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Emergence in the deep sea: Evidence from harpacticoid copepods

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Abstract

In coastal waters, individuals of many benthic species make temporary excursions into the water column, a behavior called emergence. The reasons for this behavior are not well established, but some that have been suggested apply equally well to the deep sea, and some sediment-trap data suggest that emergence occurs in the deep sea. To investigate this possibility, we collected sediment cores and placed inverted-funnel traps at 3087 m depth on the continental slope off central California (36°41.91'N 123°0.14'W) for 36 days and investigated a representative taxon, the harpacticoid copepods. Although our methods probably produced underestimates, at least 4 of 55 species emerged, so conceptualizations about the ecology of deep-sea-sediment communities should include the idea that some benthic species use the near-bottom flow to change locations.

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1. Introduction

A benthic animal that actively leaves the seabed, spends time in the water column, and then returns to the seabed is said to emerge. The behavior is common in shallow water; species of many taxa emerge (e.g., amphipods, ostracods, and polychaetes), and emergence has been observed in many habitats (e.g., intertidal sands, mud flats, sea-grass meadows, and shelf sands; see Mees and Jones, 1997, for a review). Numerous possible explanations

for emergence have been offered, and at least some appear to apply equally well in the deep sea. For example, it may be an efficient way to escape from deteriorating food conditions or accumulating predators. Emergence has not been studied explicitly in the deep sea, but in sediment traps that collected 4 m above bottom at 2347 m depth, L. Guidi-Guilvard (personal communication) found benthic copepods that had either emerged or been resuspended. Here, we report data that suggest that emergence occurs in the deep sea.

We focused on harpacticoid copepods because many shallow-water harpacticoid species emerge (Bell et al., 1988; Walters, 1988; Thistle, 2003).

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Moreover, harpacticoids are abundant enough in the deep sea that emergence traps of a size that could be manipulated by a remotely operated vehicle had a reasonable prospect of catching useful numbers of individuals if emergence occurred. Also, harpacticoids are ubiquitous and speciose in deep-sea sediments and are, in this sense, a representative deep-sea group.

2. Materials and methods

2.1. Study site

The study site was at 3087 m depth on the continental slope off central California (36°41.91'N, 123°0.14'W; Fig. 1). The sediment was a mud, and the seafloor was macroscopically flat in the approximately 200 m × 200 m area we explored. The salinity, temperature, and oxygen concentration of the near-bottom water during our visits (December 2004 and January 2005), as determined by sensors mounted on the remotely operated vehicle *Tiburon* of the Monterey Bay Aquarium Research Institute, were 34.6 (Falmouth Ocean OTM), 1.58 °C (Falmouth Ocean OCM), and 115.6 μM (SeaBird 43), respectively. Because reliable sensors for measuring parameters of the ocean carbon dioxide system in deep-sea environments are not readily available, we used reported values (WOCE Station P17-10; woce.nodc.noaa.gov) of two carbon-system parameters (alkalinity and total carbon dioxide) to calculate *in situ* pH of 7.78 (seawater scale), using a program developed for

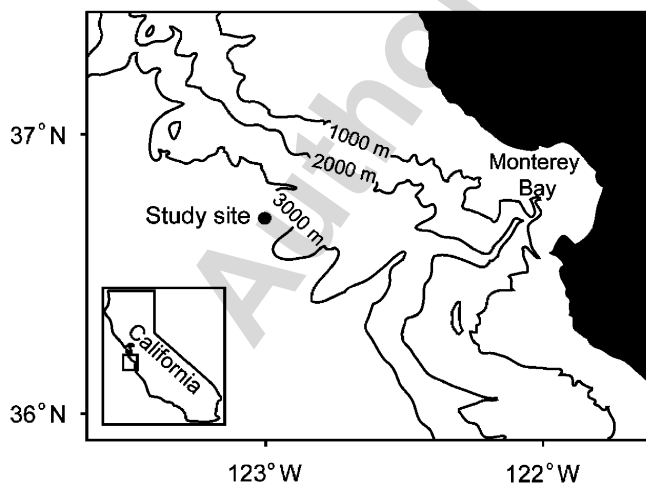


Fig. 1. A chart of the eastern Pacific off central California showing the location of the study site.

calculations of the CO₂ system (cdiac.ornl.gov/oceans/co2rprt.html). See DOE (1994) and Millero (1995) for a discussion of the ocean carbon dioxide system.

