1	The Death Assemblage as a Marker for Habitat and an Indicator of Climate
2	Change: Georges Bank, Surfclams and Ocean Quahogs
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14	Abstract
15	We utilize a comprehensive dataset for the region of Georges Bank to directly assess the
16	reliability of the death assemblage in tracking the living community at large spatial scales
17	including changes in species distributional pattern as a consequence of climate change. We focus
18	on the biomass-dominant clam species of the northwest Atlantic continental shelf: the surfclam
19	Spisula solidissima and the ocean quahog Arctica islandica, for which extensive datasets exist on
20	both the distribution of the living population and the distribution of the death assemblage. For
21	both surfclams and ocean quahogs, the distribution of shells, in the main, tracked the distribution
22	of live animals relatively closely. Thus, for both species, the presence of shells was a positive
23	indicator of present, recent, or past occupation by live animals. Shell dispersion within habitat
24	was greater for surfclams than for ocean quahogs either due to spatial time averaging, animals
25	not living in all habitable areas all of the time, or parautochthonous redistribution of shell. The
26	regional distribution of shell differed from the distribution of live animals, for both species, in a
27	biased way indicative of range shifts due to climate change. In each case this bias was consistent
28	with warming of the northwest Atlantic. Present-day overlap of live surfclams with live ocean
29	quahogs was consistent with the expectation that surfclams are moving into deeper water in
30	response to the recent warming trend. The presence of locations devoid of shells where live
31	animals nevertheless were collected measures the recentness of this event. The presence of 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 dynamics at the end of the Little Ice Age.

35

Introduction

36 Death assemblages have received much attention by taphonomists in investigations 37 relevant to the process of preservation and ultimately the interpretation of the fossil record. 38 Applications of the death assemblage in investigations of ecological change have been many 39 fewer, but these investigations demonstrate the potential of the death assemblage as a long-term 40 record of change in community structure and function. Kidwell (2007, 2008) considered 41 community change in response to anthropogenic activities such as fishing and documented the 42 record of such in the death assemblage. Aller (1995), Poirier et al., (2009), Tomašových and 43 Kidwell (2009), among others, considered the record of spatial and environmental gradients as 44 recorded in the death assemblage. Stratigraphic variation in death assemblage composition 45 records temporal changes in community structure where sedimentation rate is sufficient to 46 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 application of 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), 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 Dörges, 1988; Powell et al., 1990;
Staff and Powell, 1990a, 1999; Grill and Zuschin, 2001). Climate change is substantively
affecting community structure over large spatial scales on continental shelves today (Rose, 2005;
Lucey and Nye, 2010). Most studies emphasize commercial species because long-term time
series of composition 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., 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*.

70 Both surfclams and ocean quahogs are biomass dominants and long lived and thus 71 provide a potentially rich opportunity to study the influence of climate change on the continental 72 shelf benthos. The ocean quahog is a pan-boreal species with a western Atlantic range extending 73 south to near Chesapeake Bay (Merrill and Ropes, 1969; Dahlgren et al., 2000). The population 74 distribution has been stable in the northwest Atlantic region, probably due to the ability of the 75 species to burrow and estivate during summer months at the southern and inshore extent of the 76 range and thereby escape high summer bottom water temperatures (Taylor, 1976a; Ridgway and 77 Richardson, 2011). Recent analyses show, however, that ocean quahogs occupied their present 78 range beginning near the end of the Little Ice Age (Pace et al., submitted: for more on the Little 79 Ice Age, see Cronin et al. 2010, Mann et al. 2009). That is, the species has shifted its range over 80 historical time beginning more or less coincident with a period of rapid warming that began in 81 the early 1800s with the present range established between 1860 and 1910. Present bottom water 82 temperatures impinge on this species' thermal limits along the inshore boundary of the range, 83 however, so that the species is becoming increasingly sensitive to ongoing climate change (see 84 also Dahlgren et al. 2000 for a historical perspective).

85 In contrast, surfclams have proven to be much more sensitive to climate change over the 86 last two decades. Surfclams are generally not found in areas where bottom temperature exceeds 87 25°C (Cargnelli et al. 1999), so that the southern and inshore range boundaries are controlled 88 primarily by bottom water temperatures in late summer-early fall (August-October). The 89 sensitivity of surfclams to warm water temperatures (Munroe et al. 2013, Narváez et al. 2015) 90 positions the species to be sensitive to warming of the Mid-Atlantic Bight, the most recent phase 91 of which began circa 1970 and accelerated circa 1990 (Nixon et al., 2004; Friedland and Hare, 92 2007). At one time, the range of the Atlantic surfclam extended from Georges Bank almost to 93 Cape Hatteras and encompassed the inner half of the continental shelf from the Chesapeake Bay

94 mouth to Hudson Canyon at depths of 10 m to 50 m, with nearshore populations along Long 95 Island and Southern New England (Goldberg and Walker 1990; Weinberg 1998; Jacobson and 96 Weinberg 200), extending onto the shallower portion of Georges Bank (NEFSC, 2013). As a 97 consequence of rising bottom water temperatures, the southern and inshore range boundary of 98 the Atlantic surfclam has shifted north and into deeper waters (Cargnelli et al. 1999; Weinberg 99 2005; Munroe et al. 2013). Early evidence of this trend is the disappearance of surfclams from 100 Virginia and Maryland state waters between the 1970s and the 1990s (Loesch and Ropes 1977; 101 Powell 2003) and the development of the New Jersey state fishery in the 1990s. During the 1997 102 to 1999 period, the surfclam population was judged to be near carrying capacity throughout most 103 of its range (NEFSC 2013). However, surveys in 2002 revealed a large mortality event after 104 1999 that eliminated surfclams from the southern inshore region off the Delmarva Peninsula, an 105 event followed soon thereafter by stock declines in both state and federal waters off New Jersey 106 (Kim et al. 2004). The results of an additional survey conducted in 2004 (Weinberg et al. 2005) 107 confirmed the northward and offshore range shift.

108 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 109 110 appears to have extended into federal offshore waters off eastern Long Island, but the degree to 111 which this will continue and be substantive for the stock remains unclear. The northern limit of 112 the stock is primarily a result of limited habitat for surfclams north of Georges Bank where only 113 a limited extension into the inshore region of the Gulf of Maine is documented (Palmer, 1991). 114 Thus, the trends in aggregate have resulted in a contraction of the surfclam's range. Munroe et al. 115 (2016) have shown that maximum size also has declined over much of the stock since 1980. 116 Simulation modeling of surfclam population dynamics demonstrates that this outcome can be 117 derived solely from rising temperatures, as temperature influences scope for growth primarily 118 through its effect on filtration rate (Munroe et al. 2013, 2016), although a change in food supply 119 would provide the same outcome.

Here, we utilize a comprehensive long-term dataset for the region of Georges Bank to directly assess the reliability of the death assemblage in tracking the living community at large spatial scales including 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

125 North Atlantic range of ocean quahogs, see Brey et al., 1990; Rowell et al., 1990; Ragnarsson 126 and Thórarinsdóttir, 2002; Butler et al., 2009). Georges Bank provides a unique opportunity 127 because clam fishing has been limited in this region by a multidecadal fishery closure (Jacobson 128 and Weinberg, 2006), the bank is primarily self-recruiting (Zhang et al., 2015, 2016), habitat 129 complexity is pronounced, surfclams and ocean quahogs are both benthic biomass dominants on 130 the bank, and their survey data are extensive (e.g., Lewis et al., 2001; NEFSC, 2009; NEFSC, 131 2013). In addition, an extensive dataset documents the geographic distribution of surfclam and 132 ocean qualog shells on the bank, as well as a selection of substrate types that permit 133 consideration of habitat as a modulator of clam distribution.

