

Euphausiid Invasion/Dispersal in Gulf Stream Cold-core Rings

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Abstract

Invasion/dispersal patterns in the distribution and abundance of euphausiid species in four 2-8-month-old cold-core rings from the Gulf Stream suggest that several different physical exchange mechanisms are operating. The most important of these appear to be horizontal mixing in the mixed layer and exchange due to movement into or out of the trapped region at depth. A zone of minimum exchange is evident between 150 and 400 m. Changes in vertical distribution and abundance of warm-water species invading the ring environs suggest that only a few species, such as *Stylocheiron carinatum*, are able to penetrate and take advantage of the changing ring conditions in young- to middle-aged rings (2-8 months). Other near-surface warm-water species penetrate at slower rates regardless of whether they are vertical migrators (*Euphausia brevis*, *E. hemigibba*, *E. tenera*, *Thysanopoda aequalis*) or non-migrators (*S. suhmii*, *S. abbreviatum*). Deeper-living species such as *S. affine*, *S. elongatum*, *Nematoscelis microps*, and *N. tenella*, show minimal penetration of core waters in these four rings. Cold-water species expatriated in cold-core rings also show a varied response to ring decay, with some species disappearing rapidly—3-4 months (*Thysanopoda longicaudata*)—and others persisting for substantial periods—0.5-1 year (*N. megalops*, *E. krohnii*). Distribution of the latter two species indicates dispersal out beyond the ring core at the surface in the case of *E. krohnii* and at depths of 400-1000 m in the case of *N. megalops*.

Introduction

Cold-core rings spawned by the Gulf Stream through the meandering process described by Fuglister (1972), Parker (1971) and Lai and Richardson (1977) are mesoscale physical features (150-300 km in diameter and 1000-4000 m in vertical extent) that exist as hydrographically distinguishable entities for months to years. They have, for a significant portion of their existence, a biomass structure and species composition distinctly different from the adjacent Sargasso Sea waters (Jahn 1976; Wiebe 1976; Wiebe *et al.* 1976a; Ortner 1977; Ortner *et al.* 1978; Wiebe and Boyd 1978). By virtue of the distribution of rings, there is in the North-western Atlantic Ocean, a mosaic pattern of expatriated communities interspersed throughout home-range communities. This pattern is continuously changing because of the horizontal movement of rings and because of hydrographic changes resulting from air-sea interactions and physical exchange processes with adjacent waters, which foster change in ring biotic structure towards that of the surrounding Sargasso Sea.

Although some details of change in species abundance through time in rings have been reported (Wiebe *et al.* 1976a; Ortner *et al.* 1979; the Ring Group 1981), the patterns of invasion of warm-water species into cold-core rings and the dispersal of cold-water species out into the Sargasso Sea in relation to the hydrographic changes taking place in rings have not been described in detail except for the euphausiid *Nematoscelis megalops* (Boyd *et al.* 1978; Wiebe and Boyd 1978). In this paper, the cold-core ring distributions of

euphausiids typically found in the Slope Water, the Sargasso Sea, and cold-core rings are examined, and various processes by which invasion and dispersal may take place, especially within the upper 300 m, are described.

Methods

During 1976–1977, four cruises were made to Gulf Stream cold-core rings to study changes in their physics, chemistry and biology through time (the Ring Group 1981). Three rings, Al, Bob and Franklin, were sampled for zooplankton extensively, ring Bob on two different cruises. Details of the cruises and the net tows are summarized in Table 1. Bob was observed 2 months (time 1) and 6 months (time 2) after its formation.

Zooplankton were collected by a nine-net MOCNESS (multiple opening/closing net and environmental sensing system), described by Wiebe *et al.* (1976b). The nets were constructed of 335- μ m Nitex nylon gauze and when towed at a 45° angle, had a mouth area of 1 m². The standard oblique tow was to 1000 m with the first net open from the surface to the maximum depth of tow and the remaining eight nets opened and closed sequentially so as to sample 150-m intervals from 1000 to 400 m and 100-m intervals from 400 m to the surface. Occasionally, this sampling procedure was altered to permit the bracketing of sharp hydrographic features. Volumes of water typically filtered by each net ranged from 400 to 1000 m³.

The electronics package used to control the nets from the ship was a modified Neil Brown CTD system (Wiebe *et al.* 1976b). In addition to conductivity, temperature, and depth, we recorded flow past the nets with a reed-switch equipped TS flowmeter, angle of the net frame from the vertical, and movement of a net bar once released by means of a net response mechanism located halfway down the net-bar guides. A shipboard computer (HP 2100) was used to calculate salinity, speed of the net through the water, and volume of water filtered by the net during the tow.

At the end of a tow, the nets were washed down and the catch preserved in a 10% (v/v) buffered formalin solution. Except when very high numbers of euphausiids were present, all adult and juvenile individuals were sorted from the samples and identified to species. In cases where subsampling had to be done, aliquots between $\frac{1}{2}$ and $\frac{3}{4}$ were used. In all, 46 tows and 367 samples were analysed. In this paper, we present data on the 15 species of euphausiids that occurred most frequently and in greatest abundance in our samples.

On each cruise, tows were made at various distances and compass bearings from the centre of the ring. The long time required for sampling makes it impossible to collect a true cross-section, given the speed of ring rotation and its variation with depth and radius. We have chosen to present all data as functions of depth and radius from the estimated centre location at the time of the station. Centre locations were derived from satellite-tracked drogue paths (Richardson 1980) and from horizontal temperature maps (Olson 1980). There were times when the rapid motion of the ring and the speed at which changes occurred due to interaction with the Gulf Stream made even this procedure somewhat unsatisfactory. We have assumed (and the smoothness of the data seems to bear this out) that the rapid rotation of the ring mixes any azimuthal gradients fairly rapidly so that properties were relatively homogeneous around the ring on a given radius. For species that show strong diel vertical migration, we have treated the day and night data in the sections differently: night data are contoured, and day data are given as the range (vertical bar) with an arrow indicating the centre of the distribution.

Results

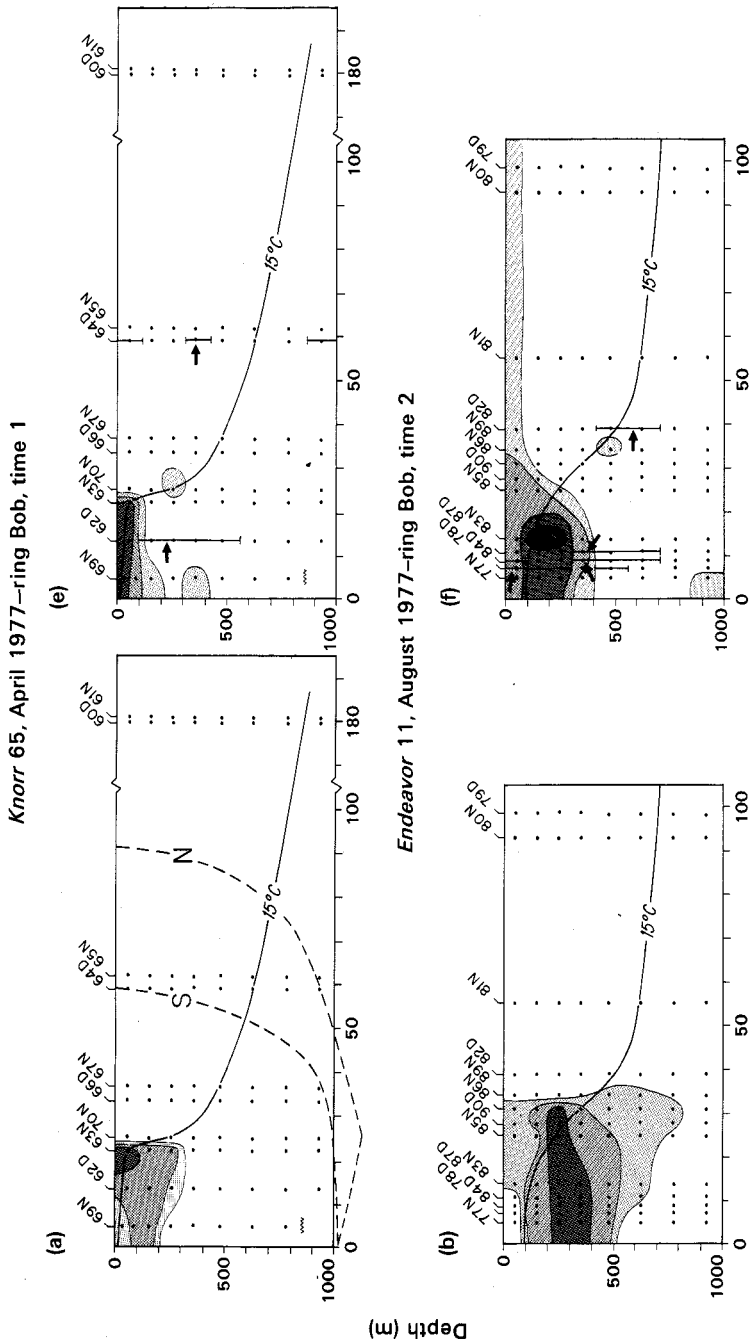
Ring Bob, Age 2 Months (Knorr 65)

The patterns of distribution of euphausiids within the ring area are strongly dependent upon the age of the ring, the affinity of a species for a particular hydrographic regime, the vertical distribution of the species, and the particular composition of the Slope Water population at the time of ring formation. This latter point is especially important, both because the evolution of the species composition within the ring in terms of absolute abundance is strongly dependent on the starting composition and because absolute abundances vary strongly with the seasonal cycles, which may be proceeding differently within or outside the ring (Wiebe 1976; Wiebe *et al.* 1976a; Ortnier *et al.* 1978; Wiebe and Boyd 1978; Ortnier *et al.* 1979). As a result of these factors, we have chosen to discuss the

Table 1. Data collected by multiple opening/closing net and environmental sensing system (MOCNESS) tow, used to prepare ring section plots of abundance versus depth

