 1997	18 May 2018	38	+	MP†, NL
x*	Laredo Sound*	N	52.4 to 52.8	–128.8 to –129.3	24 July 1997 and 12–13 July 1998	7 July 2019	82	–	MP, NL†
xi	Dundas Island	N	52.6 to 54.4	–130.7 to –131.0	2 July 2000	4 July 2019	114	–	MP, NL†

Table 2. Summary of data sources used for timeseries analysis. Asterisks (\*) indicate timeseries data sets that are geographically within subregions from the snapshot analyses (see Table 1). Note that timeseries are generally not continuous but include some gap years. For specific years and dates used in each timeseries, see Table S3. For region, S: Southern; C: Central; N: Northern. For species, MP: *Macrocystis pyrifera*; NL: *Nereocystis luetkeana*; † indicates which species is more common when both are present

Data set	Region	Nearest subregion	Start date	End date	No. of timepoints	Data type	Species	Methods	Reference
T1	S	Valdes/Gabriola (subregion i)	2013/2014	2022	24–34 per site	Presence–absence at 2 sites	NL	SCUBA surveys and videos	
T2*	S	Mayne Island (subregion ii)	2010	2021	8	Kelp forest area (m <sup>2</sup> ) at 5 sites	NL	Kayak surveys	
T3*	S	Cowichan Bay (subregion iii)	2004	2017	5	Presence–absence along 360 shoreline segments (% occupied)	NL	High-resolution satellite imagery	Schroeder et al. (2020)
T4*	S	Barkley Sound (subregion vi)	2007	2022	7	Presence–absence along 36 shoreline segments (% occupied)	MP†, NL	Aerial image, satellite, boat surveys	Starko et al. (2022)
T5*	N	South Central Coast (subregion ix)	1984	2021	38	Kelp forest area (m <sup>2</sup> ) across large area	MP†, NL	LandSat satellite imagery	
T6	N	South Central Coast (subregion ix)	2008	2022	8–11 per site	Kelp forest area (m <sup>2</sup> ) at 2 sites	MP, NL	RPAS	
T7*	N	Laredo Sound (subregion x)	2007	2019	3	Presence–absence along 103 shoreline segments (% occupied)	MP, NL†	Aerial image, satellite	

between 2017 and 2021 as 'recent' data (Timepoint 2). The large window of years used for Timepoint 1 offers a potential limitation for interpretation. However, survey efforts tended to be clustered geographically, with Timepoint 1 surveys earlier towards northern parts of the province. Therefore, to avoid making direct comparisons between data with Timepoint 1 surveys that occurred more than a few years apart, we split our snapshot data set into 3 regions (Northern, Central and Southern regions), and 11 subregions (subregions i–xi). Importantly, these regions do not reflect regional districts or other political boundaries but rather are meant to ensure that data from each timepoint are from similar years (within 5 yr) within each region (Table 1). Consequently, we do not draw statistical comparisons across regions but instead compare subregions or individual datapoints (i.e. segments; see Section 2.2) within each region.

Where possible, we also compiled various timeseries data from areas within or nearby the 11 subregions described above to contextualise any patterns inferred from the snapshot analyses. In total, we were able to assemble 7 timeseries data sets that differ in spatial scale from the area of an entire subregion to a set of individual sites ( $n = 2$  to 5) within or near subregions evaluated with our snapshot analyses (Tables 1 & 2). While timeseries data sets differ in methodology, spatial scale/coverage and response variable (e.g. presence–absence vs. total kelp area; see Section 2.3), each of these factors is internally consistent within a data set and therefore should provide insight into the trajectories of kelp forests where data were collected. It is important to note, however, that certain response variables are likely to be intrinsically more variable than others (e.g. presence–absence is likely more stable than abundance; Bastow Wilson 2012).

## 2.2. Snapshot analyses of kelp distributions

To first approximate changes in linear extent (measured here as presence–absence of kelp along shoreline segments; hereafter 'extent'), we performed snapshot analyses to identify localities that may be experiencing major changes in kelp distributions because of recent environmental and biotic shifts. For 10 subregions, we used oblique aerial imagery collected by the ShoreZone initiative (Howes et al. 1994, Cook et al. 2017) and Environment & Climate Change Canada (ECCC) between 1994 and 2021 as data sources for both timepoints. However, for one of the subregions (Cowichan Bay, subregion iii), we used 2 years from a data set derived from high-resolution

satellite imagery from Schroeder et al. (2020) (see below). A summary of data sources for each subregion is provided in Table S1 in the Supplement at [www.int-res.com/articles/suppl/m733p001\\_supp.pdf](http://www.int-res.com/articles/suppl/m733p001_supp.pdf).

For the 10 subregions with data derived from oblique aerial imagery, we created shoreline segments to classify stretches of shoreline as either a 'gain' (colonisation; kelp absent in Timepoint 1 imagery but present in Timepoint 2 imagery) or a 'loss' (extirpation; kelp present at Timepoint 1 but absent at Timepoint 2), or as 'stable' (kelp remained present at both timepoints) for each segment between the 2 time periods. These images are very high resolution and taken from low elevations (usually <100 m). Thus, they are generally of sufficient resolution to distinguish individual kelp plants, offering a highly reliable tool for visual detection of kelp. Oblique imagery was also taken at low tidal heights when most kelp canopy can be expected to be floating at the surface (Schroeder et al. 2019, Timmer et al. 2022, Gendall et al. 2023). However, because the imagery was collected at an oblique angle, we were unable to assess changes in kelp canopy area over time and restricted these analyses to presence–absence. Therefore, kelp canopy was determined to be either present or absent within each image for each segment, and the segment was accordingly classified. If the kelp or water in either image was not clearly identifiable due to glint on the water surface or choppy water, or if the image was too grainy to reliably identify kelp, the segment was not used.

For these 10 subregions, shoreline segments (~20–100 m in length) were established based on recognisable shoreline features in the aerial images that could be georeferenced in Google Earth (to georeference the shoreline segment). However, while some of the aerial imagery surveys (i.e. ShoreZone and ECCC) covered the majority of the coast (e.g. west coast of Vancouver Island; Csordas et al. 2023), other surveys (often earlier ShoreZone surveys) involved taking an image only every few hundred metres. Thus, methods varied slightly across data sets, depending on the availability or coverage of imagery and/or the length of shoreline surveyed. In 7 subregions (subregions i, ii, vii–xi), coverage of high-resolution images from Timepoint 1 was limited, and therefore segments were created based on which stretches of shoreline were visible in imagery. ShoreZone oblique aerial surveys involved both high-resolution imagery and lower-resolution video footage. Due to data limitations in these subregions, some segments were created based on still images captured from the video data. Otherwise, data were derived directly from the high-resolution imagery. Segments

were created anywhere that kelp was visible in imagery from at least 1 timepoint and the shoreline was visible in both timepoints.

For 3 subregions, where historical oblique imagery was not limiting and nearly the entire coast was photographed at high quality (subregions iv–vi), various approaches were employed to systematically survey photographic data. For the West Coast Trail (subregion v) and Juan de Fuca entrance (subregion iv), which collectively represent more than 80 km of shoreline, a systematic subsampling method was used. First the coastline was split into 250 m grid cells, and at the start of each grid cell, a single shoreline segment was established, provided the image met the quality criteria described above in imagery from both timepoints. For Barkley Sound (subregion vi), we systematically surveyed the majority (i.e. where data allowed) of a 16 km stretch of coast using oblique aerial imagery at both timepoints (see Starko et al. 2022). The coast was segmented as described above. We note that for this region, we had both oblique aerial survey and *in situ* survey data from 2021 (see Section 2.3), allowing us to determine that accuracy of classifying shoreline units using oblique aerial imagery was >97%, at least according to this sub-regional data set (see Table S2).

For Cowichan Bay (subregion iii), shoreline segments (100 m in length) were established as described by Schroeder et al. (2020) and relied on high-resolution satellite imagery (Digital Globe; 2.5 m resolution or higher) rather than oblique aerial imagery. For this data set, a timeseries was produced from imagery in 2004, 2012, 2015, 2016 and 2017 from <2 m tidal elevation in July–September, from which we used data from 2004 and 2017 for the snapshot analysis, such that Timepoint 1 data closely matched other Southern subregions. Methodological details for this data set are given in Section 2.3.

### 2.3. Timeseries analysis

We assembled 7 timeseries data sets, 5 of which fell directly within subregions examined in the snapshot analyses (see Table 2 for summary of years and data types): Mayne Island (subregion ii), Cowichan Bay (subregion iii), Barkley Sound (subregion vi), South Central Coast (subregion ix) and Laredo Sound (subregion x). The other 2 subregions with timeseries data sets cover areas adjacent to, but not directly overlapping with, subregions included in the snapshot analyses. Specifically, the Central Strait of Georgia timeseries (T1) is from north of the Valdes/Gabriola

subregion (subregion i) but does not include the same stretches of shoreline (see Fig. 2; Fig. S1). Similarly, Calvert Island (timeseries T6) is adjacent to the South Central Coast (subregion ix) but is not contained within the subregion analysed for the snapshot analysis (see Fig. 2; Fig. S2).

Where available, *in situ* data were used for time-series analyses. This was the case for 2 data sets: the Central Strait of Georgia (T1) and Mayne Island (T2). To contextualise changes in bull kelp (*Nereocystis*) occupancy (i.e. presence–absence) in T1, near subregion i (where *Macrocystis* is not present), we extracted data from citizen SCUBA diver videos (available online or through a local dive shop) and from the logbooks of authors. At one site (Eagle Rock, Denman Island; data set T1b), dives were conducted intentionally looking for kelp forests by 3 of the authors (A. & R. Zielinski, W. Heath) as part of a restoration and monitoring initiative. Here, logbooks recorded whether *Nereocystis* was present, and this was converted into presence–absence data for the site. At the other site (Tyee Cove, Nanoose Bay; data set T1a), we assembled recreational SCUBA diver videos (from a local dive shop and online, e.g. YouTube; Table S3) and determined whether *Nereocystis* was present in each video over an 11 yr period. While videos were generally not taken with the intention of tracking kelp, *Nereocystis* was a frequent occurrence in the shallows at this site alongside other kelp species, and therefore we would expect it to appear in citizen SCUBA diver videos either on purpose or incidentally while filming in the ‘kelp zone’. We included observations from April to October, to reflect the growing season of *Nereocystis*. While we included all videos or blog posts where *Nereocystis* was visible as observations of canopy kelp being ‘present’, we required that videos cover at least 20 s of footage in the ‘kelp zone’ (i.e. understorey kelp present), where conditions would be suitable for bull kelp, to include a video as an absence observation.

