

# Emergent and non-emergent species of harpacticoid copepods can be recognized morphologically

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**ABSTRACT:** Emergence—the active movement of benthic organisms into the water column and back—has consequences for many ecological processes, e.g. benthopelagic coupling. Harpacticoid copepods are conspicuous emergers, but technical challenges have made it difficult to determine which species emerge, impeding the study of the ecology and evolution of the phenomenon. We examined data on harpacticoid emergence from 2 sandy, subtidal sites (~20 m deep) in the northern Gulf of Mexico and found 6 species that always emerged and 2 species that never emerged. An examination of the locomotor appendages revealed that the number of segments in the endopods of pereopods 2–4 and the number of setae and spines on the distal exopod segments of pereopods 2–4 can be used to distinguish emergers from non-emergers. We then successfully used these characters to predict the behavior of 3 additional species. Certain morphological differences may therefore allow differentiation of emergers from non-emergers.

**KEY WORDS:** Emergence · Harpacticoid copepods · Continental shelf · Benthopelagic coupling

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## INTRODUCTION

The active movement of individual benthic animals from the seabed into the water column and back, often with a diel periodicity, is termed 'emergence' (see review by Mees & Jones 1997). Emergers include species of polychaetes, turbellarians, amphipods, cumaceans, and harpacticoid copepods. Their emergence has importance for many phenomena, including benthopelagic coupling (Marcus & Boero 1998).

Harpacticoid copepods are small crustaceans (body length < 1.0 mm) that occur in large numbers ( $10^5$  to  $10^6$  ind.  $m^{-2}$ ) in marine sediments (Hicks & Coull 1983). In some locations, a substantial portion of the population emerges every 24 h (Walters & Bell 1986, 1994, Arlt 1988, Buffan-Dubau & Castel 1996, Thistle 2003). Harpacticoid emergence has been studied extensively (Fleeger et al. 1984, Hicks 1986, Walters & Bell 1986, Armonies 1988, Buffan-Dubau & Castel 1996) and has been important in attempts to develop generalizations about emergence (see review by Palmer 1988, Armonies 1989, Thistle 2003).

What appear to be emergent harpacticoids have been found in such varied environments as sandy beaches, seagrass meadows, mudflats, coral reefs, and the continental shelf; therefore, harpacticoid emergence might be widespread. At the same time, few studies have been carried out, so the behavior of a species is unlikely to be known *a priori*. For many purposes (e.g. prediction of habitat use, Bell et al. 1987), the ability to identify species that emerge without observation of their behavior would be useful. Also, the discovery of characteristics common to emergers could help in studies of the ecology and evolution of the behavior.

Bell et al. (1987) searched for morphological similarities among harpacticoid emergers, but their task was made more difficult as the data available to them did not separate experimentally induced from true emergence. That is, harpacticoid emergence had been investigated primarily with traps sealed to the seabed (Hicks 1986, Walters & Bell 1986). Such traps created still water, which was suspected to stimulate emergence (Palmer 1988). Recent field work has shown that this concern was well founded (Thistle 2003). As a

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consequence, Bell et al. (1987) may have inadvertently considered some animals to be emergers that were not, making it more difficult to identify characters that united among the group.

To circumvent this problem, we assembled data that allowed us to separate species that emerged artifactually from species that emerged naturally. Following Remane (1952) and Noodt (1971), we asked (1) whether certain characters united emergers, (2) whether certain characters united non-emergers, and (3) whether certain characters differentiated the 2 groups.

## MATERIALS AND METHODS

**Study sites.** We used data from Thistle (2003) and L. Sedlacek & D. Thistle (unpubl.). Thistle's site was a  $3 \times 10$  m plot at 18 m depth in the northern Gulf of Mexico ( $29^{\circ}40.63'N$ ,  $84^{\circ}22.80'W$ ; Thistle 2003). The seabed was an unvegetated, moderately sorted, medium sand with  $<1\%$  silt and clay by weight (see Thistle et al. 1995, their Table 1). Sedlacek & Thistle's site was a  $1.5 \times 60$  m plot at 20 m depth ( $30^{\circ}22.65'N$ ,  $86^{\circ}38.69'W$ ) about 230 km west of Thistle's. Seabed properties were similar to those at Thistle's (2003) site.