2.2. Trap design, deployment, and recovery

As is routine in emergence studies (see for example Hicks, 1986; Walters and Bell, 1986; Thistle, 2003), we used an inverted-funnel trap (Fig. 2). The collecting chamber was a 14.6-cm-tall section of polyvinyl chloride (PVC) pipe. To it, we fitted a removable PVC lid and a custom-made, PVC funnel with openings of 22 and 1.8 cm diameter. The lid incorporated a 1.9-cm-diameter vent covered with 30-μm-aperture mesh and a 1.9-cm-diameter port closed by a nylon screw. Four legs, each with two horizontal flanges, held the collecting chamber 4 cm above the seabed. The distance from the seabed to the top of the funnel spout (i.e., the entrance to the collecting chamber) was 9.6 cm.

When emergence traps are sealed to the seabed (see for example Walters and Bell, 1986), the animals found in the collecting chamber are known

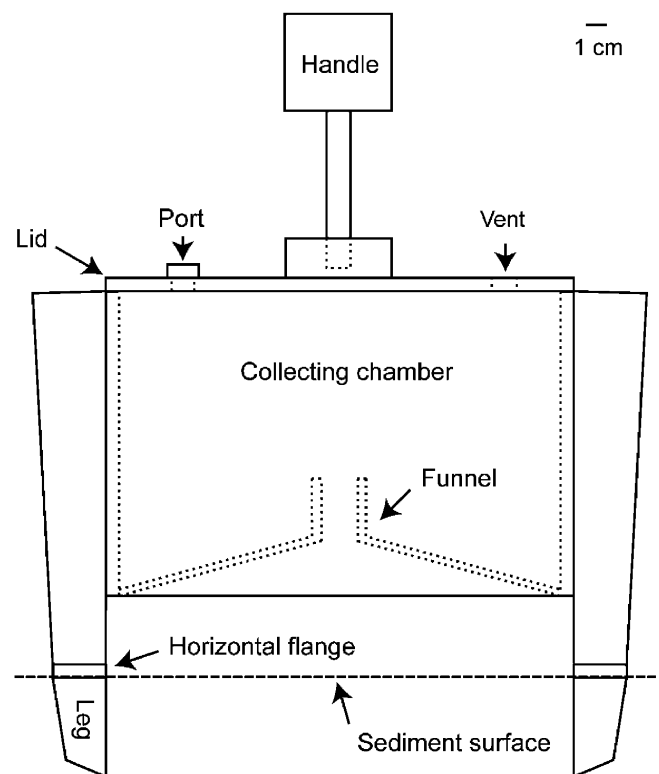


Fig. 2. A diagrammatic representation of the emergence trap showing its components.

to have come from the seabed enclosed by the trap, and the emergence rate can be measured. Such traps are usually deployed for 24 h or less, and oxygen depletion in the trap, when it has been examined, has not been problematic (Walters and Bell, 1986). In contrast, our traps were to be deployed for ~30 days. Given the antipathy of most harpacticoids to reduced oxygen concentration (Powell, 1989), traps sealed to the seabed might have created conditions that affected emergence, so we used an unsealed trap (see Fleeger et al., 1984, and Walters, 1988) and accepted that the emergence rates could only be estimated. This style of trap does have the advantage that the presence of moving water beneath the funnel should suppress the artifactual emergence that can occur in traps sealed to the seabed (Thistle, 2003).

