

# Harpacticoid copepod emergence at a shelf site in summer and winter: implications for hydrodynamic and mating hypotheses

David Thistle\*

Department of Oceanography, Florida State University, Call Street, Tallahassee, Florida 32306-4320, USA

**ABSTRACT:** Emergence (in which benthic animals swim into the overlying water and then return to the seabed) has consequences for issues such as benthopelagic coupling and benthic community organization. Harpacticoid copepods are conspicuous among emergers; however, to achieve a predictive understanding of their behavior will require much further study. In particular, little is known about variability in their emergence among seasons. I report the results of an emergence-trap study done at 18 m depth on a sandy bottom in the northern Gulf of Mexico. Percent emergence was significantly greater in September than in December. In September, near-bottom flows are quiescent, and in December, near-bottom flows are frequently energetic. That emergence was less during the season of energetic flows fits expectations from the literature that energetic flows suppress emergence. In contrast, my observations on gender and life stage of emergers provided no support for the hypothesis that harpacticoids emerge primarily to find mates.

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

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

Some benthic animals occur temporarily in the water column (Hagerman & Rieger 1981) either because they have been eroded (Palmer & Gust 1985) or because they have moved actively into the water column (i.e. emerged, see Mees & Jones 1997 for a review.) Emergence can be important. For example, it is a component of benthopelagic coupling (Marcus & Boero 1998), because energy and nutrients are exchanged between the water column and benthos (Gregg & Fleeger 1997), and it must affect benthic community organization, because the identity of the individuals at a location in the seabed changes constantly (Service & Bell 1987).

Concerning emergence, costs and benefits have been suggested (Alldredge & King 1980, Armonies 1988a, Hicks 1988, Palmer 1988a), but no theory can yet predict which individuals will emerge, when, or in what abundance. A step toward ecological understanding of emergence would be to document the important scales of variability in space and time, because

knowledge of variability can focus the search for mechanisms and provide constraints on any proposed explanation.

To investigate scales of variability in emergence that encompassed all the emerging taxa (e.g. some species of polychaete worms, Alldredge & King 1980; some species of amphipods, Grant 1980) would present overwhelming logistic challenges. I focused on the harpacticoid copepods, because they are one of the most common metazoan emergers (Bell et al. 1984). Further, because the taxon includes species with a wide range of lifestyles (Noodt 1971), comparative studies can be readily conducted to reveal how the ecologies of emergers differ from those of nonemergers.

Previous studies of emergence of sediment-dwelling (as opposed to phytal) harpacticoids have concentrated on intertidal habitats such as tidal creeks (Palmer & Brandt 1981, Palmer & Gust 1985), vegetated areas (Fleeger et al. 1984, Hicks 1986), mudflats (McCall 1992) and beaches (Armonies 1988a). Research has also been done at wading-depths in habitats such as

\*Email: thistle@ocean.fsu.edu

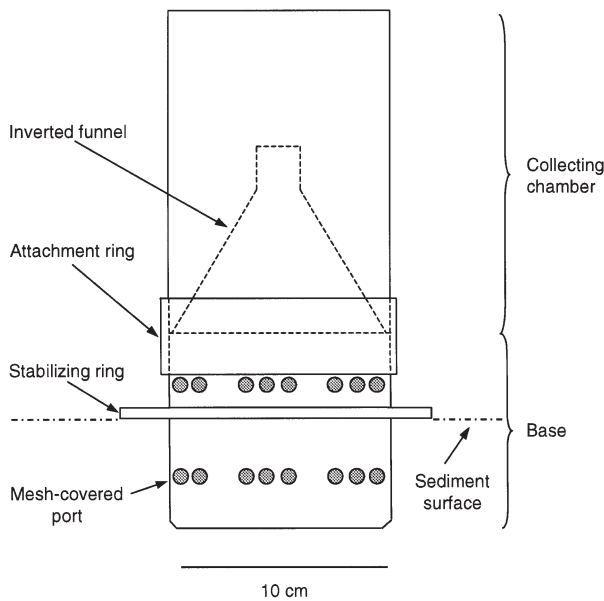


Fig. 1. Collecting chamber mounted on a base to show its components and their relationship to the seabed. In addition to the parts shown, on each base 3 stainless steel rods (0.9 by 20 cm) project horizontally just above the stabilizing ring at equal intervals around the trap to steady it

sediment patches in seagrass meadows (Walters & Bell 1986, Bell et al. 1988, Walters 1988, Buffan-Dubau & Castel 1996). Investigations have tended to focus on 24 h temporal scales and have reported variability associated with the light-dark cycle (Walters 1988, Armonies 1989) and the tidal cycle (Fleeger et al. 1984, Bell et al. 1988).

Although the studies of harpacticoid emergence were done in water of less than about 1 m depth, some authors who have published on the emergence of demersal zooplankton have reported harpacticoids from their collections in deeper water (see for example Robichaux et al. 1981, Youngbluth 1982), raising the possibility that harpacticoids emerge on the shelf. To begin to clarify the question of harpacticoid emergence at shelf depths, I chose to study a site at 18 m in the warm, temperate, northern Gulf of Mexico.

