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Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton

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Abstract. The diurnal vertical distribution of a large number of species of zooplankton, ichthyoplankton and micronekton were determined in the top 150 m in three locations in the Shelf Water, on the Nova Scotia Shelf, and Slope and on Georges Bank during spring and fall periods. Species were categorized as to their trophic level and their type of diurnal migration behaviour. The influence of temperature, salinity, and water density on the diurnal vertical distribution of the species was examined. Temperature was found to have the greatest influence on the distribution of the largest number of species. Diurnal migration behavior of the same species in Shelf and Slope water and at different times of the year was examined. Results showed that species changed their behavior in the two water masses, while some species changed their migration behavior at different times of the year. During the night in April the most abundant copepod species, *Calanus finmarchicus*, making up about 80% of the biomass, was found concentrated above the thermocline and the main chlorophyll layer. The majority of the less abundant species of copepods were found below the thermocline and the chlorophyll layer. At night in August the two most abundant copepod species, *Centropages typicus* and *Paracalanus parvus*, making up at least 80% of the zooplankton biomass, were also concentrated above the thermocline and the main chlorophyll layer. Three species of copepods were concentrated at the depth of the main chlorophyll layer and two species were concentrated below the chlorophyll layer and thermocline. The vertical distribution of other zooplankton and ichthyoplankton species was examined in relation to the thermocline and chlorophyll layer. Relationships between concentrations of six species of fish larvae and all species of copepods in the same samples showed a general increase in the numbers of larvae m^{-3} as the numbers of copepods m^{-3} increased in a range of 500–4000 m^{-3}. However, the concentration of *Merluccius bilinearis* decreased as the concentration of copepods exceeded 4000 m^{-3} suggesting that high concentrations of copepods may not be a favourable environment for the larvae.

Introduction

Recent studies on marine fish larvae have demonstrated that they actively seek out preferred environments in the vertical plane. Blaxter (1973) showed that herring (*Clupea harengus*) and plaice (*Pleuronectes platessa*) changed their vertical migration in response to light intensity, while Reynolds and Thomson (1974) found the grunion (*Leuresthes sardina*) responded to gradients of light, temperature, turbulence and oxygen, and the anchovy (*Engraulis mordax*) was demonstrated to seek out high concentrations of food (Hunter and Thomas, 1974; Lasker, 1975).

The lack of a clear relationship between concentrations of food particles and the density of fish larvae in the field has perplexed marine fisheries ecologists for a long time. Lasker (1975) presented evidence that the mean density of food for fish larvae was too low to support a reasonable survival of the larvae through metamorphosis. As a consequence, the fine scale vertical distribution of both larvae and their zooplankton prey is now considered an important component in understanding the feeding and survival of fish larvae (Ellertsen *et al.*, 1981; Owen, 1981; Kauffman *et al.*, 1981).

After reviewing the literature, May (1974) concluded that food concentration could affect the survival of fish larvae even though the field data did not show that it was a decisive factor. Laboratory experiments have shown that there is a critical abundance of food below which survival of larvae decreases quickly. Also the food densities needed for survival and a good condition factor were generally in the high end of the range for field concentrations of microzooplankton (Houde, 1978). Many studies reported good survival only at concentrations of prey much higher than reported in nature (Laurence, 1977; Saksena and Houde, 1972.

Discontinuities in the distribution of salinity and temperature have been described as regions in which different species of zooplankton concentrate (Cushing, 1951). Hansen (1951) found that the dominant species of zooplankton in a Norwegian fjord were closely associated with strong temperature and salinity discontinuities. Harder (1968) found experimentally that the majority of zooplankton species he tested accumulated at a salinity discontinuity of 3.6–17.4°/oo. Boyd (1973) reported that euphausiids were concentrated at temperature gradients. Angel (1968) found that different species of ostracods reacted differently when encountering a thermocline, and Hensen and Dunbar (1970) described the accumulation of *Limacina helicina* at a salinity discontinuity in the Arctic. Marlowe and Miller (1975) stated that the diel vertical migration of a number of Pacific subarctic copepods stopped at the thermocline.

Previously most zooplankton diel vertical distribution studies have concentrated the sampling during a single time period and looked at a narrow size range of animals. An exception was the work of Ortner *et al.* (1980) that looked at the vertical migration of zooplankton and macrozooplankton during three different seasons in slope water and the Sargasso Sea. They did not identify the animals to species, but rather to broad groups within different size classes.

The objectives of this study were to determine changes in diel vertical distribution of individual species of zooplankton, ichthyoplankton and micronekton in the top 150 m of two different water masses, the shelf and slope water, at different times of the year and to examine the depth relationships between fish larvae and their potential zooplankton prey. In addition, the physical structure of the water was examined to determine the influence of temperature, salinity and density on the vertical distribution of the different species.

Methods

Area sampled

The Nova Scotia Shelf was sampled in August 1976, Georges Bank was sampled in October 1978 and the Nova Scotian Slope region was sampled in April 1979 at which time two different water masses were sampled, the shelf water and the warmer slope water (Figure 1). All biological samples were taken with the BIONESS (Sameoto *et al.*, 1980), a sampler capable of collecting samples over

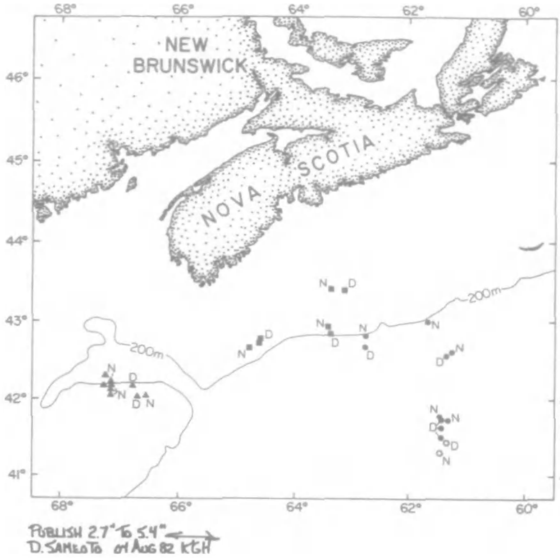


Fig. 1. Locations of stations on the Nova Scotia Shelf and Slope and on Georges Bank. (April 1979: ● – shelf water; ○ – slope water: August 1976: ■ – shelf water; ▲ – Georges Bank; D – day sample; N – night sample.)

ten separate depth intervals on command. The mouth area of the nets was 1 m^2 and the mesh size of the nets was 243 μm. The BIONESS was towed at a speed of 1.5 $m\ s^{-1}$ as it was lowered obliquely to the desired depths. The nets were opened and closed at depth intervals of either 5 or 10 m in the top 50 m and at 10 – 15 m intervals below 50 m down to 150 m depth. Samples were taken during hours of daylight and darkness. The samples were preserved in a 5% buffered formalin and seawater solution. All animals between 1 and 10 cm were removed from the sample, counted and identified. The remaining portion of the sample with animals < 1 cm in length was split a number of times with a Motoda sample splitter and one of the fractions, of 200 – 400 animals, was entirely identified to species and counted. The sorting and identification of the samples was done by MacLaren Marex of Dartmouth, Nova Scotia and the Canadian Oceanographic Identification Centre, National Museum of Natural Sciences in Ottawa, Ontario.

Temperature data were collected simultaneously with the biological samples during all the sample periods and salinity data were collected during the 1979 sample period with a Guildline Instruments conductivity cell and temperature probe mounted on the BIONESS.

Chlorophyll *a* concentrations were measured with an *in situ* Variosens fluorometer (Impulsphysik GmbH, Hamburg, West Germany) mounted on the Batfish (Herman and Denman, 1976) during the cruises of April 1979 and August 1976 and obtained from A. Herman (Bedford Institute of Oceanography, personal communication). Chlorophyll *a* concentrations were obtained from R. O'Boyle (Marine Fish Division, Bedford Institute of Oceanography, personal communication) for the Georges Bank region during the October 1978 period.

The data on the vertical distribution of species are expressed as percentages of the total populations in all the samples collected. A comparison was made of the vertical distribution of the species between the individual tows for day samples and also for night samples for each sampled area using a chi-square test for goodness of fit (Steele and Torrie, 1960) with no significant differences in distribution patterns between samples seen within the two time periods at $p \leq 0.05$. The data for all the day samples were combined to give average day time distributions and the night data were similarly treated to give the night distributions. The average numbers of each species m^{-2} for day and night periods for each region were calculated from all the samples to demonstrate their relative abundances (Figure 2). A series of unpaired 't' tests (Steele and Torrie, 1960) were calculated to determine day/night differences in abundance of numbers m^{-2} of each species for each sampled location, except the Slope water where only two stations were sampled. Nineteen out of a total of 95 species showed a significant difference ($p \leq 0.05$) in numbers between day and night.

