Temperature and food chain length, but not latitude, explain region-specific kelp forest responses to an unprecedented heatwave

Running Head: Kelp forest responses to prolonged heatwave

Samuel Starko[1,2,3*], Brian Timmer[1], Luba Reshitnyk[4], Matthew Csordas[1], Jennifer McHenry[1], Sarah Schroeder[5], Margot Hessing-Lewis[4], Maycira Costa[5], Amanda Zielinksi[6], Rob Zielinksi[6], Sarah Cook[7], Rob Underhill[8], Leanna Boyer[8,9], Christopher Fretwell[8], Jennifer Yakimishyn[10], William A. Heath[11], Christine Gruman[12], Julia K. Baum[1,3] & Christopher J. Neufeld[3*]

1 Department of Biology, University of Victoria, 3800 Finnerty Rd., Victoria, British Columbia, V8P 5C2, Canada

2 School of Biological Sciences, University of Western Australia, Crawley 6009, WA, Australia

3 Bamfield Marine Sciences Centre, 100 Pachena Rd., Bamfield, British Columbia, V0R 1B0 Canada

4 Hakai Institute, Heriot Bay, BC V0P 1H0, Canada

5 Department of Geography, University of Victoria, 3800 Finnerty Road, Victoria, British Columbia V8P 5C2, Canada

6 Hornby Island Diving Ltd. 10795 Central Road Hornby Island BC V0R 1Z0 Canada

7 Coastal and Ocean Resources, 759A Vanalman Ave, Victoria, British Columbia V8Z 3B8 Canada

8 Mayne Island Conservancy, 455-A Dixon Road, Mayne Island, British Columbia V0N 2J2, Canada

9 Stqeeye' Learning Society, PO Box 407 Salt Spring Island, British Columbia, V8K2W1, Canada

10 Pacific Rim National Park Reserve, Parks Canada Agency, 2040 Pacific Rim Highway, Ucluelet, British Columbia V0R 3A0, Canada

11 Project Watershed Society, 2536a Rosewall Crescent, Coutenay, British Columbia V9N 5N3, Canada

12 Huu-ay-aht First Nation, 170 Nookemus Road, Anacla British Columbia V0R 1B0, Canada

*Corresponding Authors:
Samuel.starko@gmail.com
chris@kelprescue.org

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Abstract

Kelp forests are among the most abundant coastal marine habitats but are vulnerable to the impacts of climate change. Between 2014 and 2016, an unprecedented heatwave and associated changes in trophic dynamics threatened kelp forests across the Northeast Pacific, with impacts documented from Mexico to Alaska. However, responses have varied substantially and remain poorly characterized across large stretches of coast, especially British Columbia (B.C.), which represents a significant percentage of the range of floating kelp species in the Northeast Pacific. Here, we explore variation in floating kelp (*Macrocystis*, *Nereocystis*) persistence pre- and post-heatwave across a >675 km latitudinal gradient, asking whether B.C. kelp forests are of conservation concern. We assembled and analyzed available quantitative kelp data, comparing snapshots of kelp extent before (1994 – 2007) and after (2018 – 2021) the heatwave in 11 regions spanning a range of temperature and sea otter-occupancy statuses, and contextualizing these with time series analyses, where available (n = 7 regions). We provide strong evidence that kelp forests have declined in many regions but with evidence of refugia at both local and regional scales. Kelp forest persistence was negatively correlated with summer sea temperatures in southern B.C., where temperatures varied by ~6°C across sites, at times exceeding species' thermal tolerances. Kelp dynamics in northern regions appeared instead to be modulated by top-down control by urchins and sea otters. Our results demonstrate that B.C.'s kelp forest have been substantially reduced in recent years but that regional and local-scale factors influence the resilience of forests to large-scale perturbations.

2

1. Introduction

Human activities are altering the distribution and structure of marine ecosystems (Halpern et al., 2008; Steffen et al., 2011). Climate change, overfishing and pollution are among the drivers causing large-scale change in our ocean ecosystems (Jackson et al., 2001; Brierley & Kingsford, 2009; Mearns et al., 2010; Smale et al., 2019). In the face of these stressors, ecosystems at times undergo rapid regime shifts to states of less desirable structure and function (Scheffer & Carpenter, 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, Burke & Pet-Soede, 2003; Pecl et al., 2017). Moreover, various ecological factors can reinforce regime shifts once they have occurred, potentially preventing ecosystems from returning to their initial state (Folke et al., 2004; Hughes et al., 2005; Filbee-Dexter & Scheibling, 2014; Filbee-Dexter & Wernberg, 2018), creating major challenges for conservation.

Coastal marine ecosystems can be especially sensitive to the impacts of climate change and other human activities with examples of regime shifts widespread across coral reefs (e.g., Graham et al., 2015; Arif et al., 2022), seagrass meadows (e.g., Moksnes et al., 2018; Chefaoui et al., 2021a) and seaweed communities (Filbee-Dexter & Scheibling, 2014; 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) 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

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97   and other seaweed species (Steneck et al., 2002; Teagle et al., 2017; Shaffer, Munsch & Cordell,

98   2020). Moreover, they are highly productive and therefore fuel the growth of higher trophic

99   levels (Duggins, Simenstad & Estes, 1989; Pessarrodona et al., 2022). Thus, declines in kelp

100   forest abundance and extent can have far reaching consequences for nearshore ecosystems and

101   beyond (Wernberg et al., 2019).

102

103   Evidence collected over the past two or more decades indicates that kelp forests are decreasing in

104   abundance and extent across certain parts of the world due to combined effects of climate change

105   and localized threats, including fishing, sewage run-off, invasive species and changes in

106   freshwater outflow (Krumhansl et al., 2016; Filbee-Dexter & Wernberg, 2018; Wernberg et al.,

107   2019; Hollarsmith et al., 2022). However, the trajectories of kelp forests around the world have

108   been highly variable, with some regions showing stability (e.g., Chile and the Falkland Islands;

109   Mora-Soto et al., 2021) or even increases in abundance (e.g., South Africa; Bolton et al., 2012),

110   highlighting the importance of refugia at global, regional and local scales (Krumhansl et al.,

111   2016; Wernberg et al., 2019). Where kelp forest ecosystem collapse has occurred, it has

112   generally been associated with transitions to urchin barrens or communities formed by other

113   (non-kelp) seaweeds (Wernberg et al., 2019), and there is evidence that transitions between these

114   states can be challenging to reverse, often failing to return to the kelp forest state even after

115   initial stressors are abated (Leinaas & Christie, 1996; Hughes et al., 2005; Pearse, 2006; Filbee-

116   Dexter & Wernberg, 2018; Feehan, Grace & Narvaez, 2019). In some areas, kelp forest losses

117   have had profound ecological and economic consequences from the collapse and closure of

118   fisheries to detrimental impacts on tourism-based industries (Rogers-Bennett & Catton, 2019). In

119   the USA, recent efforts have begun to determine whether one of the main kelp forest foundation

120   species, bull kelp (*Nereocystis luetkeana*), should be listed and protected under the Endangered

121   Species Act (Kelkar & Carden, 2022), highlighting growing efforts to restore and conserve kelp

122   forest ecosystems in the face of ongoing climate change.

123

124   Between 2014 and 2016, a large-scale marine heatwave (MHW) known as "the Blob" unfolded

125   along the west coast of North America (Lorenzo & Mantua, 2016; Tseng, Ding & Huang, 2017;

126   Robinson, Yakimishyn & Evans, 2022), threatening kelp forests in many regions (Cavanaugh et

127   al., 2019; Beas-Luna et al 2020; Starko et al. 2022). While warmer waters had direct impacts on

128   kelp forests by imposing physiological stress and die-back (Cavanaugh et al., 2019; Starko et al.,

129   2022), they also had indirect impacts on kelp forests by exacerbating the growing sea star

130   wasting disease (SSWD) epidemic (Harvell et al., 2019; Hamilton et al., 2021). SSWD resulted

131   in the functional extinction of *Pycnopodia helianthoides*, the sunflower star, across much of its

132   distribution (Harvell et al., 2019; Hamilton et al., 2021), triggering trophic cascades that

133   favoured sea urchins, the dominant herbivore of kelp forests (Schultz, Cloutier & Côté, 2016;

134   Burt et al., 2018; Rogers-Bennett & Catton, 2019; McPherson et al., 2021; Starko et al., 2022).

135   The combined effects of warming and expanding urchin populations have driven kelp forest

136   losses throughout the Northeast Pacific (Beas-Luna et al., 2020) with severe impacts observed in

137   populations of both major floating canopy-forming kelp species: giant kelp (*Macrocystis*

138   *pyrifera*) and bull kelp (*Nereocystis luetkeana*).

139

140   Despite the growing evidence that MHWs and other extreme events have negatively impacted

141   kelp forest ecosystems, the sheer extent and heterogeneity of these ecosystems makes it

142   challenging to assess the scale of kelp deforestation. Kelp forests occupy more than one-third of

143   the world's coastlines, an area five times that of coral reefs (Jayathilake & Costello, 2021), and

144   floating kelp occupy >30° latitude on the west coast of North America alone, suggesting that

145   widespread declines could have profound impacts on the availability of coastal habitat for

146   associated species and the extent of nearshore productivity. This could have important

147   implications for economically critical fisheries that rely on kelp habitats, such as salmon and

148   herring (Shaffer et al. 2019; Shaffer et al. 2020), throughout the Northeast Pacific and might also

149   impact the extent to which coastal ecosystems draw-down and sequester carbon from the

150   atmosphere at both global and regional scales (Krause-Jensen et al., 2018; Filbee-Dexter &

151   Wernberg, 2020). To assess the spatial scale and extent of kelp forest loss, we must work to

152   include historically understudied regions, including those that lack detailed multi-decadal time

153   series, leveraging and scrutinizing all available data to draw inferences about kelp forest spatial

154   contractions and associated concerns for conservation.

155

156   One region in which kelp forests have historically been understudied is British Columbia (B.C.),

157   Canada. Past glaciation has left B.C.'s coast scarred with bays, fjords and channels that create

158   inshore pockets of water that warm up in the summer to temperatures comparable to near the

159   southern limit of either kelp species (Starko et al., 2022). For example, waters in both the Strait

160   of Georgia and the west coast of Vancouver Island have reached temperatures greater than 20°C

161   in recent summers (stations 3-5 in Fig 1; Starko et al. 2022). This is warmer than known growth

162   optima for both canopy-forming kelp species (Supratya, Coleman & Martone, 2020; Fernández

163   et al., 2020), suggesting that kelp forests may be threatened by these warm sea surface

164   temperatures. Moreover, recent focal fieldwork along small stretches of the B.C. coast suggest

165   that kelp forests have also declined in response to growing urchin populations (Schultz, Cloutier

166   & Côté, 2016; Burt et al., 2018; Starko et al., 2022). However, the extent to which these threats

167   are a concern across B.C.'s nearly 26,000 km coastline (more than twice that of California,

168   Oregon and Washington combined) remains largely unclear.

169

170   Here, we ask whether kelp forest extent in coastal B.C. has changed over the past two to three

171   decades in response to recent environmental and biotic drivers. We assemble available

172   quantitative data on kelp forest distributions from B.C. Because many regions lack long-term

173   monitoring programs, we begin with numerous "snapshot" analyses–primarily using oblique

174   shoreline photography supplemented with in situ data and satellite imagery when available–from

175   two time points, one before recent heatwave and SSWD events (1994 – 2007) and one following

176   (2017 – 2021). We then use time series data from all regions where they are available (n = 7) to

177   contextualize large-scale patterns of change observed in the snapshot analyses. Moreover, we

178   discuss how spatial patterns of change correlate with environmental variation and evidence of

179   biotic interactions to make inferences about the drivers of kelp forest dynamics across a poorly

180   studied region. This assessment aims to inform whether floating kelp forests (*Macrocystis* and

181   *Nereocystis*) are of conservation concern in the province.

