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Meso- and bathypelagic fish interactions with seamounts and mid-ocean ridges

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Abstract

The World Ocean's midwaters contain the vast majority of Earth's vertebrates in the form of mesoand bathypelagic ('deep-pelagic,' in the combined sense) fishes. Understanding the ecology and variability of deep-pelagic ecosystems has increased substantially in the past few decades due to advances in sampling/observation technology. Researchers have discovered that the deep sea hosts a complex assemblage of organisms adapted to a "harsh" environment by terrestrial standards (i.e., dark, cold, high pressure). We have learned that despite the lack of physical barriers, the deep-sea realm is not a homogeneous ecosystem, but is spatially and temporally variable on multiple scales. While there is a well-documented reduction of biomass as a function of depth (and thus distance from the sun, ergo primary production) in the open ocean, recent surveys have shown that pelagic fish abundance and biomass can 'peak' deep in the water column in association with abrupt topographic features such as seamounts and mid-ocean ridges. We review the current knowledge on deep-pelagic fish interactions with these features, as well as effects of these interactions on ecosystem functioning. We highlight the recent discoveries from the Mid-Atlantic Ridge (via the Census of Marine Life field project MAR-ECO) that were presented at the international symposium "Into the Unknown, Researching Mysterious Deep-Sea Animals," hosted by the Okinawa Churaumi Aquarium, Okinawa, Japan, Feb 2007.

Introduction

Approximately 95% of Earth's liquid water is contained in the deep-pelagic realm (200-7000 m, encompassing the meso-, bathy- and abyssopelagic depth zones, *sensu* Menard and Smith, 1966). At roughly ten times the volume of all terrestrial ecosystems combined, the deep-pelagial is by far Earth's largest and least known aggregate ecosystem. For most of its extent the deep pelagial has no physical structure other than the properties of the water itself (e.g., temperature, salinity, pressure, light absorption,

current shear). In other words, the majority of the deep pelagial is a disphotic/aphotic (little or no solar light), fully three-dimensional, fluid environment in which the only solid objects are the biota contained within. As a general rule, living biomass decreases exponentially with depth in the open ocean (Angel and Baker, 1982). In areas where the deep pelagial intersects abrupt topographic boundaries (e.g., seamounts and mid-ocean ridges) enhanced biomass of deep-pelagic fishes has been observed. Here we review the current knowledge of the interactions of deep-pelagic fishes with seamounts and mid-ocean ridges, including recent findings of bathypelagic fish aggregations along the Mid-Atlantic Ridge.

The deep-pelagic fish fauna

In general, deep-pelagic fishes are small (i.e., 10 cm or less), although some species can reach 1 m. Most mesopelagic fishes migrate vertically into shallower layers at night to feed before returning to disphotic depths during daytime. Many fishes have species-specific ventral arrays of bioluminescent photophores that are used for camouflage against predators, prey attraction and illumination, and intra-specific communication (Herring and Morin, 1978; Young, 1983). Mesopelagic fishes (those living between 200-1000 m depth) are relatively short-lived, rapid-turnover species with life spans of 1-5 years; cold- and deep-water forms tend to grow larger and live longer than tropical, shallower species (e.g., Childress et al., 1980; Gartner, 1991). Bathypelagic fishes (those living greater than 1000 m depth), on the other hand, are morphologically, physiologically and behaviorally adapted to conserve energy in a food-limited environment. They are larger on average than mesopelagic fishes and have higher growth rates achieved by higher relative growth efficiencies (between 25 and 50%) (Childress, 1995). Vertical migration and bioluminescence are reduced or absent among bathypelagic organisms (Young, 1983).

Deep-pelagic fishes represent an important link between zooplankton and higher trophic level predators such as piscivorous fishes, squids, marine mammals, and seabirds. The primary prey of mesopelagic zooplanktivorous fishes are calanoid copepods (Hopkins et al., 1996; Sutton et al., 1998), but gelatinous prey may also be important for some deep-pelagic taxa (Arai, 2005). A large component of deep-pelagic fish assemblages includes higher-level predators, which feed primarily on migrating micronektonic fishes, shrimps and/or cephalopods (Sutton et al., 1996). Vertically-migrating mesopelagic fishes transfer particulate and dissolved organic matter from autotrophic upper waters to the heterotrophic ocean interior (Angel, 1985). At depth, vertical migrants produce fecal pellets and excrete metabolic products, such as carbon dioxide and dissolved organic carbon and nitrogen, generating the 'mesopelagic maximum' of organic matter often detected around 500 m (Walsh et al., 1988), the average day time depth of most deep-scattering layers (DSL). Our understanding of the dynamics and the magnitude of the fluxes in these processes is incomplete, but improving (Ducklow et al., 2001; Buesseler et al., 2007).

Deep-pelagic fish - seamount interactions

Most studies of seamount biota have been of plankton (see Genin, 2004) or larger, commercially-

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exploited species. There are relatively few studies of deep-pelagic micronekton (fishes, shrimps and cephalopods). Pelagic micronekton are known to aggregate over seamounts and may play an important role as food for higher trophic levels (Koslow, 1997; McClatchie and Dunford, 2003). Froese and Sampang (2004) report about 107 micronekton species that associate with seamounts, with most of these recorded in the vicinity of the Bear Seamount (Moore et al., 2003) or at the Nazca and Sala y Gómez submarine ridges (Parin et al., 1997). Porteiro and Sutton (2007) categorized deep-pelagic fish - seamount interactions into four groups:

1 - Mesopelagic fauna that migrate to the epipelagic layer (0-200 m depth) at night and interact with seamounts during the migration process. This type of interaction and accumulation of migrant DSL organisms with seamounts was first reported by Isaacs and Schwartzlose (1965). After being laterally advected over shallow topography by surface currents during the night, vertical migrators can be trapped at the summit of shallow seamounts on their way down to daytime depths or impinge the flanks of shallow seamounts during any phase of the diel cycle, and the summits of intermediate seamounts while descending to daytime depth. This phenomenon can be very important for seamount ecology (Fock et al., 2002). Feeding can be so intense that pelagic organisms can be depleted by resident benthopelagic predators, resulting in a 'daily gap formation' over seamounts (Genin et al., 1994). Because most of the migrants are confined to the mesopelagic layers, this interaction would be expected to decrease over seamounts deeper than 1000 m.

