NATIONAL UNDERSEA RESEARCH PROGRAM Research Report 88-4

Global Venting, Midwater, and Benthic Ecological Processes

Michael P. De Luca and Ivar Babb
Editors

July 1988

U.S. DEPARTMENT OF COMMERCE
C. William Verity, Secretary

National Oceanic and Atmospheric Administration
William E. Evans, Under Secretary

Oceanic and Atmospheric Research
Joseph O. Fletcher, Assistant Administrator

Office of Undersea Research
David B. Duane, Director

MIDWATER COMMUNITY STUDIES OFF NEW ENGLAND USING THE JOHNSON SEA-LINK SUBMERSIBLES

Ronald J. Larson[1], G. Richard Harbison[1], Phillip R. Pugh[2], John A. Janssen[3], Robert H. Gibbs[4], James E. Craddock[5], Claudia E. Mills[6], Richard L. Miller[7], and Ronald W. Gilmer[1]

1 - Harbor Branch Oceanographic Institution, Fort Pierce, FL

2 - Institute of Oceanographic Sciences, Wormley, England

3 - Biology Department, Loyola University, Chicago, IL

4 - Fish Division, U.S. National Museum, Washington, D.C.

5 - Woods Hole Oceanographic Institution, Woods Hole, MA

6 - Friday Harbor Laboratories, Friday Harbor, WA

7 - Biology Department, Temple University, Philadelphia, PA

ABSTRACT

The midwater community off New England was studied using manned submersibles. Twenty-three dives were made in three submarine canyons SE of Woods Hole in 800 m of water. We found a diverse community present. Gelatinous zooplankton (medusae, siphonophores and ctenophores) were represented by 38 species, several are undescribed. The vertical distributions of most were determined and it was discovered that they were mostly mesopelagic (occurring below 400 m). Ctenophores were both diverse and numerous in contradiction to the results of studies using nets. The siphonophore *Nanomia cara*, which showed evidence of a 150 m diel vertical migration, was most abundant. Crustacean micronekton consisted mostly of *Meganyctiphanes norvegica*, *Sergestes* sp., and *Themisto gaudichaudii*. These species all vertically migrated 100 m or more and were sometimes very numerous in midwater strata or near the bottom. Midwater fishes were found in the mesopelagic but some migrated into the upper 100 m at night. It is concluded that predation by visually orienting predators in surface waters may be the primary factor which determines vertical distributions. Nevertheless, the mesopelagic is not a good refuge from predators because there are large numbers of gelatinous predators there.

INTRODUCTION

Although a large number of studies have been done on the midwater fauna of the North Atlantic little is known about the species composition and vertical distribution of most taxa in this community. The major reason for this is that midwater trawls fail to capture a significant part of the fauna. Active nekton, e.g., squids and larger fishes are able to avoid the nets. Many gelatinous zooplankton are either damaged beyond recognition or they pass through the net because of their fragility. Here, we report the first detailed description of the vertical distribution of midwater animals based on direct in-situ observations made using the Johnson Sea-Link submersibles.

The study reported here was conducted near the shelf edge off New England, just south of Woods Hole, in 800 m of water. This region is referred to as the Slope Water Region (Backus and Craddock, 1977; Backus et al., 1977) and is known to be a mixture of shelf water and Gulf Stream water (Iselin, 1936).

METHODS

Twenty-three dives were made to depths of 800 m using the Johnson Sea-Link I and II manned submersibles (described by Youngbluth, 1984). Nine dives were made from 30 August to 6 September 1986 and 14 dives from 2 to 9 August 1987 in three submarine canyons (Atlantis, Hydrographer, and Veatch) south of the Grand Banks off the New England coast (Fig. 1). The dives were of 3-4 hours duration. They were made to depths ranging from 400 to 800 m and usually included the entire water column. It should be stressed that more time was spent at the deepest depths and thus some bias is present in the data. Dives were made between 1200 and 1500 hrs, and 2000 and 2300 hrs EDST so that diel vertical migrations could be documented.

During each submersible dive observations on the fauna as well as depth and temperature were narrated onto audio tape by audio recorder. Color video was recorded on 3/4-inch tape. Following each dive videotapes were reviewed and discussed by observers and the sound track transcribed. Specimens, even very fragile ones, were successfully collected using several kinds of samplers (described by Youngbluth, 1984). Because of the large volume of the samplers, specimens experienced relatively small temperature changes ($<5^{o}C$) when brought to the surface. Specimens were kept in shipboard incubators at ambient temperatures until studied (usually within 1-3 h). Representative specimens were photographed and preserved, where possible. The data reported here are limited to the macrozooplankton (>2 cm long), because smaller specimens could not be adequately visually quantified.

Scuba dives were made in the upper 20 m to document the epipelagic fauna.

Water temperatures in the upper 800 m ranged from 4.8 to $18^{o}C$ with a well marked thermocline in the top 25 m (Fig. 2).