For the second timeseries derived from *in situ* data (Mayne Island; T2 in subregion ii), data from citizen-science kayak surveys were analysed to produce a timeseries. Surveys were conducted *in situ* by encircling the surface extent of kelp forests during low tides <1.2 m above chart datum and taking GPS points to identify the perimeter of the bed. Polygons were then produced from these data to represent kelp extent at each timepoint. Because survey areas varied in their spatial coverage between years, polygons were clipped according to spatial overlap of the survey areas to maximize the temporal coverage of the surveys. The resulting data set covered 5 discontinu-

ous sites (Fig. S1) that were each sampled 9 times between 2010 and 2022.

For 5 other timeseries (T3–T7), various approaches were used to construct data sets with remote sensing technologies (satellites, aerial images from piloted vehicles, remotely piloted aircraft systems [RPAS]), with analysis type dependent on data availability and/or previously conducted subregion-specific analyses. While the Barkley Sound timeseries (T4 in subregion vi) involved a combination of remotely sensed and *in situ* data, all other subregions used remote sensing data for all timepoints. A summary of remote sensing data sources used for timeseries is provided in Table S4.

For Cowichan Bay (T3; subregion iii), high-resolution WorldView-2 satellite images were acquired at tidal height below 2.0 m from July, August and September, corresponding to the growing season of bull kelp (Table 2; Table S4 for years). In short, kelp presence and absence along each shoreline segment was assessed using an unsupervised ISODATA classification approach, considering land and 30 m bathymetry masks and a buffer along the shoreline to minimize the effects of adjacency. This data set was published and presented by Schroeder et al. (2020).

For Barkley Sound (T4; subregion iv), aerial and high-resolution satellite images from 2007, 2013 and 2014 were classified visually (see Starko et al. 2022) and compared to boat surveys conducted in 2018, 2021 and 2022. The same shoreline segments were used as described in Section 2.2; however, the data set was trimmed to ensure only the subset of segments present in all years of the timeseries were analysed.

For the South Central Coast (T5; subregion ix), we created a timeseries of satellite-derived annual maximum surface kelp canopy extent from 1984 to 2021. The methods were adapted and modified from Nijland et al. (2019) and conducted using Google Earth Engine (GEE) (Gorelick et al. 2017). We used 30 m resolution Collection 1 Level 2 Surface Reflectance Landsat image products available on GEE provided by the United States Geological Survey across 4 Landsat sensors: Landsat 4 and 5 Thematic Mapper (1984–2013), Landsat 7 Enhanced Thematic Mapper Plus (1999–2022) and Landsat 8 Operational Land Imagery (2013–present). The Landsat constellation collects repeat imagery over the same image area every 16 d. To produce a single composite of maximum summer kelp extent in our study region for each year, we selected Landsat image scenes collected between 1 May and 31 October (the peak growing season for kelp in this area), with a maximum tidal stage of 3.5 m and a maximum scene cloud cover of

90%. The Central Coast of BC experiences high cloud cover; therefore, we used a high maximum cloud cover threshold to retain image coverage from as many potentially clear parts of the coastline as possible to maximize opportunities to map the entire study area in each year. We removed pixels with cloud cover or cloud shadow using the quality assurance mask provided with each image, which allowed us to retain cloud-free areas in each individual image. To remove the potential false classifications of land or intertidal areas as kelp, we derived a custom intertidal land mask and applied a 30 m buffer (1 pixel) to the land mask to remove potential mixed pixels containing water and land which could be falsely detected as kelp. This mask was applied to the GEE kelp outputs; therefore, we consider these data outputs as the extent of 'offshore' canopy kelp explicitly. Furthermore, at 30 m resolution, it is also not possible to distinguish between co-occurring species of canopy-forming kelp in Landsat imagery. Therefore, this data set represents the extent of giant kelp (*Macrocystis*) and bull kelp (*Nereocystis*) canopy detections.

Following masking, we calculated the normalized difference vegetation index (NDVI) for each pixel and classified pixels as potential kelp if they had an NDVI > 0.02. Because each pixel was usually represented in multiple images, we generally only considered pixels to be kelp if they were classified as potential kelp in 2 or more images. In a few rare cases, this detection rate was reduced (i.e. a pixel only had to be detected as kelp once in an image) due to limitations in the availability of imagery in some years. We reviewed each annual output and, where the cloud mask was found to perform poorly, individual image scenes were removed. The final output was a raster of all pixels classified as offshore kelp canopy within each summer period. Using this approach, we were able to ensure a complete timeseries with all parts of the study area mapped in every year.

For Calvert Island (T6), total canopy kelp area was quantified at 2 sites using imagery from RPAS flown *in situ*. Meay Channel (T6a) is a site with *Macrocystis*, while North Beach (T6b) is a *Nereocystis* site. To delineate kelp canopy extent from RPAS imagery, a mask was applied to remove land and intertidal areas. The variable atmospheric resistant index (VARI), a vegetation image index which can distinguish between water and kelp pixels, was calculated for the remaining area (made up of kelp and water). VARI was calculated using:

$$\text{VARI} = (b_{\text{green}} - b_{\text{red}}) / (b_{\text{green}} + b_{\text{red}} - b_{\text{blue}}) \quad (1)$$

where  $b$  refers to an individual band of imagery.

Due to the presence of shallow waters and variable lighting in RPAS imagery, multiple thresholds defining kelp versus water were identified using a natural breaks (Jenks) classifier (ArcGIS [ArcMap] Version 10.8, Environmental Systems Research Institute). A trained analyst visually determined the appropriate threshold for a given area and generated individual raster data sets for each threshold. Each raster was then converted to a polygon shapefile where non-kelp polygons and any very small polygons ( $<0.1 \text{ m}^2$ ) were removed. The outputs were then reviewed and manually edited where required. The final data set merged all threshold classifications into a single vector shapefile from which total area was calculated.

For Laredo Sound (T7; subregion x), aerial imagery (from 2007), visible colour satellite imagery from 2013 (Google Earth) and oblique imagery from 2019 (ECCC) were compared and classified visually (as with the Barkley Sound timeseries) using 50 m segments (presence–absence only).

## 2.4. Environmental data

We used environmental data to examine (1) how the timing of changes in kelp forests revealed by the timeseries data compares to the timing of thermal anomalies and (2) whether spatial patterns of temperature, current speed and fetch predicted kelp persistence based on snapshot analyses. To assess temperature anomalies through time, as relevant to the available timeseries data sets, we analysed temperature timeseries from various BC Lighthouse stations (found at <https://www.dfo-mpo.gc.ca/science/data-donnees/lightstations-phares/index-eng.html>), focusing on those closest to the various timeseries data sets. We then calculated average monthly temperature anomalies using data from 1982 to 2012 as the baseline.

To assess how patterns of kelp persistence in snapshot analyses relate to local summer SSTs, we used average daily SST from the LiveOcean Model, a Regional Ocean Modeling System adapted to the coastal waters off of Washington, Oregon and Southern BC (Fatland et al. 2016) which dates to 2017. We extracted and averaged data from August 2017 (the first year of the model) which was chosen to approximate the warmest time of year when kelp are expected to be most threatened by environmental conditions. Although August 2017 was not part of a recent heatwave, 2017 was an anomalously warm year nonetheless (Whalen et al. 2023; Fig. 1), and therefore these data are meant to capture local and regional-scale temperature gradients that are typical of ‘warm years’. This

model has a grid size of 500–1500 m (depending on location), which is higher resolution than any other available temperature model or data set but likely still misses some fine-scale temperature variation occurring at even finer scales (e.g.  $<500 \text{ m}$ ). It captures known temperature gradients on southern Vancouver Island such as in Barkley Sound (Starko et al. 2022) and the Salish Sea (Ban et al. 2016) but does not include the Northern region (subregions ix–xi). To incorporate temperature data from subregions not included in the range of the LiveOcean model, we extracted data from the same time period from the 1 km multi-scale ultra-high resolution (MUR) SST product (Chin et al. 2017). While this product is smoothed and does not capture some of the fine-scale gradients captured by LiveOcean where they overlap, it is the highest resolution satellite temperature product available for Central and Northern BC. We merged these 2 layers, using LiveOcean data where available but otherwise using the MUR SST product. In addition to mean temperature values, we also extracted the 90<sup>th</sup> percentile temperature from summers of 2014–2017 using the MUR SST data to use as a visual. We present these data in some figures to provide an overview of broad temperature gradients in BC but only include mean temperature from August 2017 in formal analyses.

We also tested whether kelp persistence correlated with spatial variation in current velocity ( $\text{m s}^{-1}$ ). We used the average current speed for each pixel from the LiveOcean Model (Fatland et al. 2016), off of Washington, Oregon and Southern BC from the months of July and August 2017 with the goal of capturing multiple full tidal cycles. We note that while absolute values of current speed may vary across seasons and years, we expect relative measures of current speed to be consistent through time. While use of MUR SST allowed us to compare spatial variation in temperature across the entire province, we were only able to examine current velocity in the Southern and Central regions due to the limitations in the coverage and resolution of the LiveOcean Model and no alternative model that captures current velocities at a similar scale in the Northern region. For all regions, we also used a provincial fetch model produced by Fisheries and Oceans Canada (<https://open.canada.ca/data/en/dataset/412431c4-7363-410e-86a4-76feb9a6dcde>) as a proxy for exposure to waves.

## 2.5. Sea otter occupancy status

We used previously published reports (Nichol et al. 2015, 2020) to infer which of the 11 snapshot subre-

gions and 7 timeseries included in this study represent areas occupied by sea otters *Enhydra lutris*. These reports document surveys conducted to quantify population size and distribution of otter populations across the coast of BC. The results show that otters are consistently present (and with growing populations) in 3 subregions examined here: Nootka Sound (subregion vii), Quatsino Sound (subregion viii) and the South Central Coast (subregion ix). Although considered to have expanded to areas around northern Calvert Island (timeseries T6) in 2013 (Nichol et al. 2015, Rechsteiner et al. 2019), on-the-ground observations and surveys have shown that the occupation of focal sites (North Beach and Meay Channel) in this subregion was short-lived and otters were no longer using these sites after 2016 despite being present on nearby islands (E. Rechsteiner & O. Pontier pers. comm.).

