A crab swarm at an ecological hotspot: patchiness and population density from AUV observations at a coastal, tropical seamount

Jesús Pineda, Walter Cho, Victoria Starczak, Annette F. Govindarajan, Héctor M. Guzman, Yogesh Girdhar, Rusty C Holleman, James Churchill, Hanumant Singh, David K Ralston

A research cruise to Hannibal Bank, a seamount and an ecological hotspot in the coastal eastern tropical Pacific Ocean off Panama, explored the zonation, biodiversity, and the ecological processes that contribute to the seamount's elevated biomass. Here we describe the spatial structure of a benthic anomuran red crab population, using submarine video and autonomous underwater vehicle (AUV) photographs. High density aggregations and a swarm of red crabs were associated with a dense turbid layer 4-10 m above the bottom. The high density aggregations were constrained to 355-385 m water depth over the Southwest flank of the seamount, although the crabs also occurred at lower densities in shallower waters (~280 m) and in another location of the seamount. The crab aggregations occurred in hypoxic water, with oxygen levels of 0.04 ml/l. Barcoding of Hannibal red crabs, and pelagic red crabs sampled in a mass stranding event in 2015 at a beach in San Diego, California, USA, revealed that the Panamanian and the Californian crabs are likely the same species, *Pleuroncodes planipes*, and these findings represent an extension of the southern endrange of this species. Measurements along a 1.6 km transect revealed three high density aggregations, with the highest density up to 78 crabs/m^2, and that the crabs were patchily distributed. Crab density peaked in the middle of the patch, a density structure similar to that of swarming insects

1   **A crab swarm at an ecological hotspot: patchiness and population**

2   **density from AUV observations at a coastal, tropical seamount**

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Abstract

19   A research cruise to Hannibal Bank, a seamount and an ecological hotspot in the coastal

20   eastern tropical Pacific Ocean off Panama, explored the zonation, biodiversity, and the

21   ecological processes that contribute to the seamount's elevated biomass. Here we describe the

22   spatial structure of a benthic anomuran red crab population, using submarine video and

23   autonomous underwater vehicle (AUV) photographs. High density aggregations and a swarm of

24   red crabs were associated with a dense turbid layer 4-10 m above the bottom. The high density

25   aggregations were constrained to 355-385 m water depth over the Southwest flank of the

26   seamount, although the crabs also occurred at lower densities in shallower waters (~280 m) and

27   in another location of the seamount. The crab aggregations occurred in hypoxic water, with

28   oxygen levels of 0.04 ml/l. Barcoding of Hannibal red crabs, and pelagic red crabs sampled in a

29   mass stranding event in 2015 at a beach in San Diego, California, USA, revealed that the

30   Panamanian and the Californian crabs are likely the same species, *Pleuroncodes planipes*, and

31   these findings represent an extension of the southern endrange of this species. Measurements

32   along a 1.6 km transect revealed three high density aggregations, with the highest density up to

33   78 crabs/m^2, and that the crabs were patchily distributed. Crab density peaked in the middle of

34   the patch, a density structure similar to that of swarming insects.

Background

36   Seamounts are distinct oceanic habitats found in all oceans (Wessel et al. 2010), yet key

37   first-order ecological processes are not well understood (Clark et al. 2010). Communities of

38   benthic species on seamounts are regionally isolated, with elevated, shallow rocky habitat

39   patches surrounded by deep sedimentary plains. These two environmental axes, type of substrate

40   (hard vs. soft), and depth (gradients in food, light, and oxygen), create horizontal and vertical

41   patterns in faunal zonation (Pitcher et al. 2008; Thresher et al. 2014). These patterns are likely

42   determined regionally by circulation and larval dispersal, and vertically by physical factors and

43   biological interactions. In the pelagic environment, the trapping and concentration of pelagic

44   planktonic biomass around seamounts, due to hydrodynamic and behavioral processes, result in

45   local increase of predators -such as fish and marine mammals (Klimley et al. 2005; Morato et al.

46   2010; Morato et al. 2008). Thus, seamounts are ecological hotspots in the sense that many

47   biological and physical processes combine to produce high benthic and pelagic biomass, and

48   higher biodiversity. Seamounts are productive – their shallow summits have been fished for

49   centuries and the biomass of zooplankton is unusually high, but debate remains over the

50   mechanism of pelagic biomass enrichment. A commonly cited hypothesis is that zooplankton

51   and fish productivity result from phytoplankton growth due to topographic induced upwelling of

52   nutrients to euphotic waters, but the importance of this mechanism has been recently challenged

53   (Genin & Dower 2007). Seamounts harbor valuable yet slow growing resources, such as reef-

54   building corals (e.g., scleractinians), black corals (e.g., antipatharians), soft-corals (e.g.,

55   gorgonians), and fish, some of which can live over 100 years (e.g., orange roughy) (Koslow

56   1997). These habitats, however, have been under-sampled and under-studied, with less than 1%

57 of all seamounts explored (Clark et al. 2010). The occurrence of seamounts in open oceans

58 beyond national jurisdiction, and advances in deep-sea fishing practices have resulted in severe

59 anthropogenic pressure on seamount populations, which due to their life history characteristics

60 are amongst the least resilient populations in the marine environment (Koslow 1997; Schlacher

61 et al. 2010).

62   *Pleuroncodes planipes* (Stimpson, 1860) adult crabs, also known as red crabs, tuna crabs

63 and "langostilla", occur in pelagic waters and in deep continental shelf and continental slope

64 benthic habitats. Larvae and small individuals ($\sim$< 2.6 cm standard carapace length) tend to

65 dominate the pelagic fraction off western Baja California, with larger organisms occurring

66 exclusively in the benthos (Boyd 1967). Large individuals reproduce, but observations of pelagic

67 ovigerous females and their larvae in waters over bathyal and abyssal depths (~2000 – 3500 m)

68 suggests that a fraction of the pelagic population can reproduce as well (Longhurst & Seibert

69 1971). *P. planipes* can be extremely abundant, with accounts of dense pelagic patches up to 7 -

70 10 km (Gómez-Gutiérrez et al. 2000). (See also the casual account of a 16 km patch by B.

71 Shimada, quoted in Boyd 1967.) Off Baja California *P. planipes* is the main prey of large pelagic

72 predators such as yellowfin tuna and skipjack tuna (Alverson 1963). *P. planipes* is well adapted

73 to its pelagic lifestyle, where it can feed both on phytoplankton, by specialized filtration, and on

74 small zooplankton (Longhurst et al. 1967). On benthic habitats, galatheid crabs are deposit

75 feeders and scavangers (Lovrich & Thiel 2011; Nicol 1932). Benthic *P. planipes* ingest

76 particulate organic matter (detritus associated with sediments), phytoplankton cells, and small

77 crustaceans, foraminiferans and radiolarians (Aurioles-Gamboa & Pérez-Flores 1997). When

78   feeding on bottom sediments with diatoms, detritus and small organisms, galatheid crabs' "third

79   maxillipeds… act as brooms" (Nicol 1932), which would disturb and resuspend fine sediment.

80   Most studies on *Pleuroncodes planipes* have been done in pelagic waters, and have

81   provided little information on the benthic habitat. Boyd (1967) found that benthic *P. planipes*

82   ranged from ~100 to 300 m water depth off western Baja California, with smaller individuals

83   found in shallower bottoms, and population densities up to $11/m^2$. These distributions correlated

84   with oxygen minima waters, with oxygen levels below 0.5 ml/l. Boyd (1967) and Robinson and

85   Gómez-Gutiérrez (1998) found that some benthic individuals tend to migrate from the bottom to

86   the upper water column. The typical northern geographic endrange of *P. planipes* is somewhere

87   in Baja California. Intermittently, particularly during the El Niño phase of the El Niño Southern

88   Oscillation (ENSO), its geographic range expands northward to California (Longhurst 1966;

89   Smith 1985). The southernmost geographic endrange of *P. planipes* appears to be somewhere in

90   Costa Rica (Wicksten 2012), where it is thought to overlap with the southern range of

91   *Pleuroncodes monodon* (Macpherson et al. 2010; Wehrtmann et al. 2010; Wicksten 2012). The

92   center of abundance of pelagic *P. planipes* is in western Baja California (Brinton 1979; Gómez-

93   Gutiérrez et al. 2000; Longhurst 1968). The distribution and abundance of benthic *P. planipes* is

94   not well documented, particularly south of Baja California.

95   We present findings from a research cruise to Hannibal Bank, a coastal seamount in the

96   Gulf of Chiriquí, Eastern Tropical Pacific coastal ocean off Panama (Fig. 1). This cruise

97   explored the mechanisms that contribute to high densities of benthic and pelagic organisms in an

98   ecological hotspot and examined the seamount biodiversity and the benthic community zonation

99 along the depth gradient. Work included (a) submarine dives to collect, film and observe

100 firsthand the benthic habitats, with DNA extractions of collected organisms performed onboard,

101 (b) autonomous underwater vehicle (AUV) transects to map population densities of abundant

102 benthic fauna, and (c) hydrographic and velocity measurements over the seamount using a

103 conductivity, temperature, depth (CTD) and oxygen profiler and a hull-mounted acoustic

104 Doppler current profiler. Hannibal seamount and its shallow top, Hannibal Bank, are within the

105 recently created Coiba National Park, a [UNESCO World Heritage site](#), off the Pacific coast of

106 Panama. Hannibal Bank harbors abundant large fish sustaining artisanal fisheries, and is a

107 destination for international sport fishermen. The flat-topped triangular shaped seamount rises

108 from 450 m to ~40 m , occupying an area of 83 km^2 (Fig. 2). Proximate to the continental shelf

109 edge, it is ~20 km west of Coiba Island, 60 km from the main coast, and centered at about 07°

110 24' N - 82° 3' W (Cunningham et al. 2013). Hannibal seamount communities are likely

111 influenced by several physical processes, including synoptic upwelling from December to late

112 April (D'Croz & O'Dea 2007), low aragonite saturation state (Manzello et al. 2008), low oxygen

113 sub-thermocline waters, low salinity from runoff and precipitation (~3 m yearly precipitation),

114 sharp thermal stratification, large internal tides, and a 4 m tidal range (Dana 1975; Pineda et al.

115 2009; Starczak et al. 2011).

116  On the last dive of the research cruise we observed extraordinarily high densities of

117 anomuran galatheid crabs near the bottom of the seamount, and an associated turbid layer over

118 the bottom. The encounter was unexpected and mesmerizing., We documented these

119 observations with high definition video, a photo-transect, environmental water column

120 measurements and genetic analysis of crab samples. Here we report on these observations, and

121   address the following questions: What is the distribution of the crabs along a transect? What are

122   the patterns of variability in abundance within a patch? Is there a relationship between the turbid

123   layer and the crab aggregations? Are the crabs observed over the Hannibal Seamount the same

124   species as *Pleuroncodes planipes* found off of California?