To determine if a significant change in the vertical distribution occurred between day and night a chi-square test for normal approximation (Steele and Torrie, 1960) was applied to all species data. This was done by determining the depth of the top 50% of the population of a species during the day and comparing the percentage of the night population within the same depth interval by the chi-square test, using a probability level of 0.05.

Temperature, salinity and water density relationships with vertical distribution

The relationship between percentage of the population of each species and the temperature, salinity and water density (σ_t) was determined for the species collected in April 1979. Only species population percentages and temperature were compared for August and October data. The numbers of animals of each species found at each sampled temperature and salinity were calculated from the individual samples and converted to a percentage for the total population of the species. This was done separately for the day and night data for each of the four sampled locations. The temperature profiles (Figure 2) are averages for all stations sampled in each of the day and night periods. These profiles are provided to show the reader the general temperature structure of the water but were not used in the determination of the temperature preference of the various species.

Results

Vertical migration

The day and night vertical distribution of all the common species of animals collected are shown for all four sampled locations (Figures 2a – 2e). The vertical migration of the species was categorized into four types: (i) those that showed no vertical migration; (ii) those that always migrated upwards at night; (iii) those that migrated during one sampling period and not during others; and (iv) those that showed a reverse migration behavior (i.e., going deeper during the night) (Table I).

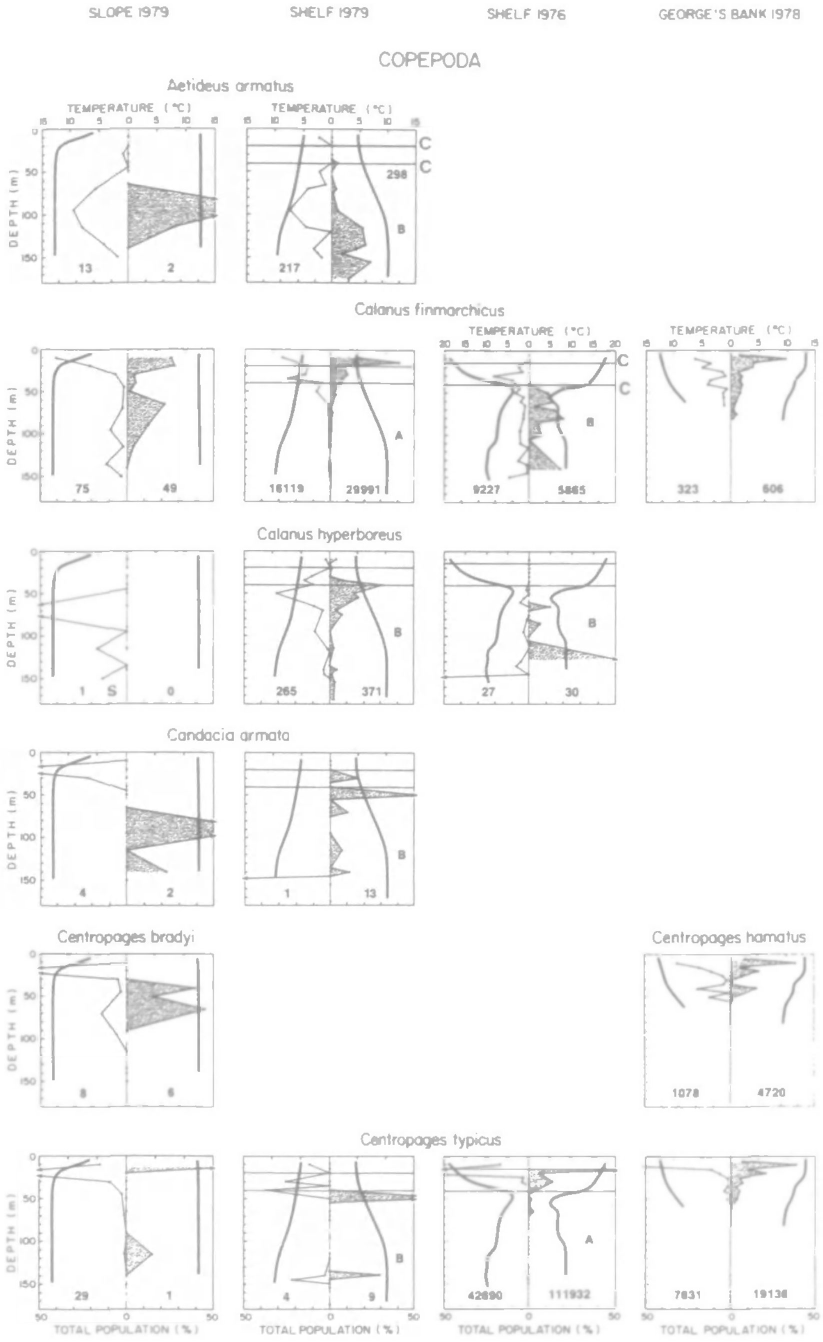
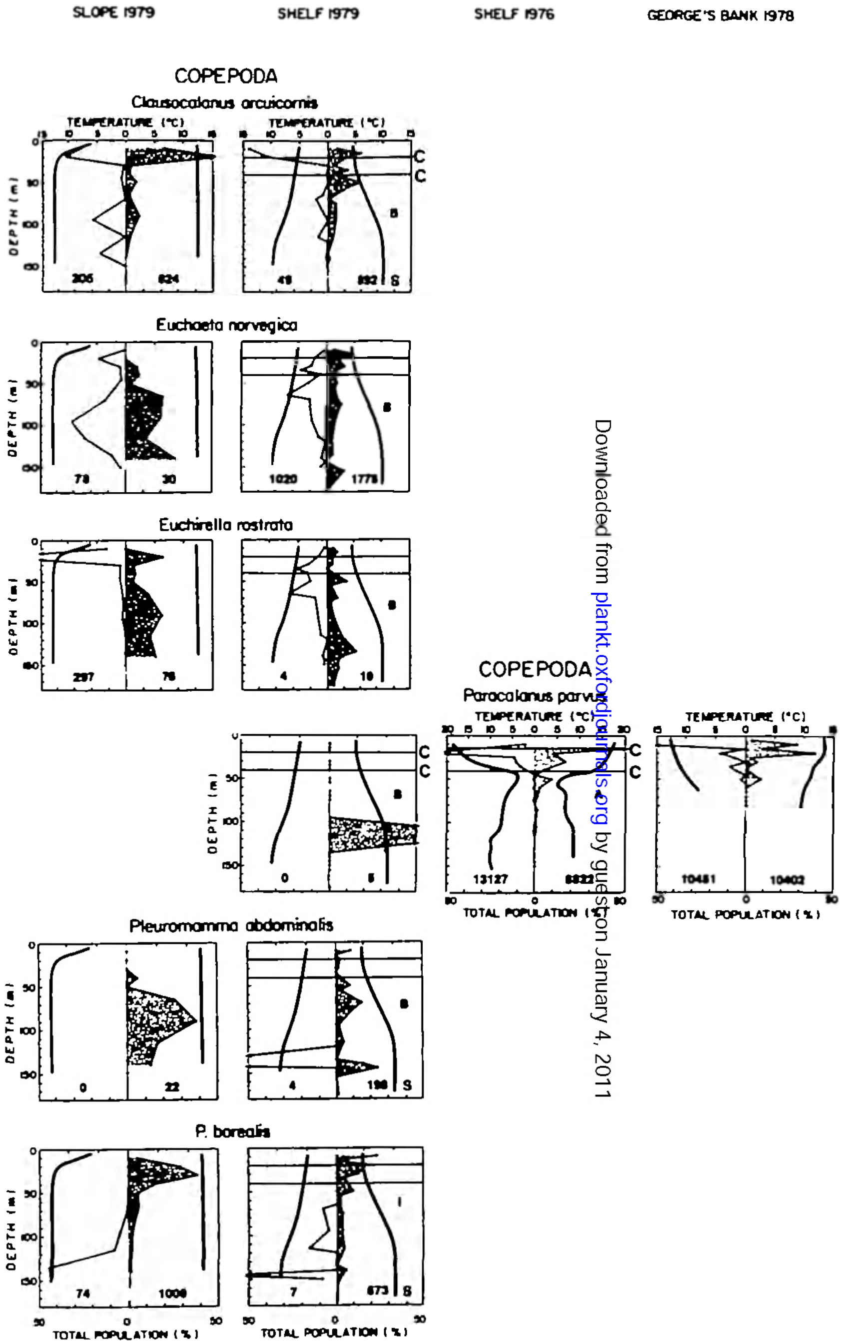
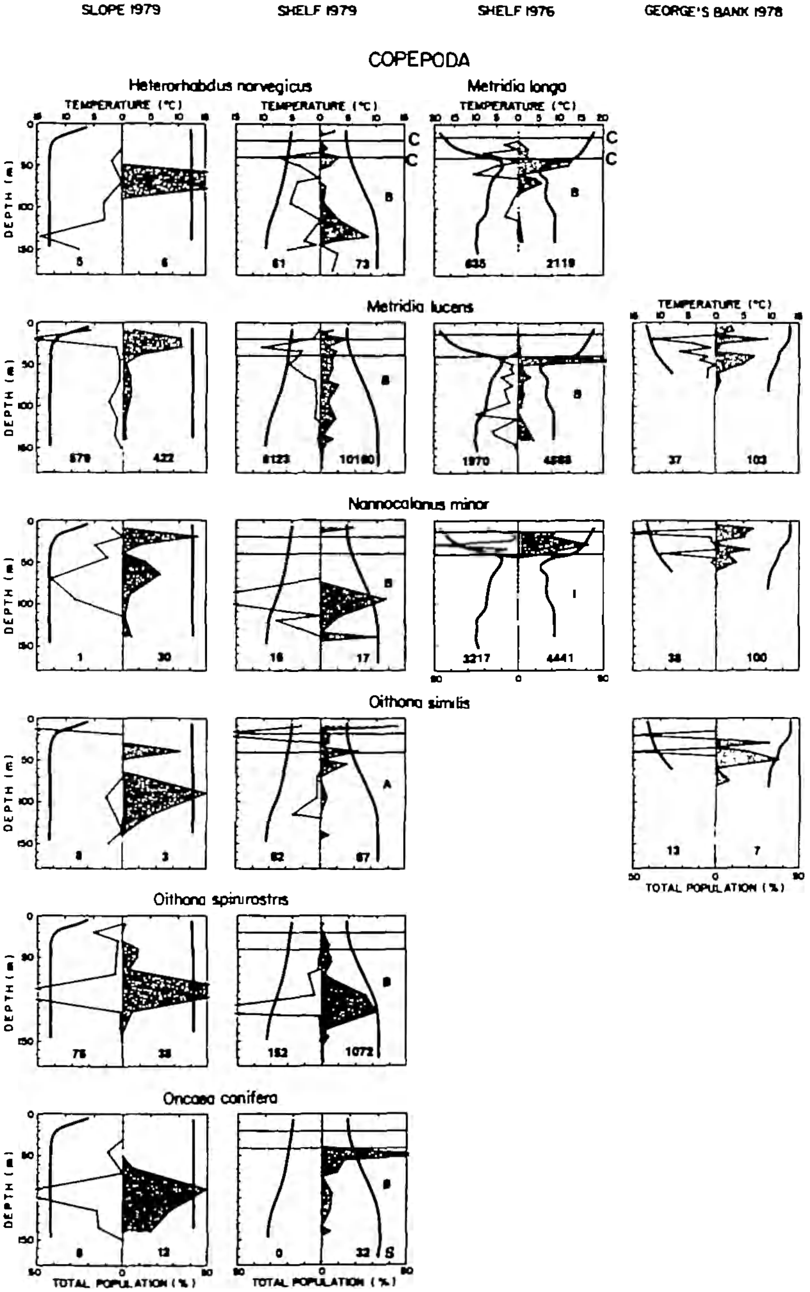
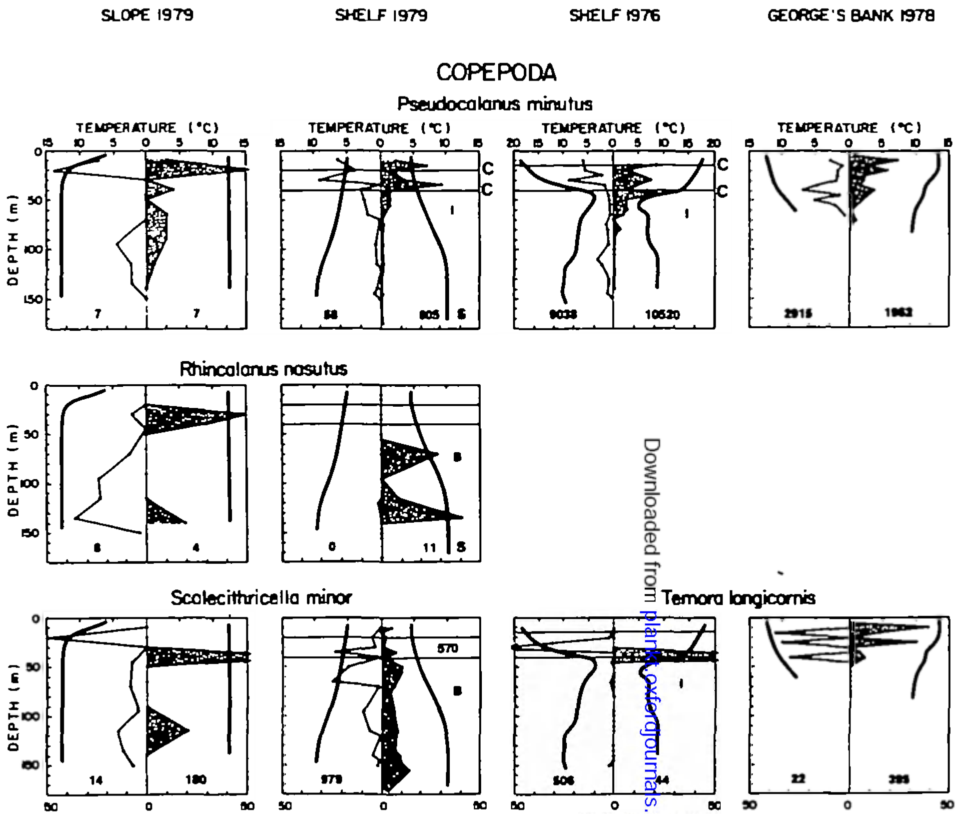
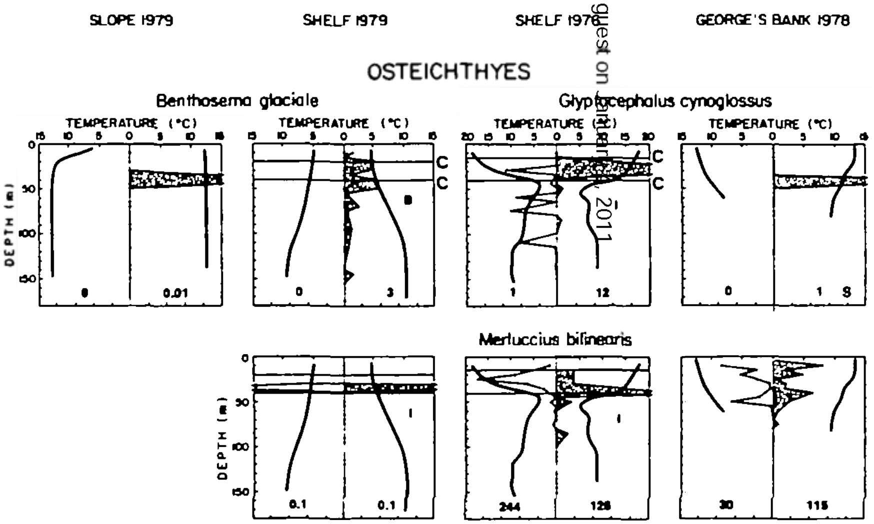