182

183   Various abiotic and biotic factors may make kelp more resilient in the face of warming and shifts

184   in trophic dynamics (Hollarsmith et al., 2022). Spatial variation in temperature and other

185   environmental variables can mediate the responses of kelp forests to large-scale warming

186   (Wernberg et al., 2016; Cavanaugh et al., 2019; Starko et al., 2019; Filbee-Dexter et al., 2020),

187   with factors like water motion, upwelling dynamics, and nutrient pollution leading to complexity

188   in the distribution of environmental variation across the coastal fringe (Druehl, 1978;

7

189   Hollarsmith et al., 2022; Spiecker & Menge, 2022; Starko et al., 2022). For example, while

190   inland waters may warm up in the summer, areas on the outer coast with high wave exposure or

191   currents can stay cool and nutrient rich through upwelling and mixing, potentially facilitating

192   kelp persistence (Berry et al., 2021; Starko et al., 2022). On the other hand, food web length and

193   structure can mediate the secondary impacts of SSWD. Specifically, when sea otters or other

194   urchin predators are present they introduce functional redundancy, limiting the effects of sea star

195   loss on the abundance of urchins and the subsequent effects on kelp forests (Burt et al., 2018;

196   Eisaguirre et al., 2020). Consequently, here we test four hypotheses: 1) that kelp forests have

197   experienced more losses (i.e., local-scale extirpations) than gains (i.e., local colonisations) across

198   B.C.; 2) that kelp loss in some regions has been near-complete, similar to patterns observed in

199   parts of California (e.g., Rogers-Bennett & Catton 2019); 3) that local environmental conditions

200   (specifically temperature) have mediated the impacts of the 2014-2016 heatwave event on kelp

201   forest distributions (with warmer areas more likely to experience kelp declines); and 4) that

202   regions with sea otters have been more stable in the face of these large-scale perturbations due to

203   top-down control on urchin populations.

204
205
206   ## 2. Materials & Methods

207
208   *2.1 Study design and regions*

209   We selected study regions based primarily on the availability of imagery, and with the goals of

210   capturing a range of sea surface temperatures as well as regions with and without sea otters. We

211   were able to assemble data for 14 regions spanning a ~675-kilometer latitudinal gradient (6

212   regions for "snapshot analyses" only, 2 regions for time series only, and 5 regions for both types

213   of analyses; see Tables 1-2). Our goal with the snapshot analyses was to quantify changes in kelp

214 linear shoreline extent (hereafter, "extent") using a timepoint from before (1995 – 2007) and a

215 timepoint from after (2017 – 2021) the major 2014-2016 marine heatwave (MHW). While

216 historical aerial images for snapshot analyses span more than a decade, all of these time points

217 occurred before recent warming (since 2014) and SSWD that were known to drive major

218 changes to kelp forest dynamics in the Northeast Pacific (Beas-Luna et al., 2020). We also

219 compiled various time series data where available; while datasets differ in methodology and

220 response variable (e.g., linear extent vs total kelp area; see below), they were internally

221 consistent and therefore provide important context for patterns of change captured by snapshot

222 analyses.

223

224 *2.2 Snapshot analyses of kelp linear extent*

225 To assess changes in linear extent (measured here as presence-absence of kelp along shoreline

226 segments), we performed analyses focused on two time points: one before the MHW and one

227 after (hereafter "snapshot analyses"). For nine regions, we used oblique aerial imagery collected

228 by the ShoreZone initiative (Howes, Harper & Owens, 1994; Cook et al., 2017) and Environment

229 & Climate Change Canada (ECCC) between 1995 and 2021 as data sources for both time points.

230 For one of the regions (Barkley Sound), more recent ShoreZone imagery from before the MHW

231 were available (2007) and we coupled these with in situ surveys conducted in 2018, while for

232 another region (Cowichan Bay), we used two years from a dataset derived from high resolution

233 satellite imagery (see below). A summary of data sources for each region is provided in Table S1

234

235 For the ten regions that involved oblique aerial imagery (including Barkley Sound), we created

236 shoreline segments to classify stretches of shoreline that could be identified in both pre- and

237 post-MHW imagery, and where either one or both of the images contained kelp canopy that was

238 clearly visible in oblique images. Oblique imagery was taken at low tidal heights when most kelp

239 canopy can be expected to be floating at the surface (Schroeder et al., 2019; Timmer et al.,

240 2022), but since the imagery was collected at an oblique angle, we were unable to accurately

241 assess changes in the area of kelp canopy over time and restricted these analyses to presence-

242 absence. Therefore, kelp canopy was determined to be either present or absent within each image

243 for each segment, and the segment was accordingly classified as either a 'gain' (colonisation;

244 absent in pre-MHW imagery but present in post-MHW imagery), a 'loss' (extirpation; present

245 pre-MHW but absent after), or as 'stable' (kelp remained present at both time points) for each

246 segment between the two time periods. Out of an abundance of caution, if the kelp in either

247 image was not clearly identifiable due to glint on the water surface, choppy water, or if the image

248 was too grainy to reliably identify kelp, the segment was not used. For these ten regions, the

249 methods varied slightly depending on the availability of imagery and/or the length of shoreline

250 surveyed.

251

252 In six regions (Valdes/Gabriola, Nootka, Quatsino, South Central Coast, Laredo Sound, Dundas

253 Island), coverage of historical images was limited. For these regions, shoreline segments (~30-60

254 m in length) were established based on recognizable shoreline features in the aerial images that

255 could be georeferenced in google earth. Due to data limitations in these regions, some segments

256 were created based on stills taken from oblique-facing aerial videos that were collected during

257 initial surveys rather than images themselves. Most photos (from either video stills or original

258 photography) only covered a single segment, but in some cases, two or three segments were

259 established from wider shot photography. To capture colonisation events or determine the extent

260   to which some stretches of shoreline lacked kelp in both survey years, we also collected

261   observations of kelp absences for any images where kelp was not present in the historical year

262   and for which there was modern imagery of that same stretch of coastline that also lacked kelp.

263   We did not quantify the length of shoreline associated with absence observations unless they had

264   been colonised by kelp between the time points. In this latter case, shoreline segments were

265   created as described above to capture kelp colonisation of a new stretch of shoreline.

266

267   For three regions, where historical oblique imagery was not limiting and virtually the entire coast

268   was photographed at high quality (Juan de Fuca Entrance - region iv, West Coast Trail – region

269   v, Barkley Sound – region vi), different approaches were employed to systematically survey

270   photographic data. For the West Coast Trail (region v) and Juan de Fuca entrance (region iv),

271   which collectively represent more than 80km of shoreline, a systematic subsampling method was

272   used. First the coastline was split into 250m pixels, and at the start of each pixel, a single

273   shoreline segment (length ~20-100m depending on shoreline features; West Coast Trail average

274   = 48m; Juan de Fuca average = 40m) was established, provided the image met the quality criteria

275   described above in imagery from both time points. For Barkley Sound (region vi), we used two

276   time points from a time series involving multiple data sources (see Starko et al 2022 and

277   description below). In short, we systematically resurveyed a 16km stretch of coast (originally

278   surveyed in 2007) in 2018, 2021 and 2022 (see Starko et al. 2022). The coast was segmented into

279   ~20 – 100m segments (32m on average) segments as above. For the snapshot analysis, we

280   compared data from 2007 to data from 2018.

281

282   Shoreline segments (100m in length) in Cowichan Bay (region iii) were established as described

283   in Schroeder et al. (2020) and relied on high resolution satellite imagery (Digital Globe; 2.5m

284   resolution or higher) rather than oblique aerial imagery. For this dataset, a time series was

285   produced from imagery in 2004, 2012, 2015, 2016 and 2017 from <2m tidal elevation in July –

286   September, from which we used data from 2004 and 2017 for the snapshot analysis.

287   Methodological details for this dataset are given in section 2.3

288
289   *2.3 Time series analysis*
290
291   We assembled time series datasets for 7 regions, five of which directly overlap with regions

292   examined in the snapshot analyses (see Table 2 for summary of years and data types). These five

293   regions are Mayne Island (region ii), Cowichan Bay (iii), Barkley Sound (vi), South Central

294   Coast (ix) and Laredo Sound (x). In contrast, the Central Strait of Georgia region (region i-b),

295   which includes a stretch of the Strait of Georgia from Denman Island down to Nanaimo is

296   adjacent to the Valdes/Gabriola region (region i) but does not include the same stretches of

297   shoreline (see Fig 2, Fig S1). Similarly, Calvert Island (region ix-b) is adjacent to the South

298   Central Coast (region ix) but is not contained within the region analysed for the snapshot

299   analysis (see Fig 2, Fig S2). Data from Central Strait of Georgia (region i-b) involved analysis of

300   SCUBA diver observations from 2 sites (see below), and Calvert Island (region ix-b), involved

301   the analysis of aerial imagery acquired from remotely piloted aerial systems (RPAS) flown at

302   two sites.

303

304   Where available, in situ data were used for time series analyses. This was the case for two

305   regions: the Central Strait of Georgia (region i-b) and Mayne Island (ii). To contextualize

306   changes in bull kelp (*Nereocystis*) occupancy (i.e., presence-absence) in the Central Strait of

12

307   Georgia (where *Macrocystis* is not present), we extracted data from citizen SCUBA diver videos

308   (available online or through a local dive shop) and from the logbooks of authors. At one site,

309   Eagle Rock (Denman Island), dives were conducted intentionally looking for kelp forests by

310   three of the authors (A. & R. Zielinski, W. Heath) as part of a restoration and monitoring

311   initiative. Here, logbooks recorded whether *Nereocystis* was present and this was converted into

312   presence-absence data for the site. At the other site (Tyee Cove, Nanoose Bay), we assembled

313   recreational SCUBA diver videos (from a local dive shop and online – e.g., YouTube; Table S2)

314   and determined whether *Nereocystis* was present in each video over an 11-year period. While

315   videos were generally not taken with the intention of tracking kelp, *Nereocystis* was a frequent

316   occurrence in the shallows of this site alongside other kelp species, and therefore we would

317   expect it to appear in citizen SCUBA diver videos either on purpose or incidentally while filming

318   in the "kelp zone". We included observations from April – October, to reflect the growing season

319   of *Nereocystis*. While we included all videos or blog posts where *Nereocystis* was visible as

320   observations of canopy kelp being "present", we required that videos cover at least 20 seconds of

321   footage in the "kelp zone" (i.e., understory kelp present), where conditions would be suitable for

322   bull kelp, to include a video as an absence observation. Both sites were selected based on direct

323   observations by the authors (Timmer, Heath, A & R. Zielinski) that the forests had disappeared

324   in recent years and therefore may offer insight into the timing of losses but not the extent of

325   losses, nor does this capture interannual variation in abundance or extent of kelp forests that have

326   persisted in this region.

327

328   For the second time series derived from in situ data (Mayne Island – region ii), data from citizen-

329   science kayak surveys were analyzed to produce a time series. Surveys were conducted in situ by

13

330   encircling the surface extent of kelp forests during low tides <1.2m above chart datum and taking

331   GPS points to identify the perimeter of the bed. Polygons were then produced from these data to

332   represent kelp extent at each time point. Because survey areas varied in their spatial coverage

333   between years, polygons were clipped according to spatial overlap of the survey areas to

334   maximize the temporal coverage of the surveys. The resulting dataset covered five discontinuous

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

336

337   For five other regions (iii, iv, ix, ix-b, x), various approaches were used to construct time series

338   with remote sensing technologies (satellites, aerial images from piloted vehicles, RPAS), with

339   analysis type dependent on data availability and/or previously conducted region-specific

340   analyses. While the Barkley Sound (region vi) time series involved a combination of remotely

341   sensed and in situ data, all other regions used remote sensing data for all time points. A summary

342   of remote sensing data sources used for time series is provided in Table S3.

343

344   For Cowichan Bay (region iii), high resolution WorldView-2 satellite images were acquired at

345   tidal height below 2.0 m from July, August and September, corresponding to the growing season

346   bull kelp (see Tables 2, S3 for years). In short, kelp presence and absence along each shoreline

347   segment was assessed using an unsupervised ISODATA classification approach, considering

348   land and 30 m bathymetry masks and a buffer along the shoreline to minimize the effects of

349   adjacency. This data set is published and presented by Schroeder et al. (2020).

350

351   For Barkley Sound (region iv), aerial and high resolution satellite images were classified visually

352   (see Starko et al., 2022) and compared to boat surveys conducted between 2018 and 2022 (see

353   snapshot methods above). The same shoreline segments were used as described in section 4.2,

354   however the dataset was trimmed to ensure only the subset of segments present in all years of the

355   time series were analysed.

