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How well do we know the infaunal biomass of the continental shelf?

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Keywords: continental shelf, benthos, biomass, sampling design, sampling density, patchiness, bivalve

Highlights:

1. A numerical model simulated survey gear types and sampling densities.
2. Boxcore and grab samplers were simulated with the Atlantic surfclam as target.
3. Typical survey sampling designs produced highly inaccurate clam densities.
4. Increased clam patchiness produced surveys with large density estimation errors.
5. Biomass of large benthos may be routinely underestimated on the continental shelf.

Abstract

Benthic infauna comprise a wide range of taxa of varying abundances and sizes, but large infaunal taxa are infrequently recorded in community surveys of the shelf benthos. These larger, but numerically rare, species may contribute disproportionately to biomass, however. We examine the degree to which standard benthic sampling gear and survey design provide an adequate estimate of the biomass of large infauna using the Atlantic surfclam, *Spisula solidissima*, on the continental shelf off the northeastern coast of the United States as a test organism. We develop a numerical model that simulates standard survey designs, gear types, and sampling densities to evaluate the effectiveness of vertically-dropped sampling gear (e.g., boxcores, grabs) for estimating density of large species. Simulations of randomly distributed clams at a density of 0.5-1 m⁻² within an 0.25-km² domain show that lower sampling densities

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4 (1-5 samples per sampling event) resulted in highly inaccurate estimates of clam density with the
5 presence of clams detected in less than 25% of the sampling events. In all cases in which
6 patchiness was present in the simulated clam population, surveys were prone to very large errors
7 (survey availability events) unless a dense (e.g., 100-sample) sampling protocol was imposed.
8 Thus, commercial quantities of surfclams could easily go completely undetected by any standard
9 benthic community survey protocol using vertically-dropped gear. Without recourse to modern
10 high-volume sampling gear capable of sampling many meters at a swath, such as hydraulic
11 dredges, biomass of the continental shelf will be grievously underestimated if large infauna are
12 present even at moderate densities.
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21 **Introduction**

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23 Benthic infauna comprise a wide range of taxa of varying abundances and sizes. The
24 literature records a rich and diverse record of benthic surveys in which abundance and biomass
25 are reported, only a few of which will be referenced herein. Generally speaking, large animals
26 contribute substantially more to community biomass than to community abundance (e.g., Staff et
27 al., 1985). This trend suggests that estimates of benthic biomass should be designed to
28 adequately sample the larger, but numerically rarer, infauna. We ask these questions here. How
29 well do we achieve that goal? Do we really know the biomass of infauna on the continental
30 shelf? We examine this question by using the Atlantic surfclam, *Spisula solidissima*, on the
31 continental shelf off the northeastern coast of the United States as a test organism. This clam
32 supports a major commercial fishery in this region (Weinberg, 1999, 2005). The density of these
33 clams is well described based on stock surveys using hydraulic dredges with known and high
34 efficiency of capture (Weinberg et al., 2005; Hennen et al., 2012). Dredge tows reported in
35 Weinberg et al. (2005) typically sampled 1,375 m². High density populations typically exist at
36 densities of 0.5 to 2 m⁻². Taking an 140-mm surfclam as a typical individual, this density
37 contributes 14 to 56 g m⁻² (Marzec et al., 2010) to benthic biomass, a biomass that is
38 representative of typical samples obtained in many benthic surveys (e.g., Josefson and Hansen,
39 2004; Dubois et al., 2009; Bolam et al., 2010; Schonberg et al., 2014). Thus, successful sampling
40 of these large clams, were they to be present in these densities, would constitute an important
41 component of macroinfaunal biomass.
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Methods

To examine the potential for sampling and adequately quantitating clam density and hence biomass using gear and sampling densities typically employed in benthic survey designs, we developed a numerical model that simulates standard survey designs, gear types, and sampling densities. The model evaluates the effectiveness of vertically-dropped sampling gear (e.g., boxcores, grabs) for estimating density of large species such as surfclams. The model establishes a two-dimensional grid in which particles (clams) are dispersed either randomly or patchily. In the case of patches, the patches are distributed randomly, and the clams are distributed in a biased random fashion so that clams are more likely to be within a given distance from another clam than otherwise. The basic unit of the domain is cm. Simulations for this study were conducted using a domain of 500x500 m. For the purposes of this exercise, clams were sampled using either a 25x25-cm or 50x50-cm sampling device, representing typical boxcore or grab sampling gear.

Simulated sampling locations within the domain are chosen randomly using Knuth's Ran1 random number generator (Press et al., 1986). Initial trials showed that small-scale autocorrelation (2-4 numbers in a row) occurred often enough to generate biased results in some cases. Thus all random numbers were re-randomized using an independent set of random numbers. We assume that surfclams expose an 8x8-cm surface to the sampling gear; that is, clams are oriented vertically in the anterior-posterior dimension, so that the exposure is expressed by the width and height of the clam rather than the length. Chosen sampling locations defined the northwest corner of the sample. By convention, any clam falling >50% within the sampled area was considered sampled. For each simulation, the domain was seeded with enough clams to provide an average density of 0.5, 1, or 2 clams m⁻², representative of typical and high densities for surfclams in the Mid-Atlantic Bight (NEFSC, 2010).