SLOPE 1979
SHELF 1979
SHELF 1976
GEORGE'S BANK 1978
COPEPODA
Aetideus armatus
TEMPERATURE (°C)
DEPTH (m)
13
2
217
298
C
B
Calanus finmarchicus
75
49
16119
29991
A
9227
5865
323
606
Calanus hyperboreus
1
S
0
265
371
27
30
Candacia armata
4
2
1
13
Centropages bradyi
8
6
Centropages hamatus
1078
4720
Centropages typicus
29
1
4
9
42690
111932
7831
19136
TOTAL POPULATION (%)

Fig. 2.


SLOPE 1979
SHELF 1979
SHELF 1976
GEORGE'S BANK 1978
COPEPODA
Clausocalanus arcuicornis
TEMPERATURE (°C)
DEPTH (m)
0
50
100
150
205
824
41
892
C
C
B
S
Euchaeta norvegica
78
30
1020
1778
Euchirella rostrata
297
76
4
10
COPEPODA
Paracalanus parvus
0
5
13127
6822
10481
10402
TOTAL POPULATION (%)
Pleuromamma abdominalis
0
22
4
198
P. borealis
74
1008
7
673
I
50
0
50
TOTAL POPULATION (%)


SLOPE 1979
SHELF 1979
SHELF 1976
GEORGE'S BANK 1978
COPEPODA
Heterorhabdus norvegicus
Metridia longa
Metridia lucens
Nannocalanus minor
Oithona similis
Oithona spinirostris
Oncaea conifera
TEMPERATURE (°C)
DEPTH (m)
TOTAL POPULATION (%)
C
B
A
I
S
5
6
61
73
635
2119
679
422
8123
10180
1970
4888
37
103
1
30
16
17
3217
4441
38
100
8
3
82
87
13
7
76
38
152
1072
0
12
32


SLOPE 1979
SHELF 1979
SHELF 1976
GEORGE'S BANK 1978
COPEPODA
Pseudocalanus minutus
TEMPERATURE (°C)
DEPTH (m)
C
C
I
7
7
58
805
S
9038
10520
2915
1962
Rhincalanus nasutus
8
4
S
0
11
S
Scolecithricella minor
Temora longicornis
570
S
I
14
180
979
506
44
22
395
TOTAL POPULATION (%)


SLOPE 1979
SHELF 1979
SHELF 1976
GEORGE'S BANK 1978
OSTEICHTHYES
Benthosema glaciale
Glyptocephalus cynoglossus
TEMPERATURE (°C)
DEPTH (m)
C
C
S
8
0.01
0
3
1
12
0
1
S
Merluccius bilinearis
I
I
0.1
0.1
244
125
30
115

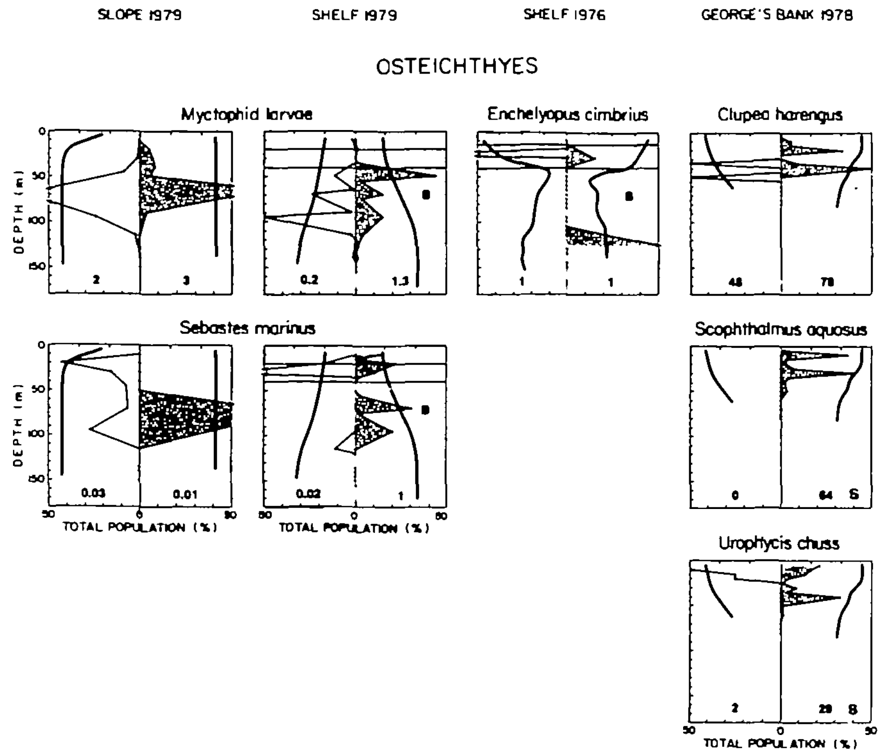


Fig. 2. Vertical distributions of populations of common species of copepods and fish larvae and adults during the day and night (shaded values) in the Nova Scotia shelf water in April 1979, August 1976 and on Georges Bank in October 1978. Each dot represents the mean depth of a sampled strata. Numbers in boxes are the mean numbers of animals m^{-2}. Letters on night side of figures mean: A – animals concentrated above chlorophyll layer depth, B – animals concentrated below chlorophyll layer depth and I – animals concentrated in the chlorophyll layer depth. Horizontal lines marked with a C on figures for shelf 1979 and 1976 represent the depth range of the chlorophyll layer. S means there were significantly ($p < 0.05$) more animals m^{-2} at night than during the day as measured with an unpaired 't' test.

A number of species were absent or found at low concentrations during the day, but were common at night (Figure 2). The most probable explanation for this was that these animals were found at a depth >150 m during the day (Sameoto, 1982a) and therefore were out of the sampled depth range. Avoidance of the BIONESS by some larger species cannot be ruled out, however, the sampler is very effective in collecting macrozooplankton (Sameoto *et al.*, 1980; Sameoto, 1983). Therefore the absence of a species during the day but its presence at night was considered evidence for vertical migration.

Copepods. Herbivorous copepod species showed three types of migration behavior, types 1, 2 and 3. Three species were classified as type 1, three species as type 2 and four species as type 3 (Table I and Figures 2a–2d). Among the omnivorous copepod species, seven species had type 1 behavior, five showed type 2, four showed type 3. Only four copepods were classified as carnivores: one had

Table I. List of species that were studied for evidence of diurnal vertical migration during April 1979 in Slope and Shelf water, August 1976, on the Nova Scotia Shelf and on Georges Bank in October 1978. 'Yes' and 'no' refer to whether diurnal migration took place; (–) means there were no data; (r) means the animals migrated deeper at night. Trophic level classifications of species as herbivores (H), omnivores (O) or carnivores (C) are given. The type of migration behavior is given.

Group	Species	April		Aug.	Oct.	Trophic classification	Type of migration
		Slope	Shelf	Shelf	Georges Bank		
Gastrapoda	*Clione* sp.	no	no	no	–	C	1
	Limacina retroversa		yes	–	–	H	2
	L. trochiformis	yes	no	–	–	H	3
	L. helicina	–	–	no	–	H	1
Cephalopoda	*Megalocranchia* sp. (larvae)	yes (r)	yes	–	–	C	4
	Illex illecebrosus (larvae)	–	yes (r)	–	–	C	4
Polychaeta	*Tomopteris helgolandica*	no	no	yes	yes	C	3
Ostracoda	*Conchoecia curta*	yes	no	–	–	O	3
	C. elegans	yes	yes	–	–	O	2
	C. haddoni	no	yes	–	–	O	3
	C. obtusata	yes	no	–	–	O	3
Copepoda	*Aetideus armatus*	no	yes (r)	–	–	C	4
	Calanus finmarchicus	no	yes	no	no	H	3
	C. hyperboreus	–	no	no	–	H	1
	Candacia armata	yes (r)	yes	–	–	C	2
	Centropages bradyi	no	–	–	–	O	1
	C. hamata	–	–	–	no	O	1
	C. typicus	no	no	no	no	O	1
	Clausocalanus arcuicornis	no	no	–	–	H	1
	Corycaeus sp.	no	yes	–	–	O	3
	Eucalanus attenuatus	yes	yes	–	–	H	2
	E. elongatus	yes	yes	–	–	H	2
	Euchaeta norvegica	no	no	–	–	C	1
Copepoda	*Euchirella rostrata*	yes	no	–	–	O	3
	Heterorhabdus norvegicus	yes	no	–	–	C	3
	Metridia longa	–	–	no	–	O	1
	Metridia lucens	no	no	yes	no	O	3
	Nannocalanus minor	yes	no	no	no	H	3

	Oithona similis	no	no	–	no	O	1
	Oithona spinirostris	no	no	–	–	O	1
	Oncaea conifera	no	yes	–	–	O	3
	Paracalanus parvus		yes	–	–	H	3
	Pleuromamma abdominalis	yes	yes	–	–	O	2
	P. borealis	yes	yes	–	–	O	2
	P. glacilis	yes	–	–	–	O	2
	P. robusta	yes	yes	–	–	O	2
	P. xiphias	yes	yes	–	–	O	2
	Pseudocalanus minutus	no	no	no	yes	H	3
	Rhincalanus nasutus	yes	yes	–	–	H	2
	Scolecithricella minor	no	no	–	–	O	1
	Temora longicornis	–	–	no	no	O	1
Amphipoda	*Parathemisto abyssorum*	no	no	no	no	C	1
	Parathemisto gaudichaudii	no	yes	–	yes	C	3
Euphausiacea	*Euphausia krohni*	yes	yes	–	no	O	2
	Meganyctiphanes norvegica	yes	yes	yes	no	O	3
	Nematoscelis megalops	yes	yes	–	no	H	3
	Thysanoessa calyptopis	no	no	no	no	H	1
	T. furciliae	no	no	–	–	H	1
	T. longicaudata	no	no	yes	no	C	3
	T. inermis	–	–	yes	–	O	1
	T. raschi	–	–	yes	–	O	1
Chaetognatha	*Sagitta elegans*	–	–	yes		C	2
	S. lyra			yes		C	2
	S. tasmanica			yes		C	2
Urochordata	*Oikopleura vanhoeffeni*	–	no	no	–	H	1
Osteichthyes	*Merluccius bilinearis*	no	no	no	no	C	1
	Sebastes marinus	no	no	–	–	C	1
	Myctophid larvae	no	yes	–	–	C	2
	Benthosema glaciale	yes	yes	–	–	C	2
	Glypocephalus sp.	–	–	yes	yes	C	2
	Enchelypus cimbrius	–	–	no	–	C	1
	Urophycis chuss	–	–	–	no	C	1
	Scophthalmus aquosus	–	–	–	yes	C	2
	Clupea harengus	–	–	–	yes	C	2

type 1 behavior, one was a type 2 migrator, one was type 3 and one was type 4.