125   **Methods**

126   The cruise onboard the M/V *Alucia* from 31 March to 20 April 2015 focused on Hannibal

127   Seamount. Work included ecological surveys over all flanks of the seamount (Fig. 2), and fifteen

128   submarine dives conducted with Nadir, a 3-person submarine, and 11 dives with RV2, a 2-person

129   submarine with more robust sampling capabilities than Nadir. On most missions, the submarines

130   surveyed starting from the bottom of the seamount and continued to the top, working in tandem,

131   within ~150 m of each other. Twelve transects with the Seabed autonomous underwater vehicle

132   (AUV) complemented the diving missions and surveyed similar areas, collecting benthic

133   imagery. On a typical cruise day, submarines were deployed during the morning and the Seabed

134   AUV in the evening. Here we focus on observations completed on 18 and 19 April 2015, when

135   crab aggregations were detected and studied. A conductivity, temperature, oxygen and depth

136   profile was taken from the M/V *Alucia* using a Seabird SBE19 plus CTD in the vicinity of the

137   submarine dive and Seabed AUV transect on 18 April 2015 (Fig. 2, blue cross in inset).

138   ***AUV observations and density estimation***

139   Seabed AUV conducted transects on the seamount, and obtained images to estimate

140   densities of bottom organisms. Designed specifically for optical imaging of the seafloor (Singh

141   et al. 2004b), the Seabed AUV has been used extensively for coral reef ecology, and other high

142   resolution imaging applications (Singh et al. 2004a; Williams et al. 2014). It is equipped with

143   high-dynamic range cameras (Singh et al. 2007)to provide species documentation via imagery

144   that can be corrected for the nonlinear attenuation of light in the water. Seabed AUV navigated at

145   a speed of ~20 – 25 cm /s and mean altitude of 3.5 – 4.5 m above the bottom along a predefined

146   track, adjusting its altitude using a high frequency acoustic Doppler profiler. Seabed took 1024

147   by 1380 pixel images of the seafloor that was illuminated with a strobe, and recorded

148   temperature, conductivity, depth, and altitude. The camera pixels are square and the field of view

149   is 45° in the horizontal and 33° in the vertical. Image width, x, is determined from altitude

150   (height above bottom), z, by noting that $0.5(x/z) = \mathrm{Tan}(45/2)$, which gives $x = 0.828z$. Because

151   the pixels are square, the image height, y, is proportional to the number of pixels; i.e.,

152    $y = x(1024/1380)$. AUV specific altitude is used for every image, and image area is calculated

153   as $x \cdot y$.

154   The Seabed AUV was programmed to take photographs every ~ 4 seconds, with image

155   overlap. We examined every third image (12 s interval), which gave a sequence with no image

156   overlap. The non-analyzed images were used to resolve ambiguities in identification. Images

157   were inspected for crabs and other organisms by eye, and all organisms were counted in each

158   image.

159   Species identification of the crabs was confirmed by DNA barcoding of individuals in

160   our samples (described below). Images from the Seabed AUV were light-corrected and inspected

161   for organisms and type of substrate. A catalog of organisms was created from the photographs,

162   and each morphospecies received a code. *Pleuroncodes planipes* were easily distinguished in the

163 video recording taken from the submarine dives, and in the Seabed AUV images. To estimate

164 crab density (#/m^2), the number of crabs was divided by estimated image area in each

165 photograph.

Patchiness estimate

167 Patchiness of *P. planipes* was estimated with I$_{mod}$ using the formula of Bez (2000)

168 modified by Décima and Ohman (2010). This index, based on Lloyd's index, considers a transect

169 that does not sample the entire range of the species:

$$
\text{I}_{\text{mod}} = \left[\frac{\sum_i z_i^2}{s \left(\sum_i z_i \right)^2} \right] N
$$

171 where z_i is the density of the crabs in a given image, s is the size of the sampling unit used in the

172 survey (mean quadrat size, 8.93 m^2), and N is the number of images analyzed. For comparison,

173 we also report the patchiness index of an unidentified stomatopod that was easily detected in the

174 photographs.

Seamount sample collection and genetic barcoding

176 The submarines collected benthic organisms opportunistically, using a robotic

177 manipulator arm, a net and a sediment scoop. (Ministerio del Ambiente de Panama permit #

178 SE/A-18-15) Collected specimens were stored in a compartmentalized honeycomb quiver or in a

179 larger "biobox". After the submarine dives, the sampled organisms were held in chilled seawater

180 until they were photographed and labelled (e.g., Fig. 3b), preliminary taxa identification based on

181   morphology was made, tissue was collected, and DNA extractions were performed onboard.

182   Here, we focus on *Pleuroncodes* crabs. DNA was extracted using the DNEasy extraction kits

183   (Qiagen) following the manufacturer's protocol. Upon return to the laboratory in Woods Hole,

184   we conducted a genetic barcoding analysis on the crabs. A portion of the mitochondrial

185   cytochrome c oxidase subunit I (COI) gene was amplified by PCR using the universal HCO-

186   2198 and LCO-1490primers (Folmer et al. 1994). PCR conditions were: 95°C for 3 minutes; 35

187   cycles of 95°C for 30 seconds, 48°C for 30 seconds, and 72°C for 1 minute; and 72°C for 5

188   minutes. PCR products were visualized on agarose gels stained with Sybr Safe (Life

189   Technologies). PCR products were purified using Qiaquick PCR purification kits (Qiagen) and

190   sequenced in both directions (MWG Eurofins Operon). Sequences were analyzed using the

191   Geneious v. 7.1.7 software platform (Biomatters). Because morphological and video examination

192   suggested that the crabs were *Pleuroncodes planipes*, we also sequenced COI from crabs

193   identified as *P. planipes* from California for comparison (collection details below). Hannibal and

194   California crab sequences were aligned with ClustalW (Larkin et al. 2007) using default

195   parameters. The ends of the alignment were trimmed so that the dataset was complete for all

196   taxa. Uncorrected p and Kimura 2-parameter distances were calculated and a neighbor-joining

197   tree was constructed in PAUP* (Swofford 2003).

198   ***Sample collection in a mass stranding event***

199   From January to August 2015 there were several mass stranding events of *Pleuroncodes*

200   *planipes* crabs on Southern California beaches, documented from news reports, the Lexis-Nexis

201   database, and informal surveys (J. Pineda, pers. obs., Table 1, *Supplemental Materials*). In June

202   2015, crabs were observed in a San Diego beach (S. Searcy, Univ. San Diego, pers. com., and J.

203   Pineda, pers. obs.), and most of the crabs on the beach were still alive. At False Point, La Jolla

204   (32°48' 28.51"N, 117°15'54.96"), we collected galatheid crabs on 2-5 June 2015, and preserved

205   them in ethanol to provide reference specimens for DNA barcoding of seamount crabs.

206   **Results**

207   ***Submarine observations and AUV mission***

208   On the last diving mission of the cruise, 18 April 2015, the two submarines dived to the

209   bottom by the westward flank of the seamount (Fig. 2). Upon approaching the bottom, a very

210   dense cloud of sediment was encountered; on no other submarine or AUV dive had such a dense

211   cloud been observed (Fig. 3a). Altitude soundings from the submarine indicated that the turbid

212   cloud extended 4 to 10 m over the ocean floor. As the submarine approached the bottom, a large

213   number of galatheid crabs were encountered. RV2 took 13 min and 40 sec high-definition video

214   of the crabs. A few still photographs and other video were taken from within the Nadir.

215   The video clips and photographs show that crabs were sometimes interacting among

216   themselves (e.g., facing each other pulling out a dead crab) and with other organisms, including a

217   sand eel. In some footage, crabs were sparsely distributed, and appeared to be sedentary. In other

218   footage, benthic crabs were very dense, touching adjacent crabs, with most crabs moving broadly

219   in the same direction (Fig. 3c and d) as a swarm (Video S1, Supplemental Materials). In this

220   footage, some crabs jumped and swam a few 10's of cm and landed in another spot. A crab

221   outside of the patch moved towards, and merged with the main patch (Fig. 3d). Sand eel, small

222   pelagic fish, shrimp, and a few stomatopods were in close proximity to the crab aggregation.

223   The population observed in the footage was composed of relatively large crabs, with no

224   visible smaller individuals, i.e., $\sim< 2.3$ cm carapace length. (See Fig. 3b for typical crabs, with ~

225   2.7 cm carapace length; carapace length as measured by Gómez-Gutiérrez et al 2000). For most

226   of the footage, the submarine hovered 2-3 m above the bottom, and the submarine and its lights

227   did not appear to affect the behavior of the crabs. The high turbidity immediately above the

228   bottom extended horizontally for at least 10's of m, and the turbid cloud appeared to be

229   associated with the crab patch. As the submarine moved up the seamount slope and abandoned

230   the patch, the density of crabs decreased abruptly, and the turbid cloud disappeared (Fig. 3d).

231   On 19 April 2015, the Seabed AUV was programmed to complete a photo-transect in the

232   same region as the crabs seen on 18 April. The AUV dived to about 325 m, and then completed a

233   1,610 m transect which included a set of turns to avoid potential high risk areas (e.g., rocky

234   pinnacles) (Fig. 2., inset) Mean image width and length for this transect were 3.46 and 2.57, m,

235   yielding a mean area per image of 8.93 m^2 (n = 580). Mean AUV altitude and speed was 4.18 m,

236   and 0.23 m/s. The 580 analyzed photos were taken at 12 s intervals, and consecutive images had

237   a gap of $2.78 - 2.57 = 0.21$ m . (See Fig. 4 for an image from the AUV, with the highest density

238   of crabs detected in the transect, 77.2 individuals / m^2).

***Pleuroncodes planipes* abundance**

240   *Pleuroncodes planipes* were detected in 12.2% of the Seabed AUV photographs. Images

241   with counts of *P. planipes* tended to center around 365-m water depth (Fig. 5). Crabs were rare

242   in the shallowest and deepest images, with bins centered at 305 and 405 m, although the number

243   of images from these depths was low. Peak densities, with up to 72.2 crabs/m^2, occurred at 360

244   – 380 depths (Fig. 7). Three high-density patches were constrained to depths between 362 and

245   381 m (Fig. 8, top panel), and were separated from each other by over 100's of meters along the

246   northing (latitudinal) axis (Fig. 8, lower panel). The distribution of abundance in these peaks

247   indicates that densities were low at the periphery, and that the maxima densities occur near the

248   middle of the patch (Fig. 9). The distribution of crabs along the transect was very patchy, with

249   I_{mod} = 5.34. Unidentified stomatopods that always occurred as singletons in the images had I_{mod} =

250   3.54. The turbid layer was not apparent in the Seabed AUV images.