356

357   For the South Central Coast (ix), the Google Earth Engine Kelp Mapping Tool was used to

358   produce a time series of annual maximum kelp extent from 1984 to 2021 using methods

359   described within Nijland et al. (2019). In brief, a time series of maximum annual kelp area (m^2)

360   was derived using the Normalized Difference Vegetation Index (NDVI) from Landsat 5 TM, 7

361   ETM+ and 8 OLI imagery with a minimum NDVI threshold of 0.02 and detection threshold of 2

362   (ie. each pixel had to be detected above the minimum NDVI threshold twice in each time period

363   to be classified as kelp) for all image scenes available between May 1 – Oct 31. In some years,

364   detection thresholds were changed due to limitations in available imagery (mostly due to cloud

365   cover). Images used had cloud cover < 90% and a tidal stage of <3.5 m (chart datum) of each

366   year. Where the Landsat cloud mask was found to perform poorly, some image scenes were

367   removed manually. A land mask was applied with a 30 m buffer (1 Landsat pixel) to remove

368   potential mixed pixels containing land which could be falsely detected as kelp. Therefore, these

369   data outputs consider "offshore" kelp explicitly.

370

371   For Calvert Island (ix-b), total canopy kelp area was quantified at two sites using imagery from

372   RPAS flown in situ. Meay Channel is a site with *Macrocystis*, while North Beach is a

373   *Nereocystis* site. Total kelp area at each time point was assessed either manually or using an

374   index and threshold method.

375

376 For Laredo Sound (x), aerial imagery (from 2007), visible colour satellite imagery from 2013

377 (Google Earth) and oblique imagery from ECCC (2019) were compared and classified visually

378 (as with the Barkley Sound time series) using 50m segments (presence-absence only).

379
380 *2.4 Environmental data*

381 We used environmental data to test 1) whether spatial patterns of temperature predicted kelp

382 persistence based on snapshot analyses; and 2) how kelp area in the longest time series (South

383 Central Coast) correlates with temporal temperature anomalies. To assess how patterns of kelp

384 persistence in snapshot analyses relate to local summer sea surface temperatures, we used

385 average daily sea surface temperature from the LiveOcean Model, a Regional Ocean Modeling

386 System adapted to the coastal waters off of Washington, Oregon, and southern British Columbia

387 (Fatland, MacCready & Oscar, 2016). We extracted and averaged data from August 2017 (the

388 first year of the model) which, although not during the 2014-2016 MHW, was still an

389 anomalously warm year. This model has a grid size of 500 – 1500m (depending on location)

390 which may miss some fine-scale temperature variation. It   captures known temperature

391 gradients on southern Vancouver Island such as in Barkley Sound (Starko et al. 2022) and the

392 Salish Sea (Ban et al., 2016) but does not include the three regions north of Vancouver Island. To

393 assess temperature anomalies relevant to the South Central Coast (region ix) time series, we used

394 a temperature time series from McInnes Lighthouse which is nearby this region. We then

395 calculated average month anomalies using data from 1982 to 2012 as the baseline.

396
397 *2.7 Sea otter occupancy status*

398 We used previously published reports (Nichol et al., 2015, 2020) to infer which of the 14 regions

399 included in this study are occupied by sea otters (*Enhydra lutris*). These reports document

16

400   surveys conducted to quantify population size and distribution of otter populations across the

401   coast of B.C. These results show that otters are consistently present (and with growing

402   populations) in three regions examined here: Nootka Sound (vii), Quatsino Sound (viii) and the

403   South Central Coast (ix). Although considered to have expanded to areas around Calvert Island

404   (region ix-b) in 2013 (Nichol et al., 2015), on-the-ground observations and surveys have shown

405   the occupation of focal sites (North Beach and Meay Channel) in this region was short-lived and

406   otters were no longer using these sites after 2016 despite being present on nearby islands.

407

408   *2.6 Statistical analysis*

409   To test whether regions varied in their trajectories in the snapshot analysis, we used a Fisher's

410   exact test to determine whether kelp change status (stable, gain, loss) was contingent on region.

411   We also tested whether summer sea surface temperature (using modelled data from August

412   2017) predicted kelp persistence from snapshot data in southern regions using a spatially explicit

413   binomial glm (0 = kelp loss, 1 = kelp gain or persistence). We then used various statistical

414   models to determine whether kelp forest extent or abundance has changed through time in the

415   time series data. Specifically, we used linear models to test for change through time for Barkley

416   Sound (extent), Cowichan Bay (extent) and Mayne Island (kelp forest area) regions because data

417   were continuous and normally distributed. For Laredo Sound, we tested whether years differed in

418   their linear extent using a binary glmm (fixed = year [categorical]; random = segment). For

419   Calvert Island region, where data were continuous but non-normal, we tested for change through

420   time across both sites using a glmm fit with a gamma distribution (fixed = year [continuous];

421   random = site). Finally, we tested for change in offshore kelp forest area through time in the

422   South Central Coast time series using a linear model and also tested whether kelp forest area

17

423 following 2014 was drawn from the same distribution as prior to the heatwave using a Wilcoxin

424 rank sum test.

425

3. Results

427

428 We found substantial changes in the linear extent of kelp forests when comparing pre- and post-

429 MHW data from snapshot analyses; however, the direction and amount of change varied across

430 regions (Fig 2; Fisher's Exact Test: p = 0.0005). Of the 11 regions that we examined with our

431 snapshot analyses, 6 had more kelp losses than gains, 2 had more gains than losses, and 3 had

432 roughly no change (<10% net loss or gain). Regions that experienced the greatest kelp loss

433 spanned the entire latitudinal gradient from Valdes/Gabriola – region ii (74 % loss; ~49° N) to

434 Laredo Sound – region x (31% loss; ~53°N) and Dundas Island – region xi (62% loss; ~55°N).

435 Moreover, losses were observed in regions dominated by both *Macrocystis* and *Nereocystis* (e.g.,

436 Barkley Sound – region vi versus Valdes/Gabriola – region i). In contrast, the South Central

437 Coast (region ix) and Quatsino Sound (region viii) regions experienced increases in linear extent

438 compared to historical snapshots, with 16% and 15% gains, while only experiencing 3% and no

439 losses, respectively. Regions on the exposed outer coast of southern Vancouver Island (Juan de

440 Fuca – region iv, West Coast Trail – region v) experienced very little change in kelp extent (<5%

441 net change) between the two time points while Nootka – region vii – experienced both increases

442 and decreases, resulting in a net change of only ~9% (Fig 1). Regions that experienced increases

443 or stability also included those dominated by both canopy kelp species.

444

445 In addition to differences amongst regions, spatial patterns in kelp persistence tended to reflect

446 the mediating impacts of fine-scale environmental variation. In southern regions without otters

18

447   (regions i to vi), kelp loss strongly correlated with local summer sea surface temperatures.

448   Coastlines along the southeast (regions i to iii) and southwest sides (regions iv to vi) of

449   Vancouver Island span multiple local and regional temperature gradients (see Fig 3) and kelp

450   persistence patterns from these regions strongly correlate with this fine-scale variation in

451   temperature. Kelp loss on Mayne/Saturna (region ii) was largely restricted to the northeastern

452   sides of islands that experience greater temperatures than other parts of the region (Fig 3).

453   Similarly, the Valdes/Gabriola regions, which experience particularly warm summer

454   temperatures, experienced significant losses across the entire region. In Barkley Sound, kelp

455   forests disappeared primarily from inner parts of the region where conditions are known to get

456   much warmer (see Starko et al., 2022; Fig 3) while remaining towards the outer shore, including

457   adjacent outer shore regions (West Coast Trail, Juan de Fuca Entrance). We specifically tested

458   whether spatial variation in temperature predicted kelp forest persistence within and across all

459   regions on southern Vancouver Island (n = 6 regions; n = 798 segments) and found that, after

460   accounting for spatial autocorrelation, kelp forest persistence was strongly predicted by local

461   temperature variation (Spatial GLM: X^2 = 24.402, p < 0.0001).

462

463   Exposure to waves and currents appeared to also influence kelp forest persistence. While there

464   was extensive kelp loss in Valdes/Gabriola (region i), there were persistent forests in the high

465   current narrows between islands. Similarly, in the Cowichan (iii) region, the most persistent

466   forests were in the narrows between Vancouver Island and Saltspring Island. This likely reflects

467   either fine-scale mixing that brings cooler waters to the surface not captured by the LiveOcean

468   Model or else it reflects impacts of water motion through other means (e.g., impacts on urchin-

469   kelp dynamics, growth rate). In the Laredo Sound (x) and Dundas Island (xi) regions, kelp

470   forests largely disappeared from more sheltered areas, specifically the eastern (leeward) side of

471   Dundas Island and Aristazabal Island, respectively (Fig 4). In both cases, urchin barrens (and in

472   some cases, groups of sea urchins) were visible as shallow as the intertidal zone in the oblique

473   aerial imagery (Fig S3-S6). However, kelp persisted on the side of each island that faces towards

474   the open ocean, where wave exposure is likely to be much greater. Thus, wave action may limit

475   the ability of urchin grazers to reach the shallowest edge of the depth range of kelp forests,

476   thereby facilitating persistence of kelp in the face of increasing urchin populations (Keats, 1991;

477   Watson & Estes, 2011).

478

479   Kelp forest gains also tended to be spatially clustered, primarily in regions with increasing sea

480   otter populations (Fig 4). Gains in Nootka Sound were focused in two parts of the region, the

481   inner islands of the sound and a small islet towards the exposed outer coast. Gains in Quatsino

482   Sound tended to be spatially clustered around the opening of the sound but were also found in a

483   few other cases further into the sound. On the South Central Coast, two stretches of coastline that

484   included multiple shoreline segments each were colonised by kelp while remaining largely stable

485   elsewhere. Kelp forest colonisations in other regions were generally patchy and uncommon but

486   tended to be found nearby other segments that had kelp in both time points.

487

488   Time series from a variety of regions provide temporal context for observed changes in the

489   distribution of kelp forests from the snapshot analyses. Across several regions with time series,

490   negative impacts from the 2014-2016 MHW appear prevalent with varying levels of recovery

491   and in some cases continued declines. The Central Strait of Georgia (region ii-b; only

492   *Nereocystis* present) and Barkley Sound (region vi; both species present but *Macrocystis* more

493   common) both experienced declines during this time-period and these have persisted for several

494   years past the event (Fig 5a, f). In contrast, while Mayne Island (region ii) and Cowichan Bay

495   (region iii) both had the lowest linear extent in the year following the MHW (2017) than in any

496   other year (including during the MHW), these declines were relatively moderate (~22 and ~34%

497   compared to lowest pre-MHW year) and for Mayne Island, recovery of the kelp forests was

498   captured in later years. However, despite this apparent recovery in the regional Mayne Island

499   time series, some individual sites experienced persistent declines during and following the MHW

500   (Fig S7). Data from part of Laredo Sound (region x) demonstrate that kelp was present

501   throughout the entire region as recently as 2013. Thus, kelp loss in Laredo Sound captured in our

502   snapshot analysis occurred sometime between 2013 and 2019, which coincides with the timing

503   of the MHW and SSWD impacts. Similar patterns were observed on Calvert Island (ix-b), where

504   kelp area declined between 2015 and 2020. Interestingly, 2014 had the greatest bull kelp

505   abundance at the North Beach site on Calvert Island but steadily decreased over the next several

506   years. This spike in kelp abundance in 2014 coincides with short-term occupation by sea otters

507   which occurred in this region between 2013 and 2014 (Burt et al., 2018). Importantly, kelp

508   abundance following the departure of sea otter populations and the 2014-2016 event was lower

509   than kelp observations beforehand (2006, 2012). Temporal variation in bull kelp abundance at

510   this site therefore lends insight into multiple ecosystem states: kelp forests with *Pycnopodia* but

511   no otters (2006 – 2013), kelp forests with both sea otters and *Pycnopodia* (2014), and kelp

512   forests without either top predator (2016 – 2021) (Burt et al., 2018).