134

Methods

135 Data Resources

136 Surfclam and ocean qualog survey data from 1980 to 2011 were obtained from the 137 NMFS-NEFSC (National Marine Fisheries Service – Northeast Fisheries Science Center) survey 138 database. These data include standardized catch of surfclams and ocean quahogs, information on 139 substrate and in particular the presence of cobbles, rocks, and boulders, and the occurrence of 140 ocean guahog and surfclam shell. The data were obtained, in most cases, from triennial surveys 141 that invoked a stratified random design. The gear was a hydraulic dredge, with well-known 142 selectivity and efficiency characteristics (NEFSC, 2009; NEFSC, 2013; see also Meyer et al., 143 1981; Smolowitz and Nulk, 1982; Hennen et al., 2012). Tows were typically of 5-min duration at 144 1.5 knots.

145 Analytical approach

146 General considerations

147 Survey tow locations were specified by the recorded position at the initiation of the tow. 148 Tows with similar initial positions were considered replicates, a replicate being defined relative 149 to a distance approximately twice the distance traveled by a typical survey tow: approximately 150 0.29 minutes of latitude or 0.39 minutes of longitude. Survey tows initiated within this distance 151 apart were considered replicates even if taken in different years. In general, the highest value 152 amongst replicates was taken for further analysis. This emphasized the presence of indicators of 153 complex habitat and also retained information on live animals that might not be stable 154 constituents over the 30+ years of the survey time series.

155 Ocean quahog and surfclam shells can be considered to be stable constituents of the death

156 assemblage over much, if not all, of the entirety of the survey time series. For ocean quahogs, for 157 example, taphonomic loss rates are low (Powell et al., 2002, 2008, 2011) and this can be 158 anticipated also to be the case for surfclams. Stability of the living population over time might 159 not be the case for surfclams as life span is less than the duration of the time series and 160 recruitment, although relatively continuous (Weinberg et al., 1999; Lewis et al., 2001; Powell et 161 al., 2016), is patchy. Thus, surfclams might vary in their presence and extent of occupation of 162 any particular location throughout the time series. In contrast, ocean quahog life spans vastly 163 exceed the duration of the time series by contrast (Ropes et al., 1984; Begum et al., 2010; 164 Ridgway and Richardson, 2011). For surfclams, presence should be interpreted to indicate the 165 potential for occupation of a site, not the expectation of continual occupancy over the 30+ year 166 time series, whereas for ocean quahogs, continuous habitation is a defensible inference.

167 *Data preparation - substrate*

168 The dredge efficiently captured large sedimentary particles such as rocks, cobbles, and 169 boulders. Cobbles encompassed anything smaller than six inches but larger than gravel. Rocks 170 were defined to be between six and twelve inches and boulders were defined as anything larger 171 than twelve inches. Over the history of the survey, the annotations regarding substrate varied. 172 From 1978 to 1980, substrate data were recorded in either liters or bushels. The survey dredge 173 used during this time period was considerably smaller than the dredge used from 1982 to 2011. 174 Due to the extreme variability of recorded data from 1978 to 1980, presence and predominance 175 values were assigned to these data. A value of 0 indicated an absence of a particular substrate 176 (e.g., cobbles). A value of 1 was given to volumes ≤ 1 bushel or where presence was indicated 177 without a volume given (e.g., "trace" was recorded). A value of 2 was assigned to any volume >1 178 bushel. Data for Georges Bank in this portion of the dataset are limited to a few stations taken in 179 1980.

From 1982 through 2011, substrate data were recorded in terms of present or predominant. In addition, the volume caught was routinely recorded, as was the percent of total volume present as substrate. To provide more quantitative and consistent values for substrate, the total volume of substrate in bushels was calculated for each tow from the percent of total volume. The total substrate volume was then divided proportionally by the sum of presence and predominance values, given values of 1 and 2 respectively, in order to estimate the number of bushels of cobbles, rocks, and boulders. This provided an estimate of the volume of each constituent present in the dredge. Thus, a substrate type listed as 'present' in a tow with a high
total substrate volume would have contributed a higher portion of the total catch relative to a
substrate type listed as 'predominant', but with a lower total substrate volume. Using these
volumetric estimates, the data were recoded as 0 for absence or <1 bushel, 1 where the volume of

191 a particular category was <30 bushels, and 2 where the volume was ≥30 bushels.

192 Data prior to 2002 were recorded on hand-written data sheets. For 2002-2011, data were 193 entered directly into an electronic database. Subsequent statistical analysis showed that the 194 substrate volumes recorded in the electronic database were consistently lower per tow than those 195 values on the pre-2002 data sheets, by a factor of 10. Further investigation, including interviews 196 with people who participated in the survey across the 1999-2002 transition, did not elucidate an 197 explanation for the differential, but evaluation across a series of surveys showed that the 198 differential coincided with the transition from data sheet to electronic file and that the differential 199 was consistent forwards and backwards in time from that point. To standardize the data, the 200 2002-2011 values were increased by a factor of 10.

201 The divisions between zero and one bushel and between 29 and 30 bushels used to 202 distinguish absent, present, and predominant were obtained by examining the corrected 203 electronic data from 2002-2011 where the tows for the entire survey domain, not just Georges Bank, could be analyzed as they were already in electronic format. The median and 75th 204 205 percentile for all tows was 0 (no substrate larger than gravel collected) for these tows, except for cobbles where the 75th percentile fell near the tail of the distribution. That is, cobbles, rocks, and 206 boulders were rarely encountered by the survey. The value of 30 fell between the 90th and 99th 207 208 percentiles of all tows for these substrate types except cobbles where it fell close to the 90th percentile (Table 1). The value 1 fell at or above the 90th percentile of all tows for these substrate 209 types except cobbles where it fell near the 75th percentile (Table 1). Thus, we defined as present 210 211 all tows where at least one bushel of material was obtained and as predominant the rare tows 212 where 30 or more bushels were obtained.

In addition, substrate information was gleaned from haul and gear codes associated with each tow. These encompass a range of incidents, mechanical problems, and miscellaneous misfortunes that might have compromised the tow. We extracted the haul and gear codes that indicated problems stemming from bottom contact. These included: (1) locations where the bottom was too rough for dredge deployment; (2) locations where dredge damage occurred, 218 including broken nipples, broken or bent knife blades, torn hoses, or damage to the dredge frame;

and (3) locations where rocks were caught in sufficient number to be judged to have

220 compromised the tow, but which did not cause significant/any damage to the dredge. We

221assigned each of these tows to the set that contained tows that returned \geq 30 bu of cobbles, rocks222and/or boulders. In nearly all cases, these same tows were identified to this substrate class based

223 on documentation obtained from the catch. In only 37 cases (3.7% of the total dataset) the was

the tow not so identified and 31 of these were cases where the tow was abandoned due to bottom

- being too rough for dredge deployment.
- 226 Data preparation shell

227 For shell, abundance data were entered as absence, presence, and predominance values 228 (0, 1, 2). Generally, shell volume as a percentage of total catch was recorded for each tow, as it 229 was for substrate. Thus, the afore-described analysis for substrate could be recapitulated for 230 shell. However, our approach was to focus on the relative importance of shell types at each 231 location rather than comparing the absolute quantity across all tows because this provided a 232 relative ranking of the habitat as a function of species preference. Determining whether total 233 quantity was interpretable with respect to the time-averaged intensity of occupation of the site 234 would require further analyses, although the present database may support such an analysis. 235 Thus, we assigned values of 0, 1, and 2 for absent, present, and predominant for each tow in the 236 time series.

