INTERTIDAL CLAM DIVERSITY, SIZE, ABUNDANCE AND BIOMASS IN GLACIER BAY NATIONAL PARK & PRESERVE
1999 ANNUAL REPORT

James L. Bodkin
Kimberly A. Kloecker
October 1999
U.S.G.S.
AK Biological Science Center
1011 East Tudor Road
Anchorage, AK 99503

≋USGS
science for a changing world

INTRODUCTION

Nearshore marine communities support a wide array of commercial, recreational and culturally valuable resources including plants, invertebrates, birds, and mammals. In order to understand, quantify and attribute cause to changes in these communities, it is imperative to understand primary sources of community structuring and of natural or background levels of variation in the ecosystem. The sea otter, once nearly extinct, is currently re-occupying previous habitat in much of the north Pacific, including Glacier Bay. The role of sea otters in structuring nearshore marine communities is recognized as significant, particularly among exposed rocky shorelines. Less is known of the effects of sea otter reintroduction into soft sediment habitats, however similar effects are expected (Kvitek et. al. 1992). It is now possible to examine effects of sea otter foraging as they begin to recolonize Glacier Bay National Park and Preserve in southeast Alaska, a predominately soft sediment marine community.

Based on data from other sites that sea otters have re-occupied, it is predicted that profound changes in the abundance, species composition, and size distribution of nearshore benthic invertebrates will occur in Glacier Bay. It is likely that cascading effects will be felt in the vertebrate fauna as well. In May 1999, 384 sea otters were censussed in Glacier Bay, yet otters are still absent from large areas of the Park (Bodkin et al. 1999). This distribution of sea otters allows for a rigorous before/after control/ treatment experimental design that will permit assigning cause to changes observed in coastal communities following reoccupation by sea otters.
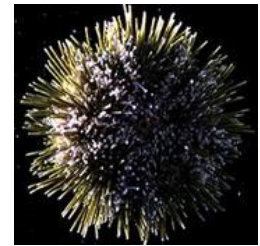
Various kinds of data are necessary to evaluate changes in nearshore marine communities and to allow careful determination of the causal role of sea otters in such changes. Information on the distribution and abundance of sea otters in and around Glacier Bay will provide a description of the spatial and temporal process of sea otter recolonization and provide the basis for study sites to evaluate changes in community structure before and after the effects of sea otters. Study of sea otter food habits will provide a measure of the direct effects of sea otter foraging. Study of sea otter diving behavior will provide a measure of the bathymetric extent of sea otters in structuring communities. Study of prey populations will allow documentation of changes in abundance and size distributions resulting from sea otter foraging and will provide discrimination among other potential factors affecting intertidal clam communities. The purpose of the intertidal clam study is to provide a quantitative description of the macroscopic clam fauna (> 10 mm) employing a sampling design that will allow inference to all of Glacier Bay and allow experimental control to describe causes of change observed over time. In this first of three annual reports we describe intertidal clam species composition, species diversity, size, abundance and biomass resulting from our initial sampling of intertidal soft sediment communities in Glacier Bay.

OBJECTIVES

A sampling program designed to meet the following objectives has been inaugurated in Glacier Bay in areas not occupied and in areas anticipated to be occupied by sea otters in the future:

- identify clam species composition
- characterize their size class distribution
- estimate intertidal clam populations' abundances