All simulated sampling was conducted using a random sampling protocol. We recognize that many biological surveys use fixed station designs (e.g., van der Meer, 1997; Petitgas and Lafont, 1997; Morehead et al., 2008) and are often transect based (e.g., Young and Rhoads, 1971; Flint and Holland, 1980; Dauer et al., 1984). King and Powell (2007) show that the uncertainties posed by insufficient sampling density, as discussed herein, plague sampling designs of the transect kind as they do random sampling designs.

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4 For patchy distributions, patchiness was defined in terms of the maximum distance
5 permitted between one clam and a second. The domain was seeded with a given number of clams
6 that defined the initial set of patches. Further clams were placed into patches if distance
7 requirements were met by means of the drawing of a limited number of random numbers. If
8 distance requirements were not met in the allotted number of draws, a new patch was initiated at
9 a random location. This permitted expansion of the number of patches, while also permitting
10 enlargement of and increased density in established patches. Patchiness was determined by
11 estimating the variance-to-mean ratio of the number of clams in a complete series of non-
12 overlapping, but contiguous, samples of “sample-size” dimension (e.g., 50 x 50 cm) covering the
13 entire domain (Taylor, 1961; Elliott, 1977). The two example scales of patchiness used in this
14 study are shown in Figures 1 and 2. Variance-to-mean ratios for simulations using these cases
15 were about 1.6 and 2.5, respectively, based on contiguous sampling of the entire domain with a
16 25x25-cm sampling gear (n=4,000,000). Clam densities inside patches reached about 80 clams
17 m⁻² within a domain where average clam density was 1 clam m⁻². Patches this dense have been
18 observed during surveys (Mann, unpubl. data).
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32 Edge effects were minimized by using a domain at least 1 million times larger than the
33 sample volume. Choice of the northwest corner of the sampling gear to establish the location of
34 sampling assured that samples would not overlap the northern and western domain boundary,
35 limiting edge effects to the southern and eastern boundary. On occasion some fraction of a
36 sample would lie beyond one of these latter boundaries. Examination of the difference between
37 simulations excluding or including such samples revealed few and always minor differences,
38 confirming that edge effects were inconsequential with the domain size employed. Similarly,
39 simulation results varied little with variation in the seed number for the random number
40 generator. Thus, only single results for each spatial distribution and sampling intensity are
41 presented.
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51 Each simulation included 1,000 trials. Clam density was calculated from the samples
52 obtained by each of these trials and the trials ranked by the density estimated. Simulation results
53 are presented as the clam density obtained for a series of percentile ranks obtained from the
54 1,000 trials. Thus, the 90th percentile value represents the density obtained in the trial ranked as
55 the 900th by clam density.
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Results

Sampling of randomly-occurring clams present at a density of 1 m^{-2} by either a 50x50-cm or a 25x25-cm boxcore or grab resulted in estimated clam densities near the true density for the interquartile half of all 100-sample sampling events (Figure 3). Not surprisingly, the larger sampling device performed modestly better. Ten samples per sampling event, a 10-fold reduction in sample density, resulted in a poorer performance for the larger gear and a marked deterioration of performance for the smaller gear. Lower sampling densities (1-5 samples per sampling event) resulted in highly inaccurate estimates of clam density with the presence of clams detected in less than 25% of the sampling events (Figure 3).

Moderate patchiness modified this pattern in specifics, but not in general outcome. One-hundred-sample events routinely returned adequate estimates of clam density. Ten-sample events performed poorly and distinctly more poorly in comparison to the case of randomly-distributed clams (Figure 4). Fewer samples per event (1-5) resulted in the failure to sample any clams in most cases. These trends were magnified in the cases where clam patchiness was even more intense (Figure 5). In all cases in which patchiness was present, surveys were prone to very large errors (survey availability events) without imposition of a dense (100-sample) sampling protocol. Generally, clam estimates biased high occurred more often for non-zero estimates, but estimates of zero were more commonplace. That is, sampling events were more likely to fail to observe clams at all, than obtain a biased estimate, whether high or low.

Results were modestly improved if clam density was doubled to 2 m^{-2} (Figure 6). Nonetheless, sampling intensities of 1 or 2 samples per 0.25 km^2 rarely revealed the presence of these clams at all and almost never estimated clam density accurately. For patchy distributions, even an intensity of 5 samples per 0.25 km^2 was gravely inadequate. Only the most intense sampling event provided adequate density estimates if clam density were only 0.5 m^{-2} (Figure 7). For these large bivalves, this density remains well within the densities supporting commercial fishing (e.g., surfclams – NEFSC, 2010). Lower, yet still high, sampling intensities of 1-2 per 0.25 km^2 , failed to reveal this clam in over 90% of such surveys. Thus, commercial quantities of clams could easily go completely undetected by any standard survey protocol using vertically-dropped gear.

Discussion

Representative Benthic Survey Designs

Benthic surveys are carried out for varied purposes using various gear types and sampling densities. Sampling density can be expressed in terms of sample area per available area or the number of samples taken per area. Here, we review a few of these designs purposefully chosen haphazardly from the literature. We compare these sampling densities to the simulation results just summarized which were obtained from simulations in which 4-20 0.0625-m² or 0.25-m² samples were taken per km² of domain, a sampling density ranging from 2.5x10⁻⁷ to 5x10⁻⁶ km² sampled per km² of domain.

