

Temporal changes in euphausiid distribution and abundance in North Atlantic cold-core  
rings in relation to the surrounding waters

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## Abstract

The species composition of euphausiids was investigated in relationship to the hydrographic conditions in the North Atlantic cold-core rings (CCR) and adjacent waters to elucidate species succession in evolving water masses. Using data, dating back to the 1970's, from as many CCRs as possible and selecting typical cases where no major physical perturbations occurred, a general pattern of euphausiid succession and change in vertical distribution in rings with time was obtained. This pattern was related to the general distribution of euphausiids in the northwestern North Atlantic Ocean, aiming at providing basic information on probable response of North Atlantic marine ecosystem to global warming. Of the 34 euphausiid species identified, 5 were cold-water species, 17 were warm-water species, 6 were wide-ranging warm-water species, 1 was transitional, 4 were cosmopolitan and the remaining was *Thysanoessa parva*. Among cold-water species, *Euphausia krohni* and *Nematoscelis megalops* were dominant in CCRs. *E. krohni* became rare in rings older than 6 months, whereas *N. megalops* survived longer, being abundant in some rings of 9 months or older, by staying within its preferred temperature range as the CCR elevated isotherms sank to depths where they are normally found in the Sargasso Sea and because it is an omnivore-carnivore. Among warm-water species, epipelagic species appeared first in rings, corresponding to the physical change occurring most rapidly in the surface layers. Mesopelagic species appeared later. Cold-water species made up 65-85% of the total euphausiid population in number in younger rings (1-5 months old), while warm-water species contributed only 2-7%. Wide-ranging warm-water species made up about up to one fourth of the total in rings 5 and 7 months old. Warm-water species, mainly *E. brevis*, increased in older rings (9 months old or older) and made up 50% of the total in

the oldest ring. The contribution of cold-water species decreased to 14% in older rings. *T. parva* made up 26-38% of the total in rings 6 months or older. CCR populations can be characterized by high species number, but intermediate evenness between the Slope Water and northern Sargasso Sea. In CCRs, only a limited number of species were dominant even if there were more species present in rings as old as 9-12 months than in the northern Sargasso Sea. In rings older than 9 months, euphausiids showed two peaks in their vertical distribution: a shallow daytime peak at about 400 m and a nighttime peak in the upper 100 m consisting of warm-water species (mainly *E. brevis*) and a deeper persistent peak at 800 m or deeper consisting of the species *N. megalops* and *T. parva*. This shallow peak in CCRs is shallower than that in the surrounding northern Sargasso Sea, and the deep peak is rarely observed in these waters.

keywords: krill, abundance, succession, distribution, cold-core rings, North Atlantic

## 1. 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). Such meso-scale eddies are not restricted to western boundary currents, but are a common phenomenon in the world oceans. These eddies have a significant impact on biogeochemical cycles in the ocean, e.g., the “PRIME” anticyclonic eddy in the Iceland Basin (Martin *et al.*, 1998; Savidge and Williams, 2001) and the SWODDIES (slope water oceanic eddies), anticyclonic eddies in the Bay of Biscay (Rodríguez *et al.*, 2003; Fernández *et al.*, 2004; Isla *et al.*, 2004). Furthermore, accurate characterization of mesoscale eddies in climate models is important because of their role in transporting heat, salt, and passive tracers used to study ocean circulation (Danabasoglu *et al.*, 1994).

Biotic feedbacks to climate change, in contrast to physico-chemical feedbacks, have a regional nature (Boyd and Doney, 2003), and therefore, ecosystem structure must be investigated for each major province. Information on zooplankton abundance and species composition in mesoscale eddies is indispensable for understanding the dynamics of marine ecosystems in the northwestern North Atlantic Ocean, because they play an important role in structuring marine food webs. Gulf Stream cold-core rings (CCR) were studied intensively in the 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 responsible processes (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). Wiebe and Flierl (1983) discussed euphausiid abundance in cross-sections of three CCRs and interpreted changes in relative abundance from inside to outside as indicating invasion or dispersal processes. In the present study, we analyzed species succession of euphausiids in rings through time, using data from as many CCRs as possible and selecting typical cases where no major physical perturbations, such as a ring-Gulf Stream interaction, occurred. Temperature structure in rings is strongly related to their age and was used to improve our understanding of the process of euphausiid species succession and change in vertical distribution in CCRs for a longer time span than previously possible.

There are several studies that addressed distribution and abundance of euphausiids in limited areas or season(s) in the northwestern North Atlantic Ocean (e.g., Bigelow, 1926; Whiteley, 1948; Grice and Hart, 1962), but no studies have covered the seasonal change based on samples widely collected in the area. We analyzed species composition of euphausiids in 139 tows collected throughout the northwestern North Atlantic Ocean including the Slope Water, warm-core rings (WCR), Gulf Stream, northern Sargasso Sea, CCRs, and southern Sargasso Sea. Our objective is to use the species composition in CCRs of various ages to see if a systematic trend in species succession with ring age exists relative to the species composition in adjacent areas.

Levitus *et al.* (2005) showed that during 1955-1998 world ocean heat content increased  $14.5 \times 10^{22}$  J corresponding to global warming, but they also noted there are cooling areas, the equatorial Pacific, the North Pacific around 40°N, and the North Atlantic centered at 60°N. Endo and Wiebe (2005) analyzed euphausiid species

succession in WCR 82B and provided basic information on possible responses of North Atlantic marine ecosystems to regional cooling accompanied by global warming. In the present paper, we provide basic information on a possible response to regional warming.