**Sampling.** Thistle (2003) and L. Sedlacek & D. Thistle (unpubl.) used the same inverted-funnel traps (see Thistle 2003, his Fig. 1) to collect emerging individuals. Each trap consisted of a cylindrical collecting chamber whose transparent walls and funnel minimized light attenuation, which might alter the behavior of the harpacticoids. The sides of the funnel sloped at  $60^{\circ}$ . Its openings were 1.5 cm and 10 cm in diameter. The collecting chambers were mounted in 2 ways. In a 'base trap', a collecting chamber was attached to a transparent cylindrical base after the base had been inserted into the sediment. A stabilizing ring limited the penetration of the base into the sediment to hold the lower opening of the funnel 4.5 cm above the seabed. Each base had 2 rows of 18 ports of 1.1 cm diameter that were covered with 50- $\mu\text{m}$ -aperture mesh to allow some exchange of water while retaining the harpacticoids. One row was centered 1.6 cm above the sediment surface, and one was centered 2.7 cm below the sediment surface. In a 'leg trap', a collecting chamber was placed on a tripod that held the lower opening of the funnel 4.5 cm above the seabed, allowing more or less free water movement beneath the chamber. In both cases, the entrance to the collecting chamber was 15 cm above the sediment. Before deployment, each collecting chamber was filled with 50- $\mu\text{m}$ -filtered seawater obtained from  $\sim 50$  cm above bottom at the study site. The smaller funnel opening was sealed with a stopper that prevented exchange during transit to the

seabed. The stopper was removed when the trap was ready to be placed on its base or tripod.

Thistle (2003) tested for differences in emergence between 2 seasons. Traps were set out in a blocked design; 1 base trap and 1 leg trap constituted a block. On a given day, 3 blocks were deployed. After  $\sim 24$  h, a SCUBA diver inserted a stopper into the smaller funnel opening of the collecting chamber of each leg trap to close it *in situ*. The collecting chamber of each base trap was released from the base and raised  $\sim 20$  cm to allow the stopper to be inserted. To estimate the number of harpacticoids remaining in the section of seabed enclosed, a diver took a 15.5-cm<sup>2</sup>-diameter core from the center of the area enclosed by the base before the base was removed from the sediment (see Walters & Bell 1986).

On deck, the water in each collecting chamber was sieved on 50- $\mu\text{m}$ -aperture mesh. Each core was mounted on a precision extruder (Fuller & Butman 1988). The water overlying the core was removed and sieved (50- $\mu\text{m}$ -aperture mesh); the sieve content was added to the 0 to 2-mm-layer sample. The top centimeter was sliced into 2 mm layers. All samples were preserved in sodium-borate-buffered seawater formaldehyde (9:1, v:v).

In the laboratory, the collecting-chamber samples and the sediment samples were stained with rose Bengal (Pfannkuche & Thiel 1988), and the harpacticoids were removed under a dissection microscope. For collecting-chamber samples, all adult harpacticoids were identified to working species. Because large numbers of harpacticoids were present in the sediment samples, only 50% of the adult harpacticoids were identified. For each adult, a random-numbers table was consulted. If the digit was odd, the individual was identified; if the digit was even (zero was treated as even), it was not (Walters & Bell [1986] solved this problem in a similar way). Most of the species encountered have not been formally described.

L. Sedlacek & D. Thistle (unpubl.) studied emergence from sediment crests and troughs. On successive days during November 1999, SCUBA divers placed traps at randomly assigned locations with the restriction that traps be at least 2.7 m (10 trap diameters) apart to minimize the possibility of hydrodynamic interference. Each day, SCUBA divers placed 4 traps—2 base traps (1 on a crest and 1 in a trough) and 2 leg traps (1 on a crest and 1 in a trough) and recovered them 24 h later. They used the same traps, trap-handling procedures, and sample-processing procedures as Thistle (2003), except that all adult individuals were identified to working species.

We used the scheme devised by Thistle (2003) to classify the emergence behavior of each species. A species absent from base traps and sediment cores,

but present in leg traps, was considered planktonic. A species found in only 1 replicate was considered too rare to classify accurately. A species absent from base traps and leg traps but present in sediment cores was classified as a non-emerger. A species present in base traps and leg traps was considered an emerger, whether or not it was present in sediment cores. A species present in base traps, but not in leg traps, was considered to have emerged as an artifact of the experiment. Species absent from base traps but present in leg traps and found in the sediment could not be classified. Of the classified species, we determined which species had been abundant enough to classify in at least 3 of the 4 data sets and had also been classified the same (e.g. as an emerger) in each data set. These species were deemed to have been consistent in their behavior.

