Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia

Jessica A Schultz, Ryan N Cloutier, Isabelle M Côté

Echinoderm population collapses, driven by disease outbreaks and climatic events, may be important drivers of population dynamics, ecological shifts and biodiversity. The northeast Pacific recently experienced a mass mortality of sea stars. In Howe Sound, British Columbia, the sunflower star *Pycnopodia helianthoides* — a previously abundant predator of bottom-dwelling invertebrates — began to show signs of a wasting syndrome in early September 2013, and dense aggregations disappeared from many sites in a matter of weeks. Here, we assess changes in subtidal community composition by comparing the abundance of fish, invertebrates and macroalgae at 20 sites in Howe Sound before and after the 2013 sea star mortality to evaluate evidence for a trophic cascade. We observed changes in the abundance of several species after the sea star mortality, most notably a four-fold increase in the number of green sea urchins, *Strongylocentrotus droebachiensis*, and a significant decline in kelp cover, which are together consistent with a trophic cascade. Qualitative data on the abundance of sunflower stars and green urchins from a citizen science database show that the patterns of echinoderm abundance detected at our study sites reflected wider local trends. The trophic cascade evident at the scale of Howe Sound was observed at half of the study sites. It remains unclear whether the urchin response was triggered directly, via a reduction in urchin mortality, or indirectly, via a shift in urchin distribution into areas previously occupied by the predatory sea stars. Understanding the ecological implications of sudden and extreme population declines may further elucidate the role of echinoderms in temperate seas, and provide insight into the resilience of marine ecosystems to biological disturbances.

1 **Evidence for a trophic cascade on rocky reefs following sea star mass**
2 **mortality in British Columbia**

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ABSTRACT

Echinoderm population collapses, driven by disease outbreaks and climatic events, may be important drivers of population dynamics, ecological shifts and biodiversity. The northeast Pacific recently experienced a mass mortality of sea stars. In Howe Sound, British Columbia, the sunflower star *Pycnopodia helianthoides* — a previously abundant predator of bottom-dwelling invertebrates — began to show signs of a wasting syndrome in early September 2013, and dense aggregations disappeared from many sites in a matter of weeks. Here, we assess changes in subtidal community composition by comparing the abundance of fish, invertebrates and macroalgae at 20 sites in Howe Sound before and after the 2013 sea star mortality to evaluate evidence for trophic cascade. We observed changes in the abundance of several species after the sea star mortality, most notably a four-fold increase in the number of green sea urchins, *Strongylocentrotus droebachiensis*, and a significant decline in kelp cover, which are together consistent with a trophic cascade. Qualitative data on the abundance of sunflower stars and green urchins from a citizen science database show that the patterns of echinoderm abundance detected at our study sites reflected wider local trends. The trophic cascade evident at the scale of Howe Sound was observed at half of the study sites. It remains unclear whether the urchin response was triggered directly, via a reduction in urchin mortality, or indirectly, via a shift in urchin distribution into areas previously occupied by the predatory sea stars. Understanding the ecological implications of sudden and extreme population declines may further elucidate the role of echinoderms in temperate seas, and provide insight into the resilience of marine ecosystems to biological disturbances.

INTRODUCTION

Echinoderms can be subject to dramatic population fluctuations (Uthicke *et al.,* 2009). Rapid declines are often driven by disease or extreme climatic events. For example, the spread of mass mortality of the black sea urchin, *Diadema antillarum*, in the 1980s suggests that it was most likely caused by a pathogen (Lessios *et al.,* 1984). The event impacted an estimated 3.5 million km^2 of the Caribbean region, causing up to 99% urchin mortality at some sites (Lessios, 1988). While the precipitous decline of *Diadema* was a unique occurrence, other echinoderm mass mortality events occur repeatedly. On the Atlantic coast of North America, an amoeboid parasite causes episodic mortality events in green sea urchins, *Strongylocentrotus droebachiensis* (Jones & Scheibling, 1985), which are linked to hurricanes and are predicted to increase in frequency with climate change (Scheibling & Lauzon-Guay, 2010). Similarly, recurring events of wasting disease involving asteroids (sea stars), echinoids (sea urchins) and holothurians (sea cucumbers) in the Channel Islands, California, are associated with climate regime shifts and extreme weather events (Engle, 1994; Eckert *et al.,* 2000).

Because sea stars and sea urchins play key ecological roles in many marine ecosystems, echinoderm population collapses can be important drivers of biodiversity, population dynamics and ecological shifts. In fact, the term 'keystone predator' was originally coined for the purple star, *Pisaster ochraceus*, after experiments showed that its absence led to significant decreases in intertidal biodiversity (Paine, 1966). Many other echinoderm species have since been shown to influence community composition through predation or herbivory. These effects are apparent on coral reefs following echinoderm population booms (e.g., coral cover declines owing to eruptive crown-of-thorns star, *Acanthaster planci* (Sano *et al.,* 1984)), or busts (e.g., the transition from

62 coral- to algae-dominated reefs following the *D. antillarum* mortality event (Carpenter, 1990)).

63 On temperate rocky reefs, fluctuations in the abundance of herbivorous urchins can also result in

64 major community shifts, from kelp forests to urchin barrens and back again (Estes & Duggins,

65 1995; Steneck *et al.*, 2003).

66 The northeast Pacific region has recently experienced a protracted mass mortality of sea

67 stars that might rival the magnitude of the *Diadema* die-off of the 1980s (Johnson, 2016). The

68 event was first noticed on the Olympic coast of Washington in June 2013 (Hewson *et al.*, 2014).

69 In affected sea stars, the signs progress from a loss of turgor pressure, to lesions and ruptures of

70 the body wall and autotomization of arms, and ultimately, disintegration and death (Fig. 1). The

71 wasting syndrome has continued through 2014 and 2015, and has so far affected some 20 species

72 from Alaska to Southern California (Stockstad, 2014). A virus may be involved (Hewson *et al.,*

73 2014), but the precise causes and contributing factors remain poorly understood. Moreover, little

74 is known so far of the extent and ecological consequences of this sea star mortality event at any

75 location.

76 Many of the affected seastars were predatory species, raising the possibility of trophic

77 cascades associated with their disappearance and marked community restructuring. In Howe

78 Sound, southern Strait of Georgia, British Columbia, the sunflower star *Pycnopodia*

79 *helianthoides* showed signs of advanced wasting in early September 2013. Dense aggregations

80 disappeared from many sites in a matter of weeks (personal observations). This species is one of

81 the world's largest predatory sea stars and it consumes a variety of prey, including echinoderms,

82 gastropods and crustaceans (Herrlinger, 1983; Shivji *et al.*, 1983). In areas that lack other

83 predators such as sea otters *Enhydra lutris*, such as in Howe Sound, sunflower stars can become

84 the dominant predator of urchins (Duggins, 1983). By altering the abundance and/or distribution

85   of sea urchins, which in turn can have a conspicuous impact on the abundance of kelp, sunflower

86   stars can influence the formation and persistence of urchin barrens, i.e. areas devoid of kelp

87   because of the grazing activity of urchins (Duggins, 1981). Indeed, most well-substantiated

88   examples of tri-trophic cascades in rocky subtidal ecosystems involve urchins as prey and major

89   herbivore (Pinnegar *et al.*, 2000). We therefore expected that *Pycnopodia* prey, in particular

90   urchins, would increase in abundance following the disappearance of their major predator,

91   leading to reductions in kelp cover.

