A crab swarm at an ecological hotspot: patchiness and population density from AUV observations at a coastal, tropical seamount (#7875)

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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 end range 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.

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Abstract

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 end range 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.

Background

Seamounts are distinct oceanic habitats found in all oceans (~~Wessel et al.~~Wessel, Sandwell & Kim, 2010), yet key first-order ecological processes are not well understood (Clark et al., 2010).

Communities of benthic species on seamounts are regionally isolated, with elevated, shallow rocky habitat patches surrounded by deep sedimentary plains. These two environmental axes, type of substrate (hard vs. soft), and depth (gradients in food, light, and oxygen), create horizontal and vertical patterns in faunal zonation (Pitcher et al., 2008; Thresher et al., 2014). These patterns are likely determined regionally by circulation and larval dispersal, and vertically by physical factors and biological interactions. In the pelagic environment, the trapping and concentration of pelagic planktonic biomass around seamounts, due to hydrodynamic and behavioral processes, result in local increase of predators -such as fish and marine mammals (Klimley et al., 2005; Morato et al., 2010; Morato et al., 2008). Thus, seamounts are ecological hotspots in the sense that many biological and physical processes combine to produce high benthic and pelagic biomass, and higher biodiversity. Seamounts are productive – their shallow summits have been fished for centuries and the biomass of zooplankton is unusually high, but debate remains over the mechanism of pelagic biomass enrichment. A commonly cited hypothesis is that zooplankton and fish productivity result from phytoplankton growth due to topographic induced upwelling of nutrients to euphotic waters, but the importance of this mechanism has been recently challenged (Genin & Dower, 2007). Seamounts harbor valuable yet slow growing resources, such as reef-building corals (e.g., scleractinians), black corals (e.g., antipatharians), soft-corals (e.g., gorgonians), and fish, some of which can live over 100 years (e.g., orange roughy) (Koslow, 1997). These habitats, however, have been under-sampled and under-studied, with less than 1%

of all seamounts explored (Clark et al., 2010). The occurrence of seamounts in open oceans beyond national jurisdiction, and advances in deep-sea fishing practices have resulted in severe anthropogenic pressure on seamount populations, which due to their life history characteristics are amongst the least resilient populations in the marine environment (Koslow, 1997; Schlacher et al., 2010).

Pleuroncodes planipes (Stimpson, 1860) adult ~~crabs~~squat lobsters, also known as red crabs, tuna crabs and "langostilla", occur in pelagic waters and in deep continental shelf and continental slope benthic habitats. Larvae and small individuals (~< 2.6 cm standard carapace length) tend to dominate the pelagic fraction off western Baja California, with larger organisms occurring exclusively in the benthos (Boyd, 1967). Large individuals reproduce, but observations of pelagic ovigerous females and their larvae in waters over bathyal and abyssal depths (~2000 – 3500 m) suggests that a fraction of the pelagic population can reproduce as well (Longhurst & Seibert, 1971). *P. planipes* can be extremely abundant, with accounts of dense pelagic patches up to 7 - 10 km (Gómez-Gutiérrez et al., 2000). (See also the casual account of a 16 km patch by B. Shimada, quoted in Boyd 1967.) Off Baja California *P. planipes* is the main prey of large pelagic predators such as yellowfin tuna and skipjack tuna (Alverson, 1963). *P. planipes* is well adapted to its pelagic lifestyle, where it can feed both on phytoplankton, by specialized filtration, and on small zooplankton (Longhurst et al. 1967). On benthic habitats, galatheid crabs are deposit feeders and scavangers (Lovrich & Thiel 2011; Nicol 1932). Benthic *P. planipes* ingest particulate organic matter (detritus associated with sediments), phytoplankton cells, and small crustaceans, foraminiferans and radiolarians (Aurioles-Gamboa & Pérez-Flores 1997). When feeding on bottom sediments with diatoms, detritus and small organisms, ~~galatheid~~ munidid ~~crabs'~~ squat lobsters' "third maxillipeds… act as brooms" (Nicol 1932), which would disturb and resuspend - fine sediment.

Most studies on *Pleuroncodes planipes* have been done in pelagic waters, and have provided little information on the benthic habitat. Boyd (1967) found that benthic *P. planipes* ranged from ~100 to 300 m water depth off western Baja California, with smaller individuals found in shallower bottoms, and population densities up to 11/m^2. These distributions correlated with oxygen minima waters, with oxygen levels below 0.5 ml/l. Boyd (1967) and Robinson and Gómez-Gutiérrez (1998) found that some benthic individuals tend to migrate from the bottom to the upper water column. The typical northern geographic end range of *P. planipes* is somewhere in Baja California. Intermittently, particularly during the El Niño phase of the El Niño Southern Oscillation (ENSO), its geographic range expands northward to California (Longhurst 1966; Smith 1985). The southernmost geographic endrange[1] of *P. planipes* appears to be somewhere in Costa Rica (Wicksten 2012), where it is thought to overlap with the northern range of *Pleuroncodes monodon* (Macpherson et al. 2010; Wehrtmann et al. 2010; Wicksten 2012). The center of abundance of pelagic *P. planipes* is in western Baja California (Brinton 1979; Gómez-Gutiérrez et al. 2000; Longhurst 1968). The distribution and abundance of benthic *P. planipes* is not well documented, particularly south of Baja California.

We present findings from a research cruise to Hannibal Bank, a coastal seamount in the Gulf of Chiriquí, Eastern Tropical Pacific coastal ocean off Panama (Fig. 1). This cruise explored the mechanisms that contribute to high densities of benthic and pelagic organisms in an ecological hotspot and examined the seamount biodiversity and the benthic community zonation

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along the depth gradient. Work included (a) submarine dives to collect, film and observe firsthand the benthic habitats, with DNA extractions of collected organisms performed onboard, (b) autonomous underwater vehicle (AUV) transects to map population densities of abundant benthic fauna, and (c) hydrographic and velocity measurements over the seamount using a conductivity, temperature, depth (CTD) and oxygen profiler and a hull-mounted acoustic Doppler current profiler. Hannibal seamount and its shallow top, Hannibal Bank, are within the recently created Coiba National Park, a UNESCOWorldHeritagesite, off the Pacific coast of Panama. Hannibal Bank harbors abundant large fish sustaining artisanal fisheries, and is a destination for international sport fishermen. The flat-topped triangular shaped seamount rises from 450 m to ~40 m , occupying an area of 83 km^2 (Fig. 2). Proximate to the continental shelf edge, it is ~20 km west of Coiba Island, 60 km from the main coast, and centered at about 07° 24’ N - 82° 3’ W (Cunningham et al. 2013). Hannibal seamount communities are likely influenced by several physical processes, including synoptic upwelling from December to late April (D'Croz & O'Dea 2007), low aragonite saturation state (Manzello et al. 2008), low oxygen sub-thermocline waters, low salinity from runoff and precipitation (~3 m yearly precipitation), sharp thermal stratification, large internal tides, and a 4 m tidal range (Dana 1975; Pineda et al. 2009; Starczak et al. 2011).

On the last dive of the research cruise we observed extraordinarily high densities of anomuran ~~galatheid crabs~~munidid squat lobsters near the bottom of the seamount, and an associated turbid layer over the bottom. The encounter was unexpected and mesmerizing~~.~~, ~~We~~ we documented these observations with high definition video, a photo-transect, environmental water column measurements and genetic analysis of squat lobster~~crab~~ samples. Here we report on these observations,

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and address the following questions: What is the distribution of the crabs along a transect? What are the patterns of variability in abundance within a patch? Is there a relationship between the turbid layer and the crab aggregations? Are the crabs observed over the Hannibal Seamount the same species as *Pleuroncodes planipes* found off of California?