513

514   The longest running time-series is that of total offshore kelp area for the South Central Coast

515   (ix). This is a region that was colonised by sea otters around the year 1990 and otter populations

516   have been increasing since (Nichol et al., 2015, 2020). Time series data from this region do not

517   include kelp within 30m of shore but offer an overall look at the abundance of kelp in offshore

518   beds (e.g. >30m from shore) which are common in this area. The time series shows no

519   directional trend through time (Linear model: P = 0.99) with some evidence of increase in kelp

520   abundance early in the dataset. Specifically, the highest abundances were found between 1999

521   and 2014 despite the dataset dating to 1984. Although kelp abundance was approximately

522   average in 2014, it dropped to its lowest value in 2015. While 2015 kelp area was only <5 % less

523   than multiple other years of the dataset, recovery following the 2014-2016 MHW was limited.

524   Kelp abundance in 2015 and later tended to be lower than the mean kelp abundance in years

525   prior, however this trend was not significant (W = 158, p = 0.06501). While past declines in kelp

526   abundance to similar levels were generally followed by rapid recovery, hinting at resilience in

527   these forests, kelp abundance following the event has stayed reduced for another six years

528   following the initial crash in 2015. It is worth noting that declines in kelp area captured in the

529   time series are not reflected in the snapshot analysis. Because kelp forests in the snapshot

530   analysis are generally fringing beds within 30m of the shoreline that are excluded from the

531   satellite time-series, this may reflect either differences in the type of kelp forest assessed by the

532   two methods or differences in the metrics used (i.e., shoreline occupancy vs. total area). This

533   highlights that changes in linear extent and total kelp area can be decoupled in some cases and

534   underscores the importance of examining differences in kelp stability according to local and

535   regional spatial scales as well as bed morphology.

536
537   **4. Discussion**
538
539   Here, we established for the first time that kelp forests in British Columbia have experienced

540   variable patterns of change over the timeframe of recent marine heatwave events, with many

22

541   regions experiencing substantial declines in kelp linear extent, consistent with our first

542   hypothesis. In the most extreme cases, kelp extent declined by more than 60% in two regions

543   (Valdes/Gabriola (i): 74% loss; Dundas Island (xi): 62% loss) and more than 30% in two others

544   (Barkley (vi): 43% loss; Laredo Sound (x): 31% loss) in the snapshot analyses, supporting our

545   second hypothesis of near-complete loss in some regions. While our snapshot analyses were not

546   comprehensive in coverage of coastal British Columbia, kelp declines were observed across the

547   coastline; with modest increases (14 – 22 % gains) observed in only two regions and little to no

548   change observed in three regions, hinting at regional-scale kelp refugia. Moreover, where

549   snapshot and time series data overlap, declines in kelp abundance and biomass are unprecedented

550   over the time periods of time series. For example, even the highly variable time series of the

551   South Central Coast (region ix) shows reduced resilience (i.e., ability to recover following a year

552   with low kelp abundance) following the 2014-2016 marine heatwave (MHW) compared to the

553   three decades prior. Similarly, kelp reached its lowest occupancy states in Barkley (vi) and

554   Laredo (x) Sounds following the heatwave compared to past timepoints spanning multiple

555   decades (Fig. 5; see Starko et al. 2022 for in depth case study of Barkley Sound to the 1970s).

556   Overall, the scale and persistent nature of concurrent kelp forest loss across several B.C. regions

557   suggests that kelp forests should be a conservation concern in this province. Importantly,

558   however, not all regions have experienced losses and instead declines have been spatially

559   clustered to particular localities within only some regions. This highlights how ecosystem-level

560   perturbations have different impacts depending on the underlying heterogeneity in the

561   environment, a phenomenon that should be strongly considered when developing management

562   plans and monitoring programs   .

563

564   *4.1 Spatial variation in kelp forest trajectories*

565   Patterns of change were strongly spatially structured, providing insight into the drivers behind

566   those changes. In areas that are naturally warmer due to seasonal patterns of warming (e.g.,

567   Central Strait of Georgia (i-b), Gabriola/Valdes (i), inner parts of Barkley Sound (vi)), kelp

568   forests largely disappeared during the 2014-2016 MHW with very minimal (if any) recovery. In

569   contrast, nearby regions (e.g., Mayne/Saturna (ii) and the West Coast Trail (v)) experienced little

570   net kelp loss, instead maintaining extensive kelp forests (Fig 4). These patterns are consistent

571   with our third hypothesis and are captured in both snapshot imagery analysis and time series

572   data, where the timing of kelp declines in both Barkley Sound and the Central Strait of Georgia

573   coincided with the 2014-2016 MHW (Fig 5). Although it is challenging to disentangle the direct

574   impacts of temperature from those of urchin expansions expected from the die-off of

575   *Pycnopodia*, recent work in Barkley Sound demonstrated that these factors together can drive

576   kelp loss in warm areas by negatively impacting kelp forests across their depth range, preventing

577   persistence in both shallow and deeper waters (Starko et al., 2022).

578

579   We attribute the loss of kelp in the two northern-most regions without otters (Laredo Sound –

580   region x and Dundas Island – region xi) to increases in urchin grazing. Both of these regions

581   experienced large declines in kelp extent, despite no evidence that these regions experience

582   temperatures warm enough to threaten kelp forests. Lighthouses nearby to both regions show that

583   temperatures remained consistently below $18^{O}C$ during the summers of 2014-2017 (Fig 1) which

584   include the warmest years in decades (see Fig 5). Instead, oblique imagery clearly shows that

585   kelp forests in these regions have transitioned to urchin barrens, with sea urchins visible as

586   shallow as the intertidal zone along several stretches of coastline where kelp has disappeared

24

587   (Figs 3, S4). Kelp losses in these areas are largely restricted to the leeward side of islands, where

588   the coast is sheltered from incoming swell. In contrast, coastlines facing west in both regions

589   generally retained kelp forests. Wave action from oncoming swell can limit the depth that sea

590   urchins can graze (Keats, 1991; Kawamata, 2010; Watson & Estes, 2011), potentially facilitating

591   kelp forest persistence in shallow waters, despite increases in the abundance and dominance of

592   sea urchins. Indeed, the West Coast Trail (v) and Juan de Fuca (iv) regions, which both face the

593   dominant direction of oncoming swell and are generally cooler due to mixing at the entrance of

594   the Juan de Fuca Strait (Fig 1; see station 1), experienced very little (<5%) change in kelp extent,

595   likely due to the absence of both environmental and biotic drivers of decline. Past work has

596   suggested that tidally driven vertical mixing might allow these regions to serve as climatic

597   refugia for marine systems in the face of climate warming and perturbations (Ban et al., 2016).

598   This hypothesis is strongly supported by our results.

599

600   The only regions to experience more increases in kelp extent than decreases were those with

601   growing sea otter populations (regions vii to ix), consistent with our fourth hypothesis that these

602   regions would be more resistant and/or resilient to changes in trophic dynamics. Although sea

603   otters were once widely distributed in British Columbia, they were extirpated from the entire

604   coast during the Fur Trade of the 18th to 20th centuries (Nichol et al. 2015). Sea otters were

605   reintroduced to Checleset Bay on Northern Vancouver Island in 1969 - 1972 and have since

606   expanded to include all three of regions vii to ix included in our study. Moreover, provincial sea

607   otter surveys conducted as recently as 2017 indicate that otter population sizes have continued to

608   increase in all study regions in which they have re-established (Nichol et al. 2020). Thus,

609   increases in kelp extent in these regions likely reflect successional dynamics associated with

25

610 changes in trophic structure (Watson and Estes 2011). Specifically, increasing otter populations

611 would be expected to drive declines in sea urchin abundance which could subsequently allow

612 kelp to colonise stretches of shoreline that were previously in the urchin barren state. We note

613 that patterns of persistence and colonisation are similar across both canopy-forming kelp species

614 in regions where the two species co-occur (Fig. S8).

615

616 *4.2 Timing of kelp forest change*

617 Time series data from seven regions capture widespread declines between 2014 and 2017,

618 coincident with the MHW and SSWD event. The Central Strait of Georgia (i-b), Barkley Sound

619 (vi), Calvert Island (ix-b) and Laredo Sound (x) all show evidence of persistent declines, with

620 little to no recovery following the heatwave (Fig 5). Where data span multiple years of the

621 heatwave (regions i-b, iii, vi, ix-b), losses were sometimes not documented until the second year

622 of the MHW or later (2015-2017), suggesting that the multi-year nature of the event was critical

623 to driving declines. In contrast to regions with persistent declines, kelp forests around Mayne

624 Island (region ii) experienced negative impacts from the 2014-2016 marine heatwave but these

625 declines were not persistent and kelp forests largely recovered in following years. However, site-

626 level analyses around Mayne Island (Fig S7) indicate that the trajectories of individual kelp

627 forests have been variable with some sites remaining stable or increasing and others experiencing

628 persistent declines. This highlights how variation in kelp forest trajectories often occurs at fine

629 scales with apparent site-level differences in the persistence of kelp forests.

630

631 *4.3 Caveats and future directions*

632   Kelp forests are naturally highly variable systems that tend to fluctuate interannually, a pattern

633   clearly demonstrated by our analysis of kelp abundance in the South Central Coast (ix) time

634   series. For this reason, there are potentially important caveats associated with our snapshot

635   analyses of two time points. In particular, the timing of both historical and modern imagery has

636   the potential to produce misleading results under some circumstances. For example, historical

637   snapshot data from the South Central Coast (ix) region were from 1997 which was during a large

638   marine heatwave (1997-1998 El Nino), an event which was known to negatively impact kelp in

639   California (e.g., Ladah & Zertuche-González, 2004; Edwards & Hernandez-Carmona, 2005) and

640   apparently drove declines in offshore kelp abundance on the South Central Coast of B.C. (Fig 6).

641   Thus, the timing of this initial survey has the potential to bias patterns towards perceived

642   increases. Importantly, however, pre-MHW imagery from nearby Laredo Sound (x), a region

643   with evidence of strong declines and no sea otter populations, was also taken during the 1997-

644   1998 event (Table 1, Fig S9). This suggests that these two regions have, in fact, experienced

645   differing trajectories and that historical sampling during the 1997-1998 event does not

646   necessitate a perception of kelp extent increases.

647

648   Similarly, due to slight differences in the timing of imagery, seasonal patterns (e.g., timing of

649   annual canopy reaching the surface or increasing canopy biomass during the growing season)

650   may confound true interannual patterns of change. Quatsino Sound (viii) was sampled initially in

651   May but resampled in July when kelp beds are expected to be larger, creating potential for

652   seasonal patterns to confound true patterns of change in kelp extent (more kelp expected later in

653   the summer). However, the South Central Coast (ix) region had the opposite issue (with initial

654   surveys occurring later in the season than modern imagery) and showed similar patterns of extent

655 increases as observed in Quatsino. Moreover, all other regions had very closely matched dates

656 for historical and modern imagery (i.e., less than one month and generally within 1-2 weeks).

657

658 Interannual variation in kelp abundance driven by environmental conditions, for example

659 associated with climatic oscillators (e.g., PDO, ENSO), was also not captured using our two time

660 point snapshot analyses, introducing an additional caveat to the interpretation of these data. Five

661 of the regions examined in the snapshot analyses were also considered using time series, as well

662 as region i-b which is adjacent to a sixth snapshot region (i.e., region i). These time series

663 support the hypothesis that declines occurred during the 2014-2016 MHW and provide additional

664 temporal context to patterns observed in a majority of regions. Moreover, snapshot comparisons

665 in the Strait of Georgia (regions i, ii, iii) were all made between 2004 and 2017-2021. In 2004,

666 PDO, ENSO and temperature anomalies were all positive (at times more so than resurvey years;

667 Fig S9), suggesting that these two time points should experience similar effects of climatic

668 oscillators. Yet, patterns of kelp loss at the latter sampling point were dramatic (e.g.,

669 Valdes/Gabriola lost kelp in 74% of segments). Snapshot analyses also focused only on

670 presence-absence and not on abundance which is generally expected to be more stable even in

671 ecologically dynamic systems (Wilson 2012). Moreover, most snapshot data were derived from

672 oblique imagery which was generally high enough resolution to detect even a single kelp

673 individual, further limiting the importance of interannual variability in abundance in our

674 presence-absence analyses. In a recent paper focused on Barkley Sound (region vi) (Starko et al.,

675 2022), presence-absence in these shoreline units was generally consistent in years prior to the

676 MHW, even when comparing to data from the 1970s and 1980s, despite likely interannual

677 variation in the abundance (i.e., total area) of kelp within these beds. Similarly, for Laredo

28

678   Sound, all three time points (1997, 2007, 2013) prior to the heatwave show consistent presence-

679   absence across most shoreline units, despite variability in interannual conditions across these

680   three years. In contrast, however, data from Cowichan Bay show much more interannual

681   variability in kelp presence-absence. Thus, the background variation in kelp presence-absence

682   likely varies across regions.