251   ***Galatheid crabs DNA barcode ID***

252   We obtained COI sequences for 6 specimens from Hannibal seamount and 4 specimens

253   from the *Pleuroncodes planipes* stranding in California. Sequences were deposited in GenBank

254   (Hannibal, KU179422-26, KU179431; La Jolla, KU179427-30). Five out of the 6 Hannibal

255   specimens were obtained from the main crab swarm on 18 April 2015. The 6th specimen was

256   obtained on 3 April 2015, at a depth of 278 m, when crabs were observed on the bottom at the

257   Northeast flank of the seamount (near 7° 21.21' N, 82° 1.37' W) at low densities. The final

258   alignment for the combined seamount and California dataset was 595 base pairs. Inspection of

259   the amino acid translation indicated that the sequences did not represent pseudogenes. Sequences

260   differed from each other by between 1 to 8 base pairs. Uncorrected p and Kimura 2-parameter

261   distances were similar to each other and ranged from 0.00168 – 0.01363. There were no shared

262   haplotypes and the mean pairwise distance (for both metrics) between Hannibal specimens was

263   greater than the mean distance between Hannibal and California specimens (Table 1, Fig. 6).

264 *Water properties*

265   The CTD cast revealed strong temperature, salinity, and oxygen stratification (Fig. 10).

266 The temperature profile showed a sharp thermocline in the upper 40 m, with a temperature drop

267 from 28.5°C at the surface to 17.4°C at 40 m, and a near-bottom temperature of 11.1 °C at ~365

268 m. A halocline was also observed, with a salinity drop from 33.4 psu at the surface to 34.8 psu at

269 40 m. Maximum salinity occurred at mid depths (34.9 psu at 180 m), with a slight freshening

270 with increasing depth (to 34.8 psu at 365 m).

271   Oxygen concentration decreased rapidly with depth, from over 4.8 ml/l at the surface to

272 1.1 ml/l at 50 m, and was less than 1.0 ml/l deeper than 250 m. The lowest oxygen value, 0.04

273 ml/l, was obtained from the deepest measurement, 365 m, ~15 m above the bottom. Thus, *P.*

274 *planipes* maximum densities occurred at depths where waters were oxygen depleted. The vertical

275 gradients of temperature and oxygen concentration changed abruptly at about 238 m, with larger

276 gradients seen below 238 m. The vertical salinity also changed at around 238 m, but more subtly.

277 Beam attenuation data from the SBE CTD revealed a turbid layer around 365 m depth in which

278 optical attenuation tripled.

279 **Discussion**

280   Based on DNA barcoding, the Hannibal seamount crabs appear to be the same species as

281 *Pleuroncodes planipes* from California. COI is the most typically used species barcode gene

282 (Bucklin et al. 2011), and sequence comparisons are frequently based on Kimura 2-parameter

283 (K2P) distances (da Silva et al. 2011). K2P distances may not necessarily be the best distance

284 metric for a given taxon (Collins & Cruickshank 2013; Srivathsan & Meier 2012), other metrics

285   may not necessarily perform better and the use of this metric permits straightforward

286   comparisons with K2P distances from studies. Uncorrected p distances were similar to the K2P

287   distances, and in both metrics, the mean distance between individuals at Hannibal Seamount was

288   greater than the mean distance between Hannibal Seamount and California. Pairwise

289   mitochondrial COI distances fell within the range of typical intraspecific distances for galatheids

290   (da Silva et al. 2011). The southern range limit of *P. planipes* is considered poorly known

291   (Hendrickx & Harvey 1999), although researchers have suggested Costa Rica (Wicksten 2012),

292   and our observations here, supported by DNA sequences, may be the southernmost record.

293   Species have distinct patterns of variation in abundance over space, and understanding

294   the factors that determine these patterns and their diversity is a central goal in ecology. Spatial

295   distribution patterns may reflect individual and population processes, including settlement,

296   dispersal, migration (Roa & Tapia 2000) and behavior. For example, gregarious behavior and

297   swarming in insects may produce characteristic spatial patterns of abundance (Okubo & Chiang

298   1974). Whereas practically all organisms have patchy distributions at some spatial scale of

299   observation, the causes and consequences of patchiness can reflect fundamental ecological and

300   life history characteristics (Marquet et al. 1993). For example, patchiness can be species specific

301   and vary ontogenetically (Décima et al. 2010; Hewitt 1981), and species that face different

302   degrees of patchiness may have evolved different life history strategies (e.g. Dagg 1977).

303   Patchiness, may be driven by external ("vectorial", environmental), reproductive, social (e.g.

304   behavioral) and competitive ("coactive") processes (Hutchinson, 1953). Physical–biological

305   interactions, such as the swimming up response of zooplankton and larvae to downwelling

306   currents (Scotti & Pineda 2007), might also produce patchiness (e.g., aggregation at fronts), and

307   explain why only certain taxa aggregate in particular hydrodynamic settings.

308   The distribution of *Pleuroncodes planipes* was highly patchy, similar to other galatheid

309   populations (Freire et al. 1992; Roa & Tapia 2000), and I_{mod} values were higher than those of a

310   stomatopod that occurred at smaller densities than *P. planipes*. The high *P. planipes* densities

311   were constrained to a narrow subset of regions and depth ranges on Hannibal seamount. From

312   the 26 submarine dives (15 missions to distinct sites) and the 12 AUV transects, we observed

313   dense aggregations of crabs in only one region, the northwestern flank of the seamount, and

314   these aggregations were constrained to ~355 – 385 m water depths. The AUV survey detected

315   three peaks in abundance (*a-c,* Fig. 9), and in peak b, the observed density was 77 individuals /

316   m^2, one of the highest that have been measured for galatheid crabs (Lovrich & Thiel 2011, Table

317   6.1). Our sampling protocol cannot resolve whether these density peaks are discrete patches or

318   whether aggregations were connected. It is unlikely, however, that crabs in density peak *c* were

319   connected to crabs in peak *b*, because crab distributions were observed to be constrained to 355-

320   385 m, and the crabs in *b* and *c* were separated by shallower depths (Figs. 2 and 8).

321   The density distribution within each of the three abundance peaks detected in the survey

322   is consistent with a pattern where density increases toward the center of distribution (Fig. 9).

323   However, we do not know whether the AUV surveyed the center of the patch. The two high-

324   density peaks at ~480 and 1440 m along the transect (Figs. 9a and 9c) each have an adjoining

325   lower-density peak. These lower-density peaks may represent budding, small aggregations that

326   have split from the main aggregation, and might grow into larger patches, or they might merge

327 into the larger, adjacent patch. These density distribution patterns are likely due to aggregation

328 driven by the crab's gregarious behavior, and coordinated movement of the aggregation, a

329 phenomenon that has been called swarming. Okubo et al. (2001) describe swarming as a

330 phenomenon where a group of organisms move together. Swarms are arguably one of the few

331 ecological phenomena that possess emergent properties, where the characteristics of the

332 aggregation cannot be simply explained by adding the individual's behaviors (Parrish &

333 Edelstein-Keshet 1999). In these complex systems, a focus on individual behavior is unlikely to

334 explain the properties of the swarm. Whether all emergent properties in swarms are functional or

335 not, is an open question (Parrish & Edelstein-Keshet 1999). The increase in density towards the

336 center is consistent with other organisms that form swarms and aggregations (e.g., insects, krill

337 and schooling fish, Okubo & Chiang 1974; Okubo et al. 2001), and patterns of abundance in

338 other gregarious benthic populations where density increases towards the middle of the

339 distribution might reveal a swarming behavior. Two other galatheid species have patterns where

340 density increases towards the middle of the patch (Freire et al. 1992) but in these European

341 *Munida* spp. species, the scale of the patches is a few tens of kilometers, compared to the ~100 m

342 scale observed in our study. It is unclear whether the abundance structure of these *Munida* spp.

343 and *Pleuroncodes planipes* patches are caused by the same processes. Dense benthic

344 aggregations of other species of anomuran and brachyuran crabs (king crabs, spider crabs, tanner

345 crabs, lyre crabs) have been observed, and some were related to reproduction (DeGoursey &

346 Auster 1992; Powell & Nickerson 1965; Stevens et al. 1992; Stevens et al. 1994).

347 Crabs densities appeared to be higher and more clumped in the submarine video

348 observations than in the AUV images (compare submarine video still frame Fig. 3 with AUV

349   Fig. 4). The submarine video still frames in Fig. 3 were taken when *Pleuroncodes planipes* were

350   moving as a group, a swarm, and most organisms appeared to be oriented in the same direction.

351   In the AUV images, a consistent crab orientation and the swarm motion were not obvious.

352   Moreover, the turbid cloud observed from the submarine (Fig. 3) was not seen in any of the

353   AUV images. The turbidity cloud was most likely produced by *Pleuroncodes planipes* activities,

354   as the turbidity disappeared at the edge of the patch, and was not observed outside of the patch or

355   in any other submarine dive or AUV missions. Diurnal patterns of activity might explain the

356   differences in turbidity. Submarine observations were early in the day, whereas the AUV survey

357   was done in the evening. However, another possibility is that crabs observed from the submarine

358   were in a location with finer, and hence more easily suspended sediments than those surveyed by

359   the AUV survey. However, the locations not far from each other (Fig. 2).

360   The resuspension of sediment initiated by crab activity may affect the benthic

361   environment over the northwest seamount flank. Feeding of king crabs in waters ~3m deep off

362   Kodiak Island, Alaska, resulted in a dense cloud of turbid water (Bradley & Stephen 2014), and

363   Yahel (2008) found that bottom fish activity was an important mechanism for sediment

364   resuspension and remineralization of organic matter between water depths of ~ 60 and 140-m in

365   Saanich Inlet (Vancouver Island, BC, Canada).

366   *Pleuroncodes planipes* occurred at water depths with very low oxygen (0.04 ml/l at ~15

367   m above the bottom where the crabs were observed). The affinity of some galatheids to low

368   oxygen waters, and *P. planipes* in particular, is known (Boyd 1967; Lovrich & Thiel 2011).

369   Depth distribution of *P. planipes* and other galatheids might be related to these low oxygen

370   levels (discussed by Lovrich & Thiel 2011), but more study is needed to test this hypothesis.