Methods

The cruise onboard the M/V *Alucia* from 31 March to 20 April 2015 focused on Hannibal Seamount. Work included ecological surveys over all flanks of the seamount (Fig. 2), and fifteen submarine dives conducted with Nadir, a 3-person submarine, and 11 dives with RV2, a 2-person submarine with more robust sampling capabilities than Nadir. On most missions, the submarines surveyed starting from the bottom of the seamount and continued to the top, working in tandem, within ~150 m of each other. Twelve transects with the Seabed autonomous underwater vehicle (AUV) complemented the diving missions and surveyed similar areas, collecting benthic imagery. On a typical cruise day, submarines were deployed during the morning and the Seabed AUV in the evening. Here we focus on observations completed on 18 and 19 April 2015, when crab aggregations were detected and studied. A conductivity, temperature, oxygen and depth profile was taken from the M/V *Alucia* using a Seabird SBE19 plus CTD in the vicinity of the submarine dive and Seabed AUV transect on 18 April 2015 (Fig. 2, blue cross in inset).

AUV observations and density estimation

Seabed AUV conducted transects on the seamount, and obtained images to estimate densities of bottom organisms. Designed specifically for optical imaging of the seafloor (Singh et al. 2004b), the Seabed AUV has been used extensively for coral reef ecology, and other high

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resolution imaging applications (Singh et al. 2004a; Williams et al. 2014). It is equipped with high-dynamic range cameras (Singh et al. 2007) to provide species documentation via imagery that can be corrected for the nonlinear attenuation of light in the water. Seabed AUV navigated at a speed of ~20 – 25 cm /s and mean altitude of 3.5 – 4.5 m above the bottom along a predefined track, adjusting its altitude using a high frequency acoustic Doppler profiler. Seabed took 1024 by 1380 pixel images of the seafloor that was illuminated with a strobe, and recorded temperature, conductivity, depth, and altitude. The camera pixels are square and the field of view is 45° in the horizontal and 33° in the vertical. Image width, *x*, is determined from altitude (height above bottom), *z*, by noting that $0.5(x/z) = \mathrm{Tan}(45/2)$, which gives $x = 0.828z$. Because the pixels are square, the image height, *y*, is proportional to the number of pixels; i.e., $y = x(1024/1380)$. AUV specific altitude is used for every image, and image area is calculated as $x{\cdot}y$.

The Seabed AUV was programmed to take photographs every ~ 4 seconds, with image overlap. We examined every third image (12 s interval), which gave a sequence with no image overlap. The non-analyzed images were used to resolve ambiguities in identification. Images were inspected for crabs and other organisms by eye, and all organisms were counted in each image.

Species identification of the ~~crabs~~ squat lobsters was confirmed by DNA barcoding of individuals in our samples (described below). Images from the Seabed AUV were light-corrected and inspected for organisms and type of substrate. A catalog of organisms was created from the photographs, and each morphospecies received a code. *Pleuroncodes planipes* were easily distinguished

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in the video recording taken from the submarine dives, and in the Seabed AUV images. To estimate ~~crab~~ squat lobster density (#/m^2), the number of crabs was divided by estimated image area in each photograph.

Patchiness estimate

Patchiness of *P. planipes* was estimated with I_{mod} using the formula of Bez (2000) modified by Décima and Ohman (2010). This index, based on Lloyd's index, considers a transect that does not sample the entire range of the species:

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

where z_i is the density of the ~~crabs~~ squat lobsters in a given image, s is the size of the sampling unit used in the survey (mean quadrat size, 8.93 m^2), and N is the number of images analyzed. For comparison, we also report the patchiness index of an unidentified stomatopod that was easily detected in the photographs.

Seamount sample collection and genetic barcoding

The submarines collected benthic organisms opportunistically, using a robotic manipulator arm, a net and a sediment scoop. (Ministerio del Ambiente de Panama permit # SE/A-18-15). Collected specimens were stored in a compartmentalized honeycomb quiver or in a larger "biobox". After the submarine dives, the sampled organisms were held in chilled seawater until they were photographed and labelled (e.g., Fig. 3b), preliminary taxa identification based on

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Sample collection in a mass stranding event

From January to August 2015 there were several mass stranding events of *Pleuroncodes planipes* crabs on Southern California beaches, documented from news reports, the Lexis-Nexis database, and informal surveys (J. Pineda, pers. obs., Table 1, *Supplemental Materials*). In June 2015, crabs were observed in a San Diego beach (S. Searcy, Univ. San Diego, pers. com., and J.

Pineda, pers. obs.), and most of the crabs on the beach were still alive. At False Point, La Jolla (32°48' 28.51"N, 117°15'54.96"), we collected galatheid crabs on 2-5 June 2015, and preserved them in ethanol to provide reference specimens for DNA barcoding of seamount crabs.

Results

Submarine observations and AUV mission

On the last diving mission of the cruise, 18 April 2015, the two submarines dived to the bottom by the westward flank of the seamount (Fig. 2). Upon approaching the bottom, a very dense cloud of sediment was encountered; on no other submarine or AUV dive had such a dense cloud been observed (Fig. 3a). Altitude soundings from the submarine indicated that the turbid cloud extended 4 to 10 m over the ocean floor. As the submarine approached the bottom, a large number of galatheid crabs were encountered. RV2 took 13 min and 40 sec high-definition video of the crabs. A few still photographs and other video were taken from within the Nadir.

The video clips and photographs show that crabs were sometimes interacting among themselves (e.g., facing each other pulling out a dead crab) and with other organisms, including a sand eel. In some footage, crabs were sparsely distributed, and appeared to be sedentary. In other footage, benthic crabs were very dense, touching adjacent crabs, with most crabs moving broadly in the same direction (Fig. 3c and d) as a swarm (Video S1, Supplemental Materials). In this footage, some crabs jumped and swam a few 10's of cm and landed in another spot. A crab outside of the patch moved towards, and merged with the main patch (Fig. 3d). Sand eel, small pelagic fish, shrimp, and a few stomatopods were in close proximity to the crab aggregation.

The population observed in the footage was composed of relatively large crabs, with no visible smaller individuals, i.e., ~< 2.3 cm carapace length. (See Fig. 3b for typical crabs, with ~ 2.7 cm carapace length; carapace length as measured by Gómez-Gutiérrez et al 2000). For most of the footage, the submarine hovered 2-3 m above the bottom, and the submarine and its lights did not appear to affect the behavior of the crabs. The high turbidity immediately above the bottom extended horizontally for at least 10's of m, and the turbid cloud appeared to be associated with the crab patch. As the submarine moved up the seamount slope and abandoned the patch, the density of crabs decreased abruptly, and the turbid cloud disappeared (Fig. 3d).

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On 19 April 2015, the Seabed AUV was programmed to complete a photo-transect in the same region as the crabs seen on 18 April. The AUV dived to about 325 m, and then completed a 1,610 m transect which included a set of turns to avoid potential high risk areas (e.g., rocky pinnacles) (Fig. 2., inset) Mean image width and length for this transect were 3.46 and 2.57, m, yielding a mean area per image of 8.93 m^2 (n = 580). Mean AUV altitude and speed was 4.18 m, and 0.23 m/s. The 580 analyzed photos were taken at 12 s intervals, and consecutive images had a gap of $2.78 - 2.57 = 0.21$ m . (See Fig. 4 for an image from the AUV, with the highest density of crabs detected in the transect, 77.2 individuals / m^2).

***Pleuroncodes planipes* abundance**

Pleuroncodes planipes were detected in 12.2% of the Seabed AUV photographs. Images with counts of *P. planipes* tended to center around 365-m water depth (Fig. 5). Crabs were rare in the shallowest and deepest images, with bins centered at 305 and 405 m, although the number of images from these depths was low. Peak densities, with up to 72.2 crabs/m^2, occurred at 360

– 380 depths (Fig. 7). Three high-density patches were constrained to depths between 362 and 381 m (Fig. 8, top panel), and were separated from each other by over 100's of meters along the northing (latitudinal) axis (Fig. 8, lower panel). The distribution of abundance in these peaks indicates that densities were low at the periphery, and that the maxima densities occur near the middle of the patch (Fig. 9). The distribution of crabs along the transect was very patchy, with I_{mod} = 5.34. Unidentified stomatopods that always occurred as singletons in the images had I_{mod} = 3.54. The turbid layer was not apparent in the Seabed AUV images.