Josefson and Hansen (2004) surveyed a series of Danish estuaries and coastal areas using a Haps corer of 0.01 m². Sampling density was about 6.1x10⁻⁸ km² per km², or about 4 samples per km², similar to or lower than our simulated sampling designs. Dubois et al. (2009) sampled sandy shoals on the Louisiana continental shelf in the Gulf of Mexico using 3 replicates of a 900 cm² GOMEX boxcore or a total of 0.27 m² per sample. Stations were distributed in roughly a 50x5 km region, a sampling density of 2.3x10⁻⁸ km² per km², or about 0.08 samples per km², much lower than densities used in our simulations. Bolam et al. (2010) sampled much of the continental shelf of the United Kingdom using an 0.1 m² Day or Van Veen grab. At each site, 3 samples were collected within 50 m, with sites approximately 44.5 km apart, equivalent to about 1.5x10⁻³ samples per km² or a sampling density of about 2x10⁻¹⁰ km² per km². This sampling density is much sparser than used in our simulations. Schonberg et al. (2014) sampled the northeast Chukchi Sea using replicate (0.1 m²) Van Veen grabs. Stations were about 19 km apart, about 2.8x10⁻³ samples per km² or a sampling density of about 6x10⁻¹⁰ km² per km². Aller et al. (2002) sampled the continental shelf off Cape Hatteras, North Carolina using a variety of boxcores yielding 0.0049 m² to 0.016 m² depending on gear details. A number of transects were sampled. On one transect, 4 stations were occupied over a distance of about 2 km, about 2 samples per km² or approximately 2x10⁻⁸ km² per km². Escobar-Briones and Soto (1997) sampled the Texas continental shelf using 2-3 replicate 0.2 m² Smith-McIntyre grabs per station with stations about 0.25 degrees of latitude apart, yielding a sampling frequency of 1.3x10⁻³ per km² or a sampling density of about 6x10⁻¹⁰ km² per km².

The purpose of this summary is to merely point out that typical sampling gear has a

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4 sampling area no higher than our highest gear sample size of 0.25 m² and typical sampling
5 densities are near to much below the lower sampling densities of 1-2 per 0.25 km² used in our
6 simulations which failed to yield a single clam in over 90% of the simulated surveys.
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10 *The Implications of Limited Sampling*

11 The limitations imposed by inadequate sample density, particularly for patchily-
12 distributed species, are well described (e.g., Findlay, 1982; Smith and Gavaris, 1993; Brown,
13 2003). King and Powell (2007) identified variations in the spatial dimension and shape of
14 patches that elicited a significant tendency for predictably biased-low density estimates or that
15 favored a high occurrence rate of biased-low and biased-high density estimates, given inadequate
16 sampling. As sampling densities are rarely very high, these survey availability events are
17 commonplace occurrences for many species. However, the failure to identify species as present
18 or to inordinately downweigh their importance is an outcome much less often identified.
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27 The sampling densities examined in this simulation study are relatively high even at the
28 low sampling densities of 1-5 per sampling event, 4-20 samples per km². This is a sampling
29 intensity of 2.5x10⁻⁷ to 5x10⁻⁶ km² per km². Very rarely are sampling densities above this
30 sampling density employed in benthic surveys, and good estimates required sampling at 1x10⁻⁴
31 km² per km², a sampling density very rarely utilized. Thus, we investigate a series of spatially
32 relatively intense sampling protocols. On the other hand, the gear used, providing samples of
33 0.25 and 0.0625 m², is representative of standard sampling instruments.
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41 Can we expect gear of this kind to provide accurate biomass estimates of large and long-
42 lived infaunal animals on the continental shelf? The answer is simply no! Even under dense
43 sampling protocols, the chance of capture of even a single large bivalve, present at a rather high
44 density of 1 m⁻², is low. Thus, without recourse to modern high-volume sampling gear capable of
45 sampling many meters at a swath, such as hydraulic dredges, infaunal biomass of the continental
46 shelf often will be grievously underestimated if large infauna are present even at moderate
47 densities.
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53 Moreover, the simulations reveal an interesting pattern of low- and high-availability
54 events, that is underestimates and overestimates of biomass, consistent with the results of King
55 and Powell (2007) who found that either species were routinely underestimated or that high- and
56 low-availability events occurred with relatively equivalent probability. No cases were observed
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4 where high-availability events were the commonplace occurrence. In our simulations, low
5 sample density produced low-availability events routinely. Somewhat increased sample density
6 increased the probability of high-availability events, but no simulation produced a bias towards
7 high-availability events. Thus, the mismatch of sample density and patch dynamics will rarely
8 result in the consistent overestimate of biomass, but commonly result in the consistent
9 underestimate of biomass.

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16 Staff et al. (1985) stressed the importance of filter feeders in the benthos of the
17 continental shelf (and elsewhere) when community structure was based on biomass rather than
18 abundance. Bivalves, today's dominant filter feeders and the only filter feeders routinely capable
19 of spatially extensive top-down control of primary production (e.g. Roditi et al., 1996; Jonsson et
20 al., 2005; Powell et al., 2012b), typically are large in comparison to most other benthic denizens.
21 Not surprisingly, bivalve biomass averages high relative to other contributing groups to the
22 benthic community, but production:biomass ratios average low (Cusson and Bourget, 2005)
23 because bivalves tend to be long-lived. In keeping with their tendency towards large size,
24 bivalves also trend towards being numerically relatively rare (Staff et al., 1985). Being
25 dominantly, though not exclusively, infaunal (Nicol, 1968, 1970; Lockwood, 2004), their
26 lifestyle and role in community structure both auger against the routine adequacy of their
27 sampling to sustain accurate estimates of their role in community biomass and energy flow.
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38 What penalties follow?

