Community shifts on rocky reefs following sea star mass mortality in British Columbia

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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 wasting event. We observed changes in the abundance of several species, most notably a four-fold increase in the number of green sea urchins, *Strongylocentrotus droebachiensis*, after the sea star mortality. 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. Behavioural experiments conducted in situ suggest predation release as a key mechanism underpinning the shift in urchin numbers. However, it remains unclear whether this mechanism has acted 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   **Community shifts on rocky reefs following sea star mass mortality in**

2   **British Columbia**

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16   **ABSTRACT**

17

18   Echinoderm population collapses, driven by disease outbreaks and climatic events, may be

19   important drivers of population dynamics, ecological shifts and biodiversity. The northeast

20   Pacific recently experienced a mass mortality of sea stars. In Howe Sound, British Columbia, the

21   sunflower star *Pycnopodia helianthoides* — a previously abundant predator of bottom-dwelling

22   invertebrates — began to show signs of a wasting syndrome in early September 2013, and dense

23   aggregations disappeared from many sites in a matter of weeks. Here, we assess changes in

24   subtidal community composition by comparing the abundance of fish, invertebrates and

25   macroalgae at 20 sites in Howe Sound before and after the 2013 sea star wasting event. We

26   observed changes in the abundance of several species, most notably a four-fold increase in the

27   number of green sea urchins, *Strongylocentrotus droebachiensis*, after the sea star mortality.

28   Qualitative data on the abundance of sunflower stars and green urchins from a citizen science

29   database show that the patterns of echinoderm abundance detected at our study sites reflected

30   wider local trends. Behavioural experiments conducted in situ suggest predation release as a key

31   mechanism underpinning the shift in urchin numbers. However, it remains unclear whether this

32   mechanism has acted directly, via a reduction in urchin mortality, or indirectly, via a shift in

33   urchin distribution into areas previously occupied by the predatory sea stars. Understanding the

34   ecological implications of sudden and extreme population declines may further elucidate the role

35   of echinoderms in temperate seas, and provide insight into the resilience of marine ecosystems to

36   biological disturbances.

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38   **Keywords** Starfish, Marine diseases, Community shifts, Mass mortality, Environmental change

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39   **INTRODUCTION**

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41   Echinoderms can be subject to dramatic population fluctuations (Uthicke *et al.,* 2009). Rapid

42   declines are often driven by disease or extreme climatic events. For example, the spread of mass

43   mortality of the black sea urchin, *Diadema antillarum* Philippi, 1845, in the 1980s suggests that

44   it was most likely caused by a pathogen that was never identified (Lessios *et al.,* 1984). The

45   event impacted an estimated 3.5 million km^2 of the Caribbean region, causing up to 99% urchin

46   mortality at some sites (Lessios, 1988). While the decimation of *Diadema* was a unique

47   occurrence, other echinoderm mass mortality events occur repeatedly. On the Atlantic coast of

48   North America, an amoeboid parasite causes episodic mortality events in green sea urchins,

49   *Strongylocentrotus droebachiensis* O. F. Müller, 1776 (Jones & Scheibling, 1985), which are

50   linked to hurricanes and are predicted to increase in frequency with climate change (Scheibling

51   & Lauzon-Guay, 2010). Similarly, recurring events of wasting disease involving asteroids (sea

52   stars), echinoids (sea urchins) and holothurians (sea cucumbers) in the Channel Islands,

53   California, are associated with climate regime shifts and extreme weather events (Engle, 1994;

54   Eckert *et al.,* 2000).

55   Because sea stars and sea urchins play key ecological roles in many marine ecosystems,

56   echinoderm population collapses can be important drivers of biodiversity, population dynamics

57   and ecological shifts. In fact, the term 'keystone predator' was originally coined for the purple

58   star, *Pisaster ochraceus* Brandt, 1835, after experiments showed that its absence led to

59   significant decreases in intertidal biodiversity (Paine, 1966). Several other echinoderm species

60   have since been shown to influence community composition through predation or herbivory.

61   These effects are apparent on coral reefs following echinoderm population booms (e.g., coral

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62   cover declines owing to eruptive crown-of-thorns star, *Acanthaster planci* Linnaeus, 1758 (Sano

63   *et al.,* 1984)), or busts (e.g., the transition from coral- to algae-dominated reefs following the *D.*

64   *antillarum* mortality event (Carpenter, 1990)). On temperate rocky reefs, fluctuations in the

65   abundance of herbivorous urchins can also result in major community shifts, from kelp forests to

66   urchin barrens and back again (Estes & Duggins, 1995; Steneck *et al.*, 2003).

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

68   stars. The event, which is regarded as the largest outbreak of marine disease ever recorded for

69   non-commercial species (C.D. Harvell, pers. comm., 2015), was first noticed on the Olympic

70   coast of Washington in June 2013 (Hewson *et al.*, 2014). In affected sea stars, the signs progress

71   from a loss of turgor pressure, to lesions and ruptures of the body wall and autotomization of

72   arms, and ultimately, disintegration and death. The wasting syndrome has continued through

73   2014 and early 2015, and has so far affected some 20 species from Alaska to Southern California

74   (Stockstad, 2014). A virus may be involved (Hewson *et al.,* 2014), but the precise causes and

75   contributing factors remain poorly understood. Moreover, little is known so far of the extent and

76   ecological consequences of this sea star mortality event at any location.

