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Can we estimate molluscan abundance and biomass on the continental shelf?

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ABSTRACT

Few empirical studies have focused on the effect of sample density on the estimate of abundance of the dominant carbonate-producing fauna of the continental shelf. Here, we present such a study and consider the implications of suboptimal sampling design on estimates of abundance and size-frequency distribution. We focus on a principal carbonate producer of the U.S. Atlantic continental shelf, the Atlantic surfclam, *Spisula solidissima*. To evaluate the degree to which the results are typical, we analyze a dataset for the principal carbonate producer of Mid-Atlantic estuaries, the Eastern oyster *Crassostrea virginica*, obtained from Delaware Bay. These two species occupy different habitats and display different lifestyles, yet demonstrate similar challenges to survey design and similar trends with sampling density. The median of a series of simulated survey mean abundances, the central tendency obtained over a large number of surveys of the same area, always underestimated true abundance at low sample densities. More dramatic were the trends in the probability of a biased outcome. As sample density declined, the probability of a survey availability event, defined as a survey yielding indices >125% or <75% of the true population abundance, increased and that increase was disproportionately biased towards underestimates. For these cases where a single sample accessed about 0.001–0.004% of the domain, 8–15 random samples were required to reduce the probability of a survey availability event below 40%. The problem of differential bias, in which the probabilities of a biased-high and a biased-low survey index were distinctly unequal, was resolved with fewer samples than the problem of overall bias. These trends suggest that the influence of sampling density on survey design comes with a series of incremental challenges. At woefully inadequate sampling density, the probability of a biased-low survey index will substantially exceed the probability of a biased-high index. The survey time series on the average will return an estimate of the stock that underestimates true stock abundance. If sampling intensity is increased, the frequency of biased indices balances between high and low values. Incrementing sample number from this point steadily reduces the likelihood of a biased survey; however, the number of samples necessary to drive the probability of survey availability events to a preferred level of infrequency may be daunting. Moreover, certain size classes will be disproportionately susceptible to such events and the impact on size frequency will be species specific, depending on the relative dispersion of the size classes.

1. Introduction

Molluscs, primarily bivalves, and echinoderms, primarily echinoids, are the dominant producers of carbonate in estuaries and on the continental shelf in temperate to arctic climes (Moore, 1972; Farrow et al., 1984; Lejart et al., 2012; Lebrato et al., 2010; Waldbusser et al., 2013). As the carbonate balance of the world's oceans becomes an increasing focal point (Cooley et al., 2009; Doney et al., 2009; Feely et al., 2009), determining carbonate production rates and the influence of climate change on these production rates becomes an expanding need (Gattuso et al., 1998;

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Kleypas and Yates, 2009; Wright and Burgess, 2005; Tomašových et al., 2006; Dorshel et al., 2007). Carbonate balance is a function of the rate of carbonate addition, the rate of taphonomic loss, and the rate of burial (Powell, 1992; Tomašových et al., 2006; Powell et al., 2012). The processes and rates of taphonomic loss and burial have received considerable attention, particularly in nearshore settings (Parsons-Hubbard, 2005; Best et al., 2007; Powell et al., 2006; Waldbusser et al., 2011), but also on the continental shelf (Parsons-Hubbard et al., 1999; Powell et al., 2002b, 2011a,b; Smith and Nelson, 2003). Carbonate production rates should also be readily acquired; however, few such estimates exist (e.g., Smith, 1971; Lebrato et al., 2010).

Estimates of carbonate production require effective estimation of population density and size frequency, as well as the implementation of population dynamics models or direct observations permitting estimation of recruitment, growth, and mortality rates (e.g., Powell et al., 2012). A number of population dynamics models have been described for carbonate-producing denizens of the continental shelf (Bradbury and Tagart, 2000; Munroe et al., 2013; NEFSC, 2013). These models require a reliable estimate of abundance; however, the adequacy of abundance estimates from benthic surveys has recently been questioned (Powell and Mann, 2016). The issue arises from the tendency of molluscs to contribute in larger measure to biomass than to abundance (Staff et al., 1985); that is, well represented among the infaunal biomass dominants are the filter-feeding bivalves and predatory gastropods that are among the larger of the continental shelf benthos and among the principal carbonate producers. Such species are present at relatively lower densities than the smaller infauna and tend to be patchy, thus estimates of their abundance and biomass are heavily dependent on sampling gear and sample density (Rago et al., 2006; Powell and Mann, 2016). The problem of sample density is well-considered in the literature (e.g., Findlay, 1982; Livingston, 1987; Kidwell et al., 2001; Battista, 2003; Bennington, 2003; Brown, 2003), but few empirical studies have focused directly on the effect of sample density on the estimation of abundance and biomass of carbonate-producing fauna, particularly the biomass-dominant molluscs of the continental shelf.

The need to accurately estimate the abundance of larger benthic species on the continental shelf goes well beyond carbonate production, and arises from manifold survey needs, including stock assessments to manage commercial species (e.g., NEFSC, 2009; NEFSC, 2013), identification of impacts of fossil fuel exploration and production (e.g., Peterson et al., 1996; Currie and Isaacs, 2005; Parr et al., 2007), documentation of multifarious anthropogenic stresses (e.g., Kidwell, 2007; Carroll et al., 2009), baseline studies documenting community structure and function (e.g., Davis and VanBlaricom, 1978; Aller et al., 2002; Dubois et al., 2009; Buhl-Mortensen et al., 2012), and elucidation of the influence of climate change (e.g., Weinberg, 2005; Lucey and Nye, 2010; Powell et al., 2017). Although many such surveys have been carried out, rarely have their designs taken into account the potential biases imposed by a mismatch of sampling density and species patchiness. Here, we report the results of such an empirical study and consider the implications of suboptimal sampling design on the estimates of abundance and size-frequency distribution as they may affect characterization of biomass dominants on the continental shelf.

We focus on the Atlantic surfclam, *Spisula solidissima*, a principal carbonate producer and biomass dominant found on the continental shelf of the U.S. East coast from the Chesapeake Bay to Georges Bank (Weinberg et al., 2005; NEFSC, 2013), where it supports a major commercial fishery (NEFSC, 2013). The species is particularly sensitive to warming of the bottom waters of the Mid-Atlantic Bight, with well-documented changes in mortality rate and geographic range (Weinberg, 2005; Narváez et al. 2015; Munroe et al., 2016; Hofmann et al., in press), such that substantial spatial and temporal variations in community structure and carbonate production and deposition can be anticipated. The species is extremely patchy (Flowers, 1973; Weinberg et al., 2002; Powell et al., 2017), creating a challenge for accurate estimation of abundance and biomass.