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40 Large bivalves are bellwethers of environmental change. They record in their growth and
41 population dynamics changes in environmental conditions (Jones et al., 1989; Ivany et al., 2003
42 Butler et al., 2009). A selection of them rank among the oldest of noncolonial animals (e.g.,
43 Peterson, 1983; Powell and Cummins, 1985; Goodwin and Pease, 1989; Philipp and Abele,
44 2009). Being particularly sensitive to environmentally-enforced shifts in range (Roy et al., 2001;
45 Kim and Powell, 2004; Munroe et al., 2013), such bivalves offer an early warning system for
46 ecologically significant reorganizations of continental shelf community structure (e.g., Roy et al.,
47 2001; Dahlgren et al., 2000; Weinberg, 2005). Such range shifts are anticipated to be of
48 particularly large scale towards the poles (Parmesan and Yohe, 2003). The effects of climate
49 change, though becoming predictable in the physical world (e.g., Bojariu and Gimeno 2003;
50 Keenlyside et al., 2008), remain resistant to predictive modeling in the biological world, due to
51 thresholds in physiological and ecological response surfaces (e.g., Cognie et al., 2006;
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4 Beaugrand et al., 2008). Thus, sentinel bivalve species can offer early indications of large-scale
5 changes in community dynamics. They are the “canaries in the coal mine” for benthic ecology.
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9 Large bivalves are also routinely employed as sentinel species for monitoring ecosystem
10 health (e.g., Green et al., 1983; O’Connor, 1996; Rittschof and McClellan-Green, 2005) and we
11 predict that they will be found to contribute disproportionately to the carbonate budget of the
12 continental shelf benthos. They are at the nexus of the feedback between community dynamics
13 and the benthic carbonate budget (e.g., Kidwell, 1986; Tomašových et al., 2006; Powell et al.,
14 2012a). Thus, no carbonate budget for the continental shelf can be accurately formulated without
15 reliable estimates of their biomass and shell production. They may prove also to be early
16 warnings of ocean acidification (e.g., Gazeau et al. 2007; Beniash et al., 2010; Talmage and
17 Gobbler, 2010; Waldbusser et al., 2013). Thus, chronic underestimation of their abundance and
18 biomass not only impairs a basic understanding of shelf community dynamics, but also
19 constrains a significant range of potential ecosystem analyses.
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29 Defeating patchiness through sampling design is an ongoing goal (e.g., Venette et al.,
30 2002; Pennington, 2003; King and Powell, 2007). King and Powell (2007) showed that not only
