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Fine-scale planktonic habitat partitioning at a shelf-slope front revealed by a high-resolution imaging system

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ABSTRACT

Ocean fronts represent productive regions of the ocean, but predator–prey interactions within these features are poorly understood partially due to the coarse-scale and biases of net-based sampling methods. We used the *In Situ* Ichthyoplankton Imaging System (ISIIS) to sample across a front near the Georges Bank shelf edge on two separate sampling days in August 2010. Salinity characterized the transition from shelf to slope water, with isopycnals sloping vertically, seaward, and shoaling at the thermocline. A frontal feature defined by the convergence of isopycnals and a surface temperature gradient was sampled inshore of the shallowest zone of the shelf-slope front. Zooplankton and larval fishes were abundant on the shelf side of the front and displayed taxon-dependent depth distributions but were rare in the slope waters. Supervised automated particle counting showed small particles with high solidity, verified to be zooplankton (copepods and appendicularians), aggregating near surface above the front. Salps were most abundant in zones of intermediate chlorophyll-*a* fluorescence, distinctly separate from high abundances of other grazers and found almost exclusively in colonial form (97.5%). Distributions of gelatinous zooplankton differed among taxa but tended to follow isopycnals. Fine-scale sampling revealed distinct habitat partitioning of various planktonic taxa, resulting from a balance of physical and biological drivers in relation to the front.

1. Introduction

Planktonic organisms experience environmental gradients that likely influence the processes of aggregation, dispersal, and differential survival, resulting in plankton patchiness (Steele, 1978). Sharp gradients in temperature and salinity typically occur in the vertical direction; the subject of numerous recent studies using high frequency sampling (Dekshenieks et al., 2001; Greer et al., 2013; McManus et al., 2005). Strong horizontal gradients in water column properties can also occur, but are typically confined to areas of the ocean where two different bodies of water meet, known as fronts. Though not exclusively so, fronts are often associated with a variety of ocean topographies such as seamounts, canyons, and shelf-breaks (see Genin, 2004 for review). Despite their prevalence, the role of fronts in structuring plankton communities at fine scales (1 m to 10 m) relevant to predator–prey interactions is poorly understood.

Shelf-slope fronts are common along the western shelves of the world's oceans (Mann and Lazier, 2006) and serve as the boundary between relatively fresh shelf water and salty slope water (Houghton, 1997). These fronts are favorable habitat for a variety of organisms, having been shown to be associated with increased productivity in phytoplankton, zooplankton, and fish (Fournier et al., 1977; Mann and Lazier, 2006). To explain shelf-slope front productivity, Chapman and Lentz (1994) created a numerical model that described the circulation and predicted that bottom boundary convergence maintained the stability of the front. The convergence leads to upward flow of water along seaward sloping isopycnals, which increases nutrient input into near surface waters and consequently, phytoplankton productivity (Gawarkiewicz and Chapman, 1992). Experimental dye injections into the bottom boundary layer confirmed that convergence and along-isopycnal upwelling occurs in the field (Houghton, 1997). Biophysical models predicted that zooplankton production at the shelf-slope front could suppress phytoplankton biomass, but overall primary production in the front was high due to the consistent upwelling (Zhang et al., 2013).

Upwelling flows near the shelf-break enhance biological productivity for a variety of taxa in addition to the phytoplankton. For primary consumers, upwelling at the shelf-break leads to phytoplankton production and a favorable feeding environment for grazers including salps, copepods, and appendicularians. The increased secondary production at fronts can allow larval fishes to access high concentrations of prey (Bakun, 2006; Miller, 2002). On the other hand, fronts also can concentrate

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potential predators of larval fishes, such as hydromedusae and ctenophores (McClatchie et al., 2012). Gelatinous zooplankton are osmoconformers that actively reduce their swimming speed and aggregate near salinity gradients, which are a characteristic of shelf-edge ocean systems (Graham et al., 2001; Jacobsen and Norrbin, 2009). Salps, unlike hydromedusae and ctenophores, are bacteria and phytoplankton grazers that occupy a similar trophic niche as prey of larval fishes (copepods and appendicularians) but have reproductive rates similar to bacteria, much faster than copepods, appendicularians, and fish (Deibel, 1982; Deibel and Lowen, 2012; Heron, 1972; Tsuda and Nemoto, 1992). Therefore, salps could have an indirect negative impact on larval fishes by quickly consuming phytoplankton in a zone that is potentially favorable to secondary production of larval fish food sources (copepods and appendicularians). Salps can also negatively impact copepods directly by consuming them and their early life stages (Hopkins et al., 1993).

Most studies of planktonic organisms around frontal features have examined mesoscale patterns, detecting changes in average zooplankton and larval fish concentrations on either side of a front (Govoni and Grimes, 1992; Kingsford and Suthers, 1994; Nielsen and Munk, 1998; Sabatés et al., 2010). While these studies are useful in describing the shifts in plankton communities at fronts, they do not reveal much about small scale structure relevant to predator–prey interactions, so more recent frontal research has emphasized finer scale observations (Landry et al., 2012; Luo et al., 2014; McClatchie et al., 2012; Munk, 2014). The interactions of predators and prey at these fronts are largely unknown mainly because spatio-temporal patterns have not been resolved on the relevant scales of these associations. Small scale feeding environments have been shown to be extremely important to larval fish survival (Davis et al., 1991; Vlymen, 1977), yet remain a critical gap in our knowledge of the biological impact of many oceanographic features. In addition, the diversity of grazers and the biases of net based sampling systems to crustacean zooplankton (Alldredge and Madin, 1982; Remsen et al., 2004) obscure the fine-scale distribution of grazers and potential predators, thereby limiting the detectability of zones of the water column potentially favorable to larval fish feeding and survival.