77   In Howe Sound, southern Strait of Georgia, British Columbia, the sunflower star

78   *Pycnopodia helianthoides* Brandt, 1835— a previously abundant predator of bottom-dwelling

79   invertebrates on subtidal rocky reefs — showed signs of advanced wasting in early September

80   2013. Dense aggregations disappeared from many sites in a matter of weeks (personal

81   observations). Here, we evaluate the extent of mortality of *P. helianthoides* in Howe Sound and

82   document benthic community shifts following the rapid decline of this predatory sea star. We

83   compare rocky reef community composition before and after the mass mortality using

84   quantitative data derived from subtidal transects and qualitative information gathered by citizen

85 scientists. In addition, we provide an experimental test of a possible behavioural mechanism

86 underpinning some of the observed community shifts. In doing so, we provide the first empirical

87 study, to our knowledge, of what might be the most geographically extensive echinoderm mass

88 mortality ever recorded.

89

90 **MATERIALS AND METHODS**

91 **Subtidal surveys**

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

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

94 British Columbia (BC), Canada (Fig. 1). Surveys before the wasting event were conducted as

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

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

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

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

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

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

101 15 m (chart datum). We quantified fish and invertebrate abundance by counting all individuals of

102 the target taxa occurring fully or partly within 0.25 m^2 quadrats placed at 15 random positions

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

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

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

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

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

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

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

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

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

115   positively identify. The abundance score is roughly logarithmic: score 1 = a single individual, 2

116   = 2-10 individuals, 3 = 11-100 individuals and 4 = > 100 individuals. Species with no

117   abundance score are assumed to be absent, which we deemed to be a fair assumption given that

118   our target taxa were easy to identify.

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

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

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

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

123

124   **Sunflower star–green urchin interactions**

125   We evaluated whether changes in green urchin abundance (see Results) might result from

126   changes in perceived or actual predation pressure by sea stars. To do so, we assessed the alarm

127   response of green urchins, as reflected by changes in urchin crawling speed, upon different types

128   of tactile contact that were meant to simulate potential predatory attacks. We compared the

129   change in crawling speed among urchins in contact with a sunflower star, leather star,

130   *Dermasterias imbricata* Grube, 1857, or a control object (a rock).   All trials were conducted in

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131   situ in Howe Sound by placing a weighted measuring tape along a flat, sandy substrate at depths

132   of 7-15 m. Each urchin was placed on the substrate adjacent to the tape and we recorded the

133   distance it moved in 60 seconds (s), before exposure to a tactile stimulus. We then placed a sea

134   star or rock next to the urchin so that at least one arm tip or portion of the rock touched the

135   urchin's spines and recorded the distance and direction (towards or away from the stimulus)

136   moved by the urchin in the subsequent 60 s. For urchins that moved towards the stimulus,

137   distance was recorded as a negative value. Urchin and sea star sizes were also recorded.

138

139   **Data analyses**

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

141   2015) to compare sunflower star abundance and kelp cover before and after sea star mortality.

142   We obtained sunflower abundance for each transect by summing the number of sunflower stars

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

144   across all quadrats within each transect. In all cases, we included 'site' as a random effect, and

145   verified the assumptions of normally distributed residuals, homoscedasticity and the absence of

146   leverage.

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

148   we ran a permutation-based, non-parametric analysis of similarity (ANOSIM; Clarke, 1993)

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

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

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

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

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

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

155   which varies between 0 (samples are as similar across groups as they are within group) and 1 (all

156   samples within groups are more similar to each other than to any sample across groups) and is

157   tested for difference from zero with a permutation test (in this study, N = 999 permutations). The

158   differences in benthic assemblages were visualized in a non-metric, multidimensional scaling

159   (MDS) plot in which samples that are more similar in community composition appear closer

160   together than more dissimilar samples. Stress values of <0.1 suggest that distances among

161   samples in an MDS plot accurately reflect the extent of community differences (Clarke

162   &Warwick, 2001). Finally, we conducted an analysis of similarity percentages (SIMPER) to

163   identify the main taxa responsible for any differences observed between pre- and post-mortality

164   assemblages. We considered a taxon to be important to community differences if their

165   individual contribution was 11% or more, which is twice the expected value if dissimilarity

166   contributions were evenly distributed among all taxa in the analysis (i.e.,100 percent divided by

167   18 taxa, multiplied by 2). The SIMPER analysis also includes an indication of evenness,

168   expressed as a consistency ratio (CR). CR is the average dissimilarity contribution of a taxon

169   divided by the standard deviation in dissimilarity values of that taxon, for each time period. CR

170   values greater than one suggest that the taxon contributed to dissimilarity between time periods

171   equally across all sites (Terlizzi *et al.*, 2005).