Although the  $\leq 24$  h time scale has received the most attention, variability in harpacticoid emergence occurs at longer time scales (Walters 1991, Walters & Bell 1994). Given the marked changes in environmental conditions on the shelf at the time scale of months in temperate and boreal regions, I chose to investigate the consistency of emergence in a relatively warm and hydrodynamically calm month (September) and a relatively cold and hydrodynamically energetic month (December). The marked difference between September and December in the proportion of harpacticoids that emerged provided an opportunity to consider

Palmer's (1988a) ideas about the effect of near-bottom flow on emergence and Hicks' (1988) view that emergence evolved to facilitate mating in harpacticoids.

## MATERIALS AND METHODS

The study site was located at 18 m depth in the northern Gulf of Mexico (29° 40.63' N, 84° 22.80' W). It was defined by two 10 m long, parallel lines separated by 3 m (area = 30 m<sup>2</sup>). The seabed was an unvegetated, moderately sorted, medium sand with <1% silt and clay by weight (see Thistle et al. 1995, their Table 1).

To sample emerging individuals, I used inverted-funnel traps (Fig. 1) (Hicks 1986). The funnel, walls, and top of the cylindrical collecting chamber were transparent. The funnel had sides that sloped at 60° and had openings of 1.5 and 10 cm diameter. The area from which animals could emerge was 81.1 cm<sup>2</sup>.

In a 'base trap', a collecting chamber was inserted into a transparent base (Fig. 1). A stabilizing ring limited the penetration of the base into the seabed such that the lower opening of the funnel was 4.5 cm above the seabed. Each base had 2 rows of 18 ports of 1.1 cm diameter that were covered with 50  $\mu$ 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. The base was inserted carefully into the seabed. After 30 s, the collecting chamber was sealed onto the base. A harpacticoid would have to swim 15 cm vertically to be trapped.

In a 'leg trap', the collecting chamber was placed on a tripod such that the lower opening of the funnel was 4.5 cm above the seabed. An emergent harpacticoid would have to swim 15 cm to be caught. Because leg traps were open to the flow, they did not collect quantitatively.

Before deployment, each collecting chamber was filled with 50  $\mu$ m filtered seawater obtained from ~50 cm above bottom at the study site. A stopper sealed the smaller funnel opening to prevent exchange until the trap was ready to be placed on the seabed. The traps were set out in a blocked design; 1 base trap and 1 leg trap constituted a block. Three blocks were deployed on a given day. The blocks were positioned at random in the direction of the long axis of the site but were constrained to be separated by at least 2 m. The 2 traps of a block were separated by 1 m along the long axis; their short-axis positions were selected at random. The relative positions of the 2 trap types were counterbalanced among blocks. Traps were deployed at approximately 13:00 h local time on 10 September and 11 December 1991. During both deployments, the moon was in its first quarter. After ~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*. For each base trap, the collecting chamber was released from the base and raised ~20 cm to allow the stopper to be inserted. For estimation of the number of harpacticoids remaining in the enclosed seabed, a 15.5 cm<sup>2</sup> diameter core was taken from the center of 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 µm aperture mesh. Each core was mounted on a precision extruder (Fuller & Butman 1988) and the top 1 cm was sliced into 2 mm layers. Before slicing, the water overlying the core was removed and sieved (50 µm aperture mesh); the sieve contents were added to the 0 to 2 mm layer samples. All samples were preserved in sodium-borate buffered seawater formaldehyde (9:1, v:v).

In the laboratory, the samples were stained with rose Bengal and the harpacticoids removed. For collecting chamber samples, subadult copepodites (hereafter juveniles) and adults were counted, but only adult harpacticoids were identified to species. Sediment samples were treated similarly, but only 50% of the adult harpacticoids, selected at random, were identified because of the large number of harpacticoids present. I used the taxonomic keys of Wells (1977) and Huys et al. (1996), but many species from this site have not been formally described.

I used the scheme shown in Fig. 2 to decide if a species was an emerger for each month separately. A species absent from base traps and sediment cores but present in leg traps was considered planktonic. A species that occurred in only 1 block (a base trap, leg trap, sediment core combination) 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 nonemerger. A species present in base traps and leg traps was considered a moving-water emerger, whether or not it was present in sediment cores. A species present in base traps but not in leg traps was considered a still-water emerger, whether or not it was present in sediment cores. Once in September and once in December, a species was absent from base traps, a single individual was present in a leg trap and the species was found in the sediment. These species were not classified. For calculations involving total adults or total juveniles, I followed the practice in the literature and treated all individuals in base traps as emergers and all those in the sediment as non-emergers.

To test for differences between 'treatments', I used a randomization approach (Manly 1991). The mean value for the parameter of interest was determined for each treatment and the difference between the treatment means calculated. The data from the 2 treatments

were then combined into 1 data set from which 2 new samples equal in size to the real samples were drawn at random. The difference in means between these new random samples was calculated. This procedure was repeated 4999 times with Resampling Stats software (Bruce 1991). From the distribution of the mean differences between treatments obtained at random, I estimated the probability of obtaining by chance alone a difference as great as or greater than that observed (2-tailed, 5% significance level). In this exploratory study, no correction was made for multiple testing.