## 2.6. Statistical analysis

To test whether subregions varied in their trajectories in the snapshot analysis, we used Fisher's exact tests to determine whether kelp change status (stable, gain, loss) was contingent on subregion. We conducted this test separately for each region (Southern, Central and Northern) to avoid direct comparisons between subregions with Timepoint 1 data from over a decade apart (see Section 2.1). We also tested whether summer SST (using modelled and satellite data from August 2017) and fetch could predict kelp persistence from snapshot data in each subregion using spatial generalised linear mixed models; i.e. models with spatial random effects (implemented in R with the 'spaMM' package; binomial: 0 = kelp loss, 1 = kelp gain or persistence). For the Southern subregion, for which data were available, we also included current speed as a predictor of kelp persistence in the 'spaMM' model. To identify the variables that best explained kelp persistence, we compared models of each combination of explanatory variables (mean SST, fetch and current velocity, where available) using Akaike's information criterion (AIC). Given strong spatial autocorrelation, we used conditional AIC (cAIC) which is considered appropriate in data sets with strong random effects (Srivastava & Kubokawa 2010). However, we also calculated and present marginal AIC (mAIC), which considers only the impact of the fixed effects. We considered models to differ significantly if differences in cAIC were >3 between models.

To test for directional changes in kelp abundance or extent through time, we fit generalised linear models

with error distributions that matched the structure of the response variable (T1 = binomial distribution, T2–T5 = Gaussian distribution, T6 = Gaussian distribution fit to log-transformed canopy area). Given data limitations (i.e. low temporal coverage), we were generally unable to fit models that explicitly accounted for temporal autocorrelation. However, for T6, which spanned more than 3 decades, we tested for stationarity in the timeseries using a Dicky-Fuller test which explicitly considers autocorrelation through time.

## 3. RESULTS

Our snapshot analysis revealed substantial changes in the linear extent of kelp forests in some parts of BC in recent decades. The direction and amount of change differed across subregions in all regions (Fisher's test: Southern region:  $p < 0.001$ ; Central region:  $p = 0.0265$ ; Northern region:  $p < 0.001$ ). Of the 11 subregions examined, 6 had more kelp losses than gains, 2 had more gains than losses, and 3 had roughly no change (<10% net loss or gain). Subregions that experienced the greatest kelp loss were in both Southern (Valdes/Gabriola, subregion i: net 74% loss, Barkley Sound, subregion vi: net 43% loss) and Northern (Laredo Sound, subregion x: 30% net loss, Dundas, subregion xi: 62% net loss) regions. However, not all subregions in either region experienced declines. Southern subregions iv (Juan de Fuca) and v (West Coast Trail) experienced very little change in kelp extent (<5% net change) between the 2 timepoints, and subregions ii (Mayne Island) and iii (Cowichan Bay) experienced only minor to moderate declines (16 and 23% net loss, respectively) but with some shifts in the exact locations of kelp forests (e.g. Cowichan also had 12% gains). Northern subregion ix (South Central Coast) even experienced a small net increase in kelp extent (16%).

Central subregions vii and viii did not experience any overall declines and instead showed evidence of increases in extent since the late 1990s (Fig. 2). In particular, Quatsino Sound (subregion viii) experienced increases in linear extent compared to Timepoint 1 snapshots (15% gains and no losses). In contrast, Nootka (subregion vii) experienced both gains and losses, resulting in a net increase of only ~9% (Fig. 2) and reflecting a shift in the distribution of kelp rather than a clear unidirectional pattern of change. Examples of all 3 responses (losses, gains, stability) were observed in subregions dominated by both *Macrocystis* and *Nereocystis* (Figs. S3–S5). For example, losses were observed in both subregions i (*Nereocystis*-dom-

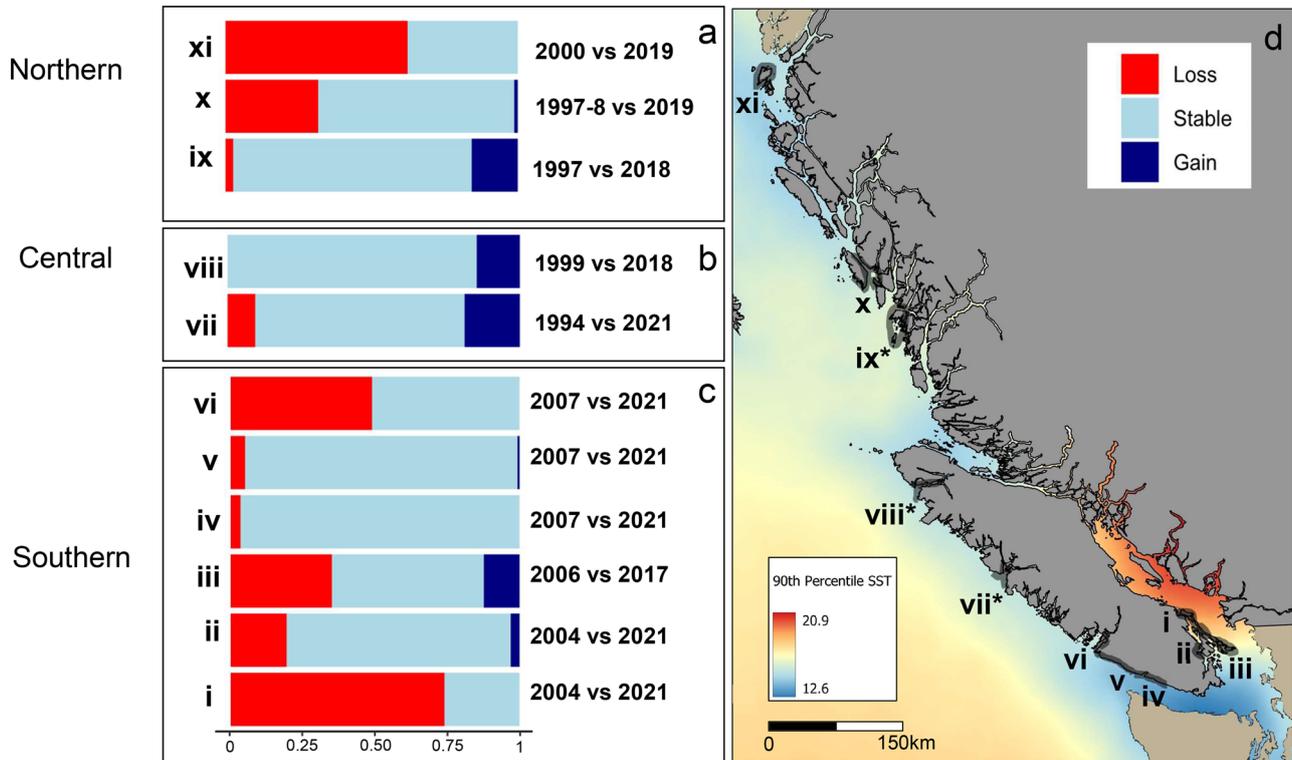


Fig. 2. Patterns of kelp persistence across the province of British Columbia inferred from snapshot analyses comparing Timepoint 1 (1997–2007) and Timepoint 2 (2016–2021) imagery. (a–c) Relative direction of change in canopy kelp presence (both *Macrocystis* and *Nereocystis*), at the level of individual segments, between the 2 timepoints based on shoreline segments visible in imagery from both timepoints. The regions with expanding other populations are indicated with asterisks in panel (d). Subregions are — i: Valdes/Gabriola, ii: Mayne/Saturna, iii: Cowichan Bay, iv: Juan de Fuca Entrance, v: West Coast Trail, vi: Barkley Sound, vii: Nootka Sound, viii: Quatsino Sound, ix: South Central Coast, x: Laredo Sound, xi: Dundas Island

inated) and vi (*Macrocystis*-dominated). Patterns of kelp persistence across the 2 timepoints tended to correlate with fine-scale environmental variation, but these patterns varied between Southern, Central and Northern regions.

### 3.1. Region 1: Southern region (Southern Vancouver Island and the Salish Sea)

In Southern subregions (i to vi), all of which lack otters, kelp loss strongly correlated with local summer SSTs (Fig. 3). Coastlines in this region span multiple local and regional temperature gradients (Fig. 3), and kelp persistence patterns both within and across these subregions strongly correlated with this fine-scale variation in temperature. In particular, subregions i to iii are located within the Salish Sea, a marginal sea that creates a persistent summer temperature gradient, with inland waters heating up considerably in the summer. Kelp extent in Valdes/Gabriola (subregion i), which is located towards the inner part of the Salish Sea, and experiences particu-

larly warm summer temperatures, declined across the entire subregion. In contrast, kelp loss on Mayne/Saturna (subregion ii) was largely restricted to the northeastern sides of islands that are exposed to warm waters of the inner Salish Sea and therefore experience greater temperatures than other parts of the subregion (Fig. 3). In Mayne and Valdes/Gabriola subregions, small pockets of high current velocities between islands also tended to correlate with local persistence (Fig. S6), suggesting an interaction between temperature and water motion (or mixing). Along the west coast of Vancouver Island, kelp linear extent remained largely stable apart from Barkley Sound, which presents its own summer SST gradient. In Barkley Sound, kelp forests disappeared primarily from inner parts of the subregion where conditions are known to get much warmer (see Starko et al. 2022; Fig. 3) while remaining towards the outer shore, including adjacent outer shore subregions (Juan de Fuca, subregion iv; and West Coast Trail, subregion v). The best fit model describing kelp persistence in the Southern region included both temperature and current speed (Table 3).