92   Here, we evaluate the extent of mortality of *P. helianthoides* in Howe Sound and test

93   whether changes in the benthic community following the rapid decline of this predatory sea star

94   are consistent with the hypothesis of a trophic cascade. We compare rocky reef community

95   composition before and after the mass mortality using quantitative data derived from subtidal

96   transects and qualitative information gathered by citizen scientists. In doing so, we provide

97   empirical evidence that a trophic cascade quickly followed what might be one of the largest

98   wildlife die-off events ever recorded (Johnson, 2016).

99

100   **MATERIALS AND METHODS**

101   **Subtidal surveys**

102   We compared sunflower star abundance and benthic community composition before (2009/2010)

103   and after (2014) the 2013 wasting event using scuba-based surveys of 20 sites in Howe Sound,

104   British Columbia (BC), Canada (Fig. 2). Surveys before the wasting event were conducted as

105   part of a study of rockfish (*Sebastes* spp) habitat (Cloutier, 2011). We repeated these surveys

106   after the wasting event using the same method, at the same GPS locations, depths (within 2 m)

107   and time of year (within 14 days). Ten sites were surveyed in early summer (June – July) and 10

108   sites in late summer (August – October). In all surveys, we recorded the abundance of 18 taxa

109   (species or species groups) of common benthic fishes and invertebrates (Table 1).

110   At each site we surveyed four transects (25 m long by 4 m wide) at depths between 8 and

111   15 m (chart datum). We quantified fish and invertebrate abundance by counting all individuals of

112   the target taxa occurring fully or partly within 0.25 m² quadrats placed at 15 random positions

113   along each transect. We also estimated visually the percent cover of kelp (mainly the genera

114   *Agarum*, *Costaria*, *Laminaria* and *Saccharina*) within the same quadrats.

115

116   **Citizen-contributed (REEF) surveys**

117   To verify that the patterns of echinoderm abundance detected at our 20 study sites reflected local

118   trends accurately, we compiled qualitative data on the abundance of sunflower star and green

119   urchin in Howe Sound and adjacent Indian Arm, east of Vancouver, from the Reef

120   Environmental Education Foundation (REEF) citizen science database. Through REEF, scuba

121   divers are trained in species identification and collect data on abundance of species sighted

122   during recreational dives. Divers assign an abundance score from 1 – 4 to each species they can

123   positively identify: score 1 = a single individual, 2 = 2-10 individuals, 3 = 11-100 individuals

124   and 4 = > 100 individuals. Species with no abundance score were assumed to be absent, which

125   we deemed to be a fair assumption given that our target taxa were easy to identify.

126   We extracted the abundance scores of sunflower stars and green sea urchins for all REEF

127   surveys submitted between January 1, 2010 and November 1, 2014 in Washington and BC. To

128   depict trends in abundance over time, we plotted 60-day running averages of the abundance

129   scores for both species. Missing values were filled in using linear interpolation.

130

131   **Data analyses**

132   We used linear mixed-effects models in the R statistical platform (nlme package; Pinheiro *et al.*,

133   2015) to compare sunflower star abundance, green urchin abundance and kelp cover before and

134   after the sea star mortality. We obtained sunflower and green urchin abundance for each transect

135   by summing the number of sunflower stars and, separately, green urchins across all quadrats and

136   log-transforming the values prior to analysis. Kelp cover was averaged across all quadrats

137   within each transect. In all cases, we included 'site' as a random effect, and verified the

138   assumptions of normally distributed residuals, homoscedasticity and the absence of leverage by

139   visually examining quantile, residual vs. fitted and Cook's distance diagnostic plots,

140   respectively.

141   To depict graphically site-level changes in the abundance of sunflower stars, green sea

142   urchins and kelp, we plotted the relative difference in abundance for each group at each site.

143   Relative abundance was calculated as the abundance after the mortality event minus the

144   abundance prior to it divided by the mean abundance for both time periods. Abundance was

145   calculated as the total count of each species at each site for sunflower stars and green urchins,

146   and as the average percent cover at each site for algae.

147   To compare overall benthic community composition before and after the sea star

148   mortality, we ran a permutation-based, non-parametric analysis of similarity (ANOSIM; Clarke,

149   1993) using PRIMER (v. 1.0.3; Clarke & Gorley, 2006). Abundance matrices (species by site)

150   were compiled for each period (i.e., pre- and post-mortality), in which abundance was estimated

151   as the total count of each taxon across transects and/or quadrats at each site. The raw data were

152   square-root-transformed to reduce the influence of very abundant or very rare species. Bray-

153   Curtis similarity coefficients were computed between pairs of sites (Clarke & Warwick, 2001).

154   The ANOSIM procedure was carried out on the similarity matrix. ANOSIM generates an R

155   statistic, which varies between 0 (samples are as similar across groups as they are within group)

156   and 1 (all samples within groups are more similar to each other than to any sample across

157   groups) and is tested for difference from zero with a permutation test (in this study, N = 999

158   permutations). The differences in benthic assemblages were visualized in a non-metric,

159   multidimensional scaling (MDS) plot in which samples that are more similar in community

160   composition appear closer together than more dissimilar samples. Stress values of <0.1 suggest

161   that distances among samples in an MDS plot accurately reflect the extent of community

162   differences (Clarke &Warwick, 2001). Finally, we conducted an analysis of similarity

163   percentages (SIMPER) to identify the main taxa responsible for any differences observed

164   between pre- and post-mortality assemblages. We considered a taxon to be important to

165   community differences if their individual contribution was 11% or more, which is twice the

166   expected value if dissimilarity contributions were evenly distributed among all taxa in the

167   analysis (i.e.,100 percent divided by 18 taxa, multiplied by 2). The SIMPER analysis also

168   includes an indication of evenness, expressed as a consistency ratio (CR). CR is the average

169   dissimilarity contribution of a taxon divided by the standard deviation in dissimilarity values of

170   that taxon, for each time period. CR values greater than one suggest that the taxon contributed to

171   dissimilarity between time periods equally across all sites (Terlizzi *et al.*, 2005).

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177 **RESULTS**

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179 **Sea star mortality**

180 At our monitored sites, the abundance of sunflower stars declined by 89% ± 29% (mean ± SD),

181 from an average of 0.42 (± 0.76) sunflower stars per m^2 before the mortality event to 0.06 (±

182 0.22) individuals per m^2 after it (LME: t = 4.62, df = 139, p < 0.0001; Fig. 3). Three sites had no

183 sunflower stars in 2009/2010, and were not included in the percent decline calculation. All 17

184 sites with sunflower stars in 2009/2010 had fewer sunflower stars in 2014.

185   The REEF data included 1568 surveys carried out at 28 sites broadly distributed across

186 BC and Washington between 2010 and 2014. Although sunflower stars were sighted on 98% of

187 surveys in the years before the mortality event and on 89% of surveys in the years afterward, a

188 marked decline was evident in their abundance score trajectory (Fig. 5). At this larger geographic

189 scale, sunflower stars started declining in approximately the third week of September, some 15

190 weeks after the first report of seastar wasting in the region.

191   We were unable to detect a geographic pattern in the spread of the sea stars' mortality in

192 our study area because of the speed at which the seastar wasting progressed. It was first

193 observed in Howe Sound (at Whytecliff Park; 49°22'18.4"N, 123°17'33.8"W) on 2 September,

194 2013, and we then noted it at all of our study sites the following month.