172   Finally, we compared urchin speed before and after contact with a stimulus (sea star or

173   rock) using paired Student's t-tests. We then calculated the change in speed (i.e., the crawling

174   speed following the tactile stimulus minus the crawling speed before contact) for each urchin and

175   used a linear model in R to compare the change in speed among treatment groups, with urchin

176   size as a covariate.

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RESULTS

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Sea star mortality

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

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

183 0.22) individuals per m^2 after it (LME: t = 4.62, df = 139, p < 0.0001; Fig. 2). Three sites had no

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

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

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

187 BC and Washington between 2010 and 2014. Although sunflower stars were sighted on 100% of

188 surveys in all years, a marked decline was evident in their abundance score trajectory (Fig. 3). At

189 this larger geographic scale, sunflower stars started declining in approximately the third week of

190 September, some 15 weeks after the first report of seastar wasting in the region.

191

Benthic community composition

193 There was a significant shift in community composition following sea star mortality in Howe

194 Sound (ANOSIM: R = 0.326, p = 0.001; Fig. 4), and many species changed in abundance from

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

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

197 disappearance of sunflower stars (Table 2). This trend is supported by the REEF surveys,

198 although these qualitative data suggest that green urchin numbers began increasing in the first

199 week of September, two to three weeks before the detectable onset of sea star decline (Fig. 3).

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200   There was also an increase in the abundance of cup corals, while the numbers of small shrimps

201   and crabs decreased (Table 2). Cumulatively, these four taxa accounted for nearly two-thirds

202   (62%) of the dissimilarity in benthic community composition before and after the sea star

203   mortality, and their contributions were consistent across sites (CRs > 1; Table 2). Despite their

204   marked decline, sunflower stars did not contribute disproportionately to the dissimilarity between

205   time periods (SIMPER; individual contribution to dissimilarity = 7.15%). Overall, within-year

206   similarity was higher after than before sea stars died (SIMPER; average inter-site similarity

207   before = 46.28%, after = 58.11%; Fig. 4), suggesting that communities became more

208   homogeneous following the seastar mortality.

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

210   the abundance of kelp. Kelp cover decreased from 3.71% (± 9.93%) in 2009/2010 to 0.77% (±

211   2.44%) in 2014 (LME: t = 2.669, df = 139, p = 0.0085; Fig. 5). In all years, the kelp at our sites

212   was almost exclusively the sea colander kelp, *Agarum fimbriatum* Harvey, 1862, but also

213   included *Saccharina latissima* (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006.

214

215   **Sunflower star–green urchin interactions**

216   Urchins moved four times faster after than before contact with sunflower stars (paired t-test: t = -

217   6.92, df = 10, p-value < 0.0001; Fig. 6) and just over twice as fast after contact with leather stars

218   (paired t-test: t = -4.98, df = 12, p-value = 0.0003; Fig. 6). They did not increase their speed

219   significantly following contact with a rock (paired t-test: t = -1.97, df = 11, p-value = 0.07; Fig.

220   6). The magnitude of the change in crawling speed differed among stimulus types (LM: $F_{4,32}$ =

221   14.60, Adj. R^2 = 0.73, p < 0.0001; Table 3). The mean change in speed for urchins exposed to

222   sunflower stars was greater than the change in speed for those exposed to either leather stars

223 (post-hoc Tukey HSD, p = 0.005) or to rocks (post-hoc Tukey HSD: p < 0.0001). However, the

224 increase in crawling speed did not differ between urchins exposed to leather stars and to rocks

225 (post-hoc Tukey HSD: p = 0.154). Urchin size did not contribute significantly to change in

226 crawling speed (Table 3). Of the 36 urchins tested, only one individual, which was in the

227 control group, moved towards the stimulus; all others moved away.

228

229 **DISCUSSION**

230

231 The wasting disease that affected echinoderms in the northeast Pacific in 2013/2014 decimated

232 the populations of sunflower stars, the sea stars that formerly dominated subtidal communities

233 (Fig. 3). We found a noticeable shift in benthic community structure following the sea star

234 decline. Benthic communities were more homogeneous and had less kelp cover compared to

235 communities before the mortality event. The community changes were largely driven by

236 changes in the abundance of green sea urchins, cup corals, shrimps and crabs (Tables 1 & 2).

237 The strong and specific avoidance (i.e., crawling speed) of green urchins to sunflower stars

238 suggests a predator–prey relationship that might underpin the urchin's population response.

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

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

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

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

243 97% of *Diadema antillarum* across the Caribbean (Lessios, 1988)). The percent change in

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

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

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

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

248   present after the event. The steep decline in sunflower star numbers was clearly evident in the

249   qualitative density scores generated by citizen science (REEF) surveys, which covered a broader

250   geographic area. The time-series of REEF data suggests that sunflower star population levels

251   were somewhat variable but largely stable between the first snapshot in 2009/2010 and the onset

252   of the wasting event in 2013. It therefore seems very unlikely that the sea star population

253   declines, and concomitant changes in benthic community composition, could be ascribed to a

254   different, unreported disturbance occurring prior to 2013.