Amphipods and euphausiids. The two common species of hyperiid amphipods were both carnivores, but showed different migration behavior. *Parathemisto abyssorum* never migrated, whereas *P. gaudichaudi* (*Themisto gaudichaudi* according to Bowman *et al*. (1982)) was a type 3 migrator, always moving to the upper layers at night (Table I) in shelf water but not migrating in slope water.

The euphausiid species *Euphausia krohni* and *Meganyctiphanes norvegica* are omnivores and both migrated vertically in the Nova Scotia shelf and slope water. In August, during the day, parts of the *M. norvegica* population were found above and below the thermocline, whereas at night no animals were found below the main concentration at the base of the thermocline. None of the species of euphausiids collected on Georges Bank migrated vertically at night, whereas all the species except *Thysanoessa longicaudata* always migrated vertically in the Nova Scotia shelf and slope water. *T. longicaudata* migrated only in August from the depth of the thermocline to the mixed layer, a distance of ~20 m. The early developmental stages of *Thysanoessa* sp. never showed evidence of vertical migration on any of the sampled regions (Table I).

Osteichthyes. All species of fish, adults and larvae, collected were considered to be carnivores (Table I). Four of the nine species of larvae never showed evidence of vertical migration (type 1 behavior), whereas four species always migrated vertically (type 2 behavior) (Table I and Figure 2e) and one, the myctophid larva *B. glaciale*, migrated in shelf water but not in the slope water.

Other groups. The three species of chaeotognaths all migrated vertically at night (Table I), while the urochordate *Oikopleura vanhoeffeni* a herbivore, did not migrate. Two species of Cephalopoda were collected during April 1979, the juvenile squids *Megalocranchia* sp. and *Illex illecebrosus*, and both species showed evidence of a reverse migration (type 4 behavior). Only one species of gastropod, *Limacina retroversa*, showed an upward vertical migration at night; similar behavior was reported by Southward and Barrett (1983). *L. trochiformis*, *L. helicina* and *Clione* sp. had type 1 behavior. The polychate *Tomopteris helgolandica* migrated vertically only during August in the shelf water. The ostracod species showed a mixed behavior (type 3) in the slope and shelf water (Table I).

Species relationship between temperature, salinity and density

During April, shelf water (defined as temperature <11°C and salinity $<35.5^{o}/_{oo}$) and slope water (defined as temperature >12°C and salinity $>35.6^{o}/_{oo}$) provided a wide range of salinity, temperature and density values in which to examine species distribution. Salinity data were not routinely collected during the other sampling periods; therefore, only range of temperature preferences are given for the August and October data.

The percentage of the total population for each species in the April samples was plotted on a σ_t range of 25.0–27.5 and against salinity and temperature. The distributions relative to density and salinity were very similar, with the animals found over a wide range of both. However, animals of all species were much more concentrated around a particular temperature or narrow temperature range (Figure 3). Such centres of concentration were not always representative of a

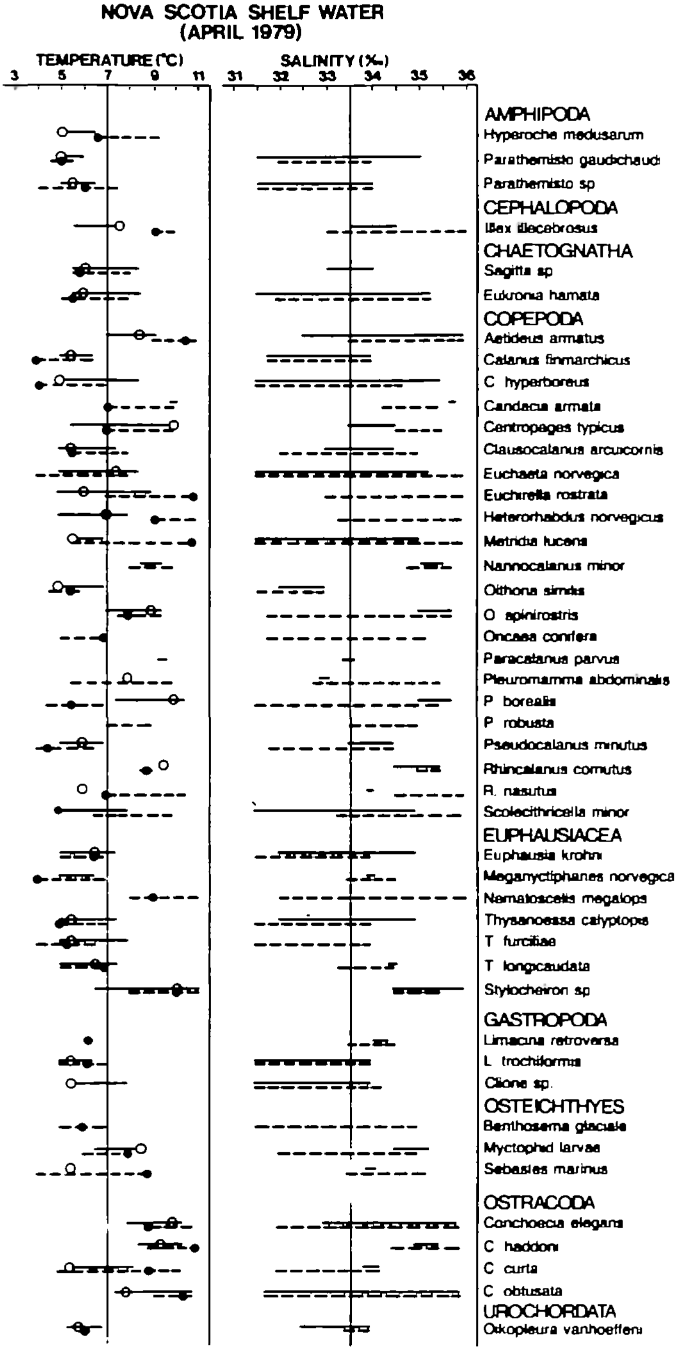


Fig. 3. The preferred day and night temperature and salinity range of 75% of the population of different species and the position of the dominant mode of the species in the shelf water sampled April 1979 (● – night data; ○ — day data). Vertical line at 7°C is the average mid-point of the thermocline. Vertical line on salinity is only to act as a guide to locate the position of the salinity ranges of species.

majority of the population but only the largest population mode within the temperature range (Figure 2). The most likely reason for the lack of a strong relationship with salinity was that a wide range of salinities (31.5 – 34.3‰) was found at the shelf water thermocline on different stations, and the animals were influenced more by temperature than the salinity gradient.

Samples taken in the slope water during April provided an opportunity to determine the depth distributions for many species in water with a relatively uniform temperature and salinity profile. During the day a layer of shelf water of 20 m depth overlay the slope water, below 20 m the temperature (12.5°C), and salinity (35.3 – 35.6‰) structure of the water was the same as the night station (Figure 2). The night station did not have a layer of shelf water at the surface.

A number of species were observed at similar depths at different stations in the slope and shelf water even though there were temperature differences as great as 7°C at the same depths between the two water masses. The copepods found at the same depths but at different temperatures were *Clausocalanus arcuicornis* (Figure 2b), *Pleuromamma borealis* (Figure 2b), and *Pseudocalanus minutus* (Figure 2d). Other species which showed similar behavior were the amphipod *P. gaudichaudi*, the gastropod *L. trochiformis* and the adults and larvae of the myctophid *Benthosema glaciale* (Figure 2e). All the other species showed a depth preference that appeared to be influenced by the temperature, either showing a much wider depth distribution in the slope water, such as *C. finmarchicus* (Figure 2a) or, in certain warm-water forms such as *Nannocalanus minor*, remaining in the warmer, deeper shelf water at night instead of migrating to the surface as at slope water station (Figure 2c).

A majority of the species in shelf water were found either in the cold-water layer or the warm layer with few species showing no temperature preference. Taking the separation between warm and cold water as the temperature in the centre of the thermocline, which was 7°C in April 1979, the dominant population modes of most species, as well as their ranges, were either above or below the thermocline during both day and night (Figure 3). Similar observations were made on Georges Bank in October and the Nova Scotia Shelf in August (Figure 4). Even species that migrated vertically at night generally did not move from one temperature extreme to the other. Southward and Barrett (1983) found that of 21 invertebrate taxa off Plymouth 48% moved across a thermocline of 2°C, 33% did not move, and some species migrated through a temperature difference of 6°C. Most migrators in this study passed through a small change in temperature and salinity, usually <4°C and <4‰. *T. longicaudata* experienced the most extreme temperature change during its migration in August, moving from 3°C water at the base of the thermocline to 18°C water above the thermocline, a depth change of ~20 m.

