

Euphausiid distribution, abundance, and succession in North Atlantic warm-core ring 82B

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Abstract

Zooplankton collections were made with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) both day and night in warm-core ring 82B in the North Atlantic Ocean and at night in the Slope Water between March and August 1982. Species succession of euphausiids in 82B was presented during the lifespan of this warm-core ring, aiming at providing basic information on possible response of North Atlantic marine ecosystem to global warming. Species succession of euphausiids (32 species) in this long-lived warm-core ring was investigated. Major physical changes of 82B occurred in March-April by convective mixing and thermostad cooling, in April/May by stratification of the surface waters, and in August by the interaction with Gulf Stream. Substantial changes in species composition were observed that corresponded to these physical changes. Four different patterns were found in temporal change in abundance of warm-water species. There were species that decreased in number from March to August, species that decreased from March to June, but increased in August, species that increased from March to August, and species that showed no systematic trend. These differences may be attributable to a species tolerance to the thermostad temperature decrease and their vertical distribution. There was also a large change from April to June with ascendance of the transition species, *Thysanoessa gregaria*. Cold-water species had variable patterns of abundance in 82B and occurred more abundantly in the Slope Water than in the ring. The monthly percentage decrease in the abundance of warm-water species in 82B was high compared with that of cold-water species in cold-core rings as a result of the more rapid changes in the physical structure and the shorter lifetimes of warm-core rings in the Western North Atlantic.

Introduction

Warm-core and cold-core rings are dominant features of western boundary currents. They have major impacts on the physics, chemistry, biology, and productivity of the regions in which they occur (Wiebe and Joyce, 1992; McGillicuddy *et al.*, 1998). Gulf Stream cold-core rings were studied extensively in 1970's and many reports were published on zooplankton. These included biomass change in zooplankton with age of rings (Wiebe *et al.*, 1976a; Ortner *et al.*, 1978), vertical fractionation of zooplankton biomass in the rings and the processes responsible for that (The Ring Group, 1981), temporal change in the vertical distribution and physiology of the euphausiid *Nematoscelis megalops* (Wiebe and Boyd, 1978; Boyd *et al.*, 1978), and physical and biological mechanisms of invasion and dispersal of euphausiids in rings (Wiebe and Flierl, 1983).

Gulf Stream warm-core rings were subsequently investigated in 1980's. Concerning zooplankton, Wiebe *et al.* (Wiebe *et al.*, 1992) studied the horizontal patchiness and vertical migration of zooplankton in ring 82H. Montoya *et al.* (Montoya *et al.*, 1992) studied abundance of $\delta^{15}\text{N}$ of various zooplankton species in ring 86A and estimated trophic relationships among them. As for the longest lived warm-core ring in the North Atlantic, 82B, the spatial distribution and temporal change in zooplankton biomass (Wiebe *et al.*, 1985a), and the size structure and taxonomic composition (Davis and Wiebe, 1985) were reported. However, little is known on the species succession of any zooplankton taxonomic group in warm-core rings. This is partly due to difficulty of surveying the same warm-core ring repeatedly during its relatively short life span compared to cold-core rings in the western North Atlantic Ocean and partly due to time-consuming process of species identification.

In this study, we investigated species succession of euphausiids in warm-core ring 82B, which was surveyed for the longest period of all warm-core rings in the North Atlantic Ocean. 82B was formed from a northward flowing Gulf Stream meander centered at 38.5°N, 70°W in February 1982, moved westward and then southwestward, and was reabsorbed by the Gulf Stream off Cape Hatteras in August 1982 (Evans *et al.*, 1985). It was surveyed over most of its life span of 6 months.

Euphausiids are major component of marine ecosystems, representing 5-10% of the total biomass of zooplankton (Mauchline, 1980), and the species composition may cause changes in the composition of primary producers through feeding activities. The tendency to form aggregations differs from species to species and vulnerability to predators differs. Therefore, species composition of euphausiids may greatly influence the energy flow through the food web. We investigated changes in species composition of euphausiids with the age of 82B, changes in the vertical distribution of dominant species, and changes in the body length and the maturity stages of warm-water euphausiids.

Method

Euphausiid samples in the warm-core ring 82B and the Slope Water were collected on four cruises between March and August 1982 (R/V Oceanus, cruises 116, 118, 121, and 125). Samples were reanalyzed because the species succession of euphausiids in warm-core rings may provide fundamental information on the response of marine ecosystems to climate change, considering the possibility that northern North Atlantic Ocean would be cooled during global warming (e.g. Curry *et al.*, 2003).

Sampling for macrozooplankton was done with a double 1-m² MOCNESS equipped with 335 μ m mesh nets, except in March 1982 (Oceanus 116), when a nine-net MOCNESS was used. The double MOCNESS is similar to that described by Wiebe *et al.* (Wiebe *et al.*, 1976b), except that the frame width has been doubled to permit two independent sets of nets to be mounted side by side (Wiebe *et al.*, 1985b). Each set contains 10 nets and had its own net bar guides, net bar release indicator, and toggle release/motor drive. The underwater sensors measured temperature, conductivity, depth, flow, net angle, and the passage of a net bar once released, except in March 1982 on Oceanus 116 cruise, when MOCNESS did not have a conductivity probe.

On each 1.5-3.5 hour haul eight samples integrating 100-m intervals from 1000 to 200 m and eight samples integrating 25-m intervals from 200 to 0 m were generally obtained. Sampling in March was the exception: four samples integrating 150-m intervals from 1000 m to 400 m were obtained as were four samples integrating 100-m intervals from 400 m to 0 m. The samples were preserved in 10% formalin buffered to a pH >8.0 with sodium tetraborate.

Euphausiid samples collected at the center of 82B both day and night, and in the Slope Water at night were examined for each sampling time (Table I, Fig. 1). Sampling in March at the center of 82B was made only at night. For information on the biomass of zooplankton, temperature, and salinity etc. of each tow, see Barber and Wiebe (Barber and Wiebe, 1985). The samples were split into aliquots, up to 1/8, according to the volume with a Folsom plankton splitter (McEwen *et al.*, 1954). All adult specimens in subsamples were identified to species and counted by examining both thelycum and petasma.

Carapace length and maturity stage of dominant warm-water (*Euphausia americana*, *E. brevis*, and *E. tenera*) and cold-water species (*E. krohni* and *Nematoscelis megalops*) were examined to investigate the temporal change in these biological characteristics, if any, of warm-water species expatriated in 82B and to see if the individuals of cold-water species that invaded 82B had special biological characteristics compared with those that did not. Carapace length was measured from the eye notch to the lateral end of the carapace under a dissecting microscope. Maturity stages were determined according to the method of Makarov and Denys

(Makarov and Denys, 1981) and shown as integrated categories according to Reid *et al.* (Reid *et al.*, 1996). Female euphausiids were assigned to 3 maturity stages: sub-adult female (FS; corresponding to stage IIB of Makarov and Denys, 1981), non-sexually mature adult female (females without spermatophores; FA1; corresponding to IIIA), and sexually active adult female (females with spermatophores; FAS; corresponding to IIIB-IIIIE). Males were assigned to 2 maturity stages: sub-adult male (MS; corresponding to IIA) and adult male (MA; corresponding to IIIA and IIIB).

Results

Physical change of 82B

WCR 82B was formed in mid-February 1982 with core waters derived from transitional waters of Gulf Stream and Sargasso Sea origin. At the time of formation, surface water temperature was 19°C and ring diameter was approximately 150 km (Joyce and Wiebe, 1983; Evans *et al.*, 1985). When 82B was first investigated in mid March, a 310 m thick, nearly isothermal layer (thermostad) of 17.5°C was observed. By mid April, the thermostad had been cooled to approximately 15.7°C and its depth had increased to over 400 m. The increase in mixed layer depth between February and mid April was mostly due to heat loss to the atmosphere (Schmitt and Olson, 1985). Thermostad temperature did not change between April and June, but a seasonal thermocline developed above 50 m by June (Wiebe *et al.*, 1985a).

Satellite observations of the surface pigment of ring core waters indicate that two plankton blooms occurred between 18 April and 7 May (Brown *et al.*, 1985). The first bloom peaked on 20 April and the second one was observed after 1 May.

The temperature profiles observed at the stations at the center of 82B for which euphausiids were examined were essentially the same as described above. The thermostad was present from March through August. The depth of the bottom of the thermostad was 300 m, 370 m, 400 m, and 300 m at the sampling of March, April, June, and August, respectively, in the present study (Fig. 2). Temperature profile in the upper 100 m in August looks peculiar, but a very similar profile was obtained with a CTD cast 8 days after the MOCNESS sampling (see Fig. 2 of Schmitt and Olson 1985). The temperature profile reflects the fact that the Gulf Stream overran the top of the ring as part of the process of ring envelopment by the Stream at the end of its existence.