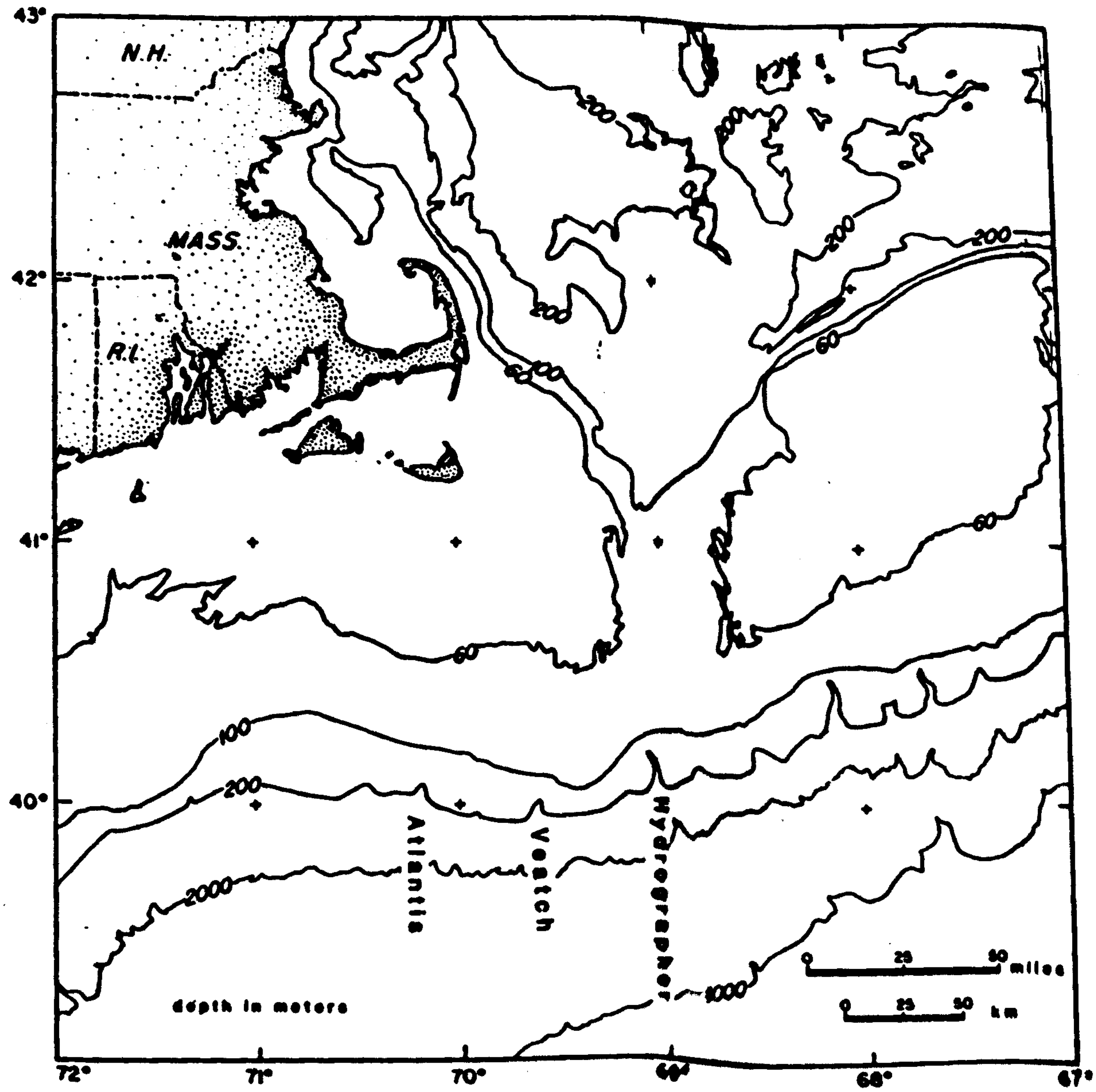

Figure 1. Chart showing locations of Atlantis, Veatch and Hydrographer canyons where dives were made.