195

196 **Benthic community composition**

197 There was a significant shift in overall community composition following sea star mortality in

198 Howe Sound (ANOSIM: R = 0.326, p = 0.001; Fig. 6), and many species changed in abundance

199 from one period to the next (Table 1). The community shift was largely driven by an increase in

200   abundance of green urchins (Table 2). Green urchin abundance quadrupled after the near-

201   disappearance of sunflower stars (LME: t = -3.10, df = 139, p = 0.0023; Fig. 3). This trend is

202   supported by the REEF surveys, although these qualitative data suggest that green urchin

203   numbers began increasing in the first week of September, two to three weeks before the

204   detectable onset of sea star decline (Fig. 5). There was also an increase in the abundance of cup

205   corals, while the numbers of small shrimps and crabs decreased (Table 2). Cumulatively, these

206   four taxa accounted for nearly two-thirds (62%) of the dissimilarity in benthic community

207   composition before and after the sea star mortality, and their contributions were consistent across

208   sites (CRs > 1; Table 2). Despite their marked decline, sunflower stars did not contribute

209   disproportionately to the dissimilarity between time periods (SIMPER; individual contribution to

210   dissimilarity = 7.15%). Overall, within-year similarity was higher after than before sea stars died

211   (SIMPER; average inter-site similarity before = 46.28%, after = 58.11%; Fig. 6), suggesting that

212   communities became more homogeneous following the seastar mortality.

213   In addition to shifts in benthic animal community composition, there was also a change in

214   the abundance of kelp. Kelp cover decreased from 4% (± 10%) in 2009/2010 to <1% (± 2%) in

215   2014 (LME: t = 2.669, df = 139, p = 0.0085; Fig. 3). In all years, the kelp at our sites was almost

216   exclusively the sea colander kelp, *Agarum fimbriatum*, but also included *Saccharina latissima*.

217   At the regional scale, the changes in abundance of sunflower stars (decline), green

218   urchins (increase) and kelp (decline) were consistent with a trophic cascade (Fig. 3). At the site

219   level, the patterns were more variable (Fig. 4). Eleven of the 17 sites that had some *P.*

220   *helianthoides* before the sea star mortality showed increases in green urchin abundance

221   concomitant with declines in sea star abundance (Fig. 4). Eight of these 17 sites showed declines

222   in kelp cover concomitant with increases in green urchin abundance (Fig. 4). A clear alternation

223   of population trajectories from predators to herbivores to kelp was clear at eight of the 16 sites

224   (Fig 4).

225

226   **DISCUSSION**

227

228   The wasting disease that affected echinoderms in the northeast Pacific in 2013/2014 heavily

229   impacted populations of sunflower stars, the sea stars that formerly dominated subtidal

230   communities. We found a noticeable shift in benthic community structure following the sea star

231   decline. Community changes were largely driven by changes in the abundance of green sea

232   urchins, cup corals, shrimps and crabs. The temporal coincidence of the alternating trajectories of

233   abundance of sea stars, urchins and kelp, as well as the overlapping distributions and

234   documented trophic linkages among these three taxa, meet the diagnostic criteria of a tri-trophic

235   cascade (Grubbs *et al.* 2016), triggered by the mass mortality of predatory sunflower stars.

236   Sunflower star densities declined by almost 90%, on average, at our sites in Howe Sound,

237   BC. Such a decline in sea stars rivals the largest magnitudes reported for disease-induced

238   echinoderm mass mortalities (e.g., 70% of *Strongylocentrotus droebachiensis* in Nova Scotia

239   (Scheibling & Stephenson, 1984); 95% of *S. franciscanus* in California (Pearse *et al.*, 1977);

240   97% of *Diadema antillarum* across the Caribbean (Lessios, 1988)). The percent change in

241   biomass of *P. helianthoides* must be even greater than the change in relative abundance because

242   the sea stars we observed following the mortality event were almost exclusively juveniles (< 6

243   cm diameter). The very large individuals (>50 cm diameter) present before the mortality event

244   likely played a proportionately larger role in structuring benthic communities than the juveniles

245   present after the event. The steep decline in sunflower star numbers, occurring some 15 weeks

246   after the first official sighting of sea star wasting, was clearly evident in the qualitative density

247   scores generated by citizen science (REEF) surveys, which covered a broader geographic area.

248   The time-series of REEF data suggests that sunflower star population levels were somewhat

249   variable, perhaps reflecting variation in the sites surveyed by divers, but largely stable between

250   the first snapshot in 2009/2010 and the onset of the wasting event in 2013. More generally, the

251   benthic species composition of the Strait of Georgia region has remained remarkably stable in

252   recent decades, even in the face of climate regime shifts (Marliave *et al.* 2011). It therefore

253   seems unlikely that the sea star population declines, and concomitant changes in benthic

254   community composition, could be ascribed to a different, unreported disturbance occurring prior

255   to 2013.

256   The most striking change we observed in community composition was a marked increase

257   in the abundance of green urchins. Overall, green urchins were nearly four times more numerous

258   following the sea star mortality event than before. However, the mechanism of this population

259   increase remains unclear. One possibility is that a recruitment pulse of green urchins coincided

260   with sea star wasting disease, which would have generated a large urchin cohort even in the

261   presence of sunflower stars. Another possibility is that urchin recruits – whether part of a normal

262   or a large cohort – were able to survive better in the absence of abundant sea star predators

263   (Duggins, 1981). The majority of urchins present a year following the seastar mortality were

264   approximately 3 - 5 cm in diameter. Green urchins of this size on the east coast of North

265   America are at least three years of age, and possibly more than a decade old (Russel, Ebert &

266   Petraitis, 1998; Vadas *et al.*, 2000). If these growth rates are similar on the Pacific coast, then

267   most of the urchins we saw could have settled several years before the sea star mortality event.

268   However, urchin growth rates can be highly variable (Vadas *et al.,* 2000), depending on food

269   supply and temperature (Thompson, 1983; Meidel & Scheibling, 1999; Pearce *et al.,* 2005) ,

270   Urchin growth rates have not yet been estimated in BC. A third possible explanation is that the

271   observed increase in urchin abundance resulted from a shift in urchin behaviour following the

272   sea star mortality event. The impact of 'intimidation' on predator–prey interactions can be as

273   important as direct consumption (Lima & Dill, 1990; Preisser, Bolnick & Benard, 2005). Under

274   risk of predation, prey individuals alter a suite of behaviours, including habitat choice, foraging

275   range, and time under cover (Werner *et al.*, 1983; Peacor & Werner, 2001; Trussell, Ewanchuk

276   & Bertness, 2003; Schmitz, Krivan & Ovadia, 2004). The effect of sunflower stars on urchin

277   behaviour is well documented. In field experiments in Alaska, both green and purple (*S.*

278   *purpuratus*) urchins moved away after *P. helianthoides* arms were placed in the centre of urchin

279   aggregations (Duggins, 1981), and urchin distribution shifted rapidly when sea star abundance

280   was experimentally increased (Duggins, 1983). Fear-released urchins could therefore respond by

281   moving from refuges, perhaps in very shallow or deep habitats or in sheltered crevices

282   inaccessible to sea stars (and divers), to more open substrates, making them easier to see and

283   count.