For deployment, each trap was placed in a carrier that contained a pedestal tipped with a rubber stopper that sealed the collecting chamber. We filled each collecting chamber with artificial seawater of salinity 35. To each, we added 50 freeze killed, adult specimens of the shallow-water harpacticoid *Schizopera knabeni* Lang obtained from a laboratory culture. These specimens allowed us to check the possibility that some harpacticoids decayed to unrecognizability in traps during the experiment. We transported three traps in their carriers to the seabed using a free-vehicle elevator. On 14 December 2004, *Tiburon* moved each trap from its carrier to its intended deployment location. During this process, the trap rested on a rubber-stopper-tipped pedestal on the *Tiburon*, so the collecting chamber was sealed until the trap was gently set on the seabed. Thirty-six days later, the *Tiburon* recovered the traps. On deck, the water in each trap was passed through a sieve of 30- μ m-aperture mesh. The sieve contents were preserved in a solution (1:9, v:v) of formalin and artificial seawater of salinity 35 that was buffered with sodium borate.

2.3. Coring

The *Tiburon* took 6 cores of 7-cm inner diameter approximately 2 m from the traps; all corers were inserted into the seabed before any were removed. On the ship, the water overlying each core was removed and passed through a sieve of 30- μ m-aperture mesh, and the sieve contents were retained. The core was placed on a precision extruder, and the top 0.5 cm sliced off. This material and the sieve contents were preserved as described above.

2.4. Sample processing

In the laboratory, the material retained on a sieve of 30- μ m-aperture mesh from each sample was stained with rose bengal and examined under a dissection microscope. Harpacticoids were removed and stored in drops of glycerin on microscope slides. We restricted our study to adults because juveniles of closely related species could not be distinguished.

2.5. Species identification

Although many deep-sea harpacticoids can be placed in families and genera, very few deep-sea species have been described (Thistle, 1978; Seifried, 2004). Accordingly, we separated our specimens into working species and used the keys of Wells (1976) and Huys et al. (1996) and the primary literature to identify our working species to the lowest formally described taxon.

2.6. Recognition of emergent species

Not all the specimens found in traps were necessarily emergers. To eliminate demersal species, we followed Thistle's (2003) rule that only species found both in traps and in cores should be considered potential emergers. To recognize the emergers among the potential emergers, we followed Thistle and Sedlacek (2004), who found that the endopods of pereopods 2–4 of emergent species had three segments and that the sum of the numbers of major setae and spines on the last segments of the exopods of pereopods 2–4 varied from 21 to 23. We assumed that these features characterize the morphologies of emergers in that, although not all species with these features are emergers, most emergers have them.

2.7. Estimating emergence rate

To estimate the minimum emergence rate, we calculated the average number of individuals per trap for all emergent species combined. We converted that average to an areal basis by assuming that the individuals caught in the trap were derived from an area equal to the area beneath the trap. We then divided that value by the 36 days of the deployment. We also determined the total number of individuals of the emergent species in each core, calculated an average, and converted that average to the same areal basis as the trap data. The ratio of

Table 1

The species found in both emergence traps and cores at our site, showing the features of pereopods 2–4 that Thistle and Sedlacek (2004) found to be useful in the identification of species that emerge

| Family | Species | P2 end | P3 end | P4 end | P2 exp | P3 exp | P4 exp |
|-----------------|--|--------|--------|--------|--------|--------|--------|
| Ameiridae | cf. <i>Nitokra</i> ^a | 3 | 3 | 3 | 7 | 8 | 8 |
| Argestidae | <i>Mesocletodes</i> cf. <i>irrasus</i> | 2 | 2 | 2 | 6 | 6 | 5 |
| Ectinosomatidae | cf. <i>Ectinosomella</i> ^a | 3 | 3 | 3 | 7 | 8 | 7 |
| Ectinosomatidae | <i>Halectinosoma</i> sp. 1 ^a | 3 | 3 | 3 | 7 | 8 | 8 |
| Ectinosomatidae | <i>Halectinosoma</i> sp. 2 | 3 | 3 | 3 | 6 | 7 | 7 |
| Ectinosomatidae | cf. <i>Sigmatidium</i> ^a | 3 | 3 | 3 | 7 | 8 | 8 |
| Huntemanniidae | cf. <i>Metahuntemannia</i> | 2 | 2 | 2 | 5 | 6 | 6 |
| Neobryidae | <i>Antarcticobryda</i> cf. <i>tenuis</i> | 2 | 2 | 2 | 6 | 6 | 5 |