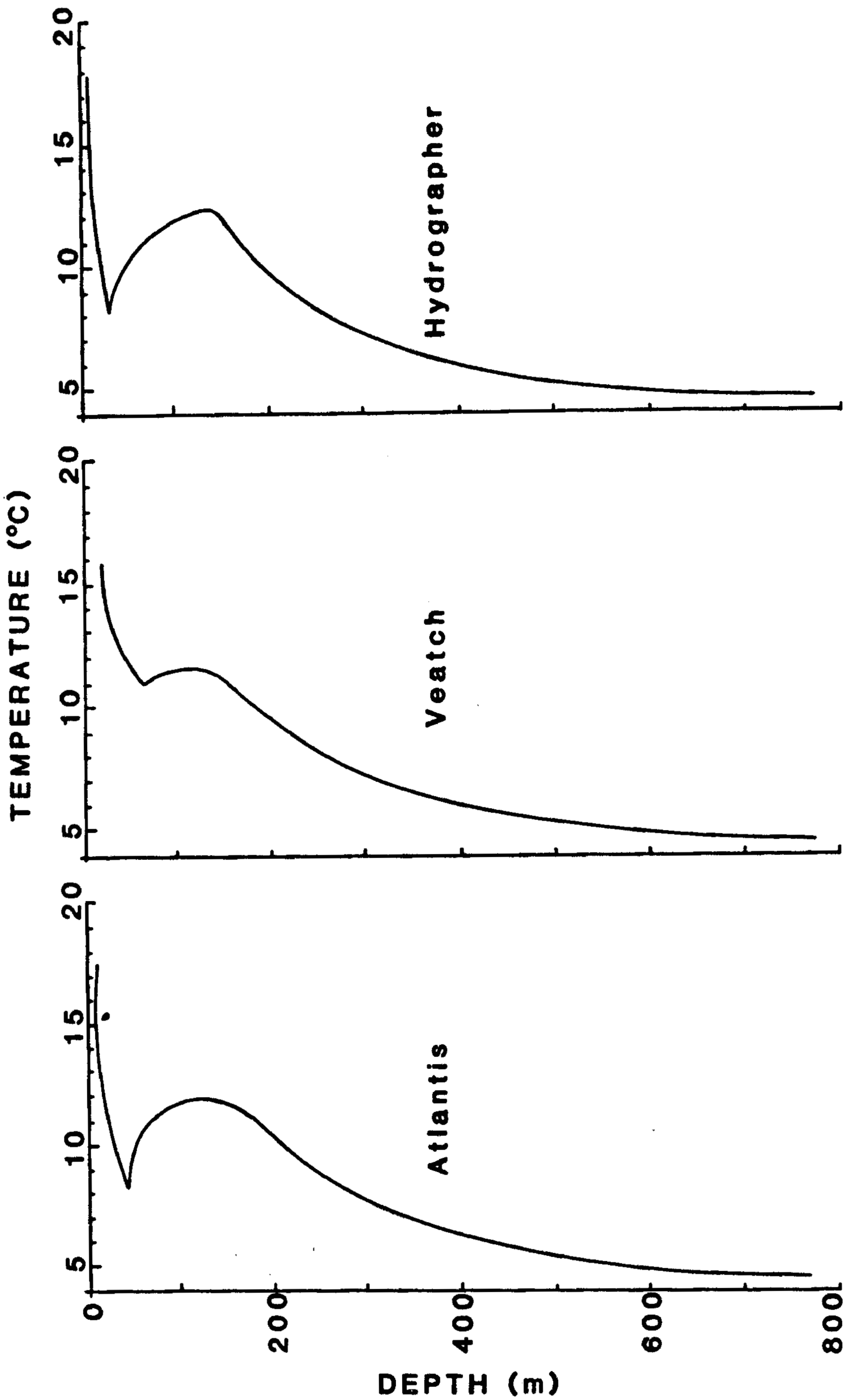

Figure 2. Temperature versus depth profiles for Atlantis, Veatch and Hydrographer canyons.

In Atlantis and Hydrographer Canyons, and to a lesser extent in Veatch Canyon, at about 40 m there was a temperature inversion where temperatures increased with depth to 150 m but thereafter decreased. Below 400 m temperatures changed only slightly (4.8-7°C). Salinities were not measured.

RESULTS

Thirty-eight species of gelatinous macrozooplankton were observed and collected (Table 1). Medusae, with 16 taxa, represented the largest group. Of these, two species of hydromedusae, Pantachogon haeckeli and Halicreas minimum, were most abundant. No new species were found, however two rare medusae were collected i.e., Poralia rufescens and Halitrephes maasi.

Siphonophores were represented by 13 species, several of which are undescribed. Nanomia cara and Forskalia spp. dominated. N. cara was the most numerous coelenterate observed. It was sometimes very abundant in midwater strata and near the bottom. The physonect Agalma okenii was the only coelenterate that was commonly seen in the surface waters by scuba divers.

Ctenophores were represented by 9 species. Several species are new to science. Bathocyroe fosteri and Beroe cucumis were most common.

Macro-crustaceans were dominated by three species, the euphausiid Meganyctiphanes norvegica. The sergestid shrimp Sergestes sp. and the amphipod Themisto (Parathemisto) gaudichaudii. M. norvegica was often very numerous in well defined depth strata and near the bottom. Neither Themisto nor Sergestes were limited to specific depth strata although their abundance was depth dependent. Large calanoid copepods were seen, mostly below 600 m but were not collected or identified.

Pelagic molluscs were represented by a number of unidentified squids and the commonly seen cranchiid Megalocranchia sp. and by the pteropods Clione limacina, Limacina helicoides, and ?Cymbulia.

Representatives of at least 13 families and many genera and numerous species of fishes were seen, video taped, and or collected. Myctophids (many taxa), hatchet fishes (Sternoptychidae, several taxa), paralepidids (mostly Notolepis rissoi), and snipe eels (Nemichthyidae, mostly Nemichthys scolopaceus) were most abundant. Other important taxa were Stomias boa ferox (Stomiidae) and Melanostigma atlanticum (Zoarcidae).