Euphausiid species that occurred in this study

A total of 32 euphausiid species occurred in this study (Tables II and III). Among them, 26 species (81%) occurred in the thermostad and 30 species were present in the top 1000 m of 82B; 25 species occurred in the top 1000 m of the Slope Water. These euphausiids were grouped as

warm-water species, cold-water species, and transition species according to the previous works (Mauchline and Fisher, 1969; The Ring Group, 1981; Wiebe, 1987; Brinton *et al.*, 1999).

Twenty-three species are categorized as warm-water species whose distributional range includes tropical and subtropical waters and sometimes extends into temperate waters. Among them, *Nematobranchion sexspinosum*, *Nematoscelis tenella*, *Stylocheiron elongatum*, *S. robustum*, *Thysanopoda monacantha*, and *Tp. orientalis* are classified as mesopelagic species (Mauchline and Fisher, 1969). All the other warm-water species are epipelagic. Five cold-water species, *E. krohni*, *Meganyctiphanes norvegica*, *N. megalops*, *Thysanoessa longicaudata*, and *Tp. acutifrons* appeared in this study. These are all epipelagic species (Mauchline and Fisher, 1969).

Distributional ranges of these species are generally restricted to the Slope Water and northern areas as well as cold-core rings. *T. gregaria* is the sole transition species in the present study. The remaining 3 species are those that have wider distribution (*Bentheuphausia amblyops*, *Nb. boopis*, and *S. longicorne*), occurring from the tropics to as far north as Icelandic waters. *B. amblyops* is a bathypelagic species and the latter 2 species are mesopelagic species (Mauchline and Fisher, 1969). One species, *Thysanoessa parva*, that has been observed in the Northwest Atlantic (Wiebe and Flierl, 1983) was not found in the samples used in this study.

Change in vertical distribution of dominant species

The nighttime vertical distribution of warm-water species in 82B generally shoaled from March to August. That is the case with *E. brevis*, *E. hemigibba*, *E. mutica* and *S. affine* (Fig. 3). The daytime distribution of *S. affine* also shoaled from April to June/August. Many of the other warm-water species occurred in the thermocline of 82B only in limited season(s), and therefore their seasonal trend in vertical distribution was not clear. At night, most of the warm-water species occurred in the thermocline. During the day, however, substantial part of the populations of warm-water species occurred below the thermocline, especially *E. hemigibba* and *E. tenera*. *E. hemigibba* occurred as deep as 600-700 m (200-300 m below the thermocline) in June and *E. tenera* as deep as 500-600 m in April and June.

A cold-water species, *E. krohni*, was distributed mainly in the thermocline at night in March-August (Fig. 4). Some part of the population occurred below the thermocline in August. Their nighttime distribution at the center of 82B was deeper than that in the Slope Water in March and August. Another cold-water species, *N. megalops*, entered into the thermocline at night only in April and June. Their nighttime distribution shoaled from March to April/June and deepened in August. Compared with their home range, the Slope Water, their residence depth was deeper in March and August at the center of 82B (100-400 m in SW vs. >400 m in 82B). The same was true for *E. krohni* i.e., 0-200 m vs. >200 m. The residence depth of another cold-water mesopelagic

species, *T. longicaudata*, was deeper than the thermocline (>400 m) throughout the survey periods of this study.

Species succession of euphausiids in 82B

In March, two warm-water species, *E. brevis* and *E. tenera*, dominated the euphausiid population both in the thermocline and in the upper 1000 m at the center of 82B at night: the sum of the contributions of these two species was 51% and 44% of total euphausiids in the thermocline and upper 1000 m, respectively (Tables II and III). The individual contribution of all other single species was less than 10%. In April, *E. tenera*, *E. brevis*, *E. krohni*, and *T. gregaria* dominated at night in the thermocline and in the upper 1000 m. Thus, species other than warm-water forms (*E. krohni* and *T. gregaria*) became abundant at night in April. In the day, *E. tenera*, *E. brevis*, and *S. longicorne* predominated in the thermocline, occupying 68% of all euphausiids. The species change between day and night may be due to descent of some proportion of populations of *E. tenera*, *E. brevis*, and *E. krohni* to the deeper layers. In June, a transition species, *T. gregaria* predominated, occupying more than 90% of all euphausiids both in the thermocline and in the upper 1000 m at night. In the day, *T. gregaria* (59%) and *E. krohni* (19%) predominated in the thermocline.

In August, two warm-water species *E. tenera* and *S. carinatum* predominated both in the thermocline and in the upper 1000 m at night. These two species were followed by *N. megalops* in the upper 1000 m. During the day, *E. tenera* and five *Stylocheiron* species, *S. affine*, *S. carinatum*, *S. elongatum*, *S. longicorne*, and *S. suhmi*, predominated in the thermocline, and *E. tenera* and *E. hemigibba* predominated in the upper 1000 m. A substantial portion of the daytime populations of *E. tenera* and *E. hemigibba* migrated down below 300 m and that may be why the five *Stylocheiron* species dominated during the day.

There were four different patterns in the temporal change in abundance of warm-water species in the thermocline (Table II). The first (Group 1) consisted of species that decreased in number from March to August. *E. brevis* and *E. mutica* showed this pattern: *E. brevis* declined less abruptly than did *E. mutica*, which was most abundant in March and then dropped to low abundance from April to August. Group 2 consisted of species that decreased from March to June, but increased in August, including *E. americana*, *E. gibboides*, *E. hemigibba*, *E. tenera*, *Nb. flexipes*, *S. affine*, *S. carinatum*, *S. suhmi*, and *Tp. aequalis*. Group 3 was composed of species that increased from March to August, including *N. microps* and *S. elongatum*. And the last, Group 4, comprised species that showed no systematic trend, including *Nb. sexspinosum*, *N. atlantica*, *N. tenella*, *S. abbreviatum*, *S. robustum*, *Tp. monacantha*, *Tp. obtusifrons*, and *Tp. tricuspidata*. Species in this last group generally were low in abundance. The species in Group 3 tolerated cold

water temperatures in 82B and were present in the deeper layers compared with the second group. *E. pseudogibba* and *Tp. orientalis* occurred below the thermocline only in a single tow and do not belong to any of these groups.

Among cold-water species, *E. krohni* increased from March to April and decreased from June to August both in the thermocline and in the upper 1000 m at the center of 82B at night (Tables II and III). In the Slope Water, this species was less abundant in April (7 individuals 1000 m⁻³ in the upper 1000 m) than the other sampling periods (42-53 individuals 1000 m⁻³). *N. megalops* appeared first in April in the thermocline and increased from April to June, but decreased in August. In the upper 1000 m at the center of 82B, this species steadily increased from March to August (12 individuals 1000 m⁻³). It was most abundant in March (31 individuals 1000 m⁻³) in the Slope Water. *M. norvegica* occurred only in April in very small numbers in the thermocline at night. In the Slope Water, this species occurred in March, April, and June, and was most abundant in April (8 individuals 1000 m⁻³). *T. longicaudata* and *Tp. acutifrons* did not occur in the thermocline at night. In the upper 1000 m, *T. longicaudata* appeared in March, April, and August and was most abundant in August (4 individuals 1000 m⁻³). In the Slope Water, however, it was most abundant in March (11 individuals 1000 m⁻³). *Tp. acutifrons* occurred only in April in the Slope Water (0.2 individuals 1000 m⁻³). All of these cold-water species occurred more abundantly in the Slope Water than at the center of 82B.

The abundance of warm-water species that occurred in the thermocline of 82B at night decreased from 195 individuals 1000 m⁻³ (97% of all euphausiids in the thermocline) in March and 127 individuals 1000 m⁻³ (77%) in April to 44 individuals 1000 m⁻³ (6%) in June (Fig. 5). Their abundance increased, however, to 280 individuals 1000 m⁻³ (98%) in August. Cold-water species in 82B increased from 0.5 individuals 1000 m⁻³ in March to 20 individuals 1000 m⁻³ in April, but decreased in August to 5 individuals 1000 m⁻³. The highest percentage of cold-water species was only 12% in April.

Species composition in the Slope Water at night was fairly different from that in 82B (Tables II and III). In March, *E. krohni*, *N. megalops*, and *T. longicaudata* predominated in the upper 1000 m in the Slope Water. In April, June, and August, *T. gregaria* and *E. krohni* were dominant: sum of contribution of these two species was 75, 73 and 82% in April, June, and August, respectively. In the Slope Water, the dominant species in the upper 1000 m and in the depth zone corresponding to the thermocline of 82B in each month were very similar.