371   *Pleuroncodes planipes* occurs in very high densities in the pelagic environment, and this

372   species mass strands yearly in shallow water and intertidal beaches near the center of its pelagic

373   abundance, Bahía Magdalena, Baja California (Aurioles-Gaamboa et al. 1994), and more

374   occasionally on California beaches (Table 1, Longhurst 1966; Smith 1985). While we were on

375   hydrographic stations over Hannibal seamount and surrounding areas, we occasionally observed

376   organisms that appeared to be pelagic red crabs swimming swiftly by the stern of the boat at

377   night, illuminated by the vessel lights. Despite multiple attempts, we were not able to capture a

378   specimen to assess its identity, so the occurrence of *P. planipes* in the water column above

379   Hannibal seamount is unknown.

380   Our observations in Panama were conducted at roughly the same time when mass

381   stranding events were registered in Southern California (Table 1, *Supplemental Material*), and

382   the Hannibal and Californian individuals appear to be the same species based on their mtCOI

383   sequences. Mass stranding of *Pleuroncodes planipes* in Southern California beaches had been

384   linked to El Niño (Smith 1985). A full El Niño had not been declared for January-June 2015,

385   when many stranding events were reported (Table 1, *Supplemental Material*). On the other hand,

386   an unusually large pool of warm water developed in late 2013 and early 2014 in the coastal

387   temperate eastern Pacific, and persisted through much of 2015 (Bond et al. 2015), apparently

388   unrelated to El Niño. The current forecast (November 2015, by NOAA Climate Prediction

389   Center), indicate that the anomalous warm-water pool condition has been followed by an El

390   Niño, and that a full El Niño is now in progress. The "pool or warm water" conditions in

391   January-June 2015 may be related to anomalously warm waters observed in Southern

392   California's nearshore in fall 2014 (Reyns, Pineda, and Lentz, unpub.). These conditions may

393   help explain the appearance of *P. planipes* in Southern California, as speculated by some news

394   outlets. Whereas it is unlikely that that our observations of benthic aggregations at Hannibal are

395   connected with the California mass stranding events, it is significant that *P. planipes* can be

396   simultaneously abundant at the two distant locations and at two different habitats. The high

397   densities of *P. planipes* likely impacted local pelagic, intertidal, and deep seamount food webs.

398   Allochthonous supply of biomass, where resources from one habitat or ecosystem

399   subsidizes another system, influences local population community and dynamics (Polis et al.

400   1997). Moreover, the episodic availability of large quantities of biomass to benthic and pelagic

401   organisms and marine mammals, including the supply of terrestrial material and whale carcasses

402   to benthic deep sea communities, the mass stranding of pelagic organisms in shallow habitats,

403   and the sudden availability of a new resource, represent an opportunistic yet important source of

404   nutrition to the "receiving" communities (Polis et al. 1997), and can influence food web structure

405   and demographic rates (Watt et al. 2000). The massive availability of *Pleuroncodes planipes*

406   might influence diverse food webs.

407   Because of its pelagic and benthic lifestyle, and its abundance, *Pleuroncodes planipes*

408   likely plays an important role in some seamount, continental shelf and shallow water food webs

409   in the subtropical and sub temperate eastern Pacific. Several authors have noticed the key role of

410   *P. planipes* in the pelagic environment, by virtue of its abundance and trophic role (Alverson

411 1963; Gómez-Gutiérrez et al. 2000; Longhurst 1966; Longhurst et al. 1967; Robinson et al.

412 2004). *P. planipes* was patchy but very abundant at Hannibal, and it might represent an important

413 resource for pelagic predators at the seamount. More research is needed to assess the distribution

414 and abundance of benthic *P. planipes*, as well as its potentially key role in semitropical and sub-

415 temperate eastern Pacific seamount and continental shelf habitats.

416 **Acknowledgements**

417   We would like to express gratitude for the help and logistical support of the Captain and

418 the crew of the M/V *Alucia*, the *Alucia'*s submarine team, Jeff Anderson, for programming and

419 running the AUV operations, and keeping it safe, Alex Bocconcelli and WHOI's Marine

420 Operations office support, the Ministerio del Ambiente de Panama for providing the research and

421 export permits, including # SE/A-18-15, and the US State Department for cruise permit support.

422 Bathymetric data in Figure 1 derived from the GEBCO_2014 Grid, www.gebco.net.

423 **References**

424 Alverson F. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean.

425   *Inter-Am Trop Tuna Comm Bull* 7:295-367.

426 Aurioles-Gaamboa D, Castro-Gonzalez MI, and Perez-Flores R. 1994. Annual mass strandings

427   of pelagic red crabs, *Pleuroncodes planipes* (Crustacea, Anomura, Galatheidae), in Bahia

428   Magdalena, Baja California Sur, Mexico. *Fishery Bulletin* 92:464-470.

429 Aurioles-Gamboa D, and Pérez-Flores R. 1997. Seasonal and bathymetric changes in feeding

430   habits of the benthic red crab *Pleuroncodes planipes* (Decapoda, Anomura, Galatheidae)

431   off the Pacific coast of Baja California Sur, Mexico. *Crustaceana* 70:272-287.

432 Bez N. 2000. On the use of Lloyd's index of patchiness. *Fisheries Oceanography* 9:372-376.

433   DOI 10.1046/j.1365-2419.2000.00148.x

434 Bond NA, Cronin MF, Freeland H, and Mantua N. 2015. Causes and impacts of the 2014 warm

435   anomaly in the NE Pacific. *Geophysical Research Letters* 42:2015GL063306.

436   10.1002/2015GL063306

437 Boyd CM. 1967. The benthic and pelagic habitats of red crab *Pleuroncodes planipes*. *Pacific*

438   *Science* 21:394-&.

439 Bradley GS, and Stephen CJ. 2014. Growth, molting, and feeding of king crabs. In: Bradley GS,

440   ed. *King Crabs of the World Biology and Fisheries Management*: CRC Press, 315-362.

441   Brinton E. 1979. Parameters relating to the distributions of planktonic organisms, especially

442   Euphausiids in the eastern tropical Pacific. *Progress in Oceanography* 8:125-189.

443   Bucklin A, Steinke D, and Blanco-Bercial L. 2011. DNA barcoding of marine metazoa. *Annual*

444   *Review of Marine Science, Vol 3* 3:471-508. DOI 10.1146/annurev-marine-120308-

445   080950

446   Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, Rogers AD, O'Hara

447   TD, White M, Shank TM, and Hall-Spencer JM. 2010. The ecology of seamounts:

448   structure, function, and human impacts. *Annual Review of Marine Science* 2:253-278.

449   Collins R, and Cruickshank R. 2013. The seven deadly sins of DNA barcoding. *Molecular*

450   *ecology resources* 13:969-975.

451   Cunningham SL, Guzman HM, and Bates RC. 2013. The morphology and structure of the

452   Hannibal Bank fisheries management zone, Pacific Panama using acoustic seabed

453   mapping. *Rev Biol Trop* 61:1967-1979.

454   D'Croz L, and O'Dea A. 2007. Variability in upwelling along the Pacific shelf of Panama and

455   implications for the distribution of nutrients and chlorophyll. *Estuarine, Coastal and*

456   *Shelf Science* 73:325-340.

457   da Silva JM, Creer S, Dos Santos A, Costa AC, Cunha MR, Costa FO, and Carvalho GR. 2011.

458   Systematic and evolutionary insights derived from mtDNA COI barcode diversity in the

459   Decapoda (Crustacea: Malacostraca). *Public Library of Science ONE* 6:e19449.

460   Dagg M. 1977. Some effects of patchy food environments on copepods. *Limnology and*
461   *Oceanography* 22:99-107.

462   Dana TF. 1975. Development of contemporary Eastern Pacific coral reefs. *Marine Biology*
463   33:355-374.

464   Décima M, Ohman MD, and De Robertis A. 2010. Body size dependence of euphausiid spatial
465   patchiness. *Limnology and Oceanography* 55:777-788.

466   DeGoursey RE, and Auster PJ. 1992. A mating aggregation of the spider crab (*Libinia*
467   *emarginata*). *Journal of Northwest Atlantic Fishery Science* 13:77-82.

468   Folmer O, Black M, Hoeh W, Lutz RA, and Vrijenhoek R. 1994. DNA primers for amplification
469   of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates.
470   *Molecular Marine Biology and Biotechnology* 3:294-299.

471   Freire J, González-Gurriarán E, and Olaso I. 1992. Spatial distribution of *Munida intermedia* and
472   *M. sarsi* (Crustacea: Anomura) on the Galician continental shelf (NW Spain): application
473   of geostatistical analysis. *Estuarine, Coastal and Shelf Science* 35:637-648.

474   Genin A, and Dower JF. 2007. Seamount plankton dynamics. In: Pitcher T, Morato T, Hart P,
475   Clark M, Haggan N, and Santos R, eds. *Seamounts: Ecology, Fisheries, and*
476   *Conservation*. Oxford, UK: Blackwell, 85-100.

477   Gómez-Gutiérrez J, Domínguez-Hernández E, Robinson CJ, and Arenas V. 2000.
478   Hydroacoustical evidence of autumn inshore residence of the pelagic red crab

479   *Pleuroncodes planipes* at Punta Eugenia, Baja California, Mexico. *Marine Ecology*

480   *Progress Series* 208:283-291.

481   Hendrickx ME, and Harvey AW. 1999. Checklist of anomuran crabs (Crustacea: Decapoda)

482   from the eastern tropical Pacific. *Belgian Journal of Zoology* 129:363-389.

483   Hewitt R. 1981. The value of pattern in the distribution of young fish. *Reun Cons int Explor Mer,*

484   178:229-236.

485   Klimley A, Richert JE, and Jorgensen SJ. 2005. The home of blue water fish. *American Scientist*

486   93:42-49.

487   Koslow JA. 1997. Seamounts and the ecology of deep-sea fisheries. *American Scientist* 85:168-

488   176.

489   Larkin MA, Blackshields G, Brown N, Chenna R, McGettigan PA, McWilliam H, Valentin F,

490   Wallace IM, Wilm A, and Lopez R. 2007. Clustal W and Clustal X version 2.0.

491   *Bioinformatics* 23:2947-2948.

492   Longhurst AR. 1966. The pelagic phase of *Pleuroncodes planipes* Stimpson (Crustacea,

493   Galatheidae) in the California Current. *CalCOFI Reports* XI:142-154.

494   Longhurst AR. 1968. The biology of mass occurrences of Galatheid crustaceans and their

495   utilization as a fisheries resource. In: Mistakidis MN, editor. Proceeding of the world

496   scientific conference on the biology and culture of shrimps and prawns FAO Fisheries

497   Reports Vol 57. Mexico City. p 95-110.

498   Longhurst AR, Lorenzen CJ, and Thomas WH. 1967. The role of pelagic crags in the grazing of

499   phytoplankton off Baja California. *Ecology* 48:190-200. 10.2307/1933100

500   Longhurst AR, and Seibert DLR. 1971. Breeding in an oceanic population of *Pleuroncodes*

501   *planipes* (Crustacea, Galatheidae). *Pacific Science* 25:426-&.

502   Lovrich GA, and Thiel M. 2011. Ecology, physiology, feeding and trophic role of squat lobsters.

503   In: Poore GCB, Ahyong, S.T., Taylor, J., ed. *The biology of squat lobsters*. Boca Raton:

504   RRC Press, 183-222.

505   Macpherson E, de Forges BR, Schnabel K, Samadi S, Boisselier MC, and Garcia-Rubies A.

506   2010. Biogeography of the deep-sea galatheid squat lobsters of the Pacific Ocean. *Deep-*

507   *Sea Research Part I-Oceanographic Research Papers* 57:228-238.

