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Deep-pelagic (0–3000 m) fish assemblage structure over the Mid-Atlantic Ridge in the area of the Charlie-Gibbs Fracture Zone

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ABSTRACT

Only a miniscule fraction of the world's largest volume of living space, the ocean's midwater biome, has ever been sampled. As part of the International Census of Marine Life field project on Mid-Atlantic Ridge ecosystems (MAR-ECO), a discrete-depth trawling survey was conducted in 2009 aboard the NOAA FSV *Henry B. Bigelow* to examine the pelagic faunal assemblage structure and distribution over the Charlie-Gibbs Fracture Zone (CGFZ) of the northern Mid-Atlantic Ridge. Day/night sampling at closely spaced stations allowed the first characterization of diel vertical migration of pelagic nekton over the MAR-ECO study area. Discrete-depth sampling from 0–3000 m was conducted using a Norwegian "Krill" trawl with five codends that were opened and closed via a pre-programmed timer. Seventy-five species of fish were collected, with a maximum diversity and biomass observed between depths of 700–1900 m. A gradient in sea-surface temperature and underlying watermasses, from northwest to southeast, was mirrored by a similar gradient in ichthyofaunal diversity. Using multivariate analyses, eight deep-pelagic fish assemblages were identified, with depth as the primary discriminatory variable. Strong diel vertical migration (DVM) of the mesopelagic fauna was a prevalent feature of the study area, though the numerically dominant fish, *Cyclothone microdon* (Gonostomatidae), exhibited a broad (0–3000 m) vertical distribution and did not appear to migrate on a diel basis. Three patterns of vertical distribution were observed in the study area: (a) DVM of mesopelagic, and possibly bathypelagic, taxa; (b) broad vertical distribution spanning meso- and bathypelagic depths; and (c) discrete vertical distribution within a limited depth range. Overall species composition and rank order of abundance of fish species agreed with two previous expeditions to the CGFZ (1982–1983 and 2004), suggesting some long-term consistency in the ichthyofaunal composition of the study area, at least in the summer. Frequent captures of putative bathypelagic fishes, shrimps, and cephalopods in the epipelagic zone (0–200 m) were confirmed. The results of this expedition reveal distributional patterns unlike those previously reported for open-ocean ecosystems, with the implication of increased transfer efficiency of surface production to great depths in the mid-North Atlantic.

1. Introduction

The deep-pelagic realm of the world ocean, the largest biome on earth, is one of the least sampled and least understood. Webb et al.'s (2010) study on global marine biodiversity underscored not only the lack of specimen records for the deep sea in general, but specifically for the midwater region. The boundaries within this region are not obvious, and it is mainly the physical properties of water itself (temperature, salinity, pressure, light penetration, currents) that provide any kind of structure (Angel, 1997; Herring, 2004). Solar radiation controls atmospheric conditions, which stratify the ocean such that environmental gradients are far more pronounced in the vertical dimension than the horizontal (Herring, 2004; Longhurst, 1976). Light penetration controls the depth of primary production and is thought to control the timing of diel vertical migration (DVM), which impacts the flux of organic matter to depth (Longhurst et al., 1990). The typical effect of these factors on pelagic community structure is that overall abundance and biomass decrease exponentially with depth in the open ocean (Angel and Baker, 1982; Robison, 2004; Sutton et al., 2010; Vinogradov, 1968), ostensibly due to diminishing food availability with increasing distance from the productive surface waters.

DVMs are not thought to occur in the bathypelagic zone (below 1000 m) for several reasons: (1) organisms cannot perceive the diel changes in light intensity below this depth (Longhurst, 1976);

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(2) the energy required for migration from these depths is greater than the energy gained from doing so, especially due to the swimming inefficiency of bathypelagic fishes, as most of their muscle mass has been replaced by energy-saving, neutrally buoyant, watery tissue (Marshall, 1971); and (3) much of what is known about DVM as a large-scale phenomenon comes from acoustic surveys which cannot detect bathypelagic fishes that do not have swimbladders (Herring, 2004); i.e., if bathypelagic DVM was occurring on the same scale as mesopelagic DVM, we may not detect it. Vinogradov (1953, 1968) proposed a "ladder of migration" theory, which suggested an overlap between diel vertical migrators of the mesopelagic and the "lie-in-wait" predators of the bathypelagic, which then descend to even greater depths in ontogenetic migrations, supplying food down to depths of 4000–5000 m. Although Longhurst (1976) found Vinogradov's theory to be unsubstantiated, he stated that "*If this model could be validated it would have important consequences in food-chain biology*." The active transfer of organic material by vertically migrating organisms, however deep, is an important part of nutrient cycling in the ocean (Angel, 1985; Dam et al., 1995; Ducklow et al., 2001; Robinson et al., 2010).