284   The data from REEF surveys support a behavioural rather than a consumptive mechanism

285   for the increase in urchin numbers. Whereas one would expect a delayed increase in urchin

286   numbers following a release from predation (Wangersky & Cunningham, 1957), green urchin

287   numbers began to increase at approximately the same time as the decline in sunflower stars was

288   evident (Fig. 5). The observed change in green urchin abundance may therefore be due, at least

289   in part, to green urchins modifying their distribution in response to the decline of sunflower stars.

290   Another conspicuous change we observed was a ~80% reduction in kelp cover (Fig. 3),

291   pointing to a potential trophic cascade triggered by the sea star mortality event. There are many

292   documented examples of urchin abundance directly influencing the abundance of algae (e.g.

293   Fletcher 1987; Carpenter, 1990; Estes & Duggins, 1995; McClanahan *et al.* 1996; Palacin *et al.,*

294   1998; Scheibling, Hennigar & Balch, 1999; Villouta *et al.* 2001). As urchin numbers rise, either

295   due to a large recruitment event (Hart & Scheibling, 1988) or the absence of a predator (Watson

296   & Estes, 2011), kelp is rapidly depleted. The alternating directions of population trends of sea

297   stars, urchins and kelp observed here are consistent with the hypothesis of a trophic cascade

298   triggered by the sea star disease. The tri-trophic cascade was clearly evident at the larger scale of

299   Howe Sound (Fig. 3), but detectable at only half of the sites, with a few additional sites showing

300   only part of the cascade (Fig. 4). It is notable that the sites surveyed earliest (i.e., sites 1-5 on

301   Figs 2 and 4) showed an increase in kelp cover, perhaps because not enough time had passed for

302   changes to take place. At other sites where the trophic cascade was not detectable, it is possible

303   that urchins moved elsewhere in search of better food sources (e.g., at sites 17 and 18 on Fig. 4),

304   or that the presence of juvenile sea stars (i.e., site 20 on Fig. 4) resulted in different trophic

305   interactions.

306   In contrast to green urchins, the abundance of many prey species did not increase in the

307   near-absence of sunflower star predators. For example, there was no change in the abundance of

308   red urchins (*S. franciscanus*) and white urchins (*S. pallidus*). Neither species is common in

309   Howe Sound, and little is known about the ecology of *S. pallidus*. However, *S. franciscanus*

310   may generally be less susceptible to sea star predation than other urchin species because they

311   grow too large to be consumed (Duggins, 1981). Moreover, although crustaceans constitute a

312   significant portion of the diet of sunflower stars (Shivji *et al.*, 1983; Estes & Duggins, 1995;

313   Lambert, 2000), shrimps and crabs declined following the sea star mortality. Several of the

314   crustaceans we monitored use kelp for both food and habitat. The spot prawn, *Pandalus*

315   *platyceros*, for instance, specifically uses the sea colander kelp as nursery habitat (Marliave &

316   Roth, 1995). The decline of some crustacean taxa could result from the reduced kelp cover and

317   therefore be a fourth step in the cascade documented here.

318   Another fourth link in the ecological cascade triggered by sea star mortality might

319   involve cup corals. Their increase in abundance was surprising as cnidarians are not normally

320   consumed by *P. helianthoides* (Shivji *et al.*, 1983; Herrlinger, 1983). However, cup corals are

321   known to fare poorly in areas dominated by macroalgae (Fadlallah, 1983). Contact with algae

322   causes coral polyp retraction, which in turn allows overgrowth by filamentous and coralline

323   algae (Coyer *et al.*, 1993). Increases in density of cup corals can be swift (< 1 year), and of the

324   magnitude observed here (3-4 times), after algae disappear (Coyer *et al.*, 1993). Of course, the

325   reduced abundance of kelp and of sea stars may also have allowed for a less obstructed view of

326   the substrate by the observers. As a number of taxa were not monitored in this study, there were

327   likely other changes following the sea star mortality event that we did not detect.

328   In conclusion, our study contributes to understanding the ecological consequences of the

329   northeast Pacific sea star mass mortality. The most notable change was a marked increase in the

330   number of green sea urchins, which might have already had trickle-down effects on other levels

331   of the ecosystem by the time we detected it. It is unclear whether the changes observed will

332   persist as long-term consequences of the near-disappearance of sea stars. Nonetheless, further

333   monitoring will help elucidate the resilience of this ecosystem in the face of acute biological

334   disturbances. Although such a sudden and drastic decline in sea star populations is alarming, it

335   provides a large-scale natural experiment that may advance our understanding of subtidal trophic

336   cascades and invertebrate population dynamics.

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338

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346

347 **REFERENCES**

348 Carpenter RC. 1990. Mass mortality of *Diadema antillarum. Marine Biology* 104:67–77.

349 Cloutier RN. 2011. Direct and indirect effects of marine protection: rockfish conservation areas as a
350   case study. MSc Thesis, Simon Fraser University.

351 Coyer JA, Ambrose RF, Engle JM, Carroll JC. 1993. Interactions between corals and algae on a
352   temperate zone rocky reef: mediation by sea urchins. *Journal of Experimental Marine Biology*
353   *and Ecology* 167(1): 21-37.

354 Dayton PK. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal
355   community. *Ecological Monographs* 45:137–159.

356 Duggins DO. 1981. Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia*
357   48:157–163.

358 Duggins DO. 1983. Starfish predation and the creation of mosaic patterns in a kelp-dominated
359   community. *Ecology* 64:1610-1619.

360 Estes JA, Duggins DO. 1995. Sea Otters and Kelp Forests in Alaska: Generality and Variation in a
361   Community Ecological Paradigm. *Ecological Monographs* 65(1):75-100.

362 Fadlallah YH. 1983. Population dynamics and life history of a solitary coral, *Balanophyllia elegans*,
363   from central California. *Oecologia* 58(2): 200-207.

364 Fletcher WJ. 1987. Interactions among subtidal Australian sea urchins, gastropods and algae:
365   effects of experimental removals. *Ecological Monographs* 57 (1): 89-109.

366 Grubs RD, Carlson JK, Romine JG, Curtis TH, McElroy WD, McCandless CT, Cotton CF, Musick JA.
367   2016. Critical assessment and ramifications of a purported marine trophic cascade. *Scientific*
368   *Reports* 6, 20970.

369 Hart MW, Scheibling RE. 1988. Heat waves, baby booms, and the destruction of kelp beds by sea
370   urchins. *Marine Biology* 99:167–176.

371 Hewson I, Button JB, Gudenkauf BM, Miner B, Newton AL, Gaydos JK, Wynne J, Groves CL, Hendler G,
372   Murray M, Fradkin S, Breitbart M, Fahsbender E, Lafferty KD, Kilpatrick AM, Miner CM,
373   Raimondi P, Lahner L, Friedman CS, Daniels S, Haulena M, Marliave J, Burge CA, Eisenlord ME,
374   Harvell CD. 2014. Densovirus associated with sea-star wasting disease and mass mortality.
375   *Proceedings of the National Academy of Sciences* 111:17278–17283.

376 Herrlinger TJ. 1983. The diet and predator-prey relationships of the sea star *Pycnopodia*
377   *helianthoides* (Brandt) from a central California kelp forest. M. A. Thesis, San Jose State
378   University.

379 Johnson, L. (2016, January 21). Sea star wasting disease among worst wildlife die-offs say
380   scientists. *CBC News.* Retrieved from http://www.cbc.ca/news/canada/british-columbia/sea-
381   star-wasting-die-off-1.3414607.

