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Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold core rings. II. Physiological and biochemical effects of expatriation

by Steven H. Boyd¹, Peter H. Wiebe¹ and James L. Cox²

ABSTRACT

Nematoscelis megalops, a cold water euphausiid commonly found in Northwestern Atlantic Slope Water, is frequently transported in the cores of Gulf Stream cyclonic rings into the Sargasso Sea. The inner core made of cold Slope Water gradually assumes physical and biological characteristics of the surrounding Sargasso Sea. These changes gradually lead to a localized extinction of this species in the core of the ring. Samples of *N. megalops* taken from the same ring at 6 and 9 months after its formation show a weakened physiological and biochemical condition.

Deterioration of ring individuals is evidenced by an increase in body water content and a reduction in total body lipid, carbon, respiration rates, and nitrogen relative to Slope Water individuals. By 6 months it appears that ring *N. megalops* must supplement food intake by metabolizing some of their body protein and by 9 months they appear to use lipids as well.

A shipboard starvation experiment involving 40 Slope Water individuals showed that physiological and biochemical states similar to those found in individuals from the 9 months old ring could be duplicated in 4 days of complete starvation.

1. Introduction

A fundamental question in the study of oceanic plankton has been: what range of environmental conditions permits both the long-term survival and the reproduction of a species? These conditions define the normal living space of the species, both vertically and horizontally. Spatial limits are typically determined by the presence or absence of individuals at different locations and hence the limits do not, by themselves, provide a measure of suitability. Factors such as food, temperature, salinity, or predation pressure may become stressful at the extremes of the spatial distribution of the species. Such conditions may lead to reproductive failure or death only after a protracted period of degradation of the physiological conditions of the organisms, as reflected by changes in biochemical composition and energy metabolism. These biochemical changes may prove to be more realistic in defining the

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limits of viable populations, especially in the case of plankton which are relatively incapable of maintaining their horizontal distribution behaviorally.

Unfavorable changes in the environment are, in the case of oceanic planktonic crustacea, determinative of their biochemical composition and metabolic rate. Energy substrates, protein or lipid, are consumed without replacement during periods of environmental stress (Orr, 1934a,b; Littlepage, 1964; Conover, 1964; Ikeda, 1974; Mayzaud, 1976; Bamstedt, 1975). Variations in biochemical composition and energy metabolism related to sex, and size of organism, latitudinal range, and seasonal effects have also been documented. However, little is known about their interaction with environmental stress.

Gulf Stream cold core rings offer a unique setting for the study of physically induced environmental stress in an oceanic environment. Gulf Stream cold core rings are formed from large meanders of the Gulf Stream which then move out into the Sargasso Sea (Parker, 1971). The central region of the ring contains Slope Water and its associated plankton community (Wiebe *et al.*, 1976; Wiebe and Boyd, 1978; Ortner *et al.*, in prep). As a ring ages, it gradually assumes the characteristics of the surrounding Sargasso Sea, through increased heating from the surface and mixing with adjacent waters. Thus the water column warms and increases in salinity, the oxygen minimum layer deepens, and the nutrient concentration of the euphotic zone decreases. After only a few months (approximately 3 to 6) the phytoplankton population in the ring approaches that of the Sargasso Sea with respect to both abundance and composition (Wiebe *et al.*, 1976; Ortner *et al.*, in prep.). The transition from a predominantly Slope Water fauna to that characteristic of the Sargasso Sea takes place more slowly (at least 12 months, Wiebe *et al.*, 1976). Rings may last as long as two years (Parker, 1971).

Nematoscelis megalops, a large, Slope Water euphausiid, found south of the Gulf Stream only in association with cold core rings, appears to be a representative cold water euphausiid species with respect to its distribution, chemical composition, growth rate, and respiration (Raymont and Conover, 1961; Mauchline and Fisher, 1969; Gopalakrishnan, 1974; Wiebe and Boyd, 1978). The alteration of *N. megalops*'s environment associated with ring decay ultimately leads to its local extinction. In this paper we present evidence to support the hypothesis that environmental alterations gradually degrade the physiological state of expatriated populations of the species. We compare biochemical and physiological properties of populations within the ring with those of populations in its home range—the Slope Water.