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

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

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

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

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

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

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

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

263   approximately 3 - 5 cm in diameter. Some studies suggest that green urchins of this size on the

264   east coast of North America are at least three years of age, and possibly more than a decade old

265   (Russel, Ebert & Petraitis, 1998; Vadas *et al.*, 2000). If these growth rates are similar on the

266   Pacific coast, then most of the urchins we saw could have settled several years before the sea star

267   mortality event. However, urchin growth rates can be highly variable (Vadas *et al.,* 2000),

268   depend on food supply (Thompson, 1983; Meidel & Scheibling, 1999) and temperature (Pearce

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269   *et al.,* 2005), and have not yet been estimated in BC. Thus, we cannot rule out increased

270   recruitment and/or survival as potential mechanisms for the increase in urchin abundance.

271   Another possible explanation is that the observed increase in urchin abundance resulted

272   from a shift in behaviour following the sea star mortality event. The impact of 'intimidation' on

273   predator–prey interactions can be as important as direct consumption (Lima & Dill, 1990;

274   Preisser, Bolnick & Benard, 2005). Under risk of predation, prey individuals alter a suite of

275   behaviours, including habitat choice, foraging range, time under cover, etc. (Werner *et al.*, 1983;

276   Peacor & Werner, 2001; Trussell, Ewanchuk & Bertness, 2003; Schmitz, Krivan & Ovadia,

277   2004). In fact, Duggins (1983) found that green urchin distribution shifted rapidly when sea star

278   abundance was experimentally increased. Similarly, purple urchins (*S. purpuratus*) fled from

279   tidepools as sunflower stars moved in (Dayton, 1975). Our behavioural experiment supports the

280   idea that *P. helianthoides* is a major predator of *S. droebachiensis,* eliciting strong avoidance

281   behaviour in the urchin (Fig. 6). The data from REEF surveys also support a behavioural rather

282   than a consumptive mechanism for the increase in urchin numbers. Whereas one would expect a

283   delayed increase in urchin numbers following a release from predation (Wangersky &

284   Cunningham, 1957), green urchin numbers began to increase at approximately the same time as

285   the decline in sunflower stars was evident (Fig. 3). The observed change in green urchin

286   abundance may therefore be due, at least in part, to green urchins modifying their distribution in

287   response to the decline of sunflower stars, emerging from spatial refuges in the near-absence of

288   the predator.

289   Another conspicuous change we observed was a nearly 80% reduction in kelp cover (Fig.

290   5), pointing to a potential trophic cascade triggered by the sea star mortality event. There are

291   many documented examples of urchin abundance directly influencing the abundance of algae

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292   (e.g. Carpenter, 1990; Estes & Duggins, 1995; Scheibling, Hennigar & Balch, 1999). As urchin

293   numbers rise, either due to a large recruitment event (Hart & Scheibling, 1988) or the absence of

294   a predator (Watson & Estes, 2011), kelp is rapidly depleted. The reduction in kelp cover may

295   account for some of the other community shifts we observed such as, for example, an increase in

296   abundance of cup corals. It is unlikely that *P. helianthoides* were consuming cup corals prior to

297   the mortality event as cnidarians are not normally consumed by this species (Shivji *et al.*, 1983).

298   Sunflower stars have also been shown to retreat upon contact with cup corals (Estes & Duggins,

299   1995). However, kelp can have a smothering effect on cup corals, and the reduced abundance of

300   kelp may have allowed for increased feeding and survival of the corals (or, alternatively,

301   unobstructed view by the observers). In contrast, crustaceans constitute a significant portion of

302   the diet of sunflower stars (Shivji *et al.*, 1983; Estes & Duggins, 1995; Lambert, 2000), but we

303   observed a decline in both shrimps and crabs following the sea star mortality (Table 2).

304   Crustaceans use kelp for both food and habitat. The spot prawn, *Pandalus platyceros*, for

305   instance, specifically uses the sea colander kelp as nursery habitat (Marliave & Roth, 1995) and

306   their apparent decline (Table 1) could be a cascade effect resulting from the reduced kelp cover.

307   In addition, as a number of taxa were not monitored in this study, there were likely other changes

308   following the sea star mortality event that we did not detect.

309   In conclusion, our study provides the first empirical evidence, to our knowledge, of

310   ecological consequences of the northeast Pacific sea star mass mortality. The most notable

311   change was a marked increase in the number of green sea urchins, which might have already had

312   trickle-down effects on other levels of the ecosystem by the time we detected it. It is unclear

313   whether the changes observed will persist as long-term consequences of the near-disappearance

314   of sea stars. Nonetheless, further monitoring will help elucidate the resilience of this ecosystem

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315   in the face of acute biological disturbances. Although such a sudden and drastic decline in sea

316   star populations is alarming, it provides a large-scale natural experiment that may advance our

317   understanding of subtidal trophic cascades and invertebrate population dynamics.