P2 end, P3 end, and P4 end are the numbers of segments of the endopods of the second, third, and fourth pereopods, respectively. P2 exp, P3 exp, and P4 exp are the numbers of major setae and spines on the terminal segments of the exopods of the second, third, and fourth pereopods, respectively.

^aSpecies identified as emergers.

these two quantities is our estimate of the minimum daily emergence rate of the population of emergent species. To estimate the minimum daily emergence rate as a proportion of all the harpacticoids in the sediment, we used the same numerator, but we calculated the denominator by determining the total number of harpacticoids in each core, calculating a per-core average, and converting that average to the same areal basis as the trap data. To obtain a maximum estimate of the daily emergence rate, we assumed that all the individuals in the trap were collected in the last 24 h of the deployment.

2.8. Other methods

To determine the proportion of the species at our site that were morphologically equipped to emerge, we examined all the species present in the sediment samples for the features that Thistle and Sedlacek (2004) suggested identify emergers.

With the aid of a drawing tube and a compound microscope, we measured body length, for a representative individual of each species, as the distance from the base of the rostrum to the base of the caudal rami in lateral view.

The field work was done during “CO₂-6,” the sixth in a series of deep-sea investigations (see Barry et al., 2005) led by J.P.B.

3. Results

We recovered 13, 39, and 42 of the 50 dead individuals of the shallow-water species *S. knabeni* we had added to the traps as an internal control.

We found 15 species in traps and 55 species in cores. Seven of the species found in traps were not found in cores, so only eight of the species at our site were considered potential emergers (Table 1). Of these, three species (in the Neobryidae, Argestidae, and Huntemanniidae) did not exhibit the pereopodal features associated with emergence. *Halectinosoma* sp. 2 met the criteria except that its total number of setae was 20, whereas the smallest sum Thistle and Sedlacek (2004) found was 21. This species was probably also an emerger, but to be conservative, we did not treat it as such. Our best estimate is therefore that four of the 55 species (7.3%) at our site emerged.

Of the 55 species, we found in the uppermost 0.5 cm, 28 (50.9%) had the pereopodal features associated with emergence.

Our maximum and minimum estimates of the daily emergence rate were 34.6% and 0.96% of the population of the emerger species and 3.2% and 0.09% of the total harpacticoid fauna respectively.

4. Discussion

4.1. Some harpacticoid species emerged

We found four species that appeared to emerge (Table 1). Three were members of the Ectinosomatidae, which are torpedo shaped, streamlined animals (Noodt, 1971). Many shallow-water species of this family are good swimmers, and some, including species of *Halectinosoma*, have been identified as emergers (Bell et al., 1987; Thistle and Sedlacek, 2004; Sedlacek and Thistle, 2006). One of

our emergers was related to species in the genus *Nitokra* (Ameiridae). Thistle (2003, see also Sedlacek and Thistle, 2006) found that a species of *Nitokra* and a species closely related to *Nitokra* emerged at his continental-shelf site.

Our evidence that these four deep-sea harpacticoid species are emergers suggests that Guidi-Guilvard (personal communication) was correct in inferring that harpacticoids emerge in the deep sea. The biology of emergence for deep-sea species is likely to differ from that of shallow-water species. For example in shallow water, maximum harpacticoid emergence often occurs at dusk, so diel changes in light intensity are important for the timing of emergence (Walters and Bell, 1986; Armonies, 1988; Teasdale et al., 2004). Diel variation in light does not occur at our 3087-m-deep study site, so an individual's emergence is probably caused by changes in its local circumstances, such as adverse changes in the chemical milieu, decreases in food availability, and increases in predator abundances.