2. Methods and materials

a. Collection techniques. Samples of *Nematoscelis megalops* were taken from both the Slope Water and a Gulf Stream cold core ring (designated Ring D by NAVOCEANO) on two successive cruises—*Chain* 125 (August 1975) and

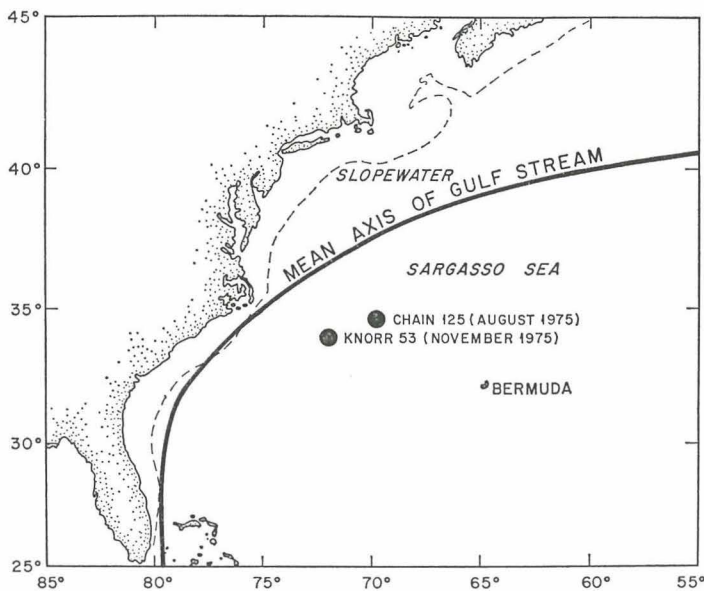


Figure 1. Position of Ring D at 6 months (*Chain 125*) and 9 months (*Knorr 53*) in the North West Atlantic.

Knorr 53 (November 1975) (Fig. 1). This ring had formed approximately six months before the first cruise. At each station *N. megalops* was removed from collections which were taken at night with a 10' Isaacs Kidd Midwater Trawl (IKMT) towed from approximately 750 m to the surface. Individuals were also obtained from night MOCNESS (1 m²) plankton tows which sampled at 100 m intervals, most often from 800 m to the surface. (See Wiebe and Boyd (1978) for more details about the plankton tows.)

Individuals for live work were collected with a closing 1 m net equipped with .505 μ mesh and an enlarged cod end bucket. The net was slowly fished for 15-25 minutes at depths of maximum *N. megalops* abundance as determined by a preceding MOCNESS tow. The ship was then stopped and the net closed. Those in the "best" condition were obtained if the net was quickly retrieved to the seasonal thermocline, and then gradually brought through the region of rapid temperature change. This procedure was the most successful presumably because it reduced thermal shock.

Our measurements included analyses of *freshly* collected individuals for sex, wet and dry weight, total lipid, carbon and nitrogen, as well as supplemental information derived from respiration and shipboard starvation experiments. Individuals for biochemical analyses were carefully picked from each collection and frozen at -15°C in plastic Petri dishes. Only those in good condition were chosen. The entire sorting process usually took less than 15 minutes. The remainder of the

plankton sample, if taken by the MOCNESS, was preserved in 5% buffered formalin and later used for estimates of numerical abundance.

b. Biomass/abundance estimates. Frozen *N. megalops* were thawed, examined microscopically for physical condition, carapace length, and sex. Individuals judged to be physically intact were weighed, dried to constant weight at 60°C and reweighed (± 0.01 mg). Carapace lengths were also determined from preserved specimens, as measured along the midline from the eye socket inner carapace edge to the most posterior leading edge (Rudd, 1936).

Estimates of numerical abundance were based on night tows taken in the ring and Slope Water on *Chain* 125 (ring age = 6 months) and *Knorr* 53 (ring age = 9 months). (See Wiebe and Boyd, 1978, for specific details.)

c. Biochemical composition. The total lipid of *N. megalops* was measured using the Bligh and Dyer (1959) modification of the gravimetric procedure of Folch, Lees and Sloane Stanley (1957). Single frozen individuals were placed in a 10 ml glass homogenizer and ground for 1 min with three successive rinses of a 6 ml chloroform methanol solution (2:1 by volume). Each rinse was filtered through a Whatman #4 qualitative filter into a separatory funnel. The residue remaining on the filter was rinsed with .05 N KCL aqueous solution. The final proportions of chloroform, methanol and water were 1:2:8. The resulting biphasic solution in the separatory funnel was allowed to sit at least 24 hours by which time the lower fraction containing the lipid had fully separated. The lower fraction was then transferred to a preweighed aluminum pan and dried in a nitrogen atmosphere. Total lipids were defined as the difference between the pan's initial and final weight.

Total carbon and nitrogen of single individuals were determined with a modified Model 185 F+M CHN analyzer. Those greater than 7.5 mg dry wt were ground and carbon and nitrogen were determined on aliquots which were then averaged.