METHODS

This study utilized the results of the aerial portion of the Glacier Bay Inventory and Monitoring protocol for site selection (Irvine 1998). In that project the coastline of Glacier Bay was broken into 5,545 200-meter segments. Every twenty-third segment was selected to be surveyed (minus a few that were dropped due to map inaccuracies or ice conditions) yielding slope and percent cover data for substrate and biota from 241 segments. For this project a line was drawn from just north of Geikie Inlet across the Bay to just north of Sandy Cove. The area from the entrance of Glacier Bay to this line constitutes the area where sea otters have colonized or are likely to in the near future. One of the aerial segments within the area was selected randomly as a starting point and every third segment was chosen for intertidal sampling, excluding sites previously utilized as intertidal inventory and monitoring sites. See Figure 1-3. To date 20 of the 28 random sites have been sampled to assess intertidal clam species composition, size distributions, and population abundance. Six additional sites (not necessarily corresponding with aerial segments) were chosen as **p**referred **c**lam **h**abitat (PCH sites) based on the abundance of shell litter scattered in the intertidal area. Two additional sites were sampled in Dundas Bay following the Wilderness Adventurer incident. At each site a 200m transect was positioned horizontally along the 0 MLLW tide level. A random starting point was selected and ten $0.25m^2$ quadrats placed 20 meters apart were excavated to a depth of 25cm. All sediments were sieved through a 10mm mesh screen then all clams (and urchins and crabs for some sites) were identified to the lowest possible taxa, counted, and measured to the nearest millimeter using dial calipers. Sediments and biota were returned following measurements. Biomass was calculated by multiplying the length of the clams by a dry weight conversion factor distinctive for each species. A modification of the Glacier Bay Coast Walker's substrate classification protocol (L. Sharman, W. Eichenlaub, pers. comm.) was used to categorize the primary and secondary substrate of each quadrat. The primary substrate (Table 1) is the type that comprised a majority of the volume of the excavated sediments while a secondary substrate was the next most abundant type based on visual estimates.

Table 1. Substrate descriptions used for sediment classifications.

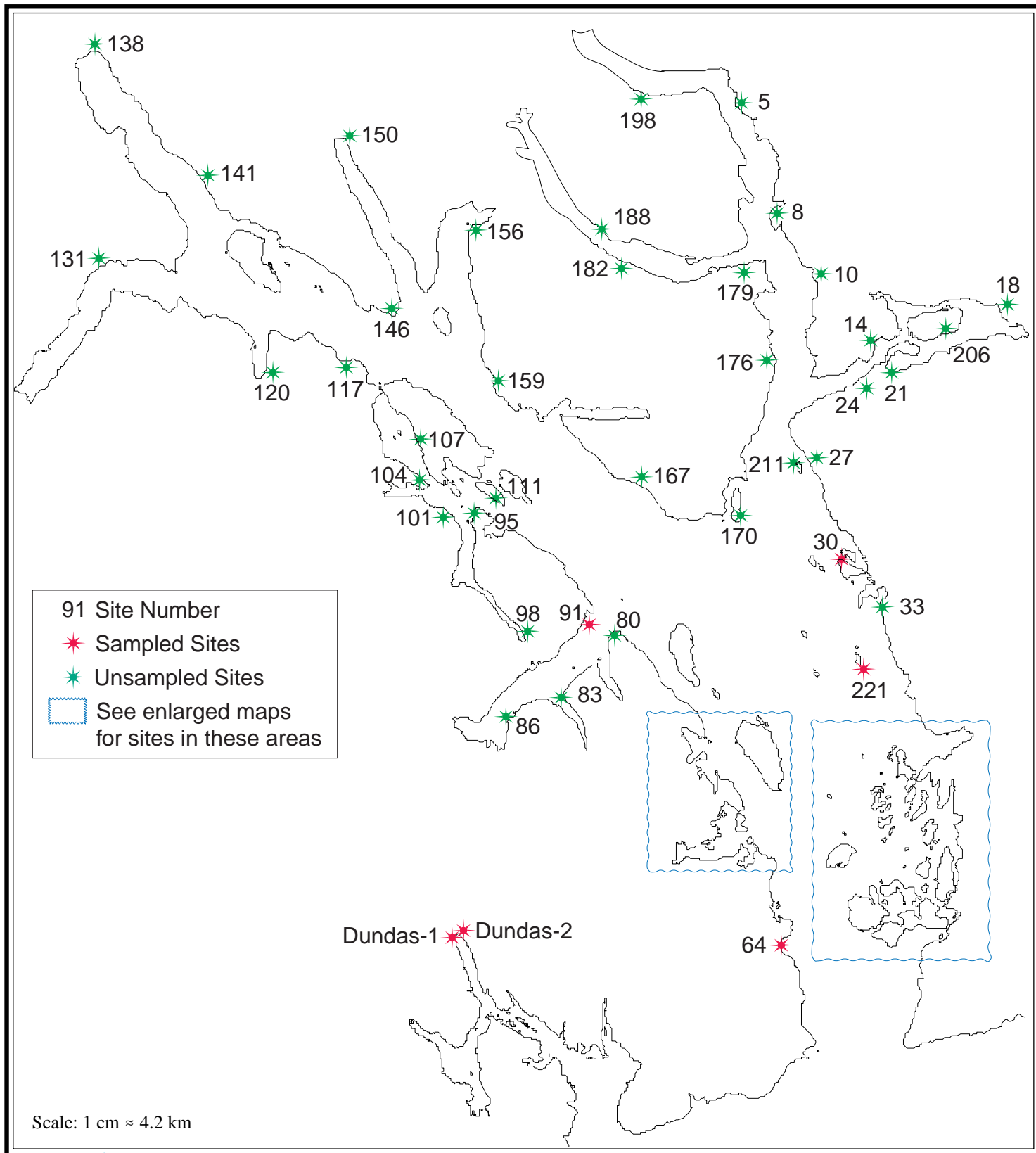| Substrate Type	Description	Diameter
Bedrock	Continuous rock surface	.
Boulder/Cobble	Billiard ball to > head	64 - > 256 mm
Pebble/Gravel	BB to billiard ball	2 - 64 mm
Coarse Sand	Pin head to BB	1 - 2 mm
Fine Sand/Silt/Mud/Clay	Fine, non-gritty to pin head	. - 1 mm
Mixed	Mixture of > 2 types	.

