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Persistent near-bottom aggregations of mesopelagic animals along the North Carolina and Virginia continental slopes

John V. Gartner Jr.
Natural Science Department SP/G, gartner.jack@spcollege.edu

Kenneth J. Sulak
Florida Integrated Science Center, US Geological Survey,, ken_sulak@usgs.gov

Steve W. Ross
Center for Marine Science, University of North Carolina, rosss@uncw.edu

Ann Marie Necaise
Center for Marine Science, University of North Carolina

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John V. Gartner Jr · Kenneth J. Sulak · Steve W. Ross · Ann Marie Necaise

Abstract Submersible observations during four missions over the North Carolina and Virginia continental slopes (184–900 m) documented the occurrence of large aggregations of mesopelagic fishes and macronektonic invertebrates near or on the bottom. Aggregated mesopelagics formed a layer up to tens of meters deep positioned from a few centimeters to 20 m, usually <10 m, above the substrate. Aggregations were numerically dominated by microvores, notably the myctophid fish *Ceratoscopelus maderensis* and the penaeid shrimp *Sergestes arcticus.* Consistently present but in relatively lower numbers, were mesopelagic predators, including the paralepidids *Notolepis rissoi* and *Lestidium atlanticum*, the eel *Nemichthys scolopaceus*, the stomiid fishes *Chauliodus sloani* and *Stomias boa ferox*, and squids *Illex* spp. Near-bottom aggregations do not appear to be an artifact due to attraction to the submersible. Based on submersible observations in three areas in 4 years spanning a decade, near-bottom aggregations of midwater organisms appear to be a geographically widespread and persistent phenomenon along the continental slope of the southeastern US Aggregations may exploit areas of enhanced food resources at the bottom.

J. V. Gartner Jr (✉)
Natural Science Department SP/G, St. Petersburg College,
6605 5th Avenue N, St. Petersburg, FL 33711, USA
e-mail: gartner.jack@spcollege.edu

K. J. Sulak
Florida Integrated Science Center,
US Geological Survey, 7920 NW 71st Street,
Gainesville, FL 32653, USA
e-mail: ken_sulak@usgs.gov

S. W. Ross · A. M. Necaise
Center for Marine Science,
University of North Carolina at Wilmington,
5600 Marvin Moss Lane, Wilmington, NC 28409, USA
e-mail: rosss@uncw.edu

Introduction

The presence of mesopelagic animals in close proximity to the bottom is not unusual in waters where the seafloor intersects the lower end of their migratory depth ranges along continental slopes, seamounts and islands. The normal diel vertical migration of mesopelagic fauna may be disrupted or truncated by proximity to land, abrupt changes in bottom topography (e.g., seamounts), and in upwelling areas (Isaacs and Schwartzlose 1965; Kinzer 1977; Young and Blaber 1986; Genin 2004). For some mesopelagic species, larger, adult members may adopt a benthopelagic lifestyle. These species discontinue or restrict vertical migrations, remaining in deep waters, often near bottom (<5 m altitude) but not resting on the substrate, to feed or avoid predation (Marshall and Merrett 1977; Marshall 1980; Gartner 1991; Stefanescu and Cartes 1992; McClain et al. 2001). These interactions of mesopelagic species with the bottom have been considered temporary and incidental to vertical migration (e.g., Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Marshall and Merrett 1977; Marshall 1980), yet there is increasing evidence that they are important to benthic, benthopelagic and demersal trophodynamics (Gordon et al. 1995; Gartner et al. 1997; Merrett and Haedrich 1997; Cartes et al. 2001; Genin 2004; Madurell and Cartes 2005).

Numerical estimations of mesopelagic animals observed from submersibles either in midwater or near the bottom are rare and inconclusive. Visual counts during one daytime dive (J. Craddock, personal communication cited by Marshall and Merrett 1977) of two species of myctophid fishes

near the bottom suggested low densities (one individual per m³ at 1,025 m), while Auster et al. (1992) observed dense near-bottom aggregations of mixed mesopelagic species on two dives, one made during the day from 390 to 610 m bottom depth and one at night at 510 m bottom depth. These 1992 data may be the first night observations of near-bottom aggregations (NBA), suggesting a lack of the expected upward migration. Other observers from submersibles have reported high numerical densities of mesopelagic animals at midwater depths, as expected (Backus et al. 1968; Auster et al. 1992).

As noted above, components of the mesopelagic fauna occur frequently on various continental slopes, topographic highs, or upwelling areas during the day; however, the issue that we address here is the persistence of this phenomenon on a diel basis. In contrast to the diel vertical migration paradigm for mesopelagic fauna, i.e., rising en masse to form a night-time layer in shallower water, we present evidence that certain migratory mesopelagic fish and crustacean species regularly form dense (>10 individuals/m³) and persistent aggregations near the bottom over the continental slope of the western North Atlantic Ocean at depths of 300–900 m. Our findings further support the growing realization that putative mesopelagic species may have a direct and significant role in the trophodynamics of the benthic boundary layer.

Materials and methods

Study sites

Data were collected from three general study areas on the Virginia and North Carolina continental slopes (Fig. 1). All three study areas were established as part of larger, ongoing projects investigating the community structure and trophodynamics of shelf edge and slope fauna. The Virginia middle slope (VMS) was sampled the least, and that area was described by Sulak and Ross (1996). The Hatteras middle slope (HMS) is an intensely studied area of complex bottom topography (canyons) and complex oceanography (see Sulak and Ross 1996; Ross et al. 2001; Bauer et al. 2002). The HMS is closest to land (∼68 km) of all areas sampled and exhibits periodic upwelling that enhances surface productivity (Lohrenz et al. 2002), both factors potentially relevant to mesopelagic faunal distributions. The HMS is also one of the most productive benthic environments sampled on the US East coast (see above references). Our stations off the Cape Lookout area (LMS) were centered on deep coral banks. These mounds appear to be formed by successive coral growth and sediment entrapment, and their tops and sides are covered by dense thickets of living and dead deep-sea corals, mostly *Lophelia pertusa*. Along the sides

and around the bases of these banks are rubble zones of dead coral branches, which extend up to hundreds of meters away from the mounds. These ridges and reef mounds rise as much as 100 m from the open substrate and accelerate bottom currents which favor attached filter-feeding corals, sponges, and other biota. The deep coral banks and surrounding rubble zones concentrate biota in much the same way as shallow coral reefs (Ross et al. unpublished data).

Submersible observations and sampling

Visual and video camera observations from the DSRV Johnson-Sea-Link (JSL) submersible were conducted on the upper to middle continental slopes (184–900 m bottom depth) off North Carolina and Virginia during four cruises (1991, 1992, 2000, 2001; Table 1; Fig. 1). We made two 1.2–3.0 hr daytime JSL dives per day, one in the morning and one in the afternoon. In 1991 and 1992, we only used the externally mounted JSL video camera to record intermittently during descent and continuously while on the bottom on each dive. Because we increased our attention to water column phenomena, in 2000 and 2001, we supplemented the external camera recordings with an internal hand held video camera, which we usually ran continuously from beginning to end of dive, except during ascent. For most of the time on bottom, video observations were obtained with the both internal and external camera lenses set to wide angle and all JSL lights on. When specimens of particular interest were observed, the cameras were zoomed in to provide as much closeup detail as possible to assist with organism identifications. Each observer recorded audio observations onto both the videotapes and onto separate audio recorders continuously during each dive. Specimens were collected as often as possible using the JSL suction sampler, often facilitated by dispensing a rotenone emulsion to narcotize mesopelagic species. A few mesopelagic fishes were collected by 1.3 cm bar size fine mesh frame mounted gill nets stacked into "sandwiches" on the lower bow platform of the JSL. Specimens collected by the JSL were returned to the laboratory and treated in a manner similar to trawl captured specimens (see below). These collections were made to both confirm field identifications of organisms and for use in the collection of ancillary biological information such as otoliths from fishes for age and growth analyses, stomachs for diet analyses, etc.