Percent water content of individual animals was calculated from the difference between the wet and dry weight.

d. Oxygen consumption measurements. Oxygen uptake measurements were made on board ship and later in the laboratory with animals taken on *Knorr* 53. We used a modified all-glass differential micro-respirometer (Greunbaum, Siegel, Schultz, and Kirk, 1955) in which the capillary bores were modified to 0.35 mm diameter and the respirometry vessels were enlarged to a 10 ml capacity. This instrument combines simplicity with small size, and makes possible semi-continuous series of measurements over a short period of time. All measurements were run at $10^{\circ} \pm 1.5^{\circ}$ C.

e. Starvation study. A shipboard study was conducted using Slope Water *N. megalops* to test the physiological and biochemical effects of starvation. Once on board the euphausiids were kept in reduced light. Those used solely for respiration

were kept in 20 liter carboys at 10° C (10-15 individuals/carboy) for at least 6 hrs before a respirometry run.

A large number of individuals were collected at night with a 1 m net tow. Nineteen of these were frozen immediately for biochemical analysis and three were used to measure oxygen uptake. These constitute the initial respiration values. An additional 40 individuals were placed in 2 liter glass containers with surface seawater, 5 to a container. Each of the eight containers was assigned a number and on consecutive days random pairs of containers were arbitrarily selected for analysis. However, by the fourth day, all individuals except one in the last four containers had died. On each day the live individuals from one container were frozen for biochemical analysis. Those in the second container were used for respiration measurements and subsequently frozen for biochemical analyses, regardless of whether they survived the respiration run. The maintenance temperature (10° C \pm 1.5) approximates the mean habitat temperature of *N. megalops* as measured by the MOCNESS. The sea water used in maintaining individuals was collected from the surface in the same area in which the individuals were collected. Sea water used in the microrespirometry was Whatman GFC glass fiber filtered, at 4.5 psi.

3. Results

a. Biochemical Composition

Water Content. Percent water content ([dry weight/wet weight] \times 100) of ring individuals (\bar{X} = 86.2, n = 29) was significantly higher than Slope Water individuals (\bar{X} = 82.8, n = 44) *Chain 125* collections (P < 0.001, Mann Whitney U test). *Knorr 53* showed a similar significant difference between ring (\bar{X} = 85.4, n = 63) and Slope Water (\bar{X} = 80.7, n = 83) specimens. Because of the higher water content of ring individuals, relationships expressed on a dry weight basis show somewhat different trends than those expressed on a wet weight basis. Wet weight based values are probably more valid for comparisons since these more closely reflect the natural state of the organisms as emphasized by Childress (1977) thus all measurements having a weight-specific component imply wet weights.

Lipid content. Variations in total lipid weight of individual *N. megalops* are shown in Figure 2. Total lipid weights ranged between 0.4 mg to 3.7 mg per individual. Lipid content expressed as % wet weight ranged between 0.3% and 5.8%. Lipid weight was positively correlated with wet weight for both of the Slope Water data sets and the 6 months (*Chain 125*) ring data set. There was no correlation between these two variables in the ring at 9 months. The lipid weights on a percentage basis were independent of body size, although the single individual observed in the large size class in the ring had the lowest percent lipid of wet weight observed.

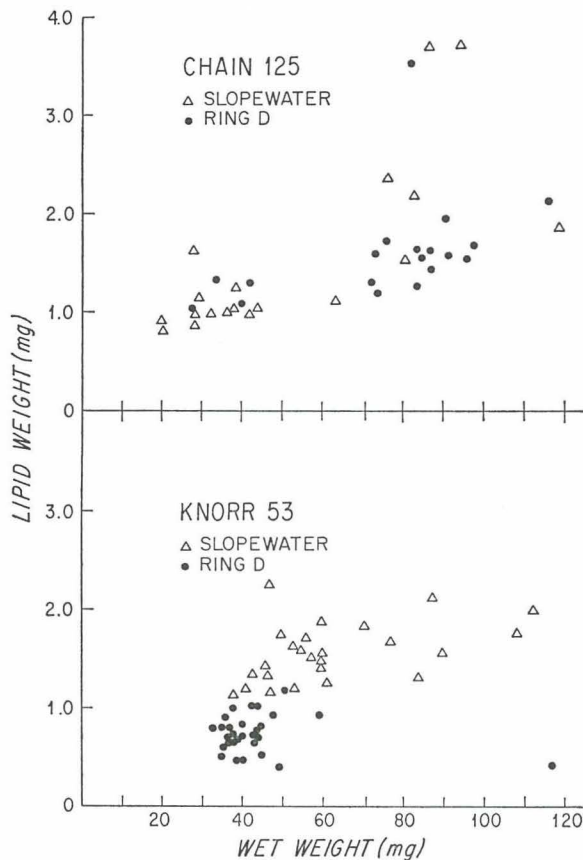


Figure 2. A comparison of *Nematoscelis megalops* total lipid weights to individual wet weights for cruises *Chain 125* and *Knorr 53*.