508   10.1016/j.dsr.2009.11.002

509   Manzello DP, Kleypas JA, Budd DA, Eakin CM, Glynn PW, and Langdon C. 2008. Poorly

510   cemented coral reefs of the eastern tropical Pacific: Possible insights into reef

511   development in a high-CO_2 world. *Proceedings of the National Academy of Sciences*

512   105:10450-10455. 10.1073/pnas.0712167105

513   Marquet P, Fortin MJ, Pineda J, Wallin DO, Clark J, Wu Y, Bollens S, Jacobi C, and Holt RD.

514   1993. Ecological and evolutionary consequences of patchiness: a marine-terrestrial

515   perspective. In: Levin SA, Powell TM, and Steele JH, eds. *Patch Dynamics*. Berlin:

516   Springer-Verlag, 277-304.

517   Morato T, Hoyle SD, Allain V, and Nicol SJ. 2010. Seamounts are hotspots of pelagic

518   biodiversity in the open ocean. *Proceedings of the National Academy of Sciences*

519   107:9707-9711.

520   Morato T, Varkey DA, Damaso C, Machete M, Santos M, Prieto R, Santos RS, and Pitcher TJ.

521   2008. Evidence of a seamount effect on aggregating visitors. *Marine Ecology Progress*

522   *Series* 357:23.

523   Nicol EAT. 1932. The feeding habits of the Galatheidae. *Journal of the Marine Biological*

524   *Association of the United Kingdom* 18:87-106.

525   Okubo A, and Chiang HC. 1974. An analysis of the kinematics of swarming of *Anarete*

526   *pritchardi* Kim (Diptera: Cecidomyiidae). *Researches on Population Ecology* 16:1-42.

527   10.1007/BF02514077

528   Okubo A, Grünbaum D, and Edelstein-Keshet L. 2001. The dynamics of animal grouping. In:

529   Levin SA, ed. *Diffusion and Ecological Problems: Modern Perspectives*: Springer New

530   York, 197-237.

531   Parrish JK, and Edelstein-Keshet L. 1999. Complexity, Pattern, and Evolutionary Trade-Offs in

532   Animal Aggregation. *Science* 284:99-101. 10.1126/science.284.5411.99

533   Pineda J, Reyns N, and Starczak VR. 2009. Complexity and simplification in understanding

534   recruitment in benthic populations. *Population ecology* 51:17-32. 10.1007/s10144-008-

535   0118-0

536   Pitcher TJ, Morato T, Hart PJ, Clark MR, Haggan N, and Santos RS. 2008. *Seamounts: ecology,*

537   *fisheries & conservation*. Oxford, UK: Blackwell Publishing.

538   Polis GA, Anderson WB, and Holt RD. 1997. Toward an integration of landscape and food web

539   ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and*

540   *Systematics*:289-316.

541   Powell GC, and Nickerson RB. 1965. Aggregations among juvenile king crabs (*Paralithodes*

542   *camtschatica*, Tilesius) Kodiak, Alaska. *Animal behaviour* 13:374-IN310.

543   Roa R, and Tapia F. 2000. Cohorts in space: geostatistical mapping of the age structure of the

544   squat lobster *Pleuroncodes monodon* population off central Chile. *Marine Ecology*

545   *Progress Series* 196:239-251.

546   Robinson CJ, Anislado V, and Lopez A. 2004. The pelagic red crab (*Pleuroncodes planipes*)

547   related to active upwelling sites in the California Current off the west coast of Baja

548   California. *Deep Sea Research Part II: Topical Studies in Oceanography* 51:753-766.

549   http://dx.doi.org/10.1016/j.dsr2.2004.05.018

550   Robinson CJ, and Goómez-Gutieérrez J. 1998. The red-crab bloom off the west coast of Baja

551   California, Mexico. *Journal of Plankton Research* 20:2009-2016.

552   Schlacher TA, Rowden AA, Dower JF, and Consalvey M. 2010. Seamount science scales

553   undersea mountains: new research and outlook. *Marine Ecology* 31:1-13. 10.1111/j.1439-

554   0485.2010.00396.x

555 Scotti A, and Pineda J. 2007. Plankton accumulation and transport in propagating nonlinear
556   internal fronts. *Journal of Marine Research* 65:117-145. 10.1357/002224007780388702

557 Singh H, Armstrong R, Gilbes F, Eustice R, Roman C, Pizarro O, and Torres J. 2004a. Imaging
558   coral I: Imaging coral habitats with the SeaBED AUV. *Subsurface Sensing Technologies*
559   *and Applications* 5:25-42.

560 Singh H, Can A, Eustice R, Lerner S, McPhee N, and Roman C. 2004b. Seabed AUV offers new
561   platform for high-resolution imaging. *Eos, Transactions American Geophysical Union*
562   85:289-296.

563 Singh H, Roman C, Pizarro O, Eustice R, and Can A. 2007. Towards high-resolution imaging
564   from underwater vehicles. *The International journal of robotics research* 26:55-74.

565 Smith PE. 1985. A case history of an anti-Niño transition plankton and nekton distribution and
566   abundances. In: Wooster WS, and David LF, eds. *El Niño North: Niño effects in the*
567   *eastern subarctic Pacific Ocean*. Seattler: Washingthon Sea Grant, 121-142.

568 Srivathsan A, and Meier R. 2012. On the inappropriate use of Kimura-2-parameter (K2P)
569   divergences in the DNA-barcoding literature. *Cladistics* 28:190-194.

570 Starczak VR, Pérez-Brunius P, Levine HE, Gyory J, and Pineda J. 2011. The role of season and
571   salinity in influencing barnacle distribution in two adjacent coastal mangrove lagoons.
572   *Bulletin of Marine Science* 87:275-299. doi:10.5343/bms.2010.1022

573   Stevens BG, Donaldson WE, and Haaga JA. 1992. First observations of podding behavior for the

574   Pacific Lyre crab *Hyas lyratus* (Decapoda: Majidae). *Journal of Crustacean Biology*

575   12:193-195. 10.2307/1549074

576   Stevens BG, Haaga JA, and Donaldson WE. 1994. Aggregative mating of Tanner crabs,

577   *Chionoecetes bairdi. Canadian Journal of Fisheries and Aquatic Sciences* 51:1273-1280.

578   Swofford DL. 2003. PAUP*. Phylogenetic analysis using parsimony (*and other methods).

579   Version 4. *Sunderland, MA: Sinauer Associates.*

580   Thresher R, Althaus F, Adkins J, Gowlett-Holmes K, Alderslade P, Dowdney J, Cho W, Gagnon

581   A, Staples D, and McEnnulty F. 2014. Strong depth-related zonation of megabenthos on

582   a rocky continental margin (∼ 700–4000 m) off southern Tasmania, Australia. *PLoS ONE*

583   9:Art. No. e85872.

584   Watt J, Siniff DB, and Estes JA. 2000. Inter-decadal patterns of population and dietary change in

585   sea otters at Amchitka Island, Alaska. *Oecologia (Berl)* 124:289-298. 10.2307/4222695

586   Wehrtmann IS, Herrera-Correal J, Vargas R, and P. H. 2010. Squat lobsters (Decapoda:

587   Anomura: Galatheidae) from deepwater Pacific Costa Rica: species diversity, spatial and

588   bathymetric distribution. *Nauplius* 18:69-77.

589   Wessel P, Sandwell DT, and Kim SS. 2010. The global seamount census. *Oceanography* 23:24-

590   33.

591   Wicksten MK. 2012. Decapod Crustacea of the Californian and Oregonian zoogeographic

592   provinces. *Zootaxa* 3371:1-307.

593   Williams G, Maksym T, Wilkinson J, Kunz C, Murphy C, Kimball P, and Singh H. 2014. Thick

594   and deformed Antarctic sea ice mapped with autonomous underwater vehicles. *Nature*

595   *Geoscience*.

596   Yahel G, Yahel R, Katz T, Lazar B, Herut B, and Tunnicliffe V. 2008. Fish activity: a major

597   mechanism for sediment resuspension and organic matter remineralization in coastal

598   marine sediments. *Marine Ecology Progress Series* 372:195-209.

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602 **Tables**

603 Table 1. Pairwise distance comparisons for uncorrected p and K2P distance metrics. Minimum

604 and maximum pairwise distances (for all comparisons) and the mean distances for pairs within

605 and between sampling localities are shown.

	Minimum	Maximum	Within - Hannibal mean	Within - California mean	Hannibal - California mean
Uncorrected p	0.00168	0.01513	0.01042	0.00336	0.00732
K2P	0.00168	0.01536	0.01055	0.00337	0.00734

