Long-term study of behaviors of two cohabiting sea urchin species, *Mesocentrotus nudus* and *Strongylocentrotus intermedius*, under conditions of high food quantity and predation risk *in situ*

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Background. In the predator–sea urchin–macrophyte trophic cascade, the ecological effect of sea urchins as grazers depends both on their density and the changes in foraging activity, which are influenced by various disturbing factors. However, the complete duration of the alarm reactions of echinoids has not been studied until now. Here, we tested a hypothesis that two cohabiting sea urchins, *Mesocentrotus nudus* and *Strongylocentrotus intermedius*, which differ morphologically, might display different behavioral responses to high hydrodynamic activity and predation. **Methods.** We used continuous time-lapse video recording to clarify behavioral patterns of *M. nudus* and *S. intermedius* in presence of a large quantity of food (the kelp *Saccharina japonica*) but under different weather conditions and different types of predation threat: (1) calm weather conditions, (2) stormy weather conditions, (3) predation risk associated with the presence of several sea star species, and (4) predation risk associated with an alarm stimulus (crushed conspecifics or heterospecifics). Three separate video recording experiments (134 days in total) were conducted under field conditions. Video recording analysis was performed to determine the number of specimens of each sea urchin species in the cameras' field of view, size of sea urchins' groups, movement patterns and the duration of the alarm responses of both sea urchin species. **Results.** We showed that in the presence of kelp, *M. nudus* and *S. intermedius* exhibited both similar and different behavioral responses to hydrodynamics and predation threat. Under calm weather, movement patterns of both echinoids were similar but *M. nudus* exhibited the higher locomotion speed and distance travelled. Furthermore, *S. intermedius* but not *M. nudus* tended to group near the food substrate. The stormy weather caused a sharp decrease in movement activity followed by escape response in both echinoids. Six starfish species failed to predate on healthy sea urchins of either species, and only a few attacks on ailing

S. intermedius specimens were successful. The alarm response of *S. intermedius* lasted approximately 90 h and 20 h for starfish attacks on ailing conspecifics and for simulated attacks (crushed conspecifics or heterospecifics), respectively, and involved several phases: (1) flight response, (2) grouping close to the food, (3) leaving the food, and (4) return to the food. Phase 3 was the more pronounced in a case of starfish attack. *M. nudus* only responded to crushed conspecifics and exhibited no grouping behavior but displayed fast escape (during 4 h) and prolonged (up to 19 days) avoidance of the food source. This outcome is the longest alarm response reported for sea urchins. **Discussion.** The most interesting finding is that two cohabiting sea urchin species, *M. nudus* and *S. intermedius*, display different alarm responses to predation threat. Both alarm responses are interpreted as defensive adaptations against visual predators.

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4

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12

13 ## ABSTRACT

14 **Background.** In the predator–sea urchin–macrophyte trophic cascade, the ecological effect of

15 sea urchins as grazers depends both on their density and the changes in foraging activity, which

16 are influenced by various disturbing factors. However, the complete duration of the alarm

17 reactions of echinoids has not been studied until now. Here, we tested a hypothesis that two

18 cohabiting sea urchins, *Mesocentrotus nudus* and *Strongylocentrotus intermedius*, which differ

19 morphologically, might display different behavioral responses to high hydrodynamic activity and

20 predation. **Methods.** We used continuous time-lapse video recording to clarify behavioral

21 patterns of *M. nudus* and *S. intermedius* in presence of a large quantity of food (the kelp

22 *Saccharina japonica*) but under different weather conditions and different types of predation

23 threat: (1) calm weather conditions, (2) stormy weather conditions, (3) predation risk associated

24 with the presence of several sea star species, and (4) predation risk associated with an alarm

25 stimulus (crushed conspecifics or heterospecifics). Three separate video recording experiments

26 (134 days in total) were conducted under field conditions. Video recording analysis was

27 performed to determine the number of specimens of each sea urchin species in the cameras' field

28 of view, size of sea urchins' groups, movement patterns and the duration of the alarm responses

29 of both sea urchin species. **Results.** We showed that in the presence of kelp, *M. nudus* and *S.*

30 *intermedius* exhibited both similar and different behavioral responses to hydrodynamics and

31 predation threat. Under calm weather, movement patterns of both echinoids were similar but *M.*

32 *nudus* exhibited the higher locomotion speed and distance travelled. Furthermore, *S. intermedius*

33 but not *M. nudus* tended to group near the food substrate. The stormy weather caused a sharp

34 decrease in movement activity followed by escape response in both echinoids. Six starfish

35 species failed to predate on healthy sea urchins of either species, and only a few attacks on ailing

36 *S. intermedius* specimens were successful. The alarm response of *S. intermedius* lasted

37 approximately 90 h and 20 h for starfish attacks on ailing conspecifics and for simulated attacks

38 (crushed conspecifics or heterospecifics), respectively, and involved several phases: (1) flight

39 response, (2) grouping close to the food, (3) leaving the food, and (4) return to the food. Phase 3

40 was the more pronounced in a case of starfish attack. *M. nudus* only responded to crushed

41 conspecifics and exhibited no grouping behavior but displayed fast escape (during 4 h) and

42 prolonged (up to 19 days) avoidance of the food source. This outcome is the longest alarm

43 response reported for sea urchins. **Discussion.** The most interesting finding is that two cohabiting

44 sea urchin species, *M. nudus* and *S. intermedius*, display different alarm responses to predation

45 threat. Both alarm responses are interpreted as defensive adaptations against visual predators.

46

47 **Subjects** Animal behavior, Ecology, Marine Biology, Zoology

48 **Keywords** Predator–prey interactions, Sea urchin behavior, Chemical alarm cues, Alarm

49 response duration, Grouping behavior, Escape response, Defensive adaptation

50

51 **INTRODUCTION**

52 The need to forage and the need to avoid predation are considered as the most important

53 evolutionary forces in the selection of morphological and behavioral characteristics of animals

54 (*Lima, 1998*; *Lima & Dill, 1990*). Sea urchins (class Echinoidea), which have a long evolutionary

55 history and a worldwide distribution, have developed a number of defense mechanisms against

56 predators promoting survival and reproduction. Possessing a locomotion speed that is

57 significantly inferior to that of many potential predators, sea urchins have a hard, internal

58 calcium carbonate skeleton (test) covered by spines. Some species are additionally protected by

59 pedicellaria with poison glands (*Jensen, 1966*; *Cannone, 1970*). Sea urchins exhibit mostly

60 nocturnal activity for both the movement/migration (*Crook et al., 2000*; *Dance, 1987*;

61 *Hasegawa, 2014*; *Hereu et al., 2005*) and spawning (*Zhadan et al., 2018*), appearing to be an
62 adaptation for enemy avoidance (*Fricke, 1973*).

63   Sea urchins lack image-forming eyes (*Ullrich-Lüter et al., 2011*); therefore, chemical
64 senses are an essential source of information on predation risk. The emergence of chemical cues
65 (substances emitted by predators and/or physically damaged con- or heterospecific prey) can
66 cause various behavioral reactions in sea urchins: 'cryptic behavior', i.e. hiding in a crack or hole
67 (*Fricke, 1973*; *Kintzing & Butler, 2014a*; *Spyksma et al., 2017*); 'associative behavior', i.e.
68 aggregation into dense groups (*Bernstein et al., 1983*; *Hagen et al., 2002*; *Kintzing & Butler,*
69 *2014a*), and 'dispersion behavior', i.e. escape (*Hagen et al., 2002*; *Urriago et al., 2011*; *Vadas &*
70 *Elner, 2003*). For some species, it has been shown that the emergence of a chemical signal from
71 predator presence was associated with a decrease in the intensity of feeding (the so-called 'fear
72 effect') (*Freeman, 2006*; *Kintzing & Butler, 2014b*; *Matassa, 2010*; *Spyksma et al., 2017*). The
73 changes in behavior, including a decrease in foraging activity, were more pronounced in young
74 individuals (*Clemente et al., 2013*; *Freeman, 2006*), and these behaviors may not occur in large
75 well-armed adults (*Parker & Shulman, 1986*; *Wirtz & Duarte, 2012*).

76   Being consumers of macrophytes, sea urchins severely affect the structure of coastal
77 benthic communities (see for review *Estes & Duggins, 1995*; *Mann, 1982*; *Steneck, 2013*). There
78 is growing evidence that in the predator–prey–plant trophic cascade, the ecological effect can be
79 not only prey density-mediated (i.e., associated with the direct influence of predators on prey
80 number) but also prey behavior-mediated (i.e., associated with inhibition of prey foraging
81 activity by predators) (*Abrams, 1995*; *Dill et al., 2003*; *Pearson, 2010*; *Schmitz et al., 2004*;
82 *Trussell et al., 2006*; *Werner & Peacor, 2003*), prompting the suggestion that the grazing effect
83 of sea urchins on macrophytes' abundance may depend on the duration of their alarm response.
84 However, the complete duration of the alarm responses of sea urchin species to waterborne
85 chemical signals emitted either from other prey (conspecific or non-conspecific), the predator
86 itself, or both has remained unknown until now. Most studies of sea urchins' responses to
87 chemical alarm signals have been conducted under laboratory conditions (*Chivers & Smith,*
88 *1998*; *Hagen et al., 2002*; *Kintzing & Butler, 2014a, 2014b*; *Manzur & Navarrete, 2011*;
89 *Matassa, 2010*; *Spyksma et al., 2017*), and field experiments conducted under conditions of calm
90 water and under unidirectional water flows (*Parker & Shulman, 1986*; *Snyder & Snyder, 1970*;
91 *Vadas & Elner, 2003*; *Wirtz & Duarte, 2012*; but see *Manzur & Navarrete, 2011*; *Urriago et al.,*

92 *2011*). All these studies have focused on the initial stage of sea urchins' alarm response, whereas

93 the entire sequence of behavioral events in sea urchins in their natural habitat, starting from the

94 onset of the alarm reaction to its complete extinction, has not been investigated.

95 The present study was undertaken to identify the temporal and spatial parameters of the

96 complete alarm reactions in two species of sea urchins, *Strongylocentrotus intermedius* (A.

97 Agassiz, 1864) and *Mesocentrotus nudus* (A. Agassiz, 1864) (= *Strongylocentrotus nudus*) under

98 conditions of food abundance using continuous time-lapse video recording (during 1.5–2 mo) of

99 animal behavior in the field. These echinoids are abundant in coastal environments of the

100 northwestern Pacific; however, their ranges overlap only partially, in the southern part of the Sea

101 of Japan washing the coasts of Korea, Japan and the Primorye region of Russia, where the lower

102 and upper geographical boundaries of *S. intermedius* and *M. nudus* occur, respectively (see for

103 review *Agatsuma, 2013a, 2013b*; *Kafanov & Pavlyuchkov, 2001*). In the Sea of Japan, these sea

104 urchins are common species in benthic communities inhabiting hard substrates at a depth of up to

105 25 m (*Kafanov & Pavlyuchkov*, 2001). Morphologically, *S. intermedius* and *M. nudus* differ from

106 each other in respect to the color (brownish-black in *M. nudus* and brownish-grey in *S.*

107 *intermedius*) and spine length and hardness (hard sharp spines of up to 30 mm in *M. nudus* and

108 less hard spines of up to 8 mm in *S. intermedius*). We hypothesized that these sea urchin species,

109 presumably sharing an evolutionary history but differing morphologically, might display

110 different behavioral responses to various disturbing factors such as high hydrodynamic activity

111 and predation.

112

113 **MATERIALS AND METHODS**

114 **Study areas, sea urchins and video recording experimental setup**

115 Field experiments were conducted in the northwestern Sea of Japan: Kievka Bay (42.830° N,

116 133.691° E) and Alekseev Bay (42.981° N, 131.730° E). Kievka Bay, with a width of 8.3 km and

117 a length of 3.3 km, is typical of the southeastern coast of the Primorye region of Russia. Being

118 open to prevailing summer winds from the southeast to the southwest, the bay is characterized by

119 high wave activity. The studies here were performed at a depth of 6 m on relatively flat bedrock

120 surrounded by large stones. Alekseev Bay has a width of 0.8 km and a length of 1.3 km, and

121 wave activity here is high only under winds from the north, a phenomenon that is quite rare in

122 summer. The studies here were performed at a depth of 2 m on a flat bottom covered with

123 medium sized gravel. Within both bays, water depth is weakly influenced by tidal activity: an
124 irregular semidiurnal tide has a maximum amplitude of approximately 50 cm (*Zhadan et al.,*
125 *2018*).

126   In both bays, the density of *S. intermedius* and *M. nudus* in the areas adjacent to the
127 experimental installations was 1 to 2 ind. m^{-2} (*Zhadan et al., 2018*). In addition, to balance the
128 density of the species in the study areas, approximately 300 specimens of *S. intermedius* were
129 collected in the bays in a radius of 100–200 m from the experimental installations and placed at a
130 distance of 10–20 m from them. The video observation of sea urchins' behaviors was performed
131 with TLC200 Pro (Brinno Incorporated) time-lapse video cameras mounted on steel stanchions
132 approximately 1 m above the bottom. Time-lapse videos were taken in 1 min intervals at a
133 resolution of 1280 × 720 pixels. The cameras were installed in such a way that the size of the
134 field of view was approximately 1.5 × 1.0 m. During the night, the cameras' fields of view were
135 illuminated by LED lamps (1 W) which were synchronized with the cameras by flash LED
136 indicator. The illumination duration was 1 s.