Lipid contents for *Chain 125* Slope Water and ring individuals were not significantly different ($P > .05$ Mann-Whitney U. Test). This implies that at least up to six months those animals in the ring were similar to those in the Slope Water with respect to total lipids. At 9 months in ring D total *N. megalops* lipid levels were significantly different from the Slope Water ($P < .01$ Mann-Whitney). While lipid contents of individuals in the Slope Water continued to increase, those in the ring decreased, not only in total lipid weight but also in % lipid of wet weight.

Carbon. Total carbon, expressed as percentage of wet weight (Fig. 3) is a relative measure of organic matter primarily in the form of lipid, carbohydrate, chitin and to a lesser degree protein. It is interesting that *N. megalops* caught in the ring at 6 months (*Chain 125*) had a significantly lower carbon content than those in the Slope Water ($P < .05$ Mann-Whitney). This implies enhanced nonlipid carbon consumption by ring animals.

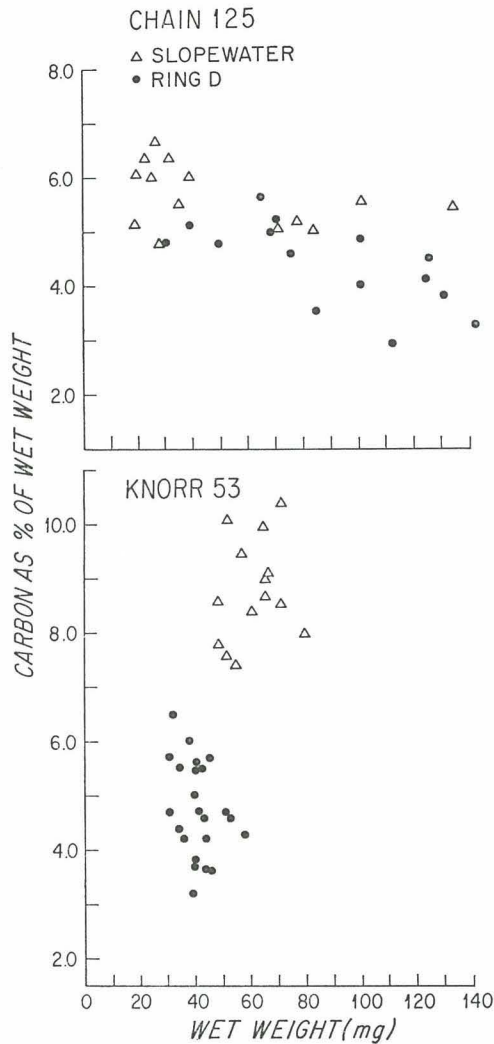


Figure 3. A comparison of *Nematoscelis megalops* total carbon as a percent of wet weight to individual wet weight for cruises *Chain 125* and *Knorr 53*.

The average carbon content of 9 month ring individuals is approximately half that of the *N. megalops* in the Slope Water. In the 3 month interval between cruises, the percent carbon of ring individuals remained unchanged while the Slope Water population nearly doubled in carbon content.

Nitrogen. Total nitrogen expressed in percent of wet weight shows a trend similar to that of carbon (Fig. 4). Analysis of the *Chain 125* ring and Slope Water nitrogen indicates that ring individuals had a significantly lower percent nitrogen content

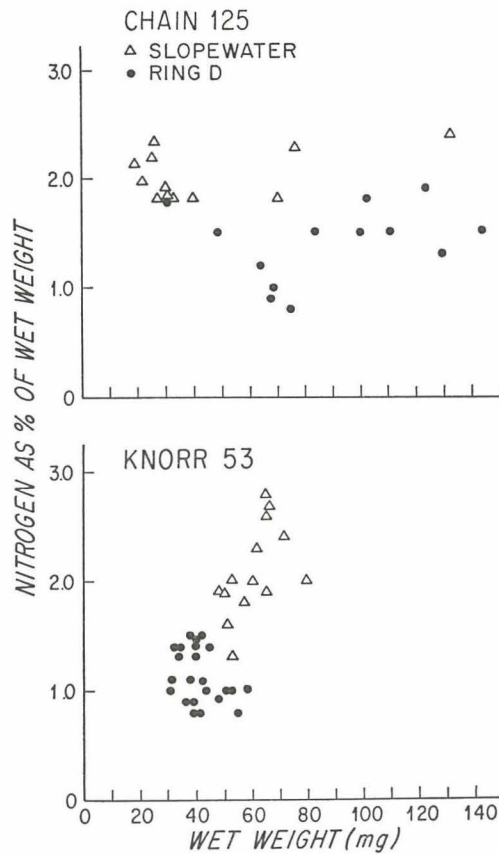


Figure 4. A comparison of *Nematoscelis megalops* nitrogen as a percent of wet weight to wet weight for cruises *Chain 125* and *Knorr 53*.

than those in the Slope Water ($P < .005$ Mann-Whitney). This relationship also suggests that a substantial change in the metabolic processes of ring individuals had occurred prior to 6 months and may be related to a change in protein, nucleic acid or chitin metabolism. Total nitrogen levels significantly declined between 6 and 9 months in ring individuals while those from Slope Water remained unchanged.