Because of variations in visibility, submersible altitude above the bottom and lack of visual reference points in midwater, it was not feasible to accurately measure the total area or volume observed by either the video cameras or the observers. However, because there were points of reference on the front of the submersible itself, mainly external equipment such as the videocamera, arc light housing and "critter gitter" frame, it was possible to establish a small volume

Fig. 1 Station map for Tucker trawls and submersible dives from three general areas along the Virginia and North Carolina continental slope. *Upper Circle* Virginia Middle Slope stations (VMS in text); *Circle* and *Inset A* Hatteras Middle Slope (HMS in text); *Circle* and *Inset B* Cape Lookout Middle Slope (LMS in text). Inset for VMS not provided because of the very close proximity of stations and small sample size (four dives)
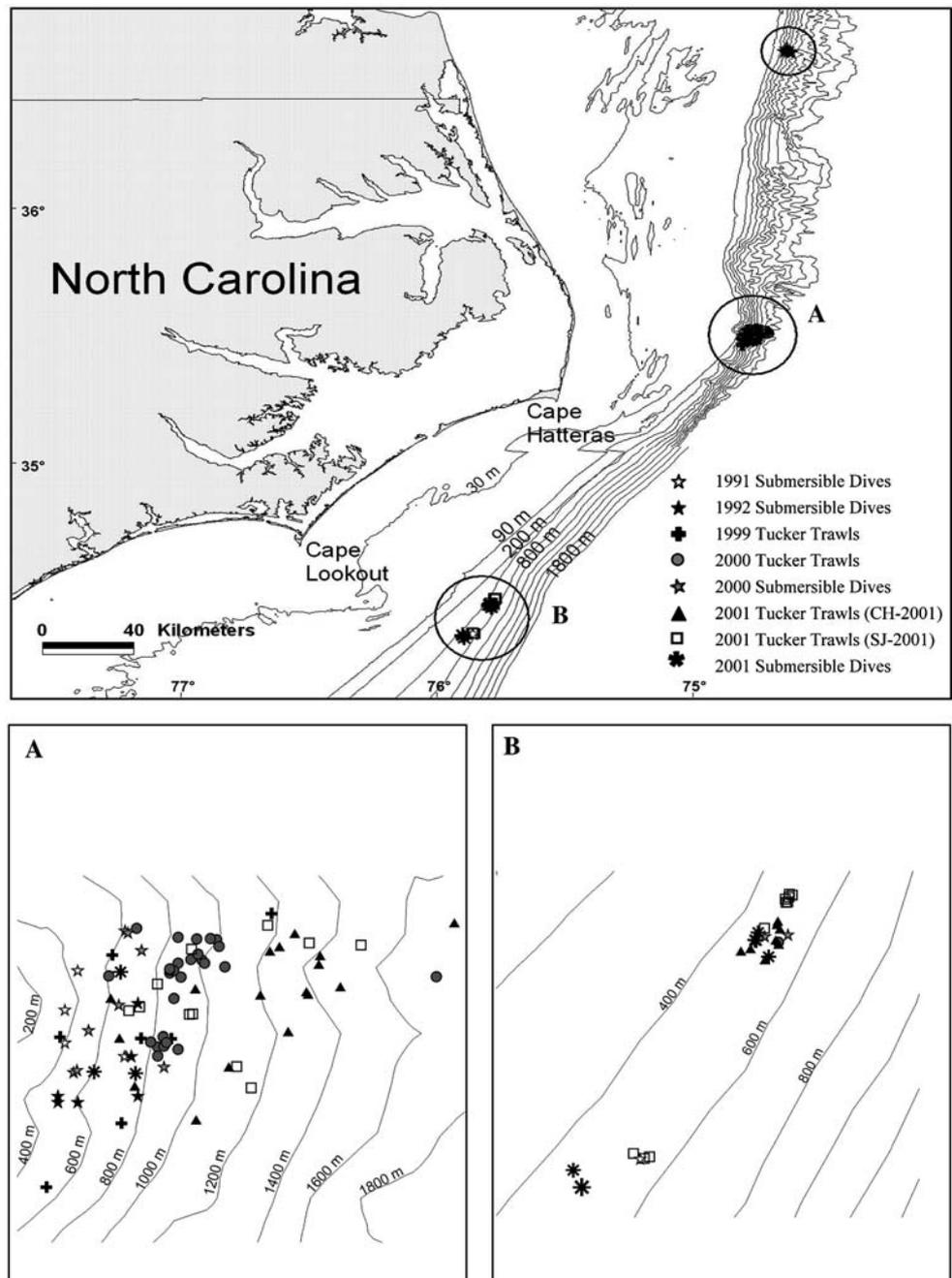
(m^3) frame of reference immediately in front of the submersible. This was used only to establish some basic density parameters, some of which are mentioned in the "Results".

For a standardized analysis of data, we estimated relative densities or abundances as numerical categories of mesopelagic animals seen by the forward observer within the field of view in front of the JSL. Abundance estimates and species identifications were later verified by review of the videotapes. The overall NBAs for all species were ranked by relative density as follows: Low ≤ 100, Medium = 100–1,000, High ≥ 1,000 individuals. Relative abundance categories were assigned for dominant mesopelagic taxa observed by the forward JSL scientist as follows: Uncommon ≤ 10, Common = 10–100, Abundant = 101–1,000, Highly Abundant ≥ 1,000.

Trawl sampling

Trawling operations during the 1991 and 1992 submersible cruises were limited (14 days, five night stations) and

Table 1 Submersible station data by area

Area	Station number	Date	Time	Depth range of DSL (m)	Bottom depth (m)	NBA-density
HMS	3063	25 July 1991	1633	365–496 (131)	727	Yes-H
	3067	27 July 1991	1644	305–381 (76)	484	Yes-H
	3068	28 July 1991	0848	487–701 (214)	808	Yes-M
	3069	28 July 1991	1611	**	325	Yes-M
	3070	29 July 1991	0834	289–457 (168)	662	No
	3211	25 June 1992	1610	274–396 (122)	722	No
	3212	27 June 1992	0852	426–480 (54)	582	Yes-L*
	3213	28 June 1992	1615	358–487 (129)	509	Yes-L
	3214	28 June 1992	0909	336–668 (332)	841	Yes-L*
	3220	01 July 1992	0840		724	No
	3221	01 July 1992	1554		807	No
	4198	23 July 2000	1702	479–640 (161)	871	No
	4199	24 July 2000	0843	393 to bottom	552	Yes-L
	4200	24 July 2000	1650		568	No
	4201	25 July 2000	0838	274–486 (202)	541	Yes-H
	4202	25 July 2000	1616	496–568 (72)	621	Yes-M
	4203	26 July 2000	1525	318–498 (180)	753	Yes-L
	4204	27 July 2000	0953	266–494 (228)	595	Yes-H
	4205	27 July 2000	1722	305 to bottom	630	Yes-M
	4358	20 September 2001	1043	190–652 (462)	883	No
	4359	21 September 2001	0852	201–528 (327)	658	Yes-L
	4360	21 September 2001	1552	225–762 (537)	887	No
VMS	3216	29 June 1992	1029	365 to bottom	741	Yes-H
	3217	29 June 1992	1703	426–701 (275)	829	Yes-L
	3218	30 June 1992	0938	420 to bottom	789	Yes-H
	3219	30 June 1992	1653	477 to bottom	566	Yes-H
LMS	4206	28 July 2000	0842	285–411 (126)	430	Yes-L
	4207	28 July 2000	1556	343 to bottom	418	Yes-L
	4361	22 September 2001	0844	294 to bottom	427	Yes-M
	4362	22 September 2001	1618	342 to bottom	399	Yes-H
	4363	23 September 2001	0902	316 to bottom	417	Yes-H
	4364	23 September 2001	1602		441	Yes-M
	4365	24 September 2001	0842		431	No
	4366	24 September 2001	1618		449	No