## **2. Materials and Methods**

The samples were collected on 15 cruises to the northwestern North Atlantic Ocean (Table 1). On all cruises, an effort was made to sample to at least a depth of 750 m at each station, and only those tows that sampled to at least 700 m were used in this study. Collections were made with three types of net systems. A 1-meter diameter ring net equipped with a flowmeter was used on the early cruises either exclusively or as a supplement to 70 cm diameter opening/closing Bongo nets (McGowan and Brown, 1966). Generally three pairs of Bongo nets were towed simultaneously on the wire so as to sample the intervals 0-250 m, 250-500 m, and 500-750 m. On cruise Chain 111, the Bongos were opened by messenger and closed by a pre-set flowmeter-triggered release; on cruise Knorr 35 they were opened and closed by messengers, with flow through each net monitored by a flowmeter in the mouth of the net. Beginning on cruise Atlantis II 85, a multiple opening/closing net and environmental sensing system (MOCNESS - Wiebe *et al.*, 1976b) was used to gather depth-specific collections. Hauls with MOCNESS were generally to 800 m with eight 100-m strata sampled as the system fished obliquely from the bottom of the haul to the surface. The mesh used on all the nets was 0.333 mm Nitex gauze. The samples were preserved in 5-10% formalin buffered to a pH 8.0 with sodium borate.

Juvenile and adult euphausiids in the collections were generally sorted from the

entire sample and enumerated according to species. When one or more species was particularly abundant, only an aliquot was counted. Identifications were made with the assistance of keys given by Boden et al. (1955) and Mauchline and Fisher (1969). The technique of Ruud (1936), whereby differences in the ratio of eye height to carapace length are compared to the carapace length, was used to separate *Nematoscelis atlantica* and *N. microps*. In addition, the qualitative differences described by Gopalakrishnan (1975) in the shape of the eyes were helpful. Our diagnosis of *Thysanopoda aequalis* is based on Brinton's (1975) definition of the species pair *Tp. aequalis* and *Tp. subaequalis*.

#### Chronology and oceanographic structure of CCRs surveyed

Five CCRs, D, Al, Bob, Emerson, and Franklin were used in the present study to examine temporal change in hydrographic conditions and euphausiid species composition, because these CCRs were well studied for their physical properties and chronology. The ages of the rings at the times of sampling and their formation dates are shown in Table 2.

Ages of CCRs were estimated from the depth of a specific isotherm (e.g., Wiebe *et al.*, 1976a) or through satellite observation on SST supplemented by sea truth (Vastano *et al.*, 1980). First we selected those cold-core rings the ages of which could be estimated from satellite observation and sea truth: Bob at 1 and 5 months old and D at 6 and 9 months old. These rings were used to establish the relationship between ring age and temperature characteristics (mean temperature in the upper 700 m, and 15°C isotherm depth). Then rings Franklin (7 months old) and Emerson (12 months old) were added to compare species composition of euphausiids with ring age. The

core water mass of ring A1 was suggested to have been partially formed from WCR H (Vastano *et al.*, 1980). Evidence for this is in the temperature characteristics and the species composition of euphausiids as will be shown later. Therefore, ring A1 was excluded from this specific analysis.

Hard copies of vertical profiles of temperature and salinity from the CTD first used with MOCNESS were available as well as values printed at 1-minute intervals. Nine-track magnetic tapes on which the original data were stored at 1-second intervals were available and the data from some tows were recovered from the tapes. The 1-minute data were used for tows where the tape data could not be read.

#### Temperature measures of ring age

Two measures of temperature were used to estimate the age of CCRs: the mean temperature in the upper 700 m, and the depth of the 15°C isotherm, which gives the thickness of warm surface water >15°C. Parker (1971) showed that in one CCR the 17°C isotherm was at a depth of 50 m at the formation and sank at a rate of 0.6 m per day. We, however, used the 15°C isotherm, because that temperature was the highest found in a newly formed CCR, Bob, at the age of one month.

#### Species composition of euphausiids

Similarity of species composition of euphausiids among tows was examined with nonmetric multidimensional scaling (nonmetric MDS) based on depth-integrated individual numbers for each species of euphausiid. The deepest depth attained by each tow varied from 700-1,100 m, but no attempt was made to standardize the integration depth layer, because in earlier cruises MOCNESS was not available and discrete depth

sampling was not possible. We used Sorensen distance as a measure of dissimilarity among tows as recommended by McCune and Grace (2002). A total of 139 tows (749 nets) collected widely from the northwestern North Atlantic Ocean were analyzed, including 34 tows from the Slope Water, 5 tows from WCRs, 4 tows from the Gulf Stream, 33 tows from the northern Sargasso Sea, 50 tows from CCRs, 1 tow from a meander from which a CCR was about to be pinched off, and 12 tows from the southern Sargasso Sea. This broad coverage allowed similarity in species composition of euphausiids to be compared not only among CCRs of different ages, but also between CCRs and adjacent areas in the northwestern North Atlantic Ocean. Species number and Pielou's evenness index  $J'$  (Pielou, 1966) were calculated to estimate the species diversity of ring communities and the communities in adjacent waters.