2 - 'Pseudoceanic' or 'neritopelagic' species (sensu Hulley and Lutjeharms, 1989; Parin et al., 1997) from primarily pelagic fish families that occur near abrupt topography, but are absent or less abundant in oceanic waters. For example, the hatchetfishes (Sternoptychidae) Argyripnus atlanticus, A. electronus and A. iridescens live in association with the Great Meteor and other seamounts south of the Azores (Badcock, 1984a; Kukuev, 2004), and with the seamounts of the Sala y Gómez and Norfolk Ridges (Parin, 1992; Parin et al., 1997). Argyripnus brocki, a member of the "mesopelagic-boundary community" (Reid et al., 1991; Benoit-Bird et al., 2001), is endemic to the Hawaiian seamount region (Harold and Lancaster, 2003). The lightfishes (Phosichthyidae) Polymetme corythaeola, P. thaeocoryla, P. andriashevi and Yarrella blackfordi also belong to this group and are known to live preferentially in continental, insular and seamount slopes (Badcock, 1984b; Parin and Borodulina, 1990). The bathypelagic tubeshoulders (Platytroctidae) Holtbyrnia anomala, H. macrops, Normichthys operosus, Sagamichthys schnakenbecki, Maulisia mauli and M. microlepis have been reported in association with many seamounts in the north Atlantic (Kukuev, 1982, 2004). Sassa et al. (2002) found enhanced mesopelagic fish numbers and biomass over the Emperor Seamount chain (Hawaii) relative to surrounding waters, due largely to dense assemblages of the seamount-endemic hatchetfish Maurolicus imperiatus (cited as M. muelleri in previous literature). Boehlert and Seki (1984) reported acoustic 'clouds' of micronekton over Southeast Hancock Seamount (Hawaii), which trawling revealed to be *Maurolicus imperiatus*, the mysidacean *Gnathophausia*

longispina (Lophogastridae), and the bobtail squid *Iridoteuthis iris* (Sepiolidae). These species remained over the seamount flanks during day, and then accumulated over the top to within 100 m of surface at night to feed (Boehlert et al., 1994). Their absence in waters away from the seamount suggested a permanent seamount boundary community. Wilson and Boehlert (2004) concluded that resistance to advection off the seamount by active swimming was likely responsible for the observed swarms.

3 - Non-migrant or weakly-migrant midwater fauna that enter the benthopelagic zone around seamounts. This group includes nearly all bathypelagic fishes as well as several groups of mesopelagic fishes that impinge seamounts, but whose densities do not appear to be enhanced. For example, at night the hatchetfish *Argyropelecus aculeatus* is equally abundant over the slope of the Great Meteor and Atlantis Seamounts and at a non-seamount oceanic reference station (Pusch et al., 2004). Bathypelagic fishes are found on the deep slopes of all seamounts and the summits of deeper seamounts, but their overall role in seamount ecosystems is poorly known.

4 - Adults of meso- and bathypelagic micronekton species that dwell in the benthopelagic zones. Adults of some species of typically mesopelagic fish families, such as the dragonfishes (Stomiidae), bristlemouths (Gonostomatidae), lanternfishes (Myctophidae), barracudinas (Paralepididae) and bigscales (Melamphaidae), dwell over seamounts and other slopes below 700 m, adopting a benthopelagic life strategy (Guschin and Kukuev, 1981).

Seamounts have higher productivity compared to the surrounding open ocean (Clark, 1999; Uiblein et al., 1999) and often support large aggregations of commercially harvested benthopelagic fishes (Rogers, 1994; Koslow et al., 2000) such as orange roughy, *Hoplostethus atlanticus*, pelagic armorhead, *Pseudopentaceros wheeleri*, alfonsinos, *Beryx* spp. and cardinalfish, *Epigonus telescopus* (Morato et al., 2006). Studies have shown that imported pelagic food supplies support large fish aggregations on seamounts. For example, Isaacs and Schwartzlose (1965) estimated that at the 100-m isobath of Banco San Isidro (Baja California) the flux of organic carbon due to topographic blockage of downward-migrating micronekton was about 40 times greater than the primary production at the most productive regions off California. Seki and Somerton (1994) reported that the diet of armorheads over the summit of SE Hancock Seamount (265 m) consisted mostly of migrating micronekton that were advected and trapped over the seamount summit at night. Fock et al. (2002) indicated that the topographic blockage mechanism could explain the distribution and diel behavior of sustained fish populations over the Great Meteor Seamount. Other studies have corroborated the topographic blockage hypothesis by showing that maximum foraging on vertically-migrating micronekton occurs in the early morning, when prey get trapped on their downward migration and become visible in the light (Pereyra et al., 1969; Genin et al., 1988).