137   To attract sea urchins in the field of view of video cameras, flat mesh containers filled
138 with the kelp *Saccharina japonica* (Laminariales, Phaeophyta; hereafter simply laminaria) were
139 used. It is known that laminaria stimulates foraging activity of *M. nudus* and *S. intermedius*
140 (*Machiguchi, 1987*; *Machiguchi et al., 1994*). The containers, each composed of 2 steel frames
141 and mesh stretched on them, 1.1 × 0.75 × 0.01 m in size, were filled with laminaria and placed in
142 the cameras' field of view. Each container (hereafter feeder) contained approximately 30 kg of
143 the kelp. Sea urchins of both species themselves found the feeders and populated them within 2–
144 3 days. All sea urchins that were in the cameras' field of view on all the feeders were taken into
145 account for further video analysis. The steel frames of the containers were pressed down by
146 stones with a diameter of 20–40 cm to protect against wave activity.

147   The indicator of the onset of sea urchins' alarm response was the escape or redistribution
148 of sea urchins in the field of view of the cameras, and the indicator of the end of the alarm
149 reaction was the return of sea urchins to their original spatial distribution pattern. Such a design
150 of the experiments allowed us to clarify (1) the features of sea urchins' behavior in the presence
151 of abundant palatable food and under different weather conditions, (2) the frequency of predator
152 attacks under natural conditions, and (3) the temporal patterns of the complete behavioral
153 response of sea urchins to a natural predator attack and simulated predator attack (crushed

154   conspecifics or heterospecifics) in sea urchin species with different morphological

155   characteristics.

156

157   **Video recording analysis**

158   The recorded videos were viewed frame by frame. We counted the numbers of specimens of

159   each sea urchin species in the each camera field of view both in the absence and in the presence

160   of disturbing factors. To access the grouping behavior of the sea urchins, we calculated the mean

161   group size as the ratio of the total number of individuals in the cameras' field of view to the

162   number of associations (*Hagen & Mann, 1994*). Following *Vadas et al.* (*1986*), we distinguished

163   between sea urchin associations and aggregations. Each group of sea urchins in two-dimensional

164   groupings, including individuals suspected of being in tactile contact (there was no visible space

165   between them) and single individuals, was considered a separate association.

166   To determine the mean group size for both sea urchin species, the video frames were

167   randomly selected over the periods of calm weather. Only the video frames showing not more

168   than 30 specimens (43 frames for each species) were chosen for the mean group size calculation

169   in order to avoid crowding effects when sea urchins might be in tactile contact due to their high

170   density on the feeders. Under such a limitation, no groups of 3 or more sea urchins in cohesive

171   three-dimensional groupings (aggregations, according to *Vadas et al., 1986*) were observed in

172   our study.

173   Sea urchins' movement was analyzed using the free software, 'Tracker', for video

174   analysis (www. open sourcephysics.org/items/detail.cfm?ID=7365). The cell size (2×2 cm) of

175   the feeder mesh was used as a scale. We tracked and measured sea urchin displacement with an

176   interval of 1 min. Following *Lauzon-Guay et al.* (*2006*), we defined a step as the distance

177   between two successive positions of the sea urchin (1 min apart), a stop as an interval when sea

178   urchin remains stationary during at least 1 min (2 successive frames) and a move as the distance

179   between two successive stops which can be composed of one or more steps. The mean

180   locomotion speed was calculated as total distance passed divided by total time.

181

182   **Long-term video recording of sea urchins' behavior**

183   We conducted 3 separate video recordings in Kievka Bay (during 51 d in August–September

184   2014 and 37 d in August–October 2015) and in Alekseev Bay (during 46 d in July–September

185   2016). In these experiments, 4 cameras were used, and 4 feeders were arranged in pairs in such a

186   way that the direction of the tidal currents coincided with the direction of the long sides of the

187   feeders. The distances between the long sides of the feeders were 0.4 m, and the distance

188   between the pairs of the feeders was 2 m. The feeders were replaced every 15–20 days (see Fig.

189   1) when approximately 80% of laminaria was consumed by sea urchins. Sea urchins were

190   carefully transferred from the old feeders to the feeders with fresh laminaria. It took

191   approximately 5 min to change one feeder.

192   We tested for behavioral differences between *M. nudus* and *S. intermedius* in presence of

193   a large quantity of palatable food but under different weather conditions and different types of

194   predation threat: (1) under calm weather conditions, (2) under stormy weather conditions, (3)

195   under predation risk associated with the presence of several sea star species, and (4) under

196   predation risk associated with simulated predator attack (crushed individuals of *M. nudus*). The

197   numbers of specimens of each sea urchin species were counted per each 6 h of observations

198   throughout all 3 long-term experiments, both in the absence and in the presence of disturbing

199   factors (see Table S1 for original data).

200   The stormy periods were determined by several signs which are clearly visible on video

201   recordings: (1) the oscillation of the feeder surface and (2) the increase in suspended particles

202   movement and water turbidity. In addition, an increase in wave height during storm was recorded

203   by the depth sensor of a multi-parameter RBRXRX-620 datalogger (Sea and Land Technologies

204   Pte, Singapore) which measured the sea level every 10 min (see for example Fig. S1).

205   We compared movement parameters (the number and length of the steps and moves, the

206   entire displacement, the number and duration of the stops, the entire stationary period and mean

207   speed) of both sea urchin species under calm and stormy weather conditions. For this purpose,

208   the distances traversed by randomly selected 10 sea urchins of each species during 240 min

209   before the storm and in the beginning of the storm (Fig. S1) were tracked and measured with an

210   interval of 1 min (see Tables S2 and S3 for raw data). Further tracking showed that a half of

211   observable sea urchins left the cameras' field of view during approximately 10 h after the

212   beginning of measurements. Locomotion speed during escape was calculated as total distance

213   passed during the period from the beginning of active movement of the sea urchin to its

214   disappearance from the field of view divided by the total time of escape (see Tables S2 and S3

215   for raw data).

216   Predation risk was associated with several species of sea stars that were present

217   simultaneously with sea urchins on the feeders or with simulation of predation attack (crushed

218   individuals of *M. nudus*). To determine behavioral responses of *S. intermedius* to starfish attacks

219   on the conspecifics which took place on September 5 and 21, 2015 (see Table S1), we measured

220   the distances of 13 sea urchins closest to the site of the attack (i.e., their entire displacement)

221   during approximately100 h after the beginning of the attack with the intervals from 2 h to 4–16

222   h. For these periods, the total numbers of *S. intermedius* specimens as well as the individuals of 2

223   starfish species, *P. pectinifera* and *L. fusca*, which were in contact with the prey, were counted.

224   Our pilot experiments showed that *M. nudus* rapidly left the area of the bottom where

225   conspecifics were crushed and avoided it for a long time. There was no similar reaction to

226   crushed *S. intermedius* specimens. Furthermore, *S. intermedius* exhibited no visible responses

227   both to crushed conspecifics and heterospecifics. Therefore, we focused on the study of the

228   phenomenon of *M. nudus* response to crushed conspecifics. We compared how quickly *M. nudus*

229   populated the feeders in the presence and in the absence of crushed conspecifics. In the first case,

230   10 *M. nudus* specimens with test diameters of 50–60 mm were crushed in the middle between the

231   pairs of the feeders when *M. nudus* were present on them (5 experiments in total; we did not

232   include the data of 1 experiment into statistical analysis because it might be influenced by the

233   experiment on storm imitation conducted 3 days earlier). In the second case, all *M. nudus*

234   specimens were removed from the cameras' fields of view and transferred to a distance of

235   approximately 10 m from the feeders (7 experiments in total; we did not include the data of 3

236   experiments into statistical analysis because they might be influenced by the previous or next

237   storm). In both cases, we estimated the temporal dynamics of the numbers of sea urchins (with

238   time intervals of 1 h and 6 h in the first and second cases, respectively).To test our assumption

239   that the storm contributes to the return of sea urchins *M. nudus* to the feeders, two experiments

240   mimicking stormy conditions were conducted several days (6 and 12 in 2014 and 2016,

241   respectively, see Table S1) after *M. nudus* left the feeders in response to crushed conspecifics.

242   The feeders were removed, and several scuba divers actively swam in the area of the

243   experimental installation. After that, the feeders with fresh laminaria were placed in their original

244   place. These procedures took 30–40 min. The average sea urchin numbers for 1 day before

245   crushing and 2 days after storm imitation were determined.

246

247 **Short-term video recording of sea urchins' behavior**

248 A set of experiments, each with a duration of approximately 6 d, was conducted in Alekseev Bay

249 from July–September 2016. The experiments were designed to elucidate behavioral patterns of

250 *M. nudus* and *S. intermedius* in response to an alarm stimulus (crushed conspecifics or

251 heterospecifics). In each of these experiments, 2 video cameras and 2 feeders were used. Two

252 days after the feeder placement, when 30–40 sea urchins of both species were gathered on the

253 feeder surface, 5 specimens of *S. intermedius* or *M. nudus* were crushed at a distance of 20 cm

254 from the feeder's short side. Three to four days after simulation of the predation threat, all the

255 sea urchins were removed from the cameras' field of view, and the experiment was repeated on

256 the other feeder with fresh laminaria and with sea urchins not previously used. In total, 4

257 experiments of this kind were carried out with each of sea urchin species used as simulated prey.

258 During 22 h before and 55 h after the treatment, we estimated the numbers of sea urchins as well

259 as the temporal dynamics of the mean group size (with time intervals from 1 to 4 h) with one

260 exception: we failed to assess the temporal dynamics of the mean group size of sea urchins *M.*

261 *nudus* in response to crushed conspecifics due to fast escape of *M. nudus*.

262   To determine movement patterns of sea urchins in response to crushed con- and

263 heterospecifics, we measured step length and locomotion speed before and after treatment.

264 Additionally, we measured with intervals of 6–9 min the distances of 10 sea urchins closest to

265 the site where simulated attack was performed. The exception was a case with response of *M.*

266 *nudus* to crushed conspecifics because sea urchins rapidly left the cameras' field of view.

267 Duration of sea urchin tracking was from 200 to 1200 min due to the species specific response of

268 sea urchins to the alarm signal.

269

270 **Statistical analysis**

271 To analyze the species-specific and treatment-specific differences in *M. nudus* and *S. intermedius*

272 behavior, the data sets on the numbers of sea urchins, mean group sizes as well as sea urchins'

273 movement parameters were formed and tested for normal distribution (D'Agostino and Pearson

274 omnibus normality test, $P < 0.05$). Normally distributed data were further analyzed by parametric

275 tests (unpaired *t*-test, 1-way ANOVA). In a case of abnormally distributed data, non-parametric

276 tests were used (Mann-Whitney test, Kruskal–Wallis test followed by Dunn's multiple

277 comparisons). To analyze the temporal dynamics of the numbers of both sea urchins in the

278   experiments on the response to crushed conspecifics or heterospecifics as well as in the

279   experiments on the repopulation the feeders by sea urchins *M. nudus* after their removal, linear

280   or nonlinear regression (curve fit) were used. All statistical analyses were run using GraphPad

281   Prism v. 6.0.The details regarding raw data and statistics are presented in the Supplementary

282   Materials. In all the Figures, the data relating to *M. nudus* is in blue color and the data relating to

283   *S. intermedius* is in red color.

284

285   **Procedural controls**

286   In our *in situ* experiments we did not use the procedural controls which are usuallyapplied in the

287   experiments with animals contained in tanks or cages, such as 'food presence – food absence',

288   'animal treatment/manipulation – imitation of animal treatment/manipulation'. First, both sea

289   urchin species exhibited clear food search behavior, and the absence of food strongly stimulated

290   them to migrate to the place where the food is present. Second, we minimized manipulations in

291   our experiments that could affect the results and conclusions. A negligible displacement of water

292   masses near a feeder associated with sea urchins' crushing as well as the swimming of the diver,

293   who served the installation, above the feeder did not cause escape reactions of both sea urchin

294   species similar to those during storm. The experiments mimicking stormy conditions were

295   conducted in the absence of the feeders. Both in long-term and short-term experiments, we used

296   short-term periods (from 1 to 3 days) just before the treatments as proper procedural controls,

297   and compared quantitative parameters (sea urchins' number and mean group size) obtained for

298   these periods with those obtained for the periods after the treatments (storms, starfish attacks or

299   crushed sea urchins).