31 the spatial extent and intensity of patches, but also patch shape, persistently compromise survey
32 estimates. One obvious solution is to increase sample number or the areal coverage of sampling
33 gear. Our simulations suggest that a simple increase in sample number is normally not an option
34 as obtaining an acceptable estimate of density for sparse or patchy fauna would require a factor
35 of 10 or greater increase in sampling intensity. A second obvious solution is to increase the areal
36 coverage per sample by the use of a dredge. Obtaining quantitative estimates of infaunal benthos
37 using dredges has proven to be difficult, however, as most dredges do not sample with 100%
38 efficiency and efficiency tends to vary as the dredge fills (Mituhasi et al., 2005; Hennen et al.,
39 2012).
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49 Can we identify regions where grave underestimates may have occurred and impose
50 adaptive survey methodologies to improve the reliability of biomass estimates? One option is to
51 seek clues from the death assemblage. Both fidelity in species composition and rank-order
52 abundance between the living community and the death assemblage are well documented (Staff
53 et al., 1986; Kidwell, 2002, 2008; Lockwood and Chastant, 2006). Large clams for the most part
54 are well preserved (Callender et al., 1994; Powell et al., 2011). Spatial and temporal averaging in
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4 the death assemblage usefully break down spatial patchiness (Powell et al., 1989; Lyman 2003;
5 Kidwell, 2008; Tomašových and Kidwell, 2010). Thus, reduced sampling intensity is required to
6 identify regions where large bivalves may be, or have been abundant. At the same time, critical
7 information on the carbonate content of the surficial sediments is obtained. Including the death
8 assemblage in an adaptive survey protocol to optimize survey effort for continental shelf biomass
9 dominants should be a considered option.
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17 Cooperative Research Center SCeMFiS (Science Center for Marine Fisheries:
18 <http://www.SCeMFiS.org>).
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4 **Figure 1.** A selected portion of the 0.25-km² domain for the case of a highly patchy population
5 (variance-to-mean ratio = 2.5). Each grid square is 25 x 25 cm, the size of a typical
6 boxcore or grab sample. Axis labels are arbitrary locations in the entire 2,000 x 2,000-
7 grid domain (2,000 grids × 25 cm = 500 m). Gray scale defines clam density. Highest
8 densities reach about 80 clams m⁻²; overall density average is 1 clam m⁻².
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14 **Figure 2.** A selected portion of the 0.25-km² domain for the case of a moderately patchy