~~*Galatheid crabs*~~*Munidid squat lobsters* DNA barcode ID

We obtained COI sequences for 6 specimens from Hannibal seamount and 4 specimens from the *Pleuroncodes planipes* stranding in California. Sequences were deposited in GenBank (Hannibal, KU179422-26, KU179431; La Jolla, KU179427-30). Five out of the 6 Hannibal specimens were obtained from the main crab swarm on 18 April 2015. The 6th specimen was obtained on 3 April 2015, at a depth of 278 m, when crabs were observed on the bottom at the Northeast flank of the seamount (near 7° 21.21' N, 82° 1.37' W) at low densities. The final alignment for the combined seamount and California dataset was 595 base pairs. Inspection of the amino acid translation indicated that the sequences did not represent pseudogenes. Sequences differed from each other by between 1 to 8 base pairs. Uncorrected p and Kimura 2-parameter distances were similar to each other and ranged from 0.00168 – 0.01363. There were no shared haplotypes and the mean pairwise distance (for both metrics) between Hannibal specimens was greater than the mean distance between Hannibal and California specimens (Table 1, Fig. 6).

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Water properties

The CTD cast revealed strong temperature, salinity, and oxygen stratification (Fig. 10). The temperature profile showed a sharp thermocline in the upper 40 m, with a temperature drop 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 m. A halocline was also observed, with a salinity drop from 33.4 psu at the surface to 34.8 psu at 40 m. Maximum salinity occurred at mid depths (34.9 psu at 180 m), with a slight freshening with increasing depth (to 34.8 psu at 365 m).

Oxygen concentration decreased rapidly with depth, from over 4.8 ml/l at the surface to 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 ml/l, was obtained from the deepest measurement, 365 m, ~15 m above the bottom. Thus, *P. planipes* maximum densities occurred at depths where waters were oxygen depleted. The vertical gradients of temperature and oxygen concentration changed abruptly at about 238 m, with larger gradients seen below 238 m. The vertical salinity also changed at around 238 m, but more subtly. Beam attenuation data from the SBE CTD revealed a turbid layer around 365 m depth in which optical attenuation tripled.

Discussion

Based on DNA barcoding, the Hannibal seamount crabs appear to be the same species as *Pleuroncodes planipes* from California. COI is the most typically used species barcode gene (Bucklin et al. 2011), and sequence comparisons are frequently based on Kimura 2-parameter (K2P) distances (da Silva et al. 2011). K2P distances may not necessarily be the best distance metric for a given taxon (Collins & Cruickshank 2013; Srivathsan & Meier 2012), other metrics

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may not necessarily perform better and the use of this metric permits straightforward comparisons with K2P distances from studies. Uncorrected p distances were similar to the K2P distances, and in both metrics, the mean distance between individuals at Hannibal Seamount was greater than the mean distance between Hannibal Seamount and California. Pairwise mitochondrial COI distances fell within the range of typical intraspecific distances for galatheids (da Silva et al. 2011). The southern range limit of *P. planipes* is considered poorly known (Hendrickx & Harvey 1999), although researchers have suggested Costa Rica (Wicksten 2012), and our observations here, supported by DNA sequences, may be the southernmost record.

Species have distinct patterns of variation in abundance over space, and understanding the factors that determine these patterns and their diversity is a central goal in ecology. Spatial distribution patterns may reflect individual and population processes, including settlement, dispersal, migration (Roa & Tapia 2000) and behavior. For example, gregarious behavior and swarming in insects may produce characteristic spatial patterns of abundance (Okubo & Chiang 1974). Whereas practically all organisms have patchy distributions at some spatial scale of observation, the causes and consequences of patchiness can reflect fundamental ecological and life history characteristics (Marquet et al. 1993). For example, patchiness can be species specific and vary ontogenetically (Décima et al. 2010; Hewitt 1981), and species that face different degrees of patchiness may have evolved different life history strategies (e.g. Dagg 1977). Patchiness, may be driven by external ("vectorial", environmental), reproductive, social (e.g. behavioral) and competitive ("coactive") processes (Hutchinson, 1953). Physical–biological interactions, such as the swimming up response of zooplankton and larvae to downwelling currents (Scotti & Pineda 2007), might also produce patchiness (e.g., aggregation at fronts), and explain why only certain taxa aggregate in particular hydrodynamic settings.

The distribution of *Pleuroncodes planipes* was highly patchy, similar to other galatheid populations (Freire et al. 1992; Roa & Tapia 2000), and I_{mod} values were higher than those of a stomatopod that occurred at smaller densities than *P. planipes*. The high *P. planipes* densities were constrained to a narrow subset of regions and depth ranges on Hannibal seamount. From the 26 submarine dives (15 missions to distinct sites) and the 12 AUV transects, we observed dense aggregations of crabs in only one region, the northwestern flank of the seamount, and these aggregations were constrained to ~355 – 385 m water depths. The AUV survey detected three peaks in abundance (*a-c*, Fig. 9), and in peak b, the observed density was 77 individuals / m^2, one of the highest that have been measured for ~~galatheid crabs~~munidid squat lobsters (Lovrich & Thiel 2011, Table 6.1). Our sampling protocol cannot resolve whether these density peaks are discrete patches or whether aggregations were connected. It is unlikely, however, that crabs in density peak *c* were connected to crabs in peak *b*, because crab distributions were observed to be constrained to 355-385 m, and the crabs in *b* and *c* were separated by shallower depths (Figs. 2 and 8).

The density distribution within each of the three abundance peaks detected in the survey is consistent with a pattern where density increases toward the center of distribution (Fig. 9). However, we do not know whether the AUV surveyed the center of the patch. The two high-density peaks at ~480 and 1440 m along the transect (Figs. 9a and 9c) each have an adjoining lower-density peak. These lower-density peaks may represent budding, small aggregations that have split from the main aggregation, and might grow into larger patches, or they might merge

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into the larger, adjacent patch. These density distribution patterns are likely due to aggregation driven by the crab's gregarious behavior, and coordinated movement of the aggregation, a phenomenon that has been called swarming. Okubo et al. (2001) describe swarming as a phenomenon where a group of organisms move together. Swarms are arguably one of the few ecological phenomena that possess emergent properties, where the characteristics of the aggregation cannot be simply explained by adding the individual's behaviors (Parrish & Edelstein-Keshet 1999). In these complex systems, a focus on individual behavior is unlikely to explain the properties of the swarm. Whether all emergent properties in swarms are functional or not, is an open question (Parrish & Edelstein-Keshet 1999). The increase in density towards the center is consistent with other organisms that form swarms and aggregations (e.g., insects, krill and schooling fish, Okubo & Chiang 1974; Okubo et al. 2001), and patterns of abundance in other gregarious benthic populations where density increases towards the middle of the distribution might reveal a swarming behavior. Two other galatheid species have patterns where density increases towards the middle of the patch (Freire et al. 1992) but in these European *Munida* spp. species, the scale of the patches is a few tens of kilometers, compared to the ~100 m scale observed in our study. It is unclear whether the abundance structure of these *Munida* spp. and *Pleuroncodes planipes* patches are caused by the same processes. Dense benthic aggregations of other species of anomuran and brachyuran crabs (king crabs, spider crabs, tanner crabs, lyre crabs) have been observed, and some were related to reproduction (DeGoursey & Auster 1992; Powell & Nickerson 1965; Stevens et al. 1992; Stevens et al. 1994).

Crabs densities appeared to be higher and more clumped in the submarine video observations than in the AUV images (compare submarine video still frame Fig. 3 with AUV

Fig. 4). The submarine video still frames in Fig. 3 were taken when *Pleuroncodes planipes* were moving as a group, a swarm, and most organisms appeared to be oriented in the same direction. In the AUV images, a consistent crab orientation and the swarm motion were not obvious. Moreover, the turbid cloud observed from the submarine (Fig. 3) was not seen in any of the AUV images. The turbidity cloud was most likely produced by *Pleuroncodes planipes* activities, as the turbidity disappeared at the edge of the patch, and was not observed outside of the patch or in any other submarine dive or AUV missions. Diurnal patterns of activity might explain the differences in turbidity. Submarine observations were early in the day, whereas the AUV survey was done in the evening. However, another possibility is that crabs observed from the submarine were in a location with finer, and hence more easily suspended sediments than those surveyed by the AUV survey. However, the locations not far from each other (Fig. 2).