**Morphological analysis.** The one thing that we knew *a priori* about emergers was that they could swim at least 15 cm from the seabed, because they were caught in the collecting chambers of emergence traps. We therefore suspected that characters associated with swimming might unite this group. In harpacticoids, pereopods 2–4 are the primary locomotor appendages. In swimming harpacticoids, one would expect these appendages to be effective paddles and thus to be relatively large, in contrast with the condition in some harpacticoids, where the numbers of segments and numbers of setae on the swimming legs are reduced (Noodt 1971). In harpacticoids, unreduced pereopods 2–4 have 3-segmented exopods and endopods and have 7, 8, and 8 setae/spines respectively on the terminal segments of the exopods (Huys & Boxshall 1991) (Fig. 1). We tabulated these characters for emergers and non-emergers.

To compare our results to those of Bell et al. (1987), we measured the characters that they found to be most informative on each of our species that had consistent behavior. Their characters were (1) the ratio of the length of the first endopodal segment of the first pereopod to that of the remainder of the endopod, (2) the projected area of the cephalosome in dorsal view, and (3) the length of the antennule of adult females. We measured these characters as illustrated in Bell et al. (1987, their Fig. 1) from *camera lucida* illustrations of our species.

We also tested the ability of our morphological characters to differentiate emergent and non-emergent species. To do so, we exploited the strict nature of our classification scheme. For example, if a single individual was caught in the base trap and a single individual was caught in the leg trap, the species was classified as an emerger, no matter how many individuals were found in the sediment. This conservatism was necessary because the number of individ-

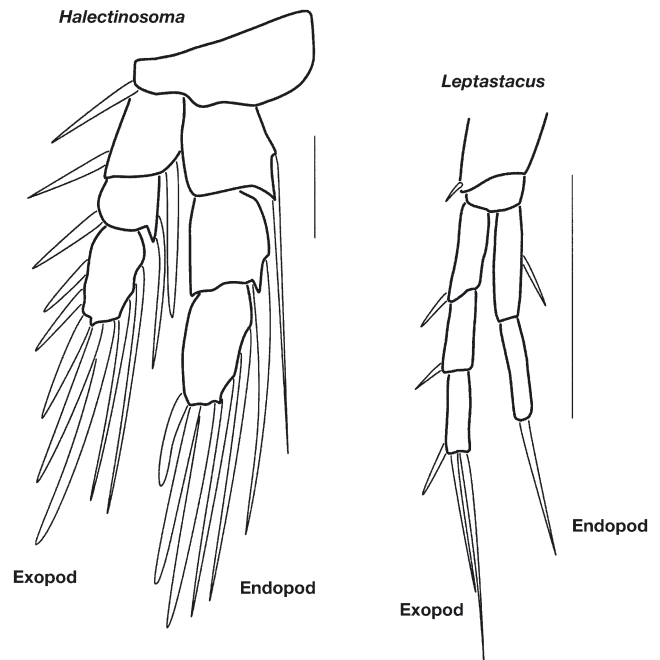


Fig. 1. Sketch of the second pereopod of *Halectinosoma* sp., representing the emergers, and *Leptastacus* cf. *coulli*, representing the non-emergers, showing the difference in number of endopodal segments and in number of terminal-segment setae of the exopod. Scale lines are 0.05 mm

uals that emerge in 24 h can be small but consistent for some species (L. Sedlacek & D. Thistle unpubl.). At the same time, in a scheme so sensitive to single individuals, mistakes in classification were possible. For example, in the process of trap installation or removal, an individual could have been caught where it did not ordinarily occur, or a species could have been rare at the location and time of the sampling, so no individual was available to enter a trap. An inspection of the abundance data revealed that 3 species had not been analyzed because a single observation caused them to be viewed as inconsistent. From the distribution of individuals among base traps, leg traps, and the sediment, we inferred the behavior of each of these species. As a test of the ability of the characters we used to predict species' behavior, we compared the morphologically predicted behavior to that inferred from the abundance data.

## RESULTS

A total of 28 species were examined for consistency of behavior. Of these, 6 species were consistent emergers, and 2 were consistent non-emergers (Table 1).