2. Methods

2.1. Data collection

Sampling Design: The option of fixed versus random sampling designs has received considerable attention (e.g., van der Meer, 1997; Morehead et al., 2008). With certain exceptions (e.g., Sammarco and Andrews, 1989; Kennicutt et al., 1996; King and Powell, 2007), benthic surveys employ random sampling (e.g., Gavaris and Smith, 1987; Smith and Gavaris, 1993; Kimura and Somerton, 2006). The purpose of the sampling program undertaken for this study was to provide a uniform array of sampled sites that could be used as potential random locations for evaluating a random sampling scheme. To the extent possible, sites were distributed equivalently in space within a region of 33.5 km^2; depth constraints modified this design in a few cases. In total, 21 stations were sampled in a 33.5-km^2 region of the continental shelf offshore southern New Jersey (Fig. 1). These stations were separated by approximately 6 min of longitude and 2.4 min of latitude.

Sampling Gear: A hydraulic dredge was used. Hydraulic dredges are fitted with a water pump on the vessel that pumps water through a hose to a manifold at the front of the dredge. Nipples affixed across the manifold direct water downward, liquefying the sediment. The dredge is towed through this liquefied sediment, capturing the larger benthic animals (Meyer et al., 1981; Smolowitz and Nulk, 1982). These dredges are used throughout the surfclam and other clam fisheries (e.g., Fogarty, 1981; Ragnarsson and Thórarinsdóttir, 2002; Gilkinson et al., 2005; Hennen et al., 2012)

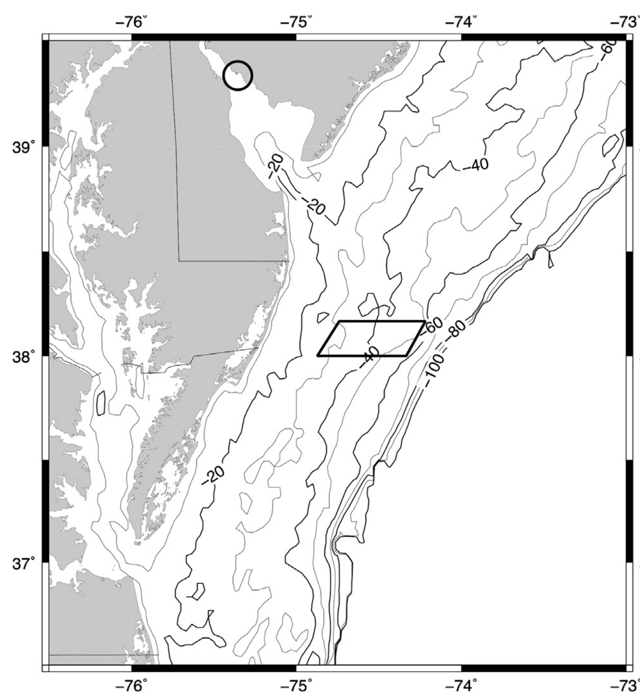

Fig. 1. The study region for the surfclam survey, marked as a quadrilateral, within the Mid-Atlantic region spanning Virginia to southern New Jersey. The circle marks the region in Delaware Bay wherein Cohansey Reef lies. Depths in m.

and typically achieve capture efficiencies for ≥120-mm surfclams of 70%–80% (NEFSC, 2013). Selectivity of smaller individuals declines as a function of the bar spacing in the cage aft of the manifold. The dredge used in this study was lined with 1-inch square wire on the bottom and knife shelf and 1x2-inch rectangular wire on the sides, back, and door. The dredge lining efficiently retained surfclams ≥40 mm, with routine capture of clams as small as 25 mm. The dredge opening was 100 in (2.54 m) across. An additional benefit of using an hydraulic dredge, beyond the high capture efficiency for large infauna, is that the swept area of a single tow is equivalent to a large number of box cores, thus eliminating the problem of small-scale patchiness that necessitates taking many box cores per station (e.g., Powell and Mann, 2016).

Tow Procedure and On-deck Sample Processing: Tows were positioned to travel across the station position. Optimal tow duration was set at 3 min. Tow duration was decreased whenever the dredge became overfull. This occurred in over half of the stations. Positions were taken every 5–10 s during the tow so that catches could be standardized to numbers per m^2. Tow swept areas varied from 224 to 660 m^2. Thus, each tow represented at least the area of 900 50*x*50-cm box cores. All live surfclams were extracted from the dredge contents and the anterior-posterior length measured to the nearest 1 mm.

Statistical Analysis: Size classes were defined to conform with the size intervals used by Kuykendall et al. (2017) which approximate surfclam age differentials based on the time required to grow to fishable size (120 mm). These size classes were obtained using von-Bertalanffy growth relationships from Munroe et al. (2016) for a series of locations across the range of the surfclam, and then interpolated for each 10-min latitude by 10 min longitude square for the region from offshore Delmarva north to Long Island (Kuykendall et al., 2017). The specific values used are the regional averages from that analysis (Kuykendall et al., 2017).

Because stations were distributed approximately evenly across the sampled region, the average of the per-m^2 standardized values was taken as the best estimate of the mean per-m^2 abundance for each size class within the sampled domain; this value will hereafter be referred to as the "true" abundance mean.

We used a Monte Carlo procedure to evaluate the bias in random sampling design imposed by a limitation in sample number. For each evaluation, 1000 random surveys were constructed by choosing randomly a specified number of station values without replacement. These 1000 surveys, when sorted by domain-average per-m^2 abundance, permitted the following metrics to be obtained: the central tendency of mean abundance taken as the median value of the simulated means, a series of percentile values of mean abundance, and the probability of obtaining a biased outcome defined as simulated surveys that recorded per-m^2 abundances >1.25 times the true abundance mean or <0.75 times the true abundance mean. The Monte Carlo procedure as implemented used a "without replacement" procedure for choosing a subset of stations for a simulated survey as a consequence of the sampling design used to obtain the dense survey dataset for oysters discussed in the next section. The alternative "with replacement" option returned results nearly identical in the surfclam case, as the simulated survey densities were always well below the total sample number in the dense survey dataset. Thus all reported simulations were carried out using the "without replacement" option.

Comparison to Oyster Survey Data. To evaluate the degree to which the results for surfclams are typical, the same analysis was carried out on a dataset for the Eastern oyster, *Crassostrea virginica*, obtained from Cohansey Reef in Delaware Bay (Fig. 1). The Delaware Bay oyster beds in New Jersey waters, including Cohansey Reef, are reviewed in Powell et al. (2008; see also Powell et al., 2007; Powell and Ashton-Alcox, 2013). The survey taken in 2009 covered an area of 8.82 km^2 and used a standard survey protocol (Powell et al., 2002a) that included a series of three 1-min dredge tows taken on each of 83 0.2′ latitude x 0.2′ longitude grids. Abundances are corrected to numbers m^{-2} using tow swept area and catchability coefficients to adjust for dredge efficiency (Powell et al., 2002a). Animals were assigned to three size categories: <60 mm, 60–75 mm, and >75 mm. The central group encompasses the animals at market size (~≥63.5 mm; Powell et al., 2005) or growing into market size in one year (Powell et al., 2005; Kraeuter et al., 2007). The 0.2′ latitude x 0.2′ longitude grid represents the survey template for station choice in the Delaware Bay survey; that is, no grid can receive more than one station in any random survey (Powell et al., 2008). Thus, the dense survey dataset includes stations at every possible sampling site. Consequently, the Monte Carlo-based simulation protocol perforce used the "without replacement" procedure earlier described.