606
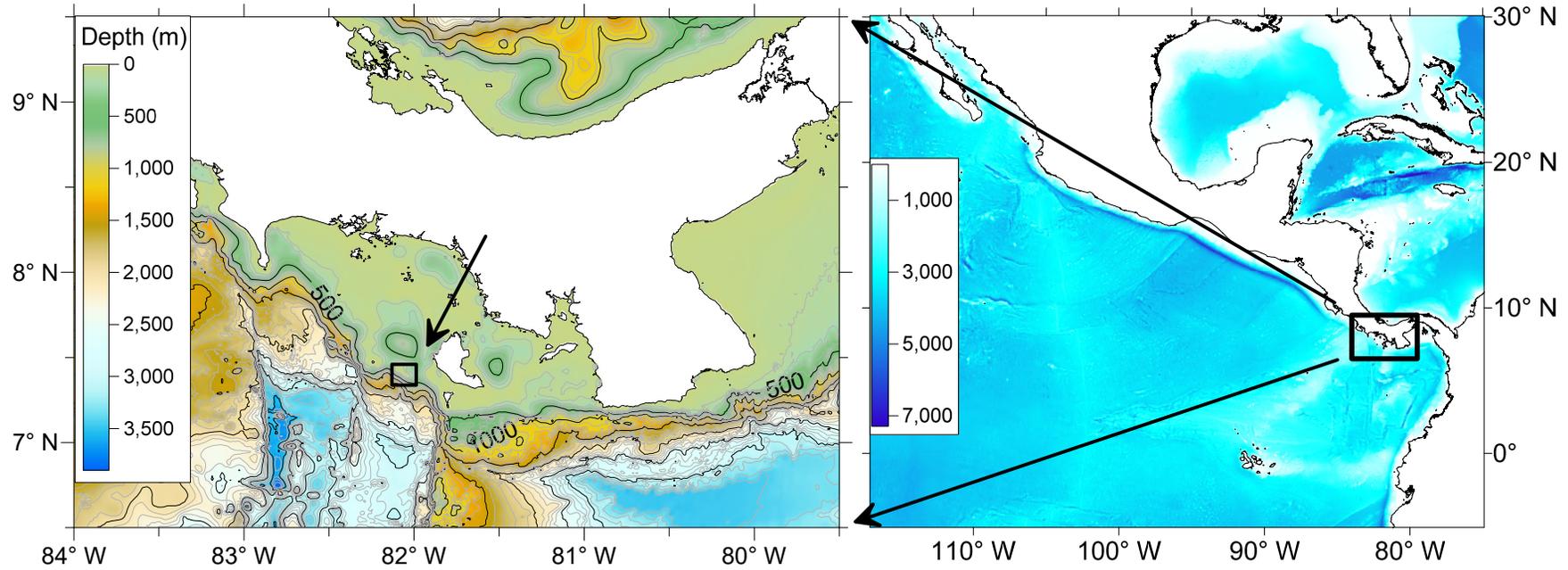
Fig 1. Map of the study area. Box in the right panel encloses the left panel, and the small box in the left panel encloses Hannibal Seamount. Bathymetry data from GEBCO.
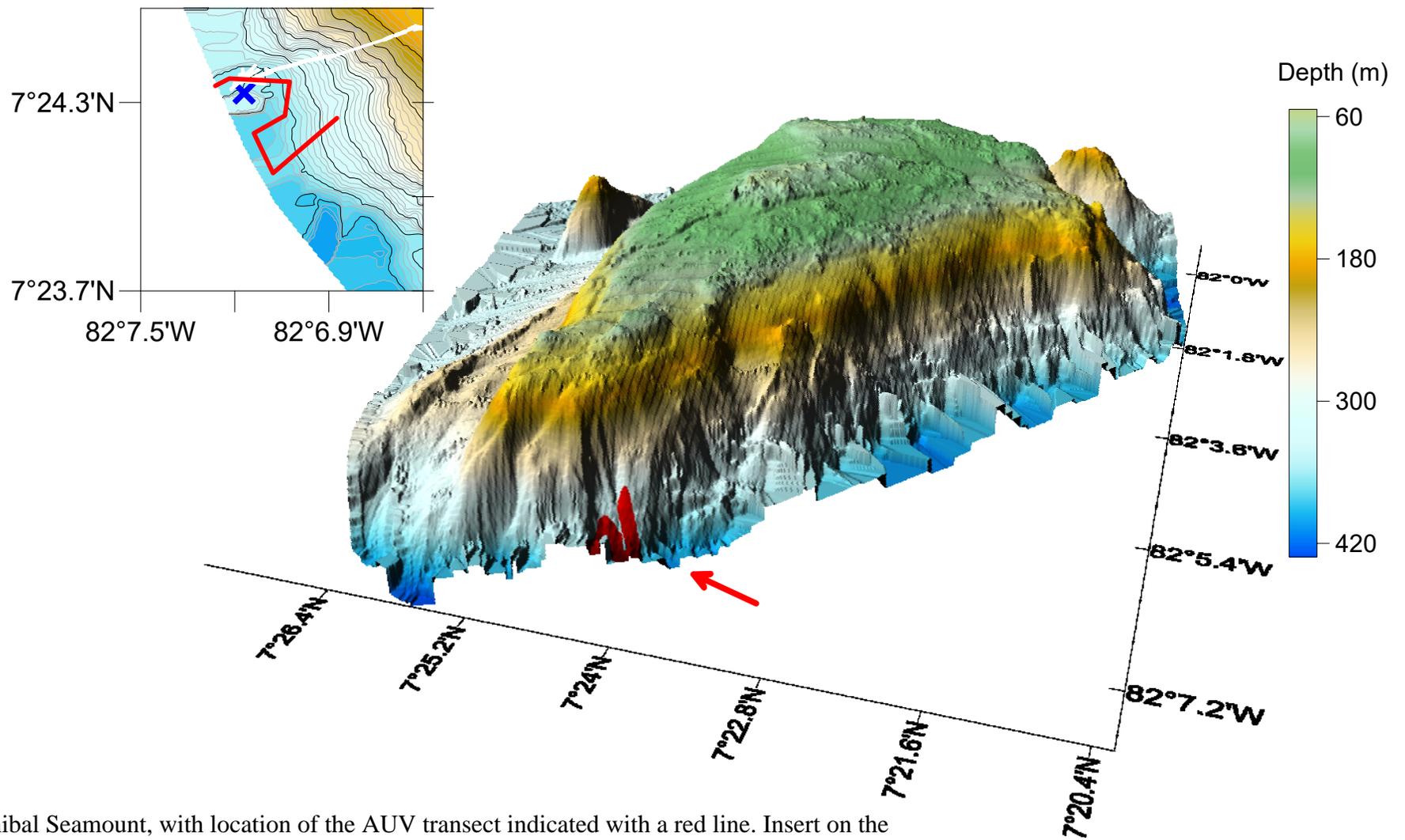
Fig. 2. Hannibal Seamount, with location of the AUV transect indicated with a red line. Insert on the left delineates AUV transect, with end of transect near the blue cross. The blue cross indicates the location of the CTD cast, and the submarine positions are in white. Depth data from Cunningham et al. (2013).
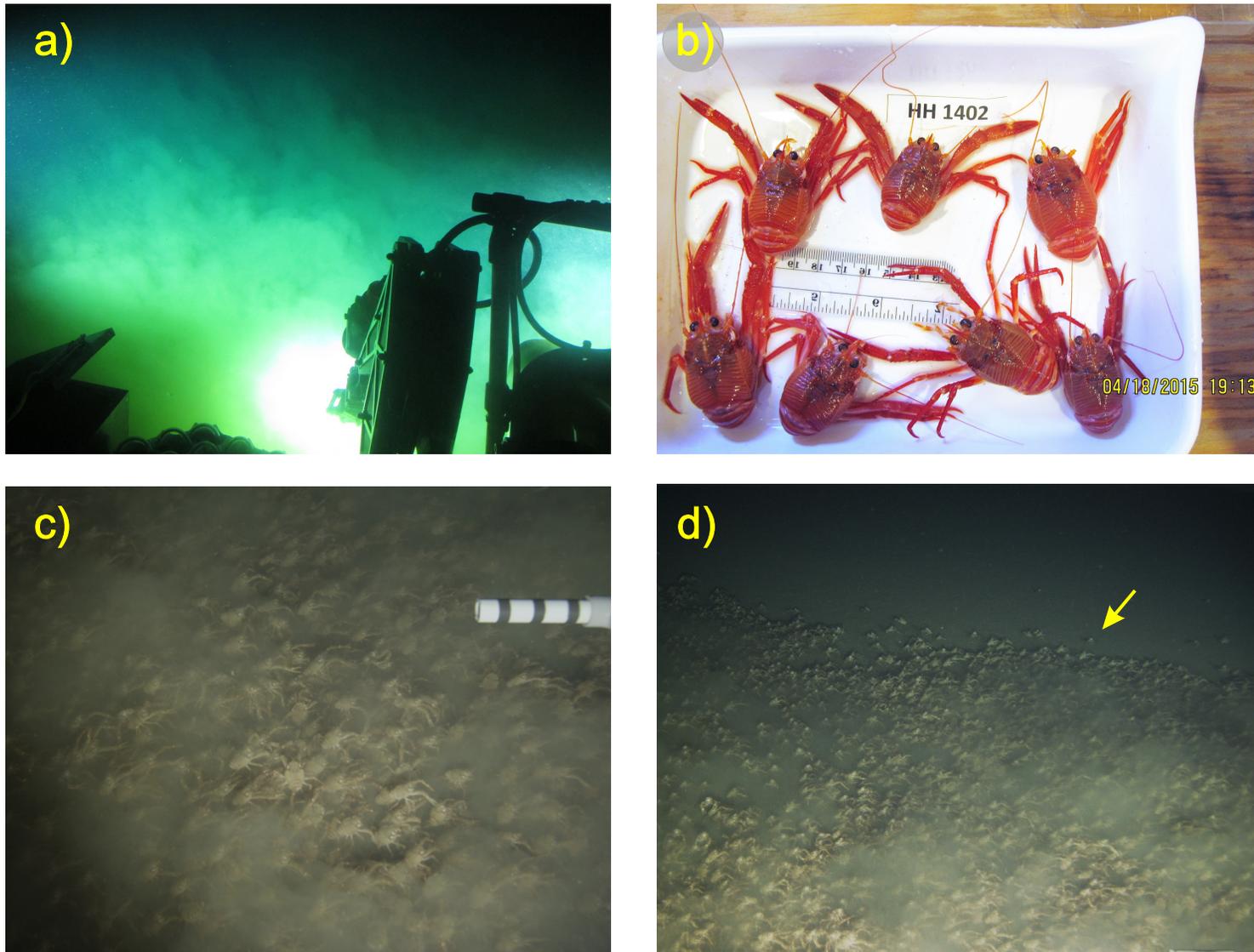
Fig. 3. Photographs and video still frames of Pleuroncodes planipes and its environment. a) Image taken within Nadir as it approached the bottom, from about 6 m above the bottom, where P. planipes aggregations were first found. b) Pleuroncodes planipes collected from the aggregation, with ruler scale in cm and English units. c) Still frame from HD video of a dense patch of P. planipes on the bottom. The white PVC segment is about 20.5 cm long d) Nearbed turbidity dropped at the edges of the Pleuroncodes patch. In the video the crabs were moving on the bottom towards the right, with a few crabs found beyond the boundary of the patch lagging behind the main aggregation. The crab marked with a yellow arrow was separate from the large patch and then merged into the patch by advancing in a direction perpendicular to the direction of patch movement.