Percent emergence was calculated as  $(A/[A + B])100$ , where  $A$  was the number of individuals of the group of

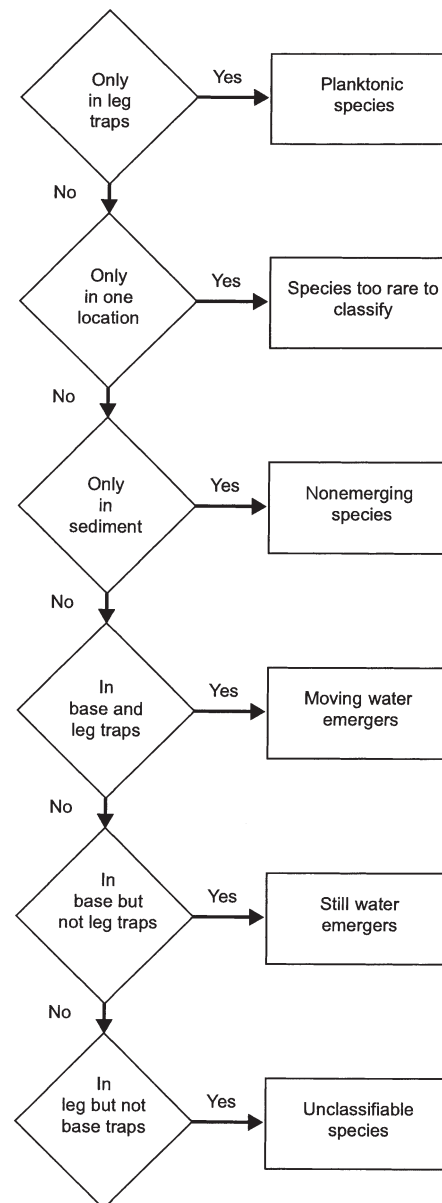


Fig. 2. Flow chart showing how the behavior of each individual was classified

interest in the collecting chamber of a base trap (i.e. the number that emerged) and  $B$  was the estimated number of individuals in the upper 1.0 cm of sediment from the same base trap. To obtain  $B$ , I multiplied the number of individuals found in the sediment samples by 5.2 to correct for the difference in area between the core and the trap. For adults, that number was multiplied by 2.0 because only 1 adult in 2 was identified from the core samples. Note that data from the leg traps were not used in the quantitative portion of the study.

## RESULTS

Table 1 lists the species considered in my study. In September, of the 32 species that could be classified,

14 (43.8%) were moving water emergers, 10 (31.3%) were still water emergers and 8 (25.0%) were non-emergers. In December, of the 37 species that could be classified, 12 (32.4%) were moving water emergers, 10 (27.0%) were still water emergers and 15 (40.5%) were nonemergers.

### Seasonal variation in percent emergence

I tested for a difference in percent emergence between the 2 sampling times in 2 ways. In the literature, reported percent emergence has been based on adults and juveniles combined; individuals found in sediment samples have been considered nonemergent, and those caught in a trap or other such device

Table 1. The species encountered showing the class to which they belonged in September and in December 1991. 'Moving' indicates moving water emergers. 'Rare' indicates species that occurred in only 1 set of samples. 'Still' indicates still-water emergers. See 'Materials and methods' and Fig. 2 for details