Carbon/Nitrogen. Carbon and nitrogen plotted as a percent of wet showed Slope Water and ring populations separating as distinct clusters for each cruise (Fig. 5). The utility of this relationship is that it allows a graphic comparison of components that best separate the two populations. For example, in the cluster for the 6 month ring it appears that percent nitrogen is a more important determinant of cluster separation, while both carbon and nitrogen in the 9 month ring cluster seem to cause a deviation from the Slope Water cluster to a similar degree.

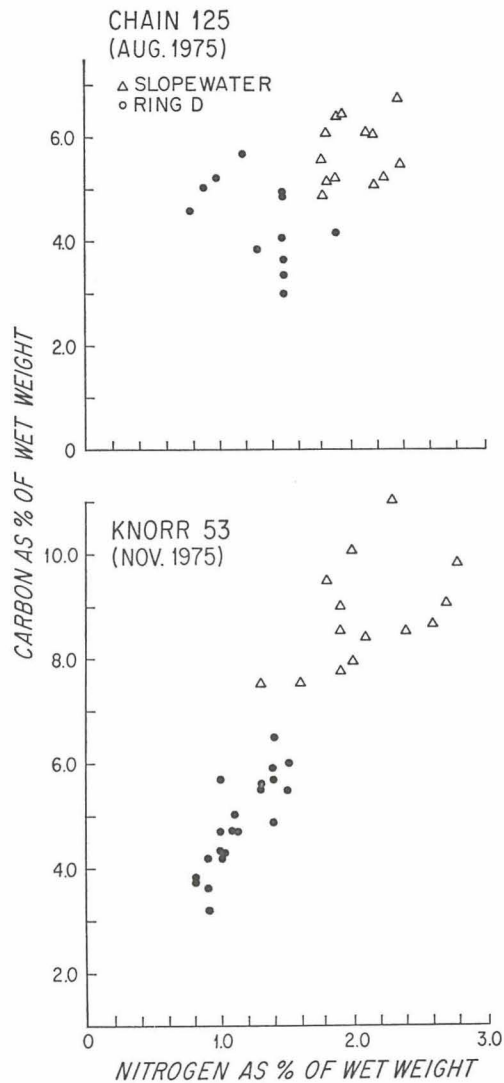


Figure 5. A comparison of *Nematoscelis megalops* percents carbon and nitrogen of wet weight for cruises *Chain 125* and *Knorr 53*.

b. Metabolism and growth

Respiration rates. Rates of oxygen consumption of animals from the *Knorr 53* (9 month) collections were measured after a 6 hour acclimation period and are considered to be between standard and active rates (Childress, 1977). Oxygen consumption of ring animals averaged $70 \mu\text{l O}_2/\text{g wet weight/hr.}$ (range 45.7-104.1, $n = 4$). These measurements were obtained from attempts on 31 animals,

Table 1. Comparison of mean wet weight of *Nematoscelis megalops* individuals in the GI and GII size classes in the Slope Waters and ring D for Chain 125 and Knorr 53. One standard deviation shown in parenthesis.

	Slope Water		Ring	
	GI	GII	GI	GII
Chain 125, August 1975	86.73 (26.16)	30.40 (8.00)	78.14 (17.10)	33.83 (5.75)
Knorr 53, November 1975	85.38 (13.33)	50.09 (9.68)	—	42.00 (6.11)

27 of which died during the 30 minute respiration experiment. In contrast, 37 Slope Water animals were measured with no mortality. Oxygen consumption averaged $680 \mu\text{l O}_2/\text{g}$ wet weight/hr. (range 492-873) almost a factor of 10 higher than ring observations. However, ring animals were less active than Slope Water animals and part of the differences in respiratory rates may be attributable to differences in equilibration rates caused by these activity differences.

Carapace lengths. Fig. 7 of Wiebe and Boyd (1978) illustrates both sets of Slope Water collections have a bimodal size distribution. Similarly, in Ring D at 6 months, carapace measurements show two contracted size frequency peaks (GI and GII) that appear to closely correspond to the similar GI and GII age classes in the Slope Water samples. In Ring D at 9 months only a single size class (GII) was present. Growth measured in terms of mean carapace length increase was most rapid in the Slope Water GI size class averaging 0.9 mm in 90 days. Animals of the GII size class in Ring D over the same interval averaged 0.1 mm.