300

301   **RESULTS**

302   **General characteristics of sea urchins' behavior**

303   During the recording periods in 2014, 2015 and 2016 (134 days in total), 24 ± 25 (mean $\pm$ SD) of

304   *M. nudus* specimens and 78 ± 42 of *S. intermedius* specimens were in the field of view of the

305   video cameras (Fig. 1A–C, Table S1). During the periods without any treatment (storms, *M.*

306   *nudus* specimens removal or crushing, starfish attacks), the numbers of *M. nudus* and *S.*

307   *intermedius* were higher, 50 ± 15 and 85 ± 42, respectively. The size composition of the two

308   echinoid species was slightly different. Only large adults of *M. nudus* with a test diameter of 62.2

309 ± 7.5 mm (mean ± SD) were present in the cameras' field of view, whereas among the adult *S.*

310 *intermedius* with test diameters from 37 to 74 mm (64.4 ± 4.3 mm), there was a small number

311 (up to 12%) of juveniles with test diameters of 10–15 mm. On the surface of the feeders, both sea

312 urchin species were relatively evenly distributed in one plane and did not form aggregates (three-

313 dimensional groups); however, they formed associations (dense two-dimensional groups).

314 Grouping behavior in *S. intermedius* was expressed to a greater extent than in *M. nudus*: when

315 from 14 to 25 of individuals were present on the surface of the feeders, the mean group size of *S.*

316 *intermedius* was approximately 2 times higher than that of *M. nudus* (2.27 ± 0.4 versus 1.12 ±

317 0.1, Mann–Whitney test, U = 0, *P* < 0.0001; see Table S4 for raw data and statistics).

318   Both sea urchin species displayed so called 'covering behavior' but it was more

319 pronounced in *S. intermedius* than in *M. nudus*. The debris covering sea urchin aboral surfaces

320 consisted mainly of pieces of the algae such as *Ulva fenestrata* Ruprecht, 1840 and *Desmarestia*

321 *viridis* (O.F. Müller) J.V. Lamouroux, 1813 in June–July, and seagrass *Zostera marina* L. in the

322 end of September. During these periods, from 87 to 100% of *S. intermedius* individuals were

323 decorated compared to from 0 to 18% for *M. nudus*.

324

325 **Behavioral responses of sea urchins to increased wave activity**

326 During the storms, the number of sea urchins of both species in the cameras' field of view

327 sharply decreased (Fig. 1A–C, see Table S1 for raw data). On the eve of the storm periods, there

328 were 54 ± 9 (mean ± SD) of *M. nudus* specimens and 76 ± 37 of *S. intermedius* specimens

329 whereas during the storms, the average numbers for both species (26 ± 15 and 34 ± 21 for *M.*

330 *nudus* and *S. intermedius*, respectively) were significantly lower (Fig. 2, see Tables S5, S6 for

331 raw data and statistics). Approximately one day after the storm, sea urchins of both species

332 restored their numbers on the feeders (Fig. 1A–C, Fig. 2, Tables S5, S6).

333   Both sea urchin species exhibited similar patterns of movement under conditions of calm

334 weather. The average numbers of moves and stops were not significantly different between

335 species, however, the moves of *S. intermedius* were shorter and consisted of higher number of

336 shorter steps whereas the locomotion speed and entire distance travelled were significantly

337 higher in *M. nudus* (Tables 1 and 2, see also Table S7 for interspecies comparison).

338   Both sea urchin species responded to increased wave activity by a sharp decrease in the

339 number of steps, length of one move and entire distance travelled (Tables 1 and 2, see also Table

340 S7 for interspecies comparison). At the same time, the duration of one stop increased

341 approximately 3 and 4 times in *S. intermedius* and *M. nudus*, respectively, and the average

342 proportions of time sea urchins spent stationary were 76 and 91%, respectively, against 33 and

343 54% under calm weather. The average locomotion speeds during storm conditions were as low

344 as 0.07 and 0.03 cm min^{-1} in *S. intermedius* and *M. nudus*, respectively. During escape, sea

345 urchin speeds sharply increased and averaged 0.82 ± 0.19 (range of 0–7.02) cm min^{-1} in *S.*

346 *intermedius* and 1.76 ± 0.30 (range of 0–11.81) cm min^{-1} in *M. nudus*, these were, respectively,

347 4.3 and 5.5 times higher than those under calm weather (see Tables S2 and S3 for raw data).

348

349 **Behavioral response of *S. intermedius* to starfish attack**

350 Over 3 periods of our studies, only three cases of the attacks of the sea stars (*Patiria pectinifera*

351 (Muller & Troschel, 1842) and *Lethasterias fusca* Djakonov, 1931) on single individuals of *S.*

352 *intermedius* were recorded (5, 10 and 21 September, 2015, see Table S1) whereas no attacks of

353 predators on sea urchins *M. nudus* were observed. Judging by the presence of injuries and

354 abnormal behavior (low motor activity and body position with the oral surface upward), only

355 sick or damaged individuals of *S. intermedius* have been attacked by sea stars (Fig. S2A). It is

356 possible that the appearance of damaged S. *intermedius* specimens that have lost a significant

357 part of the spines was due to typhoon 'Goni', which occurred on August 27–29, 2015 in the

358 northwestern Sea of Japan.

359 On September 10, sea urchin reaction to a predator attack could not be traced due to low

360 visibility caused by the storm. The behaviors of sea urchins *S. intermedius* during starfish attacks

361 on September 5 and 21, 2015 were slightly different. On September 5, one *S. intermedius*

362 specimen was consumed by 1–5 individuals of *P. pectinifera* and 1 individual of *L. fusca* in the

363 centre of one of the 4 feeders for 45 h (Fig. 3A, see also Fig. S2). Within 2 h after the beginning

364 of the attack, most of the sea urchins left the surface of the feeder and formed several groups on

365 the tops and at the base of nearby stones (Fig. S2B). The number of sea urchins in the cameras'

366 field of view was relatively stable during the first 12 h, and sea urchin distances from the site of

367 attack did not change much (Fig. 3A). Then, the distances began to increase sharply, and their

368 maximum coincided with maximum number of sea stars consuming an ailing specimen (Fig.

369 3A). 26 h after the beginning of starfish attack, the number of sea urchins in the cameras' field of

370 view began to decrease, and after 50 h, there remained approximately 30% of sea urchins (Figs.

371   3A and S2C). The number of sea urchins on the feeder began to increase between 16 and 28 h

372   after the starfish left the sea urchin remains, and this coincided with gradual decrease of sea

373   urchin distances from the site of attack (Fig. 3A). In general, the alarm reaction of *S. intermedius*

374   from the onset of the starfish attack to restoration of the initial sea urchin population on the

375   surface of the feeder (Figs. 3A and S2D) lasted for approximately 90 h.

376   On September 21, a starfish attack occurred at the short edge of the feeder. Sea urchin

377   distances from the site of attack were almost unchanged during the first 9 h and then sharply

378   increased, and this coincided with maximum number of sea stars (*P. pectinifera* and *L. fusca*)

379   consuming an ailing specimen (Fig. 3B). After 24 h, no *S. intermedius* specimens remained

380   closer than 40 cm from the site of attack. They formed associations on the feeder and the nearest

381   stones. Eight hours after the beginning the attack, the number of sea urchins in the cameras' field

382   of view began to decrease, and after 55 h, there remained approximately 50% of sea urchins.

383   Consumption of the prey by the sea stars lasted 70 h. Restoration of sea urchin abundance and

384   distribution on the feeder began 10 h after the sea stars left the remains of the prey. The total

385   duration of the sea urchin alarm reaction was 88 h (Fig. 3B).

386   It should be noted that the sea stars *P. pectinifera* and *L. fusca* were constantly present on

387   the feeders. The starfish *Asterias amurensis* Lutken, 1871, *Distolasterias nipon* (Döderlein,

388   1902), *Lysastrosoma anthosticta* Fisher, 1992 and *Aphelasterias japonica* Bell, 1881 also often

389   appeared on the feeders. With a few exceptions, these starfish did not cause visible reactions in

390   healthy sea urchins. The behavior of *P. pectinifera* was the most aggressive. In one case, during

391   28 min, *P. pectinifera* attacked an *S. intermedius* specimen, which lost approximately 20% of its

392   spines, but finally, it was left alone. In two cases, sea stars *P. pectinifera* completely crawled on

393   *S. intermedius* individuals in such a way that starfish mouth was located directly above the sea

394   urchin's anal orifice. After 11 and 15 min in the first and second cases, respectively, the sea stars

395   left the potential prey, which indicates that a healthy sea urchin can effectively resist the

396   penetration of a starfish stomach through the anus.

397

398   **Behavioral responses of *M. nudus* and *S. intermedius* to crushed *M. nudus***

399   **specimens**

400   Four experiments conducted during long-term recordings of 2014–2016 (Fig. 1A–C, Table S1)

401   showed that after the conspecifics were crushed near the feeders, approximately 90% of *M.*

402　*nudus* individuals left the cameras' field of view during 4 h (Fig. 4, see Table S8 for raw data

403　and statistics). During this period, a sharp increase in the average step length just after the

404　treatment was recorded (Fig. 5). There were 2 time intervals with the highest locomotion speed,

405　the first 55 min after the treatment when a half of *M. nudus* specimens left the cameras' field of

406　view, and the last 128 min when the rest of sea urchins escaped (Fig. S3A). These intervals were

407　interrupted by the relatively stable 1 hour period when sea urchins almost stopped moving (Fig.

408　5).

409　　　　Nine hours after the beginning of the experiment, there were no *M. nudus* specimens on

410　the feeders (Fig. 4, Table S8), and then, during a much longer period (7–19 days), only single *M.*

411　*nudus* individuals appeared (Fig. 1A–C). The restoration of the initial sea urchin numbers on the

412　feeders occurred only after the next storm event.

413　　　　The imitation of stormy weather also contributed to the return of *M. nudus* after sea

414　urchins left the feeders in response to presentation of crushed conspecifics. Sea urchins were

415　absent on the feeders during approximately 5 and 13 days in 2014 and 2016, respectively, and

416　came back within 2 days after intensive swimming and replacement of the feeders; however,

417　their number was lower than that before the experiments (Figs. 1A, C and S4, Table S1).

418　　　　Four experiments conducted during long-term recordings of 2014–2016 (Fig. 1A–C,

419　Table S1) demonstrated that, in the absence of crushed conspecifics, sea urchins *M. nudus* came

420　back 2–3 days after their removal from the surfaces of the feeders (Fig. 6, see Table S9 for raw

421　data and statistics).

422　　　　Sea urchins *S. intermedius* did not leave the cameras' field of view during the

423　experiments with presentation of crushed *M. nudus* specimens (Fig. 1A–C, Table S1); moreover,

424　statistical analysis revealed small but significant increase in *S. intermedius* numbers in 3 cases

425　when *M. nudus* was absent on the feeders (see Table S10 for statistics). Spatial pattern of *S.*

426　*intermedius* remained almost unchanged with the exception of one case: after the *M. nudus*

427　specimens were crushed, sea urchins *S. intermedius* avoided the surface of the feeder for 24 h

428　and were among the stones opposite of the crushed *M. nudus*.

429

430　**Behavioral responses of *M. nudus* and *S. intermedius* to crushed conspecifics**

431　**and heterospecifics**

432   In the 6-d short-term experiments, *M. nudus* exhibited a strong avoidance reaction in response to

433   crushed conspecifics similar to that in long-term observations (Fig. S5A, see Table S11 for raw

434   data and statistics). When *S. intermedius* individuals were crushed near the feeders, behavior of

435   sea urchins *M. nudus* remained unchanged, as evidenced by the absence of significant changes in

436   such indicators as the number of sea urchins in the cameras' field of view (Fig. S5B, see Table

437   S12 for raw data and statistics) and mean group size (Fig. S5C, see Table S13 for raw data and

438   statistics). Analysis of *M. nudus* movement activity also revealed no differences in the average

439   step length (Fig. 7A), distance from the site of simulated attack (Fig. 7B) and locomotion speed

440   (Fig. S3C).

441   In response to crushed conspecifics, *S. intermedius* moved towards the opposite side of

442   the feeder and formed associations there. Before the experiment, the mean group size was 2.25 ±

443   0.75 (mean ± SD for 21 h of observation), and this parameter was 2.5-fold higher (5.85 ± 2.18)

444   during the 14 h period after the stimulus was presented (Fig. 8A, see Table S14 for raw data and

445   statistics). The changes in the number of sea urchins in the cameras' field of view were not very

446   obvious (Fig. 9A); however, linear regression showed significant decrease in this parameter ($P <$

447   0.0001, see Table S15 for raw data and statistics). The associations were positioned in such a

448   way that sea urchins were partly on the feeder and partly outside it. On average, approximately

449   40% of the sea urchins, both grouped and alone, were located in the immediate vicinity outside

450   the feeders. Judging by the restoration of the original spatial distribution of sea urchins on the

451   feeder (the initial mean group size), the duration of the alarm reaction of *S. intermedius* was

452   approximately 18 h (Fig. 8A).

453   Analysis of *S. intermedius* movement revealed 2 time intervals of the highest activity,

454   each approximately 1.5 h in duration: the first when sea urchins formed associations and the

455   second when these associations dispersed (Figs. 10 and S3B, see Table S16 for raw data).