MOCNESS tow No.	Date	Local time (h)	Lat. (°N.)	Long. (°W.)	Depth of 15°C (m)	Comments
Cruise Knorr 62						
Moc-1-45	4.xii.76	2327	36 10.0	65 30.0	289	Ring Al centre
Moc-1-47	5.xii.76	1445	36 10.4	65 28.4	275	Ring Al centre
Moc-1-48	6.xii.76	2111	36 00.5	65 47.4	350	Ring Al fringe
Moc-1-50	7.xii.76	1431	35 55.8	67 03.3	675	Sargasso Sea
Moc-1-51	7.xii.76	2245	35 55.4	67 05.1	680	Sargasso Sea
Moc-1-52	10.xii.76	2041	36 18.3	65 16.9	315	Ring Al fringe
Moc-1-53	14.xii.76	2132	37 14.8	63 17.6	620	Sargasso Sea
Moc-1-54	15.xii.76	1516	37 15.0	63 22.7	630	Sargasso Sea
Moc-1-55	16.xii.76	1928	36 50.9	65 45.0	420	Ring Al fringe
Moc-1-56	16.xii.76	2310	36 50.0	65 44.8	370	Ring Al fringe
Cruise Knorr 65						
Moc-1-60	13.iv.77	1128	34 18.2	71 23.0	862	Sargasso Sea
Moc-1-61	13.iv.77	2142	34 19.2	71 21.1	850	Sargasso Sea
Moc-1-62	17.iv.77	1109	36 43.2	69 30.1	35	Ring Bob centre
Moc-1-63	18.iv.77	0209	36 49.0	69 33.0	28	Ring Bob centre
Moc-1-64	18.iv.77	1405	36 34.6	70 21.9	645	Sargasso Sea, edge of Gulf Stream
Moc-1-65	18.iv.77	2000	36 33.7	70 21.3	625	Sargasso Sea, edge of Gulf Stream
Moc-1-66	19.iv.77	1316	36 40.5	69 40.5	440	Ring Bob fringe
Moc-1-67	19.iv.77	2019	36 40.0	69 46.1	520	Ring Bob fringe
Moc-1-69	21.iv.77	2018	36 45.2	68 33.7	17	Ring Bob centre
Moc-1-70	22.iv.77	2243	36 32.2	68 00.0	269	Ring Bob fringe
Cruise Endeavor 11						
Moc-1-77	31.vii.77	2358	34 30.5	71 34.2	108	Ring Bob centre
Moc-1-78	1.viii.77	1810	34 25.8	71 29.6	130	Ring Bob centre
Moc-1-79	2.viii.77	1138	33 38.0	73 13.0	710	Sargasso Sea
Moc-1-80	3.viii.77	0102	33 40.0	73 09.0	695	Sargasso Sea
Moc-1-81	5.viii.77	2140	34 30.0	70 37.0	620	Sargasso Sea
Moc-1-82	6.viii.77	1017	34 29.0	70 58.0	535	Sargasso Sea
Moc-1-83	6.viii.77	2158	34 27.0	71 41.0	105	Ring Bob centre
Moc-1-84	7.viii.77	0908	34 29.7	71 50.0	105	Ring Bob centre
Moc-1-85	7.viii.77	2213	34 53.6	71 54.8	247	Ring Bob fringe
Moc-1-86	8.viii.77	0249	35 00.0	71 54.0	360	Ring Bob fringe
Moc-1-87	9.viii.77	0934	34 55.5	71 55.0	127	Ring Bob centre
Moc-1-89	13.viii.77	0044	34 33.0	71 42.0	430	Ring Bob fringe
Moc-1-90	14.viii.77	0923	34 44.8	71 59.0	307	Ring Bob fringe
Cruise Knorr 71						
Moc-1-100	30.x.77	2112	35 35.9	67 17.1	710	Sargasso Sea
Moc-1-101	31.x.77	1511	36 12.0	37 26.4	705	Sargasso Sea
Moc-1-102	3.xi.77	0838	36 40.1	65 52.1	180	Ring Franklin centre
Moc-1-103	3.xi.77	2348	36 40.0	65 53.5	175	Ring Franklin centre
Moc-1-104	4.xi.77	1750	36 42.9	64 35.5	700	Sargasso Sea
Moc-1-105	5.xi.77	1019	36 42.5	65 10.2	570	Ring Franklin fringe
Moc-1-107	5.xi.77	1905	36 41.7	65 20.0	425	Ring Franklin fringe
Moc-1-108	6.xi.77	0234	36 38.3	65 08.8	550	Ring Franklin fringe
Moc-1-109	6.xi.77	0910	36 44.1	66 00.0	152	Ring Franklin centre
Moc-1-110	6.xi.77	1957	36 49.8	65 57.8	171	Ring Franklin centre
Moc-1-111	10.xi.77	0147	36 57.5	66 18.5	198	Ring Franklin fringe
Moc-1-113	12.xi.77	2335	37 00.5	65 56.0	240	Ring Franklin fringe
Moc-1-114	13.xi.77	0309	37 01.4	65 52.1	277	Ring Franklin fringe

Fig. 1 *Nematoscelis megalops* *Euphausia krohnii*



Knorr 71, October–November 1977—ring Franklin

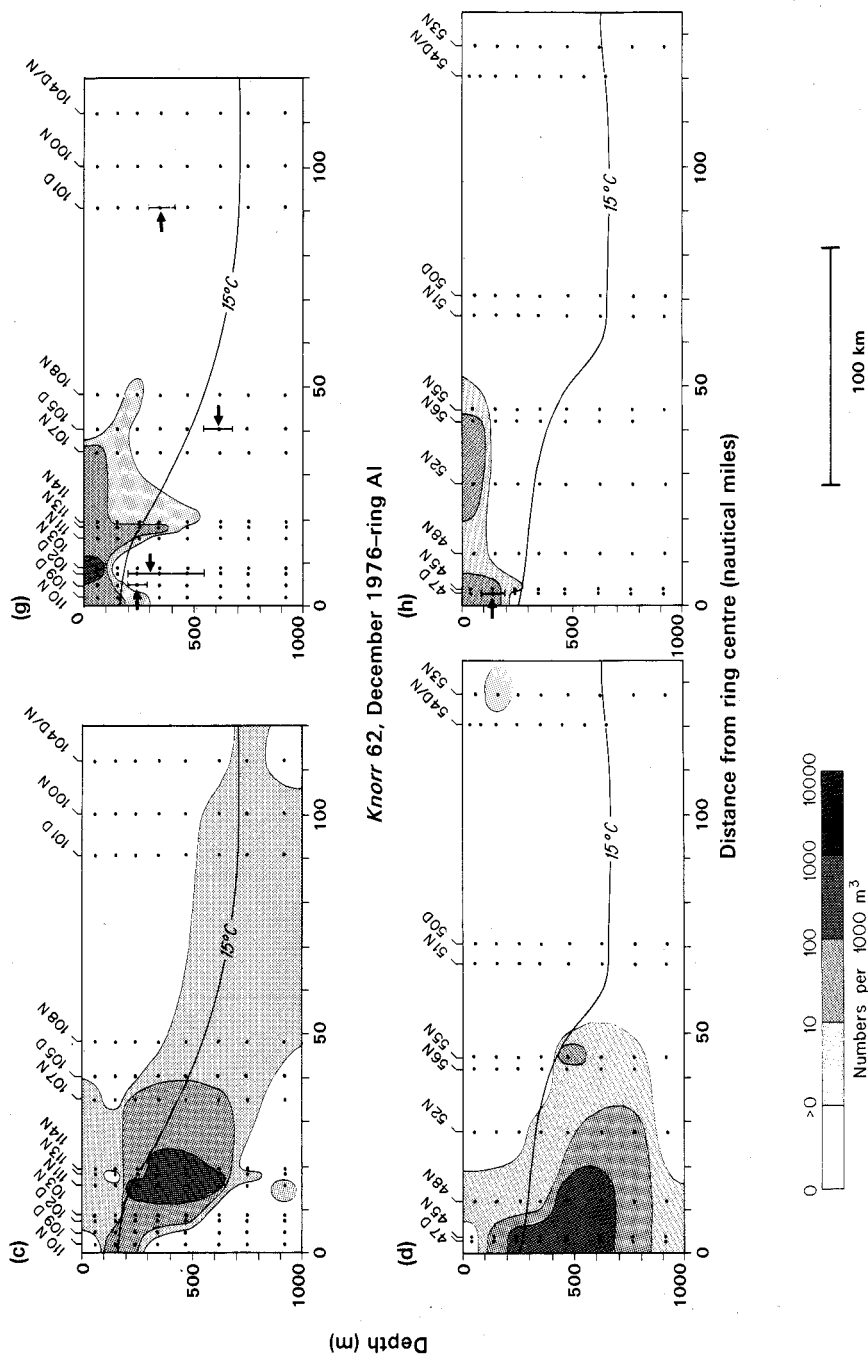
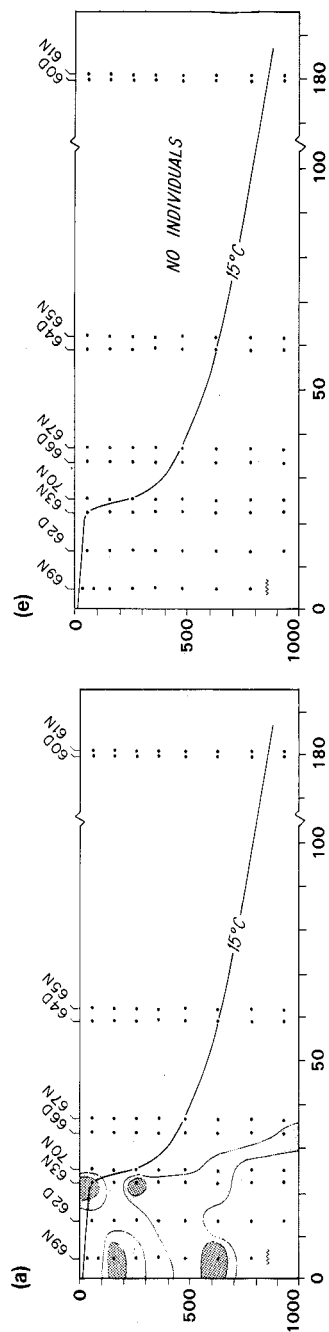


Fig. 1. Vertical sections of abundance of the Slope Water species *Nematoscelis megalops* and *Euphausia krohnii* in the cold-core ring/Sargasso Sea. Four cruises are illustrated for each species, two to ring Bob, Knorr 65 and Endeavor 11, one to ring Franklin, Knorr 71, and one to ring AI, Knorr 62. The solid line is the depth of the 15°C isotherm. For species that show strong diel vertical migration, night data are contoured and day data are given as the range (vertical bar) with an arrow indicating the centre of the distribution. The number/letter combinations along the top of each section are the MOCNESS tow numbers (D, day tow; N, night tow). The dashed lines in the top left section (N. megalops, Knorr 65) are the approximate north (N) and south (S) positions of the trapped region of a ring moving westward at 5 cm s⁻¹.

Fig. 2

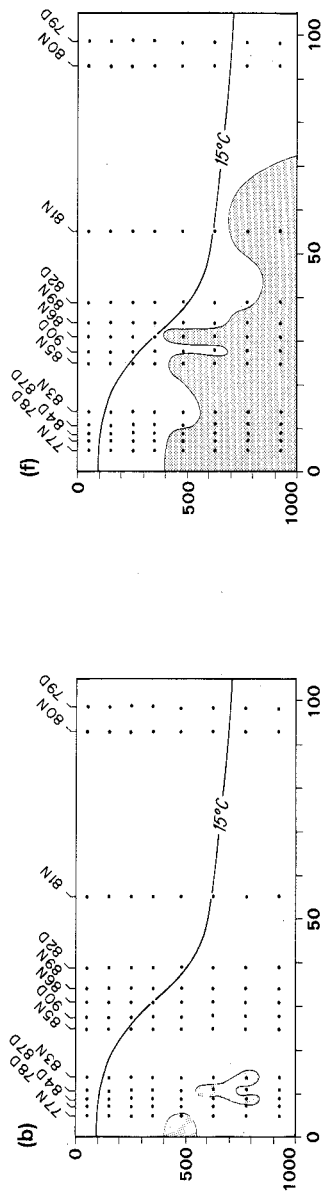
*Thysanoessa longicauda**Thysanoessa parva*

Knorr 65, April 1977—ring Bob, time 1



Depth (m)

Endeavor 11, August 1977—ring Bob, time 2



Depth (m)