Wet weight. Only mean wet and dry weight of the GI size classes can be compared owing to the reduction to a single weight frequency class in the 9 month ring (Table 1). In 90 days between collections Slope Water, *N. megalops* increased .22 mg wet wt/day while ring animals grew but .09 mg wet wt/day. After 9 months in ring D the average *N. megalops* was 84% wet wt and 67% dry wt of the corresponding size class in the Slope Water, although they were about equal when the ring was 6 months old. In the three month interval between cruises percent weight gain averaged 39% in the Slope Water and 19% in Ring D. This reduction in weight gain for ring D individuals parallels the lowered carapace length increases noted above.

c. Population structure and abundance

Sex ratio. In adult euphausiids, sex is typically determined by examination of the morphological characteristics associated with the first set of pleopods. Males have a modified endopodite known as a petasma. Females lack this modification

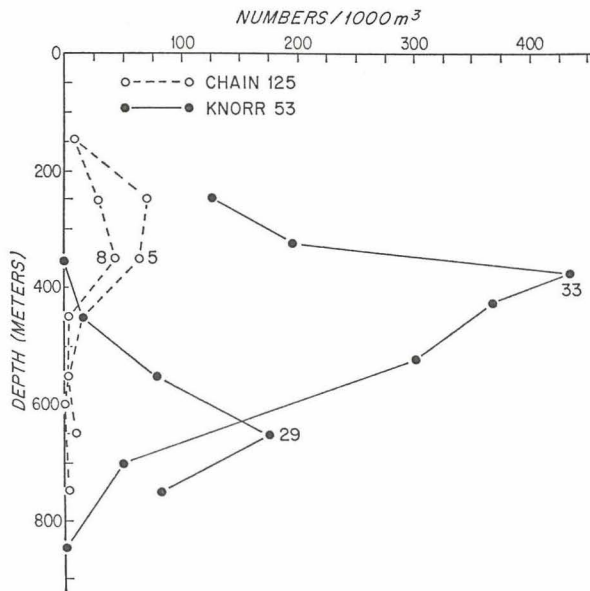


Figure 6. Vertical distributions of *Nematoscelis megalops* taken from night tows in Ring D at 6 months (MOCNESS tows 8, 5) and Ring D at 9 months (33, 29). Abundance is numbers per 1000 m³ for each interval sampled.

and have a simple leaf-like plate. In this study males were determined solely by the presence of the petasma.

In the Slope Water ratios of females to males averaged 51:1 for *Chain 125* and 1.5:1 for *Knorr 53*. The situation in the ring contrasted significantly. In ring D at 6 months the sex ratio was 114:1, whereas at 9 months no mature males were found in more than 1400 individuals inspected. The lack of or change in morphological characteristics of adult males was further investigated by microscopic examination of the endopodites of first pleopods. Males and females of Slope Water *N. megalops* were readily separable. In addition, we observed individuals collected in the ring that had rudimentary petasma development, although they were similar in size to mature males in the Slope Water.

Vertical distribution and numerical abundance

In our Slope Water collections *N. megalops* typically occurred in the upper 600 m with most individuals in the population occurring above 350 meters (see Wiebe and Boyd, 1978). The vertical distribution patterns observed in the 6 month ring (*Chain 125*) was similar except a larger fraction was present below 350 m and individuals occurred down to 800 m. On the second cruise to ring D (*Knorr 53*, 9 months) the vertical distribution exhibited a definite shift downward with the major proportion of the population occurring below 350 m. Numerical abundance

Table 2. Comparison of mean biochemical and physiological measurements for *Nematoscelis megalops* populations in the Slope Water and Ring D from *Chain 125* and *Knorr 53*. (Distribution of data is shown in Figures 2-6.)

	<i>Chain 125</i> August 1975				<i>Knorr 53</i> November 1975			
	Ring		Slope Water		Ring		Slope Water	
Weight (mg)								
Wet (Dry)	33.83	(4.97)	30.40	(5.47)	42.00	(6.17)	50.09	(9.27)
% Lipid wet weight	2.6		2.8		1.8		3.3	
% Carbon Wet (Dry)	4.4	(32.1)	5.7	(32.5)	4.8	(32.1)	9.0	(45.6)
% Nitrogen Wet (Dry)	1.4	(10.4)	2.1	(10.7)	1.0	(7.3)	1.9	(10.6)
% H ₂ O	86.2		82.8		85.4		80.7	
Respiration (ul/gm/hr)	—		—		70.0		682.0	
No. Age classes	2		2		1		2	
Sex Female:Male	113.5:1		51:1		1461:0		1.5:1	
\bar{X} Depth of occurrence m	320		240		545		280	
\bar{X} Carapace length mm	3.63		3.19		3.75		4.12	
\bar{X} Abundance m ² (range)	13.3	(17.3-9.3)	—		91.4	(148.2-34.3)	—	

of *N. megalops* taken from night MOCNESS tows in ring D at 6 and 9 months are shown in Figure 6. MOCNESS tows 5 and 8 were taken on *Chain 125* one day apart near the ring core. Tows 29 and 33 of *Knorr 53* were separated by 2 days. *Nematoscelis megalops* in ring D at 6 months average 13.3 individuals per m² under a column approximately 800 m deep, while in the 9 month ring the two tows average 91.4