Total abundance of cold-water species was largest in March (93 individuals 1000 m⁻³) and smallest in April (14 individuals 1000 m⁻³) and intermediate in June and August. The percentage of cold-water species was the highest, 91%, in March and the lowest, 29%, in August (Fig. 6). The cold-water species *E. krohni*, *N. megalops*, and *T. longicaudata* were important numerically in

this order. The total abundance of warm-water species in the Slope Water increased from 4 individuals 1000 m^{-3} in March and April to 29 individuals 1000 m^{-3} in June, and kept a similar value in August (21 individuals 1000 m^{-3}) in the upper 1000 m. The highest percentage of warm-water species, 19%, also occurred in June. The transition species, *T. gregaria* increased steadily from March (5 individuals 1000 m^{-3}) to August (115 individuals 1000 m^{-3}) in the Slope Water.

Dominant species change in body size and maturity stage composition

E. brevis males increased moderately in modal carapace length from 1.9 mm to 2.2 mm from March to June, while females increased from 2.0 mm to 2.6 mm in modal length from March to April (Fig. 7B). Too few were present in August to measure. The maturity stage of *E. brevis* did not change in the first three periods, with MA in males and FA1 and FAS in females being dominant (Table IV). The modal carapace length of *E. tenera* also increased by 0.3 mm from March to April in both sexes (Fig. 7C) and female maturity progressed during the period (Table IV). In August, however, smaller individuals in the 1.6-1.8 mm range increased in number. Although small in number, male *E. americana* also increased moderately in carapace length from March to April, while females did not (Fig. 7A). The maturity stage in males did not change from March to April, but in females it regressed during this period. In August, carapace length of *E. americana* decreased and the maturity stage correspondingly regressed.

Carapace length of *E. krohni* was largest in March and decreased by June in both sexes in the Slope Water (Fig. 8). The maturity stage of this species was also highest in March (Table V). The individuals of this species that occurred in 82B at night were similar in the carapace length to those collected in the Slope Water. The maturity stage of another cold-water species, *N. megalops*, was most advanced in March and April (Table V). Individuals that occurred in the thermostad had similar carapace length to those in the Slope Water in June (Fig. 9) when 4 measurable individuals from each sex occurred in the thermostad (3.8-4.2 mm in males and 3.5-4.5 mm in females).

Discussion

Physical change of 82B and species composition of euphausiids

Major physical changes in 82B occurred in late winter and early spring by convective mixing, in spring by surface stratification, and in August by the interaction with Gulf Stream. In March, the thermostad had a uniform temperature of 17.5°C and subsequently cooled to 15.7°C by the April sampling. This temperature change might have caused stress on warm-water species expatriated in 82B. In the northern Sargasso Sea, winter convection forms 18°C water in the surface 300-400 m (Worthington, 1959). Thus the temperature difference for warm-water euphausiids in the thermostad was over 2°C lower than that normally experienced in the upper layers of their home

range. In August, the water in the thermostad layer of 82B was largely replaced with Gulf Stream water and a new complement of warm-water species.

Substantial changes in species composition occurred from March to April and from June to August corresponding to physical changes described above. However, there was also a big change from April to June with ascendancy of *T. gregaria* during which there was no major physical change.

Four different patterns were found in the temporal change of warm-water species abundance in 82B. With the exception of the two species that increased in number from March to August (Group 3), the abundant warm-water species decreased from March to June. After that some species increased in August through the ring's interaction with the Gulf Stream. Among Group 3, *S. elongatum* is a mesopelagic species and *N. microps* inhabits deeper layers among epipelagic warm-water species in their home range (400-700 m in the daytime and mainly 100-400 m at night), and therefore the temperature decrease from March to April may have not caused them much stress.

Among cold-water species, *E. krohni*, *N. megalops*, and *M. norvegica* occurred in the thermostad at least once. The former two species increased in number from March to April and March to June, respectively. *E. krohni* especially appeared to tolerate higher temperatures better than any other cold-water species that occurred in this study. *T. longicaudata* and *Tp. acutifrons* did not occur in the thermostad. *T. longicaudata* is reported to occur between 0-400 m during the day and ascend to 0-100 m at night, and *Tp. acutifrons* mostly occurs above 140 m at night and below 500 m by day (Brinton *et al.*, 1999). However, in the Slope Water, both species rarely occurred above 300 m even at night (Endo and Wiebe, unpublished data). That may be why these species did not occur in the thermostad.

Nine warm-water species increased in number from June to August in the thermostad. The biomass increase was substantial in *E. tenera* (126 fold), *S. carinatum* (56 fold), *S. suhmi* (41 fold), *E. americana* (32 fold), *E. hemigibba* (22 fold), and *E. gibboides* (12 fold). All these species are epipelagic and their nighttime distribution is mainly shallower than 100 m. The daytime distribution of several species (*E. tenera*, *E. americana*, *E. hemigibba*, and *E. gibboides*) in the northern Sargasso Sea, however, is below 100 m (Endo and Wiebe, unpublished data). Therefore, they may have entered the thermostad at night from the Gulf Stream surface waters overrunning the ring in August.

It was unexpected to find that the species composition in the thermostad was most distinctive in June, as a result of the mass occurrence of a transition species, *T. gregaria*, relative to other sampling times. While such an occurrence may be characteristic of warm-core rings surrounded by the Slope Water (a Transition area), it was not observed in cold-core rings in which transition species such as *T. gregaria* did not proliferate (Wiebe and Flierl, 1983). *T. gregaria* is known to

form swarms and is an important food item for whales, fish, and birds (Mauchline, 1980). The species was more than six times as abundant in 82B as in the Slope Water in June and the warm-core ring may have been attractive site for such predators.

Apparent growth observed in some species

It was also unexpected that three warm-water species, *E. americana*, *E. brevis*, and *E. tenera*, expatriated in 82B increased in carapace length at least for some periods (Fig. 7). Maturity stages progressed in *E. tenera* as well (Table IV). The abundance of *E. americana* and *E. tenera* in the thermostad was similar from March to April, but decreased by June. These two species, therefore, appeared to maintain their viability during this period, making use of two phytoplankton blooms between late April and early May (Brown *et al.*, 1985). *E. brevis*, however, consistently decreased in number from March to August, and only hardy individuals may have survived in 82B. These results are in marked contrast to the biological deterioration observed in cold-water euphausiids expatriated in cold-core rings over time: an increase in water content and decrease in total body lipid, carbon, respiration rates, and nitrogen (Boyd *et al.*, 1978). The cold-core ring was surveyed at 6 and 9 months after its formation, and therefore easily observable change could be seen in cold-water euphausiids in the cold-core ring compared with changes over 82B's six month life span.

Total zooplankton biomass steadily increased from March to August in the upper 1000 m at the center of 82B (Wiebe *et al.*, 1985a). The increase between March and June occurred as an increase in the small (1.0-3.0 mm) herbivore biomass between March and April and a subsequent increase in the large herbivore (5.0-6.0 mm) and carnivore (>15 mm) biomass between April and June (Davis and Wiebe, 1985). Smaller euphausiids may have been decreased in number through predation by an increased abundance of carnivores (e.g., the Slope Water chaetognath, *Sagitta tasmanica*). This may explain the apparent growth observed in several warm-water species expatriated in 82B, in spite of the decrease in their abundance.

Change in vertical distribution

The nighttime vertical distribution of warm-water species in 82B shoaled from March to August (Fig. 3). This phenomenon looks analogous to the deepening in vertical distribution of cold-water species over time in cold-core rings (Wiebe and Boyd, 1978; The Ring Group, 1981). In cold-core rings, surface water temperature increases over time because of positive air-sea heat exchange and the cold-core ring isotherms sink because of ring spin-down (loss of potential energy). In addition, the surrounding surface Sargasso Sea water is mixed inward. In contrast, in 82B, the thermostad temperature remained the same from April to August and the vertical gradient in temperature at the bottom of the thermocline did not change. Therefore, we must seek other

explanations for the shoaling of euphausiids in 82B. Shoaling of zooplankton in general was observed in 82B and was attributed to restricted occurrence of phytoplankton to the upper 100 m (Bishop *et al.*, 1986) after the vertical stratification of water column in April. Bishop *et al.* (Bishop *et al.*, 1986) hypothesized that particulate matter was lost from thermostad waters below the euphotic layer following seasonal stratification and that the zooplankton biomass shoaled to become concentrated in the upper 100 m following the removal of deep particulate material. The same explanation may hold true for euphausiids as well.

Difference in species succession between cold-core and warm-core rings

The monthly percentage decrease in abundance of warm-water species was calculated by linear regression based on five points from March, April and June, and proved to be high, 31%, while that of cold-water species in cold-core rings in the North Atlantic was 5% per month (Endo and Wiebe, unpublished data). There are two major causes for this: first, the temperature decrease caused by convective mixing in late winter/early spring and second, the proliferation of the transition species, *T. gregaria* from April onward.