Table 1. List of midwater organisms identified from submersible dives off New England

HYDROMEDUSAE:
Aegina citrea
Aeginura grimaldii
Chromatonema rubrum
Colobonema sericeum
Halicreas minimum
Halitrephes maasi
Pandea rubra
Pantachogon haeckeli
Solmissus incisa
Solmundella bitentaculata

SCYPHOMEDUSAE:
Atolla vanhoeffeni
Atolla wyvillei
Nausithoe atlantica
Pelagia noctiluca
Periphylla periphylla
Poralia rufescens

CTENOPHORES:
Aulococtena acuminata
Bathocyroe fosteri
Beroe cucumis

Bolinopsis infundibulum
cydippid n. sp. #1 (red)
cydippid n. sp. #2 (orange)
lobate n. sp. #1
Mertensia ovum
Thalassocalyce inconstans

SIPHONOPHORES:
Apolemia spp.
Bathyphysa conifera
Chuniphyes moerae
?*Cordagalma cordiformis*
Forskalia spp.
Halistemma rubrm
Lensia conoidea
Lychnagalma utricfularia
Marrus orthocanna
Nanomia cara
physonect n. sp. #1
physonect n. sp. #2
Praya dubia

PTEROPODS:
Clione limacina
?*Cymbulia* sp.
Limacina helicoides

SQUIDS:
Order Teuthoidea
Megalocranchia sp.
Stolotheuthis leucoptera
squids undetermined species

AMPHIPODS:
Mimonectes sp.
Themisto (Parathemisto) guadichaudii
Phronima sp.

EUPHAUSIIDS:
Meganyctiphanes norvegia

DECAPODS:
Notostomus robustus
Sergestes sp.

FISHES:
Fam. Scyliorhinidae
Apristurus sp.

Fam. Bathylagidae
Bathylaqus ?*euryops*

Fam. Sternoptychidae
Argyropelecus aculeatus

Fam. Paralepididae
Notolepis rissoi
?*Paralepis* sp.

Fam. Bathysauridae
Bathysaurus sp.

Fam. Myctophidae

Table 1. (Cont'd.)

A. gigas
A. hemigymnus

Fam. Gonostomatidae
Cyclothone spp.
?*Gonostoma* sp.
others

Fam. Stomidae
Chauliodus sloani
Photonectes sp.
or *Malarosteus* sp.
Stomias boa ferox

Fam. Nemichthyidae
Nemichthys scolopaceus
others

Fam. Serrivomeridae
Serrivomer beanii

Ceratoscopelus maderensis
many unidentified

Fam. Macrouridae
early juveniles

Fam. Caristiidae
Caristius sp.

Fam. Zoarcidae
Melanostigma atlanticum

Fam. Synaphobranchidae
Synaphobranchus sp.
others

Vertical Distributions

Vertical distribution data for all dives were lumped together because there were insufficient data to determine if it varied among submarine canyons or from year to year.

The medusae were mostly found at depths in excess of 600 m (Fig. 3). Only a single macro-medusa (>2 cm diameter) species i.e. Pelagia noctiluca was found above 300 m and only three species occurred above 600 m while 15 species were found below this depth. There were no eurybathyl species. Pantachogon haeckeli occurred over the greatest depth range (425-800 m). The medusae as a group showed no evidence of a diel vertical migration.

Siphonophores were somewhat more eurybathyl than medusae. Two species i.e., Forskalia sp. and Nanomia cara, were found at depths of 100-170 m to 800 m. Nine species occurred above 600 m and only four species were not found above this depth. N. cara apparently showed a diel vertical migration of about 150 m.

During the day the mean depth of minimum occurrence was 480 m but at night it was only 330 m.

Ctenophores showed a somewhat different depth distribution. Two species i.e., Beroe cucumis and Bolinopsis infundibulum were eurybathyl, occurring from near the surface to 800 m. Four species were observed above 450 m and five species were only seen at greater depths. Ctenophores did not vertically migrate to any extent.

The only mollusc species for which we have depth data is Limacina helicoides a dark-purple pteropod which was seen below 580 m. A number of squids were seen at depths of greater than 150 m, most were seen below 300 m.

The three common macro-crustaceans mostly occurred over a broad depth range but were not seen at the surface. Meganyctiphanes norvegica was observed from 75 to 800 m but was most numerous below 200 m. Themisto gaudichaudii and Sergestes sp. were present below 150 m but were most common at depths greater than 300 m. The mean day depths of the sometime dense layers of euphausiids was 290 m but at night it had decreased to 200 m (Table 2). Themisto populations moved from an upper limit during the day of 500 m to 370 m at night and Sergestes moved from 470 m during the day to 340 m at night. Thus, these species showed a 90 to 130 m upward movement at night.

Most of the fishes occurred below 450 m (Fig. 4). Only a few species were found above this depth by day but some migrated into surface waters at night. Hatchet fishes (Sternoptychidae), myctophids, paralepidids and snipe eels showed some evidence of a