Table 2 contains a summary of the biochemical and physiological results.

d. Starvation study. Since maintenance of oceanic euphausiids under laboratory conditions is extremely difficult because of the potential for high mortality from unknown causes and because we were not able to maintain and feed individuals as controls, these data must be interpreted with caution. While no individuals sur-

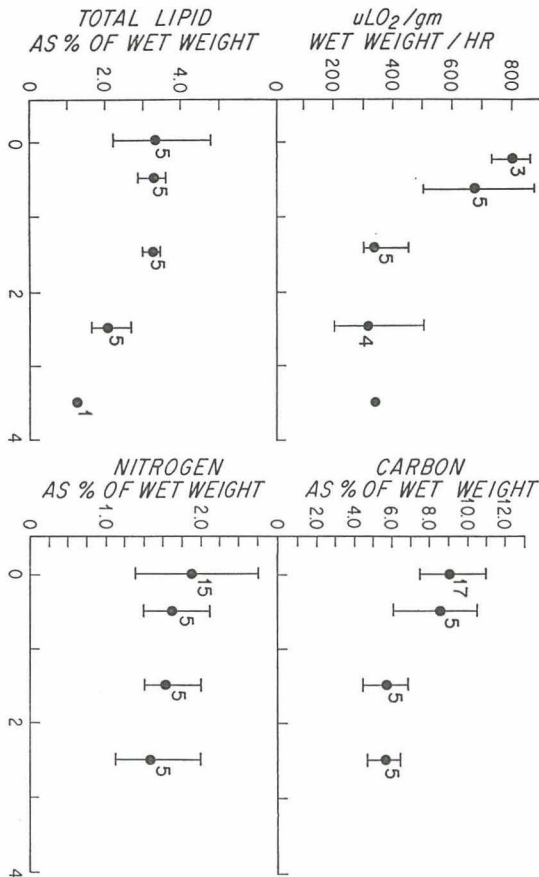


Figure 7. Shipboard starvation study comparing changes in respiration, total lipids, carbon and nitrogen percentages of wet weight through time in days. Blacked circles depict the mean and the vertical bars depict the range of each data set. Beside each circle is the number of individuals examined.

vived the shipboard study longer than 4 days, a reduction in percents carbon and nitrogen began within 2 days, with respiration rates changing more quickly (Fig. 7). Percent water was the most variable although it increased in the 4 day interval. The cursory nature of the study limits interpretation although it appears that acute stress associated with starvation and containment results in reduced carbon and nitrogen levels approximating those found in a ring 6 months of age or older. The rapidity in which complete starvation affected *N. megalops* in this experiment appears to point up the gradual nature of food deprivation in the cold core ring system and suggests that food items for *N. megalops* must be reduced or shifted in type rather slowly.

4. Discussion

Nutritional studies based on confinement of crustacean zooplankton in laboratory systems have typically shown that a lack of food results in metabolic consumption of body lipid and/or protein, often in alternating sequence. These changes are reflected in total carbon and nitrogen and in carbon to nitrogen ratios. During starvation, the percentage of water in tissues gradually increases. Respiratory rates decline and moulting and growth slow or completely stop (see review of Ikeda, 1974). Field studies have suggested that seasonal or geographic reductions in the amount and quality of food can cause changes in the physiological condition of natural oceanic populations (Omori, 1970; Ikeda, 1971; Bamstedt, 1976). Omori (1970) found that *Calanus cristatus* transported out of its home range responded to a consequent reduction in food supply by altered biochemical composition, lowered respiration rate, and sex-ratio changes.

Since the bulk of the population of *Nematoscelis megalops* lives below the euphotic zone (Wiebe and Boyd, 1978) it can reasonably be assumed that as an adult it is not a herbivore. Mauchline and Fisher (1969) state that its mouth parts are not those of a herbivore. Its position in the water column suggests that it obtains its food from euphotic zone detritus and fecal pellets and from zooplankton migrating to and from the euphotic zone. Whatever the details of its diet, the quality and quantity of food available to *N. megalops* depends upon processes in the euphotic zone. Ortner *et al.* (in prep.) have shown that ring aging produces a shift toward lower phytoplankton standing crop, smaller cell size, greater phytoplankton species diversity, and somewhat lower production. All of these changes alter primary production patterns so that they more closely resemble those of the Sargasso Sea. Moreover, zooplankton biomass in the upper 200 m declines as a consistent feature of ring aging. It is inevitable that these changes have profound effects on the food supply of *N. megalops*. The poor physiological state of this species in the ring as evidenced by changes in respiratory rate and chemical composition and by reductions in the rate of growth in terms of carapace lengths and wet weights probably reflects altered food supply.