Since the average daytime depth of the World Ocean DSL is around 500 m, aggregations of

seamount-associated benthopelagic fishes that live below that depth, such as orange roughy, cannot center their diets on migrant fauna, but rely instead on non-migrant deeper meso- and bathypelagic prey. Bathypelagic smelts (Microstomatidae), large lanternfishes and dragonfishes were found to be the main prey of orange roughy caught between 830 and 1500 m at seamounts off the Azores (Barcelos et al., 2005) and in the Rockall Trough and Porcupine Sea Bight (Mauchline and Gordon, 1984; Gordon and Duncan, 1987). Similarly, non-migrant pelagic organisms were also the prey of orange roughy caught at the seamounts off New Zealand (Rosecchi et al., 1988), Australia (Bulman and Koslow, 1992) and Chile (Labbé and Arana, 2001). Koslow (1997) concluded that seamount aggregators subsist on meso- and bathypelagic organisms that drift past seamounts. Most of these studies have not identified any clear pattern of daily feeding periodicity, which supports the idea that a constant flux of laterally-advected, non-migrant deep-pelagic fauna represents the main prey of orange roughy.

While specific mechanisms driving trophic interactions between benthopelagic fauna and water column fauna are not fully understood, it appears that a primary factor is the concentration of pelagic prey that is normally widely distributed. Greater abundances of higher trophic level predators can be supported by efficient foraging in these areas. Increased trophic efficiency may work simultaneously over several trophic levels. In some cases (e.g., Great Meteor Seamount), higher trophic levels effectively utilize all or most of the vertically-migrating prey concentrated by topographic trapping, resulting in the 'daily gap formation.' In other cases (e.g., SE Hancock Seamount), mortality of deep-pelagic fishes by the demersal seamount fauna may be offset by the benefits of increased availability of zooplankton prey, hence increasing local fish production. Whatever the mechanism, it would appear that the trophic subsidy afforded to the demersal seamount fauna (in the form of meso- and bathypelagic micronekton) is an integral part of the ecology of seamount ecosystems.

Deep-pelagic fish - mid-ocean ridge (MOR) interactions

The MOR system is the largest topographic feature of the World Ocean seafloor, larger than continental shelves and slopes where considerably more research on ecological structure has been focused. Ridges are likely to have characteristic and/or endemic faunas, and these topographic features may also interact with processes affecting the slope and shelf biota, such as intercontinental migration and dispersion (Vereshchaka and Vinogradov, 1999; Vinogradov et al., 2000). Lacking the terrigenous nutrient input received by continental slope communities, the deep-water fauna associated with mid-ocean ridges ultimately depends on local surface production. Despite limited surface production, there is evidence that near-ridge demersal fish biomass is elevated above the northern Mid-Atlantic Ridge (Fock et al., 2002; Bergstad et al. in press). Three major processes transfer organic matter to the near-ridge pelagic zone: (1) vertical migration of living animals; (2) sinking of aggregates (including marine snow) and carcasses of larger animals; and (3) lateral advection of organic matter from off-ridge sources (Angel, 1997). Along MORs, complicated topography and its effect on circulation and production at seamounts probably act to

affect distribution of the mesopelagic, bathypelagic, and benthopelagic fauna (Roden, 1987). Upwelling processes may establish an upward flux of near-bottom material into the deep pelagial. Closer to the surface, ridge systems might serve as an important source of ocean mixing through generation of internal tides, tidally rectified flows, and trapped waves (Holloway and Merrifield, 1999).

Compared to seamounts, almost nothing is known about interactions between deep-pelagic fishes and non-seamount sections of mid-ocean ridges. Despite the wide distribution and extensive area of MORs, few investigations have studied the non-vent animal communities associated with these regions (Vinogradov, 1997). Depth is the primary reason for this dearth of information as the summits of MORs generally crest below 1000 m. Bathypelagic sampling is expensive, logistically difficult, and gear selectivity often limits the spectrum of fishes caught (Aron and Collard, 1962; Kashkin and Parin, 1983). Many of the pioneering surveys of MORs were fisheries-oriented, sampling only the largest (commercially valuable) components of the communities (Troyanovsky and Lisovsky, 1995; Thomsen, 1998; Vinnichenko, 1998). The smaller, numerically dominant components (i.e., most midwater fishes) have received little effort. The perception of the bathypelagic zone as a 'biological desert' has led most biological oceanographers to ignore the organization and evolution of species distributions in this largest, least-known habitat. A related problem involves synopticity of supporting data - most oceanography vessels are poorly suited for deep trawling and most fish trawlers are ill-equipped to conduct oceanographic sampling. As a result, data on hydrography, acoustic backscatter, and plankton abundance/distribution, if available, are often offset in time and space from the fish collection. Despite these impediments, recent gains have been made in understanding these ecosystems through coordinated multidisciplinary research projects.

MAR-ECO: a mid-ocean ridge ecosystem study

The largest, most comprehensive study of a MOR ecosystem is the ongoing international research project MAR-ECO (www.mar-eco.no), a Census of Marine Life (www.coml.org) program focusing on the ecosystems associated with the northern Mid-Atlantic Ridge (MAR), from Iceland to the Azores. The principal objectives of MAR-ECO are to describe and understand the patterns of distribution, abundance and trophic relationships of organisms inhabiting the mid-oceanic North Atlantic, and to identify and model ecological processes that cause variability in these patterns (Bergstad, 2000). MAR-ECO field sampling to date has generated one of the largest (if not the largest) collections of ridge-associated deep-pelagic fishes to date. The scope and scale of multi-mode sampling spanning multiple trophic levels presents an unprecedented opportunity to understand the flow of energy between ridge systems and the overlying pelagic biota.