Fig. 4. AUV photograph with the highest density of Pleuroncodes planipes.
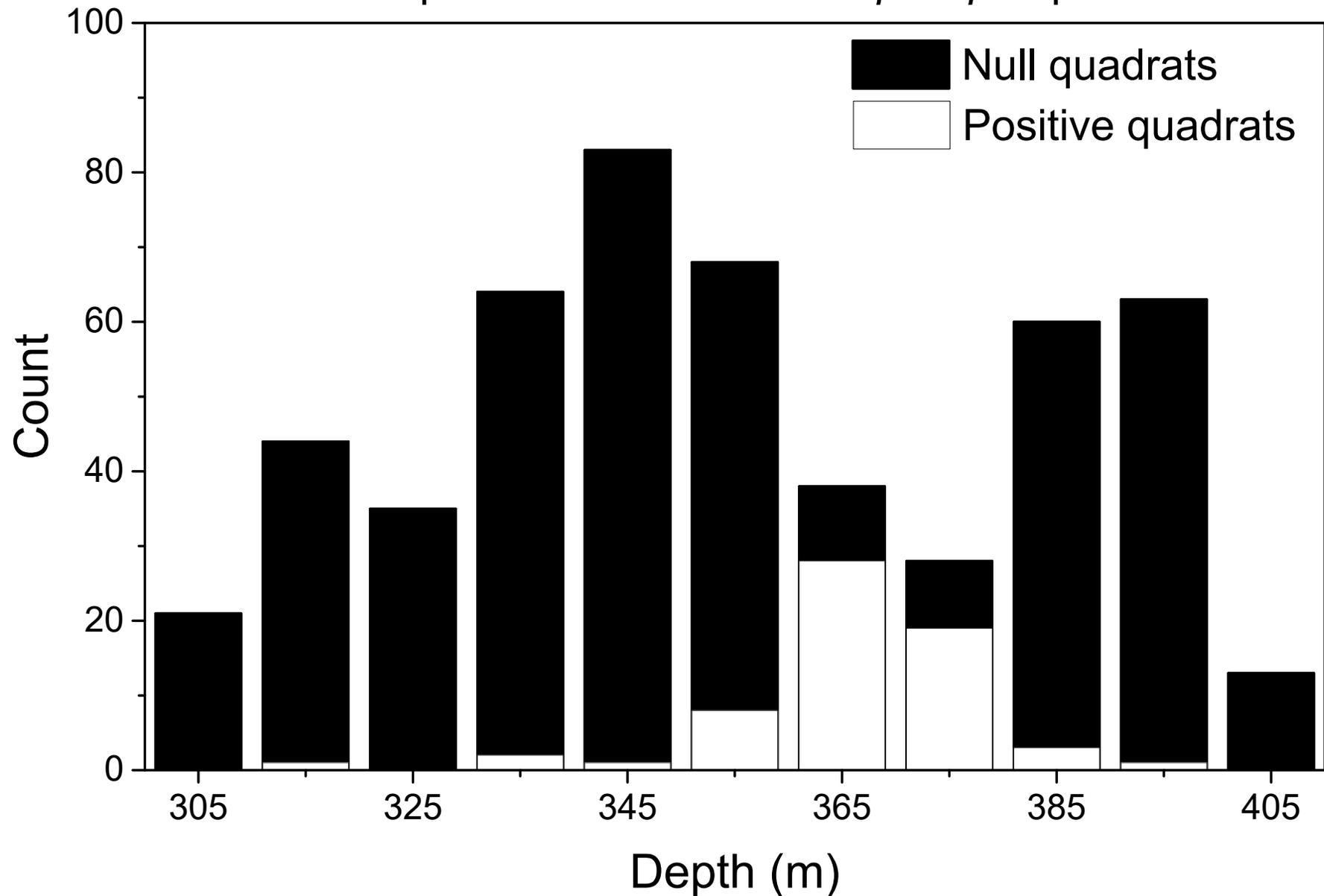
Fig. 5 Frequency distribution of quadrats with null and positive Pleuroncodes planipes counts. No P. planipes occurred in null quadrats, whereas positive quadrats are those in which at least one P. planipes was observed.
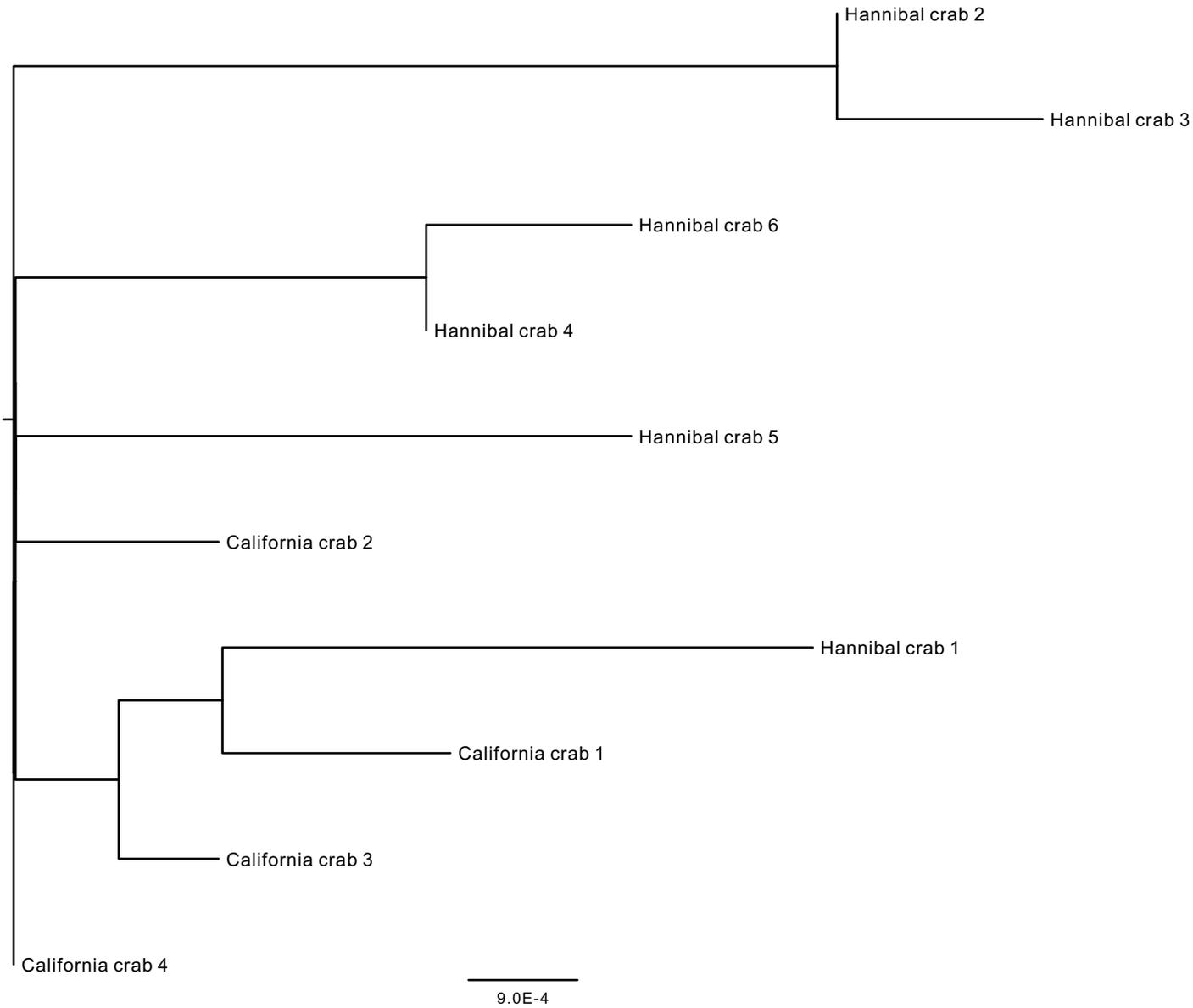
Fig. 6. Midpoint-rooted neighbor-joining topology based on mt COI Kimura 2-parameter distances. Crab number 5 was found on 3 April at another location on Hannibal seamount, and was not in an aggregation.