382 Lambert P. 2000. *Sea Stars of British Columbia, Southeast Alaska, and Puget Sound.* Royal British
383   Columbia Museum, UBC Press, Vancouver.

384   Lessios HA. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned?
385   *Annual Review of Ecology and Systematics* 19:371–393.

386   Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and
387   prospectus. *Canadian Journal of Zoology* 68:619–640.

388   Marliave JB, Gibbs CJ, Gibbs DM, Lamb AO, Young SJF. 2011. Biodiversity stability of shallow marine
389   benthos in Strait of Georgia, British Columbia, Canada through climate regimes, overfishing and
390   ocean acidification In Grillo O and Verona G (Ed.), *Biodiversity Loss in a Changing Planet*, 49-74.
391   Rijeka, Croatia: *InTech.*

392   Marliave JB, Roth M. 1995. Agarum kelp beds as nursery habitat of spot prawns, *Pandalus platyceros*
393   Brandt, 1851 (Decapoda, Caridea). *Crustaceana* 68:27–37.

394   McClanahan TR, Kamukuru AT, Muthiga NA, Gilagabher Yebio M, Obura D. 1996. Effect of sea
395   urchin reductions on algae, coral and fish populations. *Conservation Biology* 10(1): 136-154.

396   Meidel SK, Scheibling RE. 1999. Effects of food type and ration on reproductive maturation and
397   growth of the sea urchin Strongylocentrotus droebachiensis. *Marine Biology* 134:155–166.

398   Paine RT. 1966. Food web complexity and species diversity. *The American Naturalist*
399   100(910):65-75.

400   Palacin C, Giribet G, Carner S, Dantart L, Turon X. 1998. Low densities of sea urchins influence the
401   structure of algal assemblages in the western Mediterranean. *Journal of Sea Research* 39: 281-
402   290.

403   Peacor SD, Werner EE. 2001. The contribution of trait-mediated indirect effects to the net effects of
404   a predator. *PNAS* 98:3904–3908.

405   Pearce CM, Williams SW, Yuan F, Castell JD, Robinson SMC. 2005. Effect of temperature on somatic
406   growth and survivorship of early post-settled green sea urchins, *Strongylocentrotus*
407   *droebachiensis* (Müller). *Aquaculture Research* 36:600–609.

408   Pearse JS, Costa DP, Yellin MB, Agegian CR. 1977. Localized mass mortality of red sea urchin,
409   *Strongylocentrotus franciscanus* near Santa Cruz, California. *Fishery Bulletin.*

410   Pinheiro J, Bates D, DebRoy S, Sarkar D. R Core Development Team. 2015. nlme: Linear and
411   Nonlinear Mixed Effects Models. *... R-project. org/package= nlme. R package version*.

412   Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien M-L, Hereu B,
413   Milazzo M, Zabala M, D'Anna G, Piptone C. 2000. Trophic cascades in benthic marine
414   ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*
415   27(2): 179-200.

416   Preisser E, Bolnick D, Benard M. 2005. The high cost of fear: behavioral effects dominate predator-
417   prey interactions. *Ecology* 86:501–509.

418   REEF. 2014. Reef Environmental Education Foundation. World Wide Web electronic publication.
419   www.reef.org, downloaded 19 November 2014.

420

421   Russel MP, Ebert TA, Petraitis PS. 1998. Field estimates of growth and mortality of the green sea
422   urchin, *Strongylocentrotus droebachiensis. Ophelia* 48:137–153.

423   Scheibling RE, Stephenson RL. 1984. Mass mortality of *Strongylocentrotus droebachiensis*
424   (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Marine Biology* 78:153–164.

425   Scheibling RE, Hennigar AW, Balch T. 1999. Destructive grazing, epiphytism, and disease: the
426   dynamics of sea urchin-kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and*
427   *Aquatic Sciences* 56:2300–2314.

428   Schmitz OJ, Krivan V, Ovadia O. 2004. Trophic cascades: the primacy of trait-mediated indirect
429   interactions. *Ecology Letters* 7:153–163.

430   Shivji M, Parker D, Hartwick B, Smith MJ, Sloan NA. 1983. Feeding and distribution study of the
431   sunflower sea star *Pycnopodia helianthoides* (Brandt, 1835). *Pacific Science* 37:133–140.

432   Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA. 2003. Kelp forest
433   ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*
434   29(4):436-459.

435   Stockstad E. 2014. Death of the stars. *Science (New York, N.Y.)* 344:464–467.

436   Thompson RJ. 1983. The relationship between food ration and reproductive effort in the green sea
437   urchin, *Strongylocentrotus droebachiensis. Oecologia* 56:50–57.

438   Trussell GC, Ewanchuk PJ, Bertness MD. 2003. Trait-mediated effects in rocky intertidal food chains:
439   predator risk cues alter prey feeding rates. *Ecology* 96:2049–2055.

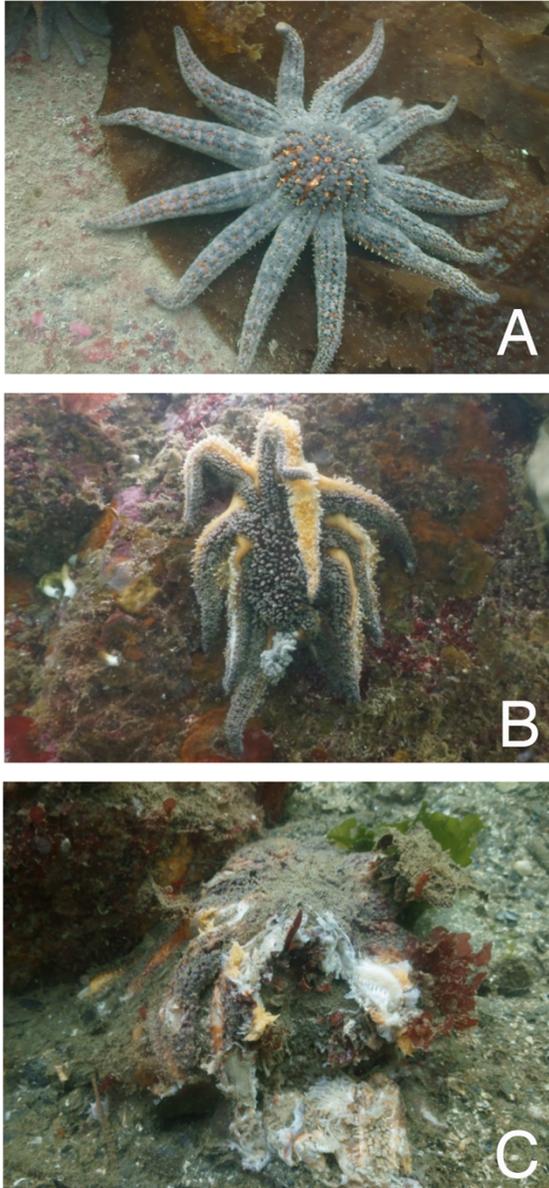
440   Vadas RL Sr., Beal B, Dowling T, Fegley JC. 2000. Experimental field tests of natural algal diets on
441   gonad index and quality in the green sea urchin, *Strongylocentrotus droebachiensis*: a case for
442   rapid summer production in post-spawned animals. *Aquaculture* 182:115–135.