## **Results**

### Age of rings

Vertical profiles of temperature at the center of 5 CCRs ( Fig. 1) revealed that the surface layer warmed first, and then the water column below the mixed layer warmed up. In rings several months old, the temperatures in the upper 100 m were higher than in a one-month old ring, and temperatures in the deeper layer, 150-800 m, were higher in rings 7 months old or older than in the younger rings. (Al was the exception: temperatures, especially at 150-800 m, were higher for its estimated age.) In order to clarify the relationship between ring age and temperature values, we selected three CCRs, D, Al and Bob, which were surveyed intensively with satellite and sea truth (XBT and CTD temperature data, Table 2).

The mean temperature in the upper 700 m, more precisely 10-700 m, at the ring

center increased at a rate of  $0.7^{\circ}\text{C}$  per month ( $y=8.06+0.65x$ ,  $r^2=0.918$ ,  $p=0.0001$ , Fig. 2). The thickness of warm surface water ( $>15^{\circ}\text{C}$ ) at the ring center increased at a rate of 30 m per month ( $y=30.86x$ ,  $r^2=0.967$ ,  $p<0.0001$ ). Ring A1, which was reported to be 2.5 months old (Vastano *et al.*, 1980; Wiebe and Flierl, 1983, Fig. 2), proved to be exceptional in terms of its temperature profile, with a higher mean temperature in the upper 700 m ( $>4^{\circ}\text{C}$ ) and a deeper  $15^{\circ}\text{C}$  isotherm ( $>200$  m) for its age. Ring A1 may have been about 9-10 months old based on mean temperature in the upper 700 m and the depth of the  $15^{\circ}\text{C}$  isotherm. In the following analysis, we used data on euphausiid species composition from rings Franklin (7 months), Emerson (12 months), Bob (1 and 5 months) and D (6 and 9 months) to investigate species succession in CCRs, because the temperature values of the former two rings are close to the regression lines in Fig. 2. These rings did not seem to have experienced major perturbations, and discrete depth layers were sampled with MOCNESS. The age of ring Emerson was estimated to be 12+ months at net sampling (Wiebe *et al.*, 1985); but the temperatures are below the regression lines in Fig. 2, and the age may be only 8 to 9 months if we assume a linear relationship between temperature and ring age. However, as will be shown later, euphausiid species composition of Emerson appeared a little older than that in ring D at 9 months. Therefore, the age of ring Emerson was set to be 12 months.

#### Change in euphausiid species with age of ring

A total of 34 euphausiid species occurred in this study (Table 3). These euphausiids were grouped as cold-water species, transition species, warm-water species, cosmopolitan, and others according to previous work (Mauchline and Fisher, 1969; The Ring Group, 1981; Wiebe, 1987; Brinton *et al.*, 1999). Five cold-water species,

*Euphausia krohni*, *Meganyctiphanes norvegica*, *Nematoscelis megalops*, *Thysanoessa longicaudata*, and *Thysanopoda acutifrons* appeared in this study. The distributional ranges of these species are generally restricted to the Slope Water and more northern areas as well as CCRs. Twenty-three species were categorized as warm-water species whose distributional range includes tropical and/or subtropical waters. We further divided warm-water species into those that can become abundant ( $>10$  indiv.m<sup>-2</sup>) in the Slope Water and those that cannot (Endo and Wiebe, unpublished data). We call them ‘wide-ranging warm-water species’ and simply ‘warm-water species’, respectively (Table 3). This is because we wanted to know the processes by which warm-water species enter CCRs and these species groups should be treated separately.

‘Wide-ranging warm-water species’ can be already abundant at the time of ring formation, but ‘warm-water species’ cannot. Wide-ranging warm-water species are not necessarily more abundant than warm-water species in the northern Sargasso Sea. For instance, the annual median abundance of two wide-ranging warm-water species, *E. tenera* and *S. carinatum*, was more than 5 indiv. m<sup>-2</sup>, but that of the remaining four species was less than 1 indiv. m<sup>-2</sup> (Endo and Wiebe, unpublished data). On the other hand, four warm-water species were more than 5 indiv. m<sup>-2</sup> in the northern Sargasso Sea (*E. brevis*, *E. hemigibba*, *S. affine*, and *S. elongatum*). Therefore, it may not be higher abundance but may be tolerance to low temperatures that makes wide-ranging warm-water species abundant in the Slope Water.

*T. gregaria* is the sole transition species in the present study. The distributional range of *T. parva* is not well known (Brinton *et al.*, 1999). In the North Atlantic, *T. parva*, a deep-living species, is reported to be a typical northern Sargasso Sea species. It regularly occurs at low to moderate abundance in the Slope Water region under the

influence of WCRs or meanders of the Gulf Stream, but rarely in the Slope Water itself (Wiebe and Flierl, 1983; Wiebe, 1987). The remaining four species, *Bentheuphausia amblyops*, a cosmopolitan, *Nematobrachion boopis*, *Stylocheiron maximum*, and *S. longicorne*, have wider distributions, occurring from the tropics to as far north as Icelandic waters. The latter three species occur further north in the Atlantic than in the Pacific because of the North Atlantic Current.