3. Results

3.1. *Spisula solidissima*

Catches per m^2 in each size class are shown in Table 1. Example distributions of representative size classes among the 21 stations, each distribution chosen to portray a differential pattern observed in the sampled domain, are shown in Figs. 2–5. The mean number of clams caught was relatively evenly distributed across the size classes. Most surfclam size classes had increased abundances in the northeast quadrant of the domain. The smaller size classes were dispersed over a larger region. The patchy nature of the species and the differential in distribution of the smaller and larger size classes are consistent with inferences from federal survey catches (NEFSC, 2013). The total number of clams averaged just under 1 m^{-2}. This is a density commonly encountered in regions of high surfclam stock density (NEFSC, 2013); thus, the surveyed region is representative of relatively dense surfclam populations as they occur in the Mid-Atlantic region.

The total number of surfclams was consistently underestimated at small sample densities, based on the median of the mean abundance values (Fig. 6). The median of the simulated survey means approached the true mean with a sampling intensity of 4 or more. Biased survey indices occurred with relatively high probability, just under 40% of the time (~20% high, ~20% low), even at a sampling intensity of 9. At sampling intensities of 5 or less, the probability of a substantial underestimate of surfclam density rapidly increased relative to the probability of a substantial surfclam density overestimate.

The median of the simulated mean abundances obtained for surfclams at or within 1 growth year of market size (>104 mm) approached the true mean with a sampling intensity of 5 or more (Fig. 7). The probability of a biased survey index was high, above 40%, even with a sampling intensity of 10 and the likelihood of an underestimate substantially exceeded the probability of a substantial overestimate at sampling intensities ≤6, reaching higher than 3 in 5 at sampling intensities of ≤4. In contrast, the median of the simulated survey mean abundances obtained for the smaller size classes (≤104 mm) fell near the true mean at any sampling intensity >1 (Fig. 8). The probabilities of a biased high or low outcome were about equally likely over most sampling densities and the probability of a biased survey index was relatively low, about 40% (~20% high, ~20% low), at sampling intensities of 6 or more.

The influence of clam size is dramatically shown by a comparison of the smallest animals with clams likely to grow into market size within 2 years (Figs. 9 and 10). For the smallest animals (≤64 mm, Fig. 9), the median of the simulated survey mean

Table 1
Number of Atlantic surfclams m^{-2}, based on catch corrected for swept area. Dredge efficiency is assumed to be near 100% for clams about 40 mm or larger.

Station	≤64	>64-80	>80-93	>93-104	>104-120	>120
1	0.050	0.007	0.007	0.010	0.013	0.016
2	0.353	0.038	0.028	0.023	0.016	0.036
3	0.123	0.018	0.015	0.020	0.047	0.165
4	0.178	0.116	0.195	0.128	0.277	0.11
5	0.023	0.003	0.007	0.021	0.045	0.010
6	0.508	0.227	0.293	0.376	0.921	0.422
7	0.292	0.070	0.280	0.375	0.660	0.255
8	0.070	0.248	0.507	0.183	0.241	0.042
9	0.200	0.143	0.258	0.141	0.323	0.078
10	0.190	0.185	0.386	0.475	1.484	0.612
11	0.244	0.091	0.235	0.431	1.049	0.331
12	0.499	0.213	0.176	0.196	0.316	0.115
13	0.009	0.013	0.002	0.004	0.006	0.017
14	0.199	0.047	0.068	0.059	0.159	0.059
15	0.093	0.029	0.020	0.020	0.039	0.138
16	0.197	0.049	0.032	0.043	0.046	0.208
17	0.150	0.040	0.032	0.022	0.030	0.067
18	0.024	0.023	0.009	0.012	0.017	0.039
19	0.067	0.000	0.000	0.000	0.000	0.000
20	0.429	0.011	0.011	0.007	0.007	0.052
21	0.282	0.031	0.028	0.012	0.025	0.045
Mean	0.199	0.076	0.123	0.122	0.272	0.134
Standard deviation (Std)	0.151	0.080	0.150	0.158	0.412	0.156
	Mean	Std				
All clams	0.927	0.951				
Submarket clams (≤104)	0.520	0.440				
Market clams (>104)	0.408	0.559				

abundances fell nearly on the true mean at all sampling intensities. The probability of a biased survey index was low, less than 40%, (~20% high, ~20% low) at sampling intensities >4, and the bias was relatively evenly distributed between biased-high and biased-low indices (~20% high, ~20% low). For a larger size class of clams (>93–104 mm, Fig. 10), the true mean was approached at sampling intensities of 2 or more, but the probability of a biased index was >40% until sampling intensity exceeded 9 and, at sampling intensities less than 6, the probability of an unduly low estimated mean relative to the true mean distinctly exceeded the probability of an unduly high estimated mean.

In every case, except for the smallest size class (≤64 mm), the median of the simulated survey mean abundances fell below the true abundance at small sample numbers and approached the true abundance asymptotically as sample density increased. That is, in most cases, not only was the probability of a biased-low survey index higher at low sample densities, but the central tendency over many surveys was also biased low. As sample density increased above this level, differential bias became unimportant, but the likelihood of obtaining a survey mean higher than 1.25 times the true mean or lower than 0.75 times the true mean remained above 40% over a substantial increment of sampling intensity. Inasmuch as the number of samples necessary to reduce differential bias, a higher probability of a biased-low index, and to reduce the overall probability of bias to <40% (~20% high, ~20% low) varied substantively among size classes, the differential in spatial distribution of the various size classes was an important modulator of the outcome.

3.2. *Crassostrea virginica*

To evaluate the degree to which the results for surfclams are typical, we performed the same analysis on a dataset for the Eastern oyster obtained from Cohansey Reef in Delaware Bay (Table 2). Unlike continental shelf surveys, a high-density sampling regimen is routinely feasible for oyster surveys and is part of the standard New Jersey stock assessment protocol (e.g., HSRL, 2012; see also Mann et al., 2016).

The median of the simulated mean abundances for small oysters (<60 mm) approached the true mean with approximately 8 random samples, about 10% of the dense 83-sample dataset (Fig. 11). The probability of a biased-low survey substantively exceeded the probability of a biased-high survey at sampling densities less than 8. The probability of a biased survey did not fall below 40% (~20% high, ~20% low) until a sampling density of about 20 tows was reached, about 25% of the dense sample dataset.