82B was formed in February and experienced winter convection. In warm-core rings formed in other seasons of the year, euphausiids would likely show slower succession rates with warm-water species being able to survive for longer time periods. Since warm-core rings are surrounded by more productive Slope Water, ring aging will produce a shift toward somewhat higher productivity in contrast to cold-core rings. However, the physical environment around warm-core rings is not stable: warm-core rings may frequently interact with the continental slope sea bottom or with the Gulf Stream, and their size, shape, and motion may be modified (Halliwell and Mooers, 1979; Evans *et al.*, 1985). Therefore, the euphausiid community in warm-core rings is generally more susceptible to perturbations through these interactions.

There are some differences in translation distance and velocity between warm-core and cold-core rings. Cold-core rings generally translate about 1478 nm during their life span of 2-3 years at a velocity of 3 km d⁻¹ or 3.5 cm s⁻¹ (Lai and Richardson, 1977). On the other hand, warm-core rings usually move shorter distance at a velocity of 3-5 km d⁻¹ (3.5-5.8 cm s⁻¹, Joyce and Wiebe, 1983). In the case of 82B, it translated 102 nm at a velocity of 4 cm s⁻¹ when it moved westward, and 7 cm s⁻¹ when it moved 166 nm southwestward (Evans *et al.*, 1985). Therefore, warm-core rings move generally shorter distance at a higher speed than cold-core rings. The concept of a trapped region states that when a ring is moving relative to the water around it, only a certain region is advected along with the ring (Wiebe and Flierl, 1983). As a result, a fast moving ring will have a smaller trapped region than one traveling slowly. Thus, fast moving warm-core rings may have a smaller trapped region, and consequently the species composition may change

faster.

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References

- Barber, V. and Wiebe, P.H. (1985) Zooplankton biomass and related MOCNESS data for tows taken on the 1981-82 warm-core rings cruises. WHOI Tech. Report 85-3.
- Bishop, J.K.B., Conte, M.H., Wiebe, P.H., Roman, M.R. and Langdon, C. (1986) Particulate matter production and consumption in deep mixed layers: observations in a warm-core ring. *Deep-Sea Res.*, **33**, 1813-1841.
- Boyd, S.H., Wiebe, P.H. and Cox, J.L. (1978) Limits of *Nematoscelis megalops* in the northwestern Atlantic in relation to Gulf Stream cold core rings. II. Physiological and biochemical effects of expatriation. *J. Mar. Res.*, **36**, 143-159.
- Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D. and Bridgeman, A.L. (1999) *Euphausiids of the World Ocean*. World Biodiversity Database CD-ROM series. ETI Expert Center for Taxonomic Identification.
- Brown, O.B., Evans, R.H., Brown, J.W., Gordon, H.R., Smith, R.C. and Baker, K.S. (1985) Blooming off the U.S. East Coast: a satellite description. *Science*, **229**, 163-167.
- Curry, R., Dickson, B. and Yashayaev, I. (2003) A change in the freshwater balance of the Atlantic Ocean over the past four decades. *Nature*, **426**, 826-829.
- Davis, C.S. and Wiebe, P.H. (1985) Macrozooplankton biomass in a warm-core Gulf Stream ring: Time series changes in size structure, taxonomic composition, and vertical distribution. *J.*

Geophys. Res., **90**, C5, 8871-8884.

Evans, R.H., Baker, K.S., Brown, O.B. and Smith, R.C. (1985) Chronology of warm-core ring 82B. *J. Geophys. Res.*, **90**, C5, 8803-8811.

Evans, R., Baker, K., Brown, O., Smith, R., Hooker, S. and Olson, D. (1984) Satellite images of warm core ring 82-B sea surface temperature and a chronological record of major physical events affecting ring structure. A report produced by the Warm Core Rings Program Service Office. pp. 1-42.

Halliwell, G.R. and Mooers, C.N.K. (1979) The space-time structure and variability of the shelf water-slope water and Gulf Stream surface temperature fronts and associated warm-core eddies. *J. Geophys. Res.*, **84**, 7707-7725.

Joyce, T. and Wiebe, P. (1983) Warm-core rings of the Gulf Stream. *Oceanus*, **26**, 34-44.

Lai, D.Y., and Richardson, P.L. (1977) Distribution and movement of Gulf Stream rings. *J. Phys. Oceanogr.*, **7**, 670-683.

Makarov, R.R. and Denys, C.J. (1981) Stages of sexual maturity of *Euphausia superba* Dana. *BIOMASS Handbook* No. 11, 1-13.

Mauchline, J. (1980) The biology of mysids and euphausiids. *Adv. Mar. Biol.*, **18**, 1-677.

Mauchline, J. and Fisher, L.R. (1969) The biology of euphausiids. *Adv. Mar. Biol.*, **7**, 1-454

McEwen, G.F., Johnson, M.W. and Folsom, T.R. (1954) A statistical analysis of the performance of the Folsom plankton sampler splitter based upon test observations. *Arch. Meteorol. Geophys. Bioklimatol.*, **7**, 502-527.

McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F., and Knap, A.H. (1998) Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature*, **394**, 263-266.

Montoya, J.P., Wiebe, P.H. and McCarthy, J.J. (1992) Natural abundance of ^{15}N in particulate

nitrogen and zooplankton in the Gulf Stream region and warm-core ring 86A. *Deep-Sea Res.*, **39**, Suppl.1, 363-392.

Ortner, P.B., Wiebe, P.H., Haury, L. and Boyd, S. (1978) Variability in zooplankton biomass distribution in the northern Sargasso Sea: the contribution of Gulf Stream cold core rings. *Fish. Bull.*, **76**, 323-334.

Reid, K., Trathan, P.N., Croxall, J.P. and Hill, H.J. (1996) Krill caught by predators and nets: differences between species and techniques. *Mar. Ecol. Prog. Ser.*, **140**, 13-20.

Schmitt, R.W. and Olson, D.B. (1985) Wintertime convection in warm-core rings: thermocline ventilation and the formation of mesoscale lenses. *J. Geophys. Res.*, **90**, C5, 8823-8837.

The Ring Group (1981) Gulf Stream cold-core rings: their physics, chemistry, and biology. *Science*, **212**, 1091-1100.

Wiebe, P.H. (1987) Macrozooplankton. In Milliman, J.D. and Wright, W.R. (eds.), *The Marine Environment of the U.S. Atlantic Continental Slope and Rise*. pp. 159-175. Jones and Bartlett Publishing Company Inc.

Wiebe, P.H. and Boyd, S.H. (1978) Limits of *Nematoscelis megalops* in the northwestern Atlantic in relation to Gulf Stream cold core rings. I. Horizontal and vertical distributions. *J. Mar. Res.*, **36**, 119-142.

Wiebe, P.H. and Flierl, G.R. (1983) Euphausiid invasion/dispersal in Gulf Stream cold-core rings. *Aust. J. Mar. Freshw. Res.*, **34**, 625-652.

Wiebe, P.H. and Joyce, T. (1992) Introduction to interdisciplinary studies of Kuroshio and Gulf Stream rings. *Deep-Sea Res.*, **39**, v-vi.

Wiebe, P.H., Copley, N.J. and Boyd, S.H. (1992) Coarse-scale horizontal patchiness and vertical migration of zooplankton in Gulf Stream warm-core ring 82-H. *Deep-Sea Res.*, **39**, Suppl 1, 247-278.

Wiebe, P.H., Burt, K.H., Boyd, S.H. and Morton, A.W. (1976b) A multiple opening/closing net and

environmental sensing system for sampling zooplankton. *J. Mar. Res.*, **34**, 313-326.

Wiebe, P.H., Flierl, G.R., Davis, C.S., Barber, V. and Boyd, S.H. (1985a) Macrozooplankton biomass in a warm-core Gulf Stream ring: Spatial distribution and temporal changes. *J. Geophys. Res.*, **90**, C5, 8885-8901.

Wiebe, P.H., Hulburt, E.M., Carpenter, E.J., Jahn, A.E., Knapp, G.P., Boyd, S.H., Ortner, P.B. and Cox, J.L. (1976a) Gulf Stream cold core rings: large-scale interaction sites for open ocean plankton communities. *Deep-Sea Res.*, **23**, 695-710.

Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Cowles, T.J., Barber, V.A. and Flierl, G.R. (1985b) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar. Biol.*, **87**, 313-323.

Worthington, L.V. (1959) The 18-degree water in the Sargasso Sea. *Deep-Sea Res.*, **5**, 297-305.

Table and Figure legends

Table I: Date and time of each MOCNESS tow used in this study.

Table II: Mean abundance (individuals 1000 m⁻³) of each euphausiid species collected in the thermostad at the center of 82B and corresponding depth layer in the Slope Water.

Table III: Mean abundance (individuals 1000 m⁻³) of each euphausiid species collected in the top 1000 m at the center of 82B and in the Slope Water.

