



The death assemblage as a marker for habitat and an indicator of climate change: Georges Bank, surfclams and ocean quahogs



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ABSTRACT

A comprehensive dataset for the Georges Bank region is used to directly compare the distribution of the death assemblage and the living community at large spatial scales and to assess the application of the death assemblage in tracking changes in species' distributional pattern as a consequence of climate change. Focus is placed on the biomass-dominant clam species of the northwest Atlantic continental shelf: the surfclam *Spisula solidissima* and the ocean quahog *Arctica islandica*, for which extensive datasets exist on the distributions of the living population and the death assemblage. For both surfclams and ocean quahogs, the distribution of dead shells, in the main, tracked the distribution of live animals relatively closely. Thus, for both species, the presence of dead shells was a positive indicator of present, recent, or past occupation by live animals. Shell dispersion within habitat was greater for surfclams than for ocean quahogs either due to spatial time averaging, animals not living in all habitable areas all of the time, or parautochthonous redistribution of shell. The regional distribution of dead shell differed from the distribution of live animals, for both species, in a systematic way indicative of range shifts due to climate change. In each case the differential distribution was consistent with warming of the northwest Atlantic. Present-day overlap of live surfclams with live ocean quahogs was consistent with the expectation that the surfclam's range is shifting into deeper water in response to the recent warming trend. The presence of locations devoid of dead shells where live surfclams nevertheless were collected measures the recentness of this event. The presence of dead ocean quahog shells at shallower depths than live ocean quahogs offers good evidence that a range shift has occurred in the past, but prior to the initiation of routine surveys in 1980. Possibly, this range shift tracks initial colonization at the end of the Little Ice Age.

1. Introduction

Death assemblages have received much attention by taphonomists in investigations relevant to the process of preservation and ultimately the interpretation of the fossil record. Applications of the death assemblage in investigations of ecological change have been many fewer, but these investigations demonstrate the potential of the death assemblage as a long-term record of change in community structure and function. Kidwell (2007, 2008) considered community change in response to anthropogenic activities such as fishing and documented the record of such in the death assemblage. Aller (1995), Poirier et al. (2009), and Tomašových and Kidwell (2009), among others, considered the record of spatial and environmental gradients as recorded in the death assemblage. Stratigraphic variation in death assemblage composition records temporal changes in community structure where sedimentation rate is sufficient to overcome time averaging (Gasse et al., 1987; Alin and Cohen, 2004; Powell et al., 1992). Warwick and Light (2002) and Tomašových and Kidwell (2010) considered applica-

tion of the death assemblage in estimating regional biodiversity.

Extracting such information from the death assemblage is compromised by a range of processes among the most important being spatial and temporal time averaging (Powell et al., 1989; Kidwell and Holland, 2002; Kidwell et al., 2005; Dexter et al., 2014), taphonomic degradation (Smith and Nelson, 2003; Kosnik et al., 2009; Powell et al., 2011), and resuspension and transport (Parsons and Brett, 1991; Zenatas, 1990; Callender et al., 1992). Nonetheless, evidence of the potential of the death assemblage in the study of recent changes in community composition over space and time continues to accumulate.

Few studies have considered the death assemblage of continental shelves, particularly over large spatial scales (e.g., MacIntyre et al., 1978; Frey and Dörjes, 1988; Powell et al., 1990; Staff and Powell, 1990a; Powell et al., 1998; Staff and Powell, 1999; Grill and Zuschin, 2001) and fewer still have addressed use of the death assemblage in tracking changes in community composition as a product of anthropogenic impact or climate change (e.g., Kidwell, 2007, 2008; Albano et al., 2016; Tomašových et al., 2017). Climate change is substantively

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affecting community structure over large spatial scales on continental shelves today (Rose, 2005; Lucey and Nye, 2010; Perry et al., 2010). Most studies emphasize commercial species because long-term time series over large spatial scales are primarily contributed by routine stock surveys (Kerr et al., 2009; Brander, 2010; Perry et al., 2010). Typically, the benthos of the continental shelf are poorly surveyed (e.g., van der Meer, 1997; Morehead et al., 2008; Powell and Mann, 2016) and few time series exist. Potentially, comparison between the death assemblage and the living community might provide evidence of shifts in distributional patterns in response to climate change when long-term time series do not exist. Unfortunately, evaluation of this potential remains unaddressed, as surveys of adequate geographic scale are extremely rare. Of the few that exist, the most important may be the survey datasets for the commercial clam species of the northwest Atlantic continental shelf: the surfclam *Spisula solidissima* and the ocean quahog *Arctica islandica*.

Both surfclams and ocean quahogs are biomass dominants and long lived and thus provide a potentially rich opportunity to study the influence of climate change on the continental shelf benthos. The ocean quahog is a pan-boreal species with a western Atlantic range extending south to near Chesapeake Bay (Merrill and Ropes, 1969; Dahlgren et al., 2000). The population distribution has been stable in the northwest Atlantic region, probably due to the ability of the species to burrow and estivate during summer months at the southern and inshore extent of the range and thereby escape high summer bottom water temperatures (Taylor, 1976a; Ridgway and Richardson, 2011). Recent documentation of population age frequencies from sites on the U.S. continental shelf, however, show that ocean quahogs occupied their present range beginning near the end of the Little Ice Age, during the late 1700s to early 1800s (Pace et al., 2017; for more on the Little Ice Age, see Cronin et al., 2010; Mann et al., 2009; for timing of initial warming in the northwest Atlantic, see Moore et al., 2017). That is, the species has shifted its range over historical time beginning more or less coincident with a period of rapid warming that began in the early 1800s with the present range established between 1860 and 1910. Present bottom water temperatures impinge on this species' thermal limits along the inshore boundary of the range, however, so that the species is becoming increasingly sensitive to ongoing climate change (see also Dahlgren et al., 2000 for a historical perspective).