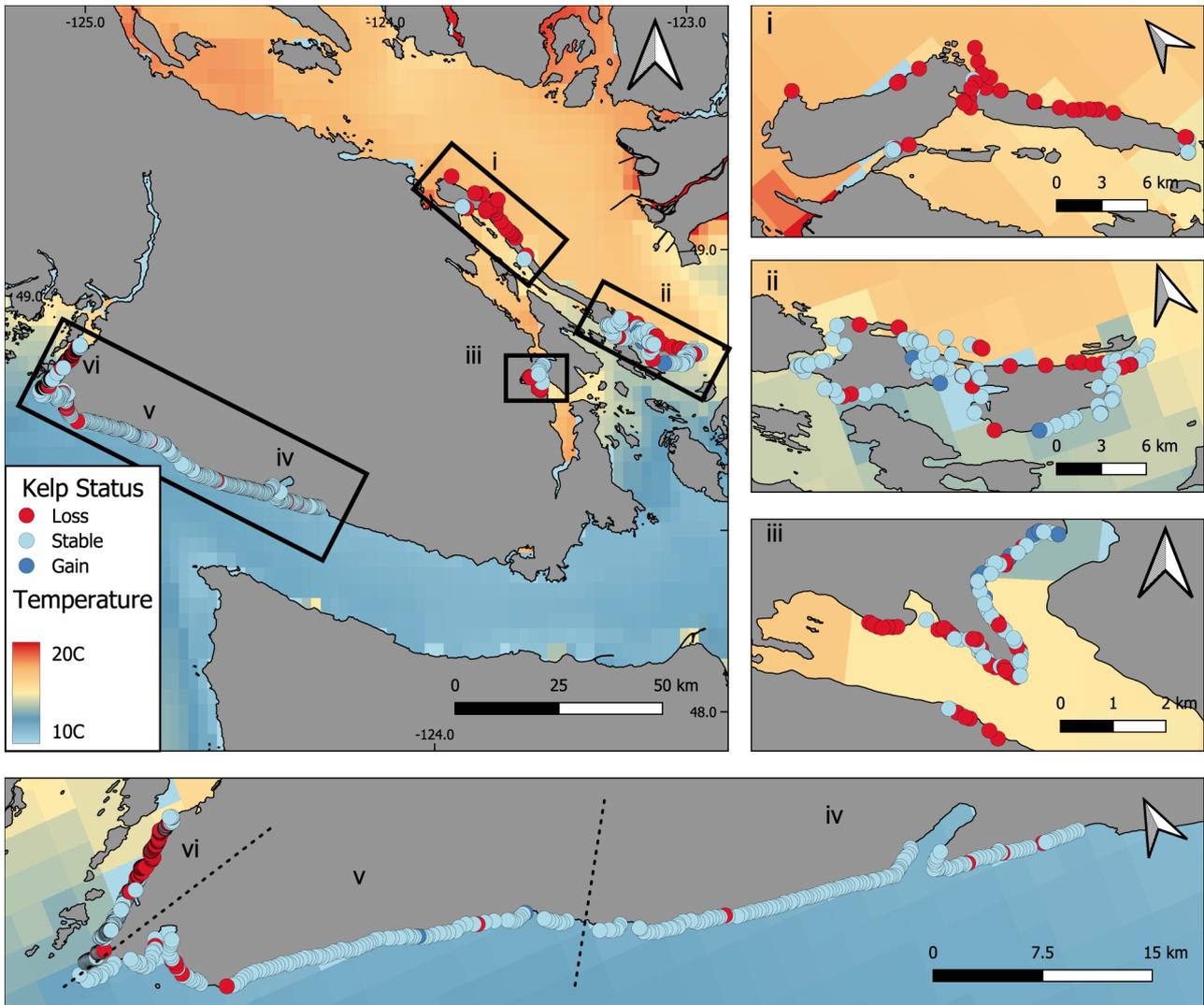


Fig. 3. Kelp persistence across the Southern region of British Columbia (subregions i–vi) overlaid on sea surface temperature (SST). Data points indicate segments from the snapshot analysis coded by their persistence status (see legend) determined by comparing data from Timepoint 1 (2004–2007) and Timepoint 2 (2017–2021); see Table 1. Coloured layer indicates mean SST in August 2017, as inferred from the LiveOcean Model. Shown are both Southeast and Southwest regions of Vancouver Island (i: Valdes/Gabriola, ii: Mayne/Saturna, iii: Cowichan Bay, iv: Juan de Fuca Entrance, v: West Coast Trail, vi: Barkley Sound)

Timeseries analyses from the Southern region support the patterns demonstrated in the snapshot analyses. Of the 4 timeseries from Southern BC (T1–T4), we detected significant directional declines in 2 of them (Fig. 4). Timeseries T1, which captures bull kelp presence–absence at 2 sites north of subregion i (that both reach particularly warm temperatures in the summer) show losses of kelp during the 2014–2016 MHW that persisted until at least 2021, at the end of the data sets (binomial GLM – T1a:  $Z = -2.580$ ,  $p = 0.0099$ ,  $df = 33$ ; binomial GLM – T1b:  $Z = -2.055$ ,  $p = 0.0399$ ,  $df = 23$ ). Timeseries T4 from Barkley Sound (subregion vi) also indicates that declines occurred during and following the 2014–2016 MHW

and have persisted until 2022 (Gaussian GLM:  $t = 4.462$ ,  $p = 0.0066$ ,  $df = 6$ ). The other 2 timeseries from the Southern region (T2 and T3 in subregions ii and iii, respectively) did not show a consistent decline in kelp through time, although only T2 was tested statistically (Gaussian GLM:  $t = -2.047$ ,  $p = 0.0799$ ,  $df = 6$ ) due to limited temporal coverage in T3. However, both reveal the lowest kelp extent or abundance in the year following the 2014–2016 MHW (i.e. in 2017) compared to any other year (including during the 2014–2016 MHW where data are available). For example, the data set from Mayne Island (T2; subregion ii) suggests that kelp forests were temporarily impacted negatively by the 2014–2016 event but then

Table 3. Comparison of models (best-fit highlighted in **bold**) explaining kelp persistence in snapshot analyses for each region. Note that not all models were fit for each region depending on data availability (see Section 2). cAIC (mAIC): conditional (marginal) Akaike's information criterion

Region	Model	cAIC	mAIC
Southern	Intercept only	431.2792	454.1205
	SST	342.2402	436.2006
	Current	432.9018	483.6026
	Fetch	427.3530	485.2468
	SST + Current + Fetch	301.9562	406.3622
	<b>SST + Current</b>	<b>273.8927</b>	<b>409.9760</b>
	SST + Fetch	331.4613	429.5025
	Fetch + Current	428.7791	479.8076
Central	<b>Intercept only</b>	<b>12.7031</b>	<b>26.9741</b>
	SST	15.2711	32.6765
	<b>Current</b>	<b>14.9583</b>	<b>28.8704</b>
	Fetch	16.0951	30.3319
	<b>SST + Current + Fetch</b>	<b>14.8045</b>	<b>27.9817</b>
	SST + Current	17.6426	31.1373
	<b>SST + Fetch</b>	<b>12.0688</b>	<b>26.1949</b>
	Fetch + Current	16.8752	30.9826
Northern	<b>Intercept only</b>	<b>202.4969</b>	<b>231.8947</b>
	<b>SST</b>	<b>201.9756</b>	<b>230.6024</b>
	<b>Fetch</b>	<b>202.4589</b>	<b>230.1529</b>
	<b>SST + Fetch</b>	<b>202.8452</b>	<b>227.3141</b>

subsequently mostly recovered. Nonetheless, these declines were relatively moderate (~22 and 34% declines relative to the lowest year before the 2014–2016 MHW). Despite this apparent recovery in T2, some individual sites (especially those towards the north of the subregion) sampled therein experienced possible declines early in the data set, while one site appeared to increase over the monitored time period (Fig. S7). Overall, time-series from the Southern region support the pattern inferred from the snapshot analyses that kelp trajectories have been variable across space with some subregions experiencing major declines and others appearing to remain stable or experiencing only minor changes in the distribution of kelp forests.

### 3.2. Region 2: Central region (Northern Vancouver Island)

Subregions in the Central region (subregions vii and viii), both of which have persistent and growing sea otter populations, experienced little

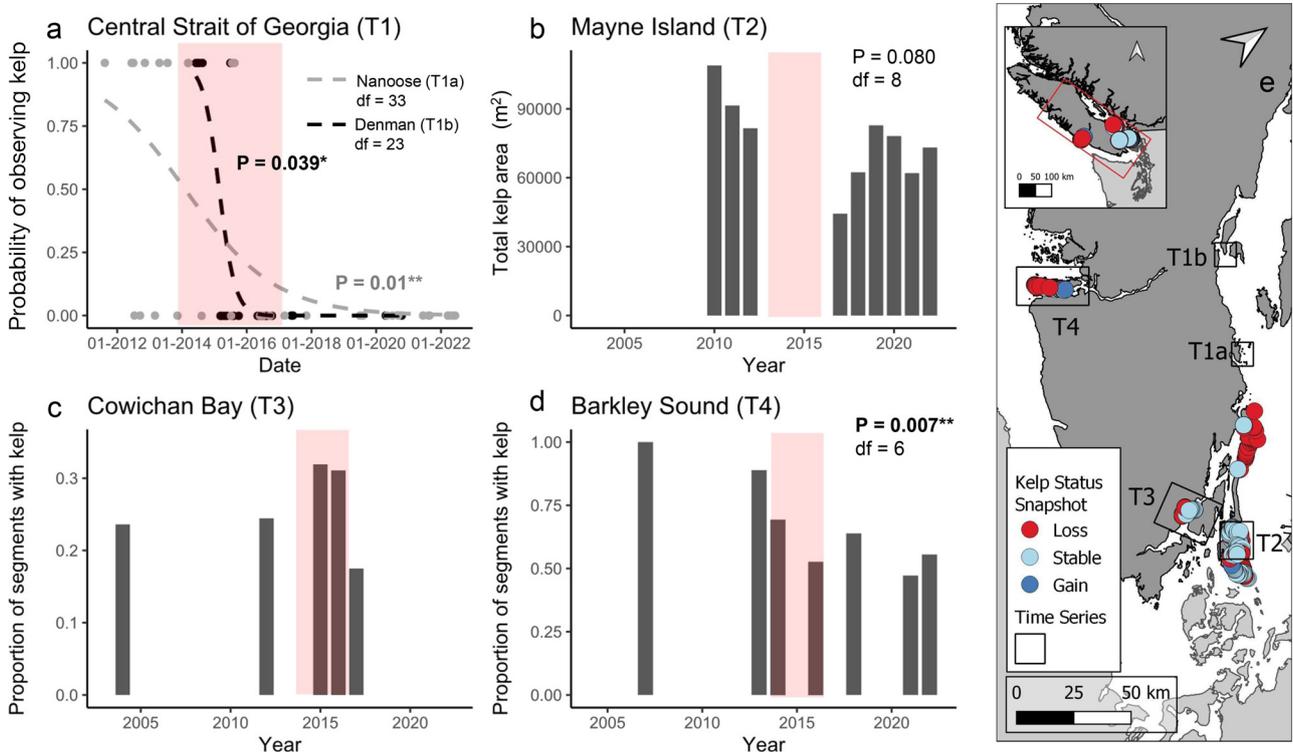


Fig. 4. Timeseries from the Southern region (data sets T1–T4). p-values of generalised linear models (see Section 2) are provided where relevant. If no p-value is shown, then no significance test was conducted due to limited number of timepoints. Dashed lines in (a) indicate significant binomial models indicative of directional trends through time. Inset in (e) shows the location of each timeseries relative to the snapshot data from nearby subregions. Asterisks indicate significant p-values (\*p < 0.05, \*\*p < 0.01)

change in kelp distributions and even possibly increases in extent, according to the snapshot analyses (Fig. 5). While kelp was lost from a small number

of shoreline segments in the 2 subregions (Fig. 2), gains were more common, resulting in net increases in kelp extent. Gains in Nootka Sound (subregion vii)