15 population (variance-to-mean ratio = 1.6). Each grid square is 25 x 25 cm, the size of a
16 typical boxcore or grab sample. Axis labels are arbitrary locations in the entire 2,000 x
17 2,000-grid domain (2,000 grids × 25 cm = 500 m). Gray scale defines clam density.
18 Highest densities reach about 80 clams m⁻²; overall density average is 1 clam m⁻².
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24 **Figure 3.** Estimated surfclam density for a randomly distributed surfclam population present at 1
25 m⁻² in a 0.25-km² domain sampled by either a 0.125-m² or a 0.25-m² boxcore using
26 five different sampling densities in which 1 to 100 samples were taken within the 0.25-
27 km² domain. The dashed line marks the true clam density in the domain: 1 clam m⁻².
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32 **Figure 4.** Estimated surfclam density for a moderately patchy surfclam population (Figure 2)
33 present at 1 m⁻² in a 0.25-km² domain sampled by either a 0.125-m² or a 0.25-m²
34 boxcore using five different sampling densities in which 1 to 100 samples were taken
35 within the 0.25-km² domain. The dashed line marks the true clam density in the
36 domain: 1 clam m⁻².
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42 **Figure 5.** Estimated surfclam density for a highly patchy surfclam population (Figure 1) present
43 at 1 m⁻² in a 0.25-km² domain sampled by either a 0.125-m² or a 0.25-m² boxcore using
44 five different sampling densities in which 1 to 100 samples were taken within the 0.25-
45 km² domain. The dashed line marks the true clam density in the domain: 1 clam m⁻².
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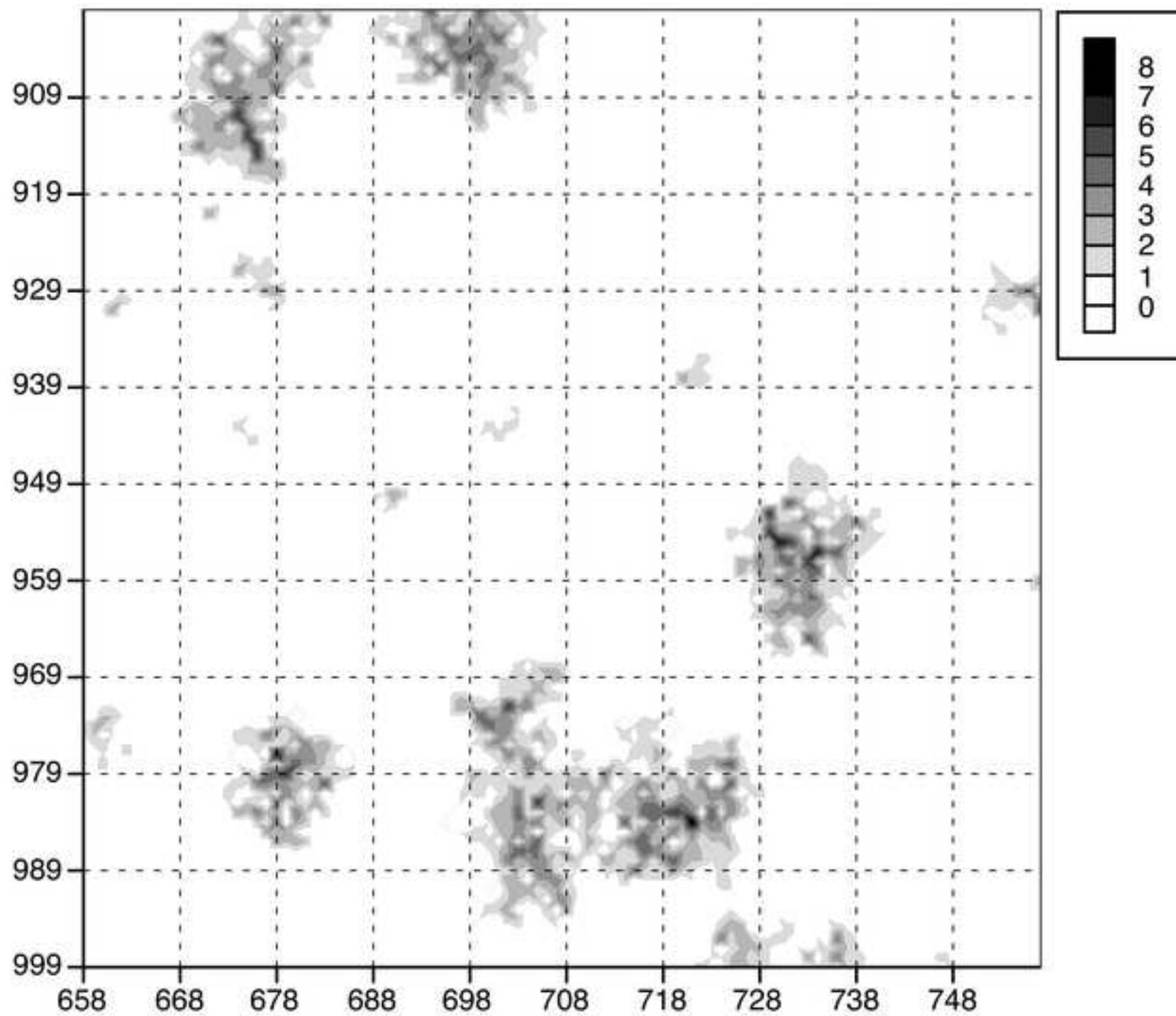
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50 **Figure 6.** Estimated surfclam density for a randomly distributed, moderately patchy, and highly
51 patchy surfclam population present at 2 m⁻² in a 0.25-km² domain sampled by a 0.125-
52 m² boxcore using five different sampling densities in which 1 to 100 samples were
53 taken within the 0.25-km² domain. The dashed line marks the true clam density in the
54 domain: 2 clams m⁻².
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59 **Figure 7.** Estimated surfclam density for a randomly distributed, moderately patchy, and highly
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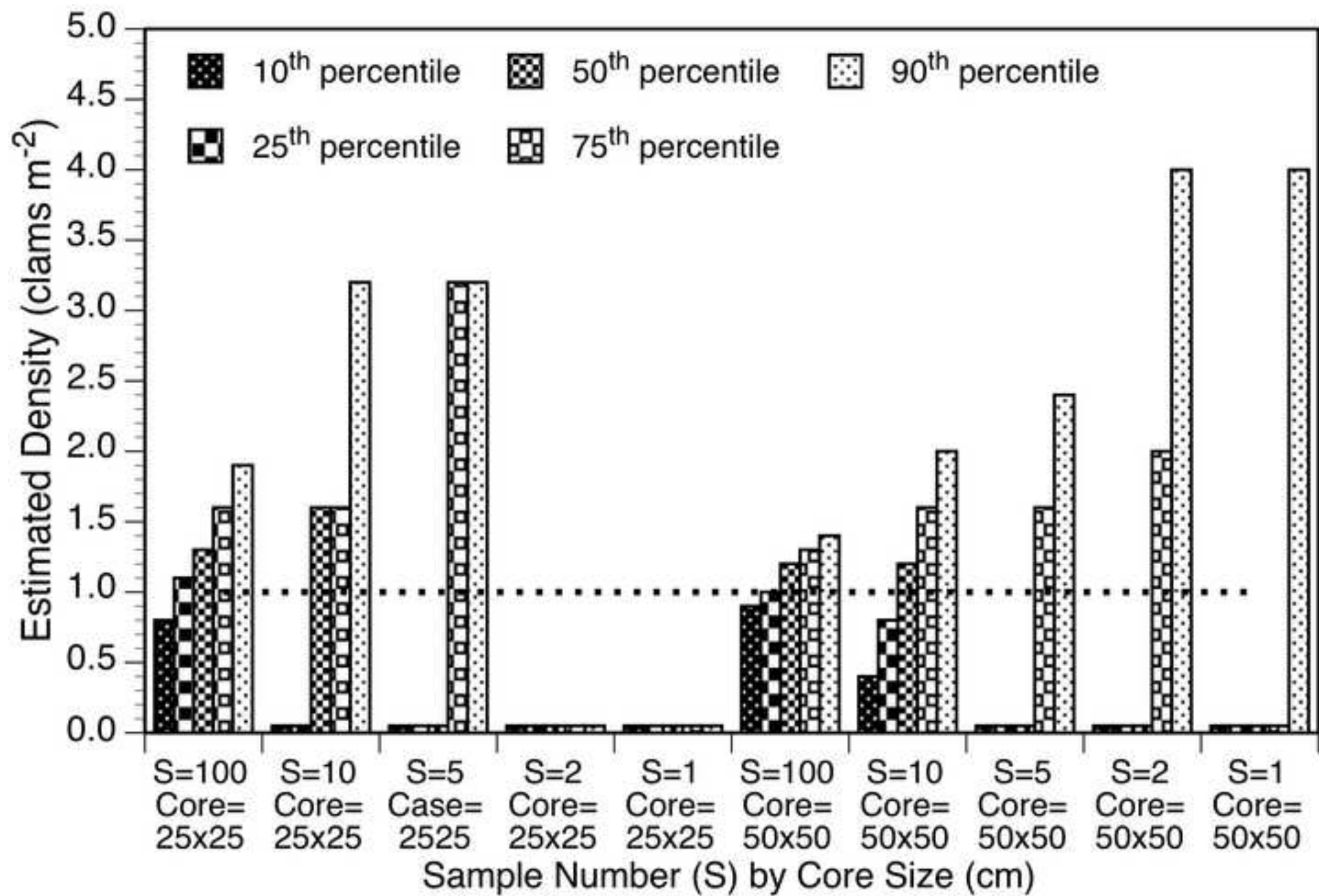
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patchy surfclam population present at 0.5 m^{-2} in a 0.25-km^2 domain sampled by a 0.125-m^2 boxcore using five different sampling densities in which 1 to 100 samples were taken within the 0.25-km^2 domain. The dashed line marks the true clam density in the domain: 0.5 clams m^{-2} .