Interactions between the deep-pelagic fauna and the northern MAR were investigated during Leg 1 of the R/V *G.O. Sars* expedition (Sutton et al., 2008; Wenneck et al., 2008), conducted during summer (Jun-Jul) 2004. This expedition mapped the pelagic fauna using: (1) continuous acoustic sampling along the

entire cruise track; and, (2) point sampling at 36 predefined stations to characterize hydrography and biotic composition, abundance and biomass. A series of sampling methods was employed at each station, including CTD deployments, plankton net tows and pelagic nekton tows. Three different double-warp midwater trawls, two commercial ('Egersund' and 'Åkra' trawls) and one oceanographic ('Krill' trawl), were used to sample from the surface to depths of 3000+ m, bottom depth permitting (see Sutton et al. in press, for more methodological detail). During this cruise the latter two trawls were equipped with a remotely operated multi-sampler with three (Åkra) or five (Krill) separate cod ends to sample depth strata discretely and consecutively during each deployment. Trawls were equipped with SCANMAR sensors to provide data on cod end number, position, UTC time and depth. In total, 115 discrete-depth samples were collected for vertical distribution characterization. Samples generally fell within one of five depth categories: 0-200 m; 200-750 m; 750-1500 m; 1500-2300 m and > 2300 m. Samples within 200 m of the bottom were noted specifically.

A total of 205 fish species were collected during Leg 1 of the 2004 G.O. Sars expedition (Sutton et al., 2008). These specimens, some of which are among the rarest known vertebrates, are housed and curated at the Bergen Museum <http://collections.uib.no/vertebrate>, the permanent repository for all 2004 MAR-ECO expedition pelagic fish specimens. In order to reduce complexity of the results, a brief faunal account by depth zone is presented here. Few fish assemblages were found wholly within the epipelagic zone, and of these only four species were abundant (the snake pipefish, Entelurus aequoreus [Syngnathidae] in the Reykjanes Ridge region and three shallow mesopelagic fishes near the Azores). Two large, vertically migrating mesopelagic assemblages were found: (1) a northern (60° - 45° N), low-diversity, high-abundance assemblage dominated by three lanternfishes (Benthosema glaciale, Protomyctophum arcticum and Myctophum punctatum), a dragonfish (Chauliodus sloani), a pearlside (Maurolicus muelleri), and a bristlemouth (Cyclothone microdon); and (2) a southern (Azorean) assemblage of high diversity (including 29 lanternfishes and 19 "dominant" species) and low abundance (half that of northern assemblage). Two discrete deep-meso/upper-bathypelagic assemblages were found near the Azores, with C. microdon, the loosejaw dragonfish (Malacosteus niger), and three large melamphaid species (Scopelogadus beanii, Scopeloberyx robustus, and Poromitra megalops) the dominant fishes. The bathypelagic zone was characterized by the presence of a single, large assemblage spanning the entire northern MAR. This assemblage was dominated numerically by C. microdon, while the main biomass contributors were C. microdon, the deep-sea smelt (Bathylagus euryops), the sawtooth eel (Serrivomer beanii), two melamphaids (S. robustus and P. crassiceps) and a tubeshoulder (Maulisia microlepis). The benthic boundary layer over the ridge (within 200 m of the bottom; variable depths between 750-2300 m) exhibited low diversity (seven main species) but contained the highest numbers and biomass per volume for the entire water column over the MAR (Fig. 1). Bathypelagic aggregators near the MAR include B. euryops, Scop. beanii, Serr. beanii, S. robustus, Eurypharynx pelecanoides, Borostomias antarcticus, and Sigmops (Gonostoma) bathyphilum.



Fig. 1.

The pooled vertical distribution of deep-pelagic fish abundance and biomass (ww = wet weight) along the northern Mid-Atlantic Ridge. Exact values listed in parentheses. Results based on 82 discrete-depth trawl samples. "Near bottom" data include all samples within 200 m of the bottom, irrespective of depth from the surface (range = 750-2300 m). After Sutton et al., 2008.

An overall view of the association of deep-pelagic fishes with the MAR can be seen using acoustic data (18 kHz) (Fig. 2). When the cruise track crossed the MAR, several acoustic features were observed relative to the bottom topography:

(1) diel vertical migration by the DSL was clearly evident, as the horizontal axis represented both distance and time (the West_East crossing took \sim 30 h);

(2) the vertical range of the diel migrant DSL was shallower than the ridge crest, suggesting that the main bulk of this assemblage passed over the ridge without obvious interaction;

(3) interactions between the ridge crest and the non-migrating sound-scatterers of the lower meso- and upper bathypelagic zones were apparent. Trawl catches suggest that these backscatter signals originated from aggregating deep-pelagic fish species. The occurrence of deep-pelagic fishes in bottom trawls taken during Leg 2 of the 2004 *G.O. Sars* expedition provided corroborating evidence. Bergstad et al., (2008) excluded as much as 60% of individual bottom trawl samples as pelagic fish 'contaminants' prior to their analyses of MAR demersal fish community structure. While these specimens could have been caught during deployment and/or retrieval of the bottom trawl, the high numbers taken relative to fishing effort compared to numbers from pelagic trawls suggest that these fishes were captured during bottom trawling.



Fig. 2.

Mean volume backscatter (Sv) data (18-kHz SIMRAD EK60 echosounder) during a cross-ridge transect (West _ East) in the Azorean region of the Mid-Atlantic Ridge (displayed in black). The transect distance and duration equaled 225 km and 30 h, respectively. Vertical grid marks represent 1000 m depth intervals; horizontal grid marks represent 50 km distance intervals. Depth displacement of the main deep-scattering layer as a function of diel vertical migration can be seen from left (night) to right (daylight).