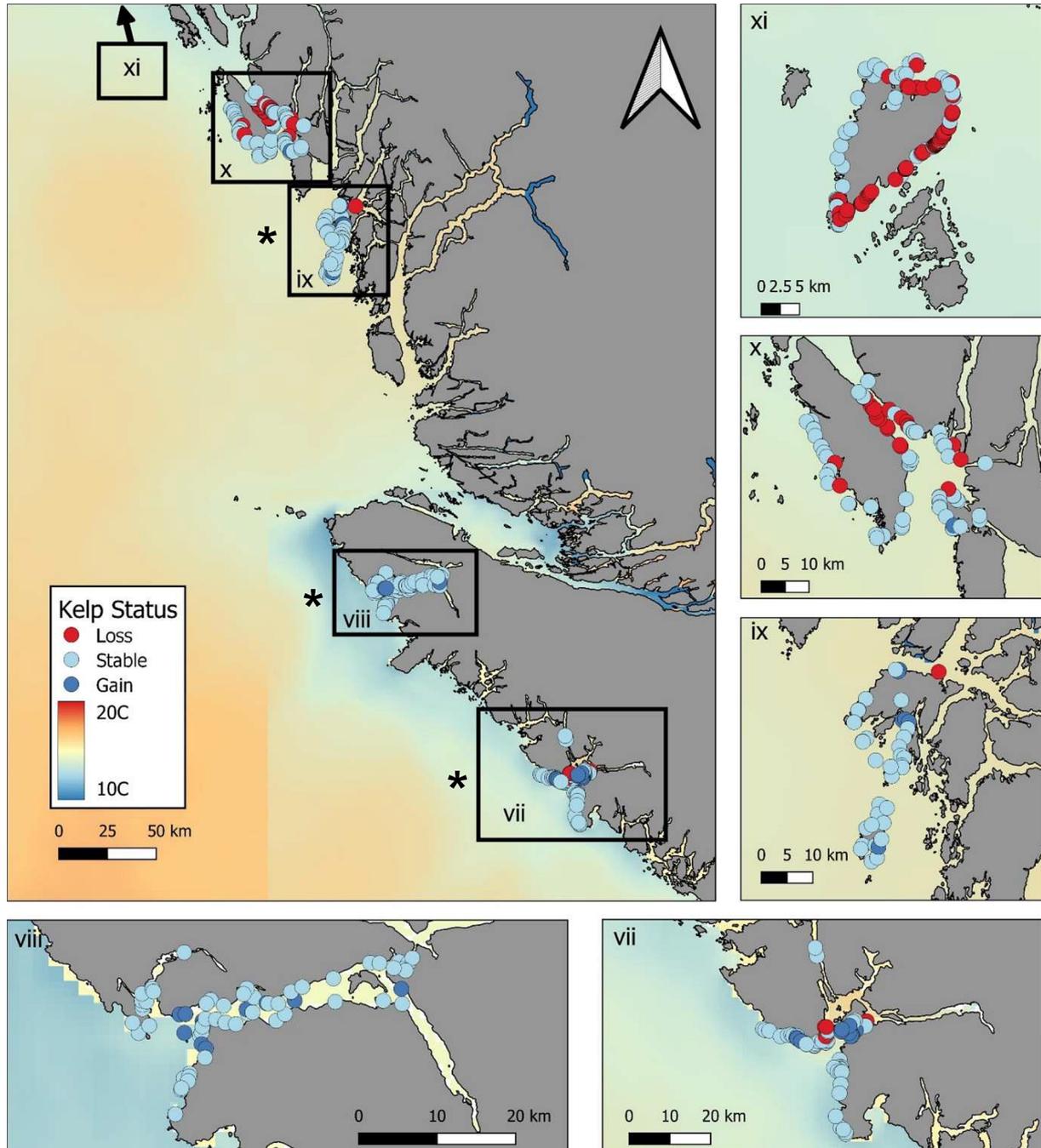


Fig. 5. Kelp persistence across the Northern and Southern regions of British Columbia (subregions vii–xi) overlaid on sea surface temperature (SST). Data points indicate segments from the snapshot analysis coded by their persistence status (see key) determined by comparing data from Timepoint 1 (1994–2000) and Timepoint 2 (2017–2021); see Table 1. Coloured layer indicates mean SST in August 2017, as inferred from the LiveOcean Model or the MUR SST product (see Section 2). Shown are subregions from both Central (vii: Nootka Sound, viii: Quatsino Sound) and Northern (ix: South Central Coast, x: Laredo Sound, xi: Dundas Island) regions. Colour scale depicting temperature is the same as in Fig. 3. Subregions with persistent sea otter populations are indicated with asterisks

were focused in 2 parts of the subregion, the inner islands of the sound and a small islet towards the exposed outer coast (Fig. 5). Gains in Quatsino Sound (subregion viii) tended to be spatially clustered around the opening of the sound but were also found in a few other cases further into the sound. Presumably due to the high stability across the region, no univariate or multivariate model performed significantly better than the intercept-only (i.e. no predictor variables) model (Table 3). No timeseries are available for this region, limiting our ability to attribute these limited changes in kelp extent to particular timeframes.

### 3.3. Region 3: Northern region (Central Coast and North Coast)

According to snapshot analyses, 2 Northern subregions both experienced substantial declines in the distribution of kelp: Laredo Sound (subregion x) lost kelp from 31% of shoreline segments between 1997 and 2019 (net loss of 30%), while Dundas (subregion xi) lost kelp from 62% of shoreline segments between

2000 and 2019 (with no gains). In both cases, declines were concentrated along stretches of coastline with low fetch, indicative of lower wave exposure (Fig. S8). In both subregions, kelp mostly persisted along west-facing, outer coastlines, while losses tended to be concentrated on inner shore stretches of coastline such as the east side of Dundas Island. In contrast to subregions x and xi, the one Northern subregion with persistent populations of sea otters, the South Central Coast (subregion ix), remained considerably more stable and even increased slightly (net increase of 13%) between 1997 and 2018. Overall, no model with predictor variables performed better than the intercept-only model, highlighting inconsistencies in the relationships of kelp persistence to environmental variables across Northern subregions.

Timeseries T5 from the South Central Coast (subregion ix) generally provides additional support for the results of the snapshot analysis from this subregion (Fig. 6). This is the longest running timeseries in our study and is satellite-derived (see Section 2.3), covering the southern part of the South Central Coast (subregion ix) which experienced very little change in the snapshot analysis (12/13 segments stable; 92%).

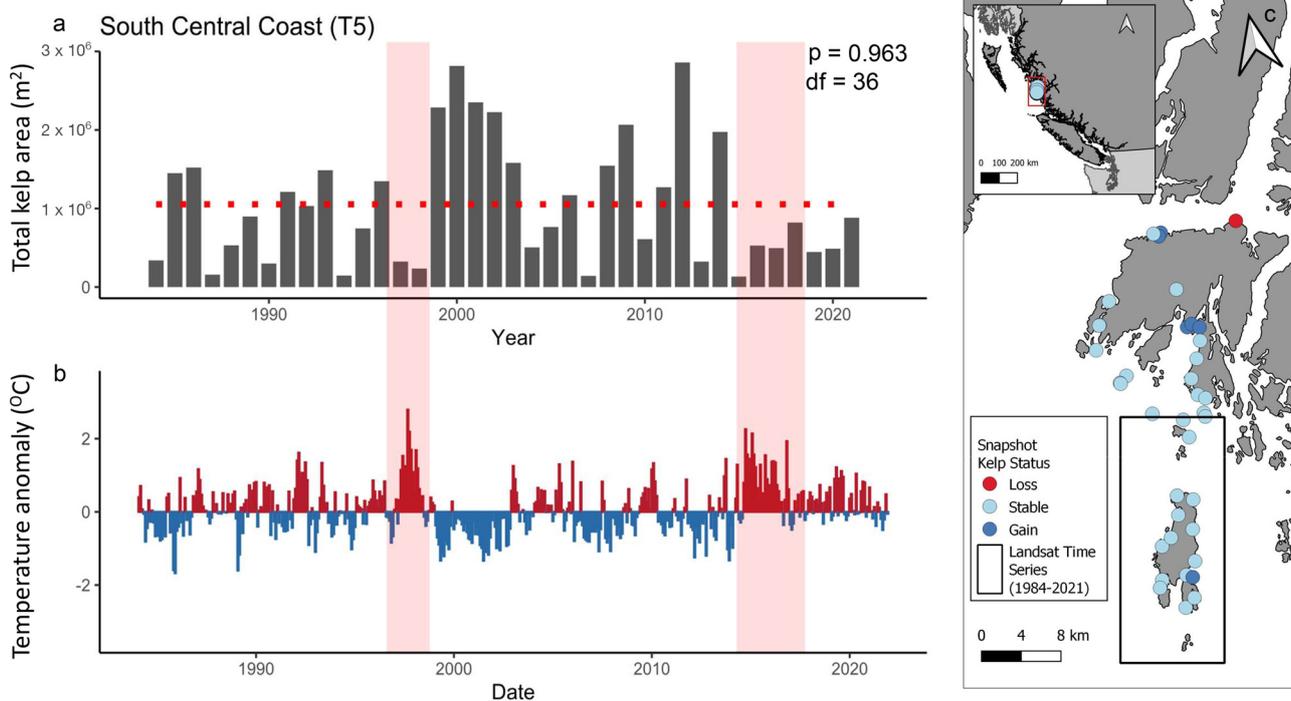


Fig. 6. Timeseries of offshore kelp forest area from South Central Coast (data set T5) subregion showing high variability (including recovery following declines) prior to the 2014–2016 heatwave, followed by consistently depressed values. (a) Total kelp area as inferred from LandSat imagery (Google Earth Engine method), excluding kelp forests within 30 m of shore. Red dotted line indicates mean total kelp area across the whole dataset. (b) Temperature anomalies based on measurements from nearby McInnes Island lighthouse (Stn 9 in Fig. 1). Red shading highlights the timing of the 1997–1998 El Niño and 2014–2016 marine heatwave. (c) Inset shows the location of the timeseries data set T5 relative to the snapshot data from the South Central Coast (subregion ix)