New imaging technology is addressing some of the fundamental issues with sampling larval fishes and the surrounding biological community by quantitatively describing plankton in relation to fine-scale environmental variables that characterize shelf-slope boundaries. A distinct advantage of optical systems is the ability to automatically count and size marine particles using image analysis software. Particle size and abundance provide a suite of information relating to trophic interaction, reproduction, and carbon export to deeper waters (Sheldon et al., 1972; Stemmann and Boss, 2012; Woodward et al., 2005). In addition, the metric equivalent spherical diameter (ESD) commonly used in particle size estimation may not be applicable in coastal waters where particles (marine snow) vary in shape, composition, and optical properties (Kranck and Milligan, 1991). The *In Situ* Ichthyoplankton Imaging System (ISIIS) combined with image analysis software allows for the automated counting, sizing, and simple feature extraction of particles, while providing the resolution adequate for the identification of many specimens to the family or genus level. The central goal of this study was to quantitatively describe the fine-scale abundances of larval fishes, gelatinous zooplankton, and particles of different size classes and composition, and use this high resolution data to better understand biological interactions at sharp physical gradients associated with the shelf edge.

2. Methods

2.1. Imaging system

The *In Situ* Ichthyoplankton Imaging System (ISIIS) was used to quantify a variety of planktonic organisms in the size range of 680 μm to 13 cm. ISIIS utilizes a Piranha II line scan camera (Dalsa) to shoot a continuous image with a scan rate of 36,000 lines s^{-1}. The images are produced by projecting collimated light across an imaged water parcel, and plankton blocking the light source are imaged as shadows, allowing for a range of transparent (gelatinous) and opaque (crustaceans) organisms to be imaged with no discernible bias in detectability (Cowen and Guigand, 2008; Cowen et al., 2013). Although ISIIS shoots a continuous image, software (Boulder Imaging, Inc.) breaks up the image into 13 cm * 13 cm frames with a 40 cm depth of field. At typical tow speeds of 2.5 m s^{-1}, it takes approximately 7.7 s to sample 1 m^3 of water. ISIIS was also equipped with motor actuated fins for depth control, a Doppler velocity log (600 micro, Navquest) and environmental sensors including a conductivity, temperature, and depth sensor (CTD) (SBE 49, Seabird electronics) and fluorometer (ECO FL (RT), Wetlabs chlorophyll-*a* fluorescence). The CTD and fluorometer sampled ~30 cm and ~1 m above the imaged water parcel, respectively.

2.2. Sampling scheme

Two ISIIS transects were performed in the same location on separate sampling days in August 2010, beginning on the shelf in waters approximately 75 m deep during different stages of the tidal cycle. The transect on August 27 was performed between 0710 and 1348, spanning 60.1 km, while the transect on August 29 was slightly shorter, lasting from 1656 to 2248 for a total distance of 52.7 km. The August 27 transect was performed during the flood tide, and the August 29 transect was during ebb tide, though tides were expected to have little effect near the shelf edge. Transects occurred in the shelf-break zone east of Georges Bank, off the coast of Massachusetts, USA, where there are consistent horizontal gradients in salinity and temperature (Fig. 1).

2.3. Bongo net samples

After each ISIIS transect, 3–4 net tows using a 61 cm bongo sampler with 335 μm mesh size were performed along the transect path at approximately evenly spaced stations. A flowmeter was attached in the center of the bongo mouth opening to quantify the volume of water filtered by the net. A CTD (SeaCAT SBE 19) was also attached to the tow wire above the bongo net to measure environmental variables and real time depth of the sampler during deployment. The bongo tows were conducted following the method of Jossi and Marak (1983). For each tow, the wire was paid out at a rate of 50 m min^{-1} to a depth of ~5 m above the bottom. The wire was then retrieved to the surface obliquely at 20 m min^{-1} while the ship was moving at 0.75–1 m s^{-1}. At the end of each tow, the bongo net was brought onboard and samples were rinsed onto a 333 μm sieve, and then preserved in 95% ethanol. After 24 h, sample ethanol was replaced with fresh 95% ethanol to enhance preservation. Samples were then shipped to the Plankton Sorting and Identification Center in Szczecin, Poland for sorting, identification, and measurement.

2.4. Image processing

ISIIS images were viewed and analyzed in ImageJ (v1.46r, Rasband, 1997–2012). Prior to analysis, images underwent a standard 'flat-fielding' procedure to remove background variation and vertical lines from the line scan imaging. All images were viewed manually, and larval fishes were identified to the family level, with species level identification made possible by examining the taxa captured in the bongo nets. Standard length was measured in pixels and converted to mm using the known pixel resolution and field of view. A potential source of small measurement error was the orientation of the larval fish relative to the camera (±200–300 μm), but this was not quantified. For each ISIIS downcast, gelatinous organisms, including salps, hydromedusae (*Clytia hemisphaerica* and *Persa incolorata*), ctenophores (lobate ctenophores and *Beroe* spp.), and siphonophores, were identified to the lowest taxonomic level possible (typically at least to family level).