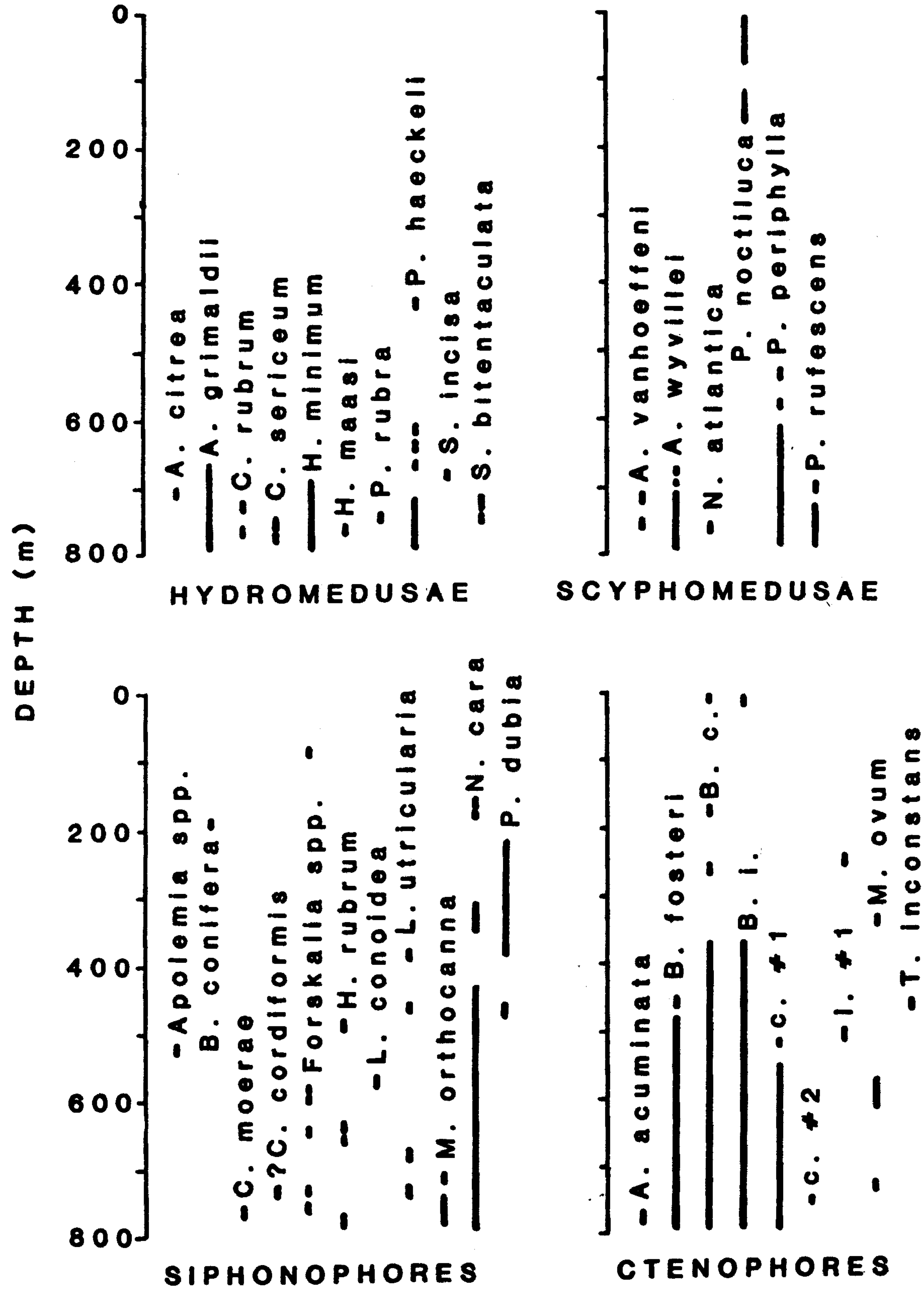

Figure 3. Bathymetric distributions of gelatinous macroplankton. Solid lines = individuals seen more or less throughout entire range. Dashes = individuals mostly confined to strata.

Table 2. Day versus night depth ranges for midwater crustaceans

TAXON	DAY DEPTH (M) $\bar{X}$ (RANGE)	NIGHT DEPTH (M) $\bar{X}$ (RANGE)
Meganyctiphanes norvegica	290 (240-370)	200 (150-300)
Sergestes sp.	470 (340-580)	340 (120-460)
Themisto gaudichaudii	500 (240-660)	370 (110-610)