Table IV: Maturity stage composition of three warm-water and two cold-water euphausiid species collected in the thermostad at night. Each entry in the table is the number of individuals examined

and found to be in the particular stage.

Table V: Maturity stage composition of two cold-water euphausiid species collected in the Slope Water at night.

Fig. 1. Location of 82B and tow positions of MOCNESS at the center of 82B during the day (open circles) and at night (solid circles) and in the Slope Water at night (crosses). Location of 82B was plotted based on the data of Evans *et al.* (1984). The coastline and 200 m isobath are indicated.

Fig. 2. Seasonal changes in vertical temperature structure at the center of 82B at night.

Fig. 3. Seasonal change in vertical distribution of five warm-water euphausiid species at the center of 82B: *Euphausia brevis* (A); *E. hemigibba* (B); *E. mutica* (C); *E. tenera* (D); and *Stylocheiron affine* (E).

Fig. 4. Seasonal change in vertical distribution of three cold-water euphausiid species at the center of 82B and in the Slope Water: *Euphausia krohni* (A); *Nematoscelis megalops* (B); and *Thysanoessa longicaudata* (C).

Fig. 5. Seasonal change in abundance of warm-water, cold-water, and transition euphausiid species that occurred in the thermostad at the center of 82B at night.

Fig. 6. Seasonal change in abundance of warm-water, cold-water, and transition euphausiid species that occurred in the upper 1000 m of the Slope Water at night.

Fig. 7. Seasonal change in carapace length distribution of three warm-water euphausiid species that occurred in the thermostad at the center of 82B at night: *Euphausia americana* (A); *E. brevis* (B); and *E. tenera* (C).

Fig. 8. Seasonal change in the carapace length distribution of *Euphausia krohni* that occurred in the Slope Water and in the thermostad of 82B at night.

Fig. 9. Seasonal change in the carapace length distribution of *Nematoscelis megalops* that

occurred in the Slope Water at night.

Table I: Date and time of each MOCNESS tow used in this study.

Area	Tow number	Date	Local Time
82B center	MOC-1-160	15 Mar '82	19:00
	MOC-1D-172	30 Apr '82	13:05
	MOC-1D-173	30 Apr '82	18:30
	MOC-1D-180	19 Jun '82	20:12
	MOC-1D-187	25 Jun '82	11:10
	MOC-1D-194	10 Aug '82	8:15
	MOC-1D-196	11 Aug '82	20:41
Slope Water	MOC-1-157	13 Mar '82	20:10
	MOC-1D-163	20 Apr '82	19:58
	MOC-1D-177	16 Jun '82	21:08
	MOC-1D-208	21 Aug '82	20:13

Table II: Mean abundance (individuals 1000 m⁻³) of each euphausiid species collected in the thermostat at the center of 82B and corresponding depth layer in the Slope Water.

Species	82B								Slope Water					
	March		April		June		August		March		June		August	
	N	D	N	D	N	D	N	N	N	N	N	N	N	
<i>Euphausia americana</i> ^W	12.61	0.75	9.35	0.00	0.36	3.50	11.47	4.29	0.65	9.58	0.76			
<i>E. brevis</i> ^W	44.58	15.65	25.19	3.44	11.42	0.00	0.00	0.00	0.00	3.36	0.00			
<i>E. gibboides</i> ^W	1.51	0.00	0.53	1.67	0.37	1.17	4.48	0.00	0.00	0.00	2.17			
<i>E. hemigibba</i> ^W	8.44	1.49	13.56	0.00	1.16	0.00	25.79	0.00	2.13	1.34	2.57			
<i>E. krohnii</i> ^C	0.51	3.30	18.11	11.82	10.20	0.00	4.17	172.23	18.67	137.41	144.89			
<i>E. mutica</i> ^W	12.92	1.72	2.89	0.00	4.35	0.00	3.80	6.43	0.53	8.35	5.79			
<i>E. tenera</i> ^W	57.77	17.60	41.11	1.03	0.99	7.76	124.74	0.00	2.47	25.92	9.11			
<i>Meganyctiphanes norvegica</i> ^C	0.00	0.00	0.57	0.00	0.00	0.00	0.00	1.42	7.72	1.04	0.00			
<i>Nematobrachion flexipes</i> ^W	5.56	0.00	0.72	0.00	0.00	0.00	0.83	0.00	0.53	0.00	0.00			
<i>Nb. sexspinosum</i> ^W	1.00	0.00	0.00	0.00	0.50	0.00	0.83	0.00	0.00	0.90	0.00			
<i>Nematoscelis atlantica</i> ^W	2.53	0.37	3.08	0.00	2.87	0.00	0.76	3.47	0.37	0.87	2.17			
<i>N. megalops</i> ^C	0.00	0.00	1.06	0.00	4.25	0.00	0.83	90.99	5.59	17.45	21.18			
<i>N. microps</i> ^W	1.02	0.00	4.66	0.00	2.06	0.00	13.16	0.00	0.00	2.15	2.06			
<i>N. tenella</i> ^W	0.00	0.00	1.30	0.00	0.00	0.00	0.00	0.00	0.00	0.46	0.00			
<i>Stylocheiron abbreviatum</i> ^W	4.57	0.00	3.81	1.47	7.01	0.00	3.80	0.00	2.76	3.68	9.10			
<i>S. affine</i> ^W	15.54	3.90	5.27	0.62	2.67	5.77	11.72	0.00	0.00	4.84	0.00			
<i>S. carinatum</i> ^W	6.92	3.22	3.23	0.69	0.79	5.41	44.07	0.00	0.64	2.12	27.97			
<i>S. elongatum</i> ^W	5.11	2.78	5.64	0.52	8.48	4.66	14.11	0.00	0.00	0.90	0.60			
<i>S. longicorne</i>	0.00	8.21	0.00	5.16	8.98	5.38	1.66	0.00	0.65	2.33	1.42			
<i>S. robustum</i> ^W	0.00	0.00	0.00	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.00			
<i>S. suhmi</i> ^W	6.18	0.00	2.38	0.00	0.37	7.36	15.21	0.00	0.64	8.39	7.61			
<i>Thysanoessa gregaria</i> ^T	5.85	2.02	18.66	37.44	629.95	1.51	0.00	16.42	69.34	150.02	373.30			
<i>T. longicaudata</i> ^C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	33.71	3.86	0.53	0.00			
<i>Thysanopoda acutifrons</i> ^C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.00	0.00			
<i>Tp. aequalis</i> ^W	3.01	0.00	2.89	0.00	0.00	0.00	5.12	0.00	0.00	0.00	0.76			
<i>Tp. monacantha</i> ^W	0.00	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
<i>Tp. obtusifrons</i> ^W	5.36	0.00	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.00	0.00			
<i>Tp. tricuspidata</i> ^W	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			

W, warm-water species; C, cold-water species; T, transition species.

Table III: Mean abundance (individuals 1000 m⁻³) of each euphausiid species collected in the top 1000 m at the center of 82B and in the Slope Water.