The gap in our knowledge of the deep-pelagic realm was one of the inspirations for the creation of the Census of Marine Life project titled 'Patterns and Processes of the Ecosystems of the northern Mid-Atlantic Ridge' (MAR-ECO), which reached its operational stage in 2001 (Bergstad and Godø, 2003). The largest field campaign of MAR-ECO, the 2004 *G.O. Sars* expedition (Bergstad et al., 2008), mapped the large-scale distribution of pelagic, demersal, and epibenthic fauna along the northern MAR from Iceland to the Azores. Due to the logistical constraints of this expedition, there was no diel station sampling replication; sampling was conducted at whatever time of day the ship arrived on station. Due to time of year (summer) and high latitude, pelagic sampling occurred mainly during daylight. Despite the low temporal and spatial resolution of the sampling strategy, ample evidence was obtained to conclude that the Charlie-Gibbs Fracture Zone (CGFZ) region represents a 'biological hotspot' across multiple trophic levels (Vecchione et al., 2010a). The *G.O. Sars* expedition also discovered a deep daytime biomass maximum which Sutton et al. (2008) attributed to the presence of larger adult bathypelagic fishes believed to adopt a benthopelagic lifestyle, taking advantage of the ridge for feeding and perhaps spawning, similar to findings near seamounts (Porteiro and Sutton, 2007). These findings prompted a return expedition to the CGFZ in the summer of 2009 aboard the NOAA FSV *Henry B. Bigelow*. In this paper we present the findings of this expedition with respect to deep-pelagic fish assemblage structure, vertical distribution, and diel variability of the CGFZ region of the northern MAR. We also examine fine-scale variability in the geographic distribution of deep-pelagic fish species relative to the Subpolar Front, the dominant hydrographic feature of the study area.

2. Methods

The discrete-depth trawl survey was conducted in the vicinity of the CGFZ (centered on 53°N 35°W) during 20 June–6 July, 2009. Eleven fixed stations, divided into two transects, one northwest and one southeast of the CGFZ, were occupied for midwater trawling (Fig. 1). Bottom depths ranged from 1400 to 3500 m with the exception of one station at 753 m bottom depth located over a seamount.

2.1. Hydrography

Daily and weekly composite remote sensing satellite images of sea-surface temperature (SST) in the vicinity of the CGFZ during the expedition were provided by the NERC Earth Observation Data Acquisition and Analysis Service (Fig. 2). *In situ* temperature data were recorded via a Seabird SBE 39 sensor mounted on the net during each deployment. Hydrographic regimes were characterized using temperature profiles as a proxy for water mass as salinity data were not recorded. Hydrographic conditions of the CGFZ region during the 2004 *G.O. Sars* expedition were described by Søiland et al. (2008). These descriptions guided the interpretation of temperature profile data collected in this study with respect to water mass.

2.2. Sampling and sample processing

Midwater trawling was conducted using a macrozooplankton (or "krill") trawl, designed at the Institute of Marine Research, Norway (Wenneck et al., 2008). This trawl had a 6×6-m^2 mouth opening and 3-mm diamond-shaped meshes from the front of the net to the codend. The trawl was equipped with Tiburon type-8 midwater doors and a multi-sampler (remotely operated multiple codends). The multi-sampler had five 30-m long collecting nets, each equipped with a 7-L codend bucket to reduce damage to the samples. The codends were opened and closed by a pre-programmed timer based on expected depth from near bottom to the surface. This type of trawl does not have a rigid frame, so restrictor ropes were mounted in the trawl opening to avoid

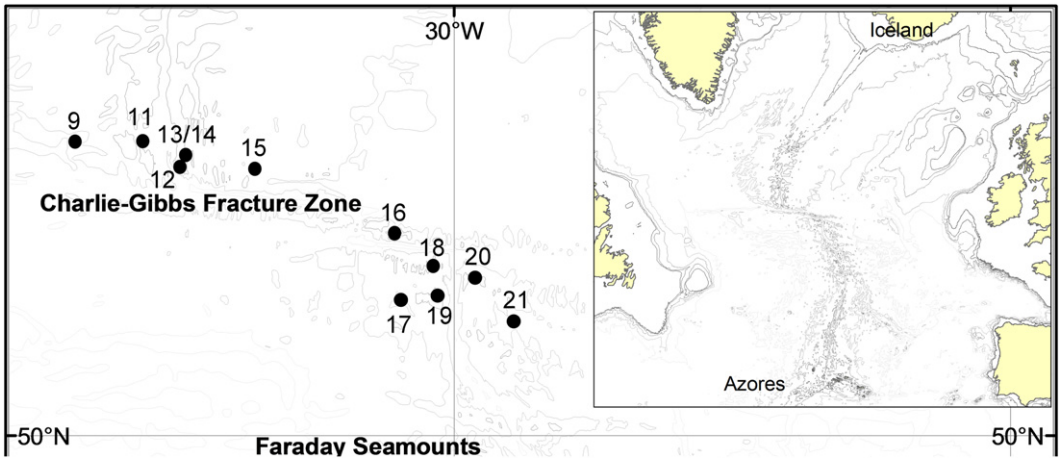

Fig. 1. Study area and trawl sampling stations of the 2009 R/V *Henry B. Bigelow* MAR-ECO expedition. Box at right shows the northern Mid-Atlantic Ridge with offset at CGFZ in center.

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