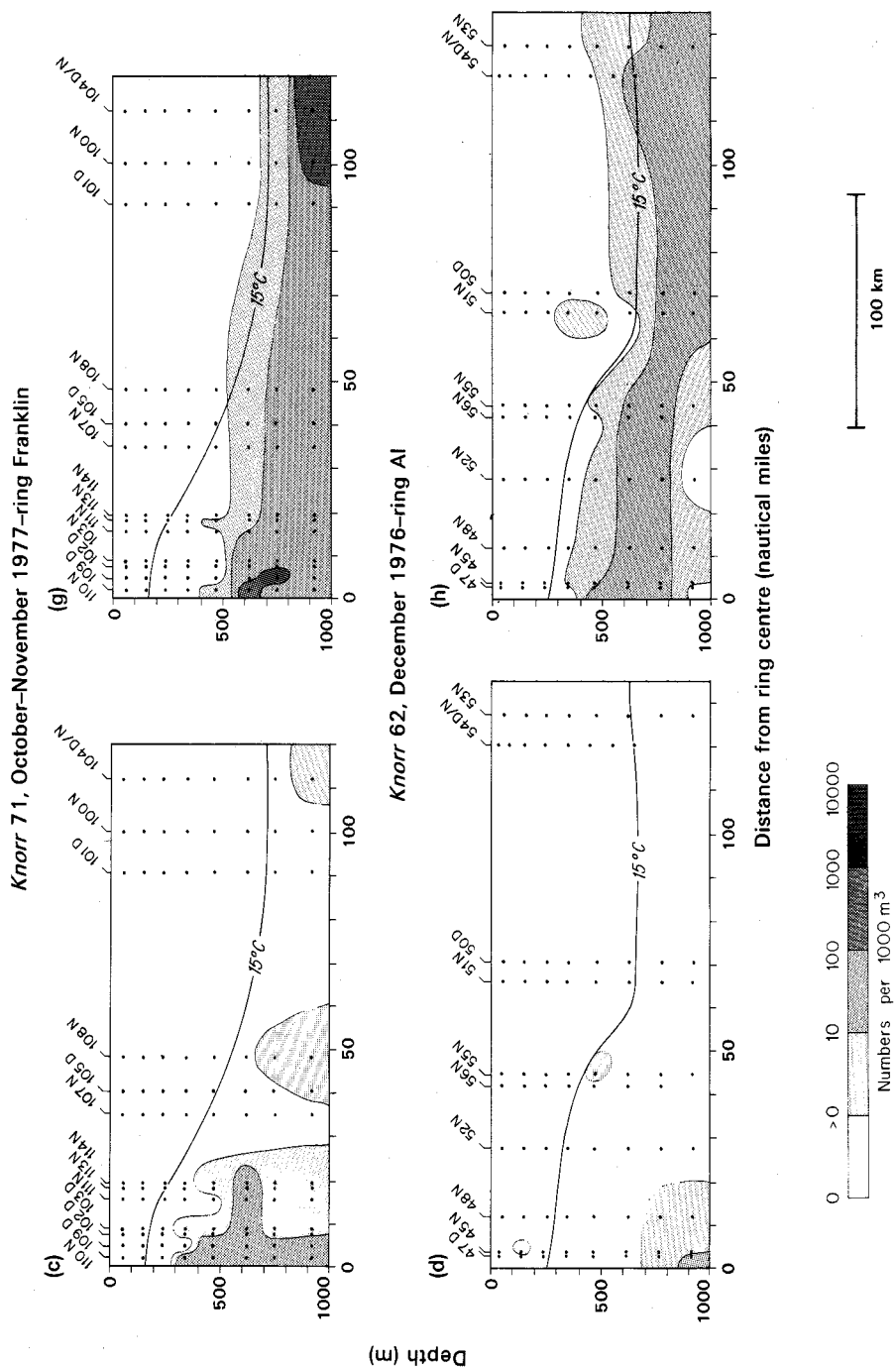


Fig. 2. Same as Fig. 1, but for the Slope Water species *Thysanoessa longicaudata* and the bathypelagic species *Thysanoessa parva*.

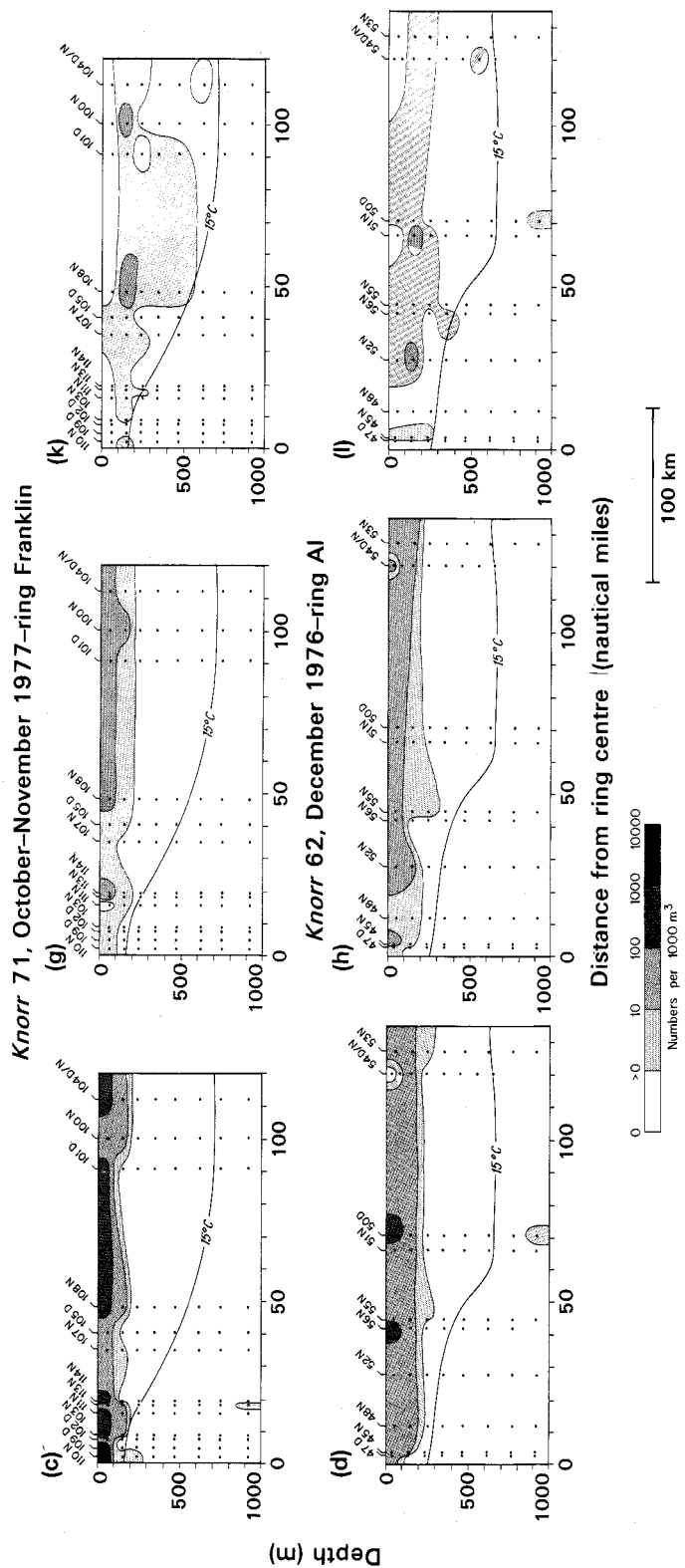
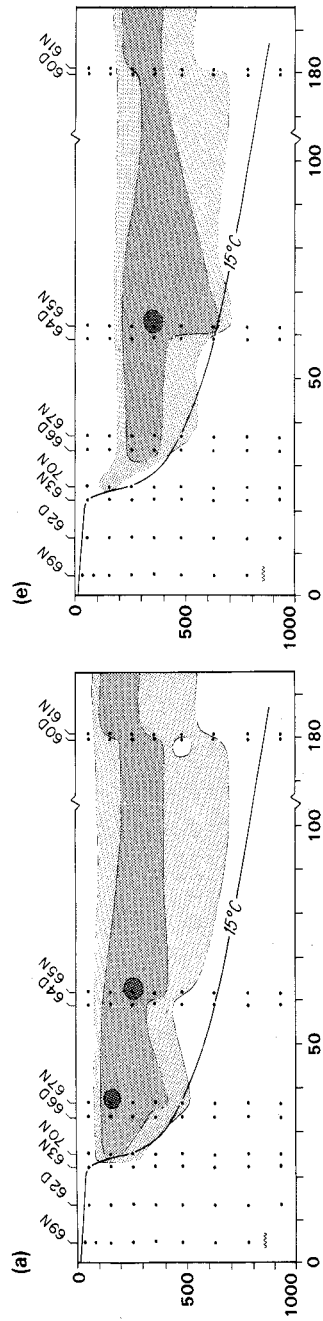


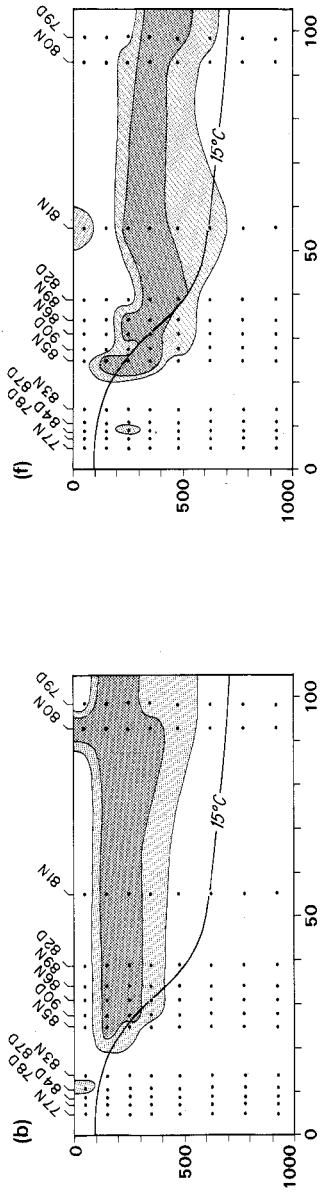
Fig. 3. Same as Fig. 1, but for the Sargasso Sea species *Stylocheiron carinatum*, *S. sulmii* and *S. abbreviatum*.