| Family<br>Species name          | Class        |              | Family<br>Species name               | Class      |              |
|---------------------------------|--------------|--------------|--------------------------------------|------------|--------------|
|                                 | September    | December     |                                      | September  | December     |
| <b>Ambungipectidae</b>          |              |              | <b>Ectinosomatidae (continued)</b>   |            |              |
| <i>cf. Ambungipectes</i>        | Moving       | Moving       | <i>Hastigerella cf. leptoderma</i>   | Still      | Still        |
| <b>Ameiridae</b>                |              |              | <i>Pseudobradya cf. exilis</i>       | Moving     | Moving       |
| <i>Ameira cf. listensis</i>     | Rare         | Still        | <i>Pseudobradya sp.</i>              | Moving     | Moving       |
| <i>Ameiriopsis sp.</i>          | Absent       | Rare         | <b>Harpacticidae</b>                 |            |              |
| <i>Leptomesochra sp.</i>        | Rare         | Absent       | <i>Mucropedia cookorum</i>           | Rare       | Nonemerger   |
| <i>cf. Nitokra</i>              | Rare         | Moving       | <i>Mucropedia kirstenae</i>          | Absent     | Nonemerger   |
| <i>Nitokra sp.</i>              | Moving       | Unclassified | <i>Zausodes arenicolus</i>           | Absent     | Rare         |
| <i>Praeleptomesochra sp.</i>    | Nonemerger   | Absent       | <b>Laophontidae</b>                  |            |              |
| <b>Canthocamptidae</b>          |              |              | <i>Laophonte cf. cornuta</i>         | Rare       | Absent       |
| <i>cf. Mesochra</i>             | Still        | Still        | <i>Paralaophonte brevisrostris</i>   | Nonemerger | Still        |
| <i>Mesochra cf. pygmaea</i>     | Moving       | Moving       | <b>Leptastacidae</b>                 |            |              |
| <i>Mesochra sp.</i>             | Moving       | Absent       | <i>Leptastacus cf. coulli</i>        | Nonemerger | Nonemerger   |
| <b>Diosaccidae</b>              |              |              | <b>Longipediidae</b>                 |            |              |
| <i>Actopsyllus sp.</i>          | Still        | Absent       | <i>Longipedia sp.</i>                | Moving     | Still        |
| <i>Amphiascoides sp.</i>        | Still        | Nonemerger   | <b>Normanellidae</b>                 |            |              |
| <i>Amphiascus varians</i>       | Rare         | Moving       | <i>Cletopsyllus sp.</i>              | Rare       | Nonemerger   |
| <i>Bulbamphiascus minutus</i>   | Unclassified | Still        | <i>Normanella sp.</i>                | Still      | Nonemerger   |
| <i>Bulbamphiascus sp.</i>       | Still        | Moving       | <b>Orthopsyllidae</b>                |            |              |
| <i>Haloschizopera sp. A</i>     | Nonemerger   | Nonemerger   | <i>cf. Orthopsyllus</i>              | Absent     | Rare         |
| <i>Haloschizopera sp. B</i>     | Nonemerger   | Nonemerger   | <b>Paramesochridae</b>               |            |              |
| <i>Protopsammotopa sp.</i>      | Nonemerger   | Nonemerger   | <i>Apodopsyllus sp.</i>              | Absent     | Rare         |
| <i>Robertgurneya sp. A</i>      | Moving       | Nonemerger   | <i>Kliopsyllus sp.</i>               | Rare       | Nonemerger   |
| <i>Robertgurneya sp. B</i>      | Still        | Nonemerger   | <i>Phyllopodopsyllus sp.</i>         | Nonemerger | Nonemerger   |
| <i>Robertsonia cf. knoxi</i>    | Still        | Still        | <b>Parastenheliidae</b>              |            |              |
| <i>Robertsonia sp.</i>          | Rare         | Still        | <i>Parastenhelia cf. ornatissima</i> | Moving     | Nonemerger   |
| <i>Stenhelia cf. peniculata</i> | Rare         | Rare         | <b>Rhizothricidae</b>                |            |              |
| <i>Stenhelia sp. A</i>          | Still        | Still        | Genus uncertain                      | Absent     | Rare         |
| <i>Stenhelia sp. B</i>          | Rare         | Nonemerger   | <i>Rhizothrix sp.</i>                | Nonemerger | Still        |
| <b>Ectinosomatidae</b>          |              |              | <b>Thalestridae</b>                  |            |              |
| <i>Bradyellopsis sp.</i>        | Moving       | Moving       | <i>cf. Dactylopodia</i>              | Moving     | Moving       |
| <i>Ectinosoma sp.</i>           | Moving       | Moving       | <i>Diarthrodes sp. A</i>             | Still      | Rare         |
| <i>Halectinosoma sp. A</i>      | Moving       | Moving       | <i>Diarthrodes sp. B</i>             | Rare       | Unclassified |
| <i>Halectinosoma sp. B</i>      | Moving       | Moving       |                                      |            |              |

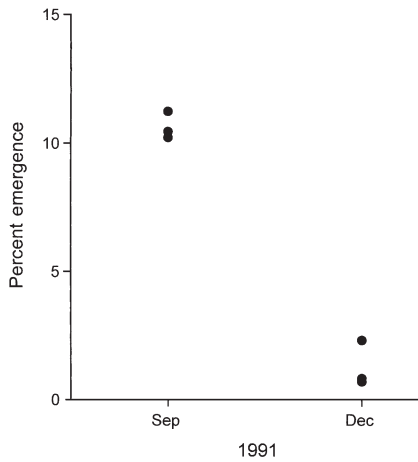


Fig. 3. Percent emergence versus season for combined adults and juveniles

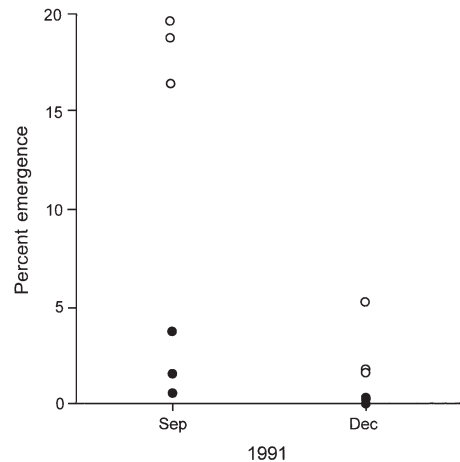


Fig. 4. Plot of percent emergence by season for adult harpacticoids (○) and juvenile harpacticoids (●)

considered emergent. At my site, the percent emergence calculated in this manner was significantly greater ( $p < 0.021$ ) in September (mean = 10.7%, range = 10.2 to 11.3%) than in December (mean = 1.4%, range = 0.8 to 2.4%) (Fig. 3). I repeated the calculation for moving-water emergers treated as a group. This difference was also significantly greater ( $p < 0.021$ ) in September (mean = 40.5%, range = 36.7 to 45.1%) than in December (mean = 9.8%, range = 5.7 to 16.4%). At the species level, percent emergence was greater in September for 8 of the 9 species classified as moving-water emergers in both September and December (Table 2).