Bottom Depth is the depth at which submersible first reached bottom, since aggregation densities were always greatest at that time. Time is Eastern Daylight Savings Time when bottom was reached

Area: *HMS* Hatteras Middle Slope; *VMS* Virginia Middle Slope; *LMS* Cape Lookout Middle Slope. *DSL* Deep Scattering Layer. *NBA* Near-bottom aggregation. Densities: *L* Low; *M* Moderate; *H* High

* NBA composed almost solely of *Sergestes arcticus*

** Data missing for descent portion of this dive. Absence of DSL may be inaccurate

provided supplemental data on distributions of the meso-pelagic fauna at the HMS and VMS. These samples were obtained with a mini-Tucker trawl (0.335 m² mouth opening, 505 μ mesh) deployed from the side of the vessel and towed for 15–45 min. The net was triggered open and closed with a messenger. Given their limited catching ability, these mini-Tucker trawl samples were omitted from comparative analyses, although the data were used to develop sampling depth horizons for later trawling operations.

Awareness of the existence of NBA based on the 1991–1992 cruise data prompted a dedicated effort in 1999–2001

to comprehensively sample the midwater fauna, covering all water column depths to within ∼100 m of the bottom during day and night. A primary objective was to determine if the "mesopelagic" NBA observed during daytime submersible dives was a persistent near-bottom feature. In order to accomplish this because night submersible dives were not feasible, we conducted discrete-depth, standardized tows of 30 min duration using large Tucker trawls towed from the stern of the research vessels and emphasizing night sampling (Figs. 1, 2a, b). During the 1999 cruise, which did not involve submersible operations, midwater trawling was only conducted at the HMS using a 3.7 m wide × 1.8 m deep Tucker trawl with 6 mm stretch mesh in the body, 1.2 mm mesh in the tailpiece, and 0.333 mm in the codend. During the 2000 and 2001 cruises, midwater sampling was conducted at the HMS and LMS sites between the two daytime dives, or when submersible dives were cancelled, and throughout the night with a Tucker trawl (2 m wide × 2 m deep, 1.59 mm mesh). Tucker trawls were opened and closed either by a clock timer release in 1999 or messenger-activated, double-trip release on the other cruises. Single net deployments on most cruises were opened at depth, fished in an oblique sweep through the target depth horizon for 30 min (Fig. 2a, b), closed and retrieved. During the 2000 cruise, the trawl frame was equipped to deploy two sequentially opened and closed nets in the same frame, providing two separate 30 min samples per deployment. For the double net rig, the two nets were opened, fished and closed in two sequential "V"-shaped sweeps through the target depth zone. The first net was always deployed open from the surface. A datalogging time-depth recorder (TDR) was attached to the upper spreader bar to record time, depth and temperature during each trawl deployment. Actual fishing depth was determined after each trawl from the TDR data and was used to adjust fishing characteristics to achieve desired sampling depths.

Laboratory procedures

All specimens collected were preserved at sea in 10% seawater formalin solution. In the laboratory, specimens were sorted, identified and transferred to 50% isopropanol. Fishes were measured to the nearest millimeter standard length (SL). Gonads of myctophid fishes were examined to determine gender and ovarian maturity stage for females (as per Gartner 1994).

Video and voice records were analyzed and written transcripts of each dive were prepared. Where possible, all individuals recorded by video devices were identified to species and enumerated by counting the number of individuals in the video field. Video identifications were confirmed as much as possible by examining submersible captured specimens.

Two species of the squid genus *Illex*, *I. illecebrosus* and *I. oxygonius*, were collected. Because these two species could not be separately identified from videotapes or submersible observations, we will refer to them hereafter as *Illex* spp.

Results

Submersible data

Overall, 34 submersible dives were accomplished at the three study areas: four dives at the VMS, 22 dives at the HMS, and eight dives at the LMS (Table 1), resulting in a total bottom time of 75.7 h. Sixteen dives were undertaken during the morning (about 0800 to 1230 hours), and 18 dives were undertaken in the afternoon (about 1500 to 2000 hours). In only five dives, two in the morning, three in afternoon, three of which were at HMS and two at LMS, no aggregations of mesopelagic species were seen either in the water column or on the bottom (Table 1). In the remaining dives two separate layers of mesopelagic animals were observed on a regular basis with most identified taxa occurring in both layers.

Deep scattering layer

A shallow midwater layer, consistent with the expected deep scattering layer (DSL), was observed during 27 of 34 dives (79%). We observed diffuse regions of commingled fishes and invertebrates of varying densities that often extended vertically for tens to hundreds of meters (54–537 m, average 211 m), with a noticeably denser central layer.

Eleven taxa, comprising nine fish and two invertebrate species, were observed in the DSL. Only two fish species, *Argyropelecus aculeatus* and *Benthosema glaciale*, were observed exclusively in the DSL (Table 2). Individuals of the paralepidid species *Lestidium atlanticum* and *Notolepis rissoi* (70.4% of dives for both species combined) and the myctophid *Ceratoscopelus maderensis* (66.7% of dives) were the most frequently observed in the DSL. These species were usually the most abundant of species observed in the DSL. The stomiid fish *Chauliodus sloani* was only observed in the DSL in one dive, while the remaining species were observed with some regularity (Table 2).

Estimated numbers of individuals in the field of view from the forward compartment of the submersible varied. The myctophid species, along with the shrimp *Sergestes arcticus* (VMS/HMS), and the sternoptychid fishes *Maurolicus weitzmani* and *Polyipnus clarus* (LMS), were the most abundant, with estimates often ranging in the hundreds, sometimes thousands, of individuals in the densest regions