In a one-month old ring (Bob), the five most abundant species, in rank order, were *N. megalops*, *E. krohni*, *T. gregaria*, *E. americana*, and *T. longicaudata* (Fig. 3). Three of the five were cold water species. In addition, *E. hemigibba* and *E. tenera* occurred at a density of 1-5 indiv. m<sup>-2</sup>. Warm-water species, *E. brevis*, *E. gibboides*, *E. hemigibba*, *Nb. flexipes*, *N. microps*, *S. suhmi*, *Tp. aequalis*, *Tp. monacantha*, *Tp. obtusifrons*, and *Tp. tricuspida* were present. In all three rings 5-7 months of age, *N. megalops* was dominant, and *E. krohni*, *E. tenera*, *S. carinatum*, *T. gregaria*, and *T. parva* were also dominants, with mean abundance of several-tens of individuals m<sup>-2</sup> in at least two of three rings. *E. krohni* and *N. megalops* were exceptionally abundant in 5 month old ring (Bob). Five more warm-water species occurred at six months compared to the ring of age 1 month: *N. tenella*, *S. abbreviatum*, *S. affine*, *S. elongatum*, and *Tp. orientalis*. In the rings 9 months or older, *E. brevis*, *N. megalops*, and *T. parva* were dominant, occurring with mean abundance of tens of individuals m<sup>-2</sup> at least at one station. Among the cold-water species, only *N. megalops* remained abundant in rings as old as 12 months. One more warm-water species, *Tp. pectinata*, occurred at this age. Thus 16 warm-water species were present in a 12 month-old CCR.

In newly formed cold-core rings, epipelagic warm-water species appeared first (Fig. 4). They include *E. brevis*, *E. gibboides*, *E. hemigibba*, *Nematobrachion flexipes*,

*Thysanopoda aequalis*, and *Tp. obtusifrons*. Many of these species are distributed in the upper 100 m at least at night in their home range, the northern Sargasso Sea. The mean abundance of *E. hemigibba* was 2 indiv. m<sup>-2</sup> in a one-month old ring (Bob) then increased slightly to 2-4 indiv. m<sup>-2</sup> thereafter. The abundance of *Tp. aequalis* was 0.4 indiv. m<sup>-2</sup> in the one-month old ring (Bob) and increased to 1-2 indiv. m<sup>-2</sup> in a 9-month old ring (D) or older. *Nb. flexipes* and *Tp. obtusifrons* usually stay deeper, but sometimes occurred in the upper 100 m at night in the northern Sargasso Sea (Endo and Wiebe, unpublished data). They appeared to slightly increase in number or had similar abundances as the rings aged, although *N. flexipes* was not observed in rings of 9 months or older. *E. brevis* appeared to increase dramatically in older rings. This species is distributed in the upper 100 m at night in the northern Sargasso Sea, but it did not increase in rings until a number of months after ring formation: the abundance was less than 1 indiv. m<sup>-2</sup> in the one-month old ring and increased to 1-2 indiv. m<sup>-2</sup> in 5-7 month old rings. It attained a maximum abundance for all warm-water species of 10-20 indiv. m<sup>-2</sup>, in rings 9 months or older.

On the other hand, species whose nighttime depth was deeper than 100 m did not appear or increase in CCRs until about six months after ring formation (Fig. 4), when the thickness of the warm surface layer had become 150 m or more (Fig. 2). These species include *Nematoscelis microps*, *N. tenella*, *S. affine*, *S. elongatum*, and *Thysanopoda orientalis*. Abundance of these species was not high, reaching at most several indiv. m<sup>-2</sup>. *S. abbreviatum*, a non-migrator usually distributed in the upper 300 m both day and night, also appeared at the center of CCRs after several months.

Four cold-water species increased in number in rings several months old and then decreased afterwards (Fig. 5). Of these *N. megalops* kept a relatively high abundance

even after 9 months, while *E. krohni* became quite rare after 7 months. As previously mentioned, two cold-water species, *E. krohni* and *N. megalops*, were exceptionally abundant in two tows made at the center of Bob at 5 months: 91.9 and 533.8 indiv. m<sup>-2</sup> in 77MOC1 and 83MOC1, respectively, for *E. krohni*, and 73.3 and 113.8 indiv. m<sup>-2</sup> in 77MOC1 and 83MOC1, respectively, for *N. megalops* (Fig. 5). Vastano *et al.* (1980) reported the physical structure of Bob throughout its life history and noted that new Slope Water was introduced from 17-21 April during interaction with the Gulf Stream, but no such event occurred afterwards. The net sampling for Bob at 1 month of age was done at exactly the same time as the Slope Water intrusion, 17-21 April.

#### Changes in species composition in CCRs

The number of euphausiid species that occurred in CCRs increased from 13 in a 1 month-old ring to 17-22 in older rings, with a maximum of 22 species in the oldest ring (Fig. 6). Pielou's evenness index, *J'*, however, ranged from 0.5 to 0.7 without an increasing trend. The mean number of euphausiid species was significantly less in the Slope Water than in the CCRs and northern Sargasso Sea (ANOVA,  $p=0.0113$ , Fisher's PLSD,  $p=0.0056$  for CCRs vs. Slope Water and  $p=0.0303$  for northern Sargasso Sea vs. Slope Water): 11-17 species in the Slope Water, 13-22 species in CCRs and 14-18 species in the northern Sargasso Sea. Therefore, CCRs may hold the highest number of species after aging for several months. However, the evenness was the highest in the northern Sargasso Sea (about 0.8) followed by cold-core rings (0.5-0.7) and the Slope Water (0.4-0.6) (ANOVA,  $p<0.0001$ , Fisher's PLSD,  $p=0.0004$  for CCRs vs. northern Sargasso Sea,  $p=0.0786$  for CCRs vs. Slope Water, and  $p<0.0001$  for northern Sargasso Sea vs. Slope Water).