**Ontogenetic differences**

I asked whether adults and juveniles differed in emergence as follows. I calculated percent emergence of juveniles using the number of juveniles caught in a trap as A and the number of juveniles estimated to be in the sediment enclosed by the trap as B. To make the

calculation for adults parallel, I used the number of adults found in a trap as A and the number of adults estimated to be in the sediment enclosed by the trap as B. In September, a significantly greater proportion of adults than juveniles emerged ( $p < 0.014$ ) but not in December ( $p \approx 0.077$ ) (Fig. 4).

This result raised the question of whether the differences between months found in the previous section, where adults and juveniles were combined, existed for each group separately. For adults, the percent emergence was significantly greater ( $p < 0.022$ ) in September than in December, but months did not differ significantly in the percent emergence of juveniles ( $p > 0.9$ ) (Fig. 4).

**Gender differences**

To test for gender differences in emergence, I determined the gender of each adult of moving-water emergers. In September, 81.3% (range = 76.0 to 85.7%) of the adult males and 89.9% (range = 88.6 to

Table 2. Percent emergence in September and in December 1991 of species classified as moving-water emergers in both months, showing that percent emergence tended to be greater in September

| Family             | Species                               | September |             | December |             |
|--------------------|---------------------------------------|-----------|-------------|----------|-------------|
|                    |                                       | Average   | Range       | Average  | Range       |
| Ambungiipedidiidae | cf. <i>Ambungiipes</i>                | 100.0     | 100.0–100.0 | 100.0    | 100.0–100.0 |
| Canthocamptidae    | <i>Mesochora</i> cf. <i>pygmaea</i>   | 83.0      | 48.9–100.0  | 50.0     | 0.0–100.0   |
| Ectinosomatidae    | <i>Bradyellopsis</i> sp.              | 75.9      | 27.7–100.0  | 7.4      | 0.0–22.3    |
|                    | <i>Ectinosoma</i> sp.                 | 77.5      | 32.4–100.0  | 100.0    | 100.0–100.0 |
|                    | <i>Halectinosoma</i> sp. A            | 72.0      | 16.1–100.0  | 37.3     | 3.1–100.0   |
|                    | <i>Halectinosoma</i> sp. B            | 100.0     | 100.0–100.0 | 4.4      | 0.0–8.7     |
|                    | <i>Pseudobradya</i> cf. <i>exilis</i> | 15.2      | 3.9–22.3    | 0.5      | 0.0–1.4     |
|                    | <i>Pseudobradya</i> sp.               | 83.8      | 48.9–100.0  | 1.5      | 0.0–4.6     |
| Thalestridae       | cf. <i>Dactylopodia</i>               | 100.0     | 100.0       | 50.0     | 13.4–100.0  |

91.3%) of the adult females emerged. In December, 33.6% (range = 16.7 to 60.6%) of the adult males and 56.6% (range = 47.7 to 69.9%) of the adult females emerged. In neither case was the difference between adult male and adult female emergence significant ( $p > 0.052$  and  $> 0.142$ , respectively).

## DISCUSSION

### Techniques used to study emergence

In most studies of meiofaunal emergence, the devices used to collect emergers required them to swim a minimum vertical distance (typically 12 to 15 cm) (Hicks 1986, Walters & Bell 1986, Walters 1991). Therefore, emergers have been defined as species whose individuals swim a minimum vertical distance. Taken at face value, reported emergence figures are underestimates because they do not include emergers who swim less than the minimum vertical distance (= short emergers) (Fleeger et al. 1984, Walters & Bell 1994, Buffan-Dubau & Castel 1996).

Unfortunately, the situation is more complicated. Some harpacticoids alter their behavior in response to changes in flow speed (Palmer 1984, Armonies 1988b, Foy & Thistle 1991), avoiding the sediment surface during times of high flow (Palmer 1988a). Most studies of emergence have involved emergence into still water. For example, emergence traps are sealed to the seabed, creating still water inside them. The still water in a trap could allow short emergers to swim unnaturally far from the seabed, or it could stimulate individuals that ordinarily would not emerge to swim into the water far enough to be caught. If either behavior occurs, still-water collecting devices overestimate the emergence they purport to study, i.e. the harpacticoids that would emerge in nature and swim vertically far enough to be collected.

In September, I found 25 species in base traps (still water), 11 of which (the still-water emergers) were not collected even once in leg traps (moving water). In December, I found 10 such species. Clearly, the emergence behavior of some individuals differed when they were exposed to still water for 24 h, which has consequences for the study of emergence. For example, in September, the mean percent emergence for moving-water species was 40.5%. When still water emergers were also included in the calculation, the mean decreased to 29.4%, a significant difference ( $p < 0.034$ ). In December, the decrease (9.7 to 5.0%) was substantial but not significant. Given these results, future studies of emergence with collectors that create still water should also include a moving-water treatment (e.g. a leg trap), so species whose behavior is altered

by still water can be identified and omitted from analysis.

Although I was able to identify many species of still-water emerger with leg traps, the approach is not perfect because I might have misclassified some still-water emergers as moving-water emergers if turbulent eddies injected resuspended (as opposed to emerging) individuals into the collecting chamber. That the numbers of still- and moving-water emergers was essentially the same in September (a time of low turbulence) and December (a time of high turbulence) suggests that the problem was not severe.