456   Between these 2 peaks of activity, there was prolonged period of approximately 16 h, when the

457   average step length and locomotion speed were relatively low, and the distance from the site of

458   simulated attack was almost unchanged.

459   Judging by the dynamics of the mean group size, response of *S. intermedius* to crushed

460   individuals of *M. nudus* was generally similar to the response to crushed conspecifics (Fig. 8B,

461   see Table S17 for raw data and statistics). Movement analysis showed that just after the

462   treatment, there was an increase in the average step length (Fig. 7A), distance from the site of

463   simulated attack (Fig. 7B) and locomotion speed (Fig. S3D). A vast majority of sea urchins did

464   not leave the cameras' field of view (Fig. 9B), and linear regression showed no significant

465   decrease in this parameter ($P = 0.3485$; see Table S18 for raw data and statistics). The original

466   spatial distribution of sea urchins on the feeder was restored within approximately 20 h after the

467   beginning of simulated attack (Fig. 8B).

468

469   **DISCUSSION**

470   The present work is the first study analyzing long-term, around-the-clock behavior of sea urchins

471   exposed under field conditions to both calm and stormy weather and to presentation of two

472   competing stimuli, food and predation threat, which are assumed to be key factors influencing

473   species survival. Due to the natural turbidity of sea water, video camera cannot register the initial

474   stages of the sea urchin alarm reaction, namely, extension of the tube feet and movement of

475   spines, which are manifested in the first seconds or minutes after sea urchin exposure to an alarm

476   signal (*Morishita & Barreto, 2011*; *Urriago et al., 2011*). At the same time, the method of

477   continuous time-lapse video recording allowed analysis of the long-term dynamics of the spatial

478   distributions of sea urchins under natural conditions when both stimuli were presented.

479   Previously, several authors applied video recording in the field to quantify sea urchins at the kelp

480   grazing front (*Lauzon-Guay & Scheibling, 2007*) and to determine sea urchin movement patterns

481   (*Dumont et al., 2007*; *Lauzon-Guay et al., 2006*); however, they used separate time-lapse video

482   sequences, each lasting several hours. We showed that two sea urchin species, different in

483   morphology and living under similar conditions, exhibited distinctly different strategies for

484   avoiding predation in terms of response duration and behavioral patterns.

485

486   **Sea urchin response to hydrodynamics**

487   In the absence of predation threat, *S. intermedius* and *M. nudus* also showed somewhat different

488   behavioral patterns. Under calm weather, *S. intermedius* much more often than *M. nudus*

489   exhibited the covering behavior and tended to group on the food substrate. Despite general

490   patterns of movement (intermittent locomotion, characterized by moves interspersed with

491   pauses) in both species, *M. nudus* spent more time stationary but moved at approximately 2 times

492   higher speed than *S. intermedius*, resulting in the higher distance traversed. However, both

493   species are highly mobile, and under conditions of calm sea and presence of food, *M. nudus* and

494   *S. intermedius* would be able to move on average 4.6 and 2.7 m per day, respectively (calculated

495   based on the average locomotion speeds). These average distances are similar to those observed

496   for the sea urchins *Strongylocentrotus droebachiensis* (0.4–1.72 m; *Dumont et al., 2006*),

497   *Toxopneustes roseus* (1.65 and 2.49 m; *James, 2000*), *Tripneustes ventricosus* (3.7 and 8.8 m;

498   *Tertschnig, 1989*) and *Diadema antillarum* (3.7 m; *Tuya et al., 2004*).

499   The results of both laboratory and field experiments evidence that sea urchins are capable

500   to sense a change in hydrodynamic activity and react by changing the behavior. In our study,

501   both sea urchins responded to the stormy weather, firstly, by decreasing the movement activity

502   up to almost complete stop and secondly, by leaving the food. It is noteworthy that during escape

503   under the stormy conditions, sea urchins can move on average 4–5-fold faster than during

504   feeding under calm weather.

505   It is known that with increasing water velocity (higher than approximately 15 cm s^{-1}), sea

506   urchins decrease their displacement and cease feeding both under laboratory (*Kawamata, 1998*;

507   *Frey & Gagnon, 2016*; *Cohen-Rengifo et al., 2018*; *Tamaki et al., 2018*) and field (*Lissner, 1980*;

508   *Dance, 1987*; *Siddon & Witman, 2003*; *Dumont et al., 2006, 2007*) conditions. Escape behavior

509   was also observed in laboratory flume experiments: at flow velocity ≤ 30 cm s^{-1}, sea urchins

510   moved in a downstream direction whereas at 35–45 cm s^{-1}, individuals moved in an upstream

511   direction (*Morse & Hunt, 2013*; *Cohen-Rengifo et al., 2018*). However, escape response of sea

512   urchins to wave-induced benthic water flow *in situ* has been poorly documented. *Dance* (*1987*)

513   observed that during a period of turbulence lasting several hours, movement of *P. lividus* was

514   significantly oriented to the deep water with lower hydrodynamic activity. *Lauzon-Guay &*

515   *Scheibling* (*2007*) found that *S. droebachiensis* density at the grazing front decreased when wave

516   action increased and suggested that the 'whiplash effect' of the swaying kelp prevented sea

517   urchins from climbing onto kelp plants. In our study, the kelp was packed into mesh containers

518   and formed a kind of soft substrate. We believe that sea urchins *M. nudus* and *S. intermedius*,

519   being able to sense an oscillation of the substratum and/or increasing water flow, reduce the

520   movement activity and then make a decision to stay close to the food or escape. We noted that in

521   the case of the weaker storm, only a part of sea urchins left the food source. Remaining *S.*

522   *intermedius* individuals gathered into groups at the base of the feeders whereas *M. nudus*

523   specimens were on the surface of the feeders. However, unfortunately, we did not measure a

524   velocity of water flow and, therefore, cannot correlate it with sea urchin movement activity.

525   Further studies are thus required to elucidate such a correlation.

526

527   **Sea urchin response to predation threat**

528   During this study, no successful starfish attacks on healthy sea urchins were observed for either

529   species, and only 3 cases of consuming of single ailing *S. intermedius* individuals by several

530   starfish specimens (*P. pectinifera* and *L. fusca*) were recorded. Taking into account the

531   laboratory experimental data that the starfish, *L. anthosticta* and *P. pectinifera* in particular, are

532   predators of *M. nudus* (see for review *Agatsuma, 2013b*), we further analyzed the video records

533   of 2017 captured by 6 video cameras in the course of another project. During 44 days, 132 ± 46

534   of *M. nudus* individuals were in the cameras' field of view and no cases of predator attacks were

535   recorded (*P.M. Zhadan pers. comm., 2018*). Considering also that both sea urchin species

536   showed only a weak response to sea stars even during direct contact, we can conclude that none

537   of 6 starfish species observed on the feeders (*P. pectinifera*, *L. fusca*, *A. amurensis*, *D. nipon*, *L.*

538   *anthosticta* and *A. japonica*) are specialized predators of *S. intermedius* and *M. nudus*. Most

539   likely, starfish perform the function of scavengers.

540   The alarm response of *S. intermedius* to predation depended on the type of alarm signal

541   and involved several phases. The sea urchins: (1) moved away from a source of threat (so called

542   'flight response'), (2) exhibited grouping behavior forming dense two-dimensional groups close

543   to the food source, (3) left the food source, and (4) restored the initial spatial distribution on the

544   food source. Phase 3 was most pronounced when the alarm signals were the attack of starfish on

545   ailing specimens or simulated attack with crushed conspecifics: approximately 50 h after the

546   beginning of starfish attack, there remained only 30–50% of sea urchins on the feeders. When

547   the alarm signal was a simulated attack with crushed heterospecifics, phase 3 was much weakly

548   pronounced or absent.

549   Sea urchins *M. nudus* exhibited a fast (during 4 h) escape (flight response) and prolonged

550   (up to 19 days) avoidance of the source of attractive food near which the conspecifics were

551   crushed. Such a long fear effect of the alarm signal associated with crushed conspecifics is

552   probably due to the marking of the area with substances released by injured sea urchins. At the

553   same time, *M. nudus* exhibited no responses to damaged heterospecifics.

554   Escape of sea urchins from an alarm source is the most well-documented first phase of

555   the alarm response of sea urchins (*Snyder & Snyder, 1970*; *Parker & Shulman, 1986*; *Sheibling*

556   *& Hamm, 1991*; *Campbell et al., 2001*; *Hagen et al., 2002*; *Vadas & Elner, 2003*; *Urriago et al.,*

557   *2011*; *Wirtz & Duarte, 2012*). It has been shown that the alarm reaction in sea urchins started

558   within a few minutes of exposure to waterborne chemosensory cues from some potential

559   predators (fish, lobsters, crabs, sea stars, gastropods), as well as from crushed prey, conspecifics

560   or heterospecifics. Generally, escape response was most pronounced in the experiments with

561   damaged conspecifics.

562   To date, responses to chemosensory cues from damaged conspecifics have been

563   demonstrated in several sea urchin species: *Diadema antillarum* (*Kintzing & Butler, 2014a*;

564   *Snyder & Snyder, 1970*), *S. droebachiensis* (*Hagen et al., 2002*; *Mann, 1982*), *Echinometra*

565   *viridis* and *Lytechinus williamsi* (*Parker & Shulman, 1986*), *Echinometra lucunter* (*Morishita &*

566   *Barreto, 2011*; *Parker & Shulman, 1986*), *Echinus esculentus* and *Psammechinus miliaris*

567   (*Campbell et al., 2001*), *Lytechinus variegatus* and *Tripneustes ventricosus* (*Vadas & Elner,*

568   *2003*), and *Arbacia lixula* and *Sphaerechinus granularis* (*Wirtz & Duarte*, 2012). It should be

569   noted, however, that *Parker & Shulman* (*1986*) did not find an alarm reaction to extracts of

570   conspecifics when analyzing sea urchin motion for 1 min in *Eucidaris tribuloides*, *T. ventricosus*

571   and *L. variegatus* living in long, dense seagrass that provided protection from detection by

572   predators, and *D. antillarum* occupying crevices.

573   In our studies, both *M. nudus* and *S. intermedius* exhibited a phased escape response to

574   crushed conspecifics: (1) a sharp increase in locomotion speed just after presentation of an alarm

575   signal lasting for 1–1.5 h and resulting in an increase of a distance from a threat source and

576   grouping close to a food source (*S. intermedius*) or escape of approximately half of specimens

577   (*M. nudus*), (2) deceleration lasting for approximately 1 h in *M. nudus* and 16 h in *S. intermedius*,

578   and (3) the second increase in locomotion speed lasting for approximately 1.5 h and resulting in

579   association dispersion and repopulation of feeders (*S. intermedius*) or escape of all remaining

580   specimens (*M. nudus*). Previously, *Vadas & Elner* (*2003*) found in the field experiments that two

581   sympatric tropical sea urchin species, *L. variegatus* and *T. ventricosus*, demonstrated an initial

582   burst of speed followed by a gradual deceleration up to relatively stable level in response to

583   conspecific alarm cues. However, these movement reactions were much shorter and lasted only 2

584   min each.

585   The most striking difference of these sea urchins in the escape responses to conspecific

586   alarm cues was that *M. nudus* exhibited fast and total escape whereas only a part of *S.*

587   *intermedius* individuals left a food source, and the remaining specimens formed associations on

588   the feeder and in close vicinity to it. Our results showed that grouping behavior is a common

589   phase of the alarm response in *S. intermedius* but not in *M. nudus*. As it was shown in laboratory

590   and field studies, a number of sea urchin species are capable of forming dense groups on a food

591   substrate (*Bernstein et al., 1981, 1983*; *Garnick, 1978*; *Pearse, 2006*; *Vadas & Elner, 2003*).

592   *Bernstein et al.* (*1981, 1983*) found that the presence of predators (lobsters *Homarus americanus*

593   or crabs *Cancer irroratus*) in laboratory aquariums or in field cages triggered the formation of *S.*

594   *droebachiensis* aggregations that were larger than groups of feeding and non-feeding sea urchins

595   in the absence of predators. The researchers interpreted such aggregation behavior as a defense

596   mechanism of *S. droebachiensis* against predation. *Vadas et al.* (*1986*), however, did not find a

597   tendency to form aggregations in the same species in the presence of predators (decapods *H.*

598   *americanus*, *C. irroratus* and sea star *Asterias vulgaris*) and suggested that grouping of sea

599   urchins in tank corners or on tank walls/cage mesh may be an experimental artefact caused by

600   the accumulation of sea urchins near artificial obstacles that prevented them from escaping a

601   predator. This point of view was supported by other studies on interactions between sea urchins

602   *S. droebachiensis* and their predators in field and laboratory experiments (*Harding & Scheibling,*

603   *2015*; *Scheibling & Hamm, 1991*). In addition, *Vadas & Elner* (*2003*), investigating the reactions

604   of sympatric sea urchins *L. variegatus* and *T. ventricosus* to simulated predator attacks in field

605   experiments, also found no formation of sea urchin groups in response to an alarm signal and

606   concluded that the flight response is the primary, and perhaps only defensive behavior employed

607   by these species. However, our results showed that two other sympatric sea urchin species (*M.*

608   *nudus* and *S. intermedius*) exhibit distinctly different behavioral response strategies to predation

609   risk: *M. nudus* employs fast escape and prolonged avoidance of dangerous area while *S.*

610   *intermedius* employs both grouping and escape behaviors.