Species	82B								Slope Water			
	March	April		June		August		March	April	June	August	
	N	D	N	D	N	D	N	N	N	N	N	
<i>Bentheuphausia amblyops</i>	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	
<i>Euphausia americana</i> ^W	3.78	0.39	3.46	0.00	0.14	2.22	3.44	1.29	0.24	3.69	0.22	
<i>E. brevis</i> ^W	13.37	9.18	9.32	2.54	4.57	0.20	0.00	0.00	0.00	1.29	0.00	
<i>E. gibboides</i> ^W	0.65	0.00	0.20	0.62	0.15	0.41	1.34	0.00	0.00	0.00	0.63	
<i>E. hemigibba</i> ^W	2.53	5.71	5.02	1.83	0.65	6.62	7.74	0.00	0.79	0.51	0.74	
<i>E. krohni</i> ^C	0.15	1.98	6.70	4.84	4.26	0.00	1.69	51.67	6.91	53.11	42.04	
<i>E. mutica</i> ^W	3.88	0.81	1.07	0.00	1.74	0.00	1.14	1.93	0.20	3.21	1.68	
<i>E. pseudogibba</i> ^W	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>E. tenera</i> ^W	17.74	13.03	15.21	1.00	0.58	14.13	37.63	0.00	0.91	10.55	2.64	
<i>Meganyctiphanes norvegica</i> ^C	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.43	2.86	0.40	0.00	
<i>Nematobrachion boopis</i>	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nb. flexipes</i> ^W	1.67	0.00	0.27	0.00	0.15	0.00	0.25	0.00	0.20	0.00	0.00	
<i>Nb. sexspinosum</i> ^W	0.30	0.00	0.00	0.00	0.20	0.00	0.25	0.00	0.00	0.35	0.00	
<i>Nematoscelis atlantica</i> ^W	1.93	3.35	1.21	2.23	1.48	2.16	1.12	1.04	0.20	0.33	0.84	
<i>N. megalops</i> ^C	0.16	0.00	0.46	0.00	1.88	0.00	11.58	30.50	2.30	6.72	8.87	
<i>N. microps</i> ^W	0.31	1.67	1.73	2.88	1.37	1.38	5.73	0.00	0.00	0.83	0.60	
<i>N. tenella</i> ^W	0.00	0.00	0.94	0.62	0.00	0.00	0.00	0.00	0.00	0.18	0.00	
<i>Stylocheiron abbreviatum</i> ^W	1.76	0.00	1.41	0.54	2.80	0.00	1.14	0.00	1.02	1.42	2.64	
<i>S. affine</i> ^W	6.81	2.29	2.09	0.23	1.07	1.74	3.52	0.00	0.00	1.86	0.00	
<i>S. carinatum</i> ^W	2.08	1.19	1.20	0.26	0.32	1.52	13.46	0.00	0.24	0.82	8.11	
<i>S. elongatum</i> ^W	5.24	1.88	4.24	0.19	3.39	1.63	4.90	0.00	0.00	0.35	0.19	
<i>S. longicorne</i>	0.00	3.10	0.00	1.91	3.59	1.67	0.72	0.00	0.24	0.90	0.41	
<i>S. robustum</i> ^W	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	
<i>S. sulmi</i> ^W	1.85	0.00	1.08	0.00	0.15	2.06	4.56	0.00	0.24	3.23	2.21	
<i>Thysanoessa gregaria</i> ^T	2.15	0.75	7.04	264.77	364.28	1.12	0.00	4.93	26.53	58.08	114.50	
<i>T. longicaudata</i> ^C	1.83	0.21	1.50	0.00	0.00	0.69	4.24	10.89	1.43	3.89	3.94	
<i>Thysanopoda acutifrons</i> ^C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	
<i>Tp. aequalis</i> ^W	0.90	0.83	1.07	1.22	0.00	0.00	1.76	0.00	0.00	0.00	0.22	
<i>Tp. monacantha</i> ^W	0.00	0.00	0.18	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	
<i>Tp. obtusifrons</i> ^W	1.61	0.10	0.00	0.20	0.14	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Tp. orientalis</i> ^W	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Tp. tricuspida</i> ^W	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

W, warm-water species; C, cold-water species; T, transition species.

Table IV: Maturity stage composition of three warm-water and two cold-water euphausiid species collected in the thermostad at night. Each entry in the table is the number of individuals examined and found to be in the particular stage.

Species	Female			Male	
	FS	FA1	FAS	MS	MA
Warm-water species					
<i>E. americana</i>					
March	0	3	4	0	12
April	1	1	0	1	6
June	0	1	0	0	0
August	4	4	1	7	6
<i>E. brevis</i>					
March	2	16	18	2	41
April	0	1	25	5	31
June	0	10	11	1	12
August					
<i>E. tenera</i>					
March	0	36	14	3	52
April	1	9	67	2	37
June	0	0	0	0	3
August	4	23	77	22	111
Cold-water species					
<i>E. krohni</i>					
March	0	0	0	0	1
April	1	0	22	0	17
June	0	2	5	18	8
August	0	0	2	0	5
<i>N. megalops</i>					
March	0	1	0	0	0
April	0	0	1	0	0
June	1	5	0	4	1
August	0	11	22	0	21

Table V: Maturity stage composition of two cold-water euphausiid species collected in the Slope Water at night

Species	Female			Male	
	FS	FA1	FAS	MS	MA
<i>E. krohni</i>					
March	0	8	132	0	181
April	3	1	8	8	12
June	31	43	56	78	90
August	18	57	22	10	88
<i>N. megalops</i>					
March	0	23	64	0	68
April	0	3	4	0	7
June	7	2	1	22	8
August	1	6	14	8	11