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319   **ACKNOWLEDGEMENTS**

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Map data © 2015 WorldMap

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329 **Figure 1**. **Rocky reef survey sites in Howe Sound, British Columbia.** Benthic community
330 composition was assessed at each of the 20 sites once in 2009 or 2010 and again in 2014. A
331 mass mortality of sea stars occurred in the summer and fall of 2013 in this area. (Map data ©
332 2015 WorldMap).

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

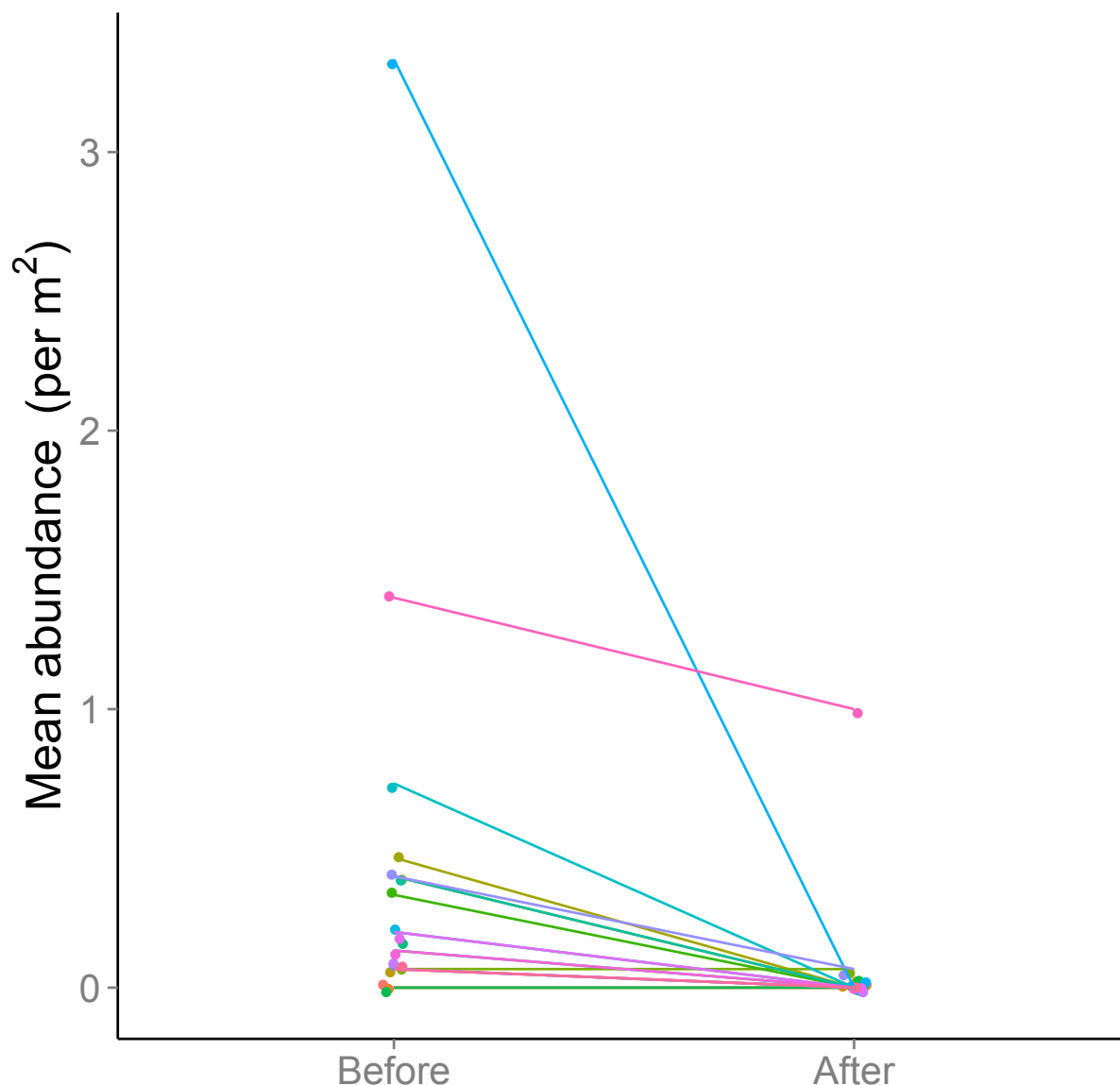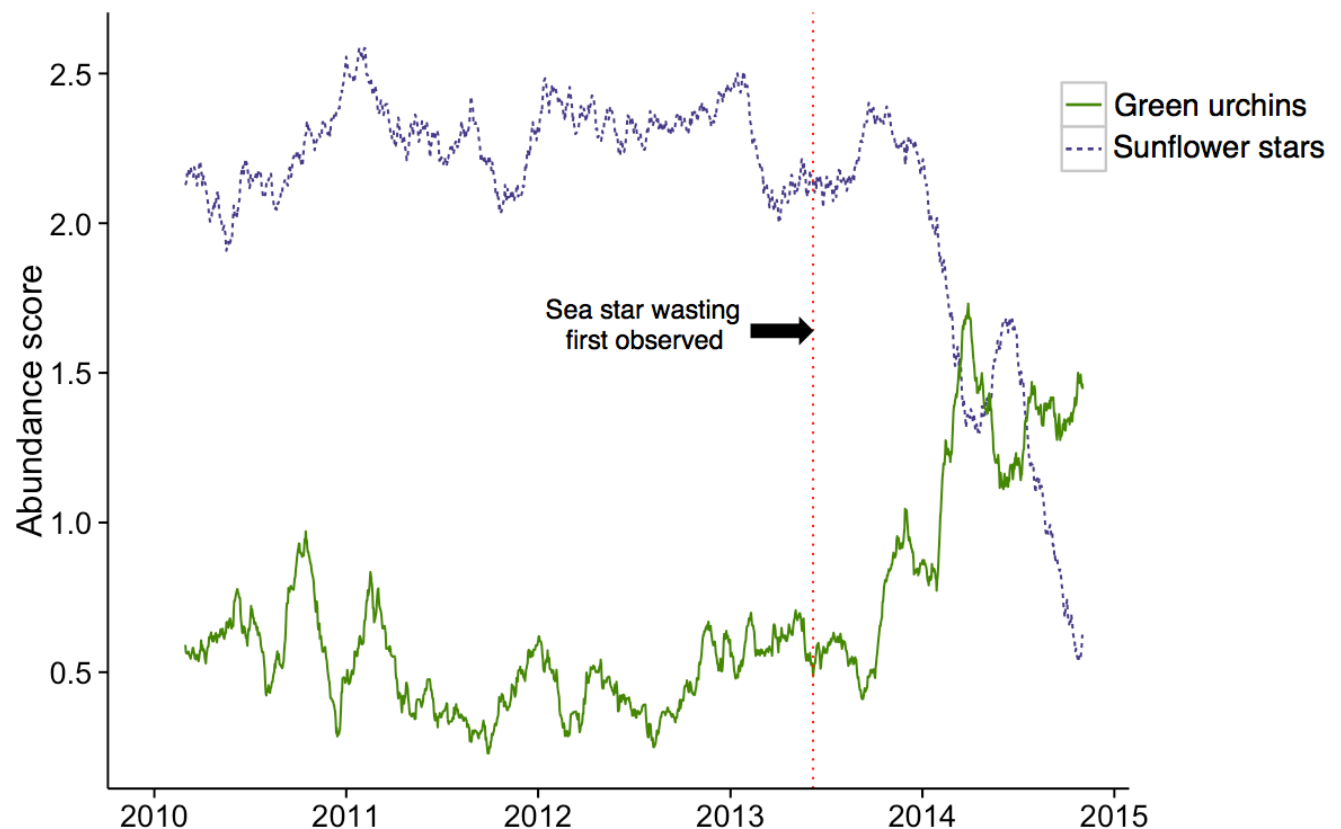| Taxon	Species or genera included in taxon	Mean density (SD)			