443   Villouta E, Chadderton WL, Pugsley CW, Hay CH. 2001. Effects of sea urchin (*Evechinus chloroticus*)
444   grazing in Dusky Sound, Fiordland, New Zealand. *New Zealand Journal of Marine and*
445   *Freshwater Research* 35(5): 1007-1024.

446   Wangersky PJ, Cunningham WJ. 1957. Time lag in prey-predator population models. *Ecology*
447   38:136-139.

448   Watson J, Estes JA. 2011. Stability, resilience, and phase shifts in rocky subtidal communities along
449   the west coast of Vancouver Island, Canada. *Ecological Monographs* 81:215–239.

450   Werner EE, Gilliam JF, Hall DJ, Mittelbach GG. 1983. An experimental test of the effects of predation
451   risk on habitat use in fish. *Ecology* 64:1540-1548.

452

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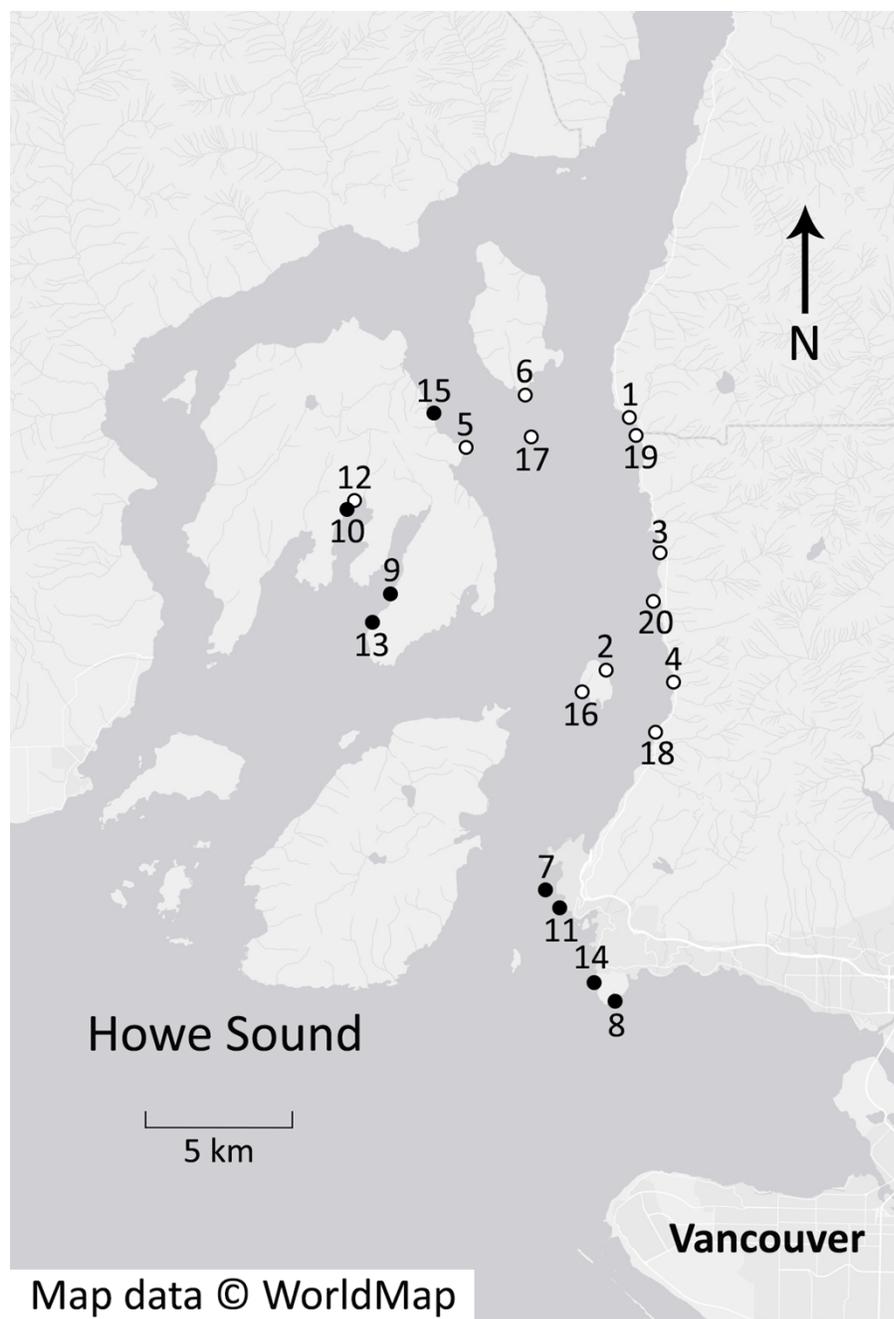
455 **Figure 1. Progression of sea star wasting disease. (A)** A healthy-looking specimen of *P.*
456 *helianthoides* moves across the kelp, *Agarum fimbiratum*. (B) Afflicted sea stars exhibit a loss of
457 turgor pressure and body wall ruptures, followed by (C) limb autotomization, disintegration and
458 death. Photos by Donna Gibbs.

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461   **Figure 2**. **Rocky reef survey sites in Howe Sound, British Columbia.** Benthic community
462   composition was assessed at each of the 20 sites once in 2009 or 2010 and again in 2014. A
463   mass mortality of sea stars occurred in the summer and fall of 2013 in this area. A site-level
464   trophic cascade following the mortality was detectable at some sites (solid circles) but not others
465   (open circles). (Map data © 2015 WorldMap).
466

467 **Table 1**. **Taxa recorded during subtidal surveys in Howe Sound, British Columbia**. Mean
468 density and standard deviation per 15 m^2 are given for each taxon as recorded before and after
469 the sea star mortality event.

Taxon	Species or genera included in taxon	Mean density (SD)			
		Before		After	
Invertebrates					
Sunflower star	*Pycnopodia helianthoides* Brandt, 1835	6.4	(11.4)	0.9	(3.3)
Green urchin	*Strongylocentrotus droebachiensis* O. F. Müller, 1776	18.3	(41.0)	77.2	(157.4)
Red urchin	*Strongylocentrotus franciscanus* Aggasiz, 1863	0.4	(0.9)	0.3	(0.6)
White urchin	*Strongylocentrotus pallidus* G. O. Sars, 1871	1.1	(2.0)	0.3	(0.4)
California cucumber	*Parastichopus californicus* Linnaeus, 1758	6.1	(9.0)	13.1	(8.9)
Dungeness crab	*Metacarcinus magister* Dana, 1852	0.1	(0.2)	0.0	
Red rock crab	*Cancer productus* Randall, 1839	0.1	(0.3)	0.4	(0.7)
Spot prawn	*Pandalus platyceros* Brandt, 1851	22.1	(89.1)	0.3	(0.8)
Squat lobster	*Munida quadrispina* Benedict, 1902	4.0	(9.0)	0.3	(0.6)
Miscellaneous crabs	Primarily anomurans, including lithode and hermit crabs; several brachyuran genera including *Cancer, Pugettia, Scyra,* and *Oregonia*	21.7	(35.0)	16.3	(23.5)
Miscellaneous shrimps	Primarily *Pandalus danae* Stimpson, 1857, but also other members of the genus *Pandalus*, as well as the genera *Lebbeus, Eualus, Heptocarpus* and possibly others	37.0	(38.6)	15.8	(11.2)
Giant Pacific octopus	*Enteroctopus dofleini* Wülker, 1910	0.1	(0.2)	0.0	
Cup corals	*Balanophyllia elegans* Verrill, 1864, *Caryophyllia alaskensis* Vaughan, 1941	6.7	(15.8)	22.1	(19.0)
Benthic fishes					
Grunt sculpin	*Rhamphocottus richardsonii* Günther, 1974	0.1	(0.2)	0.1	(0.2)
Longfin sculpin	*Jordania zonope* Starks, 1895	0.2	(0.4)	2.7	(4.1)
Sailfin sculpin	*Nautichthys oculofasciatus* Girard, 1858	0.1	(0.2)	0.0	
Scalyhead sculpin	*Artedius harringtoni* Starks, 1896	0.8	(1.6)	1.8	(2.3)
Miscellaneous sculpins	Cottid genera including *Artedius, Orthanopias, Oligocottus, Radulinus, Chitonotus* and possibly others.	5.5	(4.6)	0.7	(1.2)