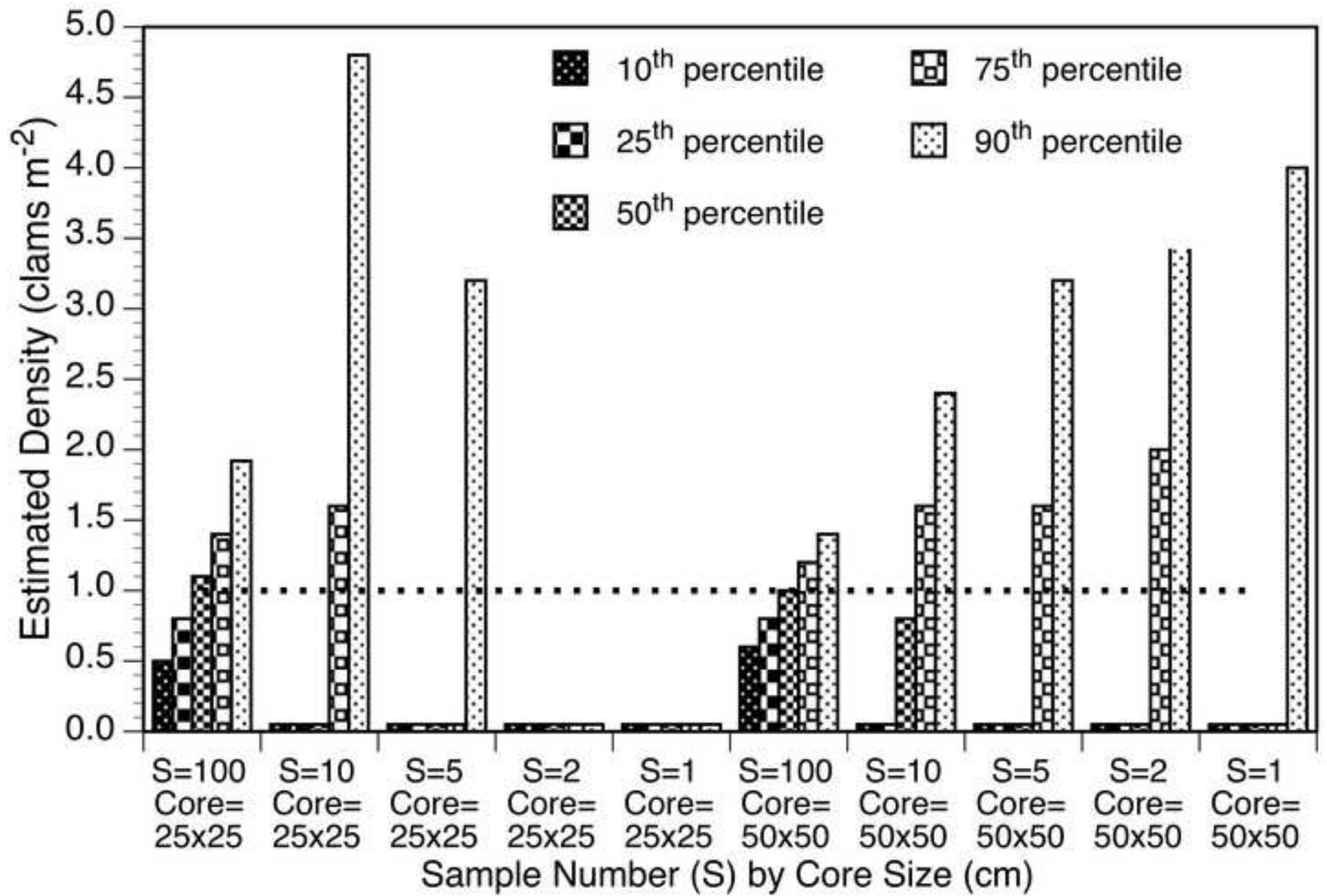
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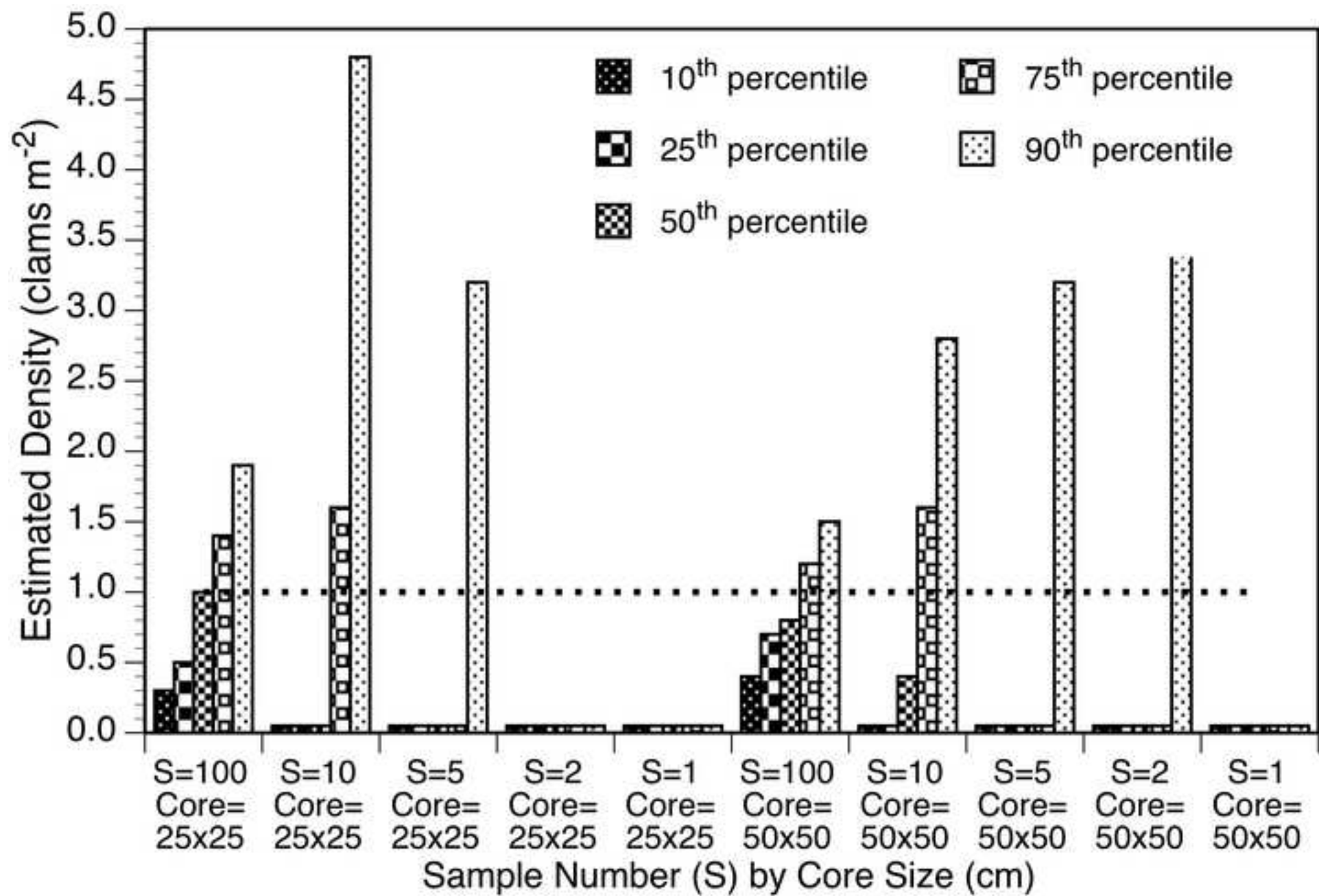