611   The duration of the alarm response of *S. intermedius* (from the appearance of the alarm

612   signal to the return to feeding) was different under different conditions. It was the longest

613   (approximately 90 h) after the attack of sea stars on ailing individuals. The eating of prey lasted

614   from 45 to 70 h, and after that, from 20 to 45 h passed before sea urchins restored their original

615   arrangement on the feeder. Considering that semidiurnal tidal cycles and constant wave activity

616   took place in the study areas, there is little reason to believe that a waterborne chemical cue from

617   the primary source (injured prey) could have persisted. The secondary source of the alarm signal

618   could be the products of predator metabolism (*Scherer & Smee, 2016*). For example, black sea

619   urchin *E. lucunter* is able to distinguish sea stars feeding on conspecifics or closely related

620   species (*Morishita & Barreto, 2011*). For predatory fish, it has been shown that substances that

621   cause the alarm response in the prey can remain active after passing through the digestive tract

622   (*Manassa & McCormick, 2012*). In addition, it is likely that waterborne chemical cues from

623   predators and/or injured prey may be sorbed on the bottom sediments and gradually released,

624   thereby increasing the time of the alarm reaction in prey.

625   Based on the above data, it may be assumed that the duration of the alarm reaction of sea

626   urchins depends on two main factors: (1) the duration of the release of substances from predators

627   and/or injured prey to the environment, and (2) the time during which sea urchins can detect

628   these substances sorbed on the sediment. In addition, species-specific previous learning might

629   also be a factor determining different behavioral patterns in sea urchin species (*Ferrari et al.,*

630   *2010*).

631   In our study, sea urchins *M. nudus* exhibited unique prolonged avoidance behavior in

632   response to crushed conspecifics, and this behavior has not been described before in sea urchins

633   and other echinoderms. The ability of *M. nudus* to avoid a site of predation for up to 19 days and

634   return to the food source only after a storm indicates that crushed *M. nudus* specimens released

635   some stable substances that marked the bottom for a long time and served as an alarm signal and

636   that the disruption and removal of the upper sediment layer during the storm probably

637   contributed to the removal of the alarm signal. The experiments with storm imitation support this

638   suggestion.

639

640   **Possible mechanisms underlying the difference in sea urchin alarm responses**

641   The mechanisms underlying different patterns of the alarm responses in cohabiting sea urchin

642   species are not yet understood. We believe that both the ability of *S. intermedius* to form

643   associations close to a food source and the ability of *M. nudus* to leave the area of predation risk

644   for a long period are useful evolutionary adaptations that enhance the likelihood of species

645   survival under permanent pressure from visual predators.

646   We suggest that sea urchin *S. intermedius* uses camouflage to protect itself from visual

647   predators because a group of these sea urchins forms a grey spot of irregular shape decorated

648   with algae, which is more difficult to be identified from air or under water than a single object

649   with a regular round shape. Furthermore, a solitary sea urchin is easier to be captured by a diving

650   predator. At the same time, such camouflage cannot be effective for sea urchin *M. nudus* because

651   its black color is in high contrast to the color of the bottom, whereas leaving the area occupied by

652   a predator increases the chances of *M. nudus* survival.

653   It is well known that in temperate waters, the most active consumers of sea urchins that

654   are able to control their abundance are the sea otter *Enhydra lutris* (*Duggins, 1980*; *Estes &*

655   *Duggins, 1995*; *Watson & Estes, 2011*) and a number of bird species, mainly gulls (*Guillemette*

656   *et al., 1992*; *Himmelman & Steele, 1971*; *Hori & Noda, 2007*; *Merkel et al., 2007*; *Wootton,*

657   *1995*). *Wootton* (*1995*) compared the densities of sea urchin *Strongylocentrotus purpuratus* in

658   several places in a lower intertidal zone both exposed to bird predators (glaucous-winged gulls

659   *Larus glaucescens*, American black oyster catchers *Haematopus bachmani* and northwestern

660   crows *Corvus caurinus*) and protected from birds by cages and showed that sea urchin

661   abundance was 59% lower after 1 year and 45% lower after 2 years in the presence of bird

662   predators compared to the absence of bird predators. For *S. intermedius*, the most abundant avian

663   predators are carrion crow *Corvus corone* and a few gull species that are able to consume a large

664   number of sea urchins, more than 4,000 specimens per 1 ha (*Hori & Noda, 2007*).

665   Data on the geographical distributions of *S. intermedius* and *M. nudus* (*Agatsuma, 2013a,*

666   *2013b*; *Bazhin, 1998*; *Kafanov & Pavlyuchkov, 2001*) and the sea otter (*Kenyon, 1969*) give

667   evidence that the ranges of these species may have partially overlapped in the past, but at

668   present, the overlapping of this predator–prey habitat seems more likely for temperate-boreal

669   species, *S. intermedius*, which inhabits the Asian Pacific coastal waters from the Kamchatka

670   Peninsula southward to the Korean Peninsula and from the Russian coast eastward to the

671   Japanese Islands. The sea urchin *M. nudus* is a subtropical species, and coastal waters of the Sea

672   of Japan near Russia (Primorye Region) and Japan (northern Hokkaido) represent the northern

673   part of its range, whereas for the sea otter, the northern Hokkaido represented the southern

674   boundary of its range in the northwestern Pacific until the 18th century, before fur hunting began

675   (*Wilson et al., 1991*).

676   Sea otters and predatory birds prefer sea urchins of medium and large size, i.e., adult

677   specimens contributing to population reproduction (*Estes & Duggins, 1995*; *Guillemette et al.,*

678   *1992*; *Himmelman & Steele, 1971*; *Hori & Noda, 2007*). The defensive behaviors of sea urchins

679   *S. intermedius* and *M. nudus* could have formed mainly under the pressure of these predators.

680   Due to natural selection, the individuals that could avoid predation attacks survived, and useful

681   genetic traits have been passed from generation to generation in the form of different defensive

682   behaviors.

683

684   **CONCLUSION**

685   Our results show that cohabiting sea urchin species, *S. intermedius* and *M. nudus*, which were

686   monitored in their natural environment under conditions of food abundance display both similar

687   and different behavioral responses to hydrodynamics and predation threat. The most interesting

688   findings are the following: (1) under calm weather, *S. intermedius* but not *M. nudus* tended to

689   group on the food substrate; movement patterns of both sea urchins were similar but *M. nudus*

690   exhibited the higher locomotion speed and distance travelled; (2) both sea urchins responded to

691   increased wave activity by a sharp decrease in the movement activity up to almost complete stop

692   and then made a decision to stay close to the food or escape; (3) several sea star species failed to

693   predate on healthy sea urchins of both species, and only a few starfish attacks on ailing *S.*

694   *intermedius* specimens were successful; (4) the alarm response of *S. intermedius* depended on the

695   type of alarm signal (consumption of ailing conspecifics by starfish or simulated attack) and

696   included the formation of dense groups close to the food source; (5) the alarm response of *S.*

697   *intermedius* lasted approximately 90 h and 20 h for starfish attacks on ailing conspecifics and for

698   simulated attacks (crushed conspecifics or heterospecifics), respectively; (6) *M. nudus* responded

699   to crushed conspecifics only and exhibited no grouping behavior but displayed fast escape

700   (during 4 h) and prolonged (up to 19 days) avoidance of the food source; (7) both sea urchins

701   exhibited a phased escape response to crushed conspecifics consisting of a sharp increase in

702   locomotion speed just after presentation of the alarm signal followed by deceleration, and the

703   second increase in locomotion speed associated with repopulation of feeders (*S. intermedius*) or

704   complete escape (*M. nudus*); (8) damaged specimens of *M. nudus* released some stable alarm

705   substances. Furthermore, our results show the benefits of using continuous time-lapse video

706   recording to study the long-term behavioral responses of sea urchins to different disturbing

707 factors such as high hydrodynamic activity and predation threat. Considering the important

708 ecological role of sea urchins as grazers of marine plants, data on the duration of the fear

709 response in sea urchin species, i.e., the periods when their foraging activity is inhibited, may be

710 of greatest use in mathematical modelling of the marine ecosystem.

711

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717

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Figure 1

Temporal dynamics of the numbers of sea urchins *Mesocentrotus nudus* and *Strongylocentrotus intermedius* in long-term experiments.

The experiments were conducted in: (A) Kievka Bay, 2014; (B) Kievka Bay, 2015; (C) Alekseev Bay, 2016. Blue and red circles connected by lines denote the numbers of *M. nudus* and *S. intermedius*, respectively, presented as the sum of all sea urchins of the given species on 4 feeders per each 6 h of observations (see Table S1 for original data). Triangles indicate the time points when sea urchins *M. nudus* were removed from the feeders. Upside down triangles denote the time points when sea urchins *M. nudus* were crushed near the feeders. Green squares denote the time points when the feeders were changed. Green rhombuses indicate the time points when the feeders were changed after the mimicking of stormy weather conditions. Shaded areas denote storm periods. Solid violet horizontal lines indicate periods of poor visibility because of high water turbidity. X-axis: month and date.

Kievka Bay 2014

A

Number of sea urchins

Kievka Bay 2015

B

Number of *M. nudus*

Number of *S. intermedius*

Alekseev Bay 2016

C

Number of sea urchins
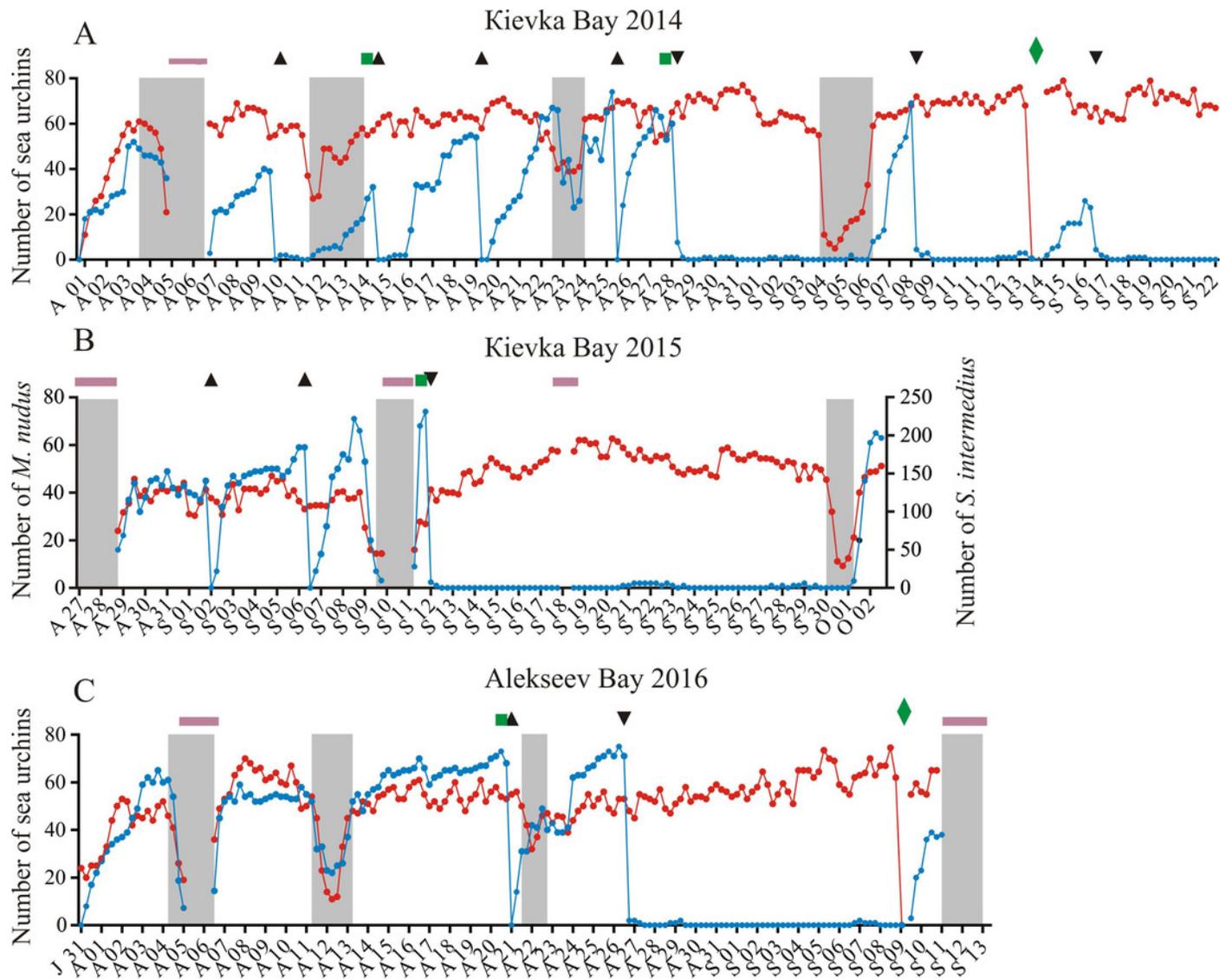
Figure 2

Changes in the numbers of sea urchins *Mesocentrotus nudus* (A) and *Strongylocentrotus intermedius* (B) in response to the stormy weather.