Our respiration rate experiments primarily indicated the relative inability of ring individuals to withstand the additional stress of a respiration experiment. Slope Water animals survived these experiments and were apparently active enough to respire at fairly high rates. Rayment and Conover (1961) recorded oxygen consumption for *N. megalops* of 110-140 $\mu\text{l O}_2/\text{g}/\text{hr}$ whereas our values averaged 680 $\mu\text{l O}_2/\text{g}/\text{hr}$ for Slope Water animals and only 70 $\mu\text{l O}_2/\text{g}/\text{hr}$ for ring animals. Comparisons of respiration rates are difficult due to the variations induced by differences in activity. While our values for ring and Slope Water *N. megalops* may differ in part due to activity differences, such a difference is in itself indicative of the better condition of Slope Water animals.

No differences in body lipid are evident between the Slope Water and ring in-

dividuals after six months, although the decline in percent nitrogen suggests that protein was used for energy metabolism. The decline in body lipid in ring individuals observed from 6 to 9 months is most likely attributable to the breakdown of constitutive lip0-protein during starvation. *N. megalops* during the study period had a relatively low lipid content in its natural condition and apparently did not possess substantial storage lipid, hence partial starvation immediately induced protein breakdown. It is possible that total lipids were conserved or maintained during the first six months for ring animals, but subsequently were utilized. This may explain the decline in lipid from six to nine months.

Changes in sex ratios in crustacean plankton accompanying dietary deficiencies have been documented by Omori (1970), Ikeda (1971), and Conover (1964), who showed that males predominate in unfavorable conditions. It was suggested that the similarity of adult male body form to previous stages may favor their transformation to adult males. Mednikov (1961) explained the predominance of females in deep sea copepods as an adaptation to increase fecundity in a food-limited population. Butler (1964) found that the hermaphroditic decapod *Pandalus danae* functions first as a male and then as a female. Sex ratios changed as the animal was carried farther from its home range.

Our study has shown a reduction of adult males in the ring by six months and their total absence after nine months. They may have been selectively eliminated from the population by some factor in their environment, although it is difficult to envision any exogenous factor with such dramatic sex selectivity. A more likely explanation involves the fact that our criterion for determining sex depends solely on the presence or absence of male characteristics. The variability of secondary sexual characteristics in adult-sized individuals on both ring cruises suggests that immature males may either be hampered in their transformation to normal adults or that mature males are retrogressing into a nonreproductive male form, indistinguishable by our criterion from the female form.

Despite the evidence showing a definite decline in the physiological state of the population age class reduction, and disappearance of mature adult males, abundance estimates of ring *N. megalops* increases nearly 7-fold between 6 and 9 months. Ordinarily, an increase in abundance might indicate the growth of a healthy population. Evidence presented above indicates that the population is in fact not healthy.

Although other explanations may be invoked to account for the increase in catch rate in the 9 month ring, such as patchiness and sampling error, the physiological and biochemical data coupled with the reduced discrepancy between day and night catches (see Wiebe and Boyd, 1978), lead us to postulate that the increased catch resulted from a decreased efficiency of net avoidance by animals in a weakened condition. Variability in responses to sensory inputs have been suggested to account for relative changes in avoidance (Mauchline and Fisher, 1969; Har-

risson, 1967). Barham (1970) has observed mesopelagic fishes and found increasing states of exhaustion cause greater capture vulnerability. If the net avoidance capabilities of stressed populations are reduced, increases in numbers caught may only reflect poor physiological condition rather than increased abundance. Our data suggest that abundance estimates per se are not sufficient to determine the viability of stressed populations.

Although the assessment of the physiological state of zooplankton is undoubtedly a complex issue, we believe that relatively simple measurements can be used as indicators. Perhaps the most useful index of nutritional condition is the measurement of carbon and nitrogen as a percentage of wet weight. The comparison of these indices between a normal "control" area and a suspected stressful environment may prove to be a valuable tool for establishing the unstressed limits of a population.

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physiological and biochemical condition.

Deterioration of ring individuals is evidenced by an increase in body water content and a reduction in total body lipid, carbon, respiration rates, and nitrogen relative to Slope Water individuals. By 6 months it appears that ring N. megalops must supplement food intake by metabolizing some of their body protein and by 9 months they appear to use lipids as well.

A shipboard starvation experiment involving 40 Slope Water individuals showed that physiological and biochemical states similar to those found in individuals from the 9 months old ring could be duplicated in 4 days of complete starvation.

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