### Why emerge?

Emergence could be a response to deteriorating conditions in the sediment. For example, at night, when photosynthesis has stopped, the 0-oxygen isocline can rise to the vicinity of the sediment surface and stress aerobic animals (Vopel et al. 1996, 1998), a stress that could be relieved if they moved temporarily into the water column. Other stresses could include a local decline in food or a local increase of competitors or predators. An individual that entered the water column could benefit from a release from these stresses, but it could also profit in other ways. For example, it could disperse much more rapidly when in the water than when in the sediment, and it would have access to the food resources of the water column (Walters & Shanks 1996, Suderman & Thistle 1998). These opportunities might have associated costs. While in the water column, an individual could be eaten by water-column predators (Palmer 1988b) or it could be expatriated (Palmer & Gust 1985). Variations in emergence behavior could therefore result from variations in a cost-benefit relationship that governs the net profitability of the behavior.

### Seasonal variation in percent emergence

I found a significant difference in percent emergence between September and December, whether calculated as in the literature (Fig. 3) or, more conservatively, with moving-water emergers alone as a group. The difference was not caused by a gross change in the fauna between months because essentially the same species were present. Rather, for most species, percent emergence was lower in December than in September (Table 2). Walters (1991) found that percent emergence was greater in August than in November or February at his site in Tampa Bay, Florida. Taken together, the reports begin to suggest that percent emergence is lower in winter than at other times in such environments.

The lower percent emergence in winter suggests that the cost-benefit trade-offs that control the behavior changed between September and December such that emergence was not as profitable during winter at my site. For example, seasonal changes in hydrodynamic conditions might cause such a change. From a review of the literature, Palmer (1988a, see also Armonies 1988b, Commito & Tita 2002) reported that the frequency of emergence was relatively greater where near-bottom flows were relatively slow (e.g. in seagrass meadows) and was lower where near-bottom flows were faster.

My results fit this pattern. At my site, when slack tide coincides with calm winds, nearly still water can occur (approximating the flow speeds in seagrass meadows). More commonly, tides and winds cause more rapid motion of the near-bottom water. Even stronger near-bottom flows occur during local storms. The duration of strong winds and the frequency of storms increase from September to December at my site (Harkema et al. 1994, Weatherly & Thistle 1997). Periods of slow flow should therefore be more frequent and last longer in September than in December. The frequency of slow flow conditions at Walters' (1991) site should also decrease in winter as calm summer weather gives way to winter weather. Also, the 'leaves' of the seagrasses at his site are shed during fall, and their baffle-like effects are lost. The decrease in percent emergence in winter could therefore arise because the winter hydrodynamic regime shifts the cost-benefit balance away from emergence. The costs associated with emerging during energetic hydrodynamic conditions are unclear. Expatriation risk might increase (Palmer 1988a), or the increased turbulence might interfere with feeding in the water column (Thistle et al. 1995, Suderman & Thistle 1998).

The decrease in percent emergence at my site between September and December could arise from other changes in environmental conditions that alter the cost-benefit trade-off. For example, the difference in hydrodynamic regime alters the gradients of biologically important chemicals in the sediment. In particular, oxygen should be pumped deeper into the sediment when the hydrodynamic regime is energetic and could decrease the number of individuals that emerge to avoid low oxygen concentrations. Also, the temperature decrease between September and December may have been involved (see Armonies 1988c), either directly affecting the physiological costs of emergence or indirectly through effects on other processes.

#### Ontogenetic effects

At his wading-depth site in a seagrass meadow, Walters (1991) found that percent emergence of adults was

roughly comparable to that of juveniles. At my site, the percent emergence of adults was significantly greater than that of juveniles in September. Further, the number of adults emerging (mean = 117.3, range = 87 to 156) was ~10 times greater than the number of juveniles emerging (mean = 9.3, range = 4 to 17) in September and in December (adult mean = 51.0, range = 29 to 86; juvenile mean = 4.7, range = 0 to 7).

The difference between Walters' (1991) results and mine could occur if our sites differed in the cost-benefit balance for juvenile emergence relative to adult emergence. The results suggest that for juveniles the return is less and/or the risks are greater at my shelf site. Because the factors in the cost-benefit trade-off have not been identified, many explanations are possible. For example, adults differ from juveniles in size, and swimming ability is a correlate of size. Walters' site differs most obviously from mine in the frequency of exposure to energetic, near-bottom flows. Rephrasing Palmer's (1988a) arguments leads us to ask whether the difference arises because adults can emerge more safely than juveniles at the shelf site.

#### Gender effects

Hicks (1988, see also Bell et al. 1988) suggested that harpacticoid emergence occurred to facilitate mating. Harpacticoid mating involves an adult male finding and clasping a subadult (usually Stage V copepodite) female until she molts, when sperm transfer occurs (Hicks & Coull 1983). Hicks (1988) and Bell et al. (1988) colleagues have argued that mating may be more readily accomplished in the water column than in the benthos because the mechanics could be easier in a fluid, and mates might be easier to locate. Under this hypothesis, subadult females and adult males should emerge. I found that in each month a substantial number of adult males emerged, which is consistent with the theory, but even more adult females emerged. Whatever the appropriateness of the mating hypothesis as an explanation for the emergence of adult males, it cannot explain why adult females (including gravid females) emerge, because mating is no longer a concern for them. Mating can be only a portion of the eventual explanation of harpacticoid emergence.