This timeseries reveals no significant, directional change through time (Gaussian GLM:  $t = -0.001$ ,  $p = 0.963$ ,  $df = 37$ ; Dicky-Fuller: D-F index =  $-2.6438$ ,  $p = 0.3217$ ), with some evidence of increases in maximum kelp abundance early in the data set. Specifically, the highest abundances were found between 1999 and 2014 despite the data set dating back to 1984. In 2015, kelp area dropped to the lowest values in the data set, though only ~5% less than multiple other years of the data set. However, unlike previous low-abundance years, recovery following this decline has been limited. Whereas past swings to similar levels were generally followed by rapid recovery (within 1 to 2 yr), kelp abundance has stayed below average for the most recent 7 yr of the data set. Nonetheless, kelp forest area remains within the range observed due to background variability for this measure, consistent with the stability inferred through the snapshot analysis. Moreover, when comparing kelp canopy area from T5 with the specific years from the snapshot analysis (1997 vs. 2018), the 2 data sets both corroborate the inferred pattern that kelp forests were similarly abundant between the 2 years and were even slightly more extensive in 2018.

Timeseries T6 from Calvert Island indicates reductions in kelp abundance not captured in the snapshot analysis of the nearby Southern Central Coast (subregion ix) (Fig. 7), highlighting how nearby stretches of coastline can experience very different dynamics. Unlike subregion ix, which has persistent and growing otter populations, the 2 sites on Calvert Island tend to lack otters, with the exception of short-term occupation between 2013 and 2015. According to this data set, kelp area declined considerably between 2015 and 2020 at the North Beach (T6b) site (*Nereocystis* forest). The greatest abundance was captured in 2014 at this site but then kelp abundance steadily decreased over the next several years. This spike in kelp abundance in 2014 coincides with short-term use of the areas by sea otters (Burt et al. 2018). Importantly, kelp abundance following the departure of sea otter populations and the 2014–2016 event was lower than kelp observations beforehand (2006, 2012), leading to a significant decline through time (log-transformed Gaussian GLM – T6b:  $t = -3.016$ ,  $p = 0.0146$ ,  $df = 10$ ). Moreover, declines continued for several years after the 2014–2016 MHW, perhaps reflecting delayed effects of SSWD. Temporal variation in kelp abundance from timeseries T6 therefore lends insight into multiple ecosystem states: kelp forests with *Pycnopodia* but no otters (2006–2013), kelp forests with both sea otters and *Pycnopodia* (ca. 2014), and kelp forests without either top predator (2016–2021). Data from the Meay Channel

*Macrocystis* site suggest that kelp declined between 2012 and 2016 and has since recovered but not to the same levels as in 2012. Nonetheless, T6a from Meay Channel did not have a significant directional trend through time (log-transformed Gaussian GLM:  $t = -0.779$ ,  $p = 0.466$ ,  $df = 7$ ).

Timeseries T7 from ~25 km of coastline in Laredo Sound (subregion x), where kelp was lost according to snapshot analyses, demonstrates that kelp forests were widespread in both 2007 and 2013 but then largely absent by 2019 (Fig. 7C; Figs. S11 & S12). Thus, kelp loss inferred from the snapshot analysis (which compares 1997/1998 to 2019) of subregion x likely occurred between 2013 and 2019, coinciding with the timing of the 2014–2016 MHW and SSWD impacts.

#### 4. DISCUSSION

Here, we established that kelp forests in BC have experienced variable patterns of change over the past 1.5–3 decades, with many subregions experiencing substantial declines in kelp linear extent. In the most extreme cases, kelp extent declined by more than 60% in 2 subregions (Valdes/Gabriola, subregion i: 74% loss; Dundas Island, subregion xi: 62% loss) and more than 30% in 2 others (Barkley Sound, subregion vi: 43% loss; Laredo Sound, subregion x: 31% loss) according to the 2-timepoint snapshot analyses. While our snapshot analyses were not comprehensive in coverage of coastal BC, kelp declines were observed in several subregions across the coastline, with modest increases (14–22% net gains) observed in only 2 subregions, and little to no change observed in 3 subregions. Thus, while some parts of the BC coast appear to have stable or even growing kelp forests, many localities have experienced considerable declines and are likely a conservation concern worthy of further research and possibly management interventions.

Both snapshot and timeseries data point to evidence of kelp forest declines in some subregions. Kelp reached its lowest occupancy states in Barkley Sound (subregion vi) and Laredo Sound (subregion x) during the most recent years surveyed (Fig. 5; see Starko et al. 2022 for an in-depth case study of Barkley Sound comparing kelp distributions back to the 1970s), a pattern supported by both snapshot and timeseries data. The timing of these declines in timeseries suggests that recent heatwaves and/or trophic changes since 2014 have driven declines in these subregions. Timeseries T1 (from near subregion i) and T5 (from near subregion

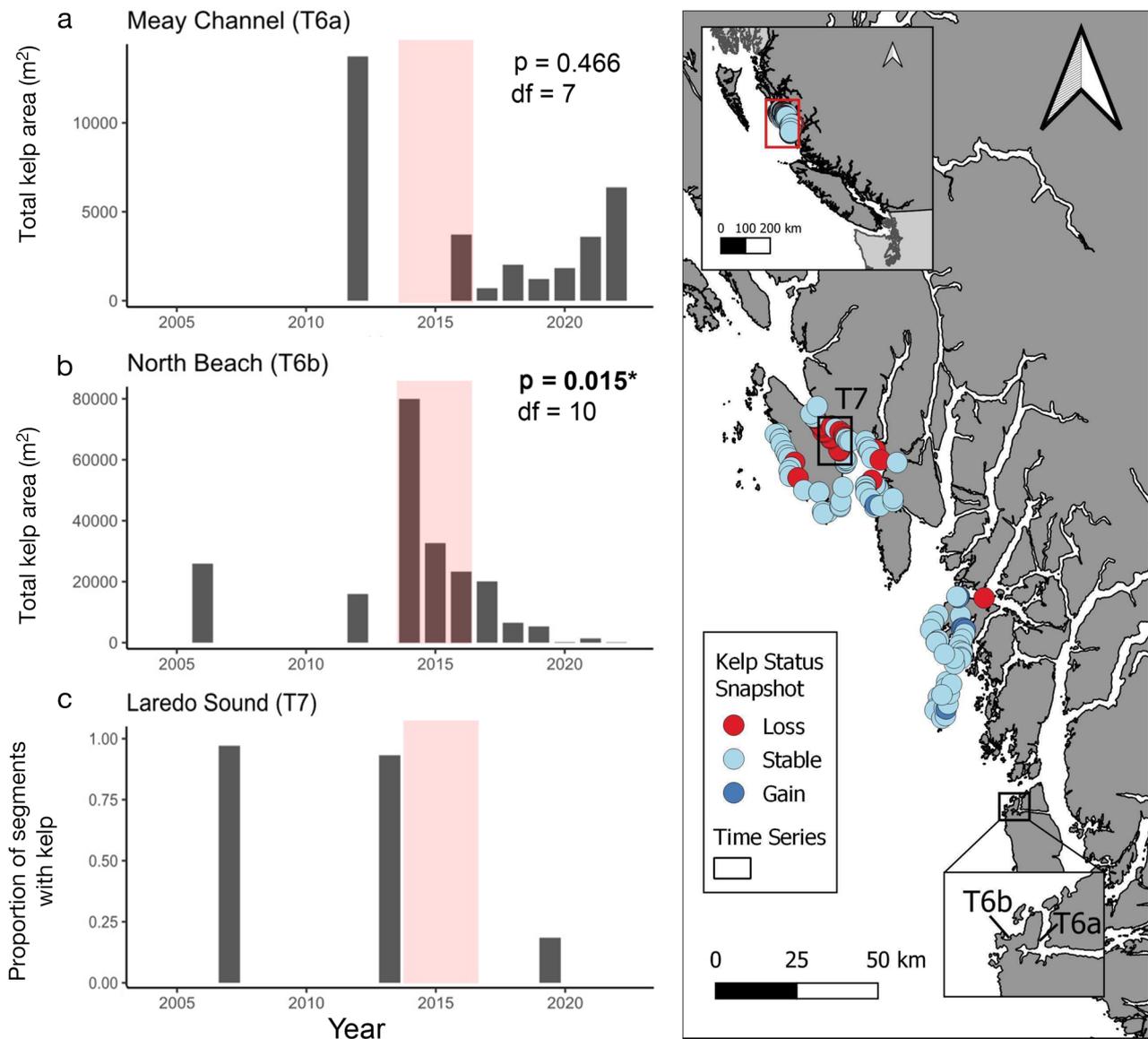


Fig. 7. Timeseries from the Central and Northern regions (data sets T6, T7). p-values of generalised linear models (see Section 2) are provided where relevant. If no p-value is shown, then no significance test was conducted due to limited number of years sampled. In (a) and (b), area ( $\text{m}^2$ ) is shown across annual summer sampling timepoints. Meay Channel site (a) is a large *Macrocystis* forest while North Beach (b) is a *Nereocystis* forest. Inset in (d) shows the location of each timeseries relative to the snapshot data from nearby subregions (ix and x). Asterisks indicate significant p-values (\* $p < 0.05$ )

ix) also reveal that kelp losses at those sites occurred around or following 2014. Where timeseries data span multiple years of the 2014–2016 heatwave (T1, T3, T4, T6), losses were sometimes not documented until 2015, 2016 or even after the event, suggesting that the multi-year nature of the event and/or the sustained conditions to follow have been critical to driving declines. In contrast to subregions with persistent declines, kelp forests around Mayne Island (subregion ii) experienced negative impacts from the 2014–2016 MHW, but then these kelp forests largely recovered in

following years. This pattern is similar to that observed along the outer coast of Washington during this same period (Tolimieri et al. 2023). However, site-level analyses of T2 around Mayne Island (subregion ii) (Fig. S7) indicate that the trajectories of individual kelp forests have been variable, with some sites remaining stable or increasing and others experiencing persistent declines. This highlights how variation in kelp forest trajectories often occurs at fine scales with apparent site-level differences in the stability and persistence of kelp forests.