The resuspension of sediment initiated by crab activity may affect the benthic environment over the northwest seamount flank. Feeding of king crabs in waters ~3m deep off Kodiak Island, Alaska, resulted in a dense cloud of turbid water (Bradley & Stephen 2014), and Yahel (2008) found that bottom fish activity was an important mechanism for sediment resuspension and remineralization of organic matter between water depths of ~ 60 and 140 m in Saanich Inlet (Vancouver Island, BC, Canada).

Pleuroncodes planipes occurred at water depths with very low oxygen (0.04 ml/l at ~15 m above the bottom where the crabs were observed). The affinity of some galatheids to low oxygen waters, and *P. planipes* in particular, is known (Boyd 1967; Lovrich & Thiel 2011).

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Depth distribution of *P. planipes* and other galatheids might be related to these low oxygen levels (discussed by Lovrich & Thiel 2011), but more study is needed to test this hypothesis.

Pleuroncodes planipes occurs in very high densities in the pelagic environment, and this species mass strands yearly in shallow water and intertidal beaches near the center of its pelagic abundance, Bahía Magdalena, Baja California (Aurioles-Ga~~a~~mboa et al. 1994), and more occasionally on California beaches (Table 1, Longhurst 1966; Smith 1985). While we were on hydrographic stations over Hannibal seamount and surrounding areas, we occasionally observed organisms that appeared to be pelagic red crabs swimming swiftly by the stern of the boat at night, illuminated by the vessel lights. Despite multiple attempts, we were not able to capture a specimen to assess its identity, so the occurrence of *P. planipes* in the water column above Hannibal seamount is unknown.

Our observations in Panama were conducted at roughly the same time when mass stranding events were registered in Southern California (Table 1, *Supplemental Material*), and the Hannibal and Californian individuals appear to be the same species based on their mtCOI sequences. Mass stranding of *Pleuroncodes planipes* in Southern California beaches had been linked to El Niño (Smith 1985). A full El Niño had not been declared for January-June 2015, when many stranding events were reported (Table 1, *Supplemental Material*). On the other hand, an unusually large pool of warm water developed in late 2013 and early 2014 in the coastal temperate eastern Pacific, and persisted through much of 2015 (Bond et al. 2015), apparently unrelated to El Niño. The current forecast (November 2015, by NOAA [ClimatePrediction Center]), indicate that the anomalous warm-water pool condition has been followed by an El

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Niño, and that a full El Niño is now in progress. The "pool or warm water" conditions in January-June 2015 may be related to anomalously warm waters observed in Southern California's nearshore in fall 2014 (Reyns, Pineda, and Lentz, unpub.). These conditions may help explain the appearance of *P. planipes* in Southern California, as speculated by some news outlets. Whereas it is unlikely that that our observations of benthic aggregations at Hannibal are connected with the California mass stranding events, it is significant that *P. planipes* can be simultaneously abundant at the two distant locations and at two different habitats. The high densities of *P. planipes* likely impacted local pelagic, intertidal, and deep seamount food webs.

Allochthonous supply of biomass, where resources from one habitat or ecosystem subsidizes another system, influences local population community and dynamics (Polis et al. 1997). Moreover, the episodic availability of large quantities of biomass to benthic and pelagic organisms and marine mammals, including the supply of terrestrial material and whale carcasses to benthic deep sea communities, the mass stranding of pelagic organisms in shallow habitats, and the sudden availability of a new resource, represent an opportunistic yet important source of nutrition to the "receiving" communities (Polis et al. 1997), and can influence food web structure and demographic rates (Watt et al. 2000). The massive availability of *Pleuroncodes planipes* might influence diverse food webs.

Because of its pelagic and benthic lifestyle, and its abundance, *Pleuroncodes planipes* likely plays an important role in some seamount, continental shelf and shallow water food webs in the subtropical and sub temperate eastern Pacific. Several authors have noticed the key role of *P. planipes* in the pelagic environment, by virtue of its abundance and trophic role (Alverson

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1963; Gómez-Gutiérrez et al. 2000; Longhurst 1966; Longhurst et al. 1967; Robinson et al. 2004). *P. planipes* was patchy but very abundant at Hannibal, and it might represent an important resource for pelagic predators at the seamount. More research is needed to assess the distribution and abundance of benthic *P. planipes*, as well as its potentially key role in semitropical and sub-temperate eastern Pacific seamount and continental shelf habitats.

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We would like to express gratitude for the help and logistical support of the Captain and the crew of the M/V *Alucia*, the *Alucia'*s submarine team, Jeff Anderson, for programming and running the AUV operations, and keeping it safe, Alex Bocconcelli and WHOI's Marine Operations office support, the Ministerio del Ambiente de Panama for providing the research and export permits, including # SE/A-18-15, and the US State Department for cruise permit support. Bathymetric data in Figure 1 derived from the GEBCO_2014 Grid, www.gebco.net.

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Tables

Table 1. Pairwise distance comparisons for uncorrected p and K2P distance metrics. Minimum and maximum pairwise distances (for all comparisons) and the mean distances for pairs within 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

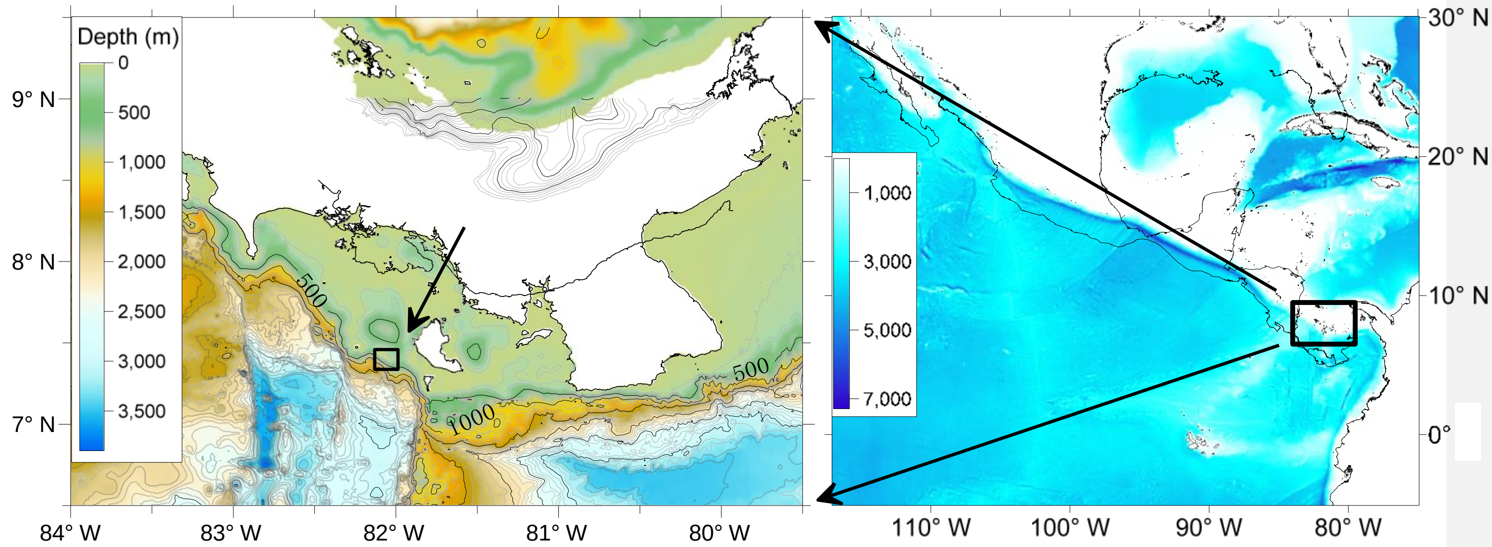

Fig 1. Map of the study area. Box in the right panel encloses the left panel, and the small box in the left panel encloses Hannibal Seamount. Bathymetry data from GEBCO.