The pattern was very similar for 60–75 mm oysters (Fig. 12) with the exception that the probability of a biased survey dipped below 40% somewhat earlier, at about 16 samples (Fig. 12). In contrast, for animals >75 mm, the median mean abundance approached the true abundance with about 6 samples, fewer than required for the smaller size classes, and the probability of a biased survey fell below 40% (~20% high, ~20% low) with about 13 samples (Fig. 13). Once again, at low sample numbers, the probability of a biased-low survey far exceeded the probability of a biased-high survey, but this dichotomy essentially disappeared with a sample number of about 6, a number fewer than required for the smaller two size classes.

For the oyster dataset, in every case, the median of the simulated mean survey abundances fell below the true abundance at small sample densities and approached the true abundance asymptotically as sample density increased. That is, not only was the probability of a biased-low survey index higher at low sample densities, but the central tendency over many surveys was also biased low. As sample density increased above this level, differential bias became unimportant, but the likelihood of obtaining a survey mean outlying the differential threshold of 1.25 times the true mean or 0.75 times the true mean remained above 40% over a substantial increment of sampling intensity.

Table 2
Number of Eastern oysters m^{-2}, based on catch corrected for swept area and dredge efficiency, for Cohansey Reef in 2009.

Station	<60 mm	60-75 mm	>75 mm	Station	<60 mm	60-75 mm	>75 mm
1	15.110	5.170	7.027	42	60.620	19.840	27.000
2	2.005	0.908	0.870	43	0.000	0.000	0.000
3	1.394	0.887	1.457	44	34.430	9.039	6.026
4	19.620	5.790	9.810	45	5.897	0.983	2.948
5	12.160	2.323	5.876	46	0.422	0.089	0.289
6	45.010	8.950	13.810	47	41.220	9.116	19.020
7	0.275	0.020	0.138	48	0.000	0.000	0.000
8	0.632	0.105	0.105	49	11.250	3.149	5.248
9	0.020	0.000	0.000	50	0.045	0.000	0.023
10	0.693	0.519	0.519	51	0.023	0.069	0.046
11	0.060	0.060	0.199	52	21.220	6.659	9.156
12	2.486	0.561	1.042	53	1.015	0.305	0.406
13	60.410	22.520	18.950	54	14.330	2.543	5.549
14	15.630	4.936	7.897	55	10.610	4.245	10.080
15	16.650	2.795	6.684	56	62.460	17.430	15.250
16	4.999	1.406	1.875	67	20.910	6.722	8.216
17	1.506	0.927	1.564	68	8.362	3.659	7.840
18	1.807	0.436	1.869	59	0.000	0.000	0.000
19	9.133	2.268	2.388	60	2.769	0.738	1.477
20	13.450	7.089	7.089	61	45.220	8.183	6.891
21	6.454	1.760	4.254	62	39.740	14.290	16.380
22	11.060	4.986	8.672	63	49.800	12.220	11.300
23	7.839	2.412	6.180	64	0.000	0.000	0.000
24	0.000	0.000	0.000	65	0.050	0.050	0.050
25	1.043	0.717	0.717	66	0.777	0.518	1.295
26	0.062	0.000	0.021	67	7.815	2.004	4.408
27	17.550	3.622	6.130	68	0.000	0.000	0.000
28	10.490	2.622	5.572	69	21.070	6.246	5.928
29	0.851	0.340	0.965	70	0.270	0.495	1.350
30	6.797	2.266	4.833	71	5.492	2.856	4.613
31	54.630	11.500	14.380	72	13.310	5.254	10.160
32	15.900	7.949	13.910	73	0.000	0.000	0.000
33	24.640	7.302	12.320	74	5.252	0.938	1.688
34	0.021	0.000	0.021	75	23.100	7.929	13.440
35	0.000	0.000	0.000	76	0.031	0.031	0.000
36	9.769	4.509	9.018	77	23.800	12.180	20.480
37	0.256	0.043	0.171	78	6.769	2.166	7.581
38	0.278	0.128	0.492	79	21.910	6.630	12.680
39	18.530	4.560	4.269	80	0.714	0.000	0.429
40	0.000	0.000	0.065	81	0.068	0.000	0.034
41	0.695	0.152	0.152	82	0.000	0.000	0.000
				83	0.310	0.620	0.103

	<60 mm	60-75 mm	>75 mm
Mean	11.699	3.491	5.045
Standard deviation (Std)	16.101	4.745	5.908

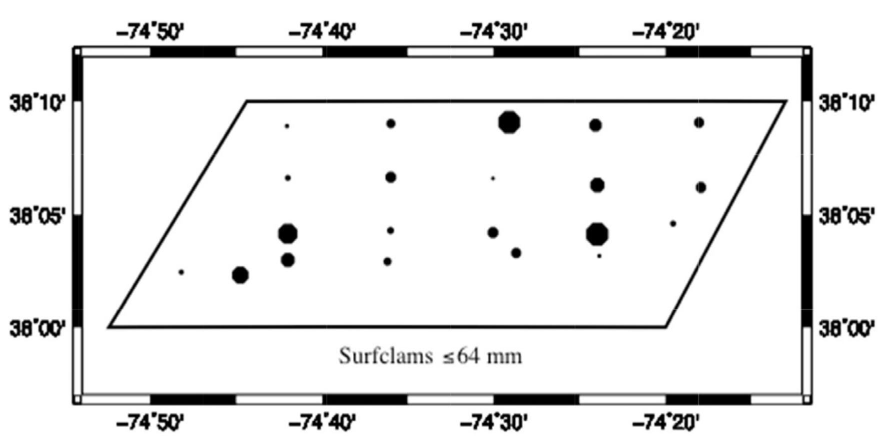

Fig. 2. Catch of clams ≤64 mm standardized to square meters of swept area from 21 sites in the sampled region. Hexagon diameters are proportional to catch and are not comparable between Figs. 2–5.

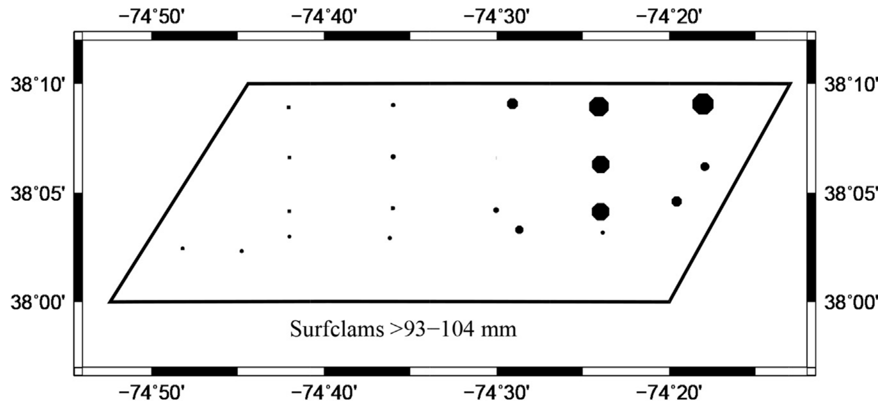

Fig. 3. Catch of clams >93–104 mm standardized to square meters of swept area from 21 sites in the sampled region. Hexagon diameters are proportional to catch and are not comparable between Figs. 2–5.