The mean abundance of total euphausiids ranged from 50 to 210 indiv. m<sup>-2</sup> in rings 1-12 months old (Fig. 7). There was no significant difference in the mean abundance of total euphausiids (ANOVA, p=0.8997) or of cold-water species (p=0.5966) among rings of various ages. On the other hand, warm-water species increased from less than 10 indiv. m<sup>-2</sup> in rings 1-7 months old to 24.5 indiv. m<sup>-2</sup> or more in rings 9 months or older. The difference in the mean abundance of warm-water species among rings of various ages was significant (p=0.0001). The total abundance of euphausiids was far more than the sum of cold-water species and warm-water species in rings 6 months or older, especially those 6 and 7 months old. The difference was caused by abundances of *T. gregaria* and *T. parva* in the ring 6 months old, and of *T. parva*, *S. carinatum*, and *E. tenera* in rings 7 months old (Figs. 3 and 7).

In WCR 82B, the maximum percentage of cold-water species was only 12% during its lifespan of 6 months (Endo and Wiebe, 2005). Species succession of euphausiids seems to have advanced further in cold-core rings, because the contribution of warm-water species reached as high as 50% in a 12-month old ring (Fig. 8).

Cold-water species occupied 65-85% of total euphausiid population abundance in younger rings (1-5 months old), while warm-water species contributed only 2-7%. The contribution of wide-ranging warm-water species was the second largest after cold-water species, 6-16%. *T. gregaria* made up 12% of the total population in a ring 1 month old, attained the maximum contribution, 38%, when 6 months old but contributed less than 7% in other rings. *T. parva* contributed 26-38% when rings were 6 months or older. The contribution of cold-water species decreased to 14% in the oldest ring while warm-water species, mainly *E. brevis*, increased in older rings (9 months old or older) and contributed 50% in the oldest ring. Therefore, cold-water

species occupied more than half of total euphausiid population in rings 5 months old or younger, wide-ranging warm-water species contributed up to one fourth in rings 5-7 months old, and warm-water species contributed about half of the population in the 12 month old ring. A transition species, *T. gregaria*, sometimes dominated in rings several months old, and a deep-living northern Sargasso Sea species, *T. parva*, occurred constantly in rings 6 months old or older.

The percentage of cold-water species decreased by 5% per month as rings aged ( $y=76.252-5.211x$ ,  $r^2=0.463$ ,  $p=0.0019$ , Fig. 9). As for the warm-water species, the abundance was low and constant in the first 6 months ( $y=6.28-0.018x$ ,  $r^2=8.852\times 10^{-5}$ ,  $p=0.9794$ ) and increased at 8% per month from 6 to 12 months ( $y=-44.933+7.846x$ ,  $r^2=0.897$ ,  $p<0.0001$ ).

Nonmetric MDS based on the euphausiid species composition in 139 tows that sampled down to 700 m depth or deeper (Fig. 10a) align the tows left to right along dimension 1 as a gradient from the southern Sargasso Sea to the northern Sargasso Sea, and the Slope Water. Therefore, dimension 1 can be characterized as a water type axis. CCR tows take the largest range of values of dimension 1, with older CCRs overlapping with northern Sargasso Sea tows and younger CCRs close to the Slope Water tows (Fig. 10b). The Gulf Stream and WCR tows share the area with those from northern Sargasso Sea, although WCR tows show higher values of dimension 2. The one meander tow (an incipient CCR) is located with tows from the Slope Water, and young CCRs.

Tows that were made at the center of CCRs were aligned in order of their age: tows from younger rings align with the Slope Water and those from older rings align with the Sargasso Sea (Fig. 6b). Exceptions are tows made at the center of ring Bob at

5 months old (77MOC1 and 83MOC1, rightmost two points), in which abundances of *E. krohni* and *N. megalops* were exceptionally high. The species composition of ring A1 (2.5 months) is also exceptional, supporting the likelihood that A1 was partially formed from a WCR.

When the abundance of cold-water and warm-water species are plotted on the same two dimensional coordinates of nonmetric MDS, it is clear that warm-water species are abundant in the northern Sargasso Sea region and cold-water species are abundant in the Slope Water region (Fig. 11).

#### Vertical distribution of euphausiids in CCRs and its change with ring age

The vertical distribution in abundance of total euphausiid species for representative day and night tows at the center of rings of various ages shows that the peak depth of occurrence descends with ring age (Fig. 12a). The euphausiids showed a single peak both day and night in a ring 1 month old: 200-300 m during the day and 0-100 m at night. There are two peaks of occurrence during the day in rings 7 months or older (300-500 m and 700-800 m) and at night in rings 9 months or older (0-100 m and 700-800 m). A peak at depths of 700-800 m does not usually appear in the Slope Water or in the northern Sargasso Sea (Endo and Wiebe, unpublished data). In the Slope Water, a cold-water species, *T. longicaudata*, sometimes forms a deeper peak (>700 m) with an abundance of more than 100 indiv. 1000 m<sup>-3</sup>; and in the northern Sargasso Sea, *T. parva* sometimes forms a similar deep peak of occurrence, but its abundance rarely exceeds 100 indiv. 1000 m<sup>-3</sup> (Endo and Wiebe, unpublished data).