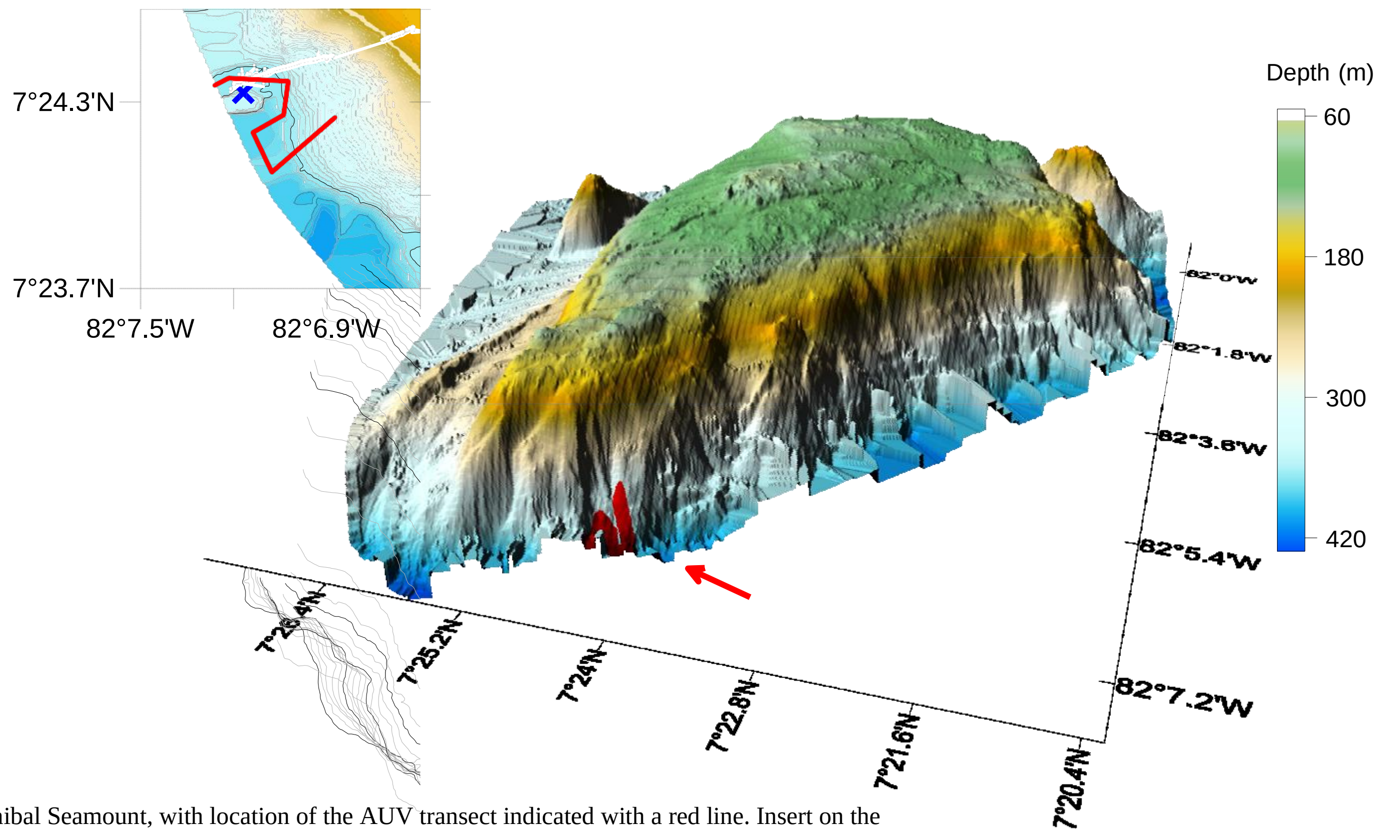

Fig. 2. Hannibal Seamount, with location of the AUV transect indicated with a red line. Insert on the left delineates AUV transect, with end of transect near the blue cross. The blue cross indicates the location of the CTD cast, and the submarine positions are in white. Depth data from Cunningham et al. (2013).

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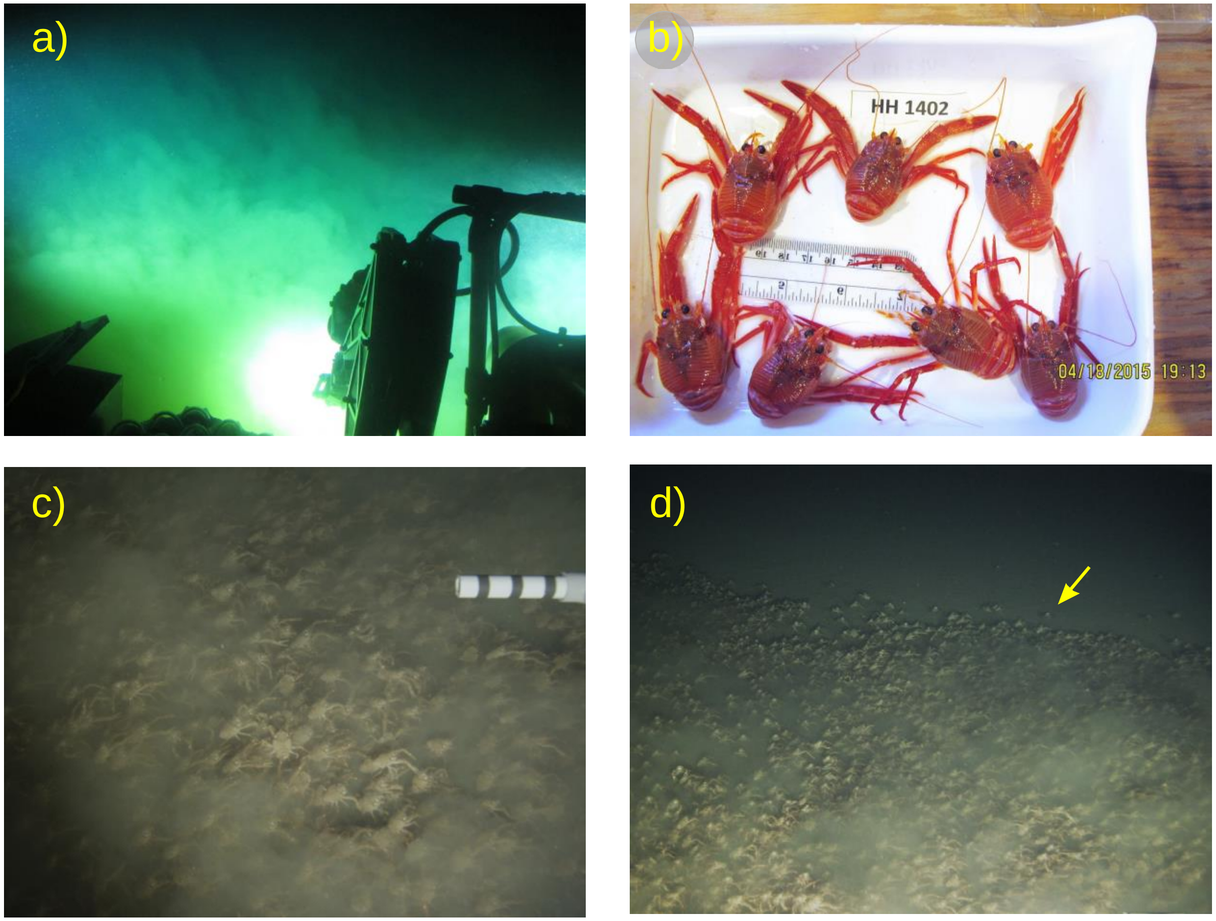

Fig. 3. Photographs and video still frames of Pleuroncodes planipes and its environment. a) Image taken within Nadir as it approached the bottom, from about 6 m above the bottom, where P. planipes aggregations were first found. b) Pleuroncodes planipes collected from the aggregation, with ruler scale 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.