Figure 1. Map of the Glacier Bay National Park coastline showing sampling locations. Red stars mark sites that have been sampled for intertidal clams as of October 1999. Green stars mark sites that have not yet been sampled. The areas outlined in blue are shown in more detail in Fig 2 and 3.
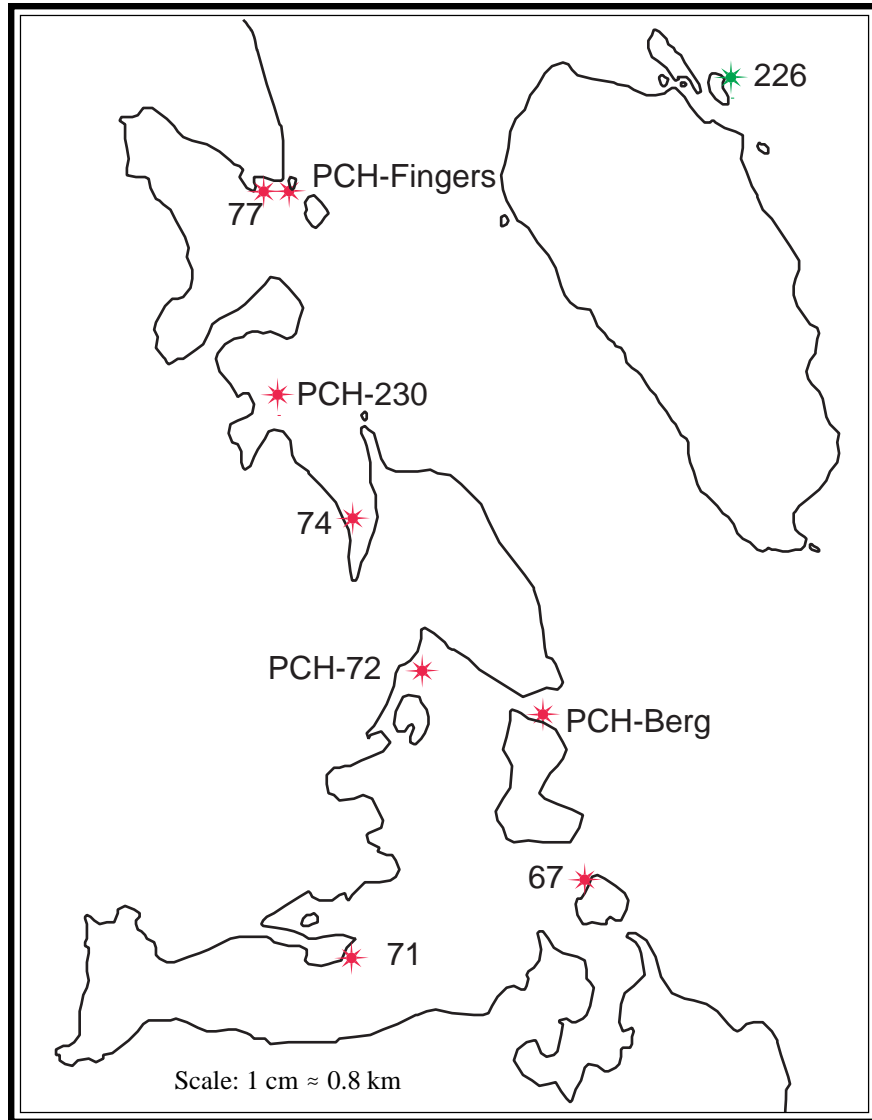
Figure 2. Map of the Fingers Bay and Berg Bay coastline showing sampling locations. Red stars mark sites that have been sampled for intertidal clams as of October 