Sutton et al., (2008) observed discernable biological 'features of interest' 100 m off the bottom near valleys and peaks of the Reykjanes Ridge (Fig. 3a) and the Azorean MAR (Fig. 3b). These backscatter patterns were similar to other signals from the mesopelagic DSL. Trawl-derived estimates of fish abundance in the mesopelagic stratum were similar to those of the near-bottom layer. The authors noted that DSLs are not limited to pelagic fish taxa, so the observed near-bottom aggregations could have been composed of demersal fishes or invertebrates. A few large demersal fishes were caught in pelagic trawls (Appendix 1; Sutton et al., 2008), the larger of which (Åkra trawl) had twice the mouth area of the demersal trawl. The authors concluded that if dense concentrations of demersal fishes were aggregating in the water column, it is likely that they would have been sampled by the pelagic gear. Conversely, demersal fish captures in the water column were relatively rare events. Thus, the acoustic data provided corollary evidence supporting the trawl-based discrimination of an assemblage of bathypelagic fishes that aggregated over a mid-ocean ridge system.



Fig. 3. Mean volume backscatter (Sv) data (18-kHz SIMRAD EK60 echosounder) showing pelagic-benthic interactions along the Mid-Atlantic Ridge. A. Reykjanes Ridge cross-ridge section; B. Azorean MAR cross-ridge section. Arrows indicate regions of enhanced, near-ridge backscatter. After Sutton et al., 2008.

In the only other semi-quantitative study of deep-pelagic fishes over the MAR, Fock et al. (2004) examined a series of 250-3200 m samples taken during a 1982 cruise in a frontal gradient area just south of the Charlie-Gibbs Fracture Zone (middle box of Fig. 1). While the focus of the Fock et al. (2004) study was primarily biogeographic, some parallels to Sutton et al. (2008) can be drawn. Using similar statistical methods, Fock et al. (2004) discriminated six clusters of species groups. Even without *Cyclothone*, which was excluded from their analysis, the Gonostomatidae (primarily *Sigmops (Gonostoma) bathyphilum)* dominated net catches at bathypelagic depths. These authors also found increased relative abundances of the Stomiidae, Melamphaidae, Serrivomeridae and Eurypharyngidae over the ridge, the same near-ridge dominants reported in Sutton et al. (2008). In a complementary analysis of the vertical distribution of the gulper eel *Saccopharynx ampullaceus* (Saccopharyngidae), Fock et al. (2004) found that the minimum depth of occurrence of this species rose from 2550 m over the Porcupine Abyssal Plain to 1000 m over the MAR.

In summation, much more work is needed to gain a robust understanding of deep-pelagic fish interactions with MORs. Available data suggest that special features of MOR environments likely cause changes in the ecological structure of deep-fish assemblages. If extrapolations of the trophic subsidy provided to seamounts by mesopelagic fish interactions prove appropriate for bathypelagic MORs, then the trophic consequences of enhanced bathypelagic biomass over MORs are obvious for MOR demersal communities. Sutton et al. (2008) further proposed that this topographic aggregation strategy could also be important for the individual populations of deep-pelagic fishes. Predatory deep-pelagic fishes situated near the ridge could wait for food to be advected horizontally by tidal currents, or intercept prey swimming downward from above. Planktivorous deep-pelagic fishes would benefit from higher concentrations of zooplankton in the benthic boundary layer (Wishner, 1980a-c; Vinogradov, 2005). A second, longer-term function of the topographic association could be inferred from the preponderance of large, gravid adults of pelagic fishes captured in 2004 G.O. Sars expedition near-ridge samples (unpubl. data), namely the concentration of the largest, 'fittest' males with the largest (and most fecund), 'fittest' females for reproduction, thus increasing the relative percentage of offspring from the 'best' of the gene pool. Given the immense areal extent of the global MOR system, any increase in spawning activity at these sites by the bathypelagic fauna may have a non-trivial effect on the ocean-wide genetic structure, evolution, and production of bathypelagic populations.

References

- Angel, M.V. 1985. Vertical migrations in the oceanic realm: possible causes and probable effects. Contributions in Marine Science 27, suppl.
- Angel, M.V. 1997. Pelagic biodiversity. In: R.F.G. Ormond, J.D. Gage, and M.V. Angel (Eds) Marine biodiversity: patterns and processes. Cambridge University Press, 449 pp.
- Angel, M.V. and A. Baker. 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the Northeast Atlantic. Biological Oceanography 2: 1-30.