Table 1. Selected characters of species that had consistent emergence behavior, showing that non-emergers differed from emergers. P2–P4 end segs = number of segments in the endopods of pereopods 2–4 respectively. P2–P4 exp setae = number of setae and spines on the distal exopod segments of pereopods 2–4 respectively

Family	Species	Behavior	P2 end segs	P3 end segs	P4 end segs	P2 exp setae	P3 exp setae	P4 exp setae
Leptastacidae	<i>Leptastacus</i> cf. <i>coulli</i>	Non-emerger	2	2	2	3	4	4
Tetragonicipitidae	<i>Phyllopodopsyllus</i> sp.	Non-emerger	2	2	2	4	4	4
Ambunguipedidae	cf. <i>Ambunguipes</i>	Emerger	3	3	3	7	8	8
Diosaccidae	<i>Amphiascus</i> cf. <i>varians</i>	Emerger	3	3	3	7	7	8
Ectinosomatidae	<i>Halectinosoma</i> sp.	Emerger	3	3	3	7	8	7
Ectinosomatidae	<i>Pseudobradya</i> cf. <i>exilis</i>	Emerger	3	3	3	7	8	8
Ectinosomatidae	<i>Ectinosoma</i> sp.	Emerger	3	3	3	7	8	8
Thalestridae	cf. <i>Dactylopodia</i>	Emerger	3	3	3	7	8	7

Table 2. Characters used by Bell et al. (1987), showing that non-emergers differed from emergers in cephalosome area. N = non-emerger, E = emerger. P1 ratio = ratio of the length of the first endopodal segment of pereopod 1 to the length of the remainder of the endopod. Cephalosome area = projected area of the cephalosome in dorsal view. A1 length = length of the antennule

Species	Behavior	P1 ratio	Cephalosome area (mm <sup>2</sup> )	A1 length (mm)
<i>Leptastacus</i> cf. <i>coulli</i>	N	1.08	0.004	0.101
<i>Phyllopodopsyllus</i> sp.	N	3.50	0.007	0.089
cf. <i>Ambunguipes</i>	E	5.08	0.153	0.234
<i>Amphiascus</i> cf. <i>varians</i>	E	2.14	0.013	0.112
<i>Ectinosoma</i> sp.	E	0.49	0.014	0.051
cf. <i>Dactylopodia</i>	E	6.60	0.079	0.180
<i>Halectinosoma</i> sp.	E	0.38	0.050	0.080
<i>Pseudobradya</i> cf. <i>exilis</i>	E	0.37	0.010	0.026

The character states of 6 locomotor-appendage characters distinguished the emergers from the non-emergers (Table 1). For example, the endopods of the second pereopods of the non-emergers had 2 segments, but those of the emergers had 3. We also compared the groups using Bell et al.'s (1987) characters. Table 2 shows that the values of their pereopod and antennule characters for the emergers encompassed

those of the non-emergers, but the non-emergers and the emergers did differ in cephalosome area.

The 3 species whose inconsistency of classification turned on a single observation were *Bradyellopsis* sp., *Longipedia* sp., and *Rhizothrix* sp. (Table 3). From an examination of the distribution of abundance among the base trap, leg trap, and sediment samples (Table 3), we inferred that *Rhizothrix* was a non-emerger and that *Bradyellopsis* and *Longipedia* were emergers. The character states of *Rhizothrix* sp. matched those of the 2 non-emergers (Tables 1 & 4).

The character states of *Bradyellopsis* matched those of the emergers (Tables 1 & 4). For *Longipedia*, the number of segments in the endopods of pereopods 2–4 matched those of the emergers (Tables 1 & 4), but the numbers of terminal setae on the exopod of pereopods 2–4 were 6, 6, and 5 respectively, lower than those of the emergers but higher than those of non-emergers (Tables 1 & 4).

Table 3. Species whose inconsistent classifications were caused by single observations, showing the problematic observations (italics). B = number of individuals collected in base traps. S = estimated number of individuals in the sediment enclosed by base traps, L = number of individuals collected in leg traps

Species	Data set 1			Data set 2			Data set 3			Data set 4		
	B	S	L	B	S	L	B	S	L	B	S	L
<i>Bradyellopsis</i> sp.	1	15	0	1	5	2	14	10	6	3	42	11
<i>Longipedia</i> sp.	395	381	422	387	647	514	110	10	13	2	94	0
<i>Rhizothrix</i> sp.	0	52	0	0	26	0	0	21	0	1	10	0