1999. Green stars mark sites that have not yet been sampled. PCH refers to sites with Preferred Clam Habitat. The entire sampling area is shown in Fig 1.
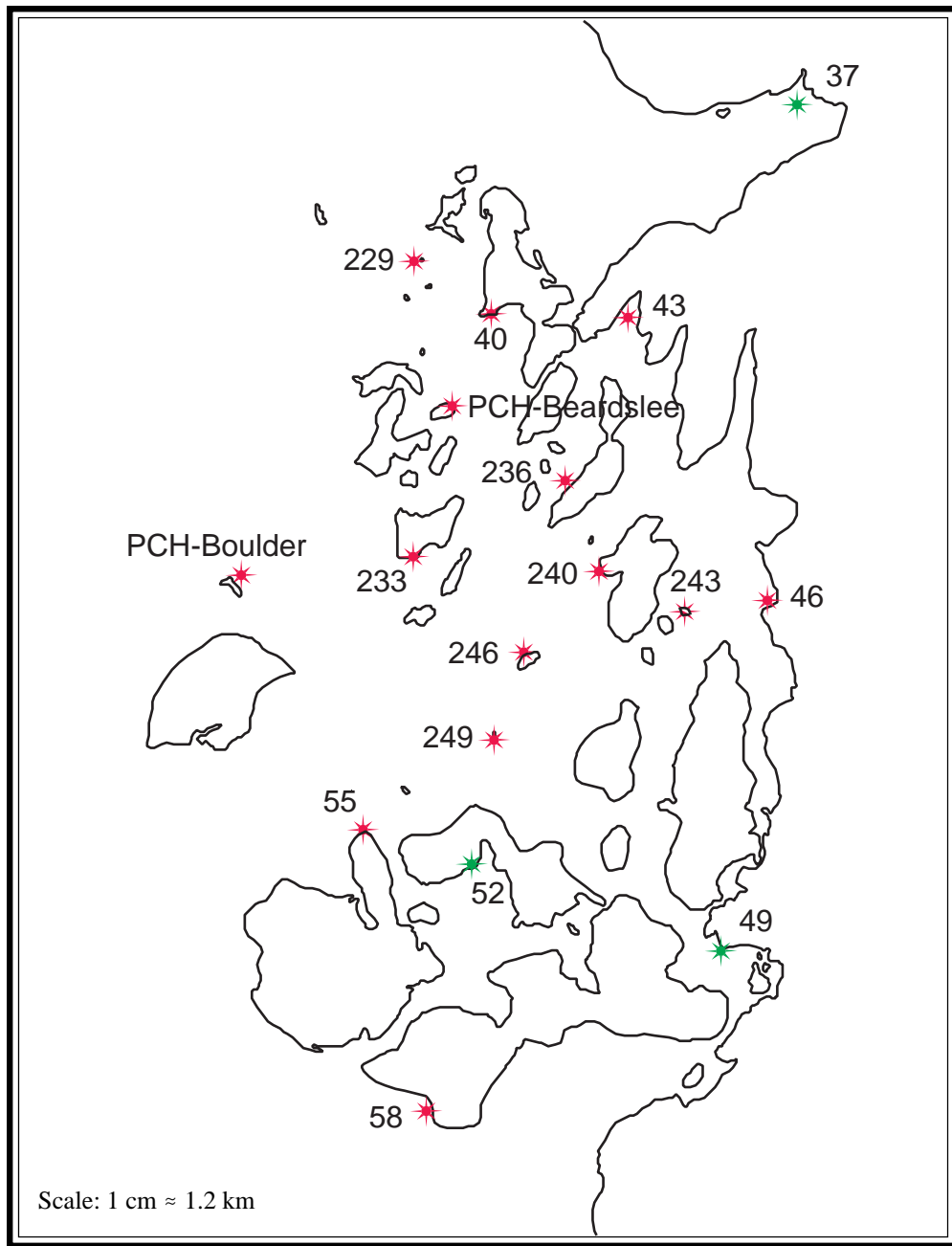
Figure 3. Map of the Beardslee Island coastline showing sampling locations. Red stars mark sites that have been sampled for intertidal clams as of October 1999. Green stars mark sites that have not yet been sampled. PCH refers to sites with Preferred Clam Habitat. The entire sampling area is shown in Fig 1.