Stylocheiron elongatum

Knorr 65, April 1977—ring Bob, time 1

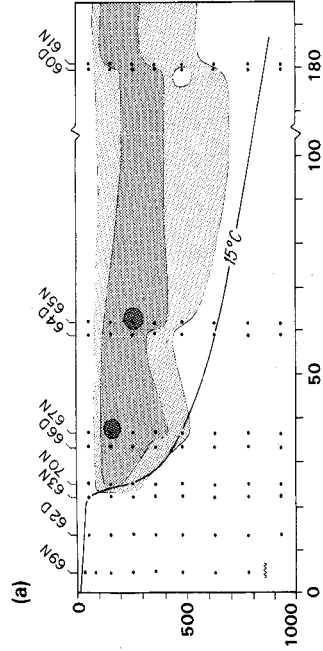


Endeavor 11, August 1977—ring Bob, time 2

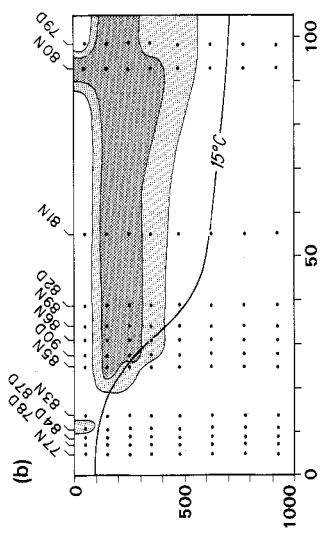


Stylocheiron affine

Knorr 65, April 1977—ring Bob, time 1



Endeavor 11, August 1977—ring Bob, time 2



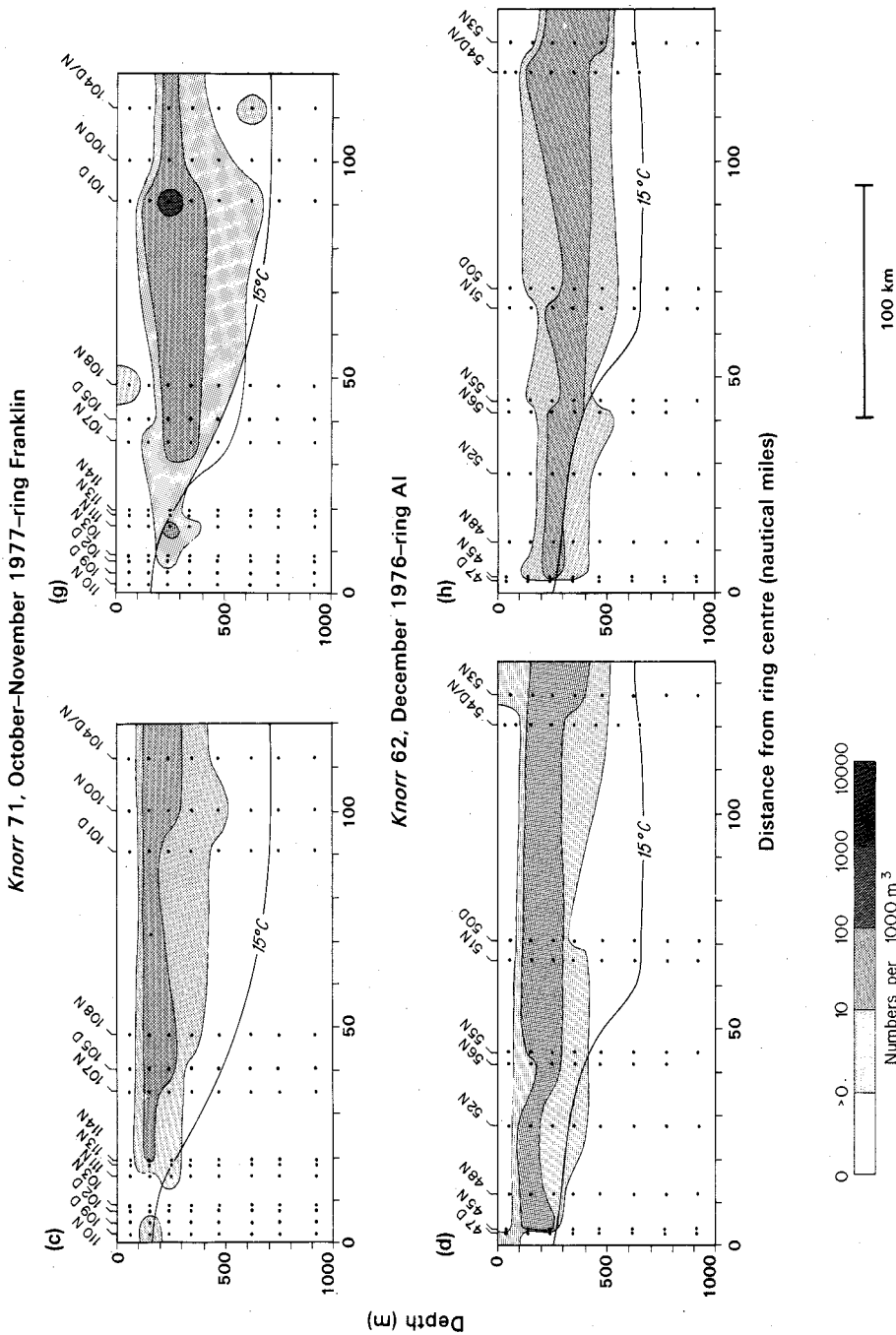


Fig. 4. Same as Fig. 1, but for the Sargasso Sea species *Stylocheiron affine* and *S. elongatum*.

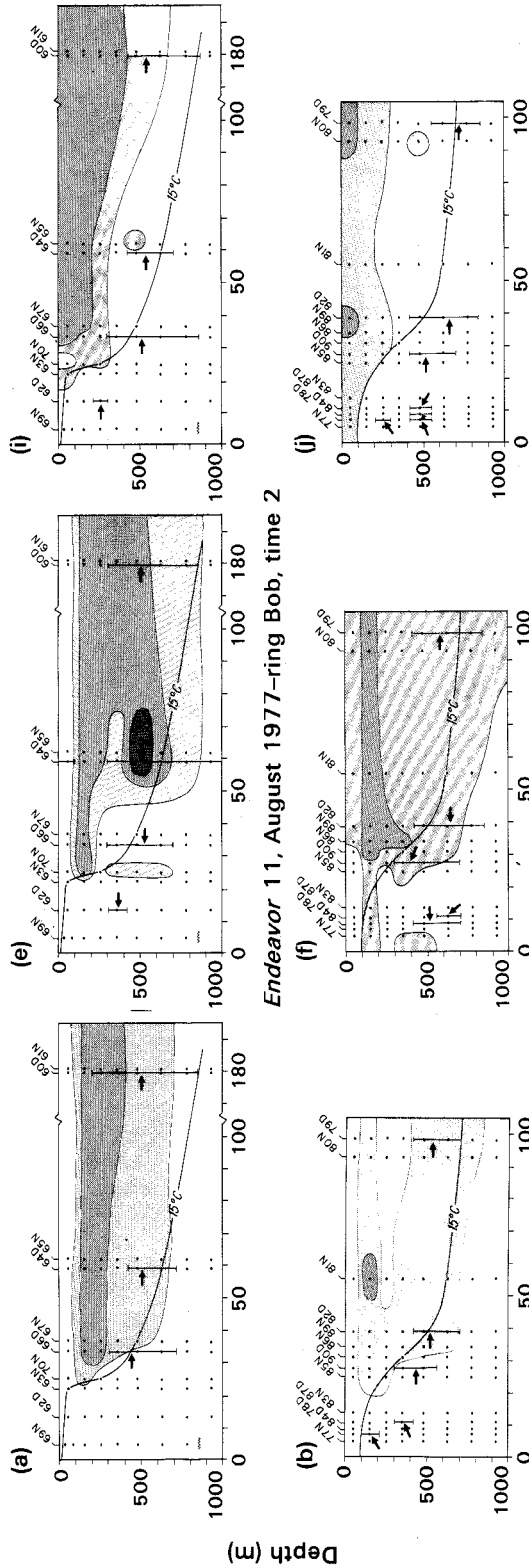
Thysanopoda aequalis

Nematoscelis microps

Nematoscelis tenella

Knorr 65, April 1977—ring Bob, time 1

Endeavor 11, August 1977—ring Bob, time 2



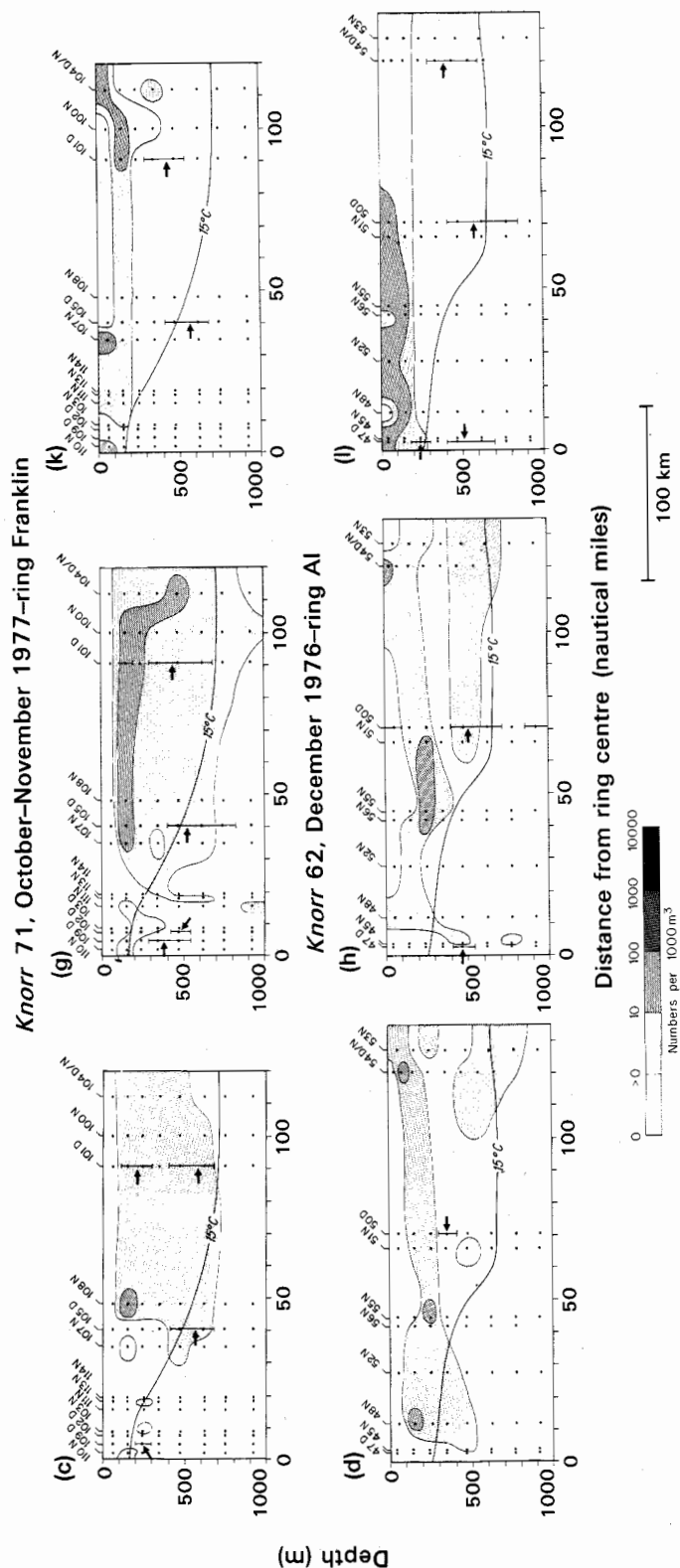


Fig. 5. Same as Fig. 1, but for the Sargasso Sea species *Nematocelis tenella*, *N. microps* and *Thysanopoda aequalis*.