Changes in vertical migration behavior

Samples taken in two water masses and at different seasons showed changes in the migration behavior of species with time and area. Three copepod species migrated in the slope water but not in the shelf water in April or the other sampled periods, these were *Heterorhabdus norvegicus*, a carnivore, *N. minor*, a

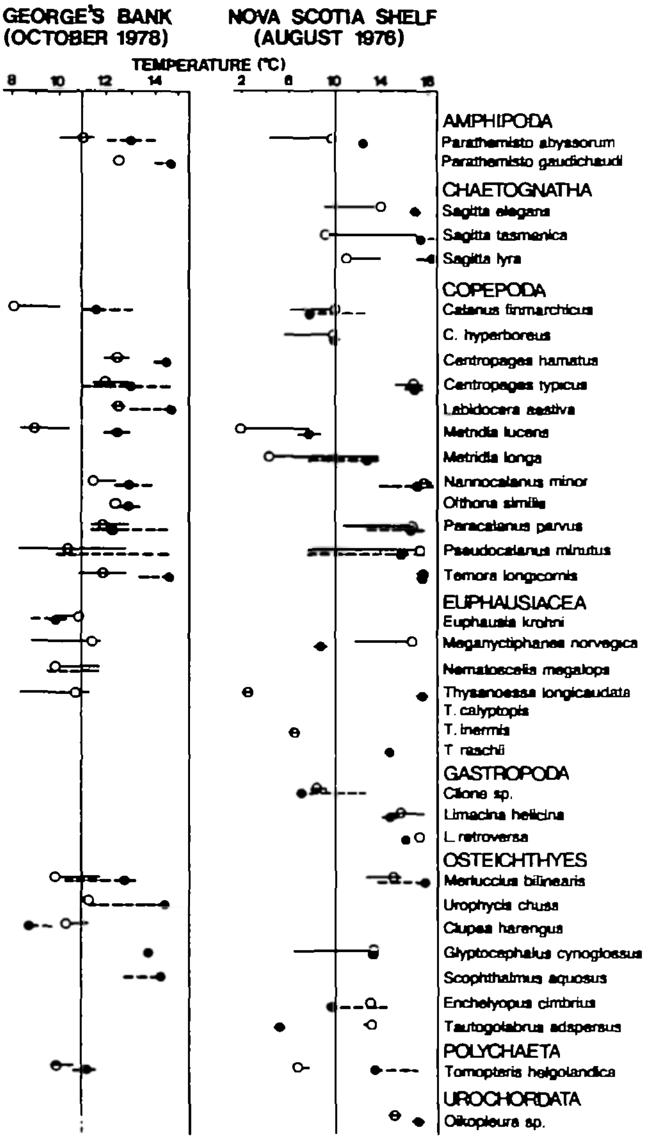


Fig. 4. The preferred day and night temperature range of 75% of the population of different species and the position off the dominant population mode of the species in shelf water sampled August 1976 and Georges Bank sampled October 1978. (● – night data; O — day data). Vertical lines at 11°C (1978) and 10°C (1976) mark the average mid-point of the thermocline.

herbivore (Figure 2c), and *Scolecithricella minor*, an omnivore (Figure 2d). Species that only migrated in shelf water during April were *C. finmarchicus*, a herbivore (Figure 2a), and *Oncaea conifera*, an omnivore (Figure 2c). Sameoto (1982b) showed *O. conifera* was found at 400 m during the day in shelf water during April 1979. The only copepod to show a change in migration behavior with season in shelf water was *Metridia lucens*, an omnivore, which showed a distinct night time vertical migration in August but not during any of the other periods (Figure 2c). The polychaete *T. helgolandica*, and the euphausiid *T. longicaudata*, both carnivores, migrated in the shelf water during August but not at any other time. All the other species showed consistent behavior during the different sampling periods.

A number of species were found in three or all four locations and, for these species, it was possible to describe their depth and temperature ranges at different times of the year. *C. finmarchicus* was found in the cold surface waters during April at a depth of 10 – 20 m. It was found in the cold water at and below the thermocline during August with most of the population below 50 m depth. However, on Georges Bank in October a large percentage of the population of *C. finmarchicus* was found in the warm water both during the day and night at a depth of 20 m similar to the April distributions (Figure 2a). The *C. finmarchicus* were not separated into copepodite stages and therefore it was possible that what appeared to be a change in behavior with the different seasons and locations may have been different distributions of various stages of the species. Williams and Conway (1980) showed younger stages of *C. finmarchicus* overlying the older stages during May. *Calanus hyperboreus* was found in deeper and warmer water than *C. finmarchicus* during April and August (Figures 2a and 4). *Centropages typicus* had similar depth distributions in the slope water in April, the shelf water in August and on Georges Bank in October, but it was significantly deeper in the shelf water in April (i.e., at 50 m) (Figure 2a) than during the other three periods. *M. lucens* showed the greatest depth variability of all the copepod species. It was concentrated between 20 – 30 m in the slope water and on Georges Bank, and was found over a wide range of depths during the night in the shelf water in April and concentrated in the thermocline at night during August (Figure 2c). *Oithona similis* had similar depth distributions in the shelf water in April and on Georges Bank during October, but a larger percentage of the population in the slope water in April was below 75 m depth than during the other seasons (Figure 2c). *Paracalanus parvus* was found at ~100 m in the shelf water during April, but it was in the upper 30 m of shelf water during August and on Georges Bank in October (Figure 2b), tending to be concentrated in the warmer water.

The distribution of *P. minutus* appeared to be independent of temperature (Figure 2e). The majority of the population was concentrated between 10 – 40 m at all the sampled locations and times, even though the temperature at these depths varied greatly (4.5 – 18°C).

The non-copepod species *P. abyssorum, M. norvegica, T. longicaudata* and *T. helolandica*, all showed significant changes in vertical distribution in the shelf water in August from other sampled periods, showing a concentration in the region of the thermocline not seen in April. Only one species of fish larva, *Merluccius bilinearis*, was found at three different sampling periods. In the shelf water, in April and August, the larvae showed a preference for a very narrow depth range concentrating at ~30 m, whereas on Georges Bank in October the larvae were distributed from 5 m to below 50 m (Figure 2e), suggesting that biological factors such as the food supply, rather than the physical environment, may be the dominant influence in their depth selection.

In the shelf water during August, a sharp thermocline seemed to be the dominating influence affecting the vertical distribution of all the species. Some such as the copepods *C. typicus* (Figure 2a), *N. minor* (Figure 2c), *P. parvus* (Figure 2b), *P. minutus* (Figure 2d), and the gastropods, *L. helicina* and *L. retroversa*, and the urochordate, *Oikopleura* sp., were always found above the thermocline. Other species, such as the *Sagitta* sp., *Thysanoessa inermis, T. longicauda* and *T. raschii* were also found above the thermocline at night; however, during the day a major portion of the *Sagitta* sp. populations were found below the thermocline, as were the three *Thysanoessa* species. Three species tended to concentrate in the thermocline both day and night, *M. longa, M. lucens* (Figure 2c) and *Temora longicornis* (Figure 2d), whereas other species, *P. abyssorum, Clione* sp. and *M. norvegica* concentrated near the base of the thermocline, particularly at night.

Chlorophyll a and zooplankton distributions

A chlorophyll *a* concentration of ~1–2 mg m^{-3} was found in the shelf water during April at a depth of 20–40 m, whereas in the slope water there was a uniform distribution of chlorophyll *a* from the surface to 40 m at a concentration of 2–3 mg m^{-3} (A. Herman, Bedford Institute of Oceanography, personal communication). During August a chlorophyll *a* maximum, with levels up to 2 mg m^{-3}, was found within the thermocline with very low levels of chlorophyll *a* (<0.5 mg m^{-3}) above 15 m and below 40 m (A. Herman, Bedford Institute of Oceanography, personal communication). On Georges Bank the chlorophyll *a* concentration was uniformly mixed throughout the entire water column (O'Boyle *et al.*, 1979).

The depths of the main night time concentrations of the various species were compared with the depth of the main chlorophyll layer in the shelf water during April and August (Figure 2). This was not done for the Georges Bank samples since the data showed that there were no well developed chlorophyll layers in the region where the samples were taken. Only night sample data were used for this comparison since many species migrated vertically into the upper layers of water at night; therefore, this period had the maximum number of species in or above the chlorophyll layer. Because the zooplankton and chlorophyll concentrations were not measured simultaneously a wide depth range encompassing the chlorophyll layer was compared to the depth of concentrations of the different species of zooplankton. No attempt was made to relate zooplankton to the chlorophyll maximum depth since it could vary as much as 10 m within the depth range given for the chlorophyll layer.