The peak of warm-water species is a little deeper than that of cold-water species during the day in rings 5 months or younger (weighted mean depth (WMD) is 359-425

m vs. 236-367 m) but becomes shallower and is clearly segregated from that of cold-water species both day and night in rings 9 months or older (Fig. 12b and c). Daytime WMD is 367-444 m and 697-723 m and nighttime WMD is 87-160 m and 575-672 m for warm-water species and cold-water species, respectively in those older rings. The vertical distribution of warm-water species is largely determined by two migrant species, *E. brevis* and *E. hemigibba*. In rings 1 and 5 months old, *E. hemigibba* was more abundant than *E. brevis*. In rings 6 and 7 months old, both species occurred with similar abundance, and in rings 9 months or older, *E. brevis* outnumbered *E. hemigibba* (Fig. 3). Both species performed a similar range of vertical migration with a little deeper depth distribution for *E. hemigibba* during the day (not shown). *E. hemigibba* deepened its daytime depth from 300-400 m in a one-month old ring to 500-600 m (the typical depth range of this species in the northern Sargasso Sea) in a 6-month old ring.

The vertical distributions of the dominant species, *E. krohni* and *N. megalops* as cold-water species, *E. brevis* as a warm-water species and *S. carinatum* as a wide-ranging warm-water species, are shown in Fig. 13. Daytime distribution of *E. krohni* deepened from 100-300 m (WMD=228 m) in a one-month old ring to 300-500 m (337-431 m) in 5-7-month old rings and then to 400-600 m (475-496 m) in 9 months or older rings. The nighttime depth distribution of *E. krohni* was mostly shallower than 100 m but a little deeper in rings 5 and 12 months old. This species performed diel vertical migration with the magnitude of 200-300 m. The vertical distribution of *N. megalops* deepened with ring age. In the Slope Water and young rings the center of distribution was about 250 m. It shifted to between 200 and 500 m (382-444 m) in 5 to 7 month old rings and in rings 9 months or older the peak of occurrence was 600-800 m

(701-737 m). This species is believed not to be a vertical migrator (Wiebe *et al.*, 1982; Brinton *et al.*, 1999) and seems to stay in a similar depth layer both day and night in old rings. The depth of occurrence of epipelagic warm-water species *E. brevis* was shallower than 100 m at night in all rings except in a one-month old ring in which a small number of individuals occurred at 100-200 m. The species occurred between 200 and 500 m in rings 7 months or older during the day, well into the cold water below surface warm water: the temperature at 500 m depth was about 6°C colder when a ring was 12 months old and up to 9°C colder when 7 months old compared with the adjacent Sargasso Sea. The vertical range of their DVM was 200-400 m. Another epipelagic species, *S. carinatum*, did not descend as deep as *E. brevis* did. *S. carinatum* is probably a non-migrator, and its depth of peak abundance was mostly shallower than 100 m at night and shallower than 200 m during the day as in the northern Sargasso Sea (Endo and Wiebe, unpublished data).

It is apparent that the shallower peak of euphausiids during the day in older rings (9 months or older) was formed by *E. brevis* and the deeper peak at night by *N. megalops*. *T. parva* also contributed to the deeper euphausiid peak.

## **Discussion**

### Species-specific changes

Epipelagic warm-water species appeared faster in CCRs than mesopelagic species did. This pattern was also reported by Wiebe and Flierl (1983) and is attributable to the fact that physical change occurs first in the surface layers, namely, surface layers warms first.

The total abundance of warm-water species in CCRs increased because that of

several individual warm-water species increased, especially *E. brevis*, starting from none to low abundance in young rings and increasing as the rings aged. In the northern Sargasso Sea, *E. brevis* is one of the dominant species throughout the year. It is most abundant in spring, with mean abundance of 50 indiv. m<sup>-2</sup>, and less abundant, about one fifth, in the other seasons (Endo and Wiebe, unpublished data). Sample collections in rings 9 and 12 months old were made in November and October, respectively, so this species was not particularly abundant in the northern Sargasso Sea at the times of sampling for these CCRs. Rather, the environment in cold-core rings might have been more suitable for this warm-water species during this period.

*E. brevis* did not increase for several months after ring formation, while another abundant warm-water species, *E. hemigibba*, increased rather linearly with ring age (Fig. 4). Wiebe and Flierl (1983) reported that *E. brevis* increased in a 6-month old ring (Bob) but did not appear in the center. Unlike *E. hemigibba*, *E. brevis* occurred abundantly in the southern as well as northern Sargasso Sea (Wiebe, 1987; Endo and Wiebe, unpublished data). Therefore, *E. brevis* may have a stronger affinity for warmer waters than *E. hemigibba* and thus took longer to increase in number at the center of cold-core rings.

In the northern Sargasso Sea, dominant species change seasonally: *E. brevis*, *E. hemigibba*, *E. tenera*, *S. carinatum*, and *T. gregaria* dominate the euphausiid population in spring; *E. brevis*, *E. hemigibba*, *S. affine*, *S. carinatum*, and *S. elongatum* dominate in summer and autumn; and *E. americana*, *E. krohni* and *T. gregaria* dominate in winter (Endo and Wiebe, unpublished data). Warm-water *Stylocheiron* species *S. affine* and *S. elongatum* became abundant only in the oldest rings investigated in this study (Figs. 3 and 4), probably because their vertical distribution is deeper. *S. affine*, a non-migrator

(Brinton *et al.*, 1999) was distributed at 100-300 m depth both day and night, and *S. elongatum* was distributed at 200-400 m at night and 200-600 m during the day in the northern Sargasso Sea (Endo and Wiebe, unpublished data). Among wide-ranging warm-water species, *E. tenera* and *S. carinatum* became abundant in rings several months old (Fig. 3).