N = 10 pairs of day/night observations

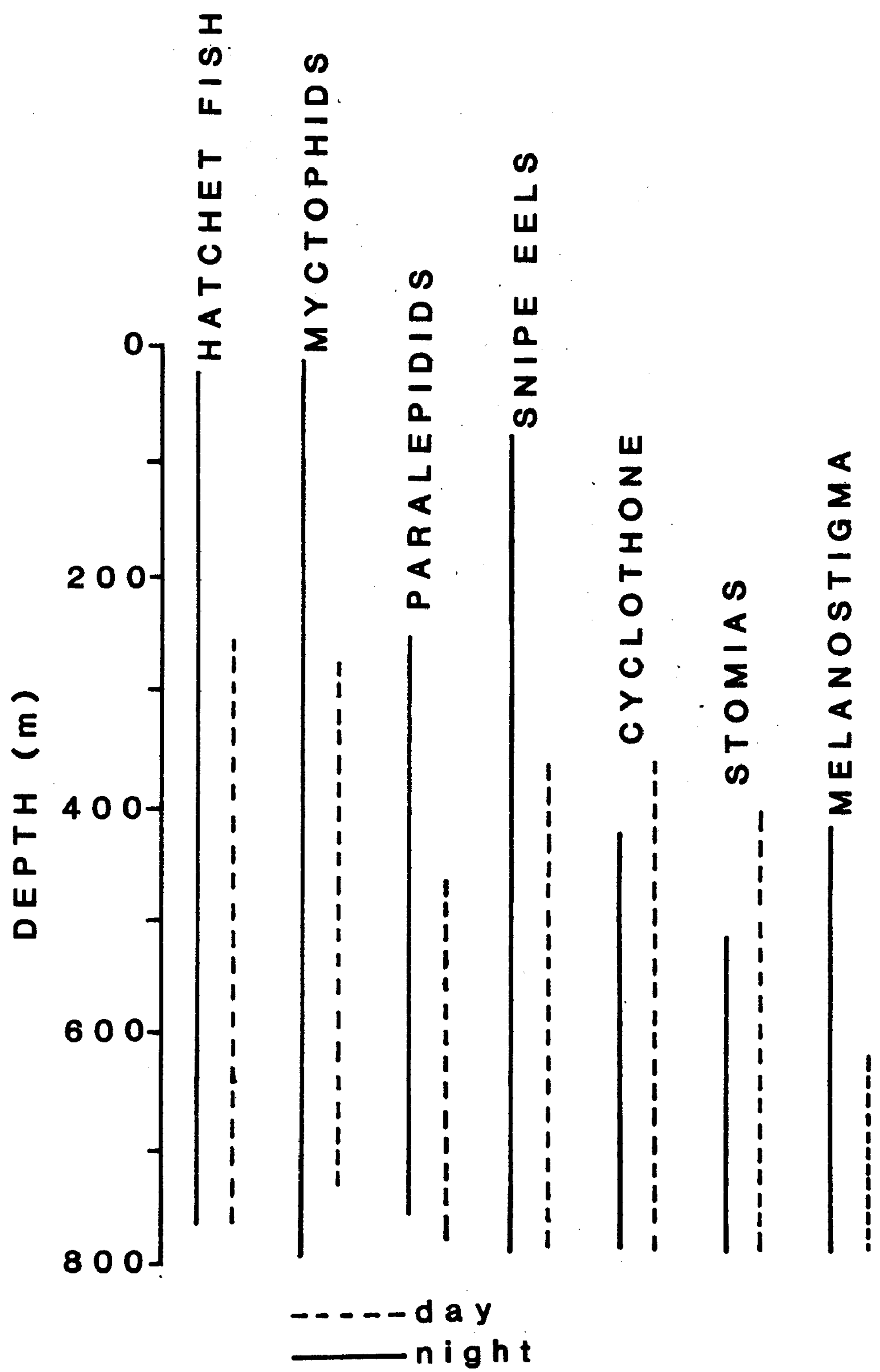

Figure 4. Day and night vertical distributions of dominant fishes.

diel vertical migration. Hatchet fishes and myctophids were found below 250 m by day but were found in the upper 100 m at night. Snipe eels (Nemichthyidae) were found deeper than 350 m by day but move up into the upper 100 m at night. Paralepidids were found somewhat deeper, >450 m, by day but were found above 250 m at night.

Melanostigma atlanticum, which we nicknamed the "Cheerio" fish because it was mostly seen motionless, curled in a circle, also showed some evidence of a diel vertical migration. During the day it was found at a minimum depth of 600 m but this decreased to 400 m at night. Other common fishes, e.g., Cyclothone spp. and Stomias boa ferox apparently did not vertically migrate or they had a reverse migration since their minimum day depth was slightly shallower than their night depth.

There is some evidence to suggest that some midwater taxa may be more abundant just above the bottom (Wishner, 1980; Smith, 1983). During 1987 we found that on some dives there was an increased number of gelatinous zooplankton near the bottom. Nanomia, an undescribed red cydippid, Beroe, and trachymedusae were sometimes most numerous near the bottom. On several dives Nanomia were so numerous within 10 m of the bottom that many could be seen at any time. Euphausiids sometimes occurred in dense swarms near the bottom at depths of 400 to 600 m. Also the numbers of fishes was sometimes higher near the bottom where midwater and benthopelagic species co-occurred.

DISCUSSION

For the invertebrate macroplankton and micronekton it was evident that the fauna was dominated, both in terms of species and individuals, by those that were found at depths in excess of 400 m. Only about 20% of the species were observed at depths of less than 300 m and 50% were only seen below 600 m.

Only a single species (Pelagia noctiluca) was found to only occur in surface waters (<300 m). Most of the species which were found in the upper 100 m were eurybathic species e.g., Beroe cucumis, Bolinopsis infundibulum, Meganyctiphanes norvegica, which also were found much deeper and generally were more abundant at greater depths. Thus the midwater invertebrate macroplankton and micronekton fauna in slope waters south of Georges Bank was mostly mesopelagic and although some species occupied a relatively broad depth range the fauna was most diverse at greatest depths.