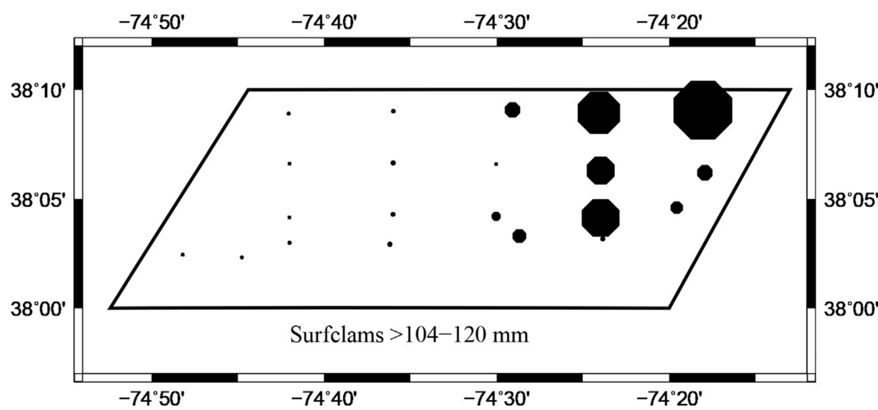

Fig. 4. Catch of clams >104–120 mm standardized to square meters of swept area from 21 sites in the sampled region. Hexagon diameters are proportional to catch and are not comparable between Figs. 2–5.

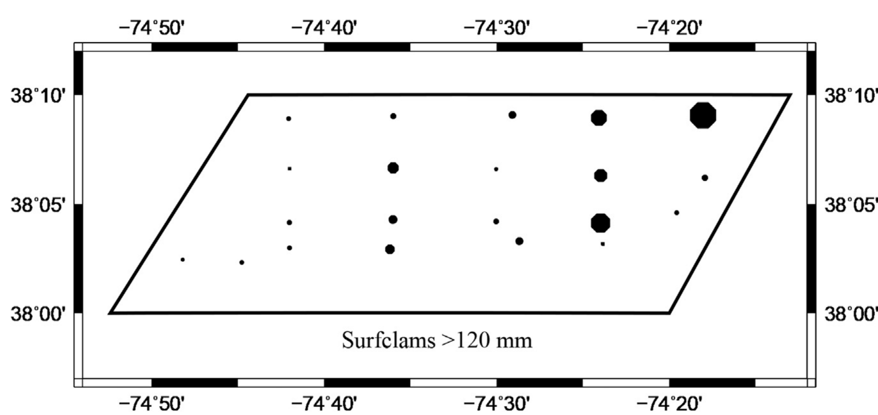

Fig. 5. Catch of clams >120 mm standardized to square meters of swept area from 21 sites in the sampled region. Hexagon diameters are proportional to catch and are not comparable between Figs. 2–5.

3.3. *Variance*

In patchy populations, one anticipates that the variance will follow Taylor's Power Law (Taylor, 1961; Vézina, 1988; Green, 1989), a consequence of which is the tendency for variances to average low when so does the mean. Example plots of simulated variances as a function of sampling density for total surfclams and total oysters are shown in Fig. 14. In both cases, as anticipated, the central tendency of the variance is biased low relative to the population variance at low sample densities. This bias can be attributed to the tendency for the simulated mean to be biased low and, thus, so too must be the variance. Moreover, as the differential bias in the estimated mean disappears with increasing sample density, so too should the differential bias in the variance (Bros and Cowell, 1987). This expected tendency is observed in both datasets.

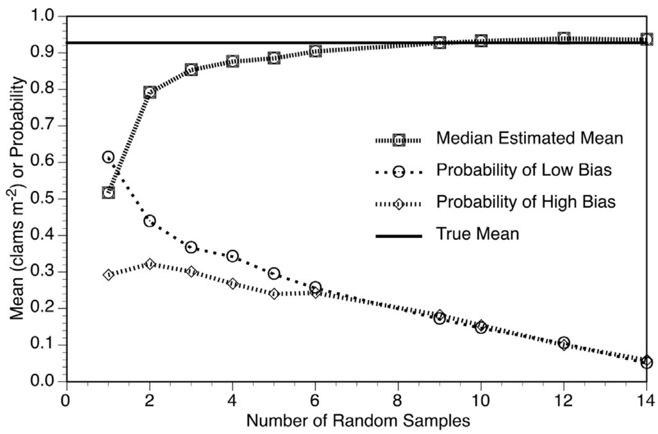

Fig. 6. The true mean ($\bar{x}$) number of surfclams m^{-2} and the median value of the mean based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

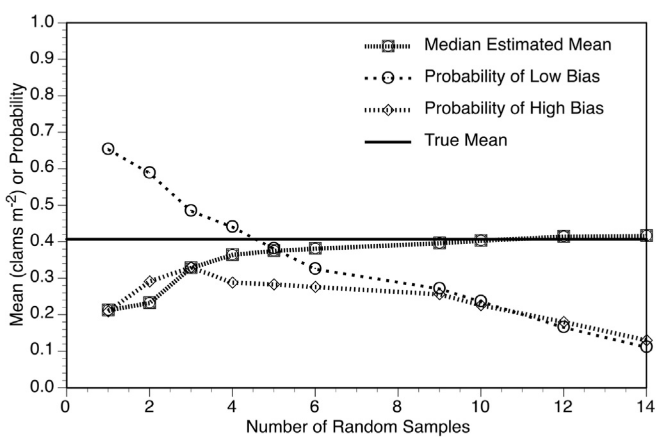

Fig. 7. The true mean ($\bar{x}$) number of surfclams m^{-2} >104 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. This size class encompasses the clams typically marketed or growing into market size within about 1 year (Kuykendall et al., 2017). Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