683

684   The dates of both pre- and post-MHW snapshot imagery vary across regions, yet the data tell a

685   consistent story in line with our hypotheses; declines in most areas without otters (especially

686   areas of warming) and stability or increases in places with sea otters or persistent mixing. Thus,

687   in the regions where widespread declines occurred, they were likely not restricted to a single year

688   despite our use of only two time points to characterise them. Overall, these factors make us

689   confident that declines observed in our snapshot analysis describe true changes in kelp linear

690   extent with important ecological and conservation implications.

691

692   For both snapshot analyses and time series data, the data type used may have also influenced the

693   observed patterns. Where shoreline segments were used, variation in their length may have

694   influenced the patterns inferred from these analyses. In particular, absence observations are more

695   likely when segments are shorter. Importantly, regions were mostly compared only to

696   themselves, and segment length was consistent through time within each region. Moreover, in

697   Laredo Sound, where two different segment methods were used (variable length for snapshot

698   analysis, fixed length of 50m for time series), the same pattern was recovered in both cases,

699   suggesting that these minor differences in length did not impact inferred patterns. The Cowichan

700   Bay time series had larger segments (100m), which would make absences less likely. However,

29

701   counter to expectation, this region was the most variable through time in terms of presence-

702   absence along segments. Thus, this variability cannot be explained by segment length. It is worth

703   noting that because Cowichan Bay data were derived from high resolution satellite rather than

704   oblique aerial imagery, small fringing beds may have been classified as kelp absence points (see

705   discussion of accuracy in Schroeder et al. 2019). Further, this region is characterized by high

706   currents which can easily submerge fringing kelp and reduce the ability to detect it at the surface

707   (Britton-Simmons, Eckman & Duggins, 2008; Timmer et al., 2022). Thus, false negatives are

708   probably more likely in this one region than in other regions analyzed using two time points. For

709   the time series analyses, a number of different survey methods and response variables were

710   assessed based on the availability of data. While we may expect these different metrics to be

711   sensitive to different types of patterns, it is important to note that time series were not compared

712   to each other but rather used to assess changes through time within a region.

713

714   Future work should aim to expand on this study in multiple ways. Firstly, the growing

715   availability of satellite imagery (including some products dating back decades) will allow

716   researchers to reconstruct time series in regions for which they are not already available

717   (Cavanaugh et al., 2021; Gendall, 2022), especially in regions with large offshore beds (Nijland

718   et al. 2019). This approach may help facilitate a province-wide assessment of canopy kelp

719   persistence, rather than focusing on a subset of regions as we have done here. Alternatively,

720   qualitative approaches may also be useful in assessing the extent of kelp forest loss in some

721   regions. For example, Traditional and Local Ecological Knowledge could help to identify

722   regions of major change for which there is no alternative data or could supplement and increase

723   confidence in quantitative approaches (Reid et al., 2021). Similarly, herbarium records

724   (Wernberg et al., 2011) and historical nautical charts (Costa et al., 2020) may offer insights into

725   the historical distribution of kelp species, especially if records are available from regions that no

726   longer support any kelp forests. Finally, in the face of environmental change, it will be essential

727   to not only reconstruct past kelp forest distributions but also make predictions about future

728   change. This can be accomplished by coupling species distribution models with climate

729   projections that could help to identify areas of resilience or vulnerability in the face of global

730   change (e.g., Martínez et al., 2018; Chefaoui et al., 2021b).

731

732   *4.4 Conclusions and implications*

733   Here we showed that kelp forests have experienced variable patterns of change across coastal

734   British Columbia, with recent and substantial declines in some focal regions. Declines in kelp

735   forest linear extent and/or abundance appear linked to both rapid warming experienced during

736   and after the prolonged 2014-2016 MHW and to increases in herbivorous urchins driven by the

737   loss of *Pycnopodia* sea stars. Importantly, microclimate, wave exposure and food chain length

738   strongly mediated the impacts of these drivers on kelp forest ecosystems in B.C., causing some

739   regions to be particularly sensitive to these drivers while others remained stable or increased,

740   indicative of climatic refugia. Large-scale concurrent evidence of declines suggests that kelp

741   forest ecosystems in B.C. should be of significant conservation concern across much of the

742   province. However, to be effective, conservation and management efforts should focus on parts

743   of the coast that are most sensitive to environmental and biological drivers of change, rather than

744   treating kelp forests across all regions as equally sensitive to environmental change. Overall, our

745   findings highlight how local or regional scale conditions can be essential in determining the

746   impacts of extreme warming events on coastal marine ecosystems and demonstrate that kelp

747   forest loss in B.C. offers a major conservation challenge in the face of ongoing global change.

748

5. Acknowledgements

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750

6. References

Arif S, Graham NA, Wilson S, MacNeil MA. 2022. Causal drivers of climate mediated coral reef regime shifts. *Ecosphere* 13:e3956.

Ban SS, Alidina HM, Okey TA, Gregg RM, Ban NC. 2016. Identifying potential marine climate change refugia: A case study in Canada's Pacific marine ecosystems. *Global Ecology and Conservation* 8:41–54.

Beas-Luna R, Micheli F, Woodson CB, Carr M, Malone D, Torre J, Boch C, Caselle JE, Edwards M, Freiwald J, Hamilton SL, Hernandez A, Konar B, Kroeker KJ, Lorda J, Montaño-Moctezuma G, Torres-Moye G. 2020. Geographic variation in responses of kelp forest communities of the California Current to recent climatic changes. *Global Change Biology* 26:6457–6473. DOI: 10.1111/gcb.15273.

Berry HD, Mumford TF, Christiaen B, Dowty P, Calloway M, Ferrier L, Grossman EE, VanArendonk NR. 2021. Long-term changes in kelp forests in an inner basin of the Salish Sea. *PLOS ONE* 16:e0229703. DOI: 10.1371/journal.pone.0229703.

Bolton J, Anderson R, Smit A, Rothman M. 2012. South African kelp moving eastwards: the discovery of Ecklonia maxima (Osbeck) Papenfuss at De Hoop Nature Reserve on the south coast of South Africa. *African Journal of Marine Science* 34:147–151. DOI: 10.2989/1814232X.2012.675125.

Brierley AS, Kingsford MJ. 2009. Impacts of climate change on marine organisms and ecosystems. *Current biology* 19:R602–R614.

Britton-Simmons K, Eckman JE, Duggins DO. 2008. Effect of tidal currents and tidal stage on estimates of bed size in the kelp Nereocystis luetkeana. *Marine Ecology Progress Series* 355:95–105.

793   Burt JM, Tinker MT, Okamoto DK, Demes KW, Holmes K, Salomon AK. 2018. Sudden

794   collapse of a mesopredator reveals its complementary role in mediating rocky reef regime

795   shifts. *Proc. R. Soc. B* 285:20180553. DOI: 10.1098/rspb.2018.0553.

796   Cavanaugh KC, Bell T, Costa M, Eddy NE, Gendall L, Gleason MG, Hessing-Lewis M, Martone

797   R, McPherson M, Pontier O. 2021. A Review of the Opportunities and Challenges for

798   Using Remote Sensing for Management of Surface-Canopy Forming Kelps. *Frontiers in*

799   *Marine Science*:1536.

800   Cavanaugh KC, Reed DC, Bell TW, Castorani MCN, Beas-Luna R. 2019. Spatial Variability in

801   the Resistance and Resilience of Giant Kelp in Southern and Baja California to a

802   Multiyear Heatwave. *Frontiers in Marine Science* 6. DOI: 10.3389/fmars.2019.00413.

803   Cesar H, Burke L, Pet-Soede L. 2003. The economics of worldwide coral reef degradation.

804   Chefaoui RM, Duarte CM, Tavares AI, Frade DG, Cheikh MS, Ba MA, Serrao EA. 2021a.

805   Predicted regime shift in the seagrass ecosystem of the Gulf of Arguin driven by climate

806   change. *Global Ecology and Conservation* 32:e01890.

807   Chefaoui RM, Duarte CM, Tavares AI, Frade DG, Cheikh MS, Ba MA, Serrao EA. 2021b.

808   Predicted regime shift in the seagrass ecosystem of the Gulf of Arguin driven by climate

809   change. *Global Ecology and Conservation* 32:e01890.

810   Costa M, Le Baron N, Tenhunen K, Nephin J, Willis P, Mortimor JP, Dudas S, Rubidge E. 2020.

811   Historical distribution of kelp forests on the coast of British Columbia: 1858–1956.

812   *Applied geography* 120:102230.

813   Deyoung B, Barange M, Beaugrand G, Harris R, Perry RI, Scheffer M, Werner F. 2008. Regime

814   shifts in marine ecosystems: detection, prediction and management. *Trends in Ecology &*

815   *Evolution* 23:402–409.

816   Druehl LD. 1978. The distribution of Macrocystis integrifolia in British Columbia as related to

817   environmental parameters. *Canadian Journal of Botany* 56:69–79.

818   Duggins DO, Simenstad CA, Estes JA. 1989. Magnification of secondary production by kelp

819   detritus in coastal marine ecosystems. *Science* 245:170–173.

820   Edwards MS, Hernandez-Carmona G. 2005. Delayed recovery of giant kelp near its southern

821   range limit in the North Pacific following El Niño. *Marine Biology* 147:273–279.

822   Eisaguirre JH, Eisaguirre JM, Davis K, Carlson PM, Gaines SD, Caselle JE. 2020. Trophic

823   redundancy and predator size class structure drive differences in kelp forest ecosystem

824   dynamics. *Ecology* 101:e02993. DOI: 10.1002/ecy.2993.

825   Fatland R, MacCready P, Oscar N. 2016. Chapter 14 - LiveOcean. In: Vance TC, Merati N,

826   Yang C, Yuan M eds. *Cloud Computing in Ocean and Atmospheric Sciences*. Academic

827   Press, 277–296. DOI: 10.1016/B978-0-12-803192-6.00014-1.

828   Feehan CJ, Grace SP, Narvaez CA. 2019. Ecological feedbacks stabilize a turf-dominated

829   ecosystem at the southern extent of kelp forests in the Northwest Atlantic. *Scientific*

830   *Reports* 9:7078. DOI: 10.1038/s41598-019-43536-5.

831   Fernández PA, Gaitán-Espitia JD, Leal PP, Schmid M, Revill AT, Hurd CL. 2020. Nitrogen

832   sufficiency enhances thermal tolerance in habitat-forming kelp: implications for

833   acclimation under thermal stress. *Scientific Reports* 10:3186. DOI: 10.1038/s41598-020-

834   60104-4.

835   Filbee-Dexter K, Scheibling R. 2014. Sea urchin barrens as alternative stable states of collapsed

836   kelp ecosystems. *Marine Ecology Progress Series* 495:1–25. DOI: 10.3354/meps10573.

837   Filbee-Dexter K, Wernberg T. 2018. Rise of Turfs: A New Battlefront for Globally Declining

838   Kelp Forests. *BioScience* 68:64–76. DOI: 10.1093/biosci/bix147.

839   Filbee-Dexter K, Wernberg T. 2020. Substantial blue carbon in overlooked Australian kelp

840   forests. *Scientific Reports* 10:1–6.

841   Filbee-Dexter K, Wernberg T, Grace SP, Thormar J, Fredriksen S, Narvaez CN, Feehan CJ,

842   Norderhaug KM. 2020. Marine heatwaves and the collapse of marginal North Atlantic

843   kelp forests. *Scientific Reports* 10:13388. DOI: 10.1038/s41598-020-70273-x.

844   Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS. 2004.

845   Regime shifts, resilience, and biodiversity in ecosystem management. *Annual review of

846   ecology, evolution, and systematics*:557–581.

847   Gendall L. 2022. Drivers of Change in Haida Gwaii Kelp Forests: Combining Satellite Imagery

848   with Historical Data to Understand Spatial and Temporal Variability.