For medusae, the results of two previous studies of the midwater fauna of the North Atlantic can be compared with the present study. Thurston (1977) and Roe et al. (1984) working in the eastern North Atlantic, at 53-60° N 20° W and 44° N 13° W respectively, both employed discrete depth open-closing midwater trawls to examine vertical distributions. The overall vertical distributions are similar for the three geographic areas although there are differences. The major difference in the studies is that even though Roe et al., (1984) worked at 44° N their data showed a more shallow distribution for most medusae (the exception was Periphylla periphylla which was taken at the surface at 53-60° N) than does ours at 40°N. All three studies found highest species diversity and greatest numbers of individuals at depths of 600 m and greater. Some of the differences among these studies is due to numbers of samples taken and their depths.

Thurston (1977) and Roe et al. (1984) found evidence for diel vertical migrations, up to 200 m, for a number of midwater medusae including Atolla vanhoeffeni, Pantachogon haeckeli, and Periphylla periphylla. But others e.g., Atolla wyvillei and Halicreas minimum did not migrate.

The most abundant midwater coelenterate off the Grand Banks was the physonect Nanomia cara. Previously N. cara was known to be abundant at shallower depths in this region (Rogers et al., 1978) but its importance at mesopelagic depths was unknown.

We found evidence that midwater siphonophores undertook diel vertical migrations of up to 150 m. Previous studies in the North Atlantic have documented similar diel migrations but this was mainly for calycophorans (Pugh, 1977, 1986).

Because of the extreme fragility of ctenophores almost nothing is known about their existence in midwater (Madin and Harbison, 1978; Harbison, 1986). For example, in one of the most comprehensive studies of the midwater community in the North Atlantic, Roe et al., (1984) only listed a single ctenophore species, Beroe cucumis. Until about a decade ago only three ctenophore species were definitely known to occur in the deep-sea (Madin and Harbison, 1978). However recently, direct observations using submersibles (Madin and Harbison, 1978; Youngbluth, 1984; Mackie, 1985; Harbison, 1986) has shown that the number of midwater ctenophores is large and, in fact, Harbison (1986) states that "the vast majority of ctenophores live in the deep-sea." Our results supports Harbison's conclusion.

Here we found that midwater fishes were mainly below 400 m, day and night. Backus et al., (in preparation) working in the same area found that midwater fish were concentrated in the 400-800 m zone regardless of time of day. We also noted that at night, hatchet fishes, myctophids, and snipe eels occurred above 100 m. Other studies have documented mesopelagic concentrations of midwater fishes and diel vertical migrations (Badcock, 1970; Clarke, 1973, 1974; Roe, 1974; Pearcy et al., 1977; Howell and Krueger, 1987; Karnella, 1987). In some regions 50% of the midwater fauna may vertically migrate (Young, 1983) but in others the proportion is much less (Pearcy et al., 1977). Although the exact causes of diel vertical migrations are unknown there is good evidence that they are mediated by light and are related to feeding behavior (Zaret and Suffern, 1976).

Possibly if we could determine what factors affect midwater vertical distributions we might be able to better understand vertical migrations. The major environmental parameters which affect vertical distributions are light, temperature, and abundance of prey and predators (Roe, 1974; Merrett and Roe, 1974; Zaret and Suffern, 1976; Enright, 1977; Young, 1983; Larson, 1986; Pugh, 1986). It appears that physical factors, most importantly temperature, may determine the overall vertical limits of a given midwater species but biological parameters, mainly food availability and predation pressure, determine the normal range. Vertical migrators must be able to cope with a broad range of temperatures, up to 25°C in the tropics. They probably do this so that they can feed on the more abundant zooplankton in the upper 100 m (Roe, 1972).

Although light is important in determining vertical distributions it mostly acts indirectly through feeding success and predation (however, we have observed the lethal effects of light on siphonophores). As a result the mesopelagic may act as a partial refuge from visual predators. However, even in the lower mesopelagic where vision may be limited, tentaculate, gelatinous predators are abundant and they may be significant causes of mortality.

Direct observations on the behavior and associations between midwater organisms are needed to provide essential data for understanding the vertical distributions and ecology of midwater organisms. Our results will be the subject of future papers.

This contribution is number 16 of Direct Studies of Mesopelagic Communities.

LITERATURE CITED

Backus, R. H. and J. E. Craddock. 1982. Mesopelagic faunal provinces and sound-scattering levels in the Atlantic Ocean. In: N. R. Anderson and B. J. Zahuranec (eds.), Ocean sound scattering production. Mar. Sci., Vol. 5, , pp. 529-547.

Badcock, J. 1970. The vertical distribution of mesopelagic fishes collected on the SOND cruise. J. Mar. Biol. Assoc. U.K., Vol. 50, pp. 1004-1044.

Clarke, T. A. 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific near Hawaii. Fish. Bull., Vol. 71, pp. 401-434.

Clarke, T. A. 1974. Some aspects of the ecology of stomiatoid fishes in the Pacific near Hawaii. Fish. Bull., Vol. 72, pp. 337-351.

Enright, J. T. 1977. Diurnal vertical migration: Adaptive significance and timing. Part 1. Selective advantage: A metabolic model. Limnol. Oceanogr., Vol. 22, No. 5, pp. 856-872.