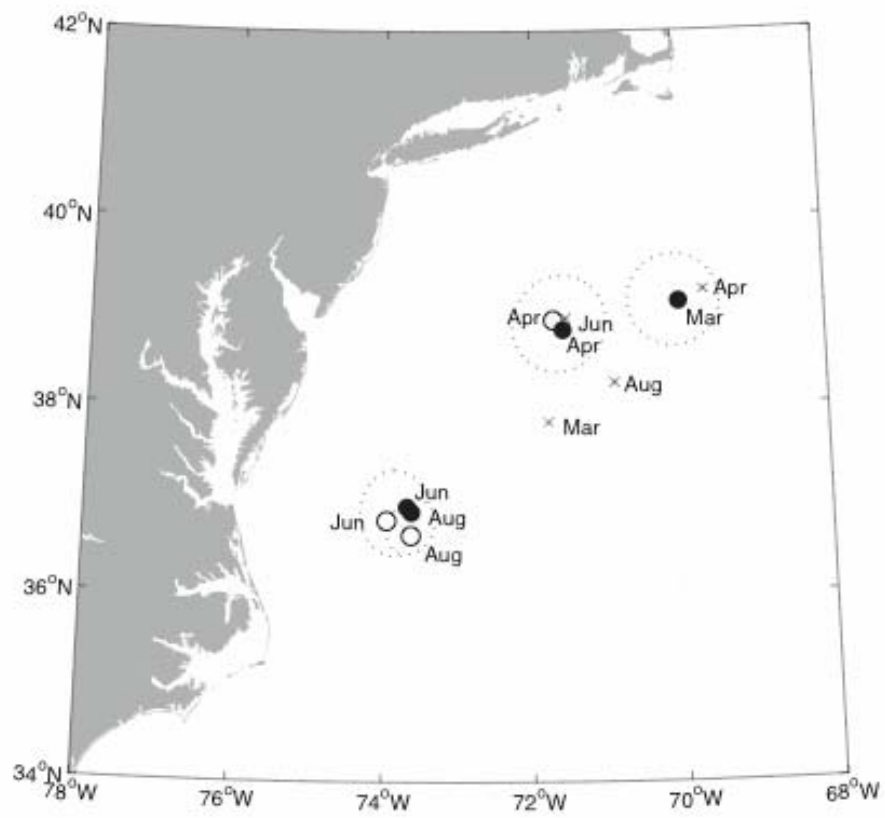


Fig. 1

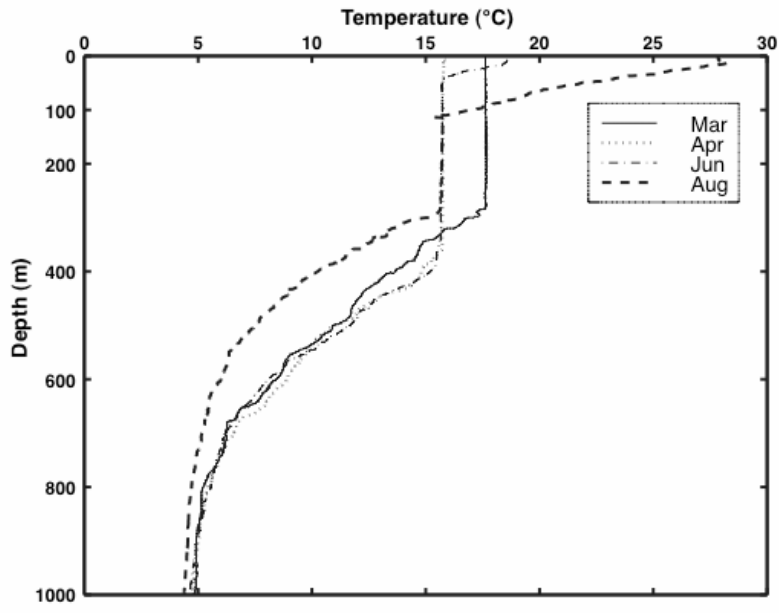


Fig. 2

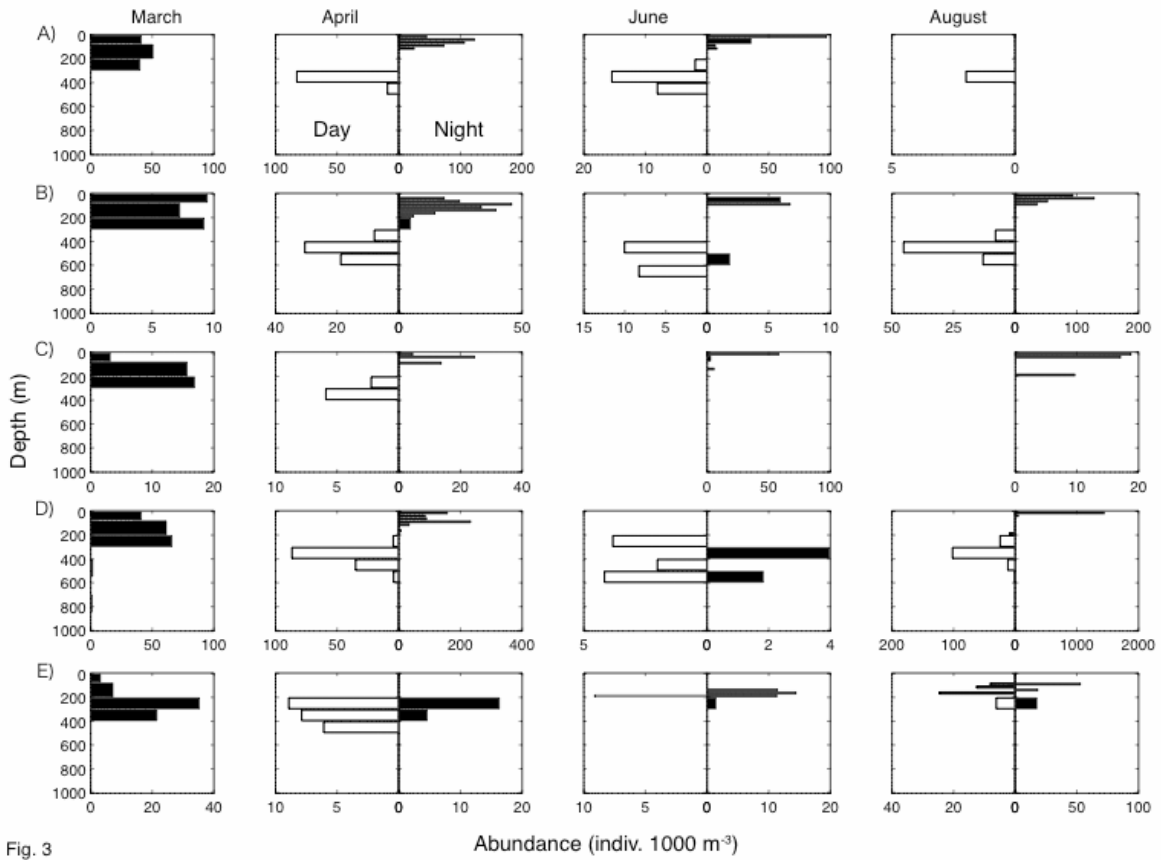


Fig. 3

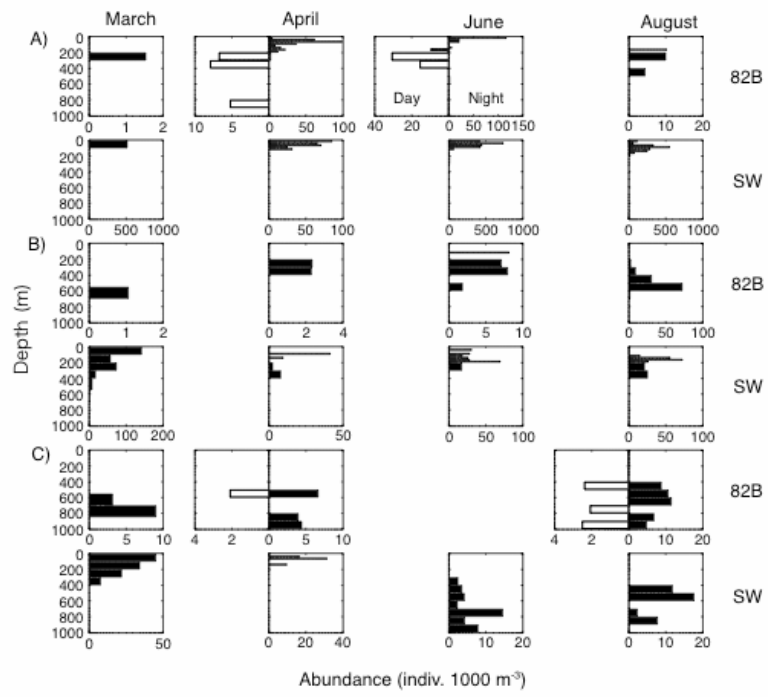


Fig. 4

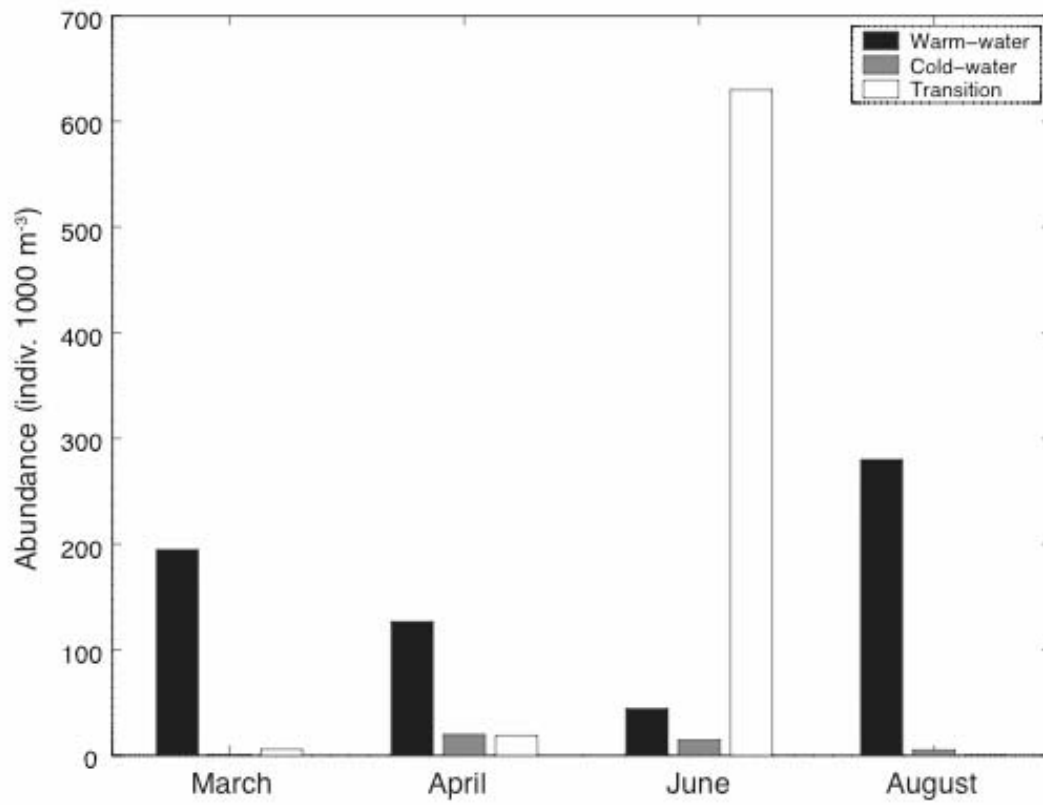