Table 4. Character states and predicted behavior of 3 species, showing that those of *Bradyellopsis* sp. matched the pattern for emergers and those of *Rhizothrix* sp. matched that for non-emergers (Table 1). P2–P4 end segs = number of segments in the endopods of pereopods 2–4 respectively. P2–P4 exp setae = number of setae and spines on the distal exopod segments of pereopods 2–4 respectively

Species	P2 end segs	P3 end segs	P4 end segs	P2 exp setae	P3 exp setae	P4 exp setae	Predicted behavior
<i>Bradyellopsis</i> sp.	3	3	3	8	8	8	Emerger
<i>Longipedia</i> sp.	3	3	3	6	6	5	No prediction
<i>Rhizothrix</i> sp.	2	2	2	4	4	4	Non-emerger

## DISCUSSION

Inspection of Table 1 reveals that the species we classified as emergers or non-emergers were not grouped taxonomically. In particular, emergence occurred in distantly related families (Ambungiopidae, Ectinosomatidae, Thalestridae), raising the possibility that it evolved more than once. Because species of the Ectinosomatidae dominated the list of emergers, the behavior might be particularly common in this family.

Emergers did prove to share the characteristics of good swimmers. The only variation within the group was that some species had 7 rather than 8 setae on the terminal segments of pereopods 3 or 4 (Table 1). We inferred therefore that all members were adapted to be swimmers to essentially the same degree, despite the taxonomic and therefore evolutionary heterogeneity of the group. This conclusion is consistent with the concept of *Lebensformtypen* (Remane 1952, Noodt 1971). The emergers also had relatively large cephalosome area (Tables 1 & 2), but the adaptive significance of this feature was not clear.

The non-emergers also shared morphological features. Their endopods had fewer than 3 segments on pereopods 2–4, and their exopods had 4 or fewer setae on the terminal segments of pereopods 2–4 (Table 1, Fig. 1). These features are similar to those of species living in the sediment that move by crawling or burrowing (e.g. *Cylindropsyllidae*, *Paramesochridae*) (Noodt 1971). The endopods of pereopods 2–4 in such species often have fewer than 3 segments, and the terminal segments of the exopods of pereopods 2–4 have fewer than 7 setae (see Lang 1948, his plates 347–350 and 476–477, Fig. 1). That the morphology of the endopods of pereopods 2–4 of the non-emergers approximated those of species known to live in the sediment suggests that non-emergers are less effective swimmers than emergers and are better adapted for life in the seabed. Our results are parallel with those

of Nilsson et al. (2000), who found morphological differences between migrating (i.e. emerging) and non-migrating oligochaetes.

We found a set of morphological characters that distinguished 6 emergent species from 2 non-emergent species. Although this result was promising, it required testing. As a first step, we examined the morphology of 3 species that were not among the 8 species considered above. We used the distribution of their abundance among base trap, leg trap, and sediment samples to infer their

behavior, then predicted their behavior using our characters. Our prediction for 2 of the species was unambiguous and correct. The situation for *Longipedia* was more complex. The segmentation of the endopods of its pereopods 2–4 matched that of the emergers, but the number of terminal setae on the exopods of pereopods 2–4 did not. Because the terminal-seta character states did not match those of either group, we could not make a prediction. Because its abundance distribution among our samples was that of an emergent, and it has been reported from the near-bottom plankton (Huys et al. 1996), we concluded that it was an emergent, and that our hypothesis should be modified to state that emergers can have as few as 5 terminal setae on the exopods of pereopods 2–4.

We conclude that certain morphological characteristics unite the emergers we have studied, and different characteristics unite the non-emergers. If these results could be extended to other species and other locations, the characteristics would be useful for inferring emergence behavior in the absence of behavioral information and for correcting classifications based on trap data. Any common characteristics among emergers could also serve as foci for investigations of the ecology and evolution of the behavior.

Earlier, we raised the possibility that Bell et al.'s (1987) inferences about the emergence behavior of the species they examined was affected by their technique (see 'Introduction'). They identified species of *Ectinosoma*, *Longipedia*, *Metis*, *Paradactylopodia*, and *Zausodes* as emergers. In our material, *Metis* and *Zausodes* were too rare to study, but we found a species of *Ectinosoma*, a species of cf. *Dactylopodia* (which is closely related to *Paradactylopodia*; Huys et al. 1996), and a species of *Longipedia* to be emergers. The coherence between our results and those of Bell et al. (1987) suggests that the latter classified their emergers correctly, and adds weight to the notion that morphology will be efficacious in detecting emergent species.

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