237 Data analysis

238 We defined the domain for analysis as Georges Bank and the westward extension across 239 the Great South Channel to approximately 69° 40' W (Figure 1). In total, the dataset 240 encompassed approximately 1,000 tows, not counting replicates (996 to 1,005 depending on the 241 number of missing data for each datum type). Each of the datum types were patchily distributed 242 across Georges Bank, as can be gleaned readily from the Figures referred to later in the Results 243 section. Characterizing patchiness, however, would not directly address the questions raised in 244 this contribution; namely, the reliability of the death assemblage in tracking the living 245 community and in recording changes in species distributional pattern over large spatial scales. 246 Consequently, analysis focused on the characteristics of neighboring tows in order to assess the 247 degree to which different tow characteristics such as the presence of live surfclams and surfclam 248 shells agreed with the expectation that, in this case, the distribution would be similar. We thus

adopted a modified nearest neighbor analysis without invoking the statistical evaluation of
patchiness as is often done (e.g., Clark and Evans, 1954; Solow, 1989; Brown, 2003; Leighton
and Schneider, 2004).

252 We adopted a presence-absence approach, although information on quantity is present for 253 live animals and for shells, for several reasons. First, although the abundance of ocean quahogs 254 at any location is likely a conservative feature over the 30+ year survey time series, this time 255 span being not much longer than the time to maturity for this animal (Thórarinsdóttir and 256 Jacobson, 2005; Thórarinsdóttir and Steingrímsson, 2000), the same cannot be said for 257 surfclams, given the higher mortality rate and shorter, albeit still long, life span (Weinberg, 1999; 258 Munroe et al., 2016). Thus, for surfclams, abundance at any time is not necessarily an indicator 259 of integrated abundance over tricennial time frames. Second, the amount of shell retained in the 260 tow is not necessarily a function of shell production over time, as some shell may be transported 261 from the site of death and, at least as likely, buried to a depth beneath that accessed by the 262 hydraulic dredge (dredge exhumation depths ≤ 20 cm, see Smolowitz and Nulk, 1982; NEFSC, 263 2013, are less than the height of sand waves and megaripples, Twichell, 1983).

264 For each tow, we assigned a pair-wise set of characteristics. For example, the tow might 265 be characterized by the presence of surfclams and the presence of surfclam shells. Four possible 266 states exist. In the above example, they are: (1) no surfclams, no surfclam shells; (2) surfclams, 267 no surfclam shells; (3) no surfclams, surfclam shells; and (4) surfclams, surfclam shells. We then 268 identified the same characteristics in the four nearest neighbors, using a modified bishops moves 269 approach. We identified the nearest neighbor in the northeast (NE), southeast (SE), southwest 270 (SW), and northwest (NW) quadrant, with one exception. Tows near boundaries typically were 271 missing one of the four neighbors. These tows were excluded as parent tows from further 272 analysis, although retained as neighboring tows. For each of the four possible characteristics of 273 the parent tow, we tallied the characteristics of these four nearest neighbors and evaluated the 274 degree to which the tallies were randomly distributed using a chi-square test for goodness of fit 275 (Daniel, 1978).

The previous analysis targets the degree to which a given characteristic pair resides in a region surrounded by that or another characteristic pair. To further examine the complexity of the surrounding region, we tallied the number of times a given characteristic pair was surrounded by a set of specified characteristic pairs. For example, if the parent tow was characterized by

280 characteristic 4 listed in the preceding paragraph, both surfclams and surfclam shell being 281 present, the four nearest neighbors might be characterized by 4,3,1,1; that is, by one neighbor 282 characterized by both surfclams and surfclam shell present (4), one by no surfclams present, but 283 surfclam shell present (3), and two by the absence of surfclams and surfclam shell (1). 284 Discounting the order of appearance, a total of 36 unique tetrads exist. We compared the 285 distribution of the number of times a particular neighborhood characteristic occurred, namely the 286 sequence of the four neighboring values, against the expectation of homogeneity, using a two-287 sided one-sample exact Kolmogorov-Smirnov test (Conover, 1980). The comparison was done 288 using all possible combinations of the four neighborhood characteristics, of which there are 36. 289 However, certain of these combinations do not occur in the dataset and, arguably, are 290 combinations that are implausible given the distribution of habitat on Georges Bank. As a 291 consequence, we also conducted the test using only the observed combinations. Test results 292 depend to some extent on the order of the tetrads. For consistency, the same order was used for 293 all tests. Reference to that order can be found in the accompanying figures.

294

Results

295 Live animal comparison

296 Figure 1 depicts the distribution of stations on Georges Bank and the easternmost portion 297 of southern New England encompassing the Great South Channel characterized by each of the 298 four possible pairwise combinations defined by the presence or absence of living ocean quahogs 299 and living surfclams. The distribution of stations so characterized is obviously non-random. 300 Cases where only ocean quahogs were found are dominantly located along the southern margin 301 of Georges Bank and parts west. Stations where only surfclams are found are dominantly located 302 in the central shallower region and along the northern edge. A relatively clearly defined line 303 exists, particularly along the southern portion of the bank, where the two species comingle.

Stations where neither surfclams nor ocean quahogs were collected were neighbored primarily by stations with the same characteristic or by stations where only surfclams were found (Table 2). Stations where surfclams were found, sans ocean quahogs, dominantly neighbored stations of the same kind and rarely neighbored stations where only ocean quahogs were found. This distribution was highly non-random. The same pattern was true for ocean quahogs (Table 2). Stations where only ocean quahogs were found neighboring stations where only surfclams were present occurred less frequently. Surfclams and ocean quahogs were obtained together in a number of cases. These, interestingly, were neighbored more evenly by other stations types. In
particular, neighboring stations often had ocean quahogs only and relatively often had surfclams
only.

314 A closer look at stations where both species were present shows that nearest neighbors 315 were not distributed randomly among the tetradic possibilities. Cases where neighbors were 316 either stations with both species or surfclams only were most common; however, cases where 317 neighbors were stations with both species or ocean quahogs only also occurred with some 318 frequency (Figure 2). The distribution of stations among tetradic combinations was highly non-319 random (K-S exact test; P = 0.0068). In contrast, stations where surfclams were present without 320 ocean quahogs, were neighbored primarily by stations where either both species were found, or 321 surfclams only (Figure 2). The distribution among observed tetrads was inhomogeneous (P =322 0.024). Similarly, stations with ocean quahogs only were surrounded primarily by stations of the 323 same type or by stations where neither species was found (Figure 2). The occurrence rate of 324 tetrads among those observed was random (P = 0.296), but the occurrence rate was non-random 325 if all possible tetradic combinations were included (P=0.039). That is, in this case, many possible 326 tetradic combinations were not observed.