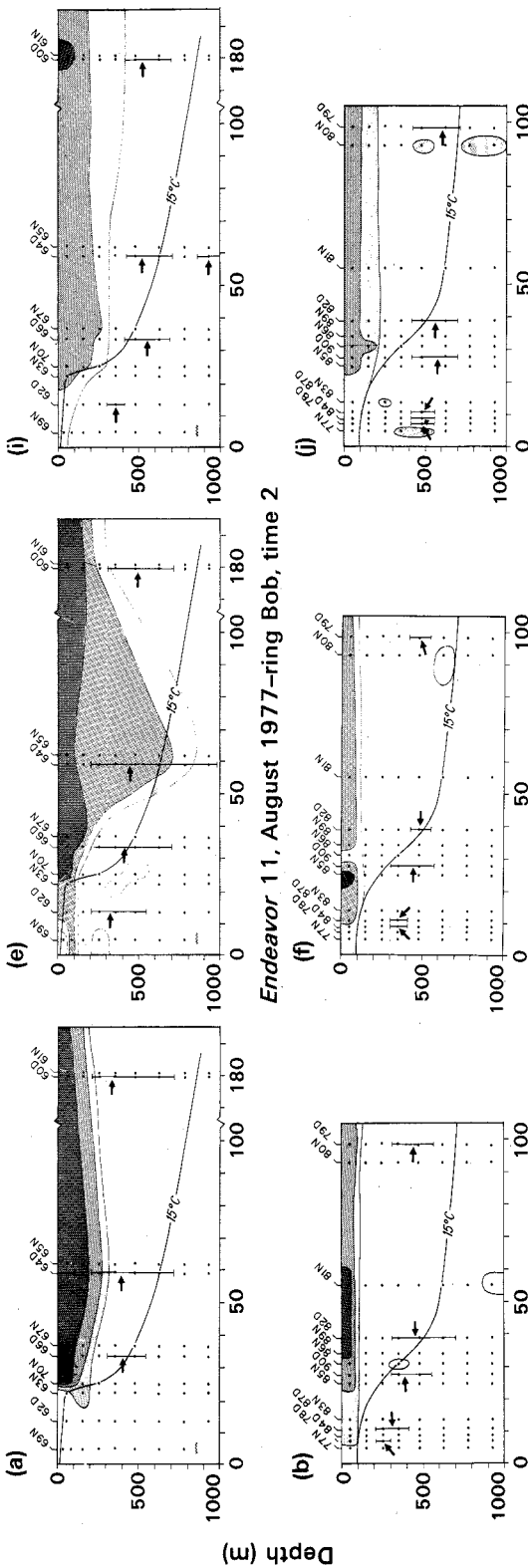
Euphausia hemigibba

Euphausia tenera

Knorr 65, April 1977—ring Bob, time 1

Endeavor 11, August 1977—ring Bob, time 2

Euphausia brevis



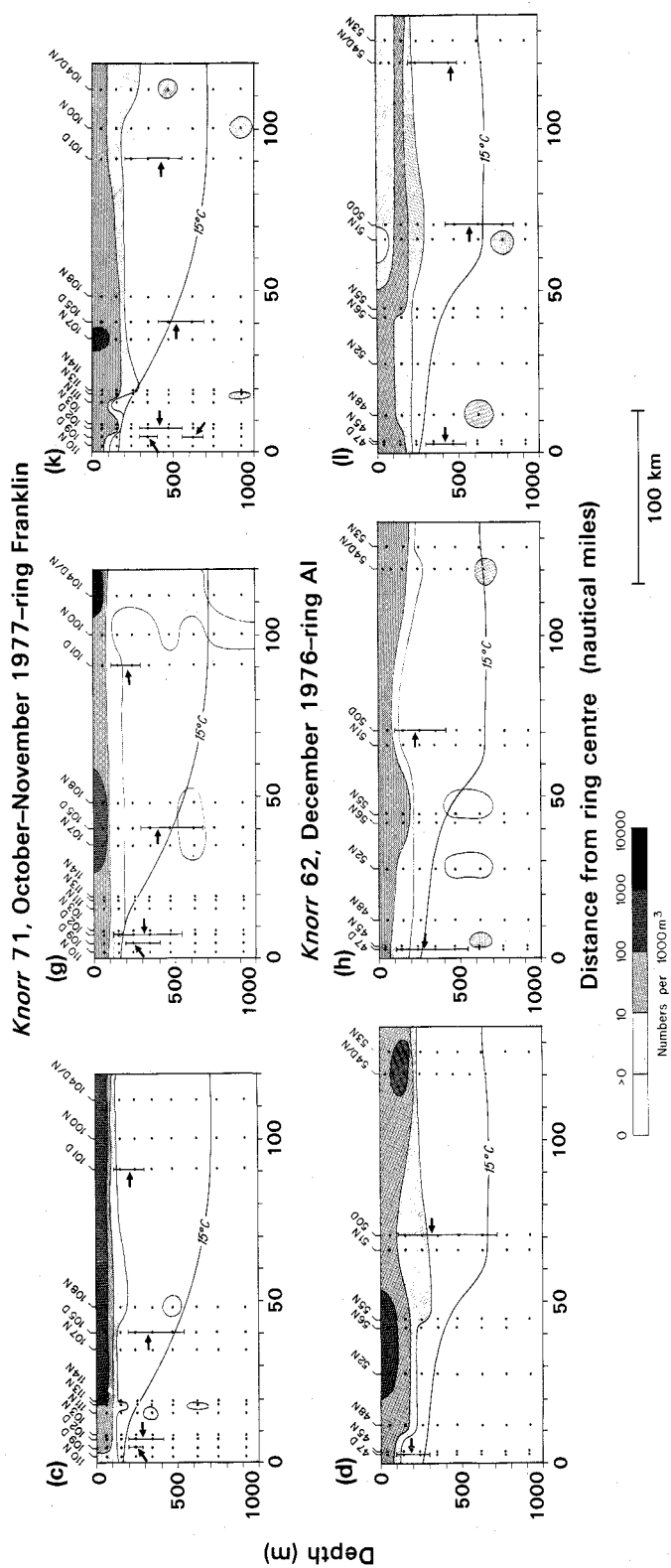


Fig. 6. Same as Fig. 1, but for the Sargasso Sea species *Euphausia brevis*, *E. tenera* and *E. hemigibba*.

patterns of abundance in cross-sections and to interpret changes in relative abundance from inside to outside as indicating invasion or dispersal processes rather than to attempt to describe abundances through time. We feel that our approach will be less biased by the fact that we have sampled different rings at somewhat different times.

In a young ring such as Bob at age 2 months (time 1), species endemic to the Slope Water (for example *Nematoscelis megalops*, *Euphausia krohnii* and *Thysanoessa longicaudata*) were mostly or wholly restricted to the ring centre (Figs 1 and 2); only a few individuals of *E. krohnii* were found 95 km from the ring centre in the outer portion of the Gulf Stream remnant encircling the ring core. Species in other taxonomic groups, such as the copepod *Pareuchaeta norvegica* and the pteropod *Limacina retroversa*, show very similar patterns (see the Ring Group 1981, fig. 6).

A number of the euphausiids that are found in the Sargasso Sea during all seasons show the opposite pattern. None of the species of the genus *Stylocheiron*, which exhibit little or no diel vertical migration in the area we sampled, were present in the centre of Bob except for a single individual of *S. suhmii* (Figs 3a, 3e, 3i and 4a, 4e). Similarly, of the two species of *Nematoscelis* with subtropical/tropical distributions that were abundant, only a few individuals of *N. microps* were found in the ring (Fig. 5e). Adults of these species occupy a broad vertical depth span and a portion of the population migrates dielily, but adults appeared only irregularly in the upper 100 m (Fig. 5).

Members of the genus *Euphausia*, a group that is characterized by strong diel vertical migration by most or all of the adult population, show different distributional patterns. In contrast to the *Stylocheiron* and *Nematoscelis* species, two of the three species of the genus *Euphausia* that were present in the Sargasso Sea in reasonably large numbers were also present in ring Bob in moderate numbers (Fig. 6). Individuals of *E. hemigibba* (Fig. 6i) and *E. tenera* (Fig. 6e) were caught on all of the tows in the ring centre in concentrations about a factor of 10 lower than in the waters of the adjacent Gulf Stream remnant and Sargasso Sea. The pteropod *Limacina inflata* as illustrated by the Ring Group (1981, fig. 6) showed a similar distribution pattern. Only *E. brevis* (Fig. 6a) was totally absent from the ring centre area.

Several other euphausiid species exhibit partial penetration of the ring core waters. *Thysanopoda aequalis* (Fig. 5i) was present in low numbers within the ring but not at the centremost station.

Thus, in this 2-month-old ring, all of the cold-water species that we have examined were basically restricted to the ring core waters of Slope Water origin, and warm-water species were either absent from this area or were present in relatively low numbers. Vertical migrators showed greater abundance in the ring than non-migrators.

Ring Bob, Age 6 Months (Endeavor 11)

We sampled ring Bob a second time when it was approximately 6 months old. Significant alterations in the distributional patterns had taken place for some species, but not others. Deeper-dwelling non-migrators showed essentially no penetration of the ring core waters; single individuals of *S. elongatum* (Fig. 4f) and *S. affine* (Fig. 4b) and only two individuals of the slightly shallower-dwelling *S. abbreviatum* (Fig. 3j) were collected in the ring. The surface forms *S. suhmii* (Fig. 3f) and *S. carinatum* (Fig. 3b) had differentially invaded the ring (compare with time 1: Figs 3a, 3e). Individuals of *S. suhmii* were present in the ring in low numbers except at the centremost station, whereas individuals of *S. carinatum* were distributed throughout the ring in numbers that exceeded by a factor of 10 those caught in the surrounding waters (Fig. 3b). *Limacina inflata* was the only other warm-water species counted thus far to show significantly higher abundance in ring Bob at time 2 than in the surrounding Sargasso Sea (the Ring Group 1981, fig. 6).

The Euphausia that were present throughout ring Bob at time 1 were still present, but their abundance levels had not changed significantly (Table 2). Similarly, *Thysanopoda aequalis* showed very little change in distribution or abundance from that observed at time 1 (Fig. 5j). *E. brevis* was found further towards the ring centre, but was absent from our tow at the innermost station (Fig. 6b).

Of the *Nematoscelis*, only *N. microps* had even limited success in invading the ring (Fig. 5f); single individuals of *N. tenella* were present in two of the three day tows, but absent from the two night tows (Fig. 5b).

The distributions of cold-water euphausiids showed divergent trends. Some individuals of *E. krohnii* appeared to have been dispersed out from the ring centre between times 1 (Fig. 1e) and 2 (Fig. 1f) and occurred in moderate numbers in ring Bob's Gulf Stream remnant. The population of *N. megalops* had increased dramatically as a result of successful reproduction of the population originally expatriated during ring formation (Figs 1a, 1b) (considerable numbers of females with eggs were observed in the ring at time 1, and the size distribution of the population was much smaller at time 2). However, no individuals were found beyond the ring's inner limits. In sharp contrast, the numbers of *Thysanoessa longicaudata* had drastically declined (Figs 2a, 2b), and at time 2 only a very reduced population was evident. The nearly complete disappearance of the pteropod *Limacina retroversa* paralleled the change in *T. longicaudata* (the Ring Group 1981).

Thus, even after a period of 6 months, there remained a substantial degree of segregation of warm- and cold-water populations. Most of the encroachment of warm-water species into the ring core and the dispersal of cold-water species out of the ring occurred for surface and near-surface forms.

Patterns in other Rings

The abundance sections of euphausiid species in the other two rings, Al and Franklin, complement patterns observed in ring Bob. Ring Franklin's time of formation is unknown, but, based on the depth of the 15°C isotherm in the ring centre, we estimate that it was 6–8 months old. The process of ring invasion had advanced beyond that observed on our second sampling of ring Bob, but it was still not complete. The distribution and abundance of the strong migrators *Euphausia hemigibba* (Fig. 6k) and *E. tenera* (Fig. 6g) were essentially the same in the ring core waters as in the adjacent Sargasso Sea, yet those for *E. brevis* (Fig. 6c) and *Thysanopoda aequalis* were not (Fig. 5k). Likewise, individuals of neither *Nematoscelis microps* (Fig. 5g) nor *N. tenella* (Fig. 5c) were as abundant in the ring as outside it. The surface forms of *Stylocheiron* (*S. carinatum* and *S. suhmii*) were well established in the ring (Figs 3c, 3g). In contrast, the deeper-living *S. abbreviatum* (Fig. 3k), *S. affine* (Fig. 4c), and *S. elongatum* (Fig. 4g) were restricted in their occurrence in this ring.