Harbison, G. R. 1986. Toward a study of the biogeography of pelagic ctenophores. In: A. C. Pierrot-Bults, S. van der Spoel, B. J. Zahuranec, and R. K. Johnson (eds.), Pelagic Zoogeography. Unesco Tech. Paper. Mar. Sci., No. 49, pp. 112-117. Paris, UNESCO.

Harbison, G. R., Madin, L. P. and N. R. Swanberg. 1978. On the natural history and distribution of oceanic ctenophores. Deep-Sea Res., Vol. 25, pp. 233-256.

Howell, W. H., and W. H. Krueger, 1987. Family Sternoptychidae, marine hatchetfishes and related species. In: R. H. Gibbs and W. H. Krueger (eds.), Biology of the midwater fishes of the Bermuda Ocean Acre. Smithsonian Cont. Zool. No. 452, p. 3250.

Iselin, C. O. 1936. A study of the circulation of the western North Atlantic. Pap. Phys. Oceanogr. Meteorol., Vol. 4, pp. 1-101.

Karnella, C. 1987. Family Myctophidae, lanternfishes. In: R. H. Gibbs and W. H. Krueger (eds.), Biology of the midwater fishes of the Bermuda Ocean Acre. Smithsonian Cont. Zool. No. 452, pp. 50-168.

Larson, R. J. 1986. Pelagic Scyphomedusae (Scyphozoa: Coronatae and Semaeostomeae) of the Southern Ocean. In: L. Kornicker (ed.), Biology of the Antarctic Seas XVI. Ant. Res. Ser., Vol. 41, pp. 59-165.

Mackie, G. O. 1985. Midwater macroplankton of British Columbia studied by submersible PISCES IV. J. Plank. Res., Vol. 7, No. 6, pp. 753-777.

Madin, L. P. and G. R. Harbison. 1978. Bathocyroe fosteri (gen. nov., sp. nov.), a mesopelagic ctenophore observed and collected from a submersible. J. Mar. Biol. Assoc. U.K., Vol. 58, pp. 559-564.

Merrett, L., and H. S. J. Roe. 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol., Vol. 28, pp. 115-126.

Pearcy, W. G., E. E. Krygier, R. Mesecar, and F. Ramsey. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res., Vol. 24, pp. 223-245.

Pugh, P. R. 1977. Some observations on the vertical migration and geographic distribution of siphonophores in the warm waters of the North Atlantic Ocean, pp. 362-378. In: Proc. Symp. on Warm Water Zooplankton. Spec. Pub. NIO. Paris, UNESCO.

Pugh, P. R. 1986. Trophic factors affecting the distribution of siphonophores in the North Atlantic Ocean. In: A. C. Pierrot-Bults, S. van der Spoel, B. J. Zahuranec, and R. K. Johnson (eds.), Pelagic Zoogeography. Unesco Tech. Paper. Mar. Sci., No. 49, pp. 230-234. Paris, UNESCO.

Roe, H. S. J. 1972. The vertical distributions and diurnal migrations of calanoid copepods collected on the SOND Cruise, 1965. 1. The total population and general discussion. J. Mar. Biol. Assoc. U.K., Vol. 52, pp. 277-314.

Roe, H. S. J. 1974. Observations on the diurnal vertical migrations of an oceanic animal community. Mar. Biol., Vol. 28, pp. 99-113.

Roe, H. S. J., and J. Badcock. 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 5. Vertical migrations and feeding of fish. Prog. Oceanog., Vol. 13, pp. 389-424.

Roe, H. S. J., P. T. James, and M. H. Thurston. 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 6. Medusae, ctenophores, amphipods and euphausiids. Prog. Oceanog., Vol. 13, pp. 425-460.

Rogers, C. A., D. C. Biggs, and R. A. Cooper. 1978. Aggregation of the siphonophore Nanomia cara in the Gulf of Maine: Observations from a submersible. Fish. Bull., Vol. 76, pp. 281-284.

Smith, K. L. 1982. Zooplankton of a bathyal benthic boundary layer: In situ rates of oxygen consumption and ammonium excretion. Limnol. Oceanogr., Vol. 27, No. 3, pp. 461-471.

Swanberg, N. 1974. The feeding behavior of Beroe ovata. Mar. Biol., Vol. 24, pp. 69-76.

Thurston, M. H. 1977. Depth distributions of Hyperia spinicera Bovallius, 1889 (Crustacea: Amphipoda) and medusae in the North Atlantic Ocean, with notes on the associations between Hyperia and coelenterates. In: M. Angel (ed.), A voyage of discovery: George Deacon 70th anniversary volume. Oxford, England, Pergamon Press, pp. 499-536.

Wishner, K. F. 1980. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Res., Vol. 27A, pp. 203-216.

Young, R. E. 1983. Oceanic bioluminescence: An overview of general functions. Bull. Mar. Sci., Vol. 33, No. 4, pp. 829-845.

Youngbluth, M. J. 1984. Water column ecology: In situ observations of marine zooplankton from a manned submersible. In: N.C. Fleming (ed.), Divers, submersibles and marine science. Mem. Univ. Occas. Pap. Biol., Vol. 9, pp. 1-118.

Zaret, T. M. and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr., Vol. 21, No. 6, pp. 804-813.