Fig. 2 Depth-time profiles for Tucker Trawl samples from 1999 through 2001 cruises. **a** Daytime samples. **b** Nighttime samples. Four nighttime samples are overlapped by others and thus appear to be missing in figure
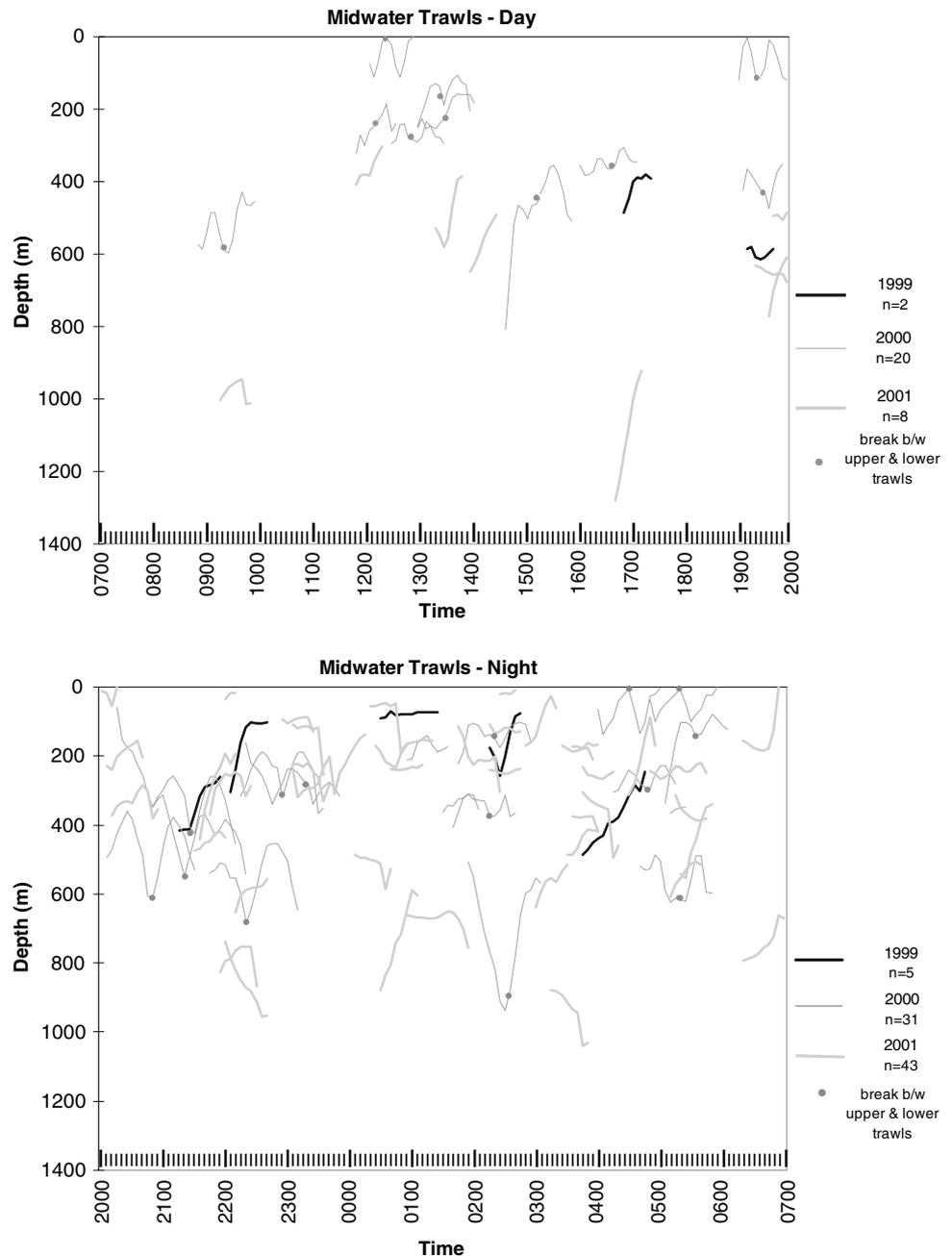
of the DSLs (1–$5/m^3$). While the paralepidid species and the mesopelagic eel *Nemichthys scolopaceus* were commonly observed, their densities were much lower, usually ≤ 10 individuals in the field of view for the two species collectively ($<1/m^3$).

Near bottom aggregations

Contrary to expectations, we also observed aggregations of varying densities of mesopelagic animals in proximity to the bottom during 24 of the 34 dives (70.5%; Table 1). Half

of these dives with NBA were in the morning and half in the afternoon, and they spanned a bottom depth range of 325–841 m. These NBA were typically first seen about 10–20 m altitude above the bottom and extended to the bottom. At some stations, aggregations were extremely dense, with large numbers of mesopelagic animals visible to the furthest extent of the field of view (Fig. 3, Table 1). Estimation of overall densities in these large aggregations ranged from 10 to 25 animals/m^3, with the most abundant species (e.g., *C. maderensis* at VMS and HMS; *P. clarus* at LMS) estimated at 5–25 individuals/m^3 (Fig. 3).

Table 2 Estimated abundances of animals in the visual field in the shallow water layer (DSL) and near bottom aggregation (NBA)

Dive	AA		BG		CM		CS		DD		IL	
	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA
3063	U				A	H						U
3067					A	H		U				U
3068					C	H					U	C
3069						A						
3070					C						U	
3211					C						U	
3212												
3213					A						U	
3214					A	C						U
3216	U				A	H					U	
3217					A	U					U	C
3218	U		A		A	H		U				U
3219					C	H						U
3220												
3221												
4198					C						U	
4199	U				A	A						
4200												
4201			A		A	H						
4202			A		A	H						
4203								U				
4204	U				A	A						
4205					A	H						
4206	U		C							C		
4207			C						C	A		
4358	C				U		U					
4359			C		U	C						
4360	C											
4361									U	U		
4362												
4363									C	A		
4364										U		
4365												
4366												

Dive	LA/NR*		MW		NS		PC**		SA		SB	
	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA
3063	U	U										
3067	U	U				U				C		
3068	U	U								C		
3069		U		A								
3070	U											
3211	U					U						U
3212	U	U				U			C	C		
3213		U	U						C	C		
3214	U		C						C	A		
3216		U			U	U				U		

Table 2 continued

Dive	LA/NR*		MW		NS		PC**		SA		SB	
	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA	DSL	NBA
3217		U			U	C				C		
3218	U	C			U	C				H		U
3219	U	C			U	U			C	U		
3220												
3221												
4198												
4199	U	C		C		U			C	C		U
4200												
4201	C	C		U		U	U		A	H		
4202	U				U				A	A		
4203	U		A		U	U			A			
4204		C			U	C	C			A		U
4205	C	U	A	A	U	U	U			A		U
4206							A	A	C			
4207			C				C					
4358	U		C		C				C			
4359	U	U			C		U		U			U
4360	U		C		U				C			
4361							A	A				
4362			U	C			A	A				
4363	U	U					C	H	U			
4364								H				
4365												
4366												

Estimates for DSL are from region of highest abundance; for NBA, estimates are based on visual field upon first contact with the bottom. Species key: AA, *Argyropelecus aculeatus*; BG, *Benthosema glaciale*; CM, *Ceratoscopelus maderensis*; CS, *Chauliodus sloani*; DD, *Diaphus dumerilii*; IL, *Illex* spp.; LA/NR*, *Lestidium atlanticum/Notolepis rissoi*; MW, *Maurolicus weitzmani*; NS, *Nemichthys scolopaceus*; PC, *Polyipnus clarus*; SA, *Sergestes arcticus*; SB, *Stomias boa ferox*. Abundance key: *U* uncommon, <10; *C* common, 11–100; *A* abundant, 101–1000; *H* highly abundant, >1,000

* *Lestidium atlanticum* and *Notolepis rissoi* were almost always sighted together in aggregations, but were the only paralepidids observed. Records often recorded both as "paralepidids or "barracudinas" without differentiating so abundances are combined

** Based on the numbers of hatchetfishes collected in midwater trawls, it is likely that many observations of "hatchetfishes" were of *P. clarus*, however, only positive i.d. records are included here

Ten taxa, comprising eight fish and two invertebrate species, were observed in the NBAs (Table 2). The stomiid *Stomias boa ferox* was the only species of mesopelagic fauna observed exclusively in the NBA (VMS and HMS). *Lestidium atlanticum*, *N. rissoi*, and *C. maderensis*, plus *S. arcticus* each occurred in >58% of the NBA dives. In general, species observed in both the DSL and NBA were noticeably more abundant, sometimes by an order of magnitude, in the NBA (Table 2). These estimated differences should be considered conservative as the visibility in the NBA was often limited by a dense nepheloid layer near the bottom at the HMS area.