Range (whiskers), upper and lower quartile (box), mean (+), and median (solid line) of the numbers of sea urchins before, during and after the storm periods are presented. Different lowercase letters above the boxes indicate significant differences in sea urchin numbers: (A) the differences between 'before the storm' and 'during the storm' numbers are significant at $P < 0.0001$, the differences between 'during the storm' and 'after the storm' numbers are significant at $P < 0.001$ (1-way ANOVA followed by Tukey's multiple comparisons test), (B) the differences between 'before the storm' and 'during the storm' numbers, 'during the storm' and 'after the storm' numbers are significant at $P < 0.0001$ (Kruskal–Wallis test followed by Dunn's multiple comparisons test) . See Table S5 and Table S6 for raw data and statistics.
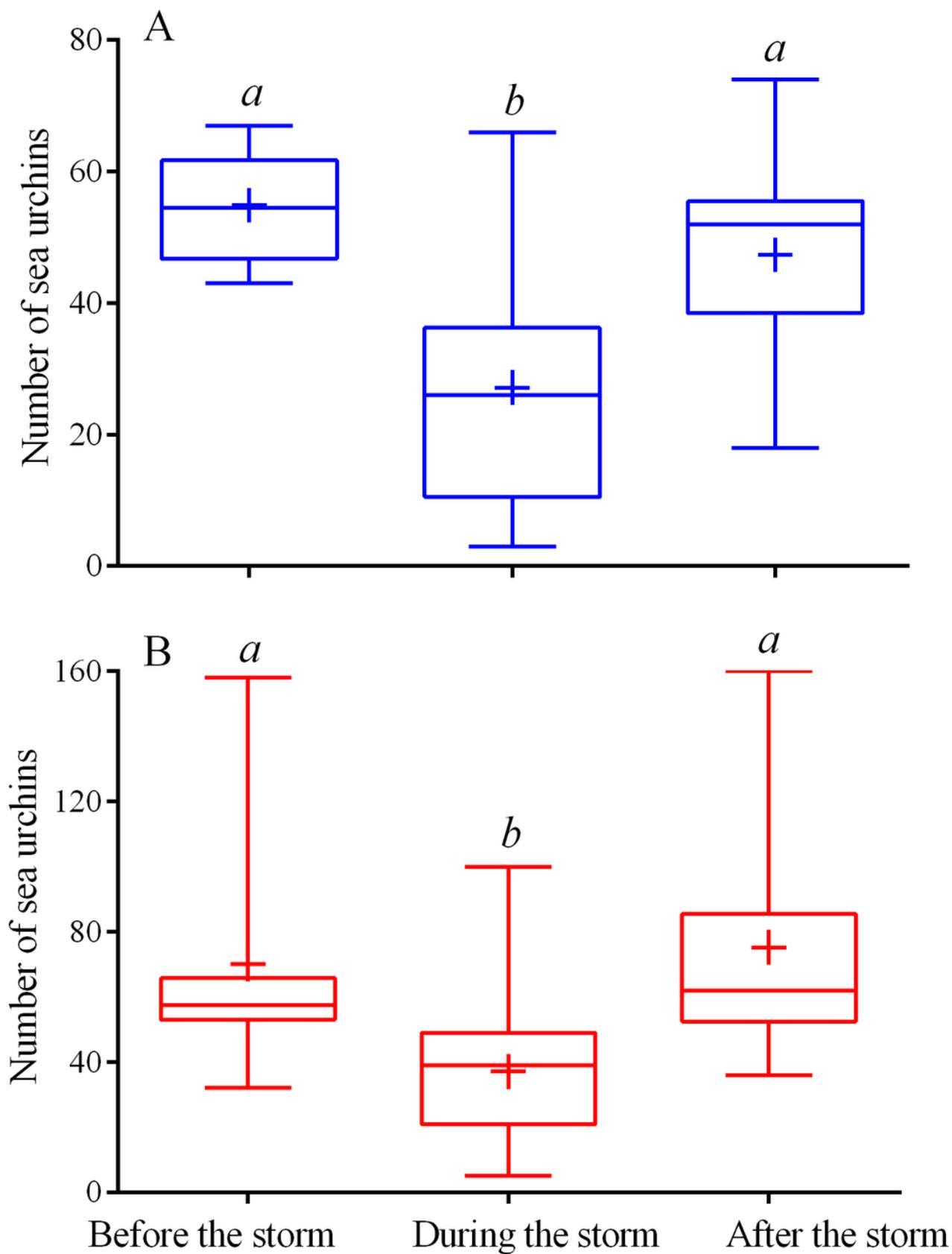
Figure 3

Movement activity of the sea urchins *Strongylocentrotus intermedius* in response to starfish attacks.

(A) Starfish attack on September 5, 2015. (B) Starfish attack on September 21, 2015. Red rhombuses denote sea urchin distances from the site of the attack, mean ± SD (n = 13). Black squares connected by dashed line denote the sum number of 2 species of sea stars (*Patiria pectinifera* and *Lethasterias fusca*) at the site of the attack. Red circles connected by solid line denote the number of sea urchins in the cameras' field of view. Time of the beginning of the attack is indicated by black asterisk.
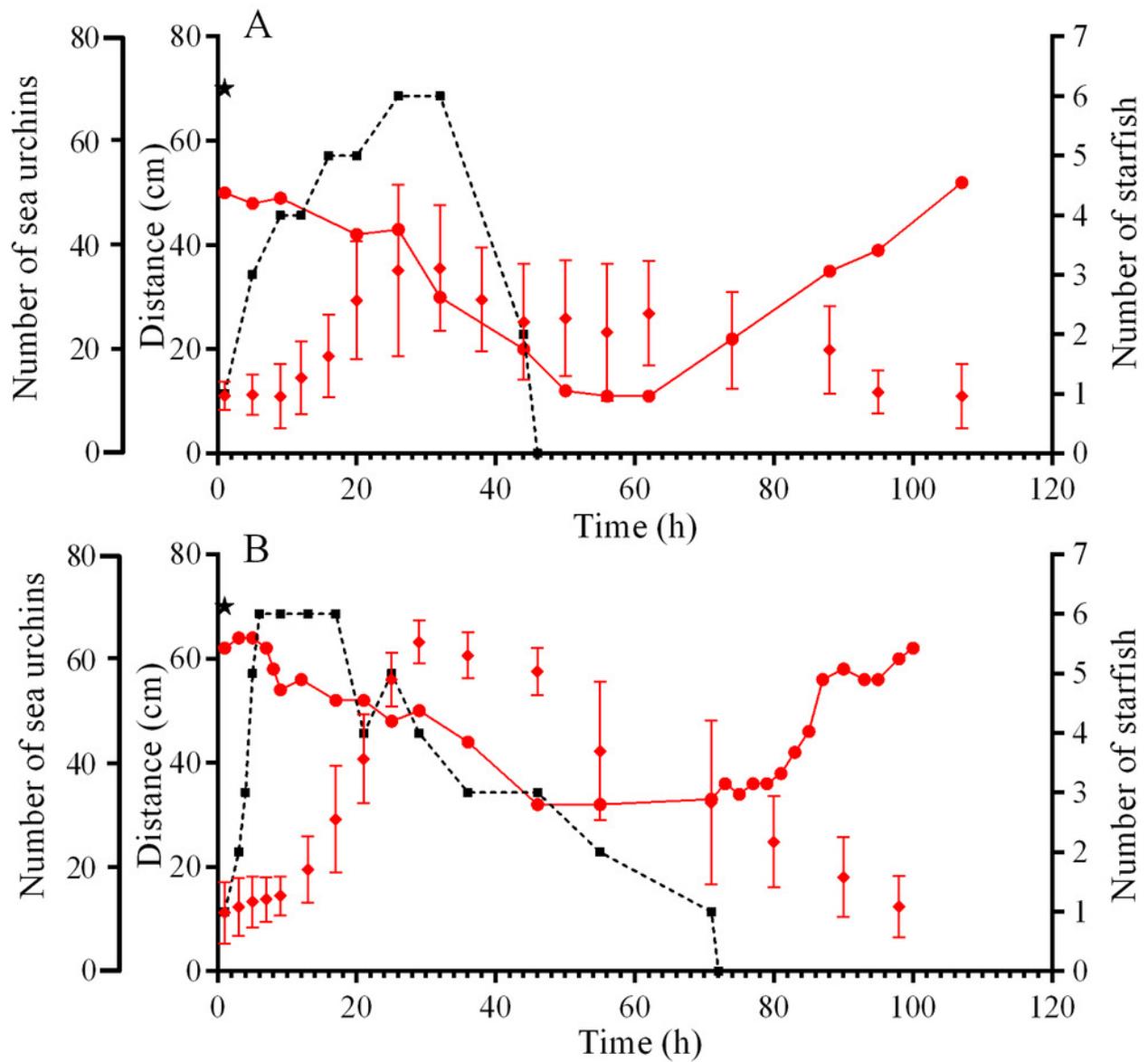
Figure 4

Changes in the numbers of sea urchins *Mesocentrotus nudus* during escape in response to crushed conspecifics in long-term experiments of 2014–2016.

The data of 4 experiments conducted during long-term recordings of 2014–2016 (see Fig. 1A–C , Tables S1, S8) are presented as median and range of the number of *M. nudus* per 1 h after crushing of conspecifics. Nonlinear regression is significant (R^2 = 0.9454, see Table S8 for raw data and statistics).
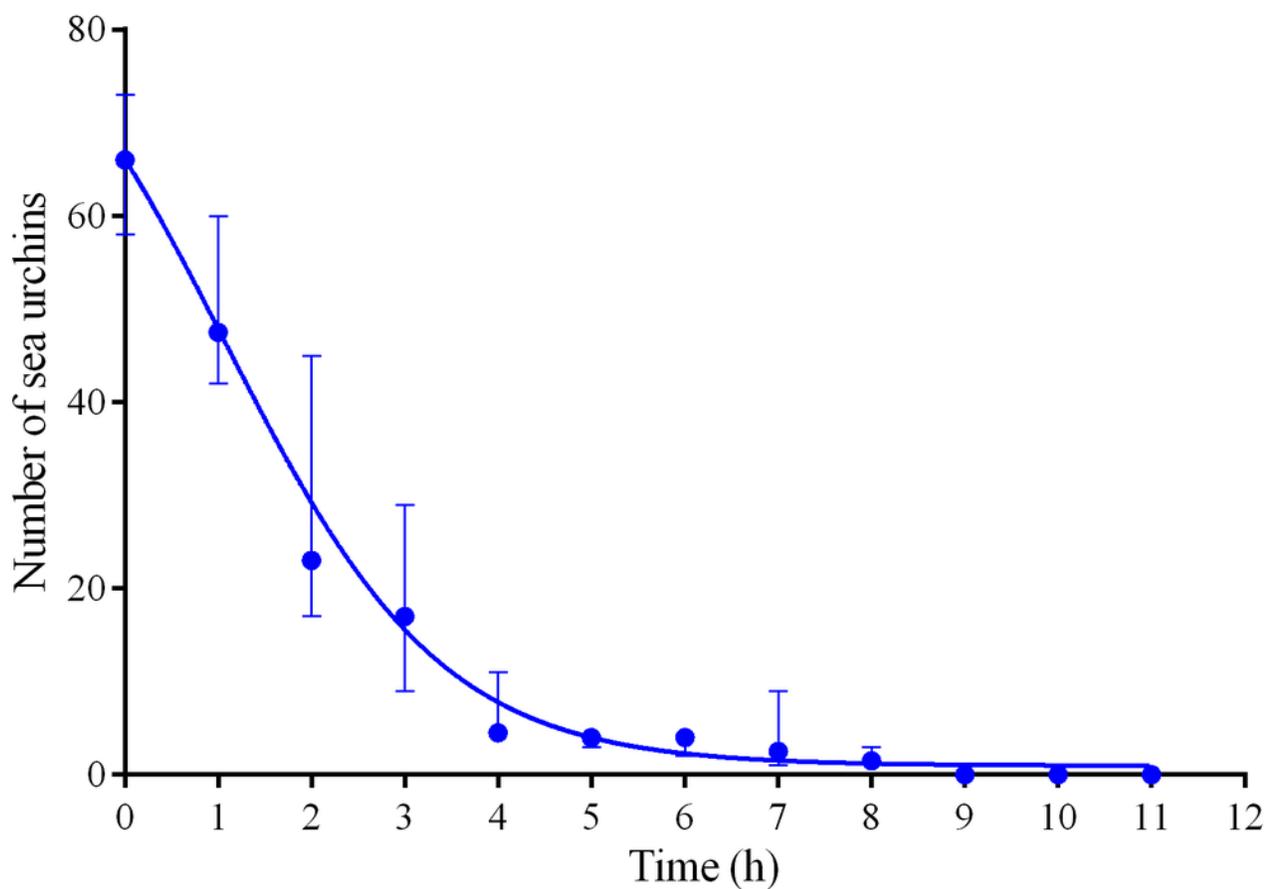
Figure 5

Movement activity of the sea urchins *Mesocentrotus nudus* in response to crushed conspecifics.