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- Angel, M.V. and P.R. Pugh. 2000. Quantification of diel vertical migration by micronektonic taxa in the Northeast Atlantic. Hydrobiology: 440, 161-179.
- Arai, M. N. 2005. Predation on pelagic coelenterates: a review. Journal of the Marine Biological Association of the United Kingdom 85: 523-536.
- Aron, W. and S.B. Collard. 1962. A study of the influence of net speed on catch. Limnology and Oceanography 14: 242-249.
- Badcock, J. 1984a. Sternoptychidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. and Tortonese, E. (eds.) Fishes of the North-eastern Atlantic and the Mediterranean. Vol 1. UNESCO, Paris, pp 302-317.
- Badcock, J. 1984b. Photichthyidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. and Tortonese, E. (eds.) Fishes of the North-eastern Atlantic and the Mediterranean. Vol 1. UNESCO, Paris, pp 318-324.
- Barcelos, L.D., F.M. Porteiro, O. Melo, M. Clarke and G. Menezes. 2005. Feeding ecology of orange roughy, *Hoplostethus atlanticus* Collett, 1889, in the Azores Archipelago. 40th European Marine Biology Symposium. Abstracts, 61-62 (poster).
- Benoit-Bird, K.J., W.W.L. Au, R.E. Brainard and M.O. Lammers. 2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. Marine Ecology Progress Series 217: 1-14.
- Bergstad, O.A. 2000. Patterns and processes of the ecosystems of the northern mid-Atlantic. A proposed Census of Marine Life initiative. Concept paper submitted to the Steering Committee of CoML, February 2001. Available on http://www.efan.no/midatlcensus/
- Bergstad, O.A., G. Menezes and Å. Høines. 2008. Distribution patterns and structuring factors of deepwater demersal fishes on a mid-ocean ridge. Deep-Sea Research II, 55: 185-202.
- Boehlert, G.W. 1988. Seamount acoustic scattering. EOS, Transactions of the American Geophysical Union, 69: 1619-1628.
- Boehlert, G.W. and T. Sasaki. 1988. Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. Fishery Bulletin, 86: 453-466.
- Boehlert G.W. and M.P. Seki. 1984. Enhanced micronekton abundance over mid-Pacific seamounts. EOS, Transactions of the American Geophysical Union, 65: 928.
- Boehlert, G.W., C.D. Wilson and K. Mizuno. 1994. Populations of the sternoptychid fish, *Maurolicus muelleri*, on seamounts in the central North Pacific. Pacific Sc., 48: 57-69.
- Buesseler, K.O., C.H. Lamborg, P.W. Boyd, P.J. Lam, T.W. Trull, R.R. Bidigare, J.K.B. Bishop, K.L. Casciotti, F. Dehairs, M. Elskens, M. Honda, D.M. Karl, D.A. Siegel, M.W. Silver, D.K. Steinberg, J. Valdes, B.Van Mooy, S. Wilson. 2007. Revisiting carbon flux through the ocean's twilight zone. Science 316 (5824): 567-570.
- Bulman, C.M. and J.A. Koslow. 1992. Diet and food consumption of a deep-sea fish, orange roughy Hoplostethus atlanticus (Pisces: Trachichthyidae), off southeastern Australia. Marine Ecology

Progress Series, 82: 115-129.

- Childress, J.J. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends in Ecology and Evolution, 10: 30-35.
- Childress, J.J., S. Taylor, G. Cailliet and M.H. Price. 1980. Patterns of growth reproduction and energy usage in some meso- and bathypelagic fishes. Marine Biology 61: 27-40.
- Clark, M. 1999. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. Oceanologica Acta, 22: 593-602.
- Ducklow, H.W., D.K. Steinberg and K.O. Buesseler. 2001.Upper ocean carbon export and the biological pump. Oceanography, 14: 50-58.
- Enrich, S. 1977. Die Fishfauna der Großen Meteorbank. Meteor-Forsch.-Ergebnisse, D 25: 1-23.
- Fock, H., B. Matthiessen, H. Zidowitz and H. von Westernhagen. 2002. Diel and habitat- dependent resource utilisation by deep sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. Marine Ecology Progress Series 244: 219-233.
- Fock, H.O., C. Pusch and S. Ehrich. 2004. Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45°-50°N). Deep-Sea Research, 51: 953-978.
- Froese, R. and A. Sampang. 2004. Taxonomy and biology of seamount fishes. In: Morato, T. and D. Pauly (eds.) Seamounts: Biodiversity and Fisheries. Fisheries Centre Research Report, 12(5). pp 25-31.
- Gartner, J.V. 1991. Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. II. Age and growth patterns. Marine Biology 111: 21-27.
- Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems 50: 3- 20.
- Genin A, L. Haury and P. Greenblatt. 1988. Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep-Sea Research 35: 151- 175.
- Genin, A., C. Greene, L. Haury, P. Wiebe, G. Gal, S. Kaartvedt, E. Meir, C. Fey and J. Dawson. 1994. Zooplankton patch dynamics: daily gap formation over abrupt topography. Deep-Sea Research 41: 941-951.
- Gordon, J.D.M. and J.A.R. Duncan. 1987. Aspects of the biology of *Hoplostethus atlanticus* and *H. mediterraneus* (Pisces: Berycomorphi) from the slopes of the Rockall Trough and the Porcupine Sea Bight (North-eastern Atlantic). Journal of the Marine Biological Association of the United Kingdom 67: 119-133.
- Guschin, A.V. and E.I. Kukuev. 1981. On the composition of ichthyofauna of the northern part of the Middle-Atlantic Ridge. In: Parin, N.V. (ed.), Fishes of the Open Ocean. Institute of Oceanology, Academy of Sciences of the USSR. (in Russian) pp 36-40.
- Harold, A.S. and K. Lancaster. 2003. A new species of the hatchetfish genus Argyripnus (Stomiiformes: Sternoptychidae) from the Indo-Pacific. Proceedings of the Biological Society of Washington, 116 (4): 883-891.