Overall, the scale and persistent nature of concurrent kelp forest losses across parts of coastal BC suggest that kelp forests should be a conservation concern in this province, warranting further efforts to map and conserve kelp populations. Importantly, however, not all areas have experienced losses, and instead, declines have been spatially clustered to only some areas of the province. This highlights how ecosystem-level perturbations have different impacts depending on the underlying heterogeneity in the environment, a phenomenon that should be strongly considered when developing management plans and monitoring programmes.

#### 4.1. Spatial variation in kelp forest trajectories

Patterns of change were strongly spatially structured, allowing insight into the drivers behind those changes. Across Southern subregions, stretches of coastline that experience greater temperatures due to seasonal patterns of warming experienced substantial kelp forest declines between Timepoints 1 (2004–2007) and 2 (2017–2021) of the snapshot analyses. Most notably, inner parts of the Salish Sea experience the highest temperatures in BC waters and showed evidence of the largest declines, with 74% loss of kelp forests on Valdes and Gabriola Islands (subregion i). Even in nearby Mayne and Saturna Islands (subregion ii), which remained mostly stable, we revealed evidence of declines in the north parts of both islands, the most inner parts of the subregion with respect to the Salish Sea. The Salish Sea is warming at a faster rate than the outer coast (Iwabuchi & Gosselin 2019), and kelp forest losses have been documented from southern parts of the Salish Sea (i.e. Puget Sound; Berry et al. 2021). Moreover, the inner Salish Sea also experiences increased freshwater input from the Fraser River (which can reduce kelp thermal tolerance; Druehl 1978). In this context, it is perhaps not surprising that these regions have seen the largest kelp forest declines. Timeseries data from both the Salish Sea (T1) and Barkley Sound (T4), which also warms up considerably in the summer (Fig. 3; Starko et al. 2022), suggest that declines mostly occurred during and following the 2014–2016 MHW and SSWD-induced trophic breakdown. Although it is challenging to disentangle the direct impacts of temperature from those of sea urchin expansions expected from the die-off of *Pycnopodia*, recent work in Barkley Sound (subregion vi) demonstrated that these factors together can drive kelp loss in warm areas by negatively impacting kelp forests across

their depth range, preventing persistence in both shallow and deeper waters (Starko et al. 2019, 2022). Thus, the combination of shifts in urchin dynamics and warm temperature may have been required to drive losses in locally warm areas (at least in Barkley Sound, subregion vi).

In contrast to Southern subregions where temperature was a key predictor of changes in kelp extent, some Northern subregions (x and xi) experienced considerable declines despite a lack of warm temperatures. Lighthouse and satellite SST data indicate that temperatures remained consistently below 16–17°C during the summers of 2014–2017 (Fig. 1), which include the warmest years in decades (see Fig. 1). Thus, thresholds lethal to kelp were likely not crossed. In many cases, these losses were instead associated with transitions to urchin barrens, where pink coralline algal pavement was clearly present from the aerial images. Sea urchins (*Strongylocentrotus purpuratus*, *Mesocentrotus franciscanus*) were also visible as shallow as the intertidal zone in a considerable number of aerial photos from these 2 subregions (examples in Figs. S9 & S10). Urchins were visible in 18% of images from Laredo Sound (subregion x) and 72% of images from Dundas Island (subregion xi). This likely indicates that sea urchins were very abundant in the intertidal zone or very shallow subtidal zone (~1–2 m depth maximum) across both subregions. In contrast, no similar phenomenon was observed in other regions, with only a single aerial photo from the West Coast Trail (subregion v) having urchins visible in the image. While a lack of visible urchins in aerial images cannot be taken to indicate that no urchins are present, their presence does provide some anecdotal evidence for spatial differences in the depths at which urchins are active. For example, while urchins were almost certainly present in the Southern and Central regions, they were either too deep to observe in the images or interspersed with kelp and other seaweeds, likely reflecting a lower abundance than would be required to produce urchin barrens similar to those seen in subregions x and xi (Fig. S10). Given the high prevalence of urchins in the shallows of subregions x and xi and the clear transition to urchin barren states that these groups of urchins represent, we hypothesise that losses of kelp in these 2 northern-most subregions were driven by urchin grazing, likely exacerbated by declines in *Pycnopodia*. Distribution models of *Pycnopodia* presented by Hamilton et al. (2021) indicate considerable declines in the probability of encountering this species in either of the Northern subregions following SSWD. Thus, these transitions to urchin barrens likely reflect ecological release of the

sea urchins as observed elsewhere in BC (Schultz et al. 2016, Burt et al. 2018).

Kelp losses in the 2 northern-most subregions are largely restricted to the leeward side of islands, where fetch is low and therefore the coast is likely to be sheltered from incoming swell. In contrast, coastlines facing west in both subregions generally retained kelp forests. Wave action from oncoming swell can limit the depth that sea urchins can graze (Keats 1991, Kawamata 2010, Watson & Estes 2011), potentially facilitating kelp forest persistence in shallow waters, despite increases in the abundance and dominance of sea urchins. We hypothesise that this process has allowed for the persistence of kelp forests along high-fetch coastlines in the 2 northern-most subregions. Similarly, the West Coast Trail (subregion v) and Juan de Fuca (subregion iv) regions, which both face the dominant direction of oncoming swell (i.e. higher fetch) and are generally cooler due to mixing at the entrance of the Juan de Fuca Strait (Fig. 1; see Stn 1), experienced very little (<5%) change in kelp extent, likely due to the absence of both environmental and biotic drivers of decline. Past work has suggested that tidally driven vertical mixing might allow these subregions to serve as climatic refugia for marine systems in the face of climate warming and perturbations (Ban et al. 2016). Our results provide support to the hypothesis that these represent particularly stable areas (at least for kelp forest ecosystems) by demonstrating the least amount of change in these subregions compared to all others. Unfortunately, we lack timeseries data from these subregions to explore interannual variability but note that they could be good candidate subregions to reconstruct timeseries using remote sensing technologies due to the presence of large offshore beds (similar to Washington outer coast; Pfister et al. 2018, Tolimieri et al. 2023).

The only subregions to experience more increases in kelp extent than decreases in the snapshot analyses were those with growing sea otter populations (subregions vii to ix), consistent with the hypothesis that sea otters make kelp forest ecosystems more resistant and/or resilient to changes in trophic dynamics. Although sea otters were once widely distributed in BC, they were extirpated from the entire coast during the fur trade of the 18<sup>th</sup> to 20<sup>th</sup> centuries (McTaggart-Cowan & Guiguet 1960, Nichol et al. 2015). Sea otters were reintroduced to Checleset Bay on Northern Vancouver Island in 1969–1972 (Bigg & MacAskie 1978) and have since expanded to include all 3 of subregions vii to ix included in our study. Moreover, provincial sea otter surveys conducted as recently as 2017 indicate that otter population sizes

have continued to increase in all study regions in which they have re-established (Nichol et al. 2020). Thus, increases in kelp extent inferred from snapshot analyses could reflect successional dynamics associated with changes in trophic structure occurring over the past 2–3 decades (Watson & Estes 2011). Specifically, increasing otter populations would be expected to drive declines in sea urchin abundance, which could subsequently allow kelp to colonise stretches of shoreline that were previously in the urchin barren state.

Six of the subregions were also represented in time-series data sets that were either directly overlapping with, or near to, the same areas evaluated using the snapshot analyses (Table 2; Table S5). This offers an opportunity to put snapshot data sets into a more robust temporal context and provides multiple lines of evidence for observed patterns of change. T1 and nearby snapshot data from Valdes/Gabriola (subregion i) both showed severe declines despite the independent sources of these data sets and the differences in spatial scale across methodologies (individual sites vs. tens of kilometres). T2 was also consistent with snapshot analyses from Mayne Island (subregion ii) despite representing 2 independent data sources, with snapshot data revealing a minor decrease (16% decline) and timeseries data revealing no significant direction trend but a possible pattern of minor decrease. Notably, both data sets provide evidence for site-specific declines along the north side of Mayne Island (Fig. 3; Fig. S7), which experiences the warm SSTs of the inner Salish Sea. The South Central Coast data sets (subregion ix; T5) also offer consistent results across independent data sets with no clear trend in the timeseries and only a minor (16%) increase inferred from the snapshot data. Finally, timeseries and snapshot data from Barkley Sound (T4; subregion vi) and Laredo Sound (T7; subregion x) both reveal consistent, major declines. However, this is not surprising, since these data sets are not fully independent and instead share some of the same imagery between snapshot and timeseries data sets. Similarly, both data sets from Cowichan Bay (subregion iii; T3) were derived from the same methods and therefore are not particularly informative in evaluating differences in approaches. The only timeseries that present substantially different patterns from nearby snapshot analyses were the 2 timeseries from Calvert Island (T6a and T6b). However, this likely reflects genuine differences in the dynamics of kelp forests around Calvert Island compared to the nearby South Central Coast subregion (subregion ix), as described earlier.

Timeseries data suggest that many observed declines occurred during or following the 2014–2016 MHW, consistent with patterns documented elsewhere in the Northeast Pacific (e.g. Arafeh-Dalmau et al. 2019, Cavanaugh et al. 2019, Rogers-Bennett & Catton 2019, Beas-Luna et al. 2020, McPherson et al. 2021). Timeseries data from Barkley Sound (T4 from subregion vi) and Laredo Sound (T7 from subregion x) assess presence–absence of shoreline segments at each timepoint and show consistent kelp distributions before the MHW. For example, kelp distributions in Laredo (subregion x) were similar between 2008 and 2013, despite variability in climatic oscillators (e.g. positive vs. negative Pacific Decadal Oscillation [PDO]). Similarly, focused work from Barkley Sound (subregion vi) indicates that these pre-MHW distributions closely match data from even the 1970s and 1980s (Starko et al. 2022). Consequently, data from these timeseries suggest that presence–absence of shoreline units can be a stable measure of kelp distributions, in the absence of a large perturbation that drives declines. In contrast to these timeseries, however, data from Cowichan Bay (T3 in subregion iii) show much more interannual variability in kelp presence–absence. Thus, the background variation in kelp presence–absence likely varies across part of the province or across methodologies (i.e. oblique imagery versus satellite imagery; see Section 4.2).