Two cold-water species, *E. krohni* and *N. megalops*, were exceptionally abundant in two tows made at the center of Bob at 5 months. Comparing the biological characteristics of *N. megalops* collected in ring Bob at 1 and 5 months, Wiebe and Flierl (1983) noticed that considerable numbers of females had eggs when first collected and much smaller body length when next collected. The spawning seasons of these species are reported to be spring to summer (Mauchline 1980) and match the first sampling period of ring Bob. Therefore, both of these species may have reproduced in ring Bob. *E. krohni* became quite rare after 7 months, but *N. megalops* maintained a relatively high abundance even in rings of 9 months or older (Fig. 5). It is also noted that *Thysanopoda acutifrons* increased in numbers when rings sampled were 5-7 months old and then decreased afterward. This species resided deeper than 300 m both day and night in CCRs and in the Slope Water. Thus, the physical/biological change in the surface layer may not have negatively affected this species, at least for the first several months. That may also be the case with *Thysanoessa longicaudata*, which showed a similar vertical distribution.

Of the two dominant cold-water species, *N. megalops* survived longer in CCRs than *E. krohni*, although the latter species appeared faster in WCR 82B than the former species (Endo and Wiebe, 2005). The difference may result partly from ability to change vertical distribution to seek suitable temperature and partly from trophic level.

*E. krohni*, a herbivore, which did not change its depth distribution very much, may have suffered from both higher temperatures and unfavorable food conditions (low abundance and smaller size of phytoplankton). On the other hand, *N. megalops*, an omnivore–carnivore, was able to avoid unfavorable temperatures by descending without suffering as much from unfavorable food conditions. Wiebe and Boyd (1978) showed that the vertical distribution of *N. megalops* in the core of ring D at 6 months of age was similar to that of the Slope Water but that it deepened significantly with the major portion of the population occurring below 300 m at 9 months. They also found that both in the Slope Water and in the ring, 50% or more of the population was found in a restricted temperature regime centered at  $\sim 10^{\circ}\text{C}$ . In the present study, the main population in the oldest ring also was centered at  $\sim 10^{\circ}\text{C}$ . In contrast, *E. krohni* stayed in the upper 200 m at night regardless of ring age (Fig. 13) and, therefore, experienced a temperature increase of  $\sim 12^{\circ}\text{C}$ , which may have contributed to its demise.

In this analysis, information on the species vertical distribution in the northwestern North Atlantic was indispensable for better understanding why some cold-water species persist longer in CCRs than others and why some warm-water species are able to invade CCRs faster than others.

#### Euphausiid community changes

CCRs held as many or more euphausiid species than in the northern Sargasso Sea when several months old, but the numbers were dominated by only a small number of species such as *N. megalops*, *T. parva*, and *E. brevis*, which did not lead to an increase in evenness (Fig. 6). Therefore, CCR populations can be characterized by high species number, but medium evenness. CCR populations thus represent a state that changes

from the less diverse Slope Water population to the more diverse northern Sargasso Sea population, but even in CCRs as old as 9 to 12 months, only a limited number of species were dominant.

The total abundance of euphausiids were not determined by cold-water and warm-water species alone, especially in rings 6 months or older (Fig. 8). *T. gregaria*, a transition species, was abundant in the ring 6 months old, and *E. tenera* and *S. carinatum* were abundant in rings 7 months old. These latter two species are wide-ranging warm-water species that sometimes become abundant in the Slope Water (Endo and Wiebe, unpublished data), and seem to have less difficulty entering into CCRs of this age than warm-water species. *T. parva* did not occur in the ring one month old, but began to appear in a ring 5 months old.

The percentage of cold-water species decreased by 5% per month as rings aged, and the regression line predicted a zero percentage at 15 months (Fig. 9). This is supported by the fact that no *N. megalops* were sampled in a 17 month old ring (Wiebe and Boyd, 1978), although it is based on the single night sample. Endo and Wiebe (2005) reported that the monthly percentage decrease in abundance of warm-water species in WCR 82B was 31%, about 6-fold faster than the percentage decrease in cold-water species in CCRs after several months. They pointed two major causes for this: first, the temperature decrease caused by convective mixing and cooling in late winter/early spring in 82B and second, the proliferation of the transition species *Thysanoessa gregaria*.

In rings older than 9 months euphausiids showed two peaks in their vertical distribution (Fig. 12): a shallow peak, consisting of warm-water species (mainly *E. brevis*) that varied from about 400 m in the daytime to less than 100 m at night and a

deeper peak at or below 800 m, consisting of a cold-water species *N. megalops* and *T. parva*. In those old rings, *N. megalops* occurred deeper than in their home range, the Slope Water, by 300 to 400 m. *E. krohni* also occurred deeper than in the Slope Water by at least 100 m during the day. On the other hand, a dominant warm-water species, *E. brevis*, occurred in shallower depths in old rings compared to the northern Sargasso Sea. Thus, there is a peak of euphausiids that is shallower than in the surrounding northern Sargasso Sea and another deep peak that is rare in these waters. These may have significant consequence for predators and prey of euphausiids in the northern Sargasso Sea.