Species expatriated in Franklin were found beyond its boundaries. Individuals of *N. megalops* (Fig. 1c) and *Thysanoessa longicaudata* (Fig. 2c) were distributed 180 km or more away from the ring centre at depths below 500 m, and *E. krohnii* (Fig. 1g) was present in the Gulf Stream remnant and beyond at depths between 100 and 300 m. The fact that *T. longicaudata* was more abundant in ring Franklin at age 6–8 months than in Bob at 2 months is probably a reflection of the variability in population abundance in the Slope Water at the time of ring formation.

Distributions in ring Al are more complex as a result of its complicated history. Although we sampled this ring about 2 months after it was observed on satellite infrared photographs as a meander of the Gulf Stream, its physical and biological structure suggest that it is not a young ring. It may have been an older ring that coalesced with the Gulf Stream about the time the satellite photos were taken and then reformed, retaining much of its older structure. Clouds covered this region for much of this period, and an unambiguous series of photos is not available to resolve this question.

Table 2. Abundance of euphausiid species collected by each MOCNESS tow on each cruise

MOCNESS tow No.	Abundance (No. m ⁻² to 1000 m) in tow														
	<i>Sylocheiron</i> <i>carinatum</i>	<i>Sylocheiron</i> <i>suhmii</i>	<i>Sylocheiron</i> <i>abbreviatum</i>	<i>Sylocheiron</i> <i>affine</i>	<i>Sylocheiron</i> <i>elongatum</i>	<i>Euphausia</i> <i>brevis</i>	<i>Euphausia</i> <i>hemigibba</i>	<i>Euphausia</i> <i>tenera</i>	<i>Thysanopoda</i> <i>aequalis</i>	<i>Nematoscelis</i> <i>megalops</i>	<i>Euphausia</i> <i>krohnii</i>	<i>Thysanoessa</i> <i>longicaudata</i>	<i>Thysanoessa</i> <i>parva</i>	<i>Nematoscelis</i> <i>microps</i>	<i>Nematoscelis</i> <i>tenella</i>
Cruise Knorr 62—ring AI															
47	7.5	1.0	0	0.2	0	4.3	4.9	3.9	1.4	49.0	1.9	2.5	7.9	0.2	0
45	12.4	3.5	1.7	3.1	3.0	3.4	6.2	5.3	2.3	130.6	6.2	0.9	9.3	0.5	0.2
48	6.2	1.4	0	2.1	2.1	6.9	1.5	2.6	1.2	50.0	0.3	1.9	13.5	0.8	2.2
52	4.0	5.0	1.7	2.6	2.8	25.2	3.4	6.9	2.7	11.9	1.0	0	8.8	0.9	0.9
56	27.9	1.3	1.5	4.3	5.6	26.5	3.0	7.1	2.5	1.4	2.4	0	5.4	2.6	1.1
55	12.0	2.9	1.0	11.9	2.6	20.8	4.7	5.9	3.8	2.6	0.4	0.3	5.8	2.3	1.3
51	14.6	3.0	1.7	12.1	3.2	5.7	2.6	1.9	3.6	0	0	0	5.3	1.5	1.3
50	29.1	5.7	0.9	6.3	3.4	6.7	1.4	3.6	3.8	0	0	0	7.0	1.9	1.3
54	2.2	3.0	0.3	7.6	10.4	35.1	9.7	9.7	7.3	0	0	0	3.5	3.1	5.0
53	9.0	4.1	0.7	7.1	7.6	20.8	3.7	9.0	1.1	0.2	0	0	6.6	2.6	1.9
Cruise Knorr 65—ring Bob, time 1															
69	0	0	0	0	0	0	0.2	1.4	0	7.3	13.0	4.8	0	0	0
62	0	3.0	0	0	0	0	2.2	2.7	0.3	6.2	17.4	0.3	0	0.2	0
63	0	0	0	0	0	0.2	3.0	4.3	0.7	34.9	13.7	5.2	0	0	0
70	81.2	6.1	1.3	3.5	0.2	11.6	6.8	75.7	0.6	0	0.2	0.1	0	3.3	0.8
66	78.4	3.4	1.0	10.1	5.0	11.3	32.2	22.8	12.9	0	0	0.1	0	7.3	6.0
67	41.6	8.1	13.2	29.8	12.4	41.8	12.8	41.6	7.6	0	0	0	0	12.3	10.3
64	29.2	6.6	2.3	10.2	5.7	113.6	24.9	46.1	9.2	0	0.8	0	0	32.7	14.5
65	143.8	13.2	4.0	23.6	35.7	39.5	6.2	40.3	4.5	0	0	0	0	13.7	6.5
60	25.4	6.1	3.9	7.4	3.2	52.1	15.2	14.4	6.7	0	0	0	0	12.7	11.1
61	16.0	2.2	5.7	7.0	9.7	103.1	26.7	54.0	8.1	0	0	0	0	12.3	8.2

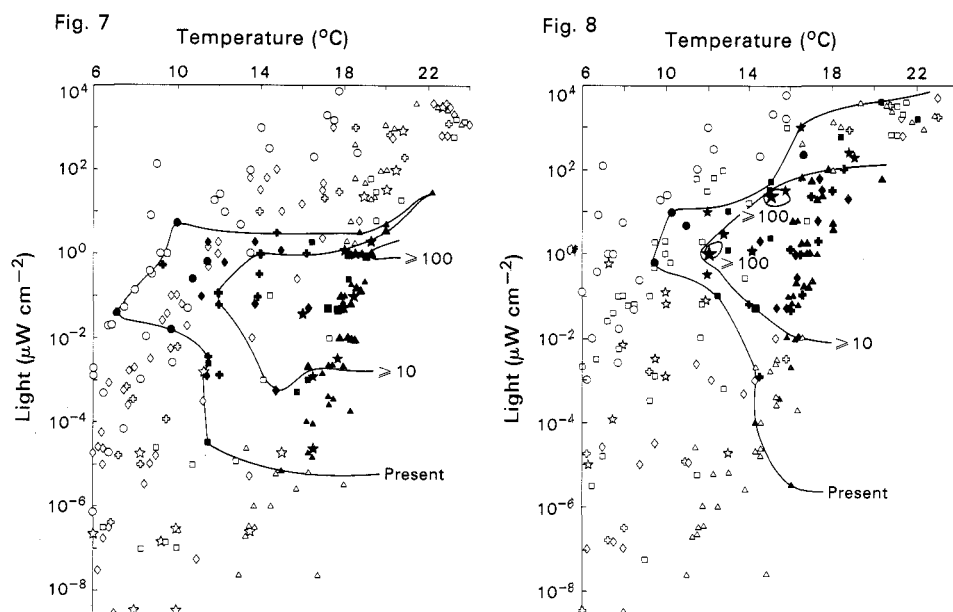
Cruise Endeavor 11—ring Bob, time 2

77	11.8	0	0	0	0	0	0	1.3	0.7	0.2	73.4	92.0	0.3	0.9	0.7	0
78	15.6	0	0	0	0	0	1.3	0.7	0	0.7	17.7	27.0	0	2.3	0	0.3
84	8.5	0.1	0	0	0.1	0	1.5	1.6	0.2	0.2	2.9	14.6	0.2	2.0	0.6	0
87	3.7	0.2	0	0.2	0	2.7	1.4	13.0	1.1	1.1	5.9	16.5	0.1	1.7	0.1	0.2
83	4.8	0.2	0	0.2	0	0.2	0.4	1.1	0.2	0.2	113.9	534.4	0.2	3.1	0.2	0
85	30.4	1.7	1.2	2.2	10.8	6.5	2.8	10.6	0.8	0.8	21.3	11.3	0	2.1	0.8	1.4
90	3.4	2.8	0.2	8.1	6.2	4.7	4.7	2.6	1.4	0	1.0	0	0	1.1	7.0	1.3
86	21.7	1.5	2.2	8.4	7.5	2.7	3.9	0.4	1.6	1.6	36.1	2.5	0	1.3	7.8	1.2
89	19.9	3.7	5.0	10.1	8.1	13.5	9.6	3.4	2.6	2.6	0.4	0.5	0	2.4	13.9	1.9
82	5.6	8.0	0.7	12.7	6.6	8.4	11.2	1.5	2.3	0	0	1.1	0	0.1	7.1	2.1
81	2.6	3.5	4.1	18.2	6.4	12.5	7.3	2.6	1.0	0	0	0.5	0	0.6	11.3	4.1
80	9.4	2.8	2.0	16.4	4.9	6.3	8.6	1.3	2.5	0	0	0.4	0	0	7.6	1.2
79	0.3	1.8	1.1	13.9	4.4	4.9	1.8	0.9	1.2	0	0	0	0	0	4.2	1.7

Cruise Knorr 71—ring Franklin

110	11.6	0.1	0.4	0.3	0	0.6	1.4	8.6	0.1	0.1	4.1	10.4	17.7	27.0	0.4	0.1
109	13.9	0.1	0	0.2	0	0.5	1.9	6.1	0	0	11.9	6.7	10.3	28.7	0.5	0.3
102	1.8	0.2	0	0	0.3	1.1	1.5	13.2	0	0	0.6	13.8	11.8	25.9	0.2	0
103	14.2	0.6	0.8	0	0.3	1.9	3.6	9.9	0.4	0.4	17.5	22.1	8.3	15.5	0.7	0.3
111	16.4	0.2	0.2	0.2	1.2	1.6	1.6	3.8	1.0	1.0	105.2	12.2	4.5	16.2	0.2	0
113	12.6	1.7	0.8	0.8	0.6	4.6	3.5	7.7	0.6	0.6	97.6	17.9	5.3	16.9	0.3	0.2
114	13.3	2.2	0.4	2.0	0.5	11.0	3.1	7.0	0.5	0.5	76.7	5.2	4.2	12.1	0.2	0
107	10.0	0.3	0.7	2.4	6.3	40.3	13.5	18.5	2.8	2.8	20.9	7.1	0	14.2	5.0	0.6
105	8.1	0.8	0.4	8.2	6.0	10.4	8.1	5.3	0.6	0.6	1.2	1.0	0.3	14.9	8.2	1.3
108	15.6	3.6	1.6	8.5	6.6	15.4	6.6	11.4	0.9	0.9	2.0	0.1	0.4	23.2	5.1	2.8
101	12.2	4.2	1.1	4.8	38.5	7.3	11.9	11.3	5.4	5.4	1.9	0.4	0	6.8	4.0	1.7
100	15.6	3.7	1.2	9.7	3.8	28.7	5.3	6.3	1.7	1.7	1.1	0	0	15.3	7.0	2.2
104	95.5	6.0	1.3	6.4	9.5	19.6	7.5	32.4	1.6	1.6	0.1	0	0.1	15.3	4.6	1.4

Ring A1 does show greater penetration by warm-water species than the previously described rings. *Thysanopoda aequalis* (Fig. 5l), the species of *Euphausia* (Figs 6d, 6h, 6l), and the shallow-dwelling *Stylocheiron* species (*S. carinatum* and *S. suhmii*; Figs 3d, 3h) all had abundances in this ring equal to or greater than those in the adjacent Sargasso Sea. However, the deeper-living *Stylocheiron* (Figs 3l, 4d, 4h) and *Nematoscelis* species still had not reached the abundance levels found outside the ring. Furthermore, cold-water species such as *N. megalops* (Fig. 1d), *Thysanoessa longicaudata* (Fig. 2d) and *E. krohnii* (Fig. 1h) were still quite abundant within the ring and occurred only in low numbers or were absent beyond the ring core.