#### 4.2. Limitations and future directions

Kelp forests are naturally highly variable systems that tend to fluctuate interannually, a pattern exemplified by our analysis of kelp abundance in T5 (Fig. 6) from the South Central Coast (subregion ix). For this reason, there are potentially important limitations associated with our snapshot analyses of 2 timepoints. In particular, the exact timing of Timepoints 1 and 2 both have the potential to produce misleading results under some circumstances. For example, Timepoint 1 snapshot data from the South Central Coast subregion were from 1997, during a large MHW (1997–1998 El Niño), an event which was known to negatively impact kelp in California (Ladah & Zertuche-González 2004, Edwards & Hernandez-Carmona 2005) and Washington (Pfister et al. 2018), and apparently drove temporary declines in offshore kelp abundance on the South Central Coast of BC (Fig. 6). Thus, the timing of this initial survey has the potential to bias patterns towards perceived increases. Importantly, however, Timepoint 1 imagery from nearby Laredo Sound (subregion x), a subregion

with evidence of strong declines and no sea otter populations, was also taken during the 1997–1998 event (Table 1; Fig. S13). This suggests that these 2 subregions have, in fact, experienced differing trajectories and that historical sampling during the 1997–1998 event does not necessitate a perception of kelp extent increases.

Similarly, due to slight differences in the timing of imagery, seasonal patterns (e.g. timing of annual canopy reaching the surface or increasing canopy biomass during the growing season) and the tidal height at the time of imagery may confound true interannual patterns of change. Quatsino Sound (subregion viii) was sampled initially in May but resampled in July when kelp beds are expected to be larger, creating potential for seasonal patterns to confound true patterns of change in kelp extent (more kelp expected later in the summer). However, the South Central Coast (subregion ix) region had the opposite issue (with initial surveys occurring later in the season than modern imagery) and showed similar patterns of increasing extent to those observed in Quatsino, both of which have sea otters. All other subregions had very closely matched dates for Timepoints 1 and 2 (i.e. less than 1 mo and generally within 1–2 wk; Table 1). With respect to tidal height, oblique aerial images were all taken at low tide, but more variability in tidal height occurred across sampling points in the satellite timeseries analyses (T3, T5), potentially contributing to perceived variability in these data sets.

Interannual variation in kelp abundance driven by environmental conditions (for example, associated with climatic oscillators, e.g. PDO, El Niño–Southern Oscillation [ENSO]), was also not captured using our 2 timepoint snapshot analyses, introducing an additional caveat to the interpretation of these data. The dates of Timepoint 1 snapshot imagery vary across subregions, yet the data tell a consistent story: declines in many areas without otters (especially areas of warming) and stability or increases in places with sea otters or persistent mixing. Thus, in the subregions where widespread declines occurred, they were likely not restricted to a single year despite our use of only 2 timepoints to characterise them. Importantly, snapshot comparisons in the Strait of Georgia (subregions i, ii, iii) were all made between 2004 and 2017–2021. In 2004, PDO, ENSO and temperature anomalies were all positive (at times more so than resurvey years; Fig. S13), suggesting that these 2 timepoints should experience similar effects of climatic oscillators. Yet, patterns of kelp loss at the latter sampling point were dramatic in some subregions (e.g. Valdes/Gabriola lost kelp in 74% of segments).

Snapshot analyses also focused only on presence–absence and not on abundance, which is generally expected to be more stable even in ecologically dynamic systems (Bastow Wilson 2012), and most snapshot data were derived from oblique imagery with high enough resolution to detect even a single kelp individual, further limiting the influence of interannual variation in our presence–absence analyses. Consequently, losses of kelp in our snapshot analyses likely reflect transitions between alternative states where an entire kelp forest is replaced by a kelp-free ecosystem state (Filbee-Dexter & Scheibling 2014, Filbee-Dexter & Wernberg 2018).

For both snapshot analyses and timeseries data, the data type used may have also influenced the observed patterns. Where shoreline segments were used, variation in their length (Fig. S14) may have influenced the patterns inferred from these analyses. In particular, absence observations are theoretically more likely when segments are shorter. Importantly, subregions were mostly compared only to themselves, and segment length was consistent through time within each subregion. Additionally, in Laredo Sound (subregion x), where 2 different segment methods were used (variable length for snapshot analysis, fixed length of 50 m for timeseries), the same pattern was recovered in both cases, suggesting that these minor differences in length did not impact inferred patterns. We also tested for an effect of segment length on kelp persistence within each region and found no significant effect in any case ('spaMM' binary models: Southern:  $\chi^2 = 2.1931$ ,  $p = 0.139$ ; Central:  $\chi^2 = 0.00042$ ,  $p = 0.998$ ; Northern:  $\chi^2 = 3.4167$ ,  $p = 0.0645$ ). The Cowichan Bay timeseries (T3) had larger segments (100 m), which would make absences less likely. However, counter to expectation, this subregion was the most variable through time in terms of presence–absence along segments. Thus, this variability cannot be explained by segment length. Notably, because Cowichan Bay data were derived from high-resolution satellite rather than oblique aerial imagery, small fringing beds may have been classified as kelp absence points (see discussion of accuracy in Schroeder et al. 2019, 2020). Further, this subregion is characterised by high currents which can easily submerge fringing kelp and reduce the ability to detect it at the surface (Britton-Simmons et al. 2008, Timmer et al. 2022). Thus, false negatives may be more likely in this subregion than in other snapshot analyses.

For the timeseries analyses, several different survey methods and response variables were assessed based on the availability of data to which these same considerations apply. Although different methodologies of

detecting kelp (e.g. *in situ* vs. 3 m resolution satellite vs. 30 m resolution) have varying abilities to capture change and are likely sensitive to different types of patterns, each data set uses consistent methodologies through time and therefore offers insight into how kelp has changed at the scale relevant to a particular data set. Despite these limitations, using and synthesising disparate sources of data can be essential to capturing patterns of change in regions that are historically understudied and therefore lack standardised assessment and monitoring programmes.

Future work should aim to expand on this study in multiple ways. Firstly, the growing availability of satellite imagery (including some products dating back decades) will allow researchers to reconstruct timeseries in areas for which they are not already available (Cavanaugh et al. 2021, Gendall 2022, Mora-Soto et al. 2024), especially where there are large offshore beds (Nijland et al. 2019). This approach may help facilitate a province-wide assessment of canopy kelp persistence, rather than focusing on a subset of areas as we have done here. As these timeseries continue to grow, statistical approaches can also be employed to better understand the role of climatic oscillators in driving interannual variation and more explicitly differentiate cyclical patterns from directional change through autocorrelation analysis. Alternatively, qualitative approaches may also be useful in assessing the extent of kelp forest loss in some areas. For example, traditional and local ecological knowledge could help to identify localities of major change for which no alternative data are available or could supplement and increase confidence in quantitative approaches (Lee et al. 2019, Reid et al. 2021). Similarly, herbarium records (Wernberg et al. 2011) and historical nautical charts (Costa et al. 2020) may offer insights into the historical distribution of kelp species, especially if records are available from places that no longer support any kelp forests. Finally, in the face of environmental change, it will be essential to not only reconstruct past kelp forest distributions but also make predictions about future change. This can be accomplished by coupling species distribution models with climate projections that could help to identify areas of resilience or vulnerability in the face of global change (e.g. Martínez et al. 2018, Chefaoui et al. 2021).

### 4.3. Management implications

We showed that kelp forests across some parts of the province have declined considerably over recent decades. This demonstrates a clear conservation issue

that should be considered by managers and rights-holders. However, these declines stand in stark contrast to the stable or even increasing trajectories of kelp forests observed in other parts of the province. Our results demonstrate that kelp forest vulnerability, and conversely resilience, are highly variable across space and that environmental heterogeneity plays an important role in contributing to these patterns. For this reason, kelp forests in close proximity should not always be assumed to have similar dynamics or be on similar trajectories. Management or conservation actions should therefore consider the need, and approach on local or regional scales. Restoration efforts involving outplanting (Eger et al. 2023, Wood et al. 2024), for instance, should be focused in parts of the province where kelp forests are actually in decline. Many of these declines are correlated with the prevalence of warmer temperatures, however, which is very challenging to combat in the context of kelp restoration and conservation (Coleman et al. 2020). This is likely especially true in areas like the Salish Sea where water temperatures regularly reach thermal tolerance thresholds of kelp (Fig. 1). Restoration and conservation of kelp forests in these warmer regions will rely on either the management of co-occurring stressors, or the use of transformative and controversial tools that facilitate increased thermal tolerance in natural populations (Coleman & Goold 2019, Coleman et al. 2020). Efforts to use hand-picked genotypes to increase ecosystem resilience are beginning in some places, and this offers a potentially powerful tool for restoration (Wood et al. 2024). Alternatively, management of urchins through culling efforts may also be needed to restore kelp forests in some parts of BC. This generally requires a substantial investment in time to remove urchins on any meaningful scale (Lee et al. 2021). However, in the absence of a top predator, urchin removal through targeted culling efforts may be the only option in the short term.

#### 4.4. Conclusions

Here we showed that kelp forests have experienced variable patterns of change across coastal BC, with recent and substantial declines in some focal areas. Declines in kelp forest linear extent and/or abundance appear to be linked to rapid warming experienced since 2014 and possibly also to increases in herbivorous urchins driven by the loss of *Pycnopodia* sea stars (evidence from BC in Schultz et al. 2016, Burt et al. 2018, Starko et al. 2022). Importantly, microclimate, water motion (waves and currents) and the

presence of otters appeared to strongly mediate the impacts of these ecosystem perturbations on kelp forest ecosystems in BC, causing some regions to be particularly sensitive to these drivers while others have remained stable or even increased despite these drivers. Interestingly, the drivers that were most important appeared to vary across different parts of the province, highlighting the need for further work to better understand the mechanisms behind spatial variation in kelp responses. Large-scale concurrent evidence of declines suggests that kelp forest ecosystems in several parts of BC are threatened and should be of significant conservation concern. To be effective, conservation and management efforts should focus on parts of the coast that are most sensitive to environmental and biological drivers of change, rather than treating kelp forests across all regions as equally sensitive to environmental change. Overall, our findings highlight how local- or regional-scale conditions can be essential in determining the impacts of environmental change on coastal marine ecosystems and demonstrate that kelp forest loss in BC offers a major conservation challenge in the face of ongoing global change.

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