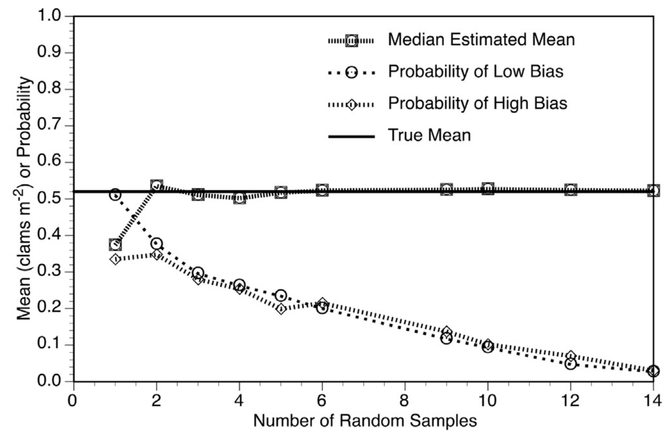

Fig. 8. The true mean ($\bar{x}$) number of surfclams m^{-2} ≤104 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. This size class encompasses the clams that require more than 1 year to grow into market size (Kuykendall et al., 2017). Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

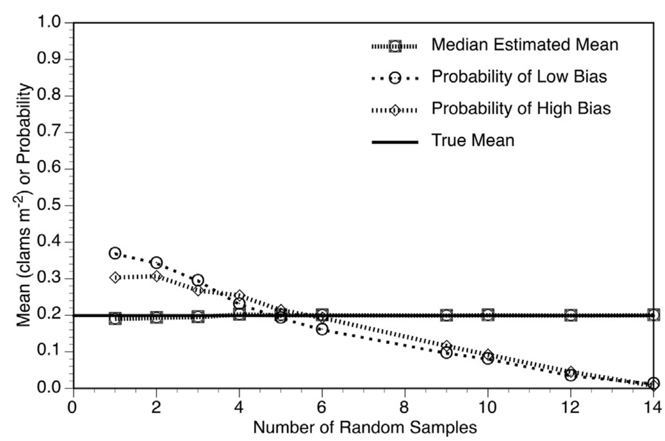

Fig. 9. The true mean ($\bar{x}$) number of surfclams m^{-2} ≤64 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

4. Discussion

The evaluation of sampling design in benthic sampling programs has received considerable attention from a variety of avenues (e.g., Gavaris and Smith, 1987; Bros and Cowell, 1987; van der Meer, 1997; Peterson et al., 2001; Morehead et al., 2008). Patchiness is the bane of all sampling programs. It exists on a range of spatial scales from very small (e.g., Jumars et al., 1977; Findlay, 1982; Powell et al., 1987; Munroe and Noda, 2009) to geographic in scope (Vézina, 1988; Ghertsos et al., 2001; Kristensen et al., 2013) and engenders an extraordinary challenge to survey programs designed to estimate the presence, abundance, and/or biological characteristics of species' populations (Livingston, 1987; Kidwell et al., 2001; McCarthy et al., 2013; Reiss et al., 2015; Powell and Mann, 2016). Today, increased warming of the temperate and boreal continental shelves warrants increased attention to the accuracy of time series of abundance of benthic dominants in order to detect shifts in population characteristics and species range and to track changes in carbonate sequestration rates. Documentation of such range shifts is already well advanced (e.g., Southward et al., 1995; Sagarin et al., 1999; Lucey and Nye, 2010; Powell et al., 2017; Hofmann et al., in press), but an understanding of the temporal dynamics of the continental shelf carbonate budget as the primary carbonate producers shift their range remains in its infancy.

The Atlantic surfclam is a dominant carbonate producer on the northwestern Atlantic continental shelf of the U.S. and is particularly sensitive to climate change. The recession of the southern and inshore boundary of the species and the movement of the leading range edge offshore is well described (Weinberg, 2005; Weinberg et al., 2005; Powell et al., 2017; Hofmann et al., in press) and well documented as an outcome of the influence of increasing bottom water temperatures in the summer and early fall on scope for growth (Kim and Powell, 2004; Narváez et al., 2015). Thus, accurate estimation of abundance and spatial distribution is becoming increasingly important. Powell and Mann (2016) examined the

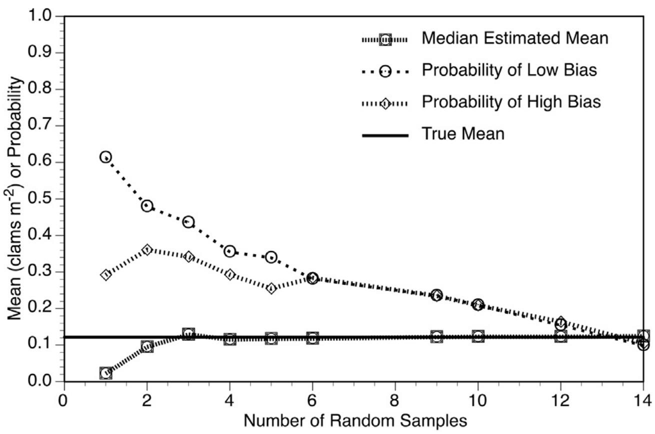

Fig. 10. The true mean ($\bar{x}$) number of surfclams m^{-2} >93–104 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

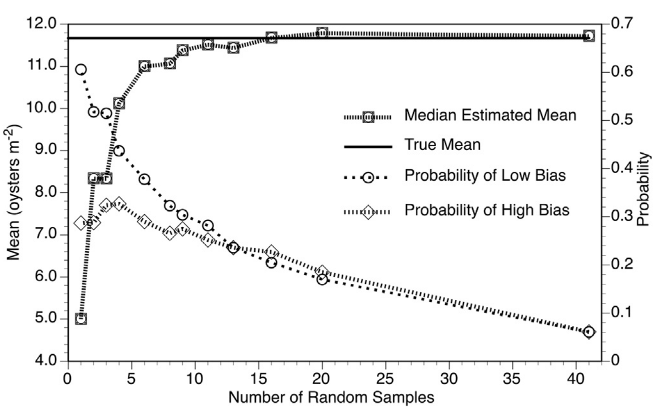

Fig. 11. The true mean ($\bar{x}$) number of oysters m^{-2} <60 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

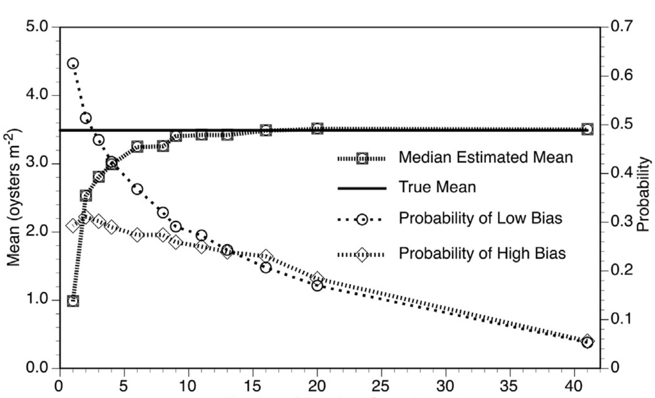

Fig. 12. The true mean ($\bar{x}$) number of oysters m^{-2} 60–75 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