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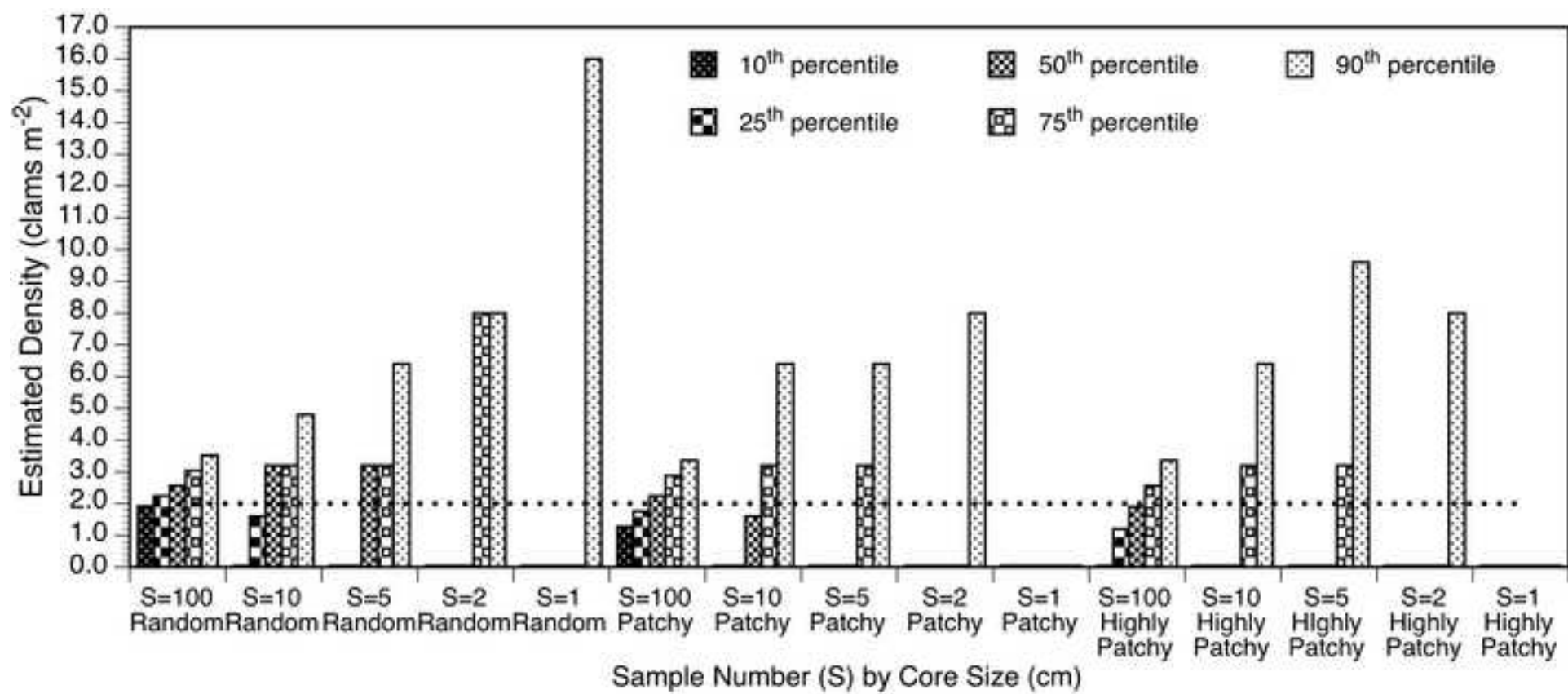
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