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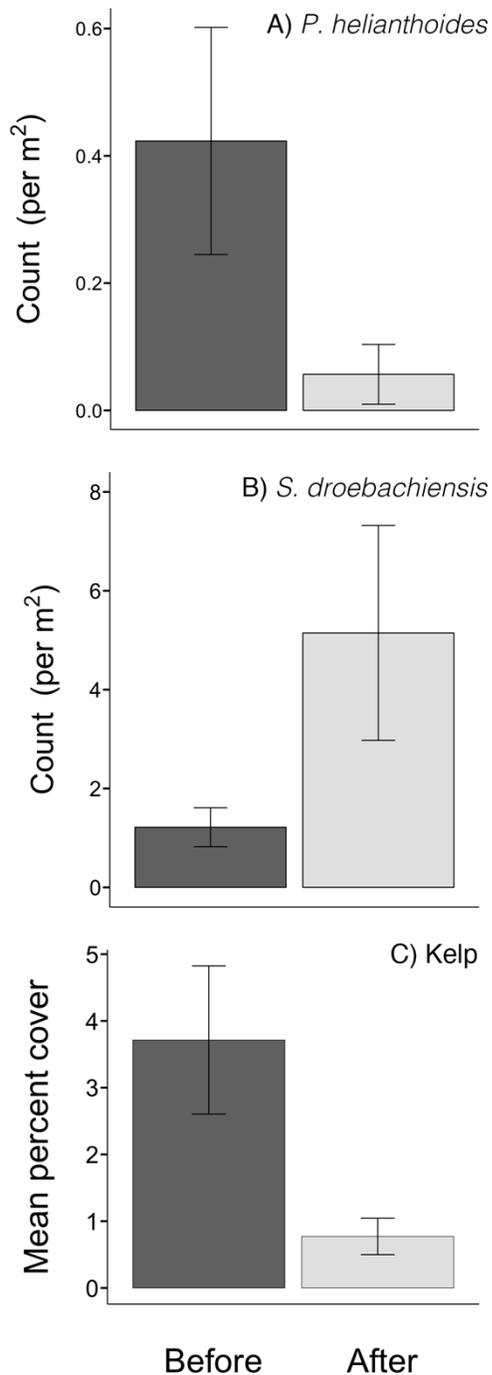
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473 **Figure 3**. **Mortality of sea stars, and subsequent change in urchin abundance and kelp**
474 **cover after sea star mortality.** Mean abundance (per m^2) of (A) sunflower stars and (B) green
475 sea urchins, and (C) percent cover of kelp on rocky reefs in Howe Sound, British Columbia, on
476 80 transects before and after the mass mortality of sea stars in 2013. Error bars represent
477 standard error. The dominant kelp was the sea colander kelp, *Agarum fimbriatum*.
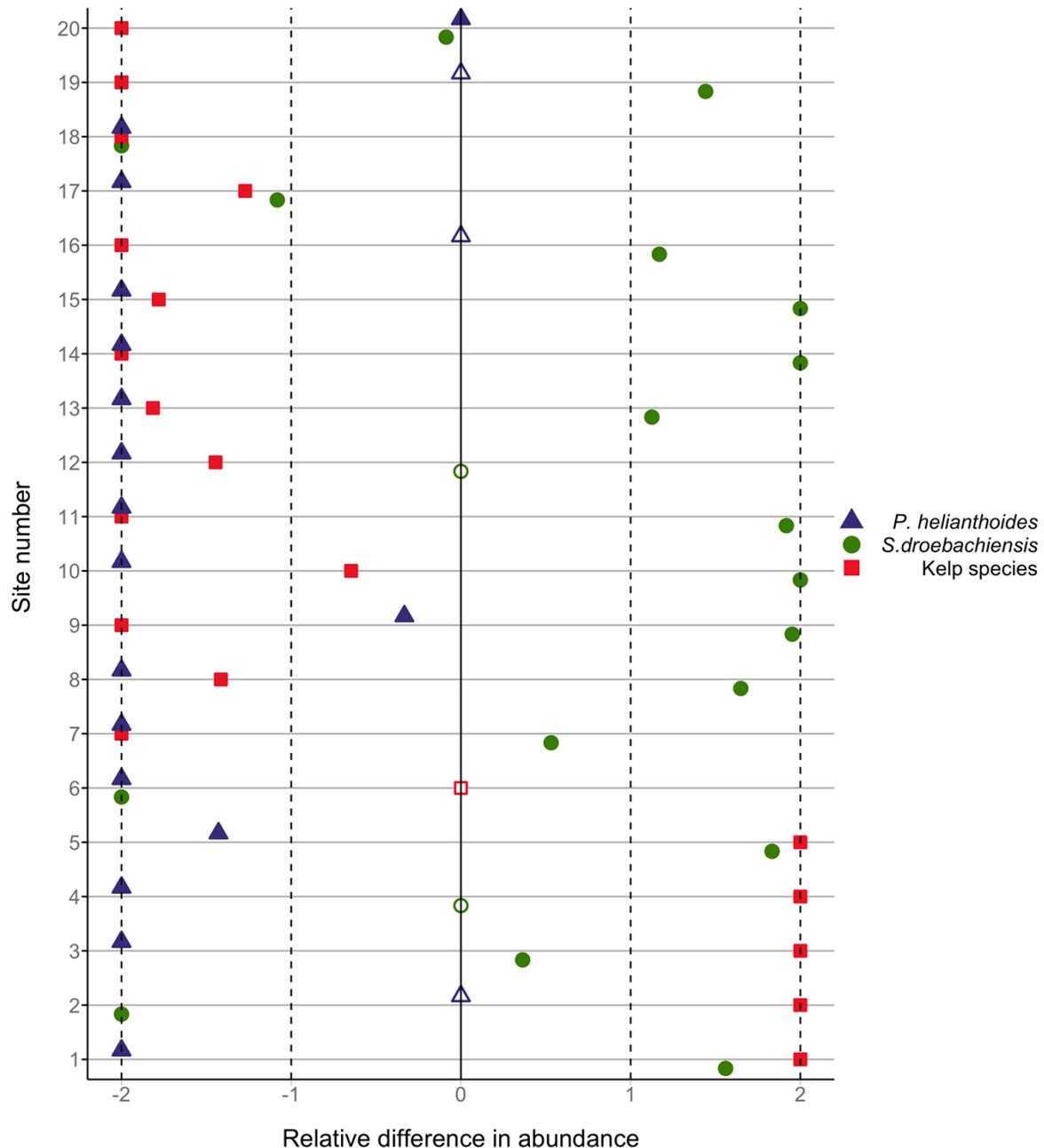
Figure 4. Relative difference in abundance of seastars, urchins and kelp by site. The
relative difference in total count of sunflower stars (blue triangles) and green urchins (green
circles), and the relative difference in the mean percent cover of algae (red squares) before and
after the sea star mass mortality. Open symbols indicate sites where population density was zero
both before and after the mass mortality. Relative difference was calculated as the change in
abundance divided by the mean abundance of both time periods. A relative difference of -2
indicates the population declined to zero. Sites are numbered chronologically according to the
order in which they were surveyed, from June to August, 2014.