		Before		After	
Invertebrates					
Sunflower star	*Pycnopodia helianthoides* Brandt, 1835	6.4	(11.4)	0.9	(3.3)
Green urchin	*Strongylocentrotus droebachiensis* O. F. Müller, 1776	18.3	(41.0)	77.2	(157.4)
Red urchin	*Strongylocentrotus 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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Figure 2. **Mass mortality of sunflower stars.** Mean site-specific abundances per m^2 of
sunflower stars on rocky reefs in Howe Sound, British Columbia, before and after the 2013 mass
mortality of sea stars. Each line/colour represents a different site; overlapping points are slightly
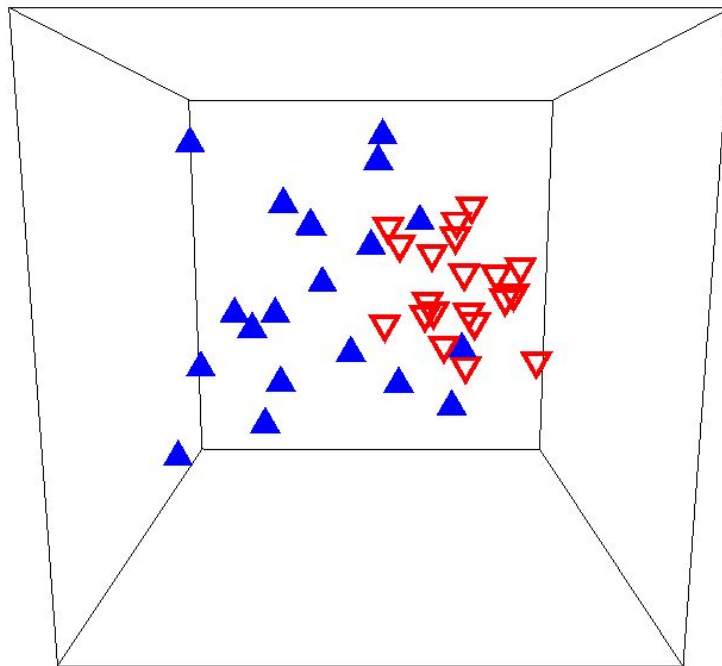offset for clarity. n = 20 sites.