Pleuroncodes planipes density with depth
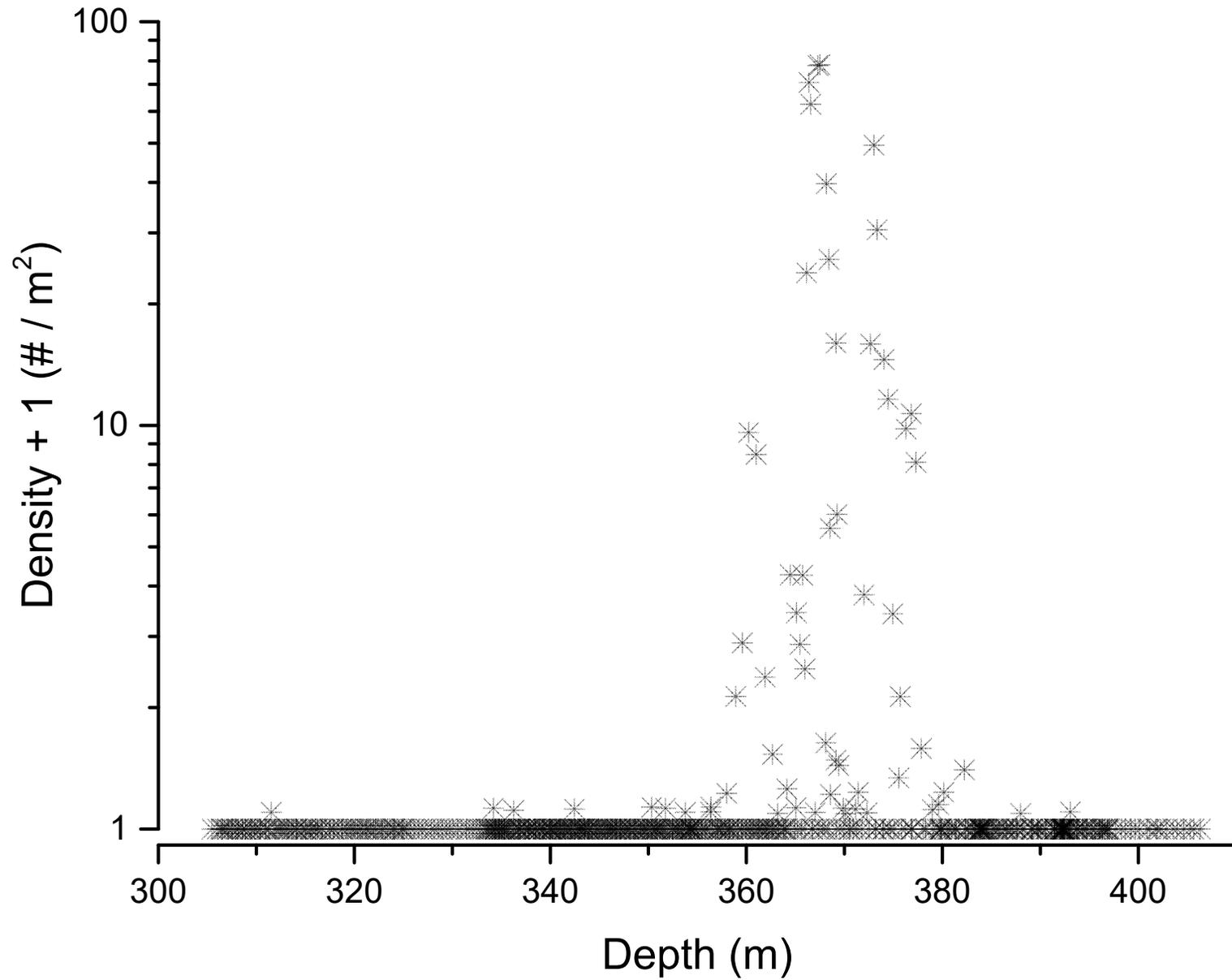
Fig. 7. Pleuroncodes planipes density with depth.
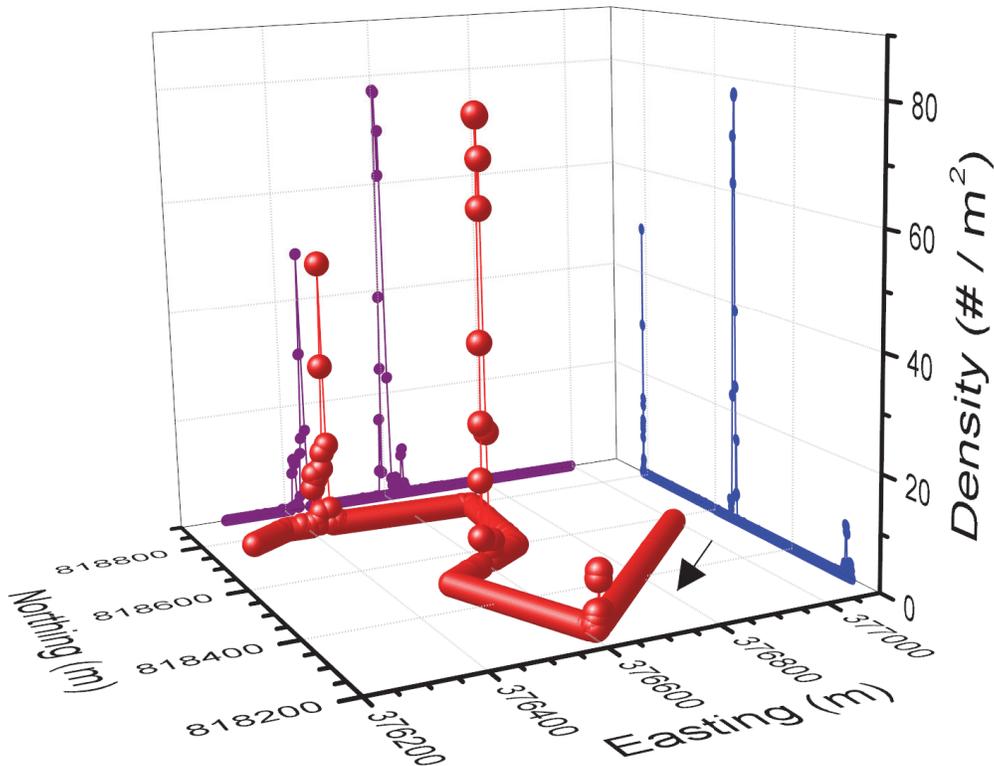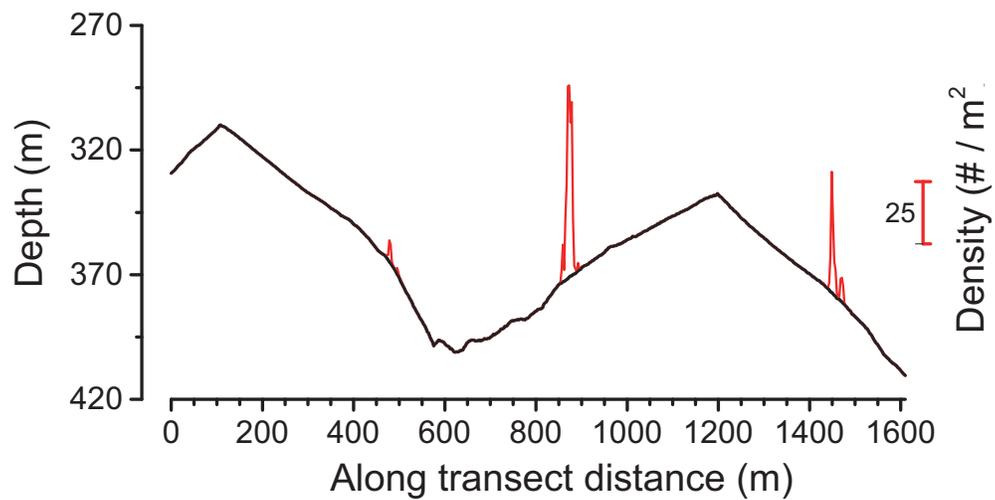
Fig. 8. Along transect Pleuroncodes planipes density on depth (top panel), and 3-d plot of density with latitude and longitude
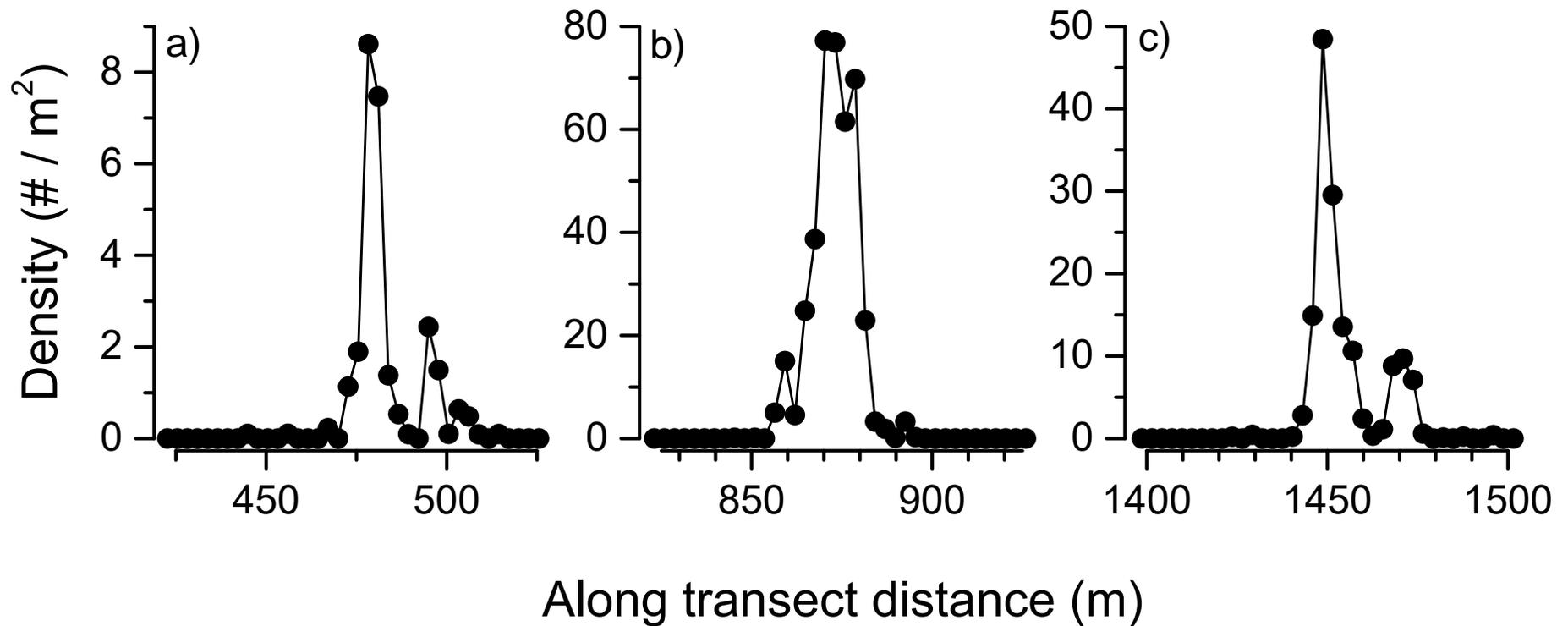
Fig. 9. Pleuroncodes planipes abundance distribution in each one of the three density peaks in Fig. 8.
For peak correspondence, see along transect distance and maximum density.
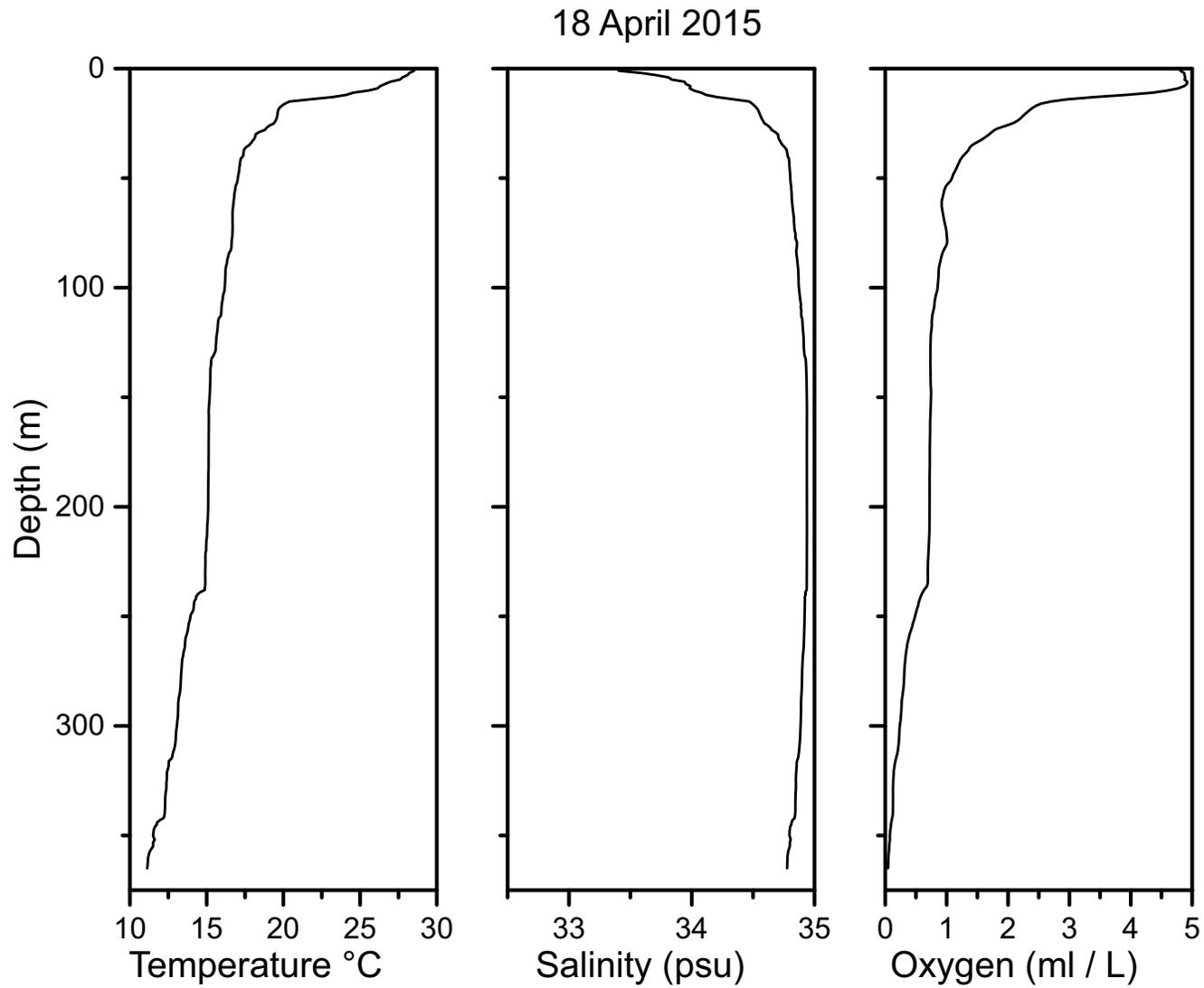
Fig. 10. Temperature, salinity and oxygen profile measurements taken with a CTD on 18 April 2015 at a station a few tens of meters from the Seabed AUV transects.