The mean lifetime of CCRs is 1 to 1.5 years (The Ring Group, 1981). It is probable that cold-water species die out at the end of a CCRs' life span. However, it would not be the case if cold water is re-supplied through a ring-Gulf Stream interaction. Most CCRs ultimately coalesce with the Gulf Stream (The Ring Group, 1981). When a relatively intense CCR becomes attached to and merges completely with the Gulf Stream, water from the ring center may be transported back into the Slope Water if the CCR is north and east of Cape Hatteras. Surviving populations of cold-water species *N. megalops* may be reunited with their home-range counterparts. When a relatively weak ring becomes attached to the Gulf Stream, it is advected downstream (The Ring Group, 1981). In this case, the ring core may not rejoin the Slope Water, and therefore, cold-water euphausiids in it may ultimately die out. However, it is still possible that cold-water species are transported back to the Slope Water upstream of Gulf-Stream meander crest (trailing flank) as shown for copepods by Ashjian (1993).

CCR populations can be similar to Slope Water populations even when 5 months old, probably by the production of offspring. On the other hand, after 9-12 months,

CCR populations can be distinct from Slope Water populations and be like northern Sargasso Sea populations that are richer in cold-water species than the typical northern Sargasso Sea populations. Therefore, CCR populations can never be like the typical northern Sargasso Sea populations in their life span, forming a mosaic pattern of zooplankton distribution in the northwest North Atlantic Ocean.

The most probable scenario of global warming is the surface warming and increased vertical stratification (Boyd and Doney, 2003), which is similar to the evolution of CCRs shown in the present study. Similar species succession and vertical fractionation of euphausiids would likely occur in the Slope Water during the process of global warming.

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**Figure caption**

Fig.1. Vertical profiles of temperature at the center of cold-core rings of various ages (months): Bob at 1 and 5 months old, Al at 2.5 months old, D at 6 and 9 months old, Franklin at 7 months old, and Emerson at 12 months old. Two or more profiles are shown for each ring depending on the number of observations made at the ring center.

Fig. 2. Relationship between ring age (months) and the mean temperature in the upper 700 m ( $^{\circ}\text{C}$ ) and depth of  $15^{\circ}\text{C}$  isotherm (m). The regressions were based on data points shown by circles (ring Bob at 1 and 5 months; ring D at 6 and 9 months) for reasons given in the text. Note the \* are for ring Al at 2.5 months; ring Franklin at 7 months; and ring Emerson at 12 months.

Fig. 3. Abundance of each euphausiid species in cold-core rings of 1 (a), 5 (b), 6 (c), 7 (d), 9 (e) and 12 (e) months old. Mean  $\pm 1$  SD are shown. Species were grouped according to their distributional types beginning from cold-water (filled squares), transition (filled triangles), wide-ranging warm-water (open circles), warm-water (filled circles), cosmopolitan (open diamonds), and *Thysanoessa parva* (filled inverted triangles). For species codes see Table 1.

Fig. 4. Abundance of warm-water species versus the age of cold-core rings. Those species whose nighttime depth is shallower than 100 m are shown in the upper panel and those whose distributional depth is deeper than 100 m at night are shown in the lower panel. Mean  $\pm 1$  SD are shown.

Fig. 5. Abundance of cold-water species versus the age of cold-core rings. Mean  $\pm 1$  SD are shown.

Fig. 6. Number of species that occurred and Pielou's J' in cold-core rings of various ages (a); seasonal change in these values in the Slope Water (b); and in the northern Sargasso Sea (c). Mean  $\pm 1$  SD are shown.

Fig. 7. Change in abundance of total euphausiids (a), cold-water species (b), warm-water species (c), wide-ranging warm-water species (d), transition species, *Thysanoessa gregaria* (e), and *Thysanoessa parva* (f) with ring age. Mean  $\pm 1$  SD are shown.

Fig. 8. Change in percentage of cold-water species, warm-water species, wide-ranging warm-water species, transition species (*Thysanoessa gregaria*), and *Thysanoessa parva* to the total euphausiid population with ring age. The calculation was based on individual number per m<sup>2</sup>.

Fig. 9. Relationship between the percentage of cold-water species (left) and warm-water species (right) and ring age. Regressions for warm-water species were taken for 1-6 months and for 6-12 months separately.

Fig. 10. Results of nonmetric MDS based on euphausiid species composition in 139 tows made in northwestern North Atlantic (a). Scores at the center of cold-core rings are selected and plotted with ring ages (months) on the same x-y coordinates (b). Note

that 2.5-month old ring and two tows in 5-month old ring (rightmost two) are exceptional.. SW: Slope Water, WCR: warm-core ring, NSS: northern Sargasso Sea, CCR: cold-core ring, SSS: southern Sargasso Sea, GS: Gulf Stream, MEA: meander.

Fig. 11. Abundance of cold-water (left) and warm-water (right) species plotted on the coordinates of nonmetric MDS.

Fig. 12. Vertical distribution of total euphausiid species (a), cold-water species (b), and warm-water species (c) during the day and at night at the center of cold-core rings of various ages (months). A typical tow each for the daytime and nighttime for each age of CCR is shown. The deepest depth layer sampled at the center of 6-months old was 600-700 m during the day and 700-800 m at night, and that of 9-month old ring was 700-800 m both day and night. Arrow heads show the weighted mean depth.

Fig. 13. Vertical distribution of *Euphausia krohni* (a), *Nematoscelis megalops* (b), *E. brevis* (c), and *Stylocheiron carinatum* (d) during the day and at night at the center of cold-core rings of various ages (months). Typical tow each for the daytime and nighttime for each age of CCR is shown. The deepest layer sampled at the center of 6-months old was 600-700 m during the day and 700-800 m at night, and that of 9-month old ring was 700-800 m both day and night. Arrow heads show the weighted mean depth.