In contrast, surfclams have proven to be much more sensitive to climate change over the last two decades. Surfclams are generally not found in areas where bottom temperature exceeds 25 °C (Cargnelli et al., 1999a); scope for growth becomes negative at temperatures above about 21 °C and animals starve to death if such high temperatures are experienced for extended periods (Kim and Powell, 2004; Narváez et al., 2015). Thus, the southern and inshore range boundaries are controlled primarily by bottom water temperatures in late summer-early fall (August–October). The sensitivity of surfclams to warm water temperatures (Munroe et al., 2013; Narváez et al., 2015) positions the species to be sensitive to warming of the Mid-Atlantic Bight, the most recent phase of which began circa 1970 and accelerated circa 1990 (Nixon et al., 2004; Friedland and Hare, 2007). In the 1960s and 1970s, and probably at earlier times, the range of the Atlantic surfclam as documented by stock surveys extended from Georges Bank almost to Cape Hatteras (e.g., Ropes, 1980, 1982) and encompassed the inner half of the continental shelf from the Chesapeake Bay mouth to Hudson Canyon at depths of 10–50 m, with nearshore populations along Long Island and Southern New England (Goldberg and Walker, 1990; Weinberg, 1998; Jacobson and Weinberg, 2006), extending onto the shallower portion of Georges Bank (NEFSC, 2013). As a consequence of rising bottom water temperatures, the southern and inshore range boundary of the Atlantic surfclam has shifted north and into deeper waters (Cargnelli et al., 1999a; Weinberg, 2005; Munroe et al., 2013). Early evidence of this trend is the disappearance of surfclams from Virginia and Maryland state waters between the 1970s and the 1990s (Loesch and Ropes, 1977; Powell, 2003) and the development of the

New Jersey state fishery in the 1990s. During the 1997–1999 period, the surfclam population was judged to be near carrying capacity throughout most of its range (NEFSC, 2013). However, surveys in 2002 revealed a large mortality event after 1999 that eliminated surfclams from the southern inshore region off the Delmarva Peninsula, an event followed soon thereafter by stock declines in both state and federal waters off New Jersey (Kim and Powell, 2004). The results of an additional survey conducted in 2004 (Weinberg et al., 2005) confirmed the northward and offshore range shift.

The contraction of the southern boundary of the surfclam's range has not been compensated by an expansion northward at the northern boundary of the range. The stock appears to have extended into federal offshore waters off eastern Long Island, but the degree to which this will continue and be substantive for the stock remains unclear. The northern limit of the surfclam stock is primarily a result of limited sandy habitat north of Georges Bank where only a limited extension into the inshore region of the Gulf of Maine is documented (Palmer, 1991). Thus, the trends in aggregate have resulted in a contraction of the surfclam's range. Munroe et al. (2016) showed that maximum size also declined over much of the stock since 1980. Simulation modeling of surfclam population dynamics demonstrates that this outcome can be derived solely from rising temperatures, as temperature influences scope for growth primarily through its effect on filtration rate (Munroe et al., 2013, 2016), although a change in food supply would provide the same outcome.

Here, we utilize a comprehensive long-term dataset for the region of Georges Bank, a database that includes documentation of the abundance of live surfclams and ocean quahogs and also their dead shells, to directly compare the distribution of these species in the death assemblage and the living community over large spatial scales and to assess the application of the death assemblage in tracking changes in species distributional pattern as a consequence of climate change. Georges Bank approaches the northern boundary of the surfclam's range while being situated well within the center of the ocean quahog's range (for additional documentation of the North Atlantic range of ocean quahogs, see Brey et al., 1990; Rowell et al., 1990; Ragnarsson and Þórarinsdóttir, 2002; Butler et al., 2009). Georges Bank provides a unique opportunity because clam fishing has been limited in this region by a multidecadal fishery closure (Jacobson and Weinberg, 2006), the bank is primarily self-recruiting (Zhang et al., 2015, 2016), habitat complexity is pronounced (Collie et al., 1997), surfclams and ocean quahogs are both benthic biomass dominants on the bank, and their survey data are extensive (e.g., Lewis et al., 2001; NEFSC, 2009, 2013). In addition, an extensive dataset documents the geographic distribution of dead surfclam and ocean quahog shells on the bank, as well as a selection of substrate types that permit consideration of habitat as a modulator of clam distribution.

2. Methods

2.1. Data resources

Surfclam and ocean quahog survey data from 1980 to 2011 were obtained from the NMFS-NEFSC (National Marine Fisheries Service – Northeast Fisheries Science Center) survey database. These data include standardized catch of live surfclams and ocean quahogs, information on substrate and in particular the presence of cobbles, rocks, and boulders, and documentation of the occurrence of ocean quahog and surfclam dead shells from each survey tow. The data were obtained, in most cases, from triennial surveys that invoked a stratified random design. The gear was a hydraulic dredge, with well-known selectivity and efficiency characteristics (NEFSC, 2009, 2013; see also Meyer et al., 1981; Smolowitz and Nulk, 1982; Hennen et al., 2012). Selectivity was good for live clams down to a size of approximately 50–55 mm. As the dredge liner controlled selectivity and no post-catch mechanical sorting occurred on the boat prior to on-deck sorting of

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