Two features of the NBAs were observed frequently. Typically within 10–15 min of the JSL's arrival on the bottom, the aggregation thinned to the extent that only scattered individuals remained in view. Unless they were physically struck by the JSL, the dispersal of the animals away from the JSL was not rapid, but rather, a slow continuous movement away from the submersible. Mesopelagic animals were also frequently observed in direct contact with the substrate. Among the myctophids and stomiids, bottom contacts consisted of quick darting movements causing them to briefly strike the sediment. These actions appeared to be disoriented startle responses to the JSL and its lights. However, regular contact with the bottom that appeared to be normal behavior was noted for vertically hovering *N. rissoi*, which were observed making repeated vertical tailsprings from the substrate. Regular contact was also
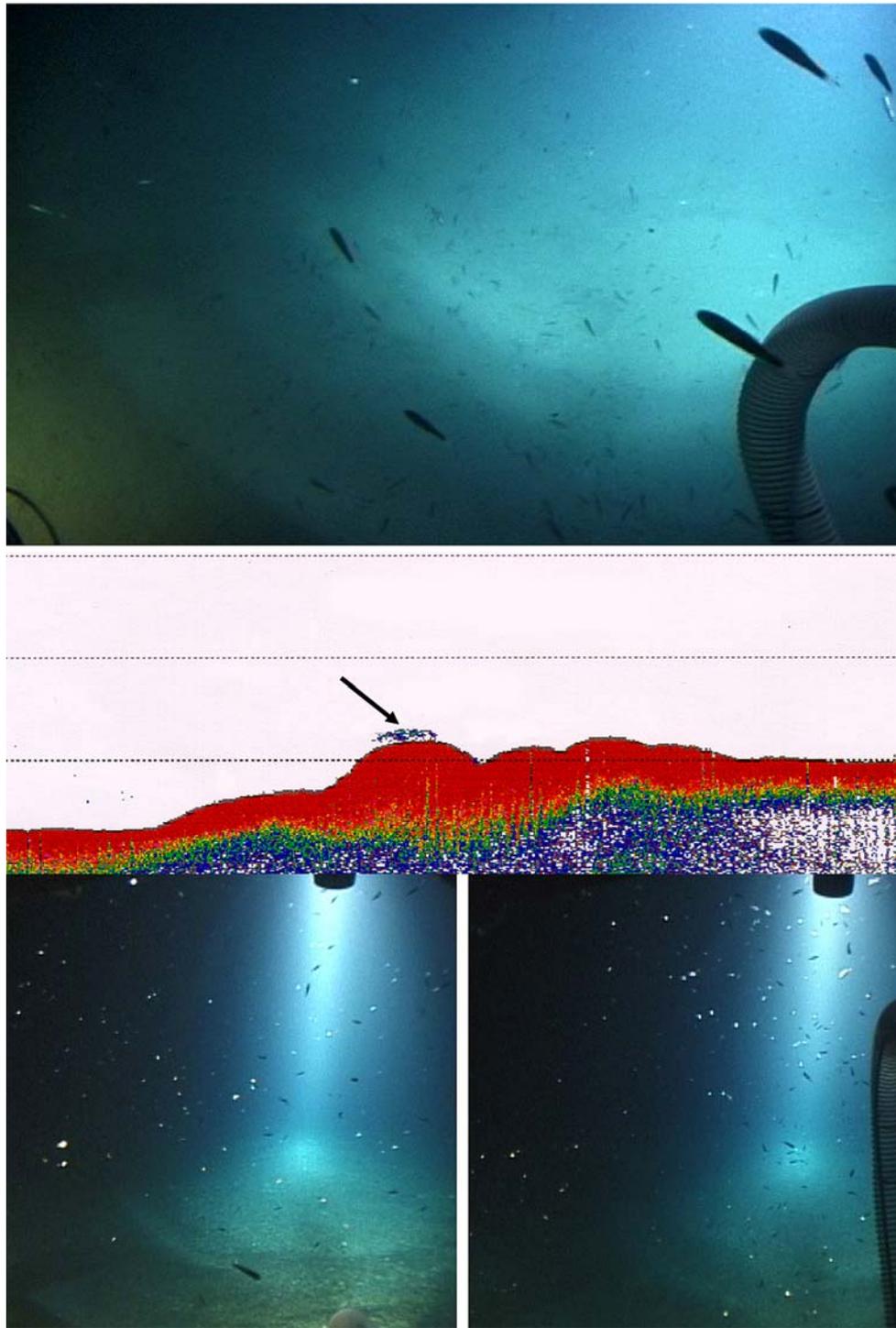
Fig. 3 Dense near bottom aggregations of mesopelagic fishes. *Top panel* is mostly *Ceratoscopelus maderensis* from JSL dive 4204 (27 July 2000, 0942 hours) over muddy substrate at 596 m at the HMS study area. *Center panel* is an echosounder profile of a coral bank in the LMS area taken just before JSL dive 4363, illustrating a large swarm of mesopelagic animals near bottom at top of ridge (*arrow*). Animals identified during the dive were mainly *Diaphus dumerilii* and *Polyipnus clarus*. *Bottom panels* are from JSL dive 4363 (23 September 2001, 0827 hours) near the base of a coral bank with coarse sandy substrate at 417 m (LMS area) illustrating a mix of *Polyipnus clarus* and *Diaphus dumerilii*. Species identifications were confirmed by simultaneous captures of specimens

observed in *Illex* spp., which were often noted resting on the bottom at the HMS site, remaining stationary with arms and retracted tentacles spread over substrate or curled (Fig. 4).

Both DSL and NBA layers were observed at all three study areas, but the species composition of the VMS and HMS sites differed markedly from the LMS sites. At the

Fig. 4 *Illex* spp. showing typical body configuration when resting on bottom. Both individuals photographed at HMS study sites

LMS sites, both layers were dominated by the myctophid *Diaphus dumerilii* and the sternoptychids *Maurolicus weitzmani* and *Polyipnus clarus*. Sergestids were uncommon and both paralepidid species and *Nemichthys scolopaceus* were absent at the LMS sites. Squids identified as *Illex* spp. were observed at all three sites.

No defined layer

In all but nine of the stations where the shallow DSL was observed (Table 1), it was well above the bottom (19–326 m off bottom, average 144 m). However, at these nine stations, once the upper part of the layer was reached, animal density was relatively consistent all the way to the bottom.

Midwater trawl data

The water column was extensively sampled by Tucker trawl. During 1999–2001, 111 tows were made over the HMS and LMS areas with 32 tows occurring during the day from 0 to 1293 m (Fig. 2a), and 79 occurring at night from 0 to 1,060 m (Fig. 2b). These samples yielded at least 88 fish species (S. W. Ross, unpublished data); however, fishes abundant in midwater trawl collections were often not those dominant in NBAs. While three NBA species were in the top five fishes collected by Tucker trawl, the two dominant

taxa, which included the gonostomatid genus *Cyclothone* with six identified species and the myctophid *Benthosema glaciale*, were absent within NBAs (Table 3). From all Tucker trawl collections, only 32 *C. maderensis* and 161 *D. dumerilii*, both dominant taxa in the NBA, were obtained. The common NBA species *N. rissoi* was not collected by Tucker trawl, although paralepidids such as *Lestidium atlanticum* were vulnerable to capture by the trawls (Table 3). Further comparisons between trawl and JSL data are in the species accounts below.

Species accounts

Family Myctophidae

Benthosema glaciale Individuals of *B. glaciale* were only identified from the shallower DSL layer during JSL dives and were usually associated with the shallower portions of the DSLs. Excluding *Cyclothone* spp., this was the most commonly collected mesopelagic fish species in both day and night Tucker trawls (Table 4) and was only collected at the HMS.

Table 3 Dominant fish species from combined 1999 to 2001 midwater Tucker trawl samples over the North Carolina Continental slope

Top Ranking Taxa	HMS	LMS
Cyclothone (6 spp.)	3,329	
Benthosema glaciale	491	
Maurolicus weitzmani	275	11
Polyipnus clarus	241	
Diaphus dumerilii	77	84
Argyropelecus aculeatus	68	7
Nemichthys scolopaceus	61	
Diaphus sp.		54
Sternoptyx diaphana	35	
Valenciennellus tripunctulatus	34	34
Ceratoscopelus maderensis	28	
Vinciguerria nimbaria		22
Sternoptyx sp.	19	
Myctophum affine		17
Myctophum selenops		16
Chauliodus sloani	15	
Lestidium atlanticum		15
Gonostoma elongatum	14	9
Vinciguerria poweriae		14
Nessorhamphus ingolfianus	12	
Notoscopelus resplendens	12	
Stomias boa ferox	12	
Diaphus mollis		11
Pollichthys mauli		8

HMS Cape Hatteras study area, *LMS* Cape Lookout study area

Ceratoscopelus maderensis This species occurred in both the DSL and NBA (Table 2). Estimated abundances of *C. maderensis* in the DSL were often an order of magnitude lower than for the NBA (Tables 2, 3). Additionally, while it predominated at VMS and HMS sites, this species was rarely observed or captured at the LMS sites (Tables 2, 3). Most specimens were trawled at night (Table 4). The typical body posture was inclined head downward about 30° off horizontal within both the DSL and NBA. In the NBA, many individuals were observed within centimeters of the bottom, although actual contact with the bottom appeared to be accidental.