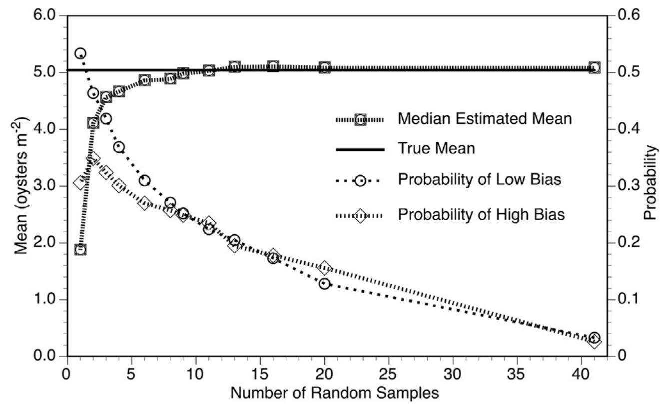

Fig. 13. The true mean ($\bar{x}$) number of oysters m^{-2} >75 mm and the median value of the mean based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated. Bias is defined as a mean value varying by more than 25% from the true mean. Bias probability is calculated as the frequency of a mean value falling below $\bar{x} - .25\bar{x}$ (low) or above $\bar{x} + .25\bar{x}$ (high).

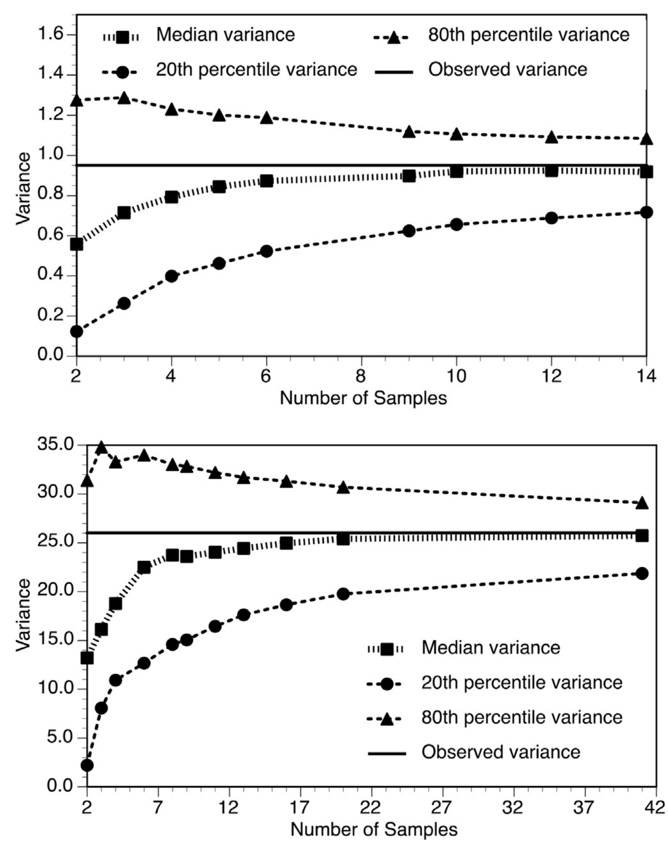

Fig. 14. The true variance (σ^2) in the number of surfclams m^{-2} (above) and oysters m^{-2} (below) and the median, 20th and 80th percentile values of the variance based on 1000 sampling events under a range of sampling intensities. Symbols identify survey sampling densities wherein the y-axis metrics were evaluated.

efficacy of box-core and grab sampling to estimate abundance for a biomass dominant such as the surfclam. Box cores and grabs are the sampling option of choice in many benthic studies. Powell and Mann (2016) concluded that tens of samples would be required in even a small area to have a reasonable probability of accurately estimating abundance. They showed also that the likelihood of a biased-low abundance estimate vastly exceeded the likelihood of one biased high when sample density was inadequate.

The study of Powell and Mann (2016) considered patchiness on a small spatial scale. Their domain was 0.25 km^2, vastly smaller than the 33.5-km^2 region surveyed in this study (Fig. 1), but the sampling device, a 0.25-m^2 box core, sampled 0.001%–0.01% of the domain depending upon simulated sample number. Sampling in this study was carried out by hydraulic dredge. Tow swept area averaged 460 m^2, equivalent to 1840 box cores of a standard 0.25-m^2 size. Thus, small-scale patchiness was integrated perforce by the sample size. The scale of patchiness investigated here is patchiness on the scale of 33.5 km^2. Nevertheless, the sampling protocol sampled about 0.0014% of the area apportioned to each sample, a fraction very similar to that of the study reported by Powell and Mann (2016). Twenty-one samples were taken in the surveyed region. To put this number in context, the U.S. National Marine Fisheries Service (NMFS) surfclam stock survey, which includes the study region, over the period of 1994–2011, took 1–4 samples per survey within the study domain (e.g., NEFSC, 1995, 1998, 2013). The NMFS survey, by comparison to many benthic surveys of the continental shelf (see Powell and Mann, 2016), is a sample dense survey. Thus, our sampling density was 5–20 times that of the density routinely used in surveying the surfclam stock, already a survey of relatively dense design.

We examined the probability of obtaining a reasonable estimate of abundance over a range of sampling intensities. We focused on the entire population, and also on size subsets of the population. A number of general trends were observed. The median of the simulated mean abundances, the central tendency that would be obtained over a large number of surveys of the same area, always underestimated the true abundance at low sample densities. For the larger animals, this underestimate lessened with sampling intensities of four or more; for smaller animals, the underestimate lessened with sampling intensities of two or more. Thus, more samples were required to accurately estimate abundance for the larger size classes. The reason for the difference in required sample number between the smaller and larger size classes is obvious from the figures showing the spatial distribution of individuals (Figs. 2–5). Smaller animals were much more widely dispersed in the domain than were larger animals. Whether this is routinely typical of the surfclam stock is not known, nor is it known whether this is a common phenomenon among bivalve molluscs.

Nevertheless, the number of samples required, on the average, to estimate the true mean was not inordinately large for any size class grouping. More dramatic were the trends in the probability of a biased outcome. Survey availability events, herein defined as surveys that yielded indices unusually high or low relative to the true population abundance, are often encountered in survey time series, though rarely reported outside of assessment documents. We defined a survey availability event as a simulated survey that yielded an abundance less than 75% of the true abundance or greater than 125% of the true abundance. As sample density declined, the probability of a survey index falling outside of this range increased and that increase was disproportionately biased towards underestimates. Generally, for the surfclam domain, 6–10 samples were required to reduce the probability of a survey index falling outside of this range to 40%. Normally, somewhat fewer samples, 4–5, were required to bring the chance of a biased-high and a biased-low survey index into approximate equality. In either case, this sample density approaches or exceeds twice the density needed to obtain an abundance value close to the true mean taking the median estimate of the mean for many separate surveys as the estimator. Trends in the variance follow as anticipated (Bros and Cowell, 1987).