Blue solid line denotes the average step length of sea urchins (n = 10). Blue circles connected by dashed line denote the number of sea urchins in the cameras' field of view. Time point of treatment is denoted by upside down triangle.
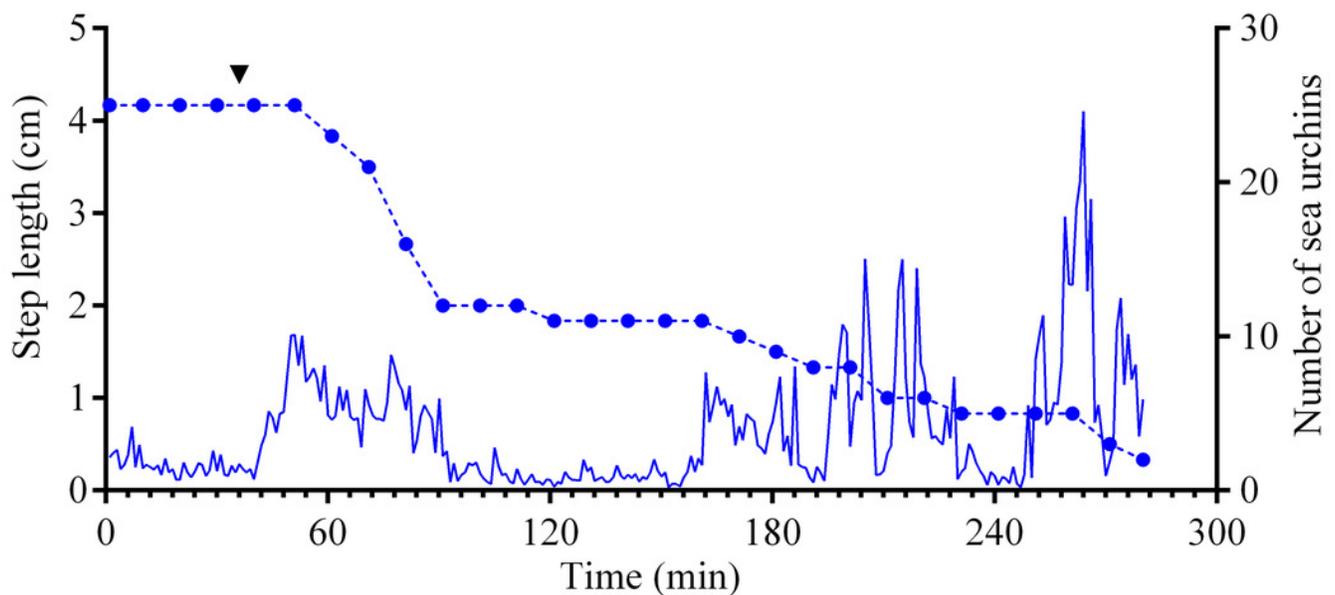
Figure 6

Temporal dynamics of repopulation of the feeders by sea urchins *Mesocentrotus nudus* after their removal in long-term experiments of 2014–2016.

The data of 4 experiments conducted during long-term recordings of 2014–2016 (Fig. 1A–C, Tables S1, S9) are presented as median and range of the number of *M. nudus* per 6 h.

Nonlinear regression is significant (R^2 = 0.731, see Table S9 for statistics).
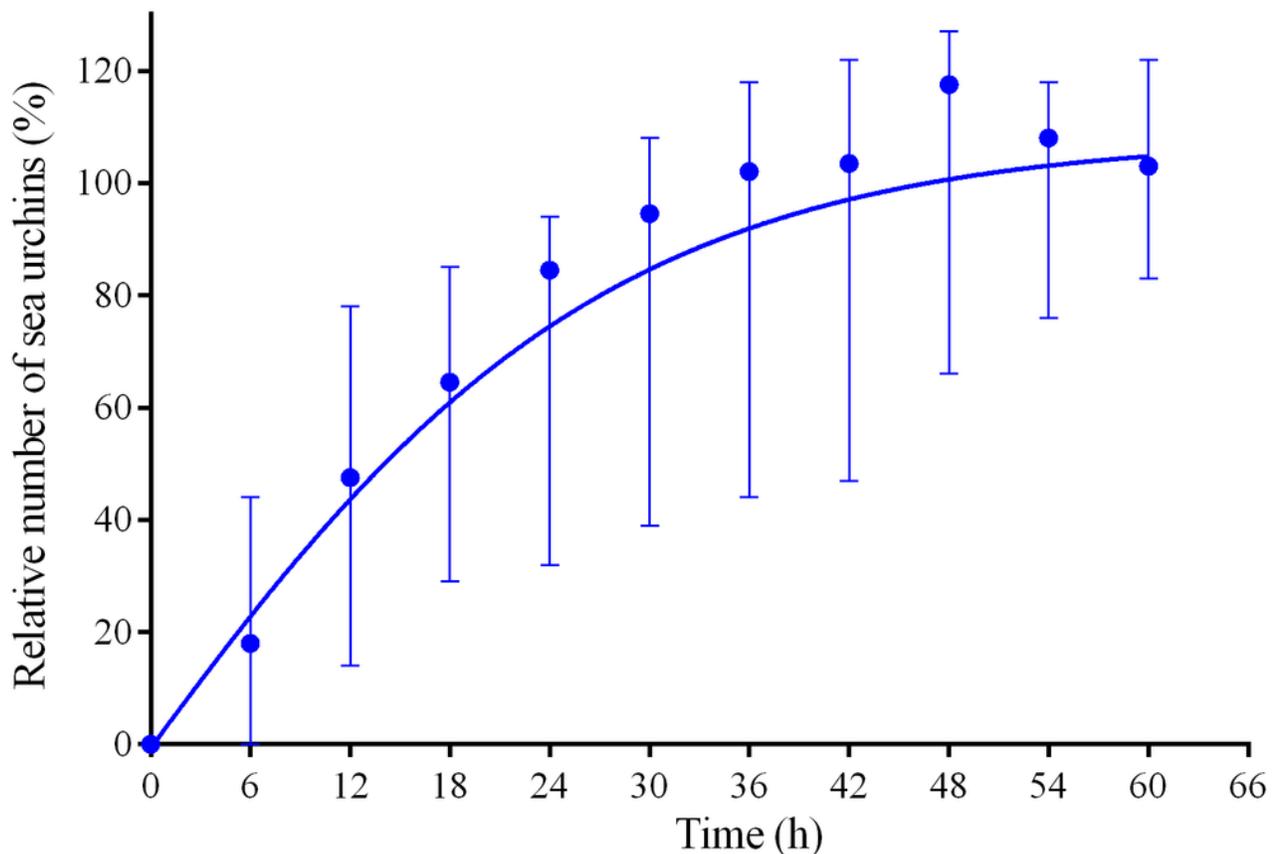
Figure 7

Movement activity of the sea urchins *Mesocentrotus nudus* (blue lines) and *Strongylocentrotus intermedius* (red lines) in response to crushed heterospecifics.

(A) The changes in the average step length of sea urchins (n = 10). (B) The changes in sea urchin distances from the site of simulated attack, mean ± SD (n = 10). SD is shown for every sixth measurement. Time of the treatment is denoted by upside down triangle.
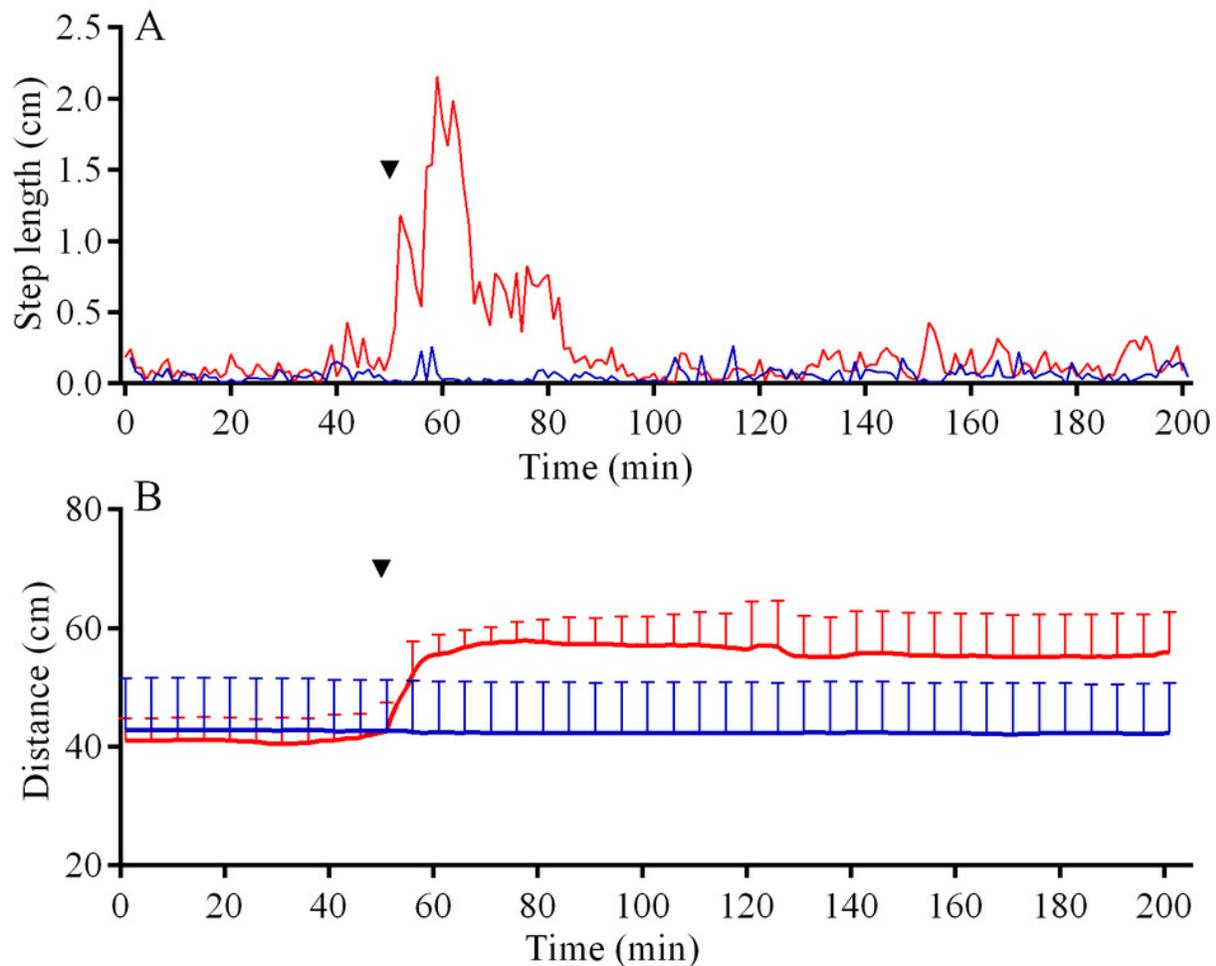
Figure 8

Temporal dynamics of the mean group size of sea urchins *Strongylocentrotus intermedius* in response to simulated predator attack.