An alternative explanation for the presence of harpacticoids in the traps is that they were swept there passively by eddies in the near-bottom flow. We believe this explanation unlikely because the speed of the near-bottom flow at our site was only a few centimeters per second, so little momentum was available to create eddies. We also tested a prediction of this passive-entry hypothesis, that the proportion of individuals in the trap that were emergers should not differ significantly from the proportion of individuals in the cores that were emergers (Table 2), other things being equal. We found that the proportion of emergers was significantly greater in the traps (24 of 30 individuals) than in the cores (17 of 154 individuals) ($p < 0.05$, chi square test of independence).

This test required the assumption that the probability of an emerger's being suspended was not systematically greater than that of other individuals in the population. Suspension should act preferentially on smaller animals because sur-

face-area-to-volume ratio increases as size decreases. Given that individuals of the four emergent species (average the body lengths = 0.50 mm, range = 0.39–0.67) were not unusually small compared to the others (average = 0.53 mm, range = 0.23–1.03), our assumption seems reasonable with respect to body size. The effect of the leg segmentation and setation differences that we used to distinguish emergent species on the probability that an animal would be suspended is unclear. Nevertheless, 50.9% of the species at our site had these characters. If possession of these characters caused individuals to be passively suspended, the traps should have contained individuals of most of the species with these characters, which they did not. We do not argue that all of the individuals we found in the trap were emergers. Given its reduced legs, we suspect that the individual of the Argestidae we found in the trap entered by being suspended. Rather, we argue that the bulk of the individuals found in the traps emerged.

No deep-sea data exist with which to compare our results. At a 20-m shelf site, Thistle (2003) found that 43.8 and 32.4% of the species of harpacticoids emerged in summer and winter respectively. We were surprised to find that only four or perhaps five of the 55 harpacticoid species at our site emerged. That 50.9% of the species at our site had the features of the swimming legs that Thistle and Sedlacek (2004) found to be associated with emergence suggests that we underestimated the number of species that emerged, a result that could arise because of some features of our experiment. (1) For an individual to be caught in an inverted-funnel trap, it must swim from the seafloor to the height of the entrance to the collecting chamber (Fig. 2). Although this distance (9.6 cm) in our trap is less than the 12–15 cm typical of those used in shallow-water studies of harpacticoid emergence (see for example Hicks, 1986; Walters and Bell, 1986; Walters, 1991), a species could emerge but never be trapped (Fleeger et al., 1984; Walters and Bell, 1994). (2) During the 36 d of the experiment, some trapped individuals could have found their way out through the spout. (3) The source population could have been depleted during the experiment if the trap caught emergers faster than they could be replaced by immigration. (4) We know that individuals did decay away during the experiment because handling losses are unlikely to account for the disappearance of *S. knabeni* individuals (Thistle et al., 2005). If individuals of some emerging species were only

Table 2
The number of individuals of emergent and nonemergent species in traps and cores, showing that emergent species are disproportionately abundant in traps

| | Emergent | Nonemergent |
|-------|----------|-------------|
| Traps | 24 | 6 |
| Cores | 17 | 137 |

caught early in the experiment, they might have decayed away before we recovered the traps, eliminating the evidence that these species emerged.

4.2. Emergence rate

The data at hand were not well suited for estimating the proportion of the population of a species or the proportion of the harpacticoid fauna that emerged per unit time because our techniques undercollected emergers. At the same time, deep-sea data are rare and expensive to obtain, so we report our estimates to begin the iterative process of discovering true values.

5. Conclusion

We have shown that at least four species emerge at our site, supporting the suggestion by Guidi-Guilvard that harpacticoids emerge in the deep sea. Our techniques undercollected emergers, so our estimates should be treated as minima, and whether emergence is common or not among deep-sea harpacticoid species is not yet clear. That it occurs at all raises interesting questions about the factors that cause the behavior and its effects on the organization of deep-sea communities.

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