- Hedgepeth, J.W. 1957. Treatise on marine ecology and paleontology. Memoirs of the Geological Society of America. 67: 1-1296.
- Herring, P.J. and J.G. Morin. 1978. Bioluminescence in fishes. In: Herring, P.J. (ed.), Bioluminescence in Action. Academic Press. New York. pp 273-329.
- Holloway, P.E. and M.A. Merrifield. 1999. Internal tide generation by seamounts, ridges and islands. Journal of Geophysical Research 104: 25937-25951.
- Hulley, P.A. and J.R.E. Lutjeharms. 1989. Lanternfishes of the southern Benguela region. Part 3. The pseudoceanic-oceanic interface. Annals of South Africa Museum, 98 (19), 409-435.
- Iglesias, S. and P.D. Munoz. 2001. Spanish investigations on deep-sea resources in northern Mid-Atlantic Ridge and adjacent areas. Working Document presented to the Workshop on the CoML project "Patterns and processes of the ecosystems of the northern Mid-Atlantic," Bergen, 12-13 february 2001. 7 pp.
- Isaacs, J.D. and R.A. Schwartzlose. 1965. Migrant sound scatterers: interactions with the sea floor. Science 150: 1810-1813.
- Kashkin, N.I. 1977. Fauna of Sound-Scattering Layers (SSL). In: Monin, A.C. (ed.), The Biological Structure in the Ocean, Oceanology. Vol. I, Moscow. pp. 299-318.
- Kashkin, N.I. and N.V. Parin. 1983. Quantitative assessment of micronektonic fishes by nonclosing gear (a review). Biological Oceanography 2: 263-287.
- Kitani, K. and K. Iguchi. 1974. Some Observations on the Feature of Fishing Ground on the Sea-Mount in the Central North Pacific Ocean As Surveyed Through the Trawl Operation. Unknown 11: 33-36.
- Koslow, A. 1996. Energetic and life-history oatterns of deeo-sea benthic, benthopelagic and seamountassociated fish. Journal of Fish Biology 49 (Supplement A): 54-74.
- Koslow, A. 1997. Seamounts and the ecology of deep-sea fisheries. American Scientist 85: 168-176.
- Koslow, J.A., G.W. Boehlert, J.D.M. Gordon, R.L. Haedrich, P. Lorance and N. Parin.(2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES Journal of Marine Science 57: 548-557.
- Kukuev, E.I. 1982. Ichthyofauna of the Corner Mountains and New England seamounts in the western North Atlantic. In: Parin, N.V. (ed.), *Poorly Known Fishes of the Open Ocean*, Institute of Oceanology, Academy of Sciences of the USSR, Moscow. (in Russian). pp 92-109.
- Kukuev, E.I. 2004. Ichtyofauna research on underwater mountain within the North Atlantic Ridge and adjacent seas. Archive of Fishery and Marine Research 51: 215-232.
- Labbé F.J. and P.M. Arana. 2001. Alimentación de orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae), en el archipiélago de Juan Fernández, Chile. Revista de Biología Marina y Oceanografía 36: 75-82.
- Linkowski, T.B. 1985. Population biology of the myctophid fish *Gymnoscopelus nicholsi* (Gillbert, (1911) from the western South Atlantic. Journal of Fish Biology 27: 683-689.

- Lorz, H.V., W.G. Pearcy and M. Fraidenburg. 1983. Notes on the feeding habits of the yellowtail rockfish, Sebastes flavidus, off Washington and in Queen Charlotte Sound. California Fish and Game 69: 33-38.
- Mauchline, J. and J.D.M. Gordon. 1984. Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. Journal du Conseil International pour l'Exploration de la Mer 41: 239-247.
- McClatchie, S. and A. Dunford. 2003. Estimated biomass of vertically migrating mesopelagic fish off New Zealand. Deep-Sea Research 50: 1263-1281.
- Melo, O. and G. Menezes. 2002. Exploratory fishing of the orange roughy (Hoplostethus atlanticus) in some seamounts of the Azores archipelago. International Council for the Exploration of the Sea, CM2002/M: 26.
- Menard, H.W. and S.M. Smith. 1966. Hypsometry of ocean basin provinces. Journal of Geophysical Research 71: 4305.
- Moore, J.A., M. Vecchione, B.B. Collette, R. Gibbons, K.E. Hartel, J.K. Galbraith, M. Turnipseed, M. Southworth and E. Watkins. 2003. Biodiversity of the Bear Seamount, New England Seamount Chain: results of exploratory fishing. Journal of Northwest Atlantic Fishery Sciences 31: 363-372.
- Morato, T., R. Watson, T.J. Pitcher and D. Pauly. 2006. Fishing down the deep. Fish and Fisheries 7: 24-34.
- Parin, N.V. 1992. Argyripnus electronus, a new sternoptychid fish from Sala y Gomez submarine ridge. Japanese Journal of Ichthyology 39: 135-137.
- Parin, N.V. and O.D. Borodulina. 1990. Review of the genus Polymetme (Phosichthyidae) with the description of two new species. Journal of Ichthyology 30: 108-121.
- Parin, N.V., A.N. Mironov and K.N. Nesis. 1997. Biology of the Nazca and Sala y Gómez submarine ridges, an outpost of the Indo-West Pacific Fauna in the Eastern Pacific Ocean: composition of the fauna, its communities and history. Advances in Marine Biology 32: 145-242.
- Pereyra, W.T., W.G. Pearcy and F.E. Carvey Jr. 1969. Sebastodes flavidus, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. Journal of the Fisheries Research Board of Canada 26: 2211 -2215.
- Porteiro, F.M. and T.T. Sutton. 2007. Midwater Fish Assemblages and Seamounts. In: T.J. Pitcher, T. Morato, P.J.B. Hart, M.R. Clark, N. Haggan and R.S. Santos, eds. Seamounts: Ecology, Conservation and Management. Fish and Aquatic Resources Series, Blackwell, Oxford, UK.
- Pusch, C., A. Beckmann, F.M. Porteiro and H. von Westernhagen. 2004. The influence of seamounts on mesopelagic fish communities. Archive of Fishery and Marine Research 51: 165-186.
- Reid, S.B., J. Hirota, R.E. Young and L.E. Hallacher. 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. Marine Biology 109: 427-440.