#### General comparisons with previous work

Two questions are of particular interest in comparisons among studies because they promise to allow insight into the interaction between emergence and environmental changes on biogeographic scales. How does the proportion of the species that emerge differ,

and how does the proportion of the individuals that emerge differ? I was able to make few comparisons because the techniques used in most studies differed from mine in ways that have profound effects (see Youngbluth 1982). To minimize such problems, I only considered field studies done with traps that were sealed to the sediment and had path lengths  $\leq 15$  cm. Even among these reports, differences in the duration of the trapping are a concern because the catch depends on the duration and time of day of the deployment (Walters & Bell 1986, Buffan-Dubau & Castel 1996).

Walters & Bell (1986) reported that 67.9% of the species they found in sediment among culms of seagrass emerged at their wading-depth site. The comparable values for my site were 75.1% in September and 59.4% in December (combining moving- and still-water emergers). The difference in percent emergence is small, so there is no reason to believe that it differs between the sites. It will be interesting to see whether future work reveals variation among habitats.

Walters & Bell (1986) trapped an average of 25.5% of the adult harpacticoids in November and 51% in April during 6 h deployments (see also Buffan-Dubau & Castel 1996). Walters' (1991) estimates of percent emergence are from 2 h collections, which are too short to be comparable. In 24 h collections, I found that 18.8% of adults emerged in September and 2.6% in December. Walters & Bell (1986) cannot have overestimated 24 h percent emergence, so percent emergence appears to be lower at my site than at theirs. As above, the difference in hydrodynamic conditions between sites (Palmer 1988a) might be responsible.

My results show that harpacticoids do emerge from a shelf sand that experiences energetic, near-bottom flows. The percent of individuals that emerge is less than that in wading-depth or intertidal habitats, but it can be nontrivial at some times of year. Work at other shelf sites will be necessary to confirm these results and to determine the bathymetric extent of harpacticoid emergence.

*Acknowledgements.* J. Winne constructed the traps. S. Boa, S. Ertman and A. Wonnacott assisted in the field. S. Boa, L. Heiman and K. Suderman helped in the laboratory. The comments of S. S. Bell, L. Sedlacek, I. Hoedl, K. Suderman, M. Teasdale, A. B. Thistle, K. Vopel, K. Walters and 3 anonymous reviewers improved the manuscript. The National Science Foundation and the Office of Naval Research supported the research; I wish to express my thanks for this kind help. Contribution No. 1099 of the Florida State University Marine Laboratory.

#### LITERATURE CITED

- Allredge AL, King JM (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. *J Exp Mar Biol Ecol* 44:133–156
- Armonies W (1988a) Active emergence of meiofauna from an intertidal sediment. *Mar Ecol Prog Ser* 43:151–159
- Armonies W (1988b) Hydrodynamic factors affecting behaviour of intertidal meiobenthos. *Ophelia* 28:183–194
- Armonies W (1988c) Physical factors influencing active emergence of meiofauna from boreal intertidal sediments. *Mar Ecol Prog Ser* 49:277–286
- Armonies W (1989) Meiofaunal emergence from intertidal sediment measured in the field: significant contribution to nocturnal plankton biomass in shallow waters. *Helgol Meeresunters* 43:29–43
- Bell SS, Walters K, Kern JC (1984) Meiofauna from seagrass habitats: a review and prospectus for future research. *Estuaries* 7:331–338
- Bell SS, Hicks GRF, Walters K (1988) Active swimming in meiobenthic copepods of seagrass beds: geographic comparisons of abundances and reproductive characteristics. *Mar Biol* 98:351–358
- Bruce PC (1991) Resampling stats. Resampling Stats Inc., Arlington, VA
- Buffan-Dubau E, Castel J (1996) Diel and seasonal vertical distribution of meiobenthic copepods in muddy sediments of a eutrophic lagoon (fishponds of Arcachon Bay). *Hydrobiologia* 329:69–78
- Commuto JA, Tita G (2002) Differential dispersal rates in an intertidal meiofaunal assemblage. *J Exp Mar Biol Ecol* 268:237–256
- Fleeger JW, Chandler GT, Fitzhugh GR, Phillips FE (1984) Effects of tidal currents on meiofauna densities in vegetated salt marsh sediments. *Mar Ecol Prog Ser* 19:49–53
- Foy MS, Thistle D (1991) On the vertical distribution of a benthic harpacticoid copepod: field, laboratory, and flume results. *J Exp Mar Biol Ecol* 153:153–163
- Fuller CM, Butman CA (1988) A simple technique for fine-scale, vertical sectioning of fresh sediment cores. *J Sediment Petrol* 58:763–768
- Grant J (1980) A flume study of drift in marine infaunal amphipods (Haustoriidae). *Mar Biol* 56:79–84
- Gregg JC, Fleeger JW (1997) Importance of emerged and suspended meiofauna to the diet of the darter goby (*Gobionellus boleosoma* Jordan and Gilbert). *J Exp Mar Biol Ecol* 209:123–142
- Hagerman GH Jr, Rieger RM (1981) Dispersal of benthic meiofauna by wave and current action in Bogue Sound, North Carolina, USA. *PSZN I: Mar Ecol* 2:245–270
- Harkema R, Weatherly GL, Burnett WC, Chanton JP (1994) A compilation of moored current meter data from the Big Bend region of the West Florida Shelf, July 1992–October 1992. Florida State University, Tallahassee, FL
- Hicks GRF (1986) Distribution and behaviour of meiofaunal copepods inside and outside seagrass beds. *Mar Ecol Prog Ser* 31:159–170
- Hicks GRF (1988) Evolutionary implications of swimming behavior in meiobenthic copepods. *Hydrobiologia* 167/168:497–504
- Hicks GRF, Coull BC (1983) The ecology of marine meiobenthic harpacticoid copepods. *Oceanogr Mar Biol Annu Rev* 21:67–175
- Huys R, Gee JM, Moore CG, Hamond R (1996) Synopses of the British fauna (new series): marine and brackish water harpacticoid copepods Part 1. Field Studies Council, Shrewsbury
- Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman & Hall, New York
- Marcus NH, Boero F (1998) Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnol Oceanogr* 43:763–768



