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Seasonal and spatial patterns of *Penilia avirostris* and three tunicate species in the southern Mid-Atlantic Bight

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ABSTRACT

The cladoceran *Penilia avirostris* and three tunicate species, *Oikopleura dioica*, *Dolioletta gegenbauri* and *Thalia democratica*, form a mesozooplankton group which ingests a wide range of particles from pico- to micro- plankton, grows rapidly due to asexual reproduction, and thus can have major impacts on phytoplankton populations. These four zooplankton species were the most abundant tunicate and cladoceran species in a study where zooplankton were sampled biweekly at five stations across the inner continental shelf in the Mid-Atlantic Bight in 2005, 2006 and 2007. Vertical tows were taken at shallow stations and depth stratified vertical tows at stations >10 m. *P. avirostris* and *O. dioica* had highly predictable seasonal cycles with peak abundances in July and August. *D. gegenbauri* also was present during this time period if upwelling favorable winds were present, which implies cross shelf transport from source populations in slope waters and the Gulf Stream. *T. democratica* only appeared in pulses when southerly winds were increasing in strength. The co-occurrence *P. avirostris* and the tunicate species with abundant *Synechococcus* and heterotrophic nanoflagellates during highly stratified summer conditions provide potential connections to microbial food webs as well as grazing opportunities on event scale blooms of dinoflagellate and diatoms species present in the area.

1. Introduction

Marine cladocerans and tunicates (appendicularians, salps and doliolids) form a unique herbivorous zooplankton group different from copepod and protozoan grazers (Sommer and Stibor, 2002). Cladocerans and tunicates are similar to protozoans in that both groups can ingest bacteria and small flagellates <5 μm (King et al., 1980; Crocker et al., 1991), but also similar to calanoid copepods, they can also ingest larger phytoplankton including diatoms and dinoflagellates (Turner et al., 1988; Crocker et al., 1991; Vargas and Madin, 2004; Bouquet et al., 2009). Although cladocerans and tunicates have a sexual reproductive phase, they grow rapidly by asexual reproduction with generation times of a few weeks (Deibel and Lowen, 2011), and produce many progeny by budding chains of individuals (salps and doliolids) or producing parthenogenic eggs (cladocerans) (Heron, 1972a, 1972b; Paffenhöfer and Orcutt, 1986; Hopcroft and Roff, 1995; Gibson and Paffenhöfer, 2000). Appendicularians only reproduce sexually but can have generation times as short as a week at temperatures of 15 °C (e.g. Bouquet et al., 2009). Since cladocerans and tunicates ingest a wide size range of food and grow rapidly, they have been considered to be colonizing species which rapidly decrease phytoplankton populations (Heron, 1972a; Nakamura et al., 1997; Deibel and Paffenhöfer, 2009). Tunicates also contribute to the biological pump by producing large fecal pellets and discarded appendicularian houses which sink rapidly removing carbon from surface layers (Anderson, 1998; Deibel, 1998).

These colonizing species appear ephemeral because their presence depends on certain oceanic conditions. Boero et al. (2008) emphasized that gelatinous zooplankton, including tunicates, play significant roles in food webs, but stated that their presence is difficult to predict. However, blooms of the doliolid *Dolioletta gegenbauri*, the salp *Thalia democratica*, and the appendicularian *Oikopleura dioica* have consistently been documented off the U.S. southeastern coast, where upwelling events triggered phytoplankton blooms which resulted in blooms between January and August (Atkinson et al., 1978; Paffenhöfer et al., 1984, 1987, 1995; Deibel 1985). Heron and Benham (1984) found *T. democratica* in winter,

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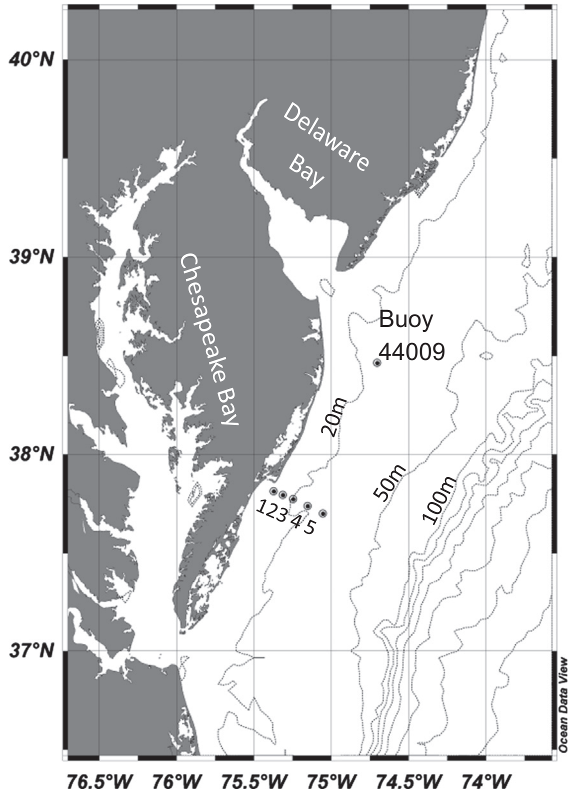

Fig. 1. A map of the southern Mid-Atlantic area showing the cruise transect off Wallops Is. on the Delmarva Peninsula, and the Delaware Bay Buoy 44009 at the southern end of Delaware Bay. The cruise transect was 32 km long starting at station 1 (9 km from shore) and ending at station 5 (41 km from shore). Figure by R. Vaillancourt.

spring and summer in coastal waters off Sydney, Australia. In tropical latitudes such as Jamaica, *O. dioica*, and the cladoceran, *Penilia avirostris*, occur year around (Hopcroft and Roff, 1998; Rose et al., 2004). However, in the temperate latitudes of the Mid-Atlantic Bight (MAB), these species have only been found during the summer (Judkins et al., 1980; Cosper and Stepien, 1984; Sherman et al., 1988).