327 Shell comparison

The distribution of surfclam and ocean quahog shell (Figure 3) is reminiscent of the distribution of live animals (Figure 1), but with less coherency. Generally, stations where both shell types were found more commonly had neighbors where only one shell type was found, in comparison to live animals (Table 2). The distribution of neighboring types remained highly significant, however (chi-square – Table 2).

333 Perusal of the characteristics of neighboring stations shows biases similar to that 334 observed for live animals, though more dispersed. The occurrence rate for neighboring tetrads of 335 parent stations containing both shell types was not randomly distributed (P = 0.00031); rather, 336 neighbors were of the same type or characterized by stations where only ocean quahog shells 337 were found (Figure 4). The occurrence rate of neighboring tetrads of parent stations containing 338 only ocean quahog shells also was inhomogeneous (P = 0.026). In contrast parent stations where 339 only surfclam shells were found were much richer in tetradic complement whether only the 340 observed tetrads were considered (P = 0.396) or all possible tetradic combinations (P = 0.11). 341 The increased dispersion was often due to the inclusion of one or more neighbors where neither

shell type was found (Figure 4). So, for example, in the live animal comparison, parent stations
characterized by surfclams only were surrounded primarily by stations of the same type or
stations also containing ocean quahogs (e.g., 4222 in Figure 2). In the shell case, the additional
tetrads containing one station with neither shell present (e.g., 4221 – Figure 4) also commonly
occurred. This increased dispersion suggests that spatial time averaging (see Powell et al., 1989)
or local transport (parautochthony) contributes importantly to the distribution of surfclam and
ocean quahog shell.

349 Surfclams and surfclam shell

Live surfclams and surfclam shell were not routinely collected together. Rather, stations where surfclam shell was collected without living surfclams were common, particularly along the southern deeper portion of Georges Bank and around the Great South Channel (Figure 5). Both being collected together occurred commonly on the shallower central portion of Georges Bank and along the northern edge. Cases where only living surfclams were collected occurred much less often (Figure 5).

356 Not surprisingly, stations where surfclams and surfclam shells were collected frequently 357 were associated with stations of the same type (Table 2). Moreover, most neighboring stations of 358 stations where surfclams were collected, but where no surfclam shells were found, were 359 characterized by the presence of both. However, many such stations also were neighbored by 360 stations without either surfclams or surfclam shells. Stations where only surfclam shells were 361 collected were also commonly neighbored by stations of the same type or by stations where 362 neither live surfclams nor shells were collected (Table 2). In very few cases were the neighbors 363 of these stations characterized by the presence only of live surfclams.

364 The distribution of tetradic sets associated with stations where both live surfclams and 365 surfclam shells were found was non-random (P = 0.0005) whereas the distribution of tetradic sets 366 associated with stations where only surfclams were found was random (P = 0.999), even if all 367 possible sets were considered (P = 0.389) (Figure 6). The tendency towards randomness is a 368 product of the frequency of tetrads in which neighbors had neither live surfclams nor shell. These 369 were proportionally more common for parent stations with surfclams only than for parent 370 stations with surfclams and surfclam shell. Many were distributed in the region where live 371 surfclams and ocean quahogs were jointly collected, indicating the newness of occupation by 372 surfclams of locations inhabited by ocean quahogs. The occurrence rate of tetradic types

373 associated with stations where only surfclam shells were caught was random if only the observed 374 tetrads were considered (P=0.155), but strongly non-random if all possible tetrads were 375 considered (P < 0.000189). That is, many possible tetradic combinations were not observed. Of 376 note is the number of stations where surfclam shells were found for which none or only one of 377 the four neighbors contained live surfclams (Figure 6). Many of these locations are associated 378 with sites where live ocean quahogs were collected: the absence of live surfclams may indicate 379 off-bank transport of surfclam shells as an important source of the increased dispersion of 380 surfclam shell relative to live surfclams, a possibility considered further in the Discussion 381 section.

382 Ocean quahogs and ocean quahog shell

Generally, stations were characterized by the joint collection of live ocean quahogs and ocean quahog shell or the collection of ocean quahog shell only (Figure 7). The former occurred along the southern deeper water portion of Georges Bank, along the southern terminus of the Great South Channel, and along a narrow northern rim of the bank. The latter were distributed in shallower portions of Georges Bank, particularly towards the east, and on the northwestern side of the Great South Channel (Figure 7).

389 In comparison to the surfclam case, the neighbors of stations containing both live ocean 390 quahogs and ocean quahog shells were highly likely to be of the same type (Table 2). Cases 391 where ocean quahogs were collected without shells were uncommon and usually were near 392 stations where both shells and live animals were collected. Cases where only ocean qualog 393 shells were found were also uncommon, but disproportionately neighbored by stations where 394 neither live animals nor shells were found. Once again, the distribution of neighbors among 395 neighbor types was significantly inhomogeneous in every case (chi square – Table 2). The 396 tetradic complement for parent stations where both live ocean quahogs and ocean quahog shells 397 were present was highly nonrandom (P < 0.000001). Such stations typically were surrounded by 398 at least 3 of 4 neighbors of the same type (Figure 8). The distribution of tetrads surrounding 399 parent stations with live ocean quahogs, sans ocean quahog shell, was also non-random (P = 400 0.061), but most neighboring stations remain stations where both live animals and shells were 401 collected (Figure 8). The same is not true for parent stations where only ocean quahog shells 402 were collected. The occurrence rate for the observed tetradic combinations was also highly non-403 random (P = 0.001), but most parent stations were neighbored by stations where only ocean

quahog shells were found or where neither live animals nor shells were found (Figure 8). As
neighboring stations only yielding ocean quahog shells rarely neighbored parent stations with
live ocean uahogs and ocean quahog shells, the influence of transportation as an explanation for

407 the observed distributional pattern seems unlikely.

408 Cross-species comparisons

409 Confirmation of the differential in distribution of shells and live animals comes from 410 cross-species comparisons. Stations where live surfclams were found with ocean quahog shells 411 were characterized by a diversity of neighbors (Table 2, Figure 9). The occurrence rate among 412 the observed tetrads was random (P = 0.137) and remained nearly so if all possible tetrads were 413 included (P = 0.073). These stations were in the zone where surfclams have invaded ocean 414 qualog territory, so that neighbors were of many different types. In comparison, cases where live 415 surfclams were found without ocean quahog shells were neighbored primarily by stations of the 416 same type with a lesser number of stations where both were found, but the few neighbors 417 characterized by the absence of surfclams and the presence of ocean quahog shells did not lessen 418 the random distribution of the occurrence rate of neighboring tetrads about these sites (P = 0.22). 419 The opposite was true for stations where surfclams were not found, but ocean guahog shells were 420 present. Most neighbors were of the same type and the distribution of tetradic types was 421 significantly non-random (P = 0.034) (Figure 9). Thus, surfclams were often found with or had 422 neighbors that contained ocean qualog shells, but the stations without live surfclams but with 423 ocean quahog shells were much more restricted in their distribution.