The lengths of individuals in the DSL were quite variable, whereas the lengths of individuals observed in the NBA were unimodal, and the average size was distinctly larger than in the DSL. The DSL layer was composed mostly of juveniles and sub-adult individuals. Measurements of *C. maderensis* collected by Tucker trawls ranged from 9 to 63 mm SL, with a mean size of 37.5 mm SL ($n = 30$). Twenty-five *C. maderensis* were captured by the JSL in NBA layers, and the males ranged from 58 to 66 mm SL ($n = 6$, mean = 61.8 mm), while females measured from 54 to 74 mm SL ($n = 19$, mean = 64.5 mm), with an overall mean size of 63.9 mm SL. A one-tail *t* test showed a highly significant difference in overall mean sizes between the DSL and NBA groups [t Stat = -4.65; P($T \leq t = 9.6 \times 10^{-5}$)]. All females were in Stages III and IV of ovarian development, which are considered vitellogenic and ripe stages of egg development, respectively (Gartner 1994). Individuals >70 mm exceeded the previously reported maximum species size from midwater trawl collections (Nafpaktitis et al. 1977).

Diaphus dumerilii *Diaphus dumerilii* individuals were captured in almost equal numbers in the DSL from the HMS ($n = 77$) and LMS ($n = 84$) study sites (Table 3); however, they were observed and captured in both the DSL and the NBA only at the LMS sites (Table 2).

A relatively uniform size range of this species was observed in the NBA. In contrast to *C. maderensis*, however, young juveniles dominated both the DSL and the NBA, with very few adults found in either layer. The size range for Tucker trawl captured individuals within the DSL was 11–64 mm SL, with a mean size of 21.5 mm SL ($n = 153$). Individuals in the NBA captured by the submersible or gill net ($n = 234$) ranged from 17 to 63 mm SL and averaged 23.7 mm SL. Only four individuals were sexually mature adults (>61 mm SL); all others were juveniles (Gartner 1994).

Family Nemichthyidae

Nemichthys scolopaceus This distinctive eel was frequently observed in both the DSL and NBA layers and was also regularly captured in Tucker trawls (Tables 3, 4). Although usually observed singly or in small numbers, at several stations they were abundant in the NBA (Table 2). In the DSL, they exhibited both vertical (head up or down)

Table 4 Midwater trawl captures of mesopelagic fish species observed in the DSL or NBA by submersible, divided into day (*D*) and night (*N*), and the depth range (m) of capture

Family/Species	1999		2000		2001	
	D	N	D	N	D	N
Fishes						
Myctophidae						
Benthosema glaciale	15 (0–615)	46 (0–487)	89 (0–808)	113 (0–938)	114 (302–1293)	126 (0–1060)
Ceratoscopelus maderensis		12 (0–487)	1 (0–625)	7 (0–673)	1 (302–409)	11 (0–880)
Diaphus dumerilii			3 (215–257)	9 (0–408)	17 (479–1293)	132 (0–880)
Nemichthyidae						
Nemichthys scolopaceus	5 (0–615)	12 (0–487)	12 (233–808)	10 (0–428)	12 (302–1293)	12 (0–880)
Paralepididae						
Lestidium atlanticum		1 (99–320)				16 (87–1060)
Sternoptychidae						
Argyropelecus aculeatus	1 (0–615)	8 (76–423)	4 (239–384)	32 (0–938)	9 (302–1016)	20 (0–966)
Maurolicus weitzmani		8 (76–258)	2 (0–384)	165 (0–673)	1 (628–812)	111 (0–966)
Polyipnus clarus		3 (0–487)	37 (121–808)	202 (0–938)		5 (0–449)
Stomiidae						
Chauliodus sloani			2 (356–808)	3 (314–673)	1 (379–580)	9 (0–880)
Stomias boa ferox		1 (0–487)	3 (231–808)	1 (0–367)	5 (379–880)	2 (0–880)

and horizontal orientation. In the NBA, they were often seen immediately over the surface of the bottom (<10 cm) swimming horizontally with a slow anguilliform motion, but were never observed to directly contact the bottom. *Nemichthys scolopaceus* was neither collected nor observed from the LMS stations.

Family Paralepididae

Lestidium atlanticum Based on dive observations, paralepidids ranked second in frequency of occurrence in both the DSL and NBA (Table 2), and both species were typically found together. *Lestidium atlanticum* was usually the less abundant of the two species. With the exception of nighttime Tucker trawl collections in 2001, it was rarely captured in nets (Table 4).

Lestidium atlanticum was a readily identifiable species that we referred to as "bronze tails" owing to the strong copper-bronze iridescence of the caudal peduncle. Specimens in the NBA were typically large, with estimated sizes of 200 mm recorded on several occasions. Their body posture tended to be horizontal or at slight head up or head down angles off the horizontal, and direct contact with the bottom was not observed. This species was not observed at the LMS study sites, although it was captured in trawls there (Table 3).

Notolepis rissoi The more abundant of the paralepidids, this bright silver species was frequently observed in both the DSL and NBA layers and outnumbered its confamilial by three or four to one. It was neither observed nor captured at the LMS sites. Of the mesopelagic species collected, *N. rissoi* was the only one never captured in Tucker trawls. This may be because it is a fast moving species that tends to move vertically, and thus is more capable of evading nets or because it spends more time near bottom.

Notolepis rissoi was typically observed in near vertical posture, usually head up, exhibiting a very rapid oscillation of the caudal peduncle and caudal fin. In the NBA, this was one of two species observed to make regular contact with the bottom. It would gradually sink tail downward from an altitude of 2–5 m off the bottom until it made contact at which point it would rapidly "spring" back upwards to the starting altitude.

Family Sternoptychidae

Argyropelecus aculeatus Although never observed in large numbers, this migratory hatchetfish was commonly seen only in the DSL. This species was regularly captured in the midwater Tucker trawls, especially at night (Table 4). Nearly all specimens were collected from the HMS area (Table 3).

Maurolicus weitzmani

This species was not as commonly observed as other fishes in the VMS and HMS sites, but was extremely common in the NBA around the deep coral banks of the LMS sites. Whenever observed, this distinctive sternoptychid was typically reported in large numbers (Table 2). As with most of the mesopelagic species, although individuals were often observed within touching distance of the bottom (<0.1 m), they usually did not make contact with the bottom. They were observed to swim among the coral branches.

Polyipnus clarus

Positive identification of this species was included in four dive logs from HMS sites and six from the LMS, with most observations from the DSL (Table 2). Our data are probably underestimates of *P. clarus* in both the DSL and especially the NBA in these areas. Some NBA records were listed as "hatchetfishes" because of low abundances (<10 individuals) and difficulty with identifications. Most of these sightings were probably of this species. *Polyipnus clarus* was commonly captured in night midwater trawls in the DSL depths at the HMS sites (Table 3).

This species was the only hatchetfish associated with the *Lophelia* coral banks in the LMS study area, where it was highly abundant near the bottom during several dives (Table 2). It was often observed in contact with the coral substrate.