- McCall JN (1992) Source of harpacticoid copepods in the diet of juvenile starry flounder. *Mar Ecol Prog Ser* 86:41–50
- Mees J, Jones MB (1997) The hyperbenthos. *Oceanogr Mar Biol Annu Rev* 35:221–255
- Noodt W (1971) Ecology of the Copepoda. *Smithson Contrib Zool* 76:97–102
- Palmer MA (1984) Invertebrate drift: behavioral experiments with intertidal meiobenthos. *Mar Behav Physiol* 10:235–253
- Palmer MA (1988a) Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar Ecol Prog Ser* 48:81–91
- Palmer MA (1988b) Epibenthic predators and marine meiofauna: separating predation, disturbance, and hydrodynamic effects. *Ecology* 69:1251–1259
- Palmer MA, Brandt RR (1981) Tidal variation in sediment densities of marine benthic copepods. *Mar Ecol Prog Ser* 4: 207–212
- Palmer MA, Gust G (1985) Dispersal of meiofauna in a turbulent tidal creek. *J Mar Res* 43:179–210
- Robichaux DM, Cohen AC, Reaka ML, Allen D (1981) Experiments with zooplankton on coral reefs, or, will the real demersal plankton please come up? *PSZN I: Mar Ecol* 2:77–94
- Service SK, Bell SS (1987) Density influenced active dispersal of harpacticoid copepods. *J Exp Mar Biol Ecol* 114:49–62
- Suderman K, Thistle D (1998) Adult female harpacticoid copepods maintain their energy reserves by feeding while suspended during storms. *Mar Ecol Prog Ser* 164:245–252
- Thistle D, Weatherly GL, Wonnacott A, Ertman SC (1995) Suspension by winter storms has an energetic cost for adult male benthic harpacticoid copepods at a shelf site. *Mar Ecol Prog Ser* 126:77–86
- Vopel K, Dehmlow J, Arlt G (1996) Vertical distribution of *Cletocamptus confluens* (Copepoda, Harpacticoida) in relation to oxygen and sulfide microprofiles of a brackish water sulphuretum. *Mar Ecol Prog Ser* 141:129–137
- Vopel K, Dehmlow J, Johansson M, Arlt G (1998) Effects of anoxia and sulphide on populations of *Cletocamptus confluens* (Copepoda, Harpacticoida). *Mar Ecol Prog Ser* 175: 121–128
- Walters K (1988) Diel vertical migration of sediment-associated meiofauna in subtropical sand and seagrass habitats. *J Exp Mar Biol Ecol* 117:169–186
- Walters K (1991) Influences of abundance, behavior, species composition, and ontogenetic stage on active emergence of meiobenthic copepods in subtropical habitats. *Mar Biol* 108:207–215
- Walters K, Bell SS (1986) Diel patterns of active vertical migration in seagrass meiofauna. *Mar Ecol Prog Ser* 34: 95–103
- Walters K, Bell SS (1994) Significance of copepod emergence to benthic, pelagic, and phytal linkages. *Mar Ecol Prog Ser* 108:237–249
- Walters K, Shanks AL (1996) Complex trophic and nontrophic interactions between meiobenthic copepods and marine snow. *J Exp Mar Biol Ecol* 198:131–145
- Weatherly GL, Thistle D (1997) On the wintertime currents in the Florida Big Bend region. *Cont Shelf Res* 17:1297–1319
- Wells JBJ (1977) Keys to aid in the identification of marine harpacticoid copepods. Zoology Department, University of Aberdeen
- Youngbluth MJ (1982) Sampling demersal zooplankton: a comparison of field collections using 3 different emergence traps. *J Exp Mar Biol Ecol* 61:111–124

*Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA*

*Submitted: May 22, 2002; Accepted: September 10, 2002  
Proofs received from author(s): January 17, 2003*