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344 **Figure 3**. **Sunflower star and green sea urchin abundance trajectories.** Sixty-day running
345 average abundance scores for green sea urchins (*Strongylocentrotus droebachiensis*; green solid
346 line) and sunflower stars (*Pycnopodia helianthoides*; purple dashed line) recorded in REEF
347 surveys from January 2010 to November 2014 in Washington and British Columbia (n = 1568
348 surveys). The vertical red dotted line indicates the date of the first recorded observation of sea
349 star wasting syndrome (7 June 2013), which was on the Olympic coast of WA.
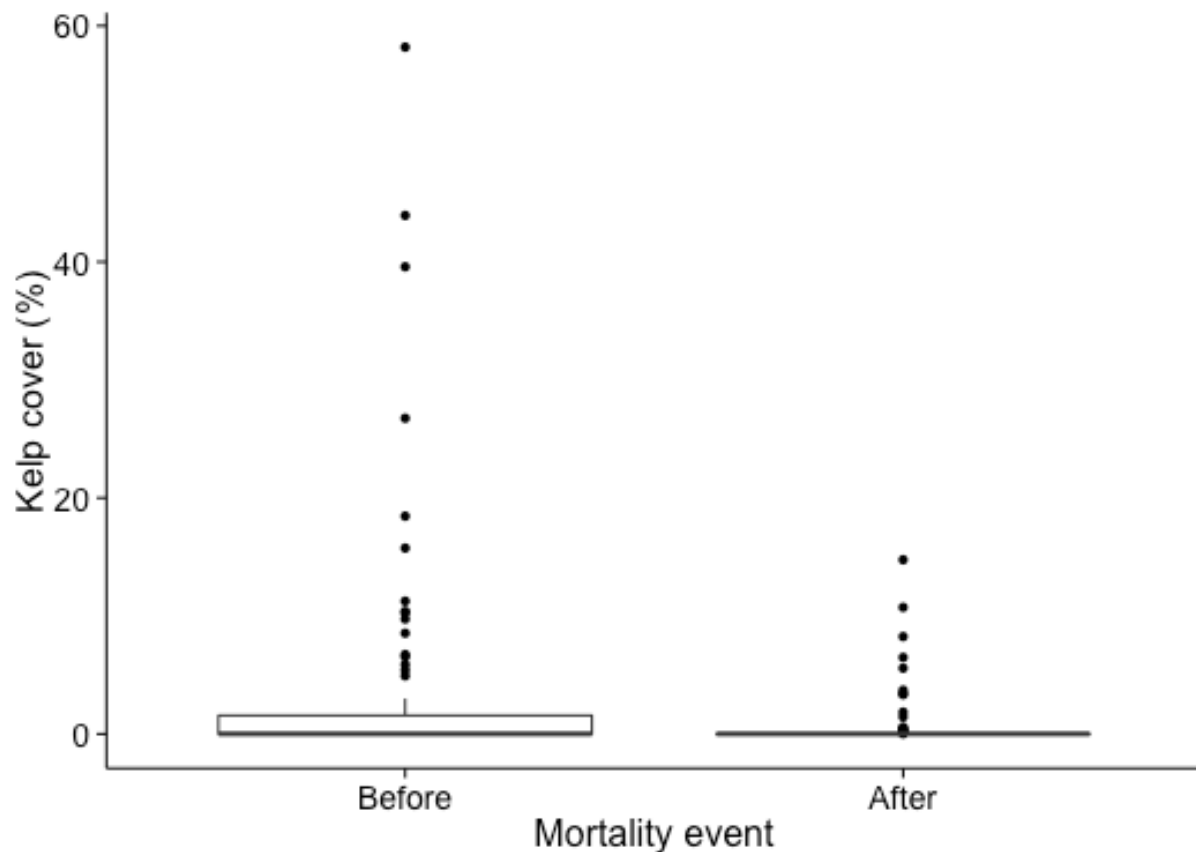
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Figure 4. **Rocky reef species assemblages before and after sea star mortality.**
Multidimensional scaling plot of benthic community composition on rocky reefs before (blue
triangles) and after (inverted red triangles) the 2013 sea star mass mortality event in Howe
Sound, British Columbia. The analysis included 18 fish and invertebrate taxa at 20 sites,
surveyed both in 2009/2010 and 2014.   The associated stress value (0.13) suggests some
distortion in the multivariate representation of the data.