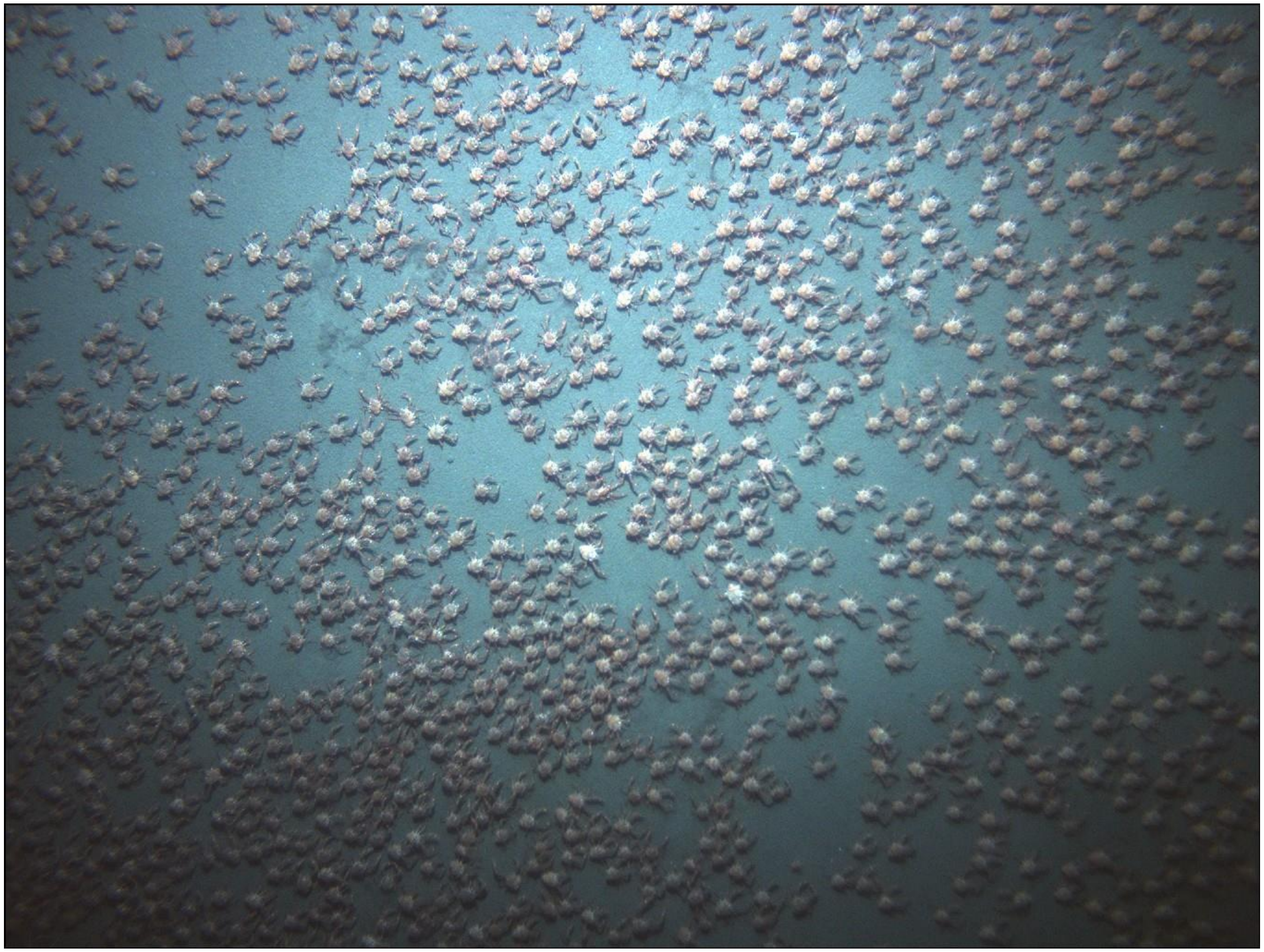

Fig. 4. AUV photograph with the highest density of Pleuroncodes planipes.

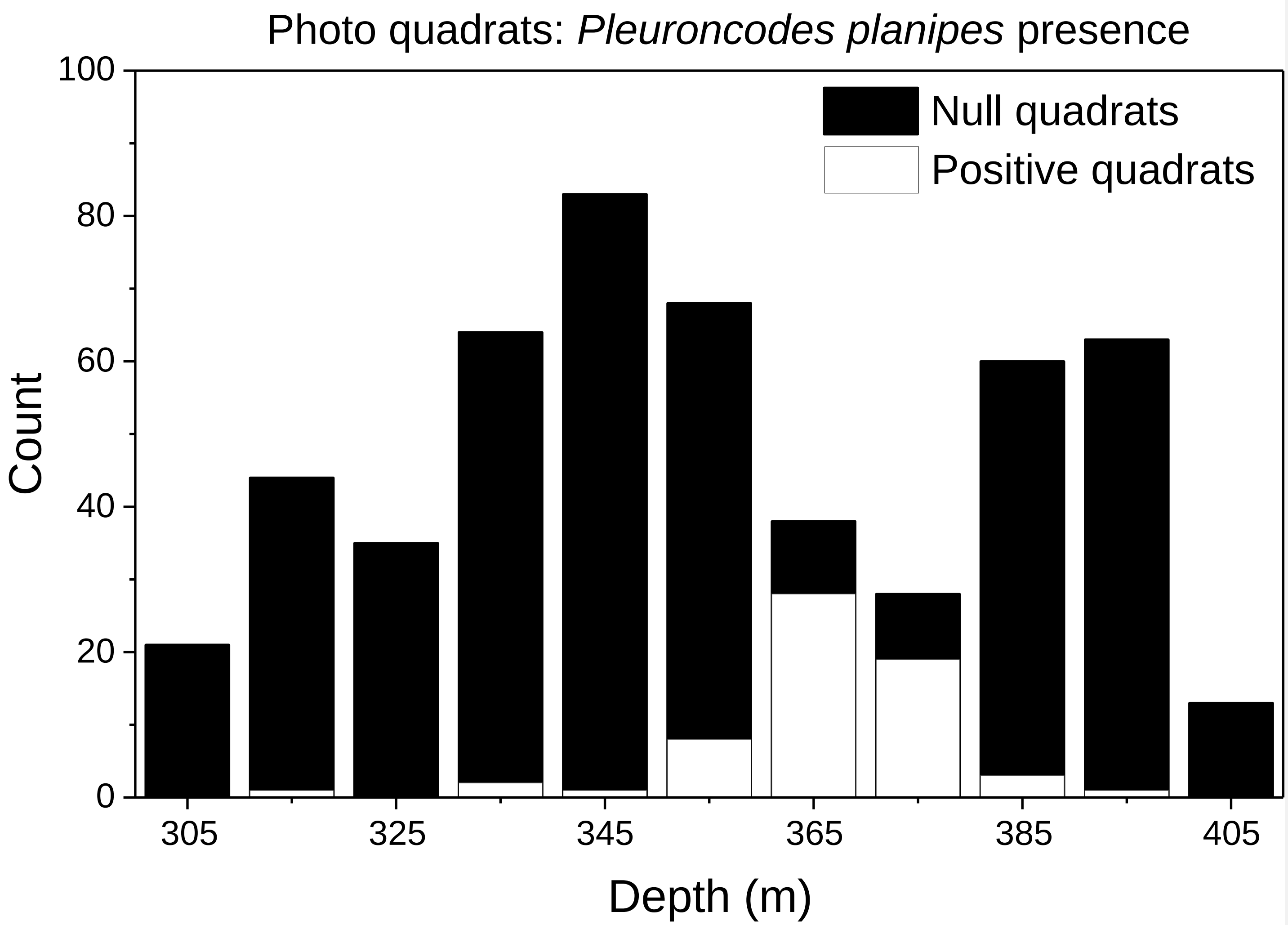

Fig. 5 Frequency distribution of quadrats with null and positive Pleuroncodes planipes counts. No P. planipes occurred in null quadrats, whereas positive quadrats are those in which at least one P. planipes was observed.