The MAB consists of three distinct water masses; the shelf, slope and the Gulf Stream. The bathymetry of the MAB shelf is simple and smooth, extending ~100 km offshore and ~800 km from Georges Bank to Cape Hatteras with an average depth of ~100 m at the shelf break (Fig. 1). The shelf water is part of a coastal current that originates near Greenland and is carried south by the mean current around Georges Bank, past Nantucket Shoals into the MAB. Within the MAB, the mean SW flow is towards Cape Hatteras, where most of the shelf water is entrained into the Gulf Stream (Chapman and Beardsley, 1989). The strip of ocean adjacent to the shelf water is the slope water, which is ~200 km wide and ~1600 km long.

Shelf-slope exchange occurs along the entire length of the MAB and constitutes an important mechanism to transfer heat, salt, nutrients, and organisms between shelf and slope waters. The Gulf Stream is on the seaward boundary of the slope water. A number of mechanisms, including Gulf Stream Rings and shelf-break eddies, contribute to the transfer of heat, chemicals and organisms across the shelf-slope region (Csanady and Hamilton, 1988).

The vernal progression of water temperature and salinity in the MAB begins in late March with increased solar radiation, increased river runoff and decreasing wind stress. This also marks the transition from horizontal to vertical density stratification in shelf waters with vertical stratification complete by June or July. The seasonal pycnocline separates the buoyant surface water from the remnant winter water near the bottom called the “cold pool”. By October, the cooling of the sea surface and increasing wind stress contribute to the deepening of the surface mixed layer, erosion and deepening of the seasonal thermocline, warming and shrinking of the cold pool, and an eventual destruction of the layered structure. By November, vertical mixing and winter cooling result in re-establishment of the winter thermal front (e.g. Kumar et al., 2006).

The physical conditions in the MAB affect the supply of nitrogen to phytoplankton populations, which influence zooplankton densities. The spring bloom in March depletes the surface nitrogen (Sherman et al., 1988). By summer, strong stratification in the MAB contributes to nitrate concentrations below detection in surface waters and a persistent deep chlorophyll maximum below the pycnocline. Nitrate concentrations also remain low in surface waters since freshwater runoff from the Delaware and Chesapeake Bays is usually at a seasonal minimum. The main input of nitrate is from the bottom cold pool water, which is the residual high nutrient water formed during winter mixing. Deep chlorophyll maxima have been documented during summer over the whole MAB (Falkowski et al., 1983).

More recently, seasonal patterns of phytoplankton abundance and diversity were described off Wallops Is., VA (Makinen and Moisan, 2012; Moisan et al., 2010). They found a winter/spring bloom and secondary fall bloom from chlorophyll concentration and satellite imagery data, but variety of seasonal blooms were displayed from microscopic counts of phytoplankton taxa. *Synechococcus* spp. cyanobacteria, which may include nitrogen fixing bacteria, were found during summer months at all depths and contributed 25% of the particulate organic carbon (Moisan et al., 2010). Flagellates which are potential predators of the cyanobacteria, and dinoflagellates also were abundant in late summer. During the fall bloom in September and October, diatom species dominated, but individual species were only present for a few weeks. All of these phytoplankton species can be ingested by pelagic tunicates and the cladoceran *P. avirostris*.

Several studies of seasonal patterns of zooplankton abundance have been done in the MAB, but these studies have not focused on cladocerans and tunicates. Sherman et al. (1988) sampled zooplankton with 333 μm mesh Bongo nets at many stations in the MAB shelf, and reported that copepod species were the most abundant animals with total zooplankton biomass peaking in late summer. However, in their study, *P. avirostris* dominated the biomass peak in late summer. Thaliacea, Doliolidae and Appendicularia were included in their figure key, but never dominated the zooplankton biomass. Their samples missed a substantial portion of the zooplankton biomass. They estimated that 30% more biomass would have been collected if zooplankton had been sampled with 53 and 65 μm mesh nets. Flagg et al. (1994) collected data from a current meter, fluorometer and an acoustic Doppler current profiler on a buoy on the outer edge of the continental shelf in the MAB to follow seasonal patterns of currents, phytoplankton and zooplankton, respectively. They documented concurrent spring (April–May) phytoplankton and zooplankton peaks, but also found plankton peaks associated with large changes in currents but not in a predictable way.

Thus, no previous studies have focused on the more fragile gelatinous tunicates, and used smaller mesh nets to collect zooplankton in nearshore MAB waters. As part of a coastal observatory study in the nearshore region off Wallops Island, VA, we studied oceanographic and biological influences on the seasonal distribution of the cladoceran *P. avirostris* and three dominant tunicate species: *O. dioica*, *D. gegenbauri*, and *T. democratica*. This study area is unique compared to most study areas in the MAB since there is minimal freshwater runoff from land. The objectives of our study were to (1) document seasonal occurrences of the