During April three herbivore species and one carnivore species had a majority of their concentrated populations above the depth of the main chlorophyll layer. Ten species were concentrated in the region of the chlorophyll layer, five herbivores, three omnivores and two carnivores. The majority of species (36) of all trophic categories were found below the depth of the main chlorophyll layer. Two copepod species had population concentrations above the main chlorophyll layer but only one, *C. finmarchicus*, was concentrated solely above the layer. The other species, *O. similis*, was concentrated above and below the layer with concentrations much lower at the depth of the chlorophyll layer (20 – 40 m), suggesting avoidance of the main chlorophyll layer (Figure 2c). The low percentages of the population at the depth of the chlorophyll layer was a consistent feature of the night samples and not an artifact of a few stations. Southward and Barrett (1983) report *O. similis* remained below the thermocline and chlorophyll *a* maximum layer at all times. *C. finmarchicus* was the most abundant copepod and as a result the maximum zooplankton biomass concentration (>80%) was also found above the chlorophyll layer (Sameoto, 1982a), a situation similar to that found by Venrick *et al.* (1973), Longhurst (1976) and Herman *et al.* (1981). Only one non-copepod species, *P. abyssorum*, was concentrated above the chlorophyll layer. Only three copepod species had concentrations at the chlorophyll layer depth, *Corycaeus* sp., *P. borealis*, both omnivores, and *P. minutus*, a herbivore, whereas 20 species of copepods were concentrated below the chlorophyll layer. *M. norvegica* was concentrated in the chlorophyll layer, whereas *T. longicaudata* was concentrated below the layer. All fish larvae species were concentrated either in or below the layer, as were the adults of *B. glaciale* (Figure 2e).

During August, as in April, three species were concentrated above the chlorophyll layer, all herbivores. Twelve species were found in the region of the chlorophyll zone, four herbivores, three omnivores and five carnivores. Ten species were concentrated below the chlorophyll zone, three herbivores, three omnivores and four carnivores.

Only two species of copepods were concentrated above the main chlorophyll layer, these were the most abundant species *C. typicus* and *P. parvus*, which meant that the maximum biomass (>80%) was found above the chlorophyll layer (Sameoto and Lewis, 1979). Southward and Barrett (1983) found *C. typicus* concentrated above the thermocline at all times of the day. *L. retroversa* was the only other species concentrated above the chlorophyll layer. Three species of copepods *N. minor, P. minutus* and *T. longicornis*, were concentrated at the depth of the chlorophyll layer as were all species of *Sagitta* and euphausiids. *C. finmarchicus* and *C. hyperboreus* were the only two species of copepods concentrated below the thermocline and subsequently the chlorophyll layer (Figure 2a).

Two species of fish larvae were concentrated at the depth of the chlorophyll layer, *M. bilinearis* and *G. cynoglossus*, whereas *E. cimbrius* was concentrated below 125 m. It is interesting to note that none of the fish larvae collected in April or August had their main concentrations above the depth of the chlorophyll layer (Figure 2e).

Relationship between fish larvae and copepod concentrations

The numbers m^{-3} of different species of fish larvae at different depths were plotted against the total number of copepods m^{-3} found in the same samples for both day and night tows for each of the areas sampled. Samples not containing larvae were omitted from the plots. In most samples the larvae were not very abundant and, in these cases, they were generally associated with low copepod numbers (Figure 5). When the numbers of copepods increased from $<500\ m^{-3}$ the concentration of larvae also increased, but above concentrations of $\sim 3000-4000$ copepods m^{-3}, there was a general decrease in larval abundance.

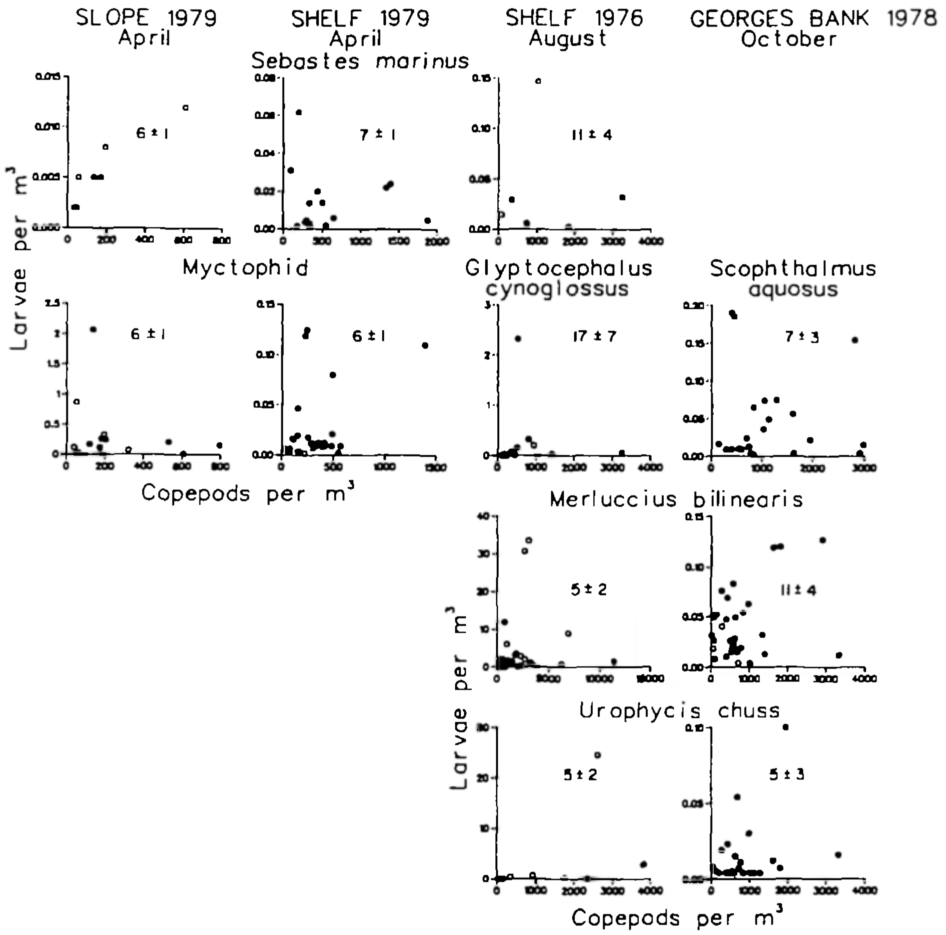


Fig. 5. Numbers of different species of fish larvae m^{-3} plotted against the total number of copepods m^{-3} in the same samples for the four regions sampled. Mean lengths ± standard deviations are given in the box for each species.

Sometimes low numbers of larvae were associated with medium numbers of copepods (i.e., 3000 – 4000 m^{-3}) but the majority of the samples with high concentrations of larvae were in water with medium copepod abundance, contrary to expectations if larvae required high concentrations of zooplankton to feed successfully.

A Pearson correlation coefficient was calculated between the total numbers of *M. bilinearis* larvae as well as between larvae of four size classes; 2 – 5 mm, 6 – 10 mm, 11 – 15 mm and > 16 mm in length and the numbers of the common species of copepods and total number of copepods m^{-3} for the August samples. These were the most common larvae in the largest data set so that if a relationship was going to be found between the larvae and numbers of copepods it would most probably be found here. Only one species of copepod, *C. typicus*, was positively correlated with the total abundance of larvae at a probability level of < 10% (r = 0.3, d.f. = 19, p = 0.08) for the day time samples. All of the correlations calculated for the night time samples were negative and non-significant except that between 2–5 mm larvae and *Temora longicornis* (r = 0.8, d.f. = 15, p = 0.005). Hence, there was no strong relationship between the total larvae and the total numbers of copepods m^{-3} or any copepod species except *T. longicornis* and *C. typicus*. In August (Figure 2) the dominant species, *C. typicus*, was distributed above the main concentration of *M. bilinearis* even though the two species were positively correlated. The larvae had only to swim upward ~10 m to be in the maximum concentration of copepods, but they were always found below the main concentration, suggesting that either the larvae were avoiding the depths containing high concentrations of copepods or only a small portion of the population made upward excursions at any one time to feed then returned to the depth below the copepod concentrations after feeding in a manner suggested by Pearre (1979). Since there was little difference in the temperature at the depths where these two groups of animals were found, it seems unlikely that temperature influenced the depth selection. Eight of the eleven groups of fish larvae had a mean length of < 10 mm (Figure 5) which meant that these larvae probably fed on copepod nauplii and early copepodite stages. Checkley (1982) found a linear relationship between the prey width and herring larvae length which showed larvae of 12 mm ingested prey up to 200 μm wide. If a similar relationship existed for the larvae collected in this study, it is probable that many of the organisms that were prey for the larvae were lost through the 243 μm nets. It is probable that some of the larvae were associated with microzooplankton concentrations which may have had a different vertical distribution than the larger forms of zooplankton caught in the nets.