849   Graham NA, Jennings S, MacNeil MA, Mouillot D, Wilson SK. 2015. Predicting climate-driven

850   regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97.

851   Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, d'Agrosa C, Bruno JF, Casey KS,

852   Ebert C, Fox HE. 2008. A global map of human impact on marine ecosystems. *science*

853   319:948–952.

854   Hamilton SL, Saccomanno VR, Heady WN, Gehman AL, Lonhart SI, Beas-Luna R, Francis FT,

855   Lee L, Rogers-Bennett L, Salomon AK, Gravem SA. 2021. Disease-driven mass

856   mortality event leads to widespread extirpation and variable recovery potential of a

857   marine predator across the eastern Pacific. *Proceedings of the Royal Society B:

858   Biological Sciences* 288:20211195. DOI: 10.1098/rspb.2021.1195.

859   Harvell CD, Montecino-Latorre D, Caldwell JM, Burt JM, Bosley K, Keller A, Heron SF,

860   Salomon AK, Lee L, Pontier O, Pattengill-Semmens C, Gaydos JK. 2019. Disease

861   epidemic and a marine heat wave are associated with the continental-scale collapse of a

862   pivotal predator (Pycnopodia helianthoides). *Science Advances* 5:eaau7042. DOI:

863   10.1126/sciadv.aau7042.

864   Hollarsmith JA, Andrews K, Naar N, Starko S, Calloway M, Obaza A, Buckner E, Tonnes D,

865   Selleck J, Therriault TW. 2022. Toward a conceptual framework for managing and

866   conserving marine habitats: A case study of kelp forests in the Salish Sea. *Ecology and*

867   *Evolution* 12:e8510. DOI: 10.1002/ece3.8510.

868   Howes D, Harper JR, Owens EH. 1994. Physical shore-zone mapping system for British

869   Columbia. *Report prepared by Environmental Emergency Services, Ministry of*

870   *Environment (Victoria, BC), Coastal and Ocean Resources Inc.(Sidney, BC), and Owens*

871   *Coastal Consultants (Bainbridge, WA).*

872   Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J. 2005. New paradigms for supporting

873   the resilience of marine ecosystems. *Trends in Ecology & Evolution* 20:380–386. DOI:

874   10.1016/j.tree.2005.03.022.

875   Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH,

876   Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi

877   JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing and

878   the recent collapse of coastal ecosystems. *Science* 293:629–637. DOI:

879   10.1126/science.1059199.

880   Jayathilake, Costello MJ. 2021. Version 2 of the world map of laminarian kelp benefits from

881   more Arctic data and makes it the largest marine biome. *Biological*

882   *Conservation*:109099.

883   Kawamata S. 2010. Inhibitory effects of wave action on destructive grazing by sea urchins: a

884   review. *Bulletin of Fisheries Research Agency* 32:95–102.

885   Kelkar M, Carden K. 2022. Petition to list bull kelp under the U.S. endangered species act.

886   Krause-Jensen D, Lavery P, Serrano O, Marbà N, Masque P, Duarte CM. 2018. Sequestration of

887   macroalgal carbon: the elephant in the Blue Carbon room. *Biology letters* 14:20180236.

888   Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD,

889   Johnson CR, Konar B, Ling SD. 2016. Global patterns of kelp forest change over the past

890   half-century. *Proceedings of the National Academy of Sciences* 113:13785–13790.

891   Ladah LB, Zertuche-González JA. 2004. Giant kelp (Macrocystis pyrifera) survival in deep

892   water (25–40 m) during El Niño of 1997–1998 in Baja California, Mexico. 47:367–372.

893   DOI: 10.1515/BOT.2004.054.

894   Leinaas HP, Christie H. 1996. Effects of removing sea urchins (Strongylocentrotus

895   droebachiensis): stability of the barren state and succession of kelp forest recovery in the

896   east Atlantic. *Oecologia* 105:524–536.

897   Lorenzo ED, Mantua N. 2016. Multi-year persistence of the 2014/15 North Pacific marine

898   heatwave. *Nature Climate Change* 6:1042–1047. DOI: 10.1038/nclimate3082.

899   Martínez B, Radford B, Thomsen MS, Connell SD, Carreño F, Bradshaw CJA, Fordham DA,

900   Russell BD, Gurgel CFD, Wernberg T. 2018. Distribution models predict large

901   contractions of habitat-forming seaweeds in response to ocean warming. *Diversity and*

902   *Distributions* 24:1350–1366. DOI: 10.1111/ddi.12767.

903   McPherson ML, Finger DJI, Houskeeper HF, Bell TW, Carr MH, Rogers-Bennett L, Kudela

904   RM. 2021. Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an

905   epizootic and marine heatwave. *Communications Biology* 4:1–9. DOI: 10.1038/s42003-

906   021-01827-6.

907   Mearns AJ, Reish DJ, Oshida PS, Ginn T. 2010. Effects of pollution on marine organisms. *Water*

908   *environment research* 82:2001–2046.

909   Moksnes P-O, Eriander L, Infantes E, Holmer M. 2018. Local regime shifts prevent natural

910   recovery and restoration of lost eelgrass beds along the Swedish west coast. *Estuaries*

911   *and coasts* 41:1712–1731.

912   Mora-Soto A, Capsey A, Friedlander AM, Palacios M, Brewin PE, Golding N, Dayton P, Van

913   Tussenbroek B, Montiel A, Goodell W, Velasco-Charpentier C, Hart T, Macaya EC,

914   Pérez-Matus A, Macias-Fauria M. 2021. One of the least disturbed marine coastal

915   ecosystems on Earth: Spatial and temporal persistence of Darwin's sub-Antarctic giant

916   kelp forests. *Journal of Biogeography* 48:2562–2577. DOI: 10.1111/jbi.14221.

917   Nichol LM, Doniol-Valcroze T, Watson JC, Foster EU. 2020. *Trends in growth of the sea otter*

918   *(Enhydra lutris) population in British Columbia 1977 to 2017*. Canadian Science

919   Advisory Secretariat (CSAS).

920   Nichol LM, Watson JC, Abernethy R, Rechsteiner E, Towers J. 2015. *Trends in the abundance*

921   *and distribution of sea otters (*Enhydra lutris*) in British Columbia updated with 2013*

922   *survey results*. Fisheries and Oceans Canada, Ecosystems and Oceans Science.

923   Pearse JS. 2006. Ecological role of purple sea urchins. *Science* 314:940–941.

924   Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK,

925   Danielsen F, Evengård B. 2017. Biodiversity redistribution under climate change:

926   Impacts on ecosystems and human well-being. *Science* 355:eaai9214.

927   Pessarrodona A, Assis J, Filbee-Dexter K, Burrows MT, Gattuso J-P, Duarte CM, Krause-Jensen

928   D, Moore PJ, Smale DA, Wernberg T. 2022. Global seaweed productivity. *Science*

929   *advances* 8:eabn2465.

930 Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck

931   K, Nicolai M, Okem A, Petzold J. 2019. IPCC special report on the ocean and cryosphere

932   in a changing climate. *IPCC Intergovernmental Panel on Climate Change: Geneva,*

933   *Switzerland* 1.

934 Reid AJ, Eckert LE, Lane J-F, Young N, Hinch SG, Darimont CT, Cooke SJ, Ban NC, Marshall

935   A. 2021. "Two-Eyed Seeing": An Indigenous framework to transform fisheries research

936   and management. *Fish and Fisheries* 22:243–261. DOI: 10.1111/faf.12516.

937 Robinson CLK, Yakimishyn J, Evans R. 2022. Minimal effects of the 2014-16 marine heatwave

938   on fish assemblages found in eelgrass meadows on the southwestern coast of Vancouver

939   Island, British Columbia, Canada. *Frontiers in Marine Science* 9.

940 Rogers-Bennett L, Catton CA. 2019. Marine heat wave and multiple stressors tip bull kelp forest

941   to sea urchin barrens. *Scientific Reports* 9:1–9. DOI: 10.1038/s41598-019-51114-y.

942 Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to

943   observation. *Trends in ecology & evolution* 18:648–656.

944 Schroeder SB, Boyer L, Juanes F, Costa M. 2020. Spatial and temporal persistence of nearshore

945   kelp beds on the west coast of British Columbia, Canada using satellite remote sensing.

946   *Remote Sensing in Ecology and Conservation* 6:327–343. DOI:

947   https://doi.org/10.1002/rse2.142.

948 Schroeder SB, Dupont C, Boyer L, Juanes F, Costa M. 2019. Passive remote sensing technology

949   for mapping bull kelp (Nereocystis luetkeana): A review of techniques and regional case

950   study. *Global Ecology and Conservation*:e00683. DOI: 10.1016/j.gecco.2019.e00683.

951 Schultz JA, Cloutier RN, Côté IM. 2016. Evidence for a trophic cascade on rocky reefs

952 following sea star mass mortality in British Columbia. *PeerJ* 4:e1980. DOI:

953 10.7717/peerj.1980.

954 Shaffer JA, Munsch SH, Cordell JR. 2020. Kelp forest zooplankton, forage fishes, and juvenile

955 salmonids of the northeast pacific nearshore. *Marine and Coastal Fisheries* 12:4–20.

956 Smale DA, Wernberg T, Oliver ECJ, Thomsen M, Harvey BP, Straub SC, Burrows MT,

957 Alexander LV, Benthuysen JA, Donat MG, Feng M, Hobday AJ, Holbrook NJ, Perkins-

958 Kirkpatrick SE, Scannell HA, Sen Gupta A, Payne BL, Moore PJ. 2019. Marine

959 heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature*

960 *Climate Change* 9:306–312. DOI: 10.1038/s41558-019-0412-1.

961 Spiecker BJ, Menge BA. 2022. El Niño and marine heatwaves: Ecological impacts on Oregon

962 rocky intertidal kelp communities at local to regional scales. *Ecological Monographs*

963 92:e1504. DOI: 10.1002/ecm.1504.

964 Starko S, Bailey LA, Creviston E, James KA, Warren A, Brophy MK, Danasel A, Fass MP,

965 Townsend JA, Neufeld CJ. 2019. Environmental heterogeneity mediates scale-dependent

966 declines in kelp diversity on intertidal rocky shores. *PLOS ONE* 14:e0213191. DOI:

967 10.1371/journal.pone.0213191.

968 Starko S, Neufeld CJ, Gendall L, Timmer B, Campbell L, Yakimishyn J, Druehl L, Baum JK.

969 2022. Microclimate predicts kelp forest extinction in the face of direct and indirect

970 marine heatwave effects. *Ecological Applications*:e2673. DOI: 10.1002/eap.2673.

971 Steffen W, Grinevald J, Crutzen P, McNeill J. 2011. The Anthropocene: conceptual and

972 historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical,*

973 *Physical and Engineering Sciences* 369:842–867.

974   Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002.

975   Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental*

976   *Conservation* 29:436–459. DOI: 10.1017/S0376892902000322.

977   Supratya VP, Coleman LJM, Martone PT. 2020. Elevated Temperature Affects Phenotypic

978   Plasticity in the Bull Kelp (Nereocystis luetkeana, Phaeophyceae). *Journal of Phycology*

979   56:1534–1541. DOI: https://doi.org/10.1111/jpy.13049.

980   Teagle H, Hawkins SJ, Moore PJ, Smale DA. 2017. The role of kelp species as biogenic habitat

981   formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and*

982   *Ecology* 492:81–98.

983   Timmer B, Reshitnyk LY, Hessing-Lewis M, Juanes F, Costa M. 2022. Comparing the Use of

984   Red-Edge and Near-Infrared Wavelength Ranges for Detecting Submerged Kelp Canopy.

985   *Remote Sensing* 14:2241.

986   Tseng Y-H, Ding R, Huang X. 2017. The warm Blob in the northeast Pacific—the bridge leading

987   to the 2015/16\hspace0.167emEl Niño. *Environmental Research Letters* 12:054019. DOI:

988   10.1088/1748-9326/aa67c3.

989   Wernberg T, Bennett S, Babcock RC, Bettignies T de, Cure K, Depczynski M, Dufois F,

990   Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B,

991   Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F,

992   Vanderklift MA, Wilson S. 2016. Climate-driven regime shift of a temperate marine

993   ecosystem. *Science* 353:169–172. DOI: 10.1126/science.aad8745.