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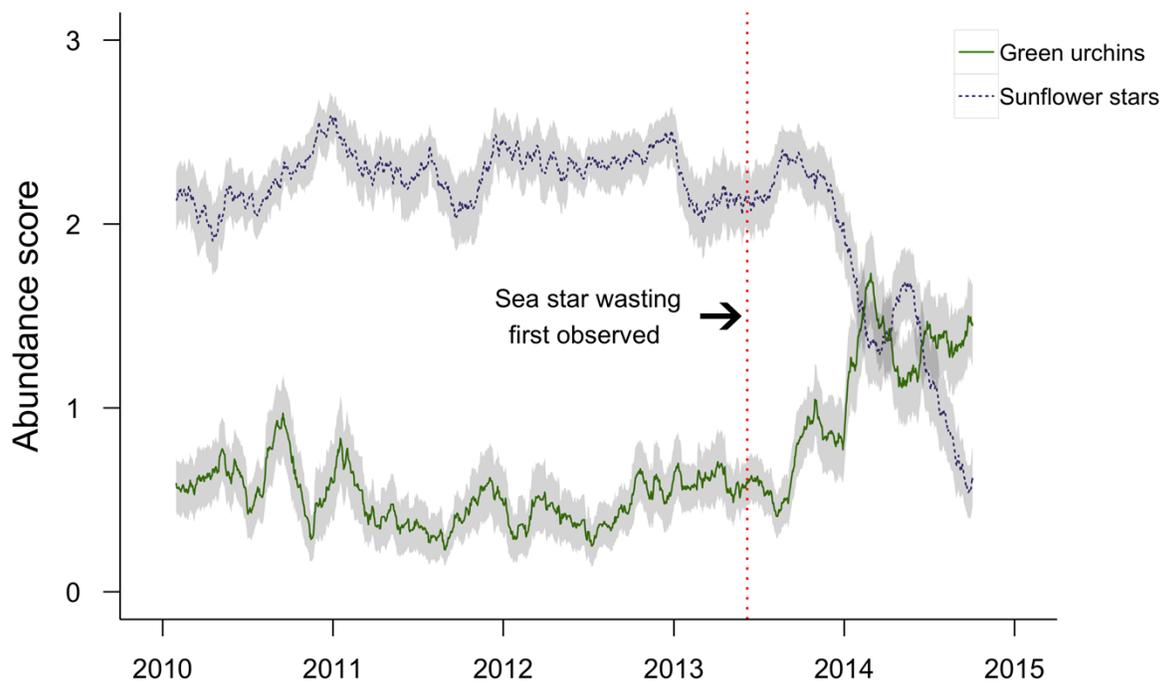
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490 **Figure 5**. **Sunflower star and green sea urchin abundance trajectories.** Sixty-day running
491 average abundance scores for green sea urchins (*Strongylocentrotus droebachiensis*; green solid
492 line) and sunflower stars (*Pycnopodia helianthoides*; purple dashed line) recorded in REEF
493 surveys from January 2010 to November 2014 in Washington and British Columbia (n = 1568
494 surveys). Grey bands indicate 95% confidence intervals of the running average. The vertical red
495 dotted line indicates the date of the first recorded observation of sea star wasting syndrome (7
496 June 2013), which was on the Olympic coast of WA.

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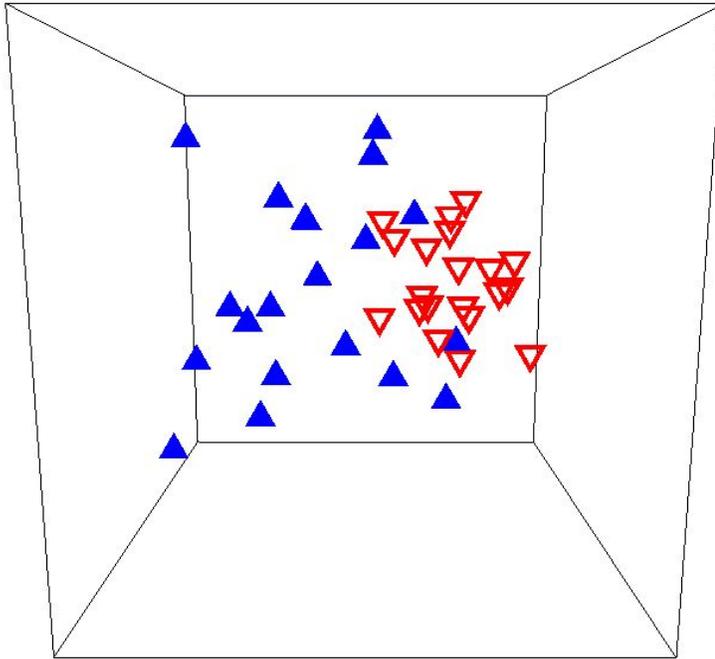
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499 **Figure 6**. **Rocky reef species assemblages before and after sea star mortality.**
500 Multidimensional scaling plot of benthic community composition on rocky reefs before (blue
501 triangles) and after (inverted red triangles) the 2013 sea star mass mortality event in Howe
502 Sound, British Columbia. The analysis included 18 fish and invertebrate taxa at 20 sites,
503 surveyed both in 2009/2010 and 2014.   The associated stress value (0.13) suggests some
504 distortion in the multivariate representation of the data.

505 **Table 2**. **Differences in pre- and post-mortality benthic assemblages.** The four taxa that
506 contributed disproportionately to dissimilarity in benthic community composition on rocky reefs
507 before and after the 2013sea star mass mortality. Mean densities (# per 30 m^2 ± 1 SD),
508 consistency ratios, and individual and cumulative contributions (in %) to differences between
509 years are shown. The consistency ratio is calculated as a species' average dissimilarity
510 contribution divided by the standard deviation of dissimilarity values. A consistency ratio > 1
511 indicates an even contribution to community dissimilarity across sites. The analysis was
512 conducted on square-root-transformed data (see Methods) but untransformed densities are
513 presented here.

Taxon	Mean density (SD)		Consistency ratio	Individual contribution (%)	Cumulative contribution (%)
	Before	After			
Strongylocentrotus droebachiensis	18.3	77.2	1.09	18.91	18.91
	(41.0)	(157.5)			
Cup corals	6.7	22.2	1.41	13.04	31.95
	(15.8)	(19.1)			
Misc. shrimps	37.0	15.9	1.3	11.29	43.23
	(38.7)	(11.2)			
Misc. crabs	21.7	16.3	1.05	11.15	54.38
	(35.0)	(23.5)			
Pycnopodia helianthoides	6.4	0.9	1.18	7.15	69.05
	(11.4)	(3.3)			

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