Family Stomiidae

Chauliodus sloani Only four individuals of this uncommon piscivore were observed, three of which were in the NBA (Table 2). These were large adults (~300 mm) hovering within 0.1–3 m of the bottom. None were observed or collected from the LMS area. These fish always hovered horizontally and remained motionless unless struck by the JSL.

Twelve of the fifteen *C. sloani* captured by midwater trawls were post-larvae and young juveniles (18–98 mm SL; mean = 39.9 mm); a thirteenth specimen was a 161 mm juvenile. These data along with our observations suggest that larger individuals remain deeper (Sutton and Hopkins 1996).

Stomias boa ferox This piscivore was reported more often than *C. sloani*, but was also only observed in the NBA (only at the HMS and VMS sites), and it was also considered an uncommon member of the aggregations (Table 2). Body posture and altitudes from the bottom were similar to *C. sloani*, hovering motionless until physically disturbed. Again, individuals observed were all in the largest reported

size range for this species. Two specimens captured by the JSL measured 176 and 255 mm SL. We obtained several close-up views of the head, and the mental barbel was always held straight forward from the head.

Twelve specimens of *S. boa ferox* were captured at DSL depths (Table 4). Six were juveniles (14–127 mm SL; mean = 68.8 mm), three were young adults (172–187 mm SL) and three were large adults (230–239 mm SL).

Cephalopods

Illex spp. *Illex* spp. squids were observed an equal number of times within the DSL and NBA, and they were sometimes more abundant in the NBA (Table 2). Frequency of occurrence and abundances may be underestimated as we often observed clouds of squid ink, which were probably from *Illex*.

Besides *Notolepis rissoi*, this was the only midwater species observed to regularly contact the bottom, and was the only species to exhibit prolonged contact. Individuals were often seen lying on the bottom, with their tentacles retracted and their arms curled downwards. They rested on the lower part of the curled arms, with the mantle lifted slightly off the bottom (Fig. 4).

Crustaceans

Sergestes arcticus This "half-red" sergestid was the most commonly observed mesopelagic crustacean and was among the top three most commonly encountered species in the DSL and NBA of the VMS and HMS study sites (Table 2). It often exhibited very high densities, especially in the NBA, where it was occasionally an order of magnitude more abundant than in the DSL (Table 2).

Individuals were usually horizontal with the antennae held stiffly forward of the body to a hinge point, from which the antennae arched posteriorly either over or alongside the body. Although many were observed within centimeters of the bottom, actual contact with the bottom was brief and appeared accidental on the few occasions when noted.

Discussion

The conventionally accepted pattern of spatial distribution for truly mesopelagic, as opposed to benthopelagic, animals is that they remain in open waters well away from the bottom throughout their lives. In contrast to this accepted distribution paradigm, our data revealed that a number of mesopelagic animals occur regularly in high abundances close to the bottom. While we also observed layers of mesopelagic species in the water column, animal densities were distinctly lower than those observed within the near-

bottom aggregations. Such NBAs may be expected and have been reported in depths similar to our study when the lower limits of the normal migratory depths of the mesopelagic fauna intersect the continental slope or other underwater bottom feature (Isaacs and Schwartzlose 1965; Mauchline and Gordon 1991). What seems unusual and has, to date, not been reported is that the NBAs appeared to persist around the clock based on our combined submersible observations and diel midwater trawling. Certain species exhibited distinct segregation, e.g., *A. aculeatus* and *B. glaciale* were observed and captured only well off the bottom, while *C. maderensis* was rarely seen or captured in midwater but was abundant near bottom, while others seemed to have less precise habitat specificity, with apparent usage of both the water column and bottom habitats. Our data suggest that persistent high-density aggregations near-bottom are a normal part of the life history of a number of species traditionally considered to be mesopelagic.

Several hypotheses, examined below, could account for near-bottom aggregations. The aggregations were the result of: (1) mesopelagic species approaching the bottom on a diel basis where it intersects their migration; (2) these species being concentrated by the unusual hydrography in the HMS region; (3) these species being concentrated by the topography along the slope; (4) these species being attracted to the submersible; (5) physiological changes related to ontogeny in some species, and; (6) behavioral changes associated with high density food resources near bottom in slope regions.

Migration interaction

Genin (2004), in a study on planktonic organisms over seamounts, coined the term "topographic blockage", in which the bottom intersects the lower vertical range of migratory species. A suggested result is that these migrators become prey to benthic or demersal predators. This near bottom interaction has been reported for a variety of vertically migrating mesopelagic fishes and invertebrates (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Marshall and Merrett 1977; Omori and Ohta 1981; Bulman and Koslow, 1992; Cartes, 1993; Gordon et al. 1995; Cartes et al. 2001; Hudson and Wigham 2003; Madurell et al. 2004; Madurell and Cartes 2005). Reid et al. (1991) discovered that pseudo-oceanic midwater species off Hawaii exhibited significant horizontal migrations in conjunction with the typical vertical pattern. They discovered that migrations were shoreward and upward at night, and offshore and downward during the day, so the potential for lateral topographic blockage should also be considered.

Virtually all lanternfish species (Backus et al. 1977; Gartner et al. 1987) plus *Chauliodus sloani* (Sutton and Hopkins 1996) undertake extensive vertical migrations.

Gonzalez et al. (2000) reported that the deep-sea scorpaenid *Sebastes mentella* collected in the North Atlantic often ate unidentified myctophids, *C. sloani*, *N. scolopaceus* and *N. rissoi*. *Sebastes mentella* occupies both demersal and pelagic habitats, so predation of these species as a demersal event cannot be confirmed; however, Gonzàlez et al. (2000) also showed that *N. scolopaceus* and *N. rissoi* occur close to the bottom; therefore, it seems likely that much of this predation took place on or near bottom. There are no reports of vertical migration in *Nemichthys scolopaceus* or *Notolepis rissoi*, so their presence in the NBA appears to be part of their natural depth range.

We have also observed benthic fishes and invertebrates feeding on species in the NBAs at the HMS and LMS regions. Myctophids, sternoptychids, sergestids and squids in the NBA were frequently observed being eaten by a variety of benthic inhabitants, including cerianthid anemones, galatheid lobsters, hagfishes and even ophiuroid brittle sea-stars.

Our sampling design does not enable us to adequately address the possibility that horizontal movements of NBA species allows them to intersect with the bottom. However, several pieces of evidence do not support the idea that the NBA's are mainly due to vertical topographic blockage. As stated, several of the species consistently present in the NBA apparently exhibited no vertical migration. Among the migrators, one would expect that both DSL and NBA size ranges would be similar, a pattern that was not observed in *Ceratoscopelus maderensis* at least. Additionally, our midwater trawl data indicated that some species such as *C. maderensis* did not ascend at night, or did so in reduced numbers, so topographic blockage would not be applicable to these species at least.

HMS hydrography

Along the western North Atlantidc slope at least, the hydrography and benthic environment of the HMS region differ markedly from other slope water regions north and south of the HMS study area, based on both published accounts and our own observations (Diaz et al. 1994; Sulak and Ross 1996; Bauer et al. 2002). This study area is composed of rugged soft sediment canyons where several current systems interact. Benthic currents are negligible, a bottom nepheloid layer is persistent, and benthic productivity is high. These unusual conditions may have produced distinctive physiological adaptations in some of the dominant benthic fish species (Moser et al. 1996; Sulak and Ross 1996). Because our first observations of NBAs came from this area, we proposed that they might be a physiological or behavioral response to hydrographic or benthic conditions. In addition to references to NBAs already noted, dense aggregations of *Ceratoscopelus maderensis* and *Diaphus*

dumerilii have been observed along the bottom around the HMS and farther north off New Jersey during both day and night dives (M. Youngbluth, personal communication), and *Maurolicus weitzmani* have been observed near the bottom north of the Yucatan Peninsula (R.G. Gilmore, personal communication). Thus, we dismiss this hypothesis mainly because NBAs, albeit with different species compositions, occur in widespread areas, including our other two study regions that are not oceanographically or ecologically comparable to the HMS.