424 A different picture comes from the distribution of live ocean quahogs and surfclam shells. 425 Most stations where ocean qualogs were found coincidentally with surfclam shells were of the 426 same type or cases where ocean quahogs were found without surfclam shells being present 427 (Table 2, Figure 10). The distribution of occurrences for neighboring tetrads was highly non-428 random (P = 0.00000059). A similar distributional pattern was found for stations where ocean 429 quahogs were found sans surfclam shell (Figure 10). The occurrence pattern for neighboring 430 tetrads was also highly non-random (P = 0.00295). The same outcome is true for stations 431 characterized by surfclam shells sans ocean quahogs (P = 0.00000173). Thus, parent stations 432 with live ocean quahogs were primarily neighbored by a limited number of station types with or 433 without surfclam shells whereas neighboring stations characterized by the absence of live ocean 434 quahogs and the presence of surfclam shell were extremely rare. The mirror distribution occurred for stations without live ocean quahogs, but with surfclam shell, where neighbors with live oceanquahogs were rare (Figure 10).

437 Substrate relationships

438 Relatively few stations returned live surfclams and evidence of complex habitat as 439 defined by the presence of any combination of cobbles, rocks, and boulders (Table 3). The 440 occurrence rate for the four nearest neighbors was not randomly distributed among the observed 441 tetrads (P = 0.0094). Nearest neighbors often were locations where surfclams were caught 442 without complex habitat being present or where no surfclams were caught, but complex habitat 443 was present (Figure 11). The occurrence of tetradic combinations of nearest neighbors for locations where surfclams were found without complex habitat was randomly distributed among 444 445 the observed tetrads (P = 0.12), although combinations in which one or more of the four 446 contained complex habitat occurred relatively infrequently.

447 The distribution of surfclam shells relative to complex habitat was almost identical. 448 Relatively few stations returned surfclam shells and evidence of complex habitat (Table 3). The 449 occurrence rate for the combinations of the four nearest neighbors was not randomly distributed 450 among the observed tetrads (P = 0.059). Nearest neighbors often were locations where surfclam 451 shells were caught without complex habitat being present or where no surfclam shells were 452 caught, but where complex habitat was present (Figure 12). The occurrence rate for tetradic 453 combinations of nearest neighbors for parent locations where surfclam shells were found without 454 complex habitat was non-randomly distributed among the observed tetrads, however (P = 455 0.0076). Combinations in which one or more of the four contained complex substrate occurred 456 relatively infrequently (Figure 12). Overall, surfclam shells were not obviously more associated 457 with complex habitat than were live surfclams, as one might expect them to be if local transport 458 of shells was important in determining the distribution of shells.

The distribution of ocean quahogs and ocean quahog shells relative to complex habitat is similar in that the trends are nearly identical between live ocean quahogs and ocean quahog shells (Table 3, Figures 13 and 14). Noticeable, however, is the fact that cases where stations with ocean quahog shells were neighbored by stations with complex habitat are more frequent than cases where live ocean quahogs were so neighbored (Table 3). This increased frequency can be mapped to the shallower water stations where ocean quahog shells were found without live ocean quahogs (Figures 7 and 8). 466

Discussion

467 **Perspective**

468 Application of the death assemblage for tracking changes in the distribution of the living 469 community over time offers an important opportunity in that many species' shifts in range as a 470 consequence of, for example, warming temperatures, cannot be assessed because time series of 471 the living community are not present. Thus, even if the present-day distribution is suspected of 472 being a product of, for example, global warming, information on the past distributional pattern, 473 being poorly known or absent, does not permit empirical validation. This challenge is 474 particularly severe for continental shelf benthos, for which we know little of distributional 475 patterns beyond a few commercial species (for exceptions, see for example, Parker, 1960; 476 Cerame-Vivas and Gray, 1966; Davis and VanBlaricom, 1978; Zuschin and Piller, 1997; Staff 477 and Powell, 1988; Buhl-Mortensen et al., 2012), particularly at large geographic scales and for 478 which sampling is insufficient to be confident in patterns for which we might have some 479 distributional data (Powell and Mann, 2016). The opportunity also presents itself to better 480 evaluate a species' habitat, as living individuals may often not be found in otherwise habitable 481 areas, either due to the vagaries of recruitment or the inadequacies of sampling design, but the 482 death assemblage reliably records occupation by most molluscan species at present or past times 483 as species' ensemble is relatively faithfully preserved (Kidwell and Flessa, 1995; Kidwell, 2001; 484 see Callender and Powell, 2000; Powell et al., 2011 for example exceptions). Powell et al. (1989) 485 termed this process spatial time averaging.

486 Unfortunately, the death assemblage also is impacted by spatial time averaging caused by 487 local to regional transport of shells (Miller, 1988; Zenotos, 1990; Callender et al., 1992) and the 488 tendency of species not to live in all habitable area all of the time [the case of *Mulinia lateralis* 489 being a particularly useful example (Levinton, 1970; Powell et al., 1986)]. Thus, the distribution 490 of shell may not always be a dependable indicator of present or past habitat, just as it may often 491 inform on the same. This ambiguity places a restriction on interpretation. In this study, we used 492 an extensive dataset for the Georges Bank region of the northwestern Atlantic continental shelf 493 to evaluate the distribution of live animals and shell for two clam species, *Spisula solidissima* 494 and Arctica islandica. For surfclams, this region has been sampled repeatedly over more than 30 495 years, so that variations in the distribution of living individuals within habitable area very likely 496 have occurred and the cumulative distribution of locations where live surfclams have been

d97 observed very likely is an effective descriptor of the habitat. For ocean quahogs, life spans are so
long that the distribution is also likely an effective descriptor of the habitat. In each case, we
compared the distribution of shell with that of the living individuals.

500 **Review and interpretation**

501 Warming of the northwest Atlantic has resulted in a documented shift in the distribution 502 of the surfclam, with this species moving north and offshore, depending on location, to remain 503 within the relatively narrow temperature range conducive to survival and growth (Weinberg, 504 2005; Hofmann et al., submitted). For ocean quahogs, no range shift has been documented. This 505 species' range has been relatively stable over the survey time frame that began, for the Georges 506 Bank region, in 1980. However, ocean quahogs invaded the region at some time in the past, the 507 precise details of which remain unknown (Dahlgren et al., 2000). Thus, we anticipate a complex 508 comparison between the distribution of surfclams and surfclam shell, with shell distributions 509 being both more diffuse than the live animals and possibly biased in space as a result of a range 510 shift. For ocean quahogs, we anticipated a less complex comparison, with shell distributions 511 being more or less mirrored by the living community.

512 Consideration can be given to the reason why increasing temperatures have resulted in a 513 northward and offshore shift in the southern and inshore boundary of the surfclam, but no 514 apparent shift in the southern and inshore boundary for the ocean quahog. For surfclams, 515 temperatures resulting in substantial loss in scope for growth are only a few degrees Celsius 516 above optimal (Munroe et al., 2013). Animals entering what Woodin et al. (2013) termed the transient event margin are rapidly compromised as ingestion drops relative to metabolic needs 517 518 (Munroe et al., 2013; Nárvaez et al., 2015). Kim et al. (2004) document the reduction in 519 condition as such animal's scope for growth becomes negative, whereupon, if persistent, they 520 ultimately die, a process termed deficit stress mortality by Nárvaez et al. (2015). Marzec et al. 521 (2010) showed that condition is also reduced offshore probably due to lower temperature leading 522 to lower ingestion rates or to lower food availability, so that the leading range edge very likely is 523 also directly temperature controlled. In contrast ocean quahogs have the ability to bury and 524 estivate for extended time periods (see Taylor, 1976a,b; Oeschger, 1990). As a consequence, 525 these animals do not experience the highest summer temperatures along their southern and 526 inshore boundary. This insulation buffers this species against rising temperatures and stabilizes 527 the range boundary. Whether the species is expanding its range northward or offshore into

528 deeper water remains unknown.