994   Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF. 2019. Chapter 3 - Status and Trends

995   for the World's Kelp Forests. In: Sheppard C ed. *World Seas: an Environmental*

996   *Evaluation (Second Edition)*. Academic Press, 57–78. DOI: 10.1016/B978-0-12-805052-

997   1.00003-6.

998   Wernberg T, Russell BD, Thomsen MS, Gurgel CFD, Bradshaw CJA, Poloczanska ES, Connell

999   SD. 2011. Seaweed Communities in Retreat from Ocean Warming. *Current Biology*

1000   21:1828–1832. DOI: 10.1016/j.cub.2011.09.028.

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1020 Table 1. Study regions used to assess changes in canopy kelp distribution from "snapshot"
1021 analyses. Asterisk (*) indicates regions that were also included in time-series analyses. For kelp
1022 species present: MP = *Macrocystis pyrifera*, NL = *Nereocystis luetkeana,* † indicates which
1023 species is more common when both are present. For otter status: + = increasing populations, - =
1024 otter populations not present.

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

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1027 Table 2. Summary of data sources used for time series analysis. Asterisk (*) indicates regions
1028 that are also included in the snapshot analyses. Note that time series are generally not continuous
1029 but include some gap years. For specific years and dates used in each time series, see Table S3.

Region	Region Name	Start date	End date	Number of time points	Data type	Methods
i-b	Central Strait of Georgia	2013/2014	2022	n = 24-34 per site	Presence-absence at two sites	SCUBA surveys and videos
ii	Mayne Island*	2010	2021	n = 8	Kelp forest area (m^2)	Kayak surveys
iii	Cowichan Bay*	2004	2017	n = 5	Presence-absence of shoreline segments (% occupied)	High resolution satellite imagery
vi	Barkley Sound*	2007	2022	n = 6	Presence-absence of shoreline segments (% occupied)	Aerial image, satellite, boat surveys
ix	South Central Coast*	1984	2021	n = 38	Kelp forest area (m^2)	LandSat satellite imagery
ix-b	Calvert Island	2008	2022	n = 7 - 10 per site	Kelp forest area (m^2) at two sites	RPAS
x	Laredo Sound*	2007	2019	n = 3	Presence-absence of shoreline segments (% occupied)	Aerial image, satellite

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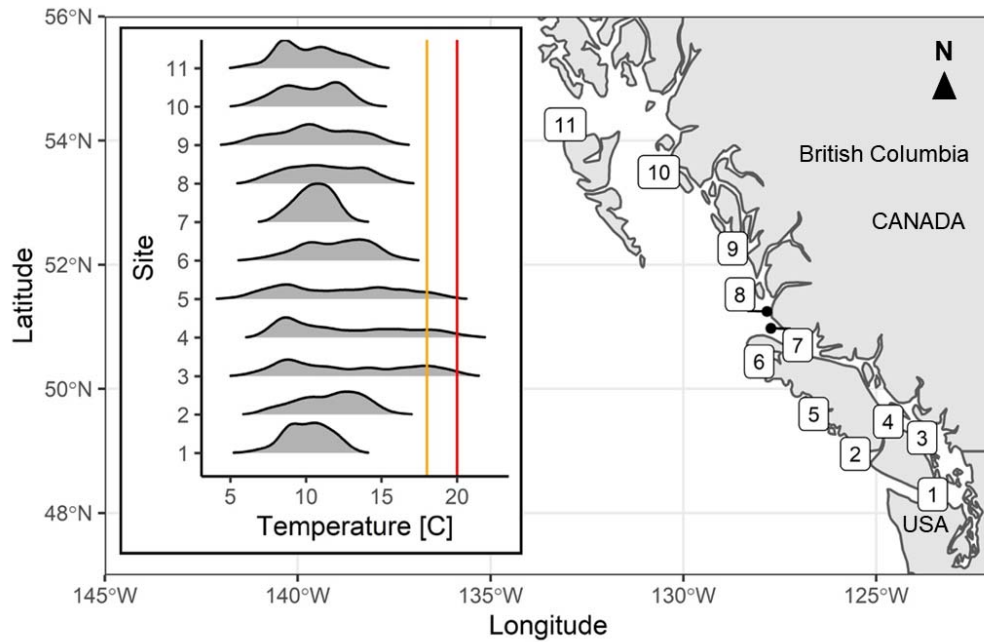
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Fig 1. Sea surface temperature measured at high tide in the summers (June 21 – Sept 20) of 2014 to 2017. Data are from Fisheries and Oceans Canada Lighthouse Stations (labelled with numbers 1 – 11) along the coast of British Columbia. Inset plots indicate the relative density of all summer temperature measurements from 2014 to 2017. Note the lack of relationship between temperature and latitude. The orange line indicates 18°C and the red line indicates 20°C.

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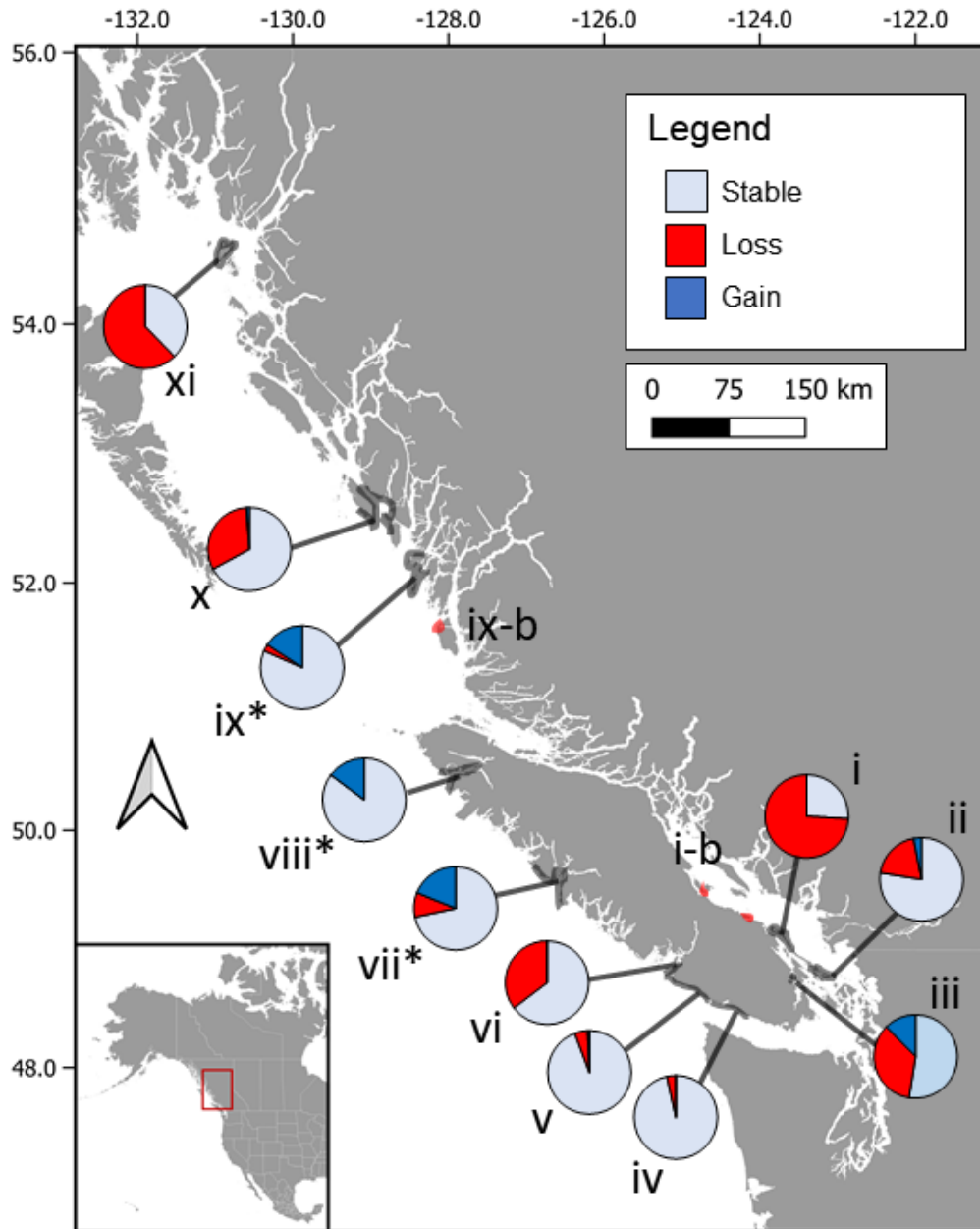
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Fig 2. Regional-scale patterns of kelp persistence comparing pre-(1997 – 2007) and post-marine heatwave (post-2016) imagery. Pie charts indicate the relative direction of change in canopy kelp presence (both *Macrocystis* and *Nereocystis*), at the level of individual segments, between the two time points based on shoreline segments visible in imagery from both time points. The regions with expanding otter populations are indicated with asterisks. Regions are as follows: 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. Region only included in the time series analysis are shown in red: i-b) Central Strait of Georgia, ix-b) Calvert Island.