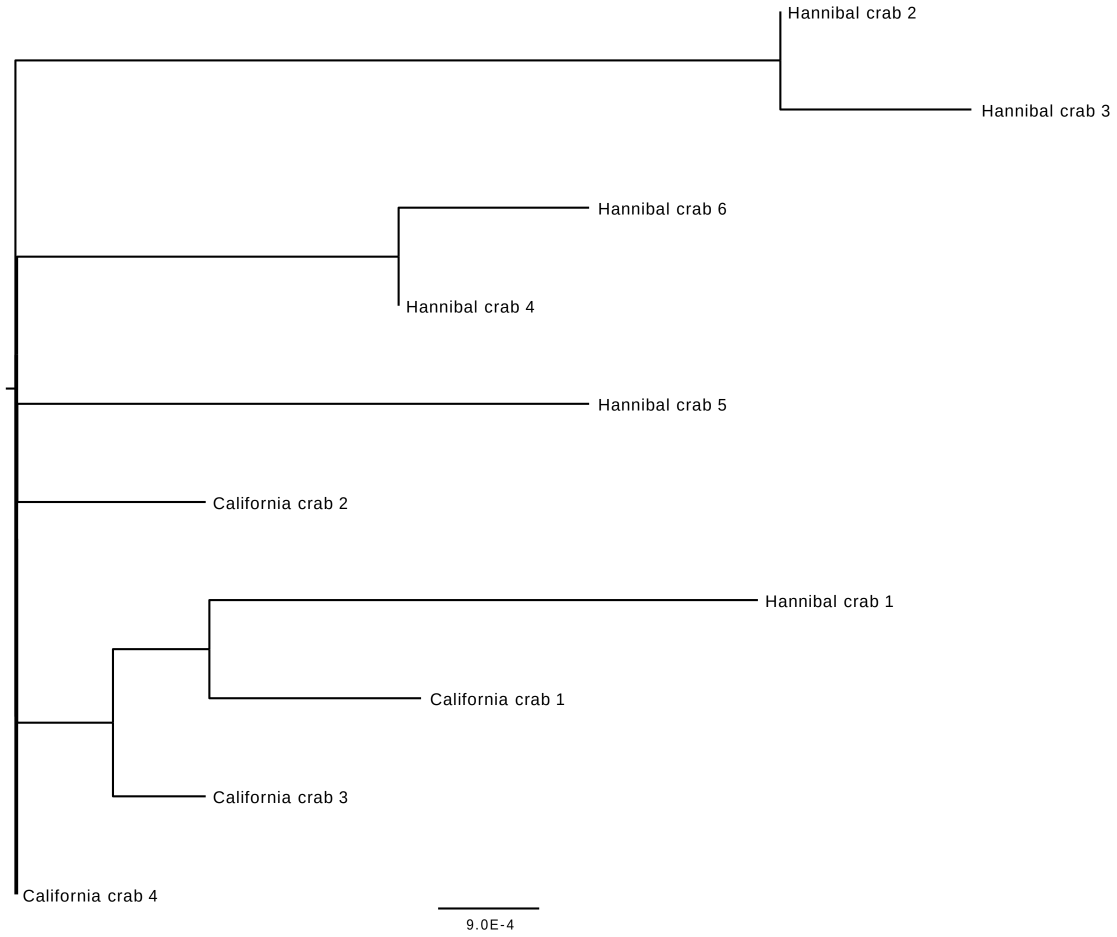

Fig. 6. Midpoint-rooted neighbor-joining topology based on mt COI Kimura 2-parameter distances. Crab number 5 was found on 3 April at another location on Hannibal seamount, and was not in an aggregation.

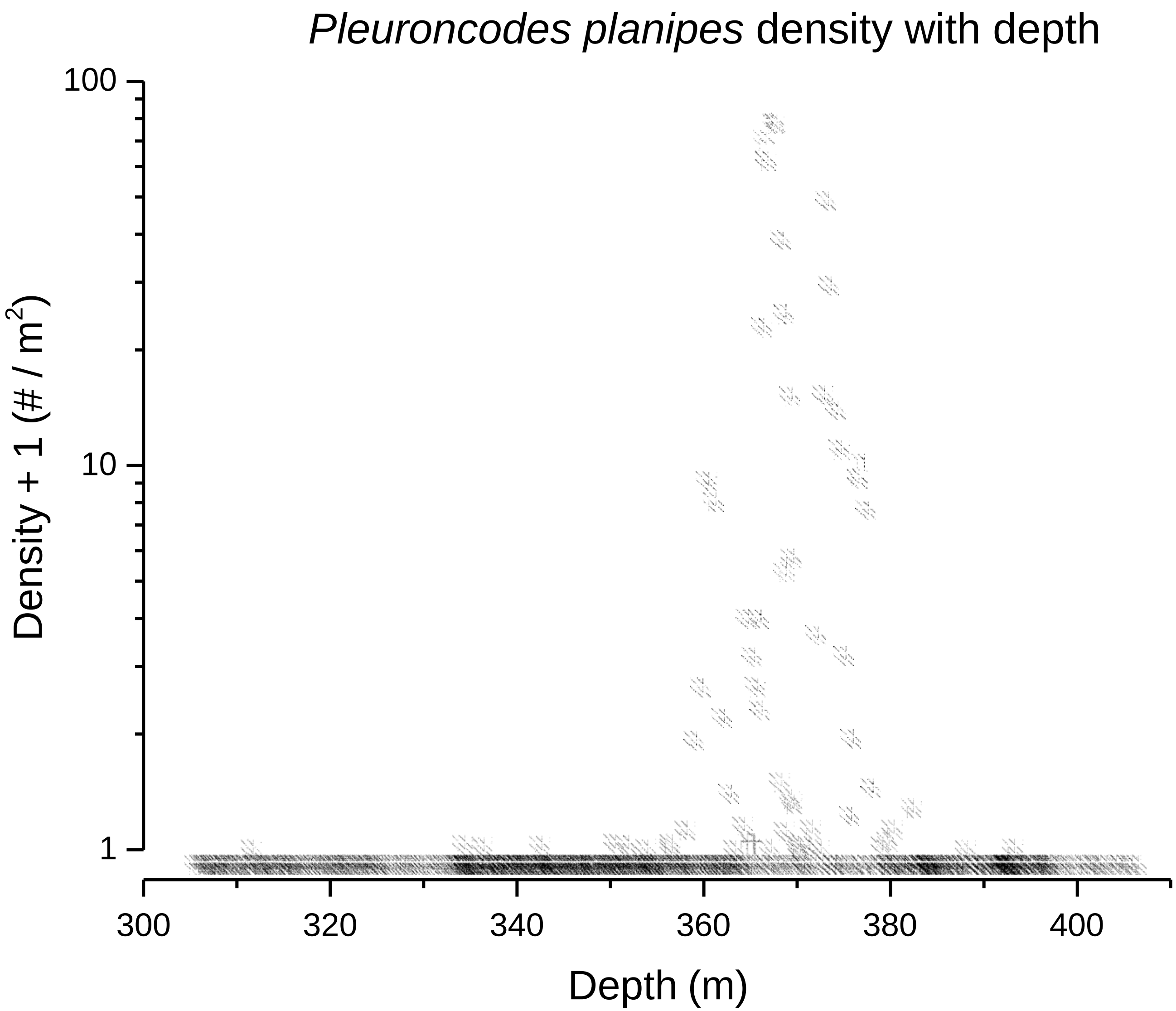

Fig. 7. Pleuroncodes planipes density with depth.