529 The two species have temperature tolerances that would normally limit distributional 530 overlap. But, during times of climate change, the insulation of the ocean quahog and expansion 531 of the surfclam result in a range overlap. This overlap is well documented (NEFSC, 2013) and is 532 readily observed in the Georges Bank dataset (Figures 1 and 2). Nearest neighbors to stations 533 having live surfclams typically also have live surfclams. The same is true for ocean quahogs. 534 However, a significant minority of stations have both species and in these cases, typically one or 535 more of the four nearest neighbors is a station where only ocean quahogs were caught or where 536 only live surfclams were caught.

537 For ocean quahogs, the distribution of live animals and shell were similar with two 538 noticeable exceptions. First, in a few cases, certain nearest neighbors were characterized by the 539 presence of live ocean quahogs, but no shell. These locales were almost always neighbored by at 540 least three of the tetradic neighboring ensemble having both ocean quahogs and ocean quahog 541 shell (Figure 8). Most were distributed near the edge of the region occupied by this species 542 (Figure 7). Likely, these sites represent recruitment in marginal habitat where total shell 543 production is low.

544 Second, although overall, the distribution of ocean quahog shell tracked the distribution 545 of live ocean quahogs very closely (Figure 8); however, in an important minority of sites, ocean 546 quahog shell was found shallower than live animals. This region was discrete spatially (Figure 547 8). Neighbors were of the same type, being characterized by ocean qualog shell but no live 548 animals; also, however, sites where neither ocean quahogs nor ocean quahog shell were collected 549 occurred as neighbors with some frequency (Figure 8). The suggestion from the regionalism and 550 neighboring site complement is that these shells document the occupation by ocean quahogs at 551 an earlier time when ocean quahogs occupied depths on Georges Bank shallower than today. 552 Over time, with warming of the northwest Atlantic that likely started at the end of the Little Ice 553 Age (Schöne et al., 2005; Cronin et al., 2010), these depths became uninhabitable. When this 554 shift in range occurred is unclear, save that the event surely preceded by many years the first 555 surveys which began in 1980, as no live ocean quahogs have ever been collected in this region 556 and the shells almost certainly represent animals that were at least 60 years old at the time of 557 death, given the normal growth rates of the species (Murawski et al., 1982; Harding et al., 2008). 558 Ocean quahogs today are rarely associated with sites where complex substrate such as

559 cobbles, rock, or boulders are found and no evidence exists that they have been in the past 560 (Figures 13 and 14). For live animals, the few such sites in the dataset have neighboring sites 561 where three or more of the tetrad do not have complex substrate associated with them (Figure 562 13). The pattern is recapitulated with ocean quahog shell (Figure 14), and the somewhat 563 increased frequency is explained by the set of sites where ocean quahog shell occurred at sites 564 shallower than the depth range of live ocean quahogs today, giving additional credence to the 565 conclusion that ocean qualog shell is rarely transported any distance beyond its original resting 566 place.

567 The distribution of surfclam shells is more complex. Sites where live surfclams and 568 surfclam shell were collected have an eclectic set of neighbors, including sites of the same kind, 569 sites where live clams were collected without shell, and sites where shell was collected without 570 live animals. The sites with live animals only tend to be in the region where surfclams and ocean 571 quahogs overlap; that is, these sites provide additional evidence of the newness of occupation as 572 surfclams colonize deeper water.

573 Sites where only surfclam shells were collected are of two types. One type consists of locations intermingled with sites having live surfclams. Possible explanations for this 574 575 distributional pattern are that these are sites capable of supporting surfclams, but none were 576 present when the sampling events occurred, or that regional transport of shell has dispersed shell 577 beyond clam habitat. Surfclams live in a region of Georges Bank that abuts complex habitat 578 where cobbles, rocks and boulders prevail. Sites where complex habitat only was found often 579 neighbor sites where both complex habitat and surfclams were collected and sites where only 580 surfclams were collected, stressing the local heterogeneity of the region (Table 3, Figure 11). 581 The distribution of surfclam shells is very similar suggesting that transport of surfclam shells 582 substantial distances is not an important process; otherwise the number of sites in which shells 583 were associated with complex habitat would be clearly higher than those where live animals 584 were associated with complex habitat. The distributional pattern appears more diffuse than that 585 of ocean quahogs and ocean quahog shell as one might expect from the shallower water, higher 586 energy habitat, but allochthonous shell beds do not appear to be an important contributor to the 587 distribution of surfclam shell.

588 Georges Bank is a relatively high-energy environment (Grant et al., 1997), leading to the 589 expectation that surfclam shell may be transported to some degree during storms. Storm waves in

shallow water are easily capable of moving molluscan shells (Allen, 1984; Frey, 1987;

591 Chattopadhyay et al., 2013) and other objects much heavier than surfclam shells (e.g., Papili et 592 al., 2014). Storms resuspend sediment across much of the continental shelf in the Mid-Atlantic 593 region and elsewhere (Hill and Nadeau, 1989; Gagan et al., 1990; Glenn et al., 2008) and can be 594 expected to do so on Georges Bank. Although long distance shell transport might occur, the 595 more likely outcome is local reworking and burial (Staff et al., 1990b; Best et al., 2000; Papili et 596 al., 2014). Of note, only rarely are surfclam shells retrieved with even minor epibiont coverage 597 (our unpubl. data). The absence of epibionts is a good indicator of nearly continuous burial 598 (Parsons-Hubbard et al., 1999; Powell et al., 2008), which leads credence to the belief that 599 although surfclam shells may be exhumed briefly during storms, only limited directional 600 transport is likely to occur.

601 The issue becomes murky, however, when the second type of site where only surfclam 602 shells were collected is evaluated. These are sites where surfclam shell is found without 603 neighboring sites with live surfclams (Figures 5 and 6). Many of these sites or nearest neighbors 604 are sites that also contain ocean quahog shell (Figure 7). Many of these sites are in deeper water where live surfclams are rarely collected (Figure 1). A question arises as to the explanation for 605 606 the distribution of deep-water surfclam shells. One possibility is that these shells are of a similar 607 species, Spisula polynyma. Spisula polynyma is the cold-water equivalent of S. solidissima with a 608 present range that extends down to Georges Bank, but the species is primarily an Arctic denizen 609 (Cassita and Hart, 2007; Kilada et al., 2009; Selin, 2010). At one time, however, the Georges 610 Bank climate may have been cold enough (see Wanamaker et al, 2011) to support significant 611 numbers of this species, as exist now on the Grand Banks and Scotian Shelf. More likely, these 612 shells are subfossil S. solidissima shells representing an earlier occupation of the bank during a 613 previous warm period (e.g., Medieval Climate Anomaly – Wanamaker et al., 2011), but off-bank 614 transport cannot be excluded; the latter, however, receives little support from the shallow water 615 distributional pattern earlier discussed.