- Richer De Forges, B. 2001. Electronic Database of ORSTOM Sampling on the Norfolk Ridge 116 (4): 883-891.
- Roden, G.I. 1987. Effect of seamount chains on ocean circulation and thermohaline structure. In: G.W. Boehlert (Ed) *Geophysical Monograph* 43. American Geophysical Union, Washington DC, pp. 335-354.
- Rogers, A.D. 1994. The biology of seamounts. Advances in Marine Biology 30: 305-350.
- Rosecchi, E., D.M. Tracey and W.R. Webber. 1988. Diet of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) on the Challenger Plateau, New Zealand. Marine Biology 99: 293-306.
- Santos, R.S, S. Hawkins, L.R. Monteiro, M. Alves and E.J. Isidrio. 1995. Marine research, resources and conservation in the Azores. Aquatic Conservation: Marine and Freshwater Ecosystems 5: 311- 354.
- Sassa, C., K. Kawaguchi, T. Kinoshita and C. Watanabe. 2002. Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. Fisheries Oceanography 11: 193-204.
- Seki, M.P. and D.A. Somerton. 1994. Feeding ecology and daily ration of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Southeast Hancock Seamount. Environmental Biology of Fishes 39: 73-84.
- Shcherbachev, Y.P., E.I. Kukuev and V.I. Shlibanov. 1985. Bottom and near-bottom ichthyocenes species composition in the underwater mountains of the southern North-Atlantic Ridge. Voprosy Ichthyologii (*Problems of Ichthyology*) 25: 35-50.
- Sutton, T.T. and T.L. Hopkins. 1996. Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: strategies, selectivity and impact of a top mesopelagic predator group. Marine Biology 127: 179-192.
- Sutton, T.T., T.L. Hopkins and T.M. Lancraft. 1998. Trophic diversity of a mesopelagic fish community. In: Pelagic Biogeography ICoPB II. IOC Workshop Report 142: 353-357.
- Sutton, T.T., F.M. Porteiro, M. Heino, I. Byrkjedal, G. Langhelle, C.I.H. Anderson, J. Horne, H. Søiland, T. Falkenhaug and O.A. Bergstad. 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea Research II*.
- Thomsen, B. 1998. Faroese quest of orange roughy in the North Atlantic. ICES C.M. 1998/0: 31.
- Troyanovsky, F.M. and S.F. Lisovsky. 1995. Russian (USSR) fisheries research in deep waters (below 500 m) in the North Atlantic. In: Hopper, A.G. (ed.) Deep-water fisheries of the North Atlantic Ocean Slope. NATO ASI Series E. Applied Sciences 296: 357-366.
- Uiblein, F., A. Geldmacher, F. Köter, W. Nellen and G. Kraus. 1999. Species composition and depth distribution of fish species collected in the area of the Great Meteor seamount, eastern central Atlantic, during cruise M42/3, with seventeen new records. Instituto Canario de Ciencias Marinas, Telde (Gran Canaria) 5: 47-85.
- Vereshchaka, A.L. and G.M. Vinogradov. 1999. Visual observations of the vertical distribution of plankton throughout the water column above Broken Spur vent field, Mid-Atlantic Ridge. Deep-Sea

Research 46: 1615-1632.

- Vinnichenko, V.I. 1997. Russian Investigations and deep water fishery on the Corner Rising Seamount in subarea 6. NAFO Scientific Council Studies 30: 41-49.
- Vinnichenko, V.I. 1998. Alphonsino (*Beryx splenens*) biology and fishery on the seamounts in the open North Atlantic. ICES C.M. 1998/0: 13.
- Vinogradov, M.E. 1997. Some problems of vertical distribution of meso- and macroplankton in the ocean. In: Blaxter, J.H.S. and Southward, A.J. (eds.) Advances in Marine Biology: The Biogeography of the Oceans. Academic Press, San Diego. pp. 1-92.
- Vinogradov, G.M. 2005. Vertical distribution of Macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible "Mir-1." Marine Biology 146: 325-331.
- Vinogradov, M.E., A.L. Vereshchaka, G.M. Vinogradov and E.I. Musaeva. 2000. Vertical distribution of zooplankton at the periphery of the North Atlantic Subtropical Gyre. Proceedings of the Russian Academy of Science (*Biology*) 4: 496-510.
- Walsh, J.J., J. Dymond and R. Collier. 1988. Rates of recycling of biogenic components of settling particles in the ocean derived from sediment trap experiments. Deep-Sea Research 35, 43-58.
- Wenneck, T. de Lange, T. Falkenhaug and O.A. Bergstad. 2008. Strategies, methods, and technologies adopted on the RV G.O. Sars MAR-ECO expedition to the mid-Atlantic Ridge in 2004.
- Wilson, C.D. 1992. Interactions of Ocean Currents and Diel Migrators at a Seamount in the Central North Pacific. PhD Dissertation Thesis, University of Hawaii, Honolulu, HI.
- Wilson, C.D. and G.W. Boehlert. 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. Journal of Marine Systems 50: 39- 60.
- Wishner, K.F. 1980a. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Research 27: 203-216.
- Wishner, K.F. 1980b. Near-bottom sound scatterers in the Ecuador Trench. Deep-Sea Research 27: 217-223.
- Wishner, K.F. 1980c. Aspects of the community ecology deep-sea benthopelagic plankton, with special attention to gymnopleid copepods. Marine Biology 60: 179-187.
- Young, R.E. 1983. Oceanic bioluminescence: an overview of general functions. Bulletin of Marine Science 33: 829-845.