(A) Response of *S. intermedius* to crushed conspecifics. (B) Response of *S. intermedius* to crushed specimens of the sea urchin *Mesocentrotus nudus*. The mean group size is presented as box-whisker plot showing the median (solid line), range (whiskers) and upper and lower quartiles (box). Upside down triangles denote the time points when sea urchins were crushed near the feeders. See Table S14 and Table S17 for raw data and statistics.
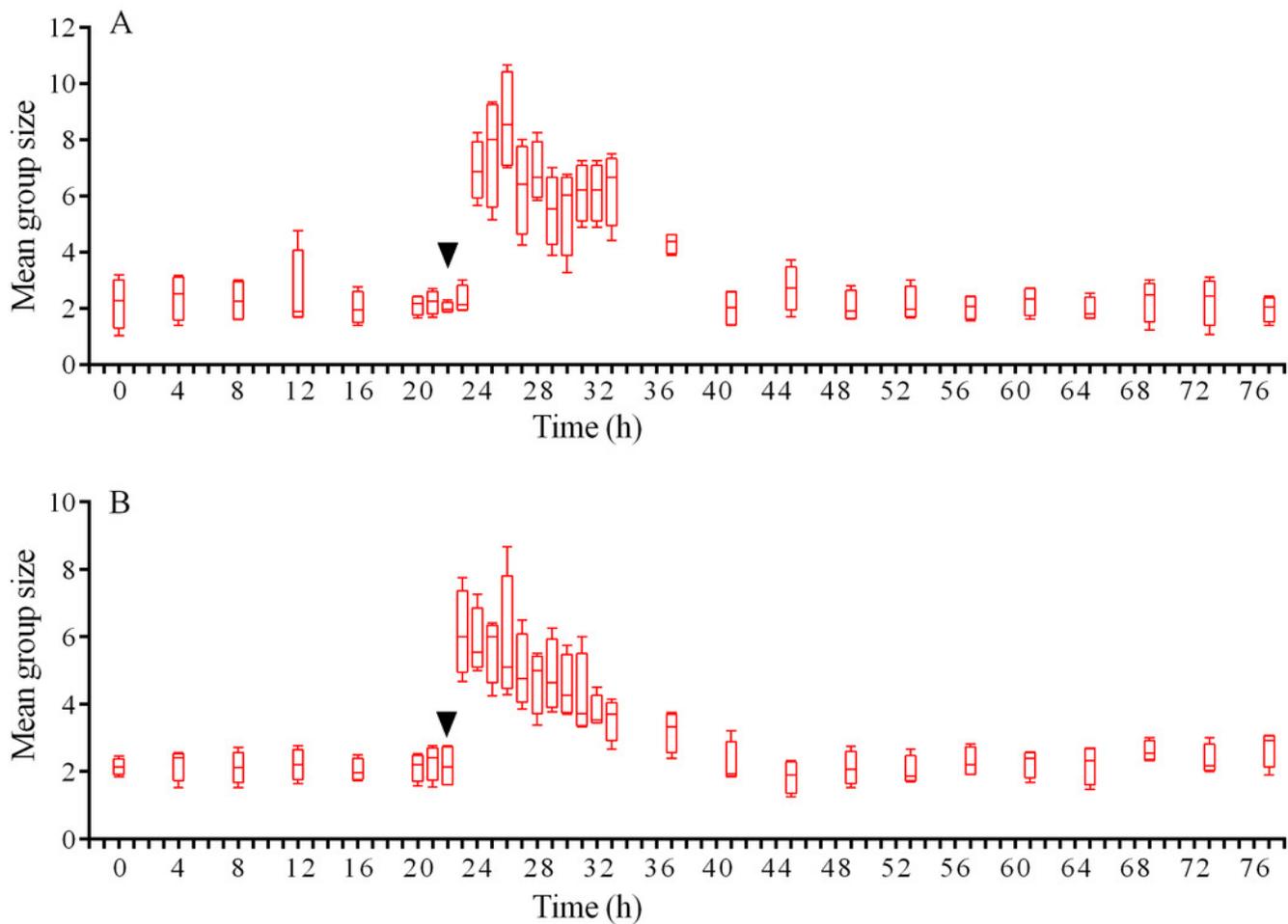
Figure 9

Temporal dynamics of the numbers of sea urchins *Strongylocentrotus intermedius* in response to simulated predator attack.

(A) Response of *S. intermedius* to crushed conspecifics. Linear regression is significant (*P* < 0.0001, see Table S15 for raw data and statistics). (B) Response of *S. intermedius* to crushed specimens of the sea urchin *Mesocentrotus nudus*. Linear regression is not significant (*P* = 0.3485, see Table S18 for raw data and statistics). The data are presented as median and range. Time of the treatment is indicated by upside down triangle.
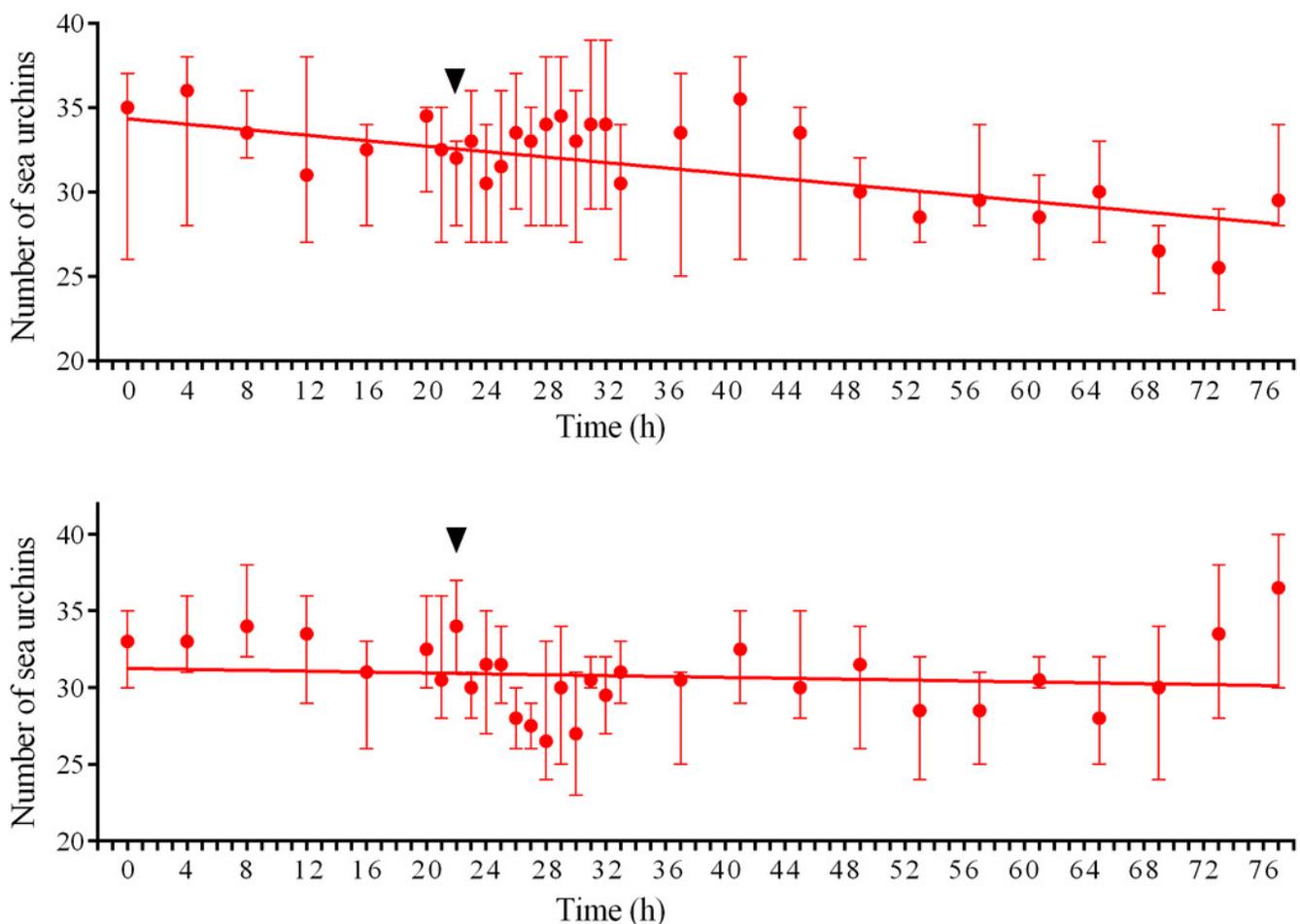
Figure 10

Movement activity of the sea urchins *Strongylocentrotus intermedius* in response to crushed conspecifics.

Red dotted line denotes sea urchin distance from the site of simulated attack, mean ± SD (n = 10). SD is shown for every ninth measurement. Red solid line denotes the average step length of sea urchins (n = 10). Time of the treatment is indicated by upside down triangle.
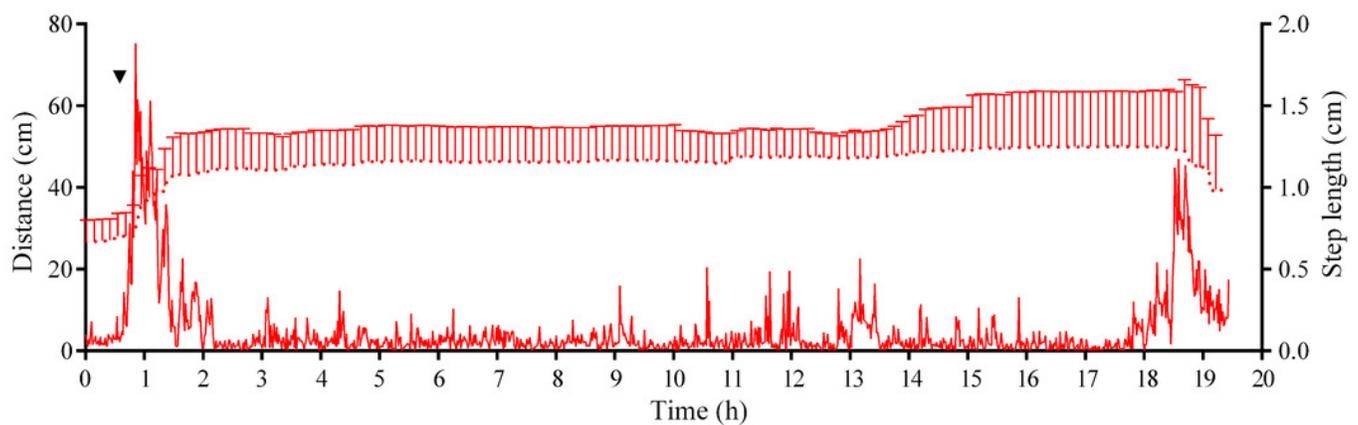
Table 1(on next page)

Parameters of movement activity of the sea urchin *Mesocentrotus nudus* under calm and stormy weather.

Data are presented as Mean ± SEM (n = 10) and the range (in the parentheses) for 240-min interval.

1

Parameter	Calm weather	Stormy weather	Statistics
Number of steps	110 ± 12 (50–160)	21 ± 3 (9–35)	$t_{10} = 7,314$; df = 9.883; $p < 0.0001$
Step length, cm	0.71 ± 0.08 (0.10–9.54)	0.29 ± 0.02 (0.10–1.34)	$t_{10} = 4.966$; df = 10.26; $p = 0.0005$
Number of moves	28 ± 2 (22–35)	13 ± 2 (5–23)	$t_{10} = 5.915$; df = 18; $p < 0.0001$
Move length, cm	2.99 ± 0.58 (0.10–56.5)	0.57 ± 0.16 (0.10–8.37)	Mann–Whitney U = 5.0; $p = 0.0002$
Entire distance traversed, cm	76.90 ± 11.86 (34.91–146.40)	5.87 ± 0.7 (3.91–9.97)	$t_{10} = 5.98$; df = 9.063; $p = 0.0002$
Number of stops	28 ± 2 (22–35)	14 ± 2 (5–24)	$t_{10} = 5.773$; df = 17.41; $p < 0.0001$
Stop duration, min	4.82 ± 0.54 (1–43)	19.69 ± 3.02 (1–87)	$t_{10} = 4.845$; df = 9.566; p = 0.0008
Entire stop duration, min	130.0 ± 11.87 (80–190)	217.9 ± 2.73 (205–231)	$t_{10} = 7.219$; df = 9.95; $p < 0.0001$
Speed, cm min^{-1}	0.32 ± 0.05 (0.15–0.61)	0.03 ± 0.003 (0.02–0.04)	$t_{10} = 6.054$; df = 9.056; $p = 0.0002$

2

Table 2(on next page)

Parameters of movement activity of the sea urchin *Strongylocentrotus intermedius* under calm and stormy weather.

Data are presented as Mean ± SEM (n = 10) and the range (in the parentheses) for 240-min interval.

1

Parameter	Calm weather	Stormy weather	Statistics
Number of steps	160 ± 10 (110–211)	57 ± 12 (18–141)	$t_{10} = 6.606$; df = 17.49; $p < 0.0001$
Step length, cm	0.28 ± 0.03 (0.10–5.46)	0.33 ± 0.08 (0.10–4.14)	Mann–Whitney U = 33.5; $p = 0.2233$
Number of moves	31 ± 2 (16–39)	26 ± 3 (13–39)	$t_{10} = 1.,147$; df = 18; $p = 0.2662$
Move length, cm	1.65 ± 0.35 (0.10–39.72)	0.65 ± 0.17 (0.10–37.7)	Mann–Whitney U = 13.0; $p = 0.0038$
Entire distance traversed, cm	44.28 ± 5.56 (29.73–88.85)	16.10 ± 4.3 (3.80–45.76)	Mann–Whitney U = 12.0; $p = 0.0029$
Number of stops	31 ± 2 (18–39)	26 ± 3 (12–38)	$t_{10} = 1.331$; df = 15.56; $p = 0.2023$
Stop duration, min	2.54 ± 0.26 (1–29)	8.63 ± 1.70 (1–80)	$t_{10} = 3.402$; df = 9.431; p = 0.0058
Entire stop duration, min	80.1 ± 10.1 (29–130)	183.2 ± 11.97 (99–222)	$t_{10} = 6.592$; df = 17.49; $p < 0.0001$
Speed, cm min^{-1}	0.19 ± 0.02 (0.12–0.37)	0.07 ± 0.02 (0.02–0.19)	Mann–Whitney U = 11.0; $p = 0.0019$

2