Fig. 5

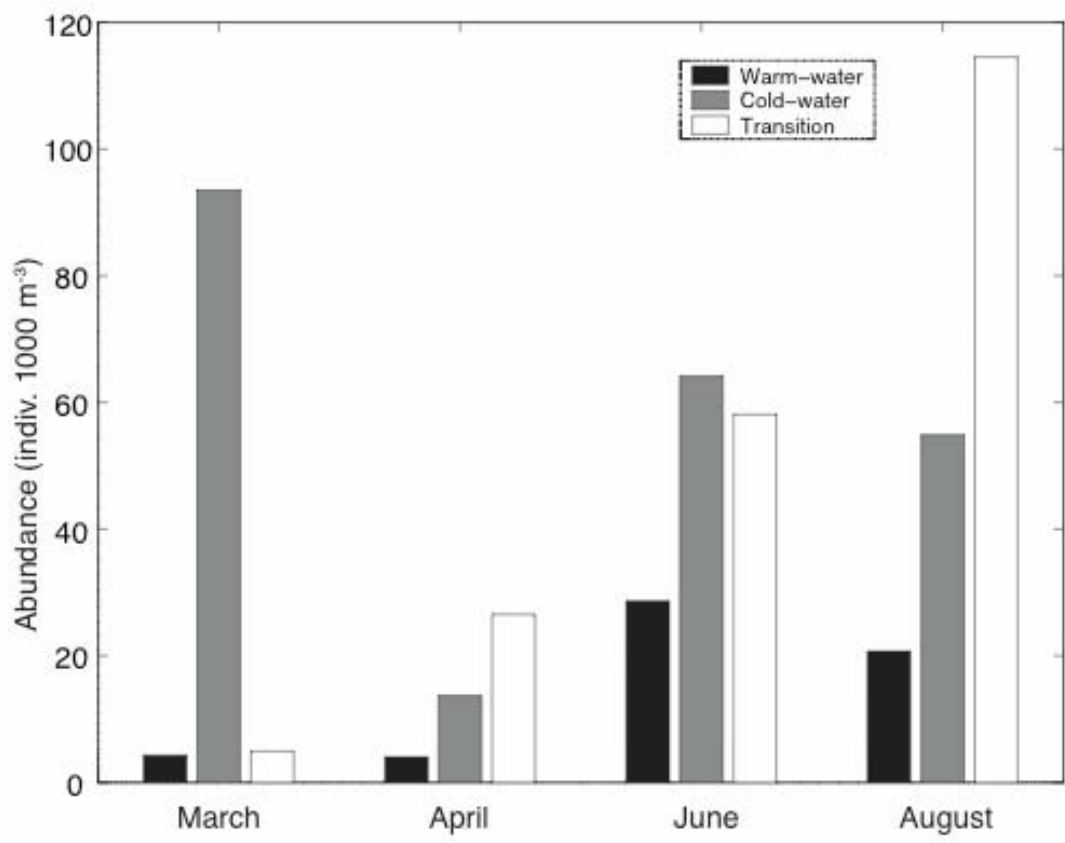


Fig. 6

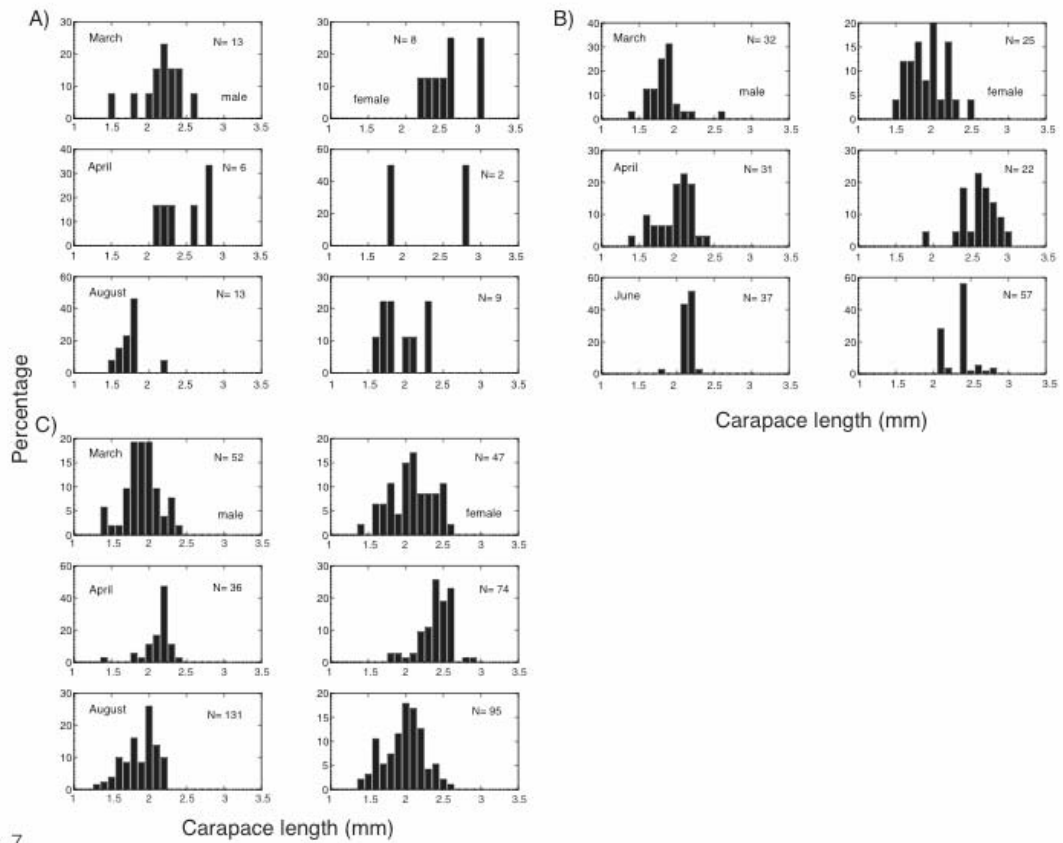


Fig. 7

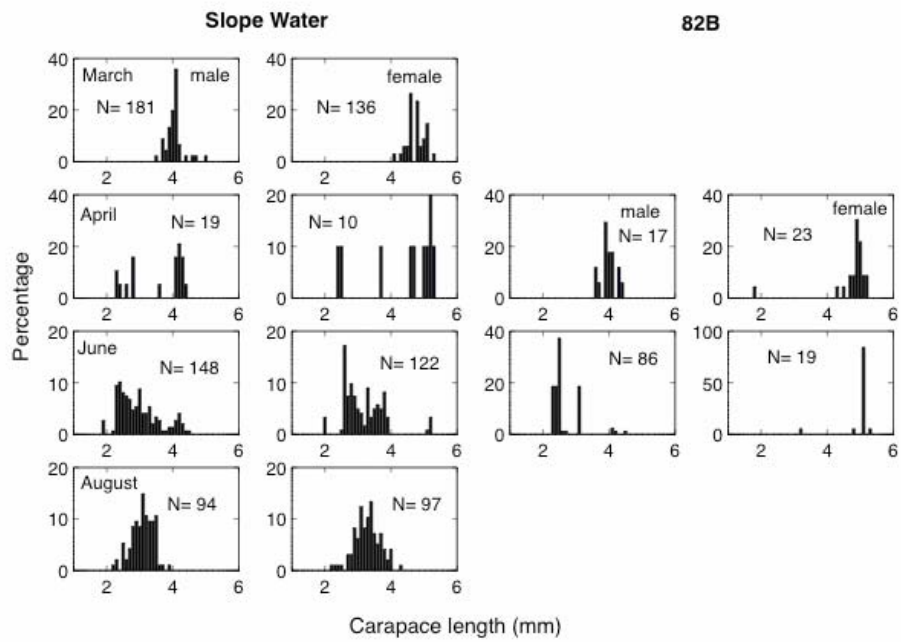


Fig. 8

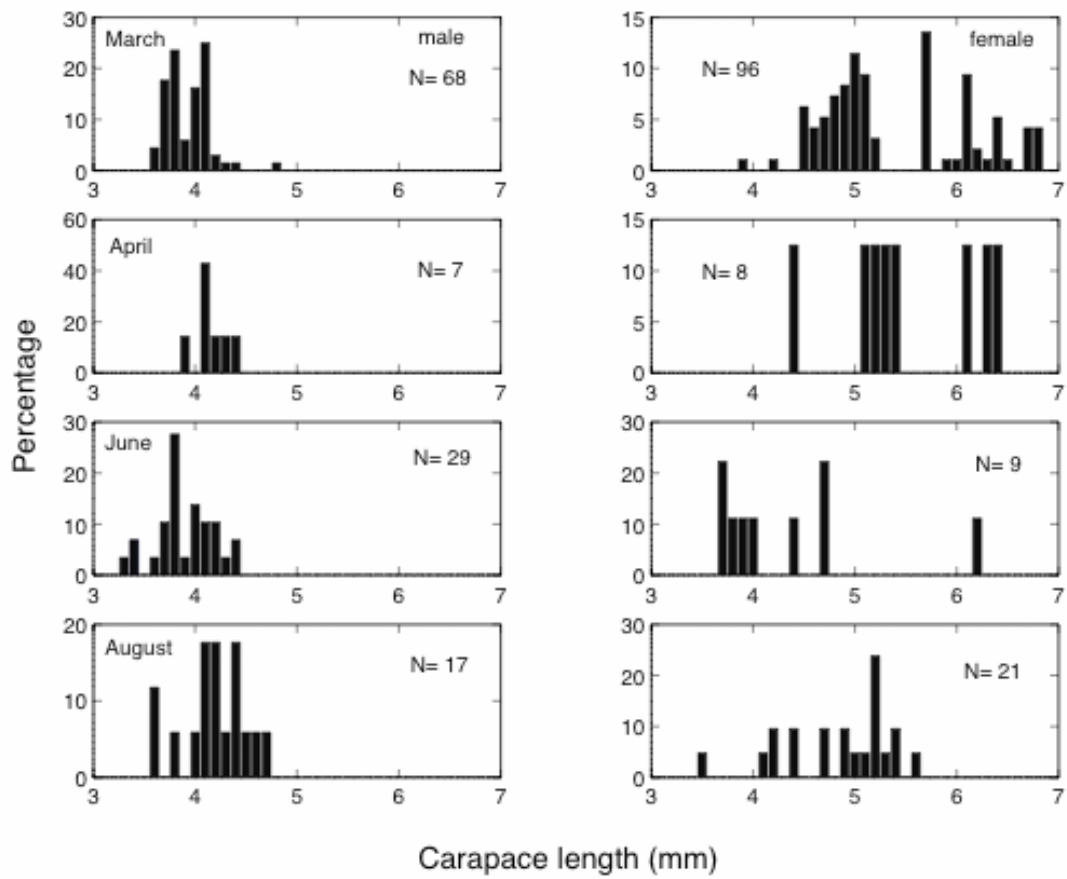


Fig. 9