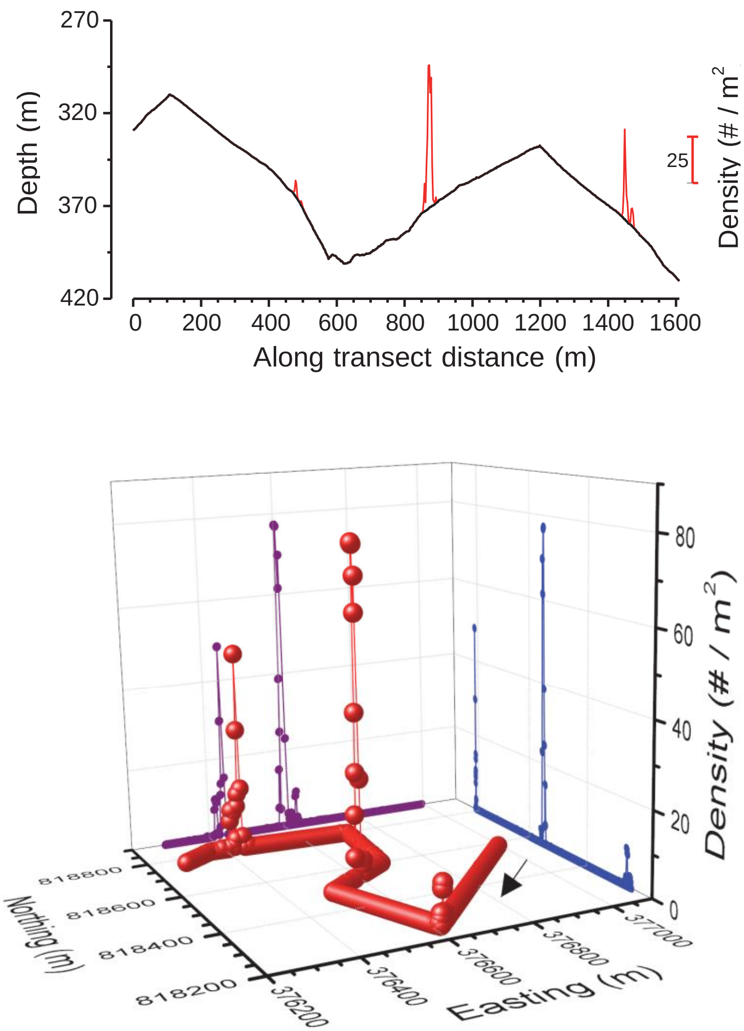

Fig. 8. Along transect Pleuroncodes planipes density on depth (top panel), and 3-d plot of density with latitude and longitude.

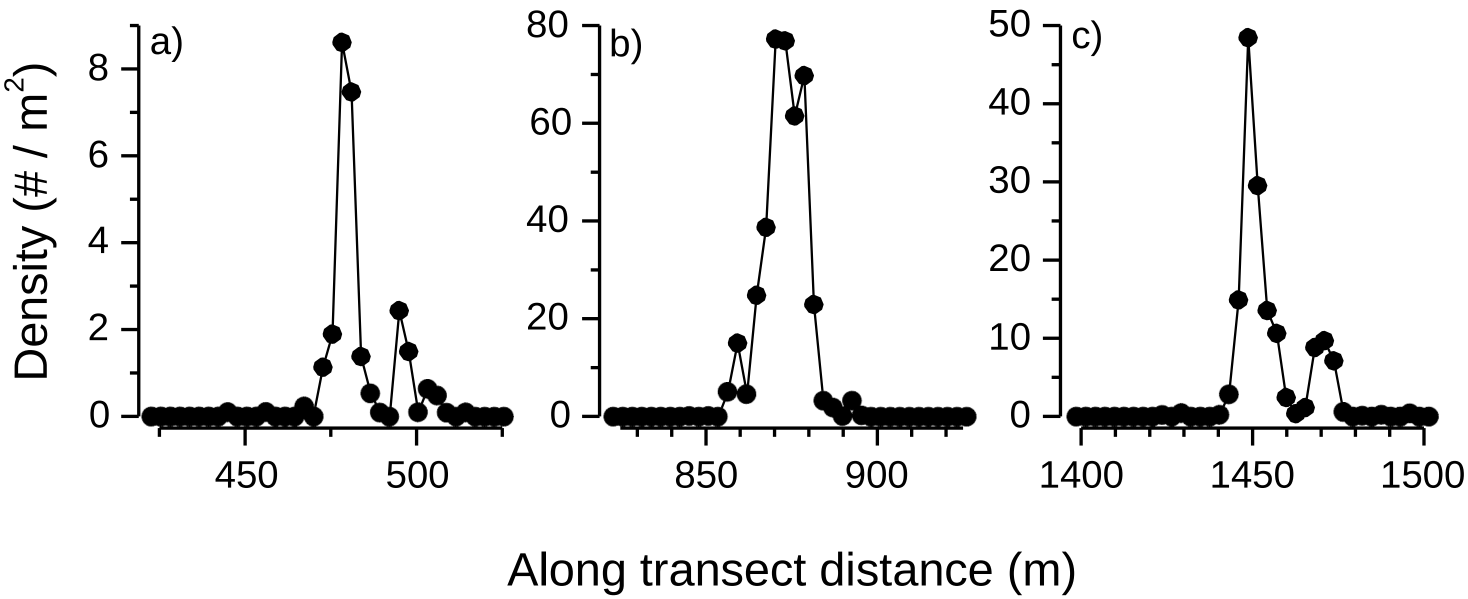

Fig. 9. Pleuroncodes planipes abundance distribution in each one of the three density peaks in Fig. 8. For peak correspondence, see along transect distance and maximum density.

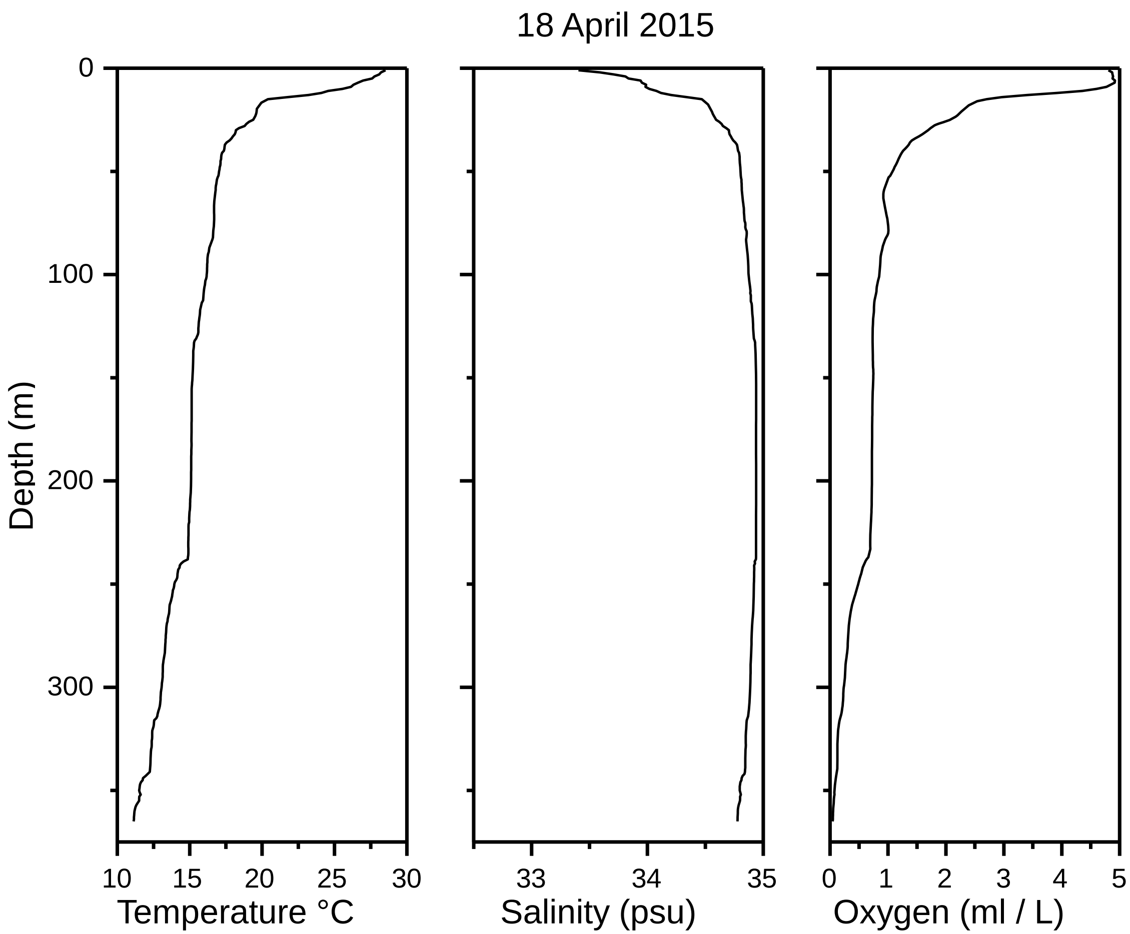

Fig. 10. Temperature, salinity and oxygen profile measurements taken with a CTD on 18 April 2015 at a station a few tens of meters from the Seabed AUV transects.