Figs 7 and 8. Abundance of *Stylocheiron elongatum* (7) and *Stylocheiron affine* (8) versus temperature and light for all MOCNESS tows taken during daytime in the North-western Atlantic. Open symbols represent samples taken in which no individuals of this species were present; solid symbols represent positive occurrences. Small symbols represent fewer than 10 individuals; medium-sized symbols represent 10 to 99 individuals; large symbols represent 100 or greater individuals. Symbols are plotted at the midpoint of temperature and light for the depth strata sampled. Lines divide the observations into particular classes; for example, the line labelled ≥ 10 encloses all observations in which 10 or more individuals were found. Note that some of the samples within this area may contain fewer or no individuals. ● Slope Water. ▲ Sargasso Sea. ★ Warm-core ring. ■ Centre of cold-core ring. ◆ Fringe of cold-core ring. + Gulf Stream.

Ring Influence on Vertical Distribution and Diel Migration

The warm-water euphausiids that penetrate cold-core rings exhibit a common reaction of shoaling in their depth distribution. In the vicinity of a ring, the shoaling often involved truncation of the lower portion of the depth distribution by 100–300 m and for deep-dwelling species, elevation of the upper limit by about 100 m. The pattern is most pronounced in young rings such as Bob and less evident in the older rings A1 and Franklin. For non-migrators living near the surface (*S. carinatum*, *S. suhmii*), the shoaling is subtle (Fig. 3). These species typically range the upper 200 m in the Sargasso Sea, but become restricted to the upper 100 m in young rings. For deeper-living non-migrators (*S. affine*, *S. elongatum*), shoaling is more dramatic (Fig. 4). The day and night vertical distributions

of migrators of *Euphausia*, *Nematoscelis*, and *Thysanopoda* species illustrated in Figs 5 and 6 show pronounced shoaling relative to the patterns of vertical distribution in the Sargasso Sea.

Although vertical temperature structure would appear to be a major factor causing the shift in the vertical distribution of most, if not all, of these species, our analysis to date does not support the idea that this is the only factor operating to regulate these patterns. Downwelling light is known to play a role in determining vertical distribution patterns and in rings seems to set an upper limit to shoaling. One example will be given here for the genus *Stylocheiron*. We have plotted species abundance versus light and temperature for all of the daytime MOCNESS tows we have taken in the North-western Atlantic. *S. elongatum* individuals did not occur at light levels higher than $10 \mu\text{W cm}^{-2}$ and optimal levels, based on where we find highest abundances, appear to be between 10^{-2} and $10^{-1} \mu\text{W cm}^{-2}$ (Fig. 7). Optimal temperatures appear on this basis to be $16\text{--}18^\circ\text{C}$. This temperature range frequently occurs in rings and in the Slope Water above the apparent upper limit for light and thus individuals in these regions seem to be unable to adjust their vertical distribution to find optimal temperatures because of light. Similar observations can be made for *S. affine* (Fig. 8). This species also appears to compensate for lower than optimal temperatures by shoaling until a threshold light level is reached (in this case, about $10^2 \mu\text{W cm}^{-2}$) and then it stops.

Effect of Rings on a Bathypelagic Species

Thysanoessa parva, a species that is generally found below 500 m in the Sargasso Sea and is often found in the Slope Water below this depth, was present in only three of the rings. It was absent from ring Bob at time 1 (Fig. 2e), but more importantly, it was absent from all 0–1000-m samples we have collected in the North-western Atlantic during February, March and April. We do not, at present, know whether the absence is due to a deepening of the species' vertical distribution to below 1000 m during this period, to a seasonal disappearance of adults with larval forms remaining in this part of the water column, or to some other as yet unknown facet of its ecology.

In rings Bob at time 2 (Fig. 2f), Al (Fig. 2g), and Franklin (Fig. 2h), the centre of abundance of *T. parva* was shoaler than in the Sargasso Sea by at least 200 m. In addition, 0–1000-m abundance of this species was 1.4–2.6 times larger in the rings.

Similarity in Species Composition across the Rings

Clearly, the invasion/dispersal processes work quite differently for different species, and it is difficult to construct an overall summary. Nevertheless, the combined effect of the patterns of abundance of the individual species makes the core of the ring noticeably different from its surroundings. We can quantify this using the percentage similarity index (S). From the integrated (to 1000 m) numbers of individuals per square metre for each species (Table 2) and the total number of individuals per square metre caught on each MOCNESS tow, S is computed as:

$$S = 100 \left(1.0 - 0.5 \sum_{i=1}^n |P_{ij} - P_{ik}| \right),$$

where P_{ij} and P_{ik} are proportions of the i th species in the j th and k th tows and n is the number of species. We have plotted in Fig. 9, S values for comparisons of each tow with the outermost tow on a section versus the depth of the 15°C isotherm (Table 1). The outer tow on a section is an indicator of the species compositional structure in the Sargasso Sea. S is low ($<30\%$) in the core of the rings, and except for ring Franklin, increases dramatically in the high-velocity region. Lowest similarity values ($<10\%$) and the sharpest change across the edge of the ring occurred in ring Bob during both sampling periods. Only ring Franklin

does not show a fairly sharp change in the compositional structure when moving out from the centre of the ring, although there is a definite break beyond a 15°C isotherm depth of 400 m. This is due primarily to individuals of species such as *S. carinatum* and *Thysanoessa parva* being abundant across the entire area and thus damping the contrast.

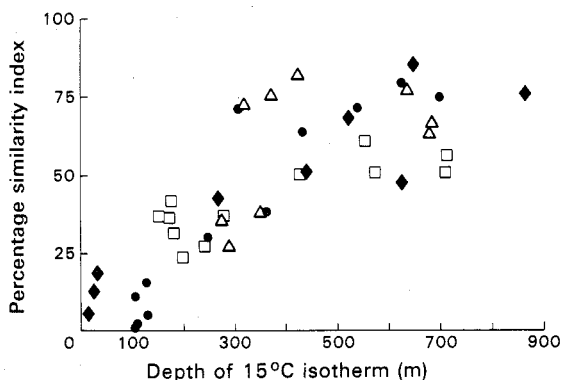


Fig. 9. Percentage similarity of the 15 euphausiid species used in this study, based on a comparison of each station in a section with the outermost station going from the ring centre to Sargasso Sea, versus the depth of the 15°C isotherm. □ Ring Franklin. △ Ring Al. ◆ Ring Bob, time 1. ● Ring Bob, time 2.

Discussion

Summary of Observations

The pattern that emerges is the following:

- (1) Warm-water species living permanently at or near the surface and those that perform diel migrations invade a ring more quickly than do species that live at subsurface depths of 150–600 m. However, even for these rapid invaders, there is often a tendency for population numbers to be lower within the ring compared to adjacent seas for 6 months or more.
- (2) Vertical migrators migrate to shallower depths in young rings and non-migrators show a strong tendency to shoal.
- (3) Cold-water species persist within the ring core for extended periods. In some cases, species can enlarge their population numbers in middle-aged rings over levels present at the time of formation; i.e., *E. krohnii* and *N. megalops*. Other species such as *Thysanoessa longicaudata* can show rather drastic declines in numbers during this same period in rings like Bob.
- (4) Cold-water species, such as *N. megalops* and *T. longicaudata*, which show submergence as a ring ages, appear to be dispersed out of a ring at depths of 400–1000 m. For the shallower-dwelling species like *E. krohnii*, which can survive surface-water modification, dispersal appears to take place near the surface.
- (5) The species compositional structure of the core of these rings remains distinctly different from the surrounding Sargasso Sea for 6–8 months after formation in spite of the exchanges of species into and out of the ring that appear to be taking place. These data corroborate the earlier findings of Wiebe *et al.* (1976a).

Mechanisms of Population Change

We cannot offer any complete explanation of how the population changes we have described arise, but we can attempt to list the various mechanisms and make estimates of the likely contribution of each process to the alteration of the distributions. These mechanisms fall into three classes:

- (1) purely physical processes that have similar effects upon the passive scalar density—diffusion, instabilities and dispersion, horizontal mixing in the mixed layer, layering, Gulf Stream interactions, and meridional circulations;
- (2) mixed processes where the biological behaviour (especially diel migration) alters the rate at which the organisms are moved by the currents—loss or gain due to long-term migration across the boundary of the trapped region, diel migration in and out of the trapped region, migration through small-scale motions, and horizontal convergence and biological reactions; and, finally,
- (3) purely biological processes that cause changes in population structure and abundance—horizontal swimming, and changes in birth, growth and death rates in response to changes in temperature, food-type distribution and abundance and predation/competition.

Purely physical processes

We can attempt to understand the role that the currents play in modifying the distributions by comparing changes in passive scalar distributions to the changes in species abundances. However, if one attempts to describe the patterns of decay of passive scalar anomalies in the ring, one finds several difficulties. The initial conditions are not always clearly defined, especially when the eddy has a complicated history involving successive interactions with the Gulf Stream. Secondly, the strength of the salinity anomaly, the most frequently measured physical tracer, decreases with depth and cannot be used to trace the water motions below about 800 m. The surface signal also tends to be quite variable.

The data collected by R.V. *Knorr* and *Endeavor* for ring Bob show little temporal change in salinity at either the 50 or 500 m depth. The surface signal at the very centre of the ring does decrease by about 25% (with the exterior salinity increasing by a like amount). A longer time series from ring D (Richardson *et al.* 1978) suggests the salt anomaly (ΔA) on the 26.7 potential density surface decreases as

$$\Delta A(t)/\Delta A(0) = 1/(1+t/T), \quad (1)$$

with a time constant $T = 4.7$ months, whereas the data for ring Bob suggest a larger time scale, $T = 12$ months. These changes can be ascribed to many different processes such as turbulent diffusion, layering, Gulf Stream interactions or meridional circulations.

The functional form in the equation above is that appropriate to the spread of an initially Gaussian distribution acted on by a constant eddy diffusion process. The constant T is related to the diffusivity K by

$$T = L^2/2K, \quad (2)$$

where L is the initial horizontal scale of the population, about 65 km for species expatriated in the ring. For species initially outside a ring, we can regard the anomaly at ring centre as being negative (fewer organisms) with the magnitude of this anomaly decreasing over a similar length scale. The estimated diffusivity, K , ranges from 0.7×10^6 to 1.7×10^6 cm² s⁻¹ for $L = 65$ km, and the T values from 4.7 to 12 months. The biota should, in as far as it is carried passively, respond likewise to these mixing processes. The changes in some biological parameters seem much larger than can be expected from those mechanisms; they are much more noticeable than the changes in ΔA . For example, the most rapid invader of the ring core, *S. carinatum*, had reached population numbers greater than those found in the Sargasso Sea by the second cruise to ring Bob (Fig. 3b).

The data from ring D, although much sparser than the data acquired during the cold-ring study, likewise indicate that the population of *N. megalops* disappeared at some point between 9 and 17 months, whereas the salinity anomaly was still visible (Wiebe and Boyd 1978).