616

Conclusions

617 Here, we utilize a comprehensive dataset for the region of Georges Bank to directly 618 assess the reliability of the death assemblage in tracking the living community at large spatial 619 scales and in recording changes in species distributional pattern over time over large spatial 620 scales. The surfclam and the ocean quahog are large long-lived species with robust shells that 621 can be expected to be retained in the death assemblage for long periods of time: preservation 622 potential is high. Thus, the death assemblage should retain a long-term record. This presents both 623 opportunities and constraints in that the death assemblage may record recent occupation or 624 occupation in the more distant past, the latter of which no longer maps the extent of the present-625 day living community. Conflation of historical and recent distributional patterns challenges 626 interpretation. For both surfclams and ocean quahogs, the distribution of shells, in the main, 627 tracked the distribution of live animals relatively closely. That is, for both species, the presence 628 of shells was a positive indicator of present, recent, or past occupation by live animals. In both 629 cases, the discrepancies in the distributional pattern were unlikely to be due to regional transport 630 of shell, although local transport, particularly for surfclams, is likely and longer distance 631 transport of surfclam shell off bank cannot be ruled out. The assemblage was primarily 632 autochthonous, likely for ocean quahogs, or parautochthonous, more likely for surfclams. 633 Dispersion within habitat originated either from spatial time averaging, animals not living in all 634 habitable areas all of the time, or within habitat redistribution of shell. Evidence of dispersion 635 was limited for ocean quahogs, likely due to the deeper-water habitat and the extended life span 636 which would promote a close mapping between shell and live animal distributions.

637 The regional distribution of shell differed from the distribution of live animals, for both 638 species, in a biased way. In each case this bias was consistent with the anticipated shift in range 639 during a period of warming of the northwest Atlantic. It is unlikely that shifts in range are a 640 product of the North Atlantic Oscillation (NAO) as the life spans of both species far exceed the 641 NAO periodicities (Hurrell and van Loon, 1997; Soniat et al., 2009; Xu et al., 2015). For 642 surfclams, shifts in range might be produced by the Atlantic Multidecadal Oscillation (AMO) as 643 the life span is half or less of the cycle's period, but the same is unlikely for ocean quahogs, as 644 that life span far exceeds the AMO periodicity (Baines and Folland, 2007; Lucy and Nye, 2010; 645 Lanci and Hirt, 2015). For ocean quahogs, response to minimally a century long warming trend 646 would be required (see Cronin et al., 2010; Shen et al., 2012). This is possibly another reason 647 why range shifts have been observed in surfclams and not ocean quahogs, as the latter responds 648 to climate change on a much different temporal scale.

649 Regardless, the distribution for surfclams was recapitulated by the present-day overlap of 650 live animals with live ocean quahogs and was consistent with the expectation that surfclams are 651 moving into deeper water in response to climate change as has been observed elsewhere throughout the species' range. The presence of locations where live animals were collected
without shells measures the recentness of this event. The distribution for ocean quahogs
equivalently explained has not been otherwise observed. That is, present-day survey data do not
record a range shift for this species. The death assemblage, however, offers good evidence that
such a range shift has occurred in the past, but much longer ago.

657 For most species occupying the continental shelf in the northwest Atlantic, data on the 658 distribution of living individuals is at best rudimentary. The very common sand dollar 659 Echinarachnius parma is a good example (e.g., Sisson et al., 2002; Murillo et al., 2016). The 660 analysis presented here suggests that the death assemblage can be used to evaluate the present 661 and past distribution of such species, and may be particularly useful if the present-day 662 distribution is at least rudimentarily known, thus permitting assessment of shifts in range over 663 recent historical time. The ocean quahog, in this study, is a particularly good example. The 664 analysis presented here also suggests that the death assemblage can be used to weigh the 665 adequacy of sampling design for long-lived species, as shells are often much more common than 666 live animals, so that the presence of shells without live animals becomes a useful indicator that 667 sample intensity may be too low. Finally, the analysis presented here suggests that the 668 distribution of shells may be a good indicator of habitat in defining survey geographic 669 boundaries, provided that shifts in range can be identified. An interesting question that remains is 670 the degree to which shell content is an indicator of habitat quality. Given the relatively good 671 agreement often observed in rank-order abundance between the living community and the death 672 assemblage (Kidwell, 2002; for limitations, see Tomašových and Kidwell, 2010), it would be 673 useful to determine if shell content indicates the degree to which an area has supported a species 674 long term. This could be an indicator of the stability of patches in the living community.

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Figure 1. The distribution of live Atlantic surfclams, *Spisula solidissima* (AS), and live ocean
quahogs, *Arctica islandica* (OQ) in the region of Georges Bank as assessed by surveys over the
1980-2011 time frame.



999 Figure 2. The characteristics of the four neighboring sites for parent sites characterized by the 1000 presence or absence of live surfclams and live ocean quahogs. The bar fills identify the 1001 characteristic of the parent site. Thus, black fill indicates parent sites where both surfclams and 1002 ocean qualogs were collected. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. For example, 4311 indicates that 1003 one neighbor had both live surfclams and live ocean guahogs (4), one neighbor had live 1004 surfclams, but no live ocean quahogs (3), and two neighbors yielded neither species (1). A (2) 1005 1006 would indicate live ocean quahogs, but no live surfclams. The y-axis records the number of times each of the tetrads occurred.

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- 1010 Figure 3. The distribution of Atlantic surfclams, *Spisula solidissima* (AS), shell and ocean
- 1011 quahogs, *Arctica islandica* (OQ), shell in the region of Georges Bank as assessed by surveys
- 1012 over the 1980-2011 time frame.



1015 Figure 4. The characteristics of the four neighboring sites for parent sites characterized by the

1016 presence or absence of surfclam shell and ocean quahog shell. The bar fills identify the

1017 characteristic of the parent site. The tetradic groups represent the characteristics of the four

- 1018 nearest neighbors using a bishops moves identification scheme. The y-axis records the number of
- 1019 times each of the tetrads occurred. For additional explanation, see Figure 2.



 $\begin{array}{c} 1020\\ 1021 \end{array}$

Figure 5. The distribution of Atlantic surfclams, *Spisula solidissima*, and Atlantic surfclam shell
in the region of Georges Bank as assessed by surveys over the 1980-2011 time frame.



Figure 6. The characteristics of the four neighboring sites for parent sites characterized by the
presence or absence of live surfclams and surfclam shell. The bar fills identify the characteristic
of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors
using a bishops moves identification scheme. The y-axis records the number of times each of the
tetrads occurred. For additional explanation, see Figure 2.



Figure 7. The distribution of ocean quahogs, *Arctica islandica*, and ocean quahog shell in the region of Georges Bank as assessed by surveys over the 1980-2011 time frame.



Figure 8. The characteristics of the four neighboring sites for parent sites characterized by the presence or absence of live ocean quahogs and ocean quahog shell. The bar fills identify the characteristic of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For additional explanation, see Figure 2.



Figure 9. The characteristics of the four neighboring sites for parent sites characterized by the

presence or absence of live surfclams and ocean guahog shell. The bar fills identify the

- characteristic of the parent site. The tetradic groups represent the characteristics of the four
- nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For additional explanation, see Figure 2.



Figure 10. The characteristics of the four neighboring sites for parent sites characterized by the presence or absence of live ocean quahogs and surfclam shell. The bar fills identify the characteristic of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For additional explanation, see Figure 2.