There are reports from other field data that suggest fish larvae may not favour regions of high copepod concentrations. Sameoto (1982b) found lower numbers of *Engraulis ringens* and *Sardinops sagax* larvae off the coast of Peru in waters where copepods were > 5000 m^{-3} than in waters with copepods concentrations of 1000– 4000 m^{-3}, and Blaxter (1971) found a negative correlation between zooplankton biomass and the condition factor of *C. harengus* larvae.

Discussion

Four types of migration behavior were recognized among the species studied and the trophic classification of species could be broadly related to the type of migratory behavior. The percentage of non-migrators was highest among the herbivores while the number of species that always migrated was greatest for carnivores (Table II). Of all species 34% never migrated and 34% always migrated. A high percentage of herbivorous non-migrators was noted by Rudyakov and Tseytlin (1976) who also found that only 13% of the zooplankton biomass in the top 600 m in the region of the Canary Islands migrated a distance > 100 m. Similarly, Longhurst and Williams (1979) found that the biomass of filter feeders in the epiplankton only increased 15–20% at night. The smallest vertical migration distance that could be detected by the sampling intervals of this study

Table II. The numbers and percentages of species in the different trophic categories and the type of migration behavior they demonstrated.

Migration behavior type	Herbivores		Omnivores		Carnivores	
	No.	%	No.	%	No.	%
Non-migrators	8	44	7	32	7	30
Always migrated	4	22	9	32	9	39
Migrated some of the time	6	33	8	36	4	17
Reverse migration	0	0	0	0	3	13

was ~10 m; if animals migrated less than this distance they probably were not detected. Vertical migrations as short as 15 m have been found for *C. typicus* in Chesapeake Bay (White *et al.*, 1979).

The reasons for vertical migration by marine organisms have been debated for over half a century, with no consensus being reached for the advantage it gives to a species (Longhurst, 1976). The advantage is probably different for each species or every stage of species. McLaren (1963) suggested that there may be a metabolic advantage for animals to migrate vertically down to colder, deeper water during the day after they have fed in the warmer surface waters at night. However, as shown here and by Sameoto (1976) many of the animals entered warmer, deeper water during the day after night time feeding and, therefore, the physiological advantage of entering colder water could not be the reason for the migration of these species; however, some species did enter cold water during day time in August. Pearre (1973) found *Sagitta elegans* continued to migrate vertically even in isothermal water. Avoidance of predators was suggested by Murray and Hjort (1912), Hutchison (1967) and Zaret and Suffern (1976) as a probable reason for vertical migration away from the surface waters during the day. This is a reasonable explanation particularly for species that are pigmented and likely to be more visible during the day, such as the euphausiids and myctophids, but does not explain why the hyperiid amphipod *P. abyssorum*, also highly pigmented, did not show a diel migration. However, it is possible that the hyperiids, which are known to be associated with gelatinous zooplankton (Madin and Harbison, 1977), were reflecting the vertical distribution of these hosts, and that the gelatinous zooplankton were destroyed by the sampling procedure. Enright and Honegger (1977) suggested that the vertical migration of *Calanus helgolandicus* was not an adaptation to avoid predators but that different stages probably benefited in different ways at different times. In some species (i.e., *M. lucens* in August) only part of the population underwent diurnal migration with the remaining population maintaining their day time depth. This suggested that there was a great amount of variability in the migration behavior within the population. Some individuals may not have migrated at all or else only a part of the population migrated each night. Pearre (1979) suggested a model for unsynchronized vertical migration that accounted for a bimodal distribution of abundance such as seen for *C. arcuicornis* and *O. similis* in April shelf water. If unsynchronized night time migration occurred for the above species then the apparent avoidance of the chlorophyll maximum depth may have been an artifact of the migration of the animals to and from the zone above and below the chlorophyll maximum depth and these species, classified as non-migrators, may have in fact been migrating; however, the suggestion of avoidance of the chlorophyll layer cannot be omitted.

Temperature was found to be more important than salinity or density in influencing the vertical distribution of the different species. Herman *et al.* (1981) showed that the main zooplankton biomass and dominant species *C. finmarchicus* were concentrated at night in the region of highest chlorophyll production above the chlorophyll maximum layer. However, below the thermocline the centroids of total number of copepods smaller than *C. finmarchicus* stage 5, followed the σ_t isopleths and not those of temperature. These 'small copepods' were not separated into species, so species differences could not be detected.

For many of the species a large percentage of the population was found outside the region of preferred depth or temperature range, particularly during the day time, whereas with other species the populations were tightly grouped around a particular depth. There was a wide diversity in how different species responded to temperature in depth selection. There appeared to be two basic species groups separated by temperature. Those that concentrated in the cold water layers and those that concentrated in the warm water. In April these two groups corresponded to species normally associated with the slope water and with the colder shelf water. The slope water species found in shelf water generally stopped their upward night time migration when they encountered the colder (usually ~7°C) water at ~75 m. The situation in the shelf water during August was different to that in April. There was no abundant slope water species, however, the shelf water species showed a vertical distribution that was influenced by the temperature, with some concentrating above the thermocline, some in the thermocline and some below the thermocline. The concentration of zooplankton in the region of the thermocline was noted by Ortner *et al.* (1980) in northwestern Atlantic slope water and the Sargasso Sea. They interpreted most of the zooplankton assemblages as being associated with the deep chlorophyll maximum which was closely associated with the thermocline. Their results were similar to those of the August data of this study which showed a number of species closely associated with the zone of high chlorophyll. However, the most abundant species, *C. typicus* and *P. parvus*, were concentrated above the main chlorophyll layer; there were as many species in the water above the chlorophyll zone as in it. The April results of this study found that the dominant copepod in numbers and biomass, *C. finmarchicus*, was concentrated above the zone of maximum chlorophyll thereby supporting the findings of Longhurst (1976) and Herman *et al.* (1981). However, the majority of both the shelf and the slope water species were found below the chlorophyll zone in April again suggesting that there is no single explanation for zooplankton vertical distribution. In this study the copepod species were not identified to stage, but Sameoto (1984) found that copepodite stages of *C. finmarchicus, C. glacialis* and *C. hyperboreus* had different vertical distributions in the top 50 m in Arctic waters. Longhurst and Williams (1979)

Williams and Conway (1980) and Williams *et al.* (1983) found different copepodite stages of *Calanus* species were often separated vertically. Therefore, it is probable that both the physical environment and quality and concentrations of phytoplankton are important factors in determining vertical distribution of different stages of many herbivores. The distribution of carnivores may also reflect the distribution of their prey. Longhurst and Williams (1979) found no correlation between the depth of the plankton layers and salinity or temperature features in a section of the northeast Atlantic, suggesting that the biological environment was the more important factor in the vertical distribution of zooplankton. Paffenhöfer (1983) in a study of the vertical distribution of zooplankton on the Florida Shelf, related to depth, temperature and concentration of particulate matter found that many species increased with depth while others were positively correlated with the abundance of particulate matter. However, when the concordance of the vertical distributions between stations were compared Paffenhöfer concluded that one could not differentiate whether depth, temperature or food were responsible for the distribution.

The vertical separation of the species, particularly in the region of the thermocline, showed that many herbivores and carnivores, particularly fish larvae, seldom came in contact with others, even though they occurred under the same m^2 of ocean. In April the main concentration of *Benthosema glaciale* larvae was below the main concentration of the dominant species of copepod, *C. finmarchicus*, but was closely associated with *C. hyperboreus*. At the same time *Sebastes marinus* larvae were closely associated with the main concentration of *C. finmarchicus* but not with *C. hyperboreus*. In August the dominant fish larvae, *M. bilinearis*, had its centre of concentration below the main concentration of the dominant copepods, *C. typicus* and *P. parvus*, suggesting that high concentrations of copepods may not make a favourable environment for larvae or that larvae may only spend a short time in the high concentrations. Further evidence to support this idea was that samples with the highest numbers of copepods generally had very low numbers of fish larvae or none at all; similar results were found by Sameoto (1982b). Wyatt (1974) found that the feeding rate and the condition factor of plaice larvae decreased with increased prey encounter suggesting that high food concentrations may not necessarily be more advantageous to the larvae than low ones. Checkley (1982) found that larval herring (*C. harengus*) selected their food according to type as well as size, further demonstrating the need for information on fine scale vertical distributions in the study of predator-prey relationships. However, other factors may be responsible for the low numbers of larvae in high zooplankton concentrations, such as predation by the zooplankton on the larvae or a lack of prey of suitable size for the larvae in these high zooplankton concentrations.

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