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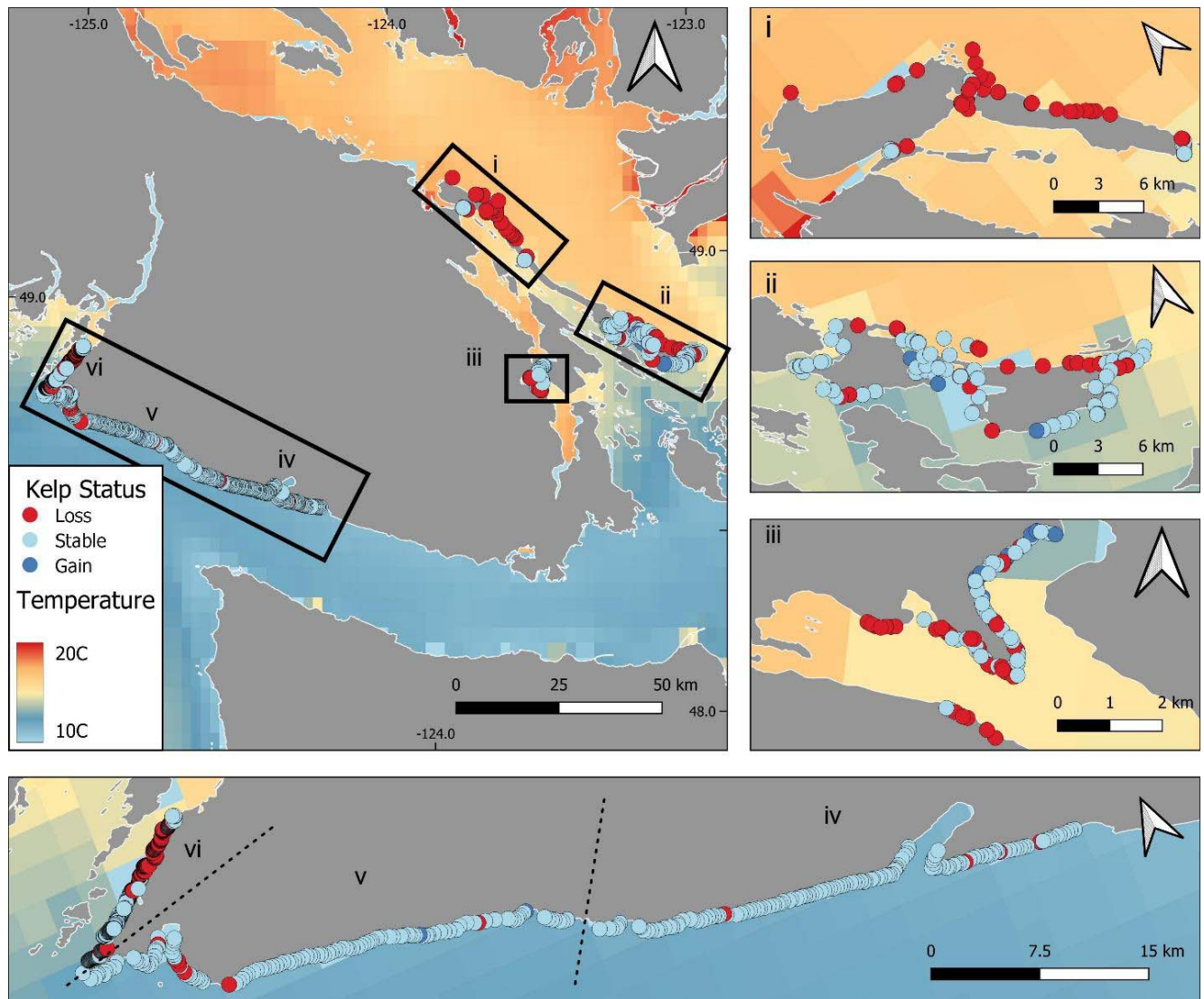
Fig 3. Kelp persistence within and across regions on southern Vancouver Island related to summer sea surface temperature. Data points indicate segments from the snapshot analysis coded by their persistence status (see inset legend) determined by comparing data from before (2004 – 2007) and after (2017 – 2021) the 2014-2016 MHW – see Table 1. Colored layer indicates mean sea surface temperature 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).
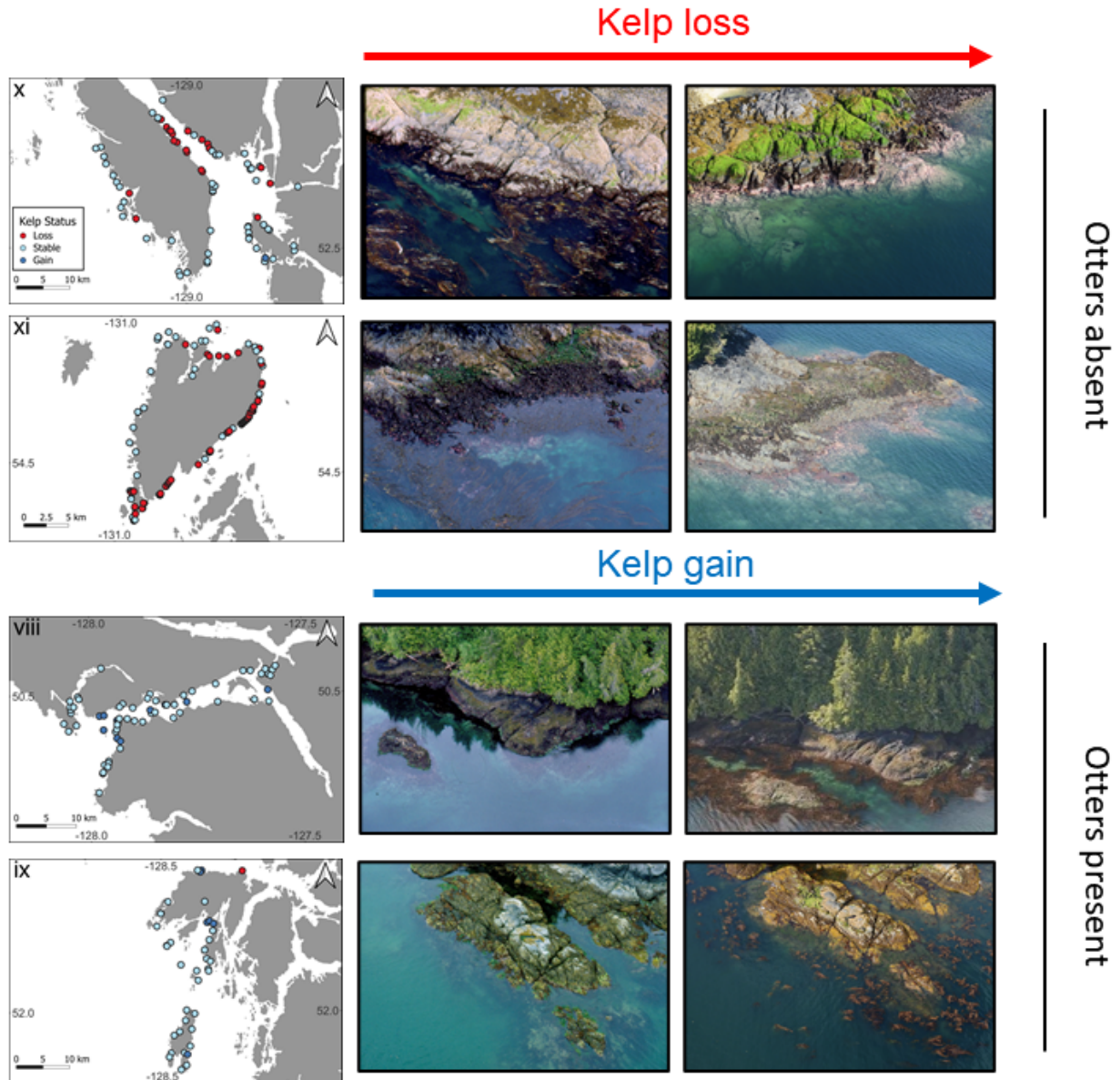
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Fig 4. Local-scale (within-region) variation in kelp persistence between historical and modern imagery in northern regions with and without growing sea otter populations. Each data point represents a shoreline segment visible from images at both time points and colour indicates whether a shoreline segment had persistent kelp forests, forests that disappeared (loss) or colonisations of shoreline segments (gains). Aerial images show examples of kelp loss (top) or gains observed in each of these regions. Images from ShoreZone BC and Environment and Climate Change Canada.

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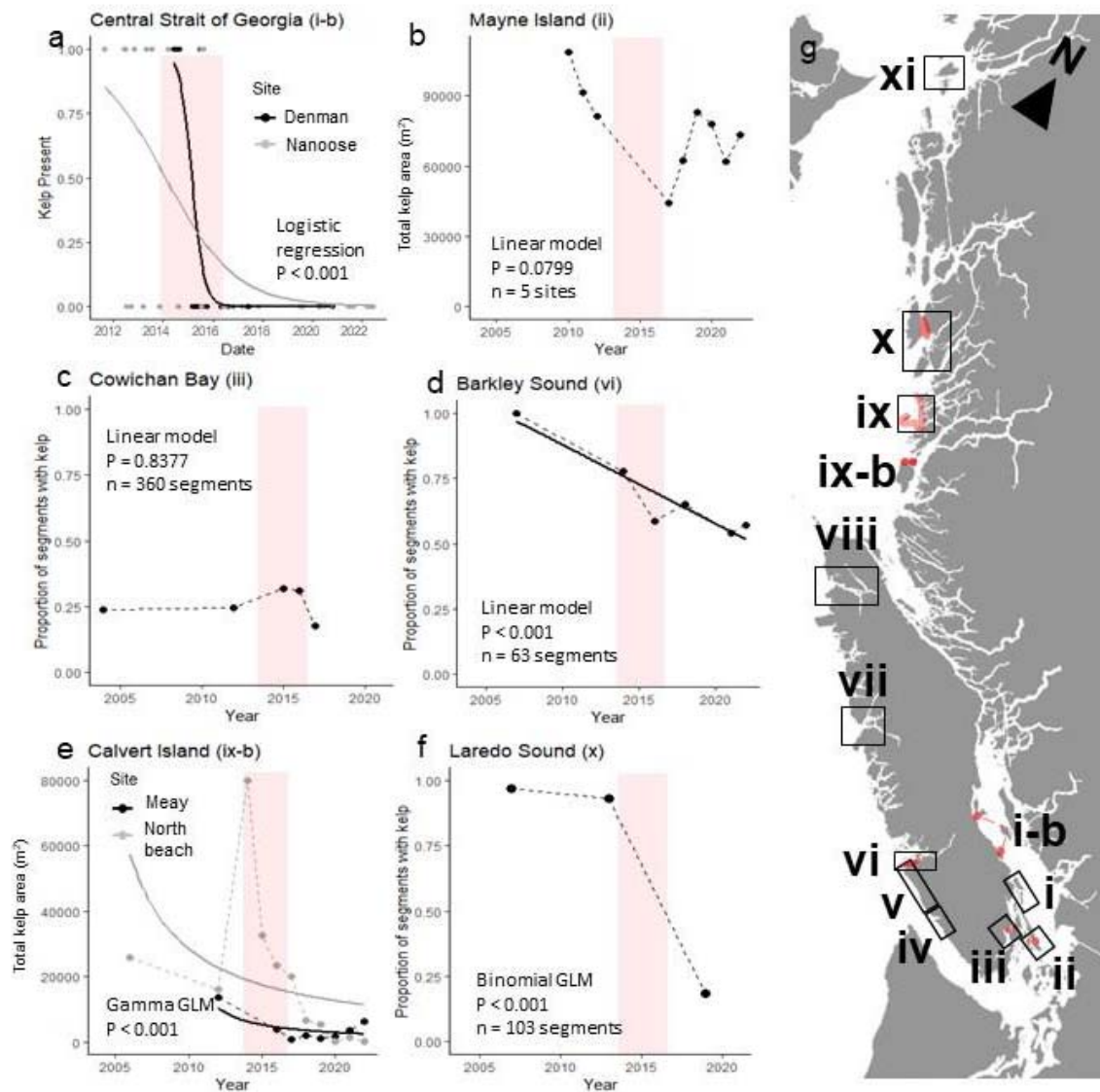
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Fig 5. Time series from six regions spanning the British Columbia coastline. Inset map shows sites or regions used for time series data highlighted in red, relative to the snapshot regions shown with boxes. Data points indicate measures of kelp abundance or occupancy years in the time series. Note that while data points are connected by dotted lines, this does not imply continuous sampling as there are gaps in the years included in each time series (see Tables 2, S3).
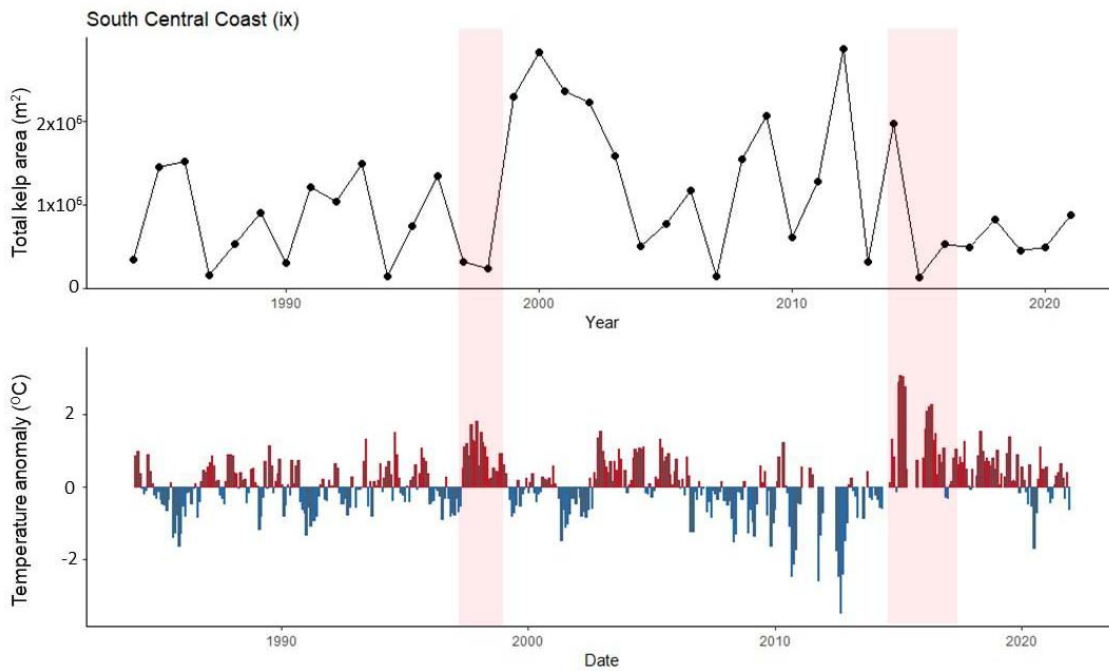
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1085 **Fig 6. Time series of offshore kelp forest area from South Central Coast region showing**
1086 **high resilience prior to the 2014-2016 heatwave**. (a) Data were generated from LandSat
1087 imagery and exclude kelp forests within 30m of the shore. (b) Temperature measurements from
1088 nearby McInnes Island lighthouse. Red shading highlights the timing of the 1997-1998 El Niño
1089 and 2014-2016 marine heatwave.

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