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

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

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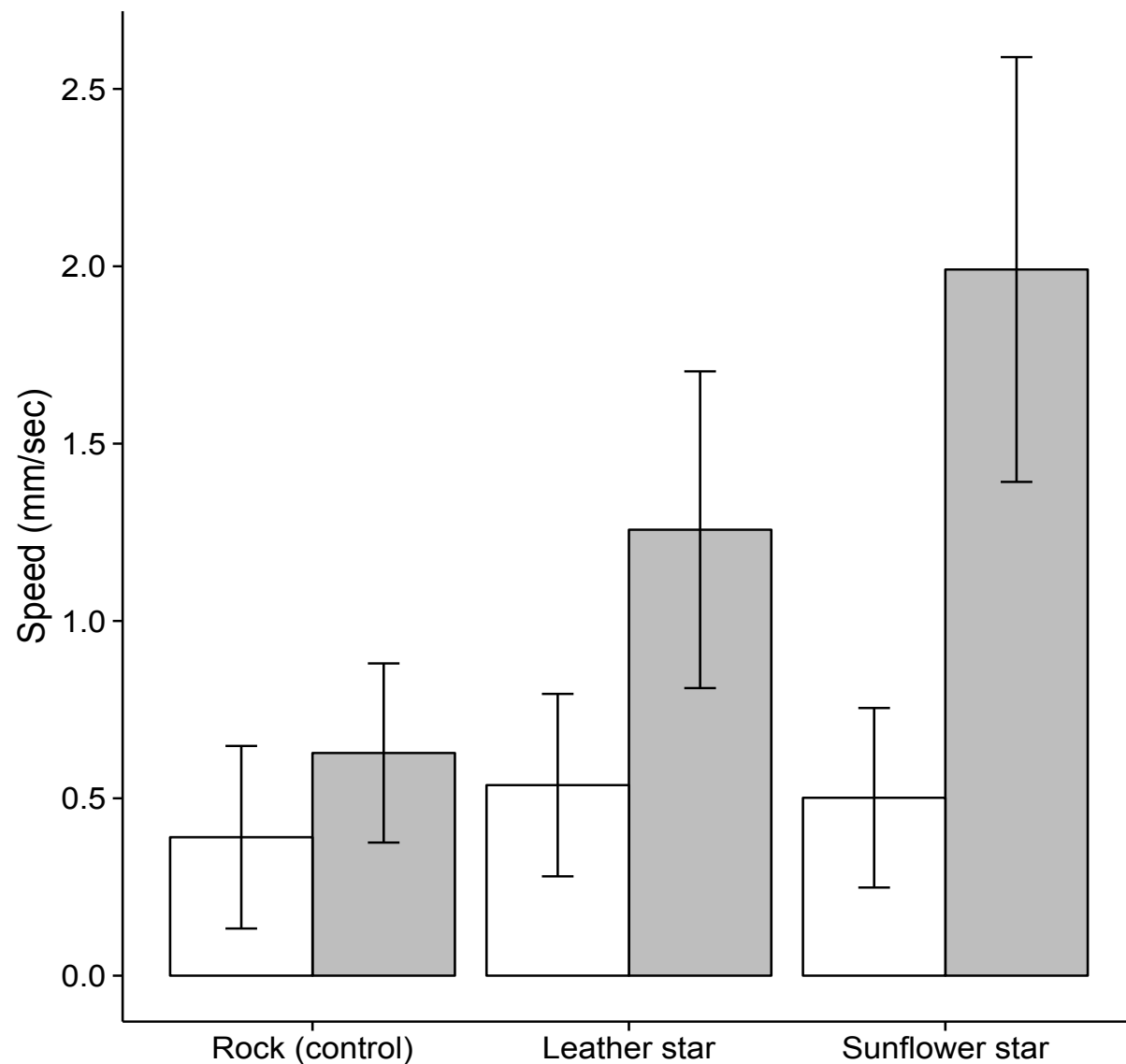
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Figure 5. **Change in kelp cover after sea star mortality.** Percent cover of kelp on rocky reefs
in Howe Sound, British Columbia, on 80 transects before and after the mass mortality of sea
stars in 2013. The thick, horizontal black line represents the median values, while the top and
bottom of the box represent the upper and lower quartiles, respectively. Outliers are indicated by
dots. The dominant kelp was the sea colander kelp, *Agarum fimbriatum*.

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376 **Figure 6**. **Escape speeds of green urchins following tactile stimuli.** Mean locomotion speed of
377 green urchins before (white bars) and after (grey bars) exposure to one of three tactile stimuli.
378 Sample sizes were n = 13 for the control, n = 12 for the leather star treatment, and n = 11 for the
379 sunflower star treatment. Error bars represent 95% confidence intervals.

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380 **Table 3**. **Parameter estimates of green urchin speed model.** Results of linear regression
381 evaluating the effect of stimulus type and urchin size on the change in crawling speed of urchins
382 when exposed to tactile contact from a potential predator (LM: $F_{4,32} = 14.60$, Adj. $R^2 = 0.73$, p <
383 0.0001).

Variable	Estimate	Std error	t value	p value
Stimulus type				
Leather star	0.95	0.34	2.80	0.009
Rock (control)	0.51	0.39	1.30	0.20
Sunflower star	1.75	0.29	4.56	< 0.0001
Urchin size	-0.006	0.008	-7.68	0.45

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