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Figure 11. The characteristics of the four neighboring sites for parent sites characterized by the presence or absence of live surfclams and complex habitat as defined by the presence of cobbles, rocks, and/or boulders. The bar fills identify the characteristic of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For

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Figure 12. The characteristics of the four neighboring sites for parent sites characterized by the presence or absence of surfclam shells and complex habitat as defined by the presence of cobbles, rocks, and/or boulders. The bar fills identify the characteristic of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For additional explanation, see Figure 2.



 $\begin{array}{c} 1075\\ 1076 \end{array}$

Figure 13. The characteristics of the four neighboring sites for parent sites characterized by the presence or absence of ocean quahogs and complex habitat as defined by the presence of cobbles, rocks, and/or boulders. The bar fills identify the characteristic of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For additional explanation, see Figure 2.



Figure 14. The characteristics of the four neighboring sites for parent sites characterized by the presence or absence of ocean quahog shells and complex habitat as defined by the presence of cobbles, rocks, and/or boulders. The bar fills identify the characteristic of the parent site. The tetradic groups represent the characteristics of the four nearest neighbors using a bishops moves identification scheme. The y-axis records the number of times each of the tetrads occurred. For additional explanation, see Figure 2.



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		1	5			
Substrate	25 th	50 th	75 th	90 th	95 th	99 th
constituent	percentile	percentile	percentile	percentile	percentile	percentile
Cobble	0.0	0.0	3.3	42.7	71.3	120.
Rock	0.0	0.0	0.0	8.8	41.6	100.
Boulder	0.0	0.0	0.0	0.0	0.0	47.5

1095 Table 1. Percentiles of bushel catch per tow for all survey tows taken in 2002-2011.

Table 2. Summary of characteristics of the four nearest neighbors to each parent site, chosen using a bishops moves strategy. Combination indicates the characteristic of the parent site, with the sequence of "no" and "yes" indicating the attribute of the first and second characteristic in the header. Numbers 1-4 are consistent with the tetradic identification scheme used in the figures. Neighbor combinations refer to the characteristics of the neighboring sites. Thus, in the first dataset the combination "no-yes" indicates parent sites where surfclams were not present, but ocean quahogs were found. The neighbor combination "yes-no" indicates neighbors where surfclams were found sans ocean quahogs. The occurrence rate indicates that such neighbors were found 21 times.

						Surfe	clams-oc	cean qua	hogs							
Combination		no-	no (1)			no-y	ves (2)			yes-	no (3)			yes-y	yes (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	239	42	255	76	56	521	21	222	260	24	603	97	86	239	100	295
Chi-square	,	235.6:	P<0.00	01		762.0: 1	P<0.000	1	:	809.5: 1	P<0.000	1		177.5: I	P<0.000	1

					Su	rfclam s	shells-o	cean qua	ahog sh	ells						
Combination		no-	no (1)			no-y	res (2)			yes-	no (3)			yes-y	/es (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	250	91	234	193	91	250	36	339	222	36	432	210	212	337	208	691
Chi-square		79.8:]	P<0.000	1		328.7: I	P<0.000	1		350.2:1	P<0.000	1		428.4: I	P<0.000	1

						Surfc	lams-su	rfclam s	hells							
Combination		no-	no (1)			no-y	res (2)			yes-	no (3)			yes-y	/es (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	356	200	96	248	191	227	48	210	98	62	51	201	265	228	201	654
Chi-square		155.4:	P<0.000)1		119.3: I	P<0.000	1		136.1:1	P<0.000	1		403.7: I	P<0.000	1

					Oce	an qua	hogs-oc	ean qual	hog she	ells						
Combinationno-no (1)no-yes (2)yes-no (3)yes-yes (4)Neighbornonoyesyesyesyesyes																
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	1002	200	52	166	210	57	12	49	59	12	16	93	174	53	95	1306

Chi-square	1	1606.1	: P<0.00	001		280.5:	P<0.000)1		98.4: F	P <0.000	1	2	2666.2:	P<0.000	1
						Surfcla	ms-ocea	n quahc	g shells	5						
Combination		no-no (1)no-yes (2)yes-no (3)yes-yes (4)no-no usenononono														
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	226	92	198	136	92	564	49	219	195	53	448	172	153	252	193	294
Chi-square		67.3:1	P<0.000	1		707.7: I	P<0.000	1		381.4: I	P<0.000	1		52.4: P	< 0.0001	

					(Dcean q	uahogs-	surfclar	n shells	5						
Combination		no-	no (1)			no-y	ves (2)			yes-	no (3)			yes-y	yes (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	238	282	53	83	291	658	28	115	63	33	262	334	87	115	338	576
Chi-square		233.4:	P<0.000)1		855.5: I	P<0.000	1		378.9:]	P<0.000	1		557.2:1	P<0.000	1

Table 3. Summary of characteristics of the four nearest neighbors to each parent site, chosen using a bishops moves strategy. Combination indicates the characteristic of the parent site, with the sequence of "no" and "yes" indicating the attribute of the first and second characteristic in the header. Numbers 1-4 are consistent with the tetradic identification scheme used in the figures. Neighbor combinations refer to the characteristics of the neighboring sites. Thus, in the first dataset the combination "no-yes" indicates parent sites where surfclams were not present, but complex habitat were found. The neighbor combination "yes-no" indicates neighbors where surfclams were found without complex habitat. The occurrence rate indicates that such neighbors were found 108 times.

						Surfel	ams-Co	mplex H	Iabitat							
Combination		no-	no (1)			no-y	es (2)			yes-	no (3)			yes-y	/es (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	598	111	325	50	109	156	108	119	382	101	550	187	48	122	176	194
Chi-square		680.0:	P<0.000)1		12.4: P	=0.0061		,	398.3: I	P<0.000	1		95.6: P	< 0.000	l

					S	Surfclan	ı shells-	Comple	x Habit	at						
Combination		no-	no (1)			no-y	ves (2)			yes-	no (3)			yes-	yes (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
Occurrence	369	66	465	100	74	193	115	122	471	124	937	200	88	124	194	210
Chi-square	4	458.3:	P<0.00	01		58.2: P	<0.0001	1		935.9: I	P<0.000	1		64.9: P	<0.0001	

					Ο	cean Q	uahogs-	Comple	x Habit	at						
Combination		no-	no (1)			no-y	res (2)			yes-	no (3)			yes-	yes (4)	
Neighbor	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-	no-	no-	yes-	yes-
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no (3)	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)		(4)	(1)	(2)	(3)	(4)
Occurrence	465	265	133	37	263	476	50	59	147	56	1235	122	39	56	104	49
Chi-square		457.8:	P<0.00	01		575.2: I	P<0.000	1	2	2452.4:	P<0.000	1		40.2: F	P<0.000	1

					Ocea	ın Quah	log Shel	ls-Com	olex Ha	bitat						
Combinationno-no (1)no-yes (2)yes-no (3)yes-yes (4)Naishbarnananananana																
Neighbor	Neighborno-no-yes-yes-no-no-yes-ye															
combination	no	yes	no	yes	no	yes	no	yes	no	yes	no (3)	yes	no	yes	no	yes
	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)		(4)	(1)	(2)	(3)	(4)

Occurrence	383	198	278	77	191	366	76	99	286	82	1275	133	81	98	123	86
Chi-square	214.0: P<0.0001				284.5: P<0.0001				2124.5: P<0.0001				10.9: P=0.012			