There are a variety of reasons why even a passive scalar may change in concentration as the ring evolves. Even though some species behave differently from the salinity anomaly, there is still much information in the distribution patterns that we can try to use in understanding the water motions. First, let us next consider conservative processes, such as meridional circulations and dispersion, which by themselves do not alter the magnitude of the concentrations but may alter the spatial patterns substantially. The deep outward motion of *N. megalops* in rings Bob and Franklin (Figs 1b, 1c) certainly does seem suggestive of the meridional circulation patterns proposed by Schmitz and Vastano (1975) and Vastano *et al.* (1980), which have inward flow near the surface, a downwelling in the centre and outward flow along about the 10°C isotherm. These models suggest inward and outward flow speeds of about 0.02 cm s⁻¹. This seems generally consistent with the observed physical changes: outflow between the 10–15°C isotherms would be accompanied by thickness changes (perhaps partially countered by diffusion). Our data from ring Bob show very complex changes in the thickness of this layer, possibly due to sampling difficulties and possibly representing real signals of the ring's complicated interactions with the Gulf Stream during the period of the cruise in April 1977. There is an increase in thickness at the centre and at distances beyond about 40 km. In spite of the variations, over most of the region with 40-km radius, the thickness decreased by about 20 m over the 4-month period from April to August. Thus, a conservative estimate of the outflowing volume (V , m³) would be:

$$\Delta V = 20 \times \pi \times (40 \times 10^3)^2.$$

This volume passes through the outside wall of the cylinder of 10–15°C water, having a thickness of 265 m, and therefore corresponding to an outward displacement of:

$$\Delta r \cong \Delta V / (2\pi \times 40 \times 10^3 \times 265) \cong 1500 \text{ m},$$

which is clearly negligible. To advect *N. megalops* the observed 23 km out of ring Bob would require divergent flows of about 0.2 cm s⁻¹ over this whole area, corresponding to vertical velocities about an order of magnitude larger than the observed sinking of isotherms. The problem is much more severe for ring Franklin when animals were found out to 220 km. These estimates of volume change are consistent with Olson's (1980) suggestion that meridional flows at depths of 200–800 m are very small, based on the existence of a downward extending tongue of anomalous potential vorticity. The biological data are not quite as consistent, however, suggesting that other processes may be responsible for the observed losses or gains in abundance.

Physical biological mechanisms

One mechanism, related both to the physical structure of the ring and the biological behavior of the species, does seem capable of explaining the deep motion of *N. megalops* away from the ring centre. This process involves loss from the trapped region due to downward shifts in the population's preferred depth range. The concept of a trapped region states that when a ring is moving relative to the water around it, only certain sections will be advected with the ring; the rest will be accelerated briefly as the ring passes, but then will be left behind. Because the swirl currents decrease with depth, the area that is advected along with the ring is largest at the surface and smaller in the deeper waters. The methods for determining the trapped region have been described by Flierl (1981). The trapped region is not azimuthally symmetric, but rather extends further north for a westward moving ring. We have sketched the boundaries on a r, z plot for comparison with the zooplankton distributions (Fig. 1a). Note that the bulk of *N. megalops* is indeed in the trapped region of three of the four rings in Fig. 1, but in ring Franklin, a lower density population maintaining itself at 10–15°C has moved below the region and appears to have been left behind. The existence of individuals 200 km from the centre after 6–8

months is no problem if a ring is moving at several centimetres per second. One prediction of this model is that these expatriates will be found only in regions over which a ring has passed (the wake region). Such individuals should not be found in the direction of propagation of the ring unless the ring has been making large anticyclonic revolutions of the kind described by Fuglister (1972) and Richardson (1980).

It is important to realize that the size and shape of the trapped region of a ring are variables that are dependent on the speed and direction of horizontal movement of the ring (Flierl 1981). For example, a fast moving ring will have a smaller trapped region than one travelling slowly. If the ring's translation velocity changes, the trapped region will shrink, grow or change direction so that one cannot assign a sharp edge to the advected volume. Furthermore, the trapped region from the time of formation includes portions of the Gulf Stream remnant and the encircling Sargasso Sea. As a result, warm-water species present in these waters when the ring is formed will be advected with the ring in the same way as the cold-water expatriates.

Loss or gain from the trapped region could affect the relative loss rates for migrating versus non-migrating species. One could hypothesize that migrating animals would be lost more rapidly from the ring (or invade more rapidly from outside) than non-migrators because they swim down into regions where the swirling motions of the ring are not intense enough to advect the water with the eddy as it moves.

This process was numerically simulated in order to evaluate whether this mechanism is significant or not. We solved for the evolution of the x and y positions of a model animal, assuming a sinusoidal migration pattern $z(t)$ over a 24-h time interval. The flow was represented by a low-pressure pattern $p(x-ct, y)F(z)$ translating at speed c , where $F(z)$ describes the strength of the currents relative to those at the surface,

$$F(z) = 3 - 5 \times 10^{-5}z - 2 \cdot 5 \times 10^{-6}z^2.$$

The horizontal velocities are derived geostrophically, and the horizontal positions predicted from:

$$\begin{aligned}\frac{dx}{dt} &= \frac{-1}{f} \frac{\partial}{\partial y} p(x-ct, y) F[Z(t)], \\ \frac{dy}{dt} &= \frac{1}{f} \frac{\partial}{\partial x} p(x-ct, y) F[Z(t)],\end{aligned}$$

where f is the Coriolis parameter and $Z(t)$ is the depth as it varies during migrations:

$$Z(t) = Z_{\text{upper}} + (Z_{\text{lower}} - Z_{\text{upper}}) \left(\sin \left(\frac{2\pi t}{24} \right) + 1 \right) / 2.$$

These equations were integrated from a specified initial point using a second-order Runge-Kutta approximation technique, and the individuals were followed over hundreds of days. Values of c from 0 to 10 cm s⁻¹ were used.

The results are somewhat surprising; the model animals persisted in the ring for as long as non-migrators. An organism originally on the back side of the ring would 'fall behind' as it migrates into the deep water, but the ring has only moved away a short distance (several kilometres) by the time the animal rises to the surface again and is caught in the more rapid currents. During the night-time periods, the animal is brought around the ring by the intense surface currents until it reaches the front side of the ring. Now, when the animal migrates down into the deep water during the day, the ring 'rides over' it so that it is again brought closer to the centre of the ring. These two tendencies—to be left behind at the back and to be ridden over at the front—essentially cancel so that the organism continues to circle the ring for many periods.

Based on the calculations, we can estimate fairly accurately the total advected region for a migrating species. Essentially, the organism circles the ring as if it were staying at an average depth Z_{av} (where the average over the day is computed by weighting by the current speed at each depth),

$$F(Z_{av}) = \frac{1}{24} \int_0^{24} dt F[Z(t)],$$

with the function F representing the vertical structure of the currents, and time t is measured in hours. For a species migrating from 0 to 800 m, the average depth is about 470 m. The trapped area can now be calculated using the methods in Flierl (1981).

Because the classes of organisms we consider are not constrained to move vertically with the water, horizontal convergences or divergences can create increases or decreases in abundance. Although the velocities involved are unlikely to be large enough to bring animals all the way into or out of a ring, they may create local maxima or minima in the distributions within the ring. In several rings, we have observed distributions of *N. megalops* and *E. krohnii* where the abundances were substantially greater at the periphery of the ring core than at the ring centre (e.g. *N. megalops* in ring Bob on *Knorr 65* and *Endeavor 11* and in ring Franklin on *Knorr 71*; *E. krohnii* in ring Bob on *Endeavor 11* and in ring Franklin on *Knorr 71*). These offsets in abundance from the ring centre do not appear to be a result of small-scale horizontal patchiness; in some cases, tows taken over a period of several days at different locations on the perimeter reproduced the abundance peaks. These peaks in abundance correspond approximately to the locations where satellite-tracked drogues tend to move when released in a ring centre (Richardson 1980). This area of a ring is characterized by high vertical shear and peak velocities in the ring current field (Olson 1980). Although vertical motion within cold-core rings is poorly known, these distributions suggest that this area is a region of convergence or frontogenesis where water from the ring core and from the Gulf Stream remnant are moving together and downward along isopycnals while the species and drogued buoys maintain a preferred depth. Vertical motions would be strongest along this convergence zone, and considerably weaker away from it, but in no case would the water velocities approach the sustainable speeds (100 m h^{-1}) that species swim during diel migrations. Based on the slope of the potential density surfaces in ring Bob on *Endeavor 11*, Olson (1980) infers the existence of a convergence zone at radius 45 km. It should be mentioned, however, that this circulation would imply upwelling in the ring centre, contrary to the observed downward sinking of the isotherms. Perhaps the sharpening or decay of the front and these associated circulations occur in a non-symmetric fashion or irregularly in time.

Biological Mechanisms

There is one biological mechanism that seems at first glance to be a likely mechanism for the distribution changes: if individuals of a species find themselves in an unpleasant environment, they swim horizontally until they reach a better one. The difficulty in this concept lies in the understanding of how an individual can orient itself in a field with gradients occurring on scales 10^6 times larger than its own body length. If one uses the rule of thumb that an organism can swim 10 body lengths per second (Barkley 1972), this implies that the animal would have to maintain this maximum rate and do it in a constant horizontal direction for a whole day in order to see substantial environmental changes. This seems extremely unlikely, given that much swimming energy at least for some species is put into vertical migration, and that horizontal movements would be interrupted by foraging and predator avoidance.

It is perhaps more reasonable to regard the effects of swimming as producing a random-walk diffusion, which may enhance any physical diffusive processes. If the animal moves a horizontal distance l in a random direction beginning afresh at separations of time τ , the effective diffusivity is:

$$K = l^2/2\tau.$$

Using the same model as used for salinity (eqn 1), the population anomaly of the ring at time t , $\Delta N(t)$ (the difference in abundance from inside to outside) satisfies:

$$\Delta N(t)/\Delta N(0) = 1/(1 + t/T),$$

with the time constant for swimming (using the above expression for K in equation 2) being:

$$T = \tau(65/l)^2.$$

If we assume the organism is 1 cm long and swims at maximum speed, V , without rest periods, then the length of an excursion l is related to the time between the start of successive excursions τ by $l = V\tau$. If the population anomaly at $t = 4$ months is 0.2 of the anomaly at $t = 0$, then at $V = 10 \text{ cm s}^{-1}$ the organism must swim for $\tau = 2$ days before changing direction randomly. Again, this is very unlikely. If we take a more reasonable guess that $\tau = 1$ h, we find that over 4 months, swimming induces an 8% decrease in the population anomaly across the eddy. This result, suggesting that invasion/dispersal by swimming is very slow, is consistent with the observations of many species that seem not to move in or out of the ring very far. Clearly, the changes in some populations, such as *Stylocheiron carinatum*, cannot be accounted for by this mechanism alone.

For many of these species with long life cycles, the effects of change in food and predator abundances will be very subtle. It may be possible for a rapidly growing species to invade a ring fairly efficiently: physical processes will carry a few individuals into the eddy where they can take advantage of the higher food concentrations and reproduce rapidly. The invasion time will be in between the population doubling time, and the time for diffusive processes to act (T above). For doubling times of the order of a few months, this time could be short enough so that biological growth could be important. Similar arguments could be made for other biological inputs, such as changes in predation, in that a decrease in death rate is closely analogous to an increase in growth rate. Still unanswered, however, are the questions of what conditions change so that the ring becomes viable living space for the warm-water species, whereas the Slope Water remains generally uninhabited by them.

Clearly, many of these questions cannot be answered without extensive work on the population biology of these species: the speculations above suggest only that the population turn-over time may play a significant role in the increases or decreases in species abundance in rings, especially for the near-surface or surface-dwelling forms.

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