Bottom topography

Bottom topography may play a role in concentrating organisms. Most of the dense near bottom aggregations occurred along steeply sloping (≥60°) ridges or canyons or other sharp relief. Some NBAs were dense enough over coral banks to be seen on echosounder traces (Fig. 3). The reason for the higher frequency of aggregations along such relief is uncertain, although these ridges may serve to concentrate and suspend organic matter as currents flow over them, allowing zooplankton and their predators to increase their numbers in such areas (Genin 2004). However, dense NBA's were also found over relatively flat regions at the VMS study area, suggesting that topography alone does not account for the formation of aggregations.

Attraction to submersible

Several examples of both positive and negative phototactic responses to the JSL were observed. The gonostomatid fish *Gonostoma elongatum* was always observed at the periphery of the light field and fled when illuminated by the arc light. In contrast, at some dive sites several species of crustaceans swarmed the lights of the JSL in enormous numbers when it reached the bottom and remained abundant until the JSL ascended. Among these crustaceans, we were able to identify the hyperiid amphipod *Parathemisto gaudiuchaudii* and the euphausiid *Megalops atlantica*.

That attraction to the JSL's presence could be a possible cause for the formation of the NBA's was discounted for several reasons. If this was the case, aggregations would be expected on almost every dive. Out of the 26 dives, notable aggregations of hundreds to thousands of individuals were observed 17 times. Attraction to the JSL should have resulted in swarming behavior by midwater animals throughout the entire portion of the dive that overlapped their habitat depths. However, the times we observed aggregations of mesopelagic species well off the bottom (DSL), the JSL usually passed through them, and the animals in the DSL did not move with or towards the JSL. In a similar fashion, the JSL also passed through the dense near-bottom aggregations, some of which were >20 m thick.

If the animals were attracted to the JSL, it seems that they would have swam alongside the JSL and moved downward with it. Although we often observed some animals swimming, not all of the movement was downward and numerous individuals remained nearly motionless, a behavior that was noted among all the stomiids unless they were physically struck by the submersible or its pressure wave. The behaviors of the mesopelagic species differed markedly from the previously noted swarming of some near-bottom crustaceans.

Invariably, observed NBA's rapidly dispersed once the JSL reached the bottom. Even massive aggregations of animals estimated to number in the thousands of individuals were almost completely gone from view within 10–15 min of the JSL's arrival. Clearly, if attracted to light or some other feature of the JSL, the aggregation densities should have increased or at least remained constant.

Ontogenetic change in physiology

Marshall (1980) suggested that some myctophid species, as well as other mesopelagic animals may adopt a benthopelagic or demersal lifestyle as they age. Based on bottom versus midwater trawl data, plus age, growth and reproductive characteristics, Gartner (1991) suggested that *Diaphus dumerilii* adopted a benthopelagic lifestyle as mature adults. However, most of the *D. dumerilii* specimens we collected in the NBA were juveniles. Characteristics of *Ceratoscopelus maderensis* within the NBA were more consistent with the hypothesis that they change to demersal habitats as they mature. The average size of bottom-collected *C. maderensis* indicated they would be near the end of their 2-year life span (Linkowski et al. 1993). The same pattern of migrating mesopelagic juveniles and more benthic adults was demonstrated for the myctophid *Lampanyctus crocodilus* in Mediterranean slope waters (Stefanescu and Cartes 1992).

Functional change based on food supply

Enhanced food supplies may be responsible for the large NBAs of mesopelagic species. The mesopelagic environment typically has a relatively low availability of food, which must be sought in three dimensions (Marshall 1980). High densities of food in essentially a two dimensional search area (i.e., near bottom) would enhance the probability of feeding success, and may serve as a mechanism retaining fauna that would otherwise migrate.

The near-bottom habitats of the HMS usually had a persistent nepheloid layer that probably contained a significant organic component (Sedberry and Musick 1978; Sulak and Ross 1996). In addition, the benthic environment of this area was reported to have the highest organic carbon depo-

sition rate on the eastern US slope (Thomas et al. 2002). The LMS coral bank sites also usually exhibited a dense marine snow layer near bottom. This high organic content would be a major food source for grazers, e.g., sergestid shrimps, mysids and euphausiids, which were observed on bottom in great numbers, especially at the HMS and/or LMS. The increased numbers of such zooplankters would lure planktivorous predators such as lanternfishes, hatchetfishes and *N. scolopaceus* that in turn, attract higher trophic feeders including the paralepidids, squids, *S. boa ferox* and *C. sloani*. Paralepidids and squids are known predators of fishes and shrimps (Rofen 1966; Wood 2002), and *S. boa ferox* and *C. sloani* are piscivorous, both feeding almost exclusively on *C. maderensis* on the western north Atlantic continental slope (Gartner, unpublished data). Genin (2004) suggested just such a concentrating mechanism over abrupt bottom topographies. Apparent feeding behaviors such as snapping of jaws and short darting "lunges" were regularly observed among the fishes within the aggregations.

The chronic near bottom presence of large numbers of animals commonly thought to be mesopelagic has significant implications for the evaluation of carbon flow in deep ocean waters. In addition to the fall of fecal matter (Robison and Bailey 1981) and decomposed organic marine "snow" (e.g., Alldredge and Silver 1988) researchers have visualized a unidirectional downward flow of energy from the mesopelagic to the benthic through direct predation (e.g., Pereyra et al. 1969; Marshall and Merrett 1977). In many regions, including continental slopes, large foodfalls (e.g., whale carcasses) are thought to be the major contributors of energy to the deep benthic and demersal macrofauna. The frequent near bottom aggregations of mesopelagic species adds to the evidence for increased carbon flow to the slope benthos. As previously stated, we repeatedly observed various benthic animals actively capturing and devouring mesopelagic animals from the aggregations.

A number of other recent reports on the diets of other benthic, benthopelagic and demersal species indicate the regular presence of putative mesopelagic species in close proximity to the bottom on a widespread geographic basis (Bulman and Koslow 1992; Cartes 1993; Cartes et al. 2001; Hudson and Wigham 2003; Madurell et al. 2004; Madurell and Cartes 2005). In all of these, various mesopelagic fish or crustacean species were regular prey items in the diet. Bulman and Koslow (1992) studied the diet of the benthopelagic fish *Hoplostethus atlanticus* collected off Tasmania and showed that they fed almost exclusively on mesopelagic prey. The frequency of *Sergestes arcticus* in their stomachs ranged from 1.9 to 7.4%, while *Chauliodus sloani* was present in 0.3–0.8% of the stomachs and three identified genera of myctophids ranged from 0.3 to 3.4% frequency of occurrence. Cartes (1993) showed that in two

species of western Mediterranean benthic pandalid shrimps, *Plesionika edwardsi* and *P. martia*, the frequency of *Sergestes arcticus* in the diet ranged from 7.0 to 29.4%, which was comparable to or exceeded the percentages of some benthic prey species. Some of the more extensive data sets show apparent seasonality in the percent contribution of mesopelagic prey to the diet (Cartes 1993, Madurell and Cartes 2005). Coupled with the findings of these reports, our data suggest that, over continental slopes and presumably shallow seamounts and other submerged features, there is a regular mesopelagic food supply for many benthic boundary layer predators in addition to the material that sinks through the mesopelagic zone from shallower waters.

There may be an energetic advantage as well for the mesopelagic residents of the near-bottom aggregations. We are investigating the diets of bottom collected midwater species to determine whether food items include epibenthic or demersal prey. Were such foods to be found, it would suggest a potentially significant upward movement of carbon in some deep ocean areas, a contrast to the typical downward energy flow paradigm.

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