Once again, the sample density required to address bias was higher for the larger animals than for the smaller animals and this differential was considerable. Thus sampling densities typically implemented by the NMFS surfclam stock survey (e.g., NEFSC, 1995, 1998, 2013), for example, should typically underestimate stock size, often appreciably, but also with some probability return a marked overestimate of stock size. Furthermore, if the dispersion between size classes is typical, then any survey satisfactorily estimating abundance of market-size surfclams will also return satisfactory estimates of submarket-size clams. Thus, survey design, in this example, could focus on a single salient size class.

How typical are these trends? The trends observed for surfclams were compared with a dense sample dataset obtained for oysters. Both species are very patchy within habitat. The oyster survey was carried out by a standard industry oyster dredge of known performance (Powell and Ashton-Alcox, 2004; Powell et al., 2007). Each set of 3 tows covered an average of 362 m^2, about 0.0041% of the surveyed 0.2′ latitude x 0.2′ longitude grid, about 4 times that of the surfclam survey analyzed herein, but still a very low percentage. Interestingly, in gross aspect, the trends in the two datasets were identical. Low sample densities consistently provided a median estimate of the survey mean abundance that underestimated the true mean. Slightly more samples were required for this median mean to approach the true mean in the oyster case in comparison to the surfclam case, typically about 6, but still a small number. As with surfclams, however, low sample densities consistently underestimated the true mean. Furthermore, as with surfclams, distinctly more samples were required to reduce the bias rate below 40%, in the range of 12–20 in this case, and at lower sample densities, the probability of a biased-low survey mean substantially outweighed the probability of a biased-high survey mean. In fact, the only noticeable difference in outcome for the oyster dataset, relative to the surfclam case, was that larger animals in the oyster case were more easily surveyed accurately than the smaller animals, the diametric opposite of the trend noted for surfclams.

For both datasets, the size of each sample represented a small fraction of the region represented by each sample ($\leq$0.004%). The results clearly show that variations in the degree of patchiness, within the constraints of the sample size relative to the domain sampled, vary significantly the outcome. Thus, two species occupying distinctly different habitats and demonstrating distinctly different lifestyles nonetheless demonstrated the same challenges to survey design given a similar sample size to domain size relationship and the same trends with sampling intensity in almost every metric of comparison. This is likely a general phenomenon (Bros and Cowell, 1987). We note, for example, that King and Powell (2007) arrived at many of the same conclusions in an analysis of the effect of patchiness on trawl catch in a finfish transect survey. In particular, King and Powell (2007) identified a strong tendency for a number of species to frequently show biased-high and biased-low survey indices with about the same probability, whereas others more often yielded an estimated abundance biased low in comparison to one biased high. King and Powell (2007) found no case where biased-high results occurred distinctly more frequently than those biased low. These trends are similar to the trends observed in this study for surfclams and for oysters, even though both datasets came from two-dimensional sampling arrays rather than the transect-based survey design of King and Powell (2007). The tendency for low sample density to produce biased-low estimates is, of course, well documented in the estimation of species richness (e.g., Staff and Powell, 1988; Walther et al., 1995; Cao et al., 2001) and in other sampling design analyses (Lewis and Stoner, 1983; Bros and Cowell, 1987; Battista, 2003). King and Powell (2007) suggested that not only the size and number of patches, but also the rarely considered aspect of patch shape, contributed to the degree to which a given sampling density yielded biased results with a certain probability. Powell and Mann (2016) show additional examples relevant to sampling the continental shelf benthos where biased-high results occur with some probability, but here too, the frequency of biased-low events consistently far surpassed the frequency of biased-high events.

Review of these trends suggests that the influence of sampling density on survey designs comes with a series of incremental challenges. At woefully inadequate sampling intensity, the probability of a biased-low survey index will substantially exceed the probability of a biased-high index. Under this circumstance, over a period of surveys, the time series will return a long-term estimate of stock dynamics that underestimates true stock abundance. If sampling intensity is increased, this bias favoring biased-low indices disappears and the frequency of bias becomes balanced between high and low. This outcome is anticipated from the central limit theorem. At this point, incrementing sample number steadily reduces the likelihood of a biased survey; however, the number of samples necessary to drive the frequency of survey availability events to a preferred level of infrequency may be high. Additionally, a high probability of survey availability events, whether biased by an increased likelihood of an underestimate or not, will introduce noise in the survey time series which may obfuscate the identification of true trends and particularly, if biased-low estimates are more likely, limit the identification of declining trends. As a consequence, understanding the probability of bias is likely to be as important as adequately minimizing it may be financially or logistically intractable. Moreover, clearly certain size classes will be disproportionately susceptible to such events and this may in some cases influence the estimate of, for example, the spawning stock as in surfclams, whereas in other cases such as the case of the Cohansey Reef oyster, the smaller size class or the recruitment index may be disproportionately affected.

The impact of climate change on the benthos of the continental shelf is likely to be profound. For a few species, this influence is becoming well documented. The carbonate content of surficial sediments is critical for the continuance of robust populations of carbonate producers, in the form of habitat creation (e.g., Kidwell, 1986; Zuschin and Pervesler, 1996; Coco et al., 2006), refuge for juveniles from predation (e.g., Gutiérrez et al., 2003; Kraeuter et al., 2003; Guay and Himmelman, 2004), and buffering of sedimentary acid for newly-settled spat (e.g., Green et al., 1998, 2004). The required continual production of carbonate may inhibit or enhance range-shift dynamics depending upon the carbonate content at the leading edge of the range and the influence of climate change on the extant producers. Tracking these events, anticipated to be of increasing consequence, requires that survey trends not be obfuscated by sampling insufficiency or compromised by the increased uncertainty produced by year-to-year variation in survey bias. This study and previous ones suggest that this challenge is severe and that a critical component of meeting this challenge is an improved understanding of the relationship of patchiness in the living community to the accuracy of the assessment of population and community metrics using survey sampling designs almost certainly biased in their estimations.

The carbonate budgets for marine ecosystems are receiving increasing attention (e.g., Sanders, 2003; Ridgwell and Zeebe, 2005; Wright and Burgess, 2005; Lebrato et al., 2010; Liu et al., 2010). Although carbonate production rates are estimated for a number of estuarine and nearshore communities (e.g., Moore, 1972; Beukema, 1980; James and Bone, 2011; Powell et al., 2012), little information is available for continental shelves. Although the population energetics of major carbonate producers likely can be modeled with some accuracy (e.g., Savina and Ménesguen, 2008; Freitas et al., 2009; Begum et al., 2010; Munroe et al., 2013), standing stock, recruitment, and mortality estimates are critical. The suggestion from this study is that, today, abundance estimates of the dominant carbonate producers of the continental shelves are substantively underestimated and as a consequence efforts to estimate carbonate budgets for these regions remain foredoomed.

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