CLAM SPECIES

Following is a list and brief description of the clam species found during preliminary 1999 intertidal clam sampling. This is not meant to be a complete list of species occurring in Glacier Bay.

Clinocardium nuttallii: (CLN)
The heart cockle can grow to 140 mm and is found from the intertidal to 30 m in sand-gravel substrates.

Gari californica: (GAC)
The California sunset clam can grow to 149 mm and is found from the intertidal to depths of 170 m in gravel substrates. *Gari* is rare in Glacier Bay, to date we have found only one.

Hiatella arctica: (HIA)
The Arctic hiatella grows to 33 mm and is found from the intertidal to 800 m. This clam attaches itself to the substrate by byssal threads therefore it is usually found in areas with larger sediment types such as pebble, cobble and boulder.

Macoma species: (MAS)
There are many species of *Macoma*, several of which have been identified in Glacier Bay (eg *M. nasuta* and *M. balthica*). *Macoma* is the most abundant intertidal clam in Glacier Bay. Most species are small (<<50 mm) although M. nasuta can grow to 75 mm. Macoma are found from the intertidal to >300 m, usually in sand-mud substrates but also in gravel. Some species are only found subtidally.

Mya species: (MYS)
Both *Mya truncata* and *Mya arenaria* are found in Glacier Bay. These clams grow to 80 and 100 mm, respectively. They are found in the intertidal (*M. Truncata* extends to 100 m) in substrates with sand/ mud.

Protothaca staminea: (PRS)
The littleneck clam grows to 75 mm and is found from the intertidal to 10 m in gravel or sand-mud substrates.

Pseudopythina compressa: (PSC)
The compressed montacutid, 'fuzzy clam', grows to 20 mm and is found from the intertidal to 100m usually in mud.

Saxidomus gigantea: (SAG)
The butter clam grows to 130 mm and is found from the intertidal to 40 m. *Saxidomus* makes up a majority of the intertidal clam biomass in Glacier Bay.

RESULTS

Diversity

The Shannon-Wiener diversity index (H') was calculated for each site. This index accounts for species richness (total number of species present) as well as their relative proportions so rare individuals do not have undue influence on H'. The theoretical maximum for H' is $\log_2$(total # species), in this case H' = 3.17. H' ranged from 0 (i.e. only one species present) to 2.194 (mean ± sd: 1.53 ± 0.6) (Figure 4). There were no apparent relationships, based on visual examination of a plot of H', between diversity and substrate type or location. H' was not different between random and selected sites. See Figure 5 for proportions of clam species per site.

Figure 4. Shannon-Wiener diversity index, H' for the intertidal clam sampling sites. Sites 91 and 233 only had one species, therefore H' is 0. Site 64 had no clams therefore it doesn't have an H'. H' max is the theoretical maximum diversity if a site were to have all 9 clam species in similar proportions. Sites are listed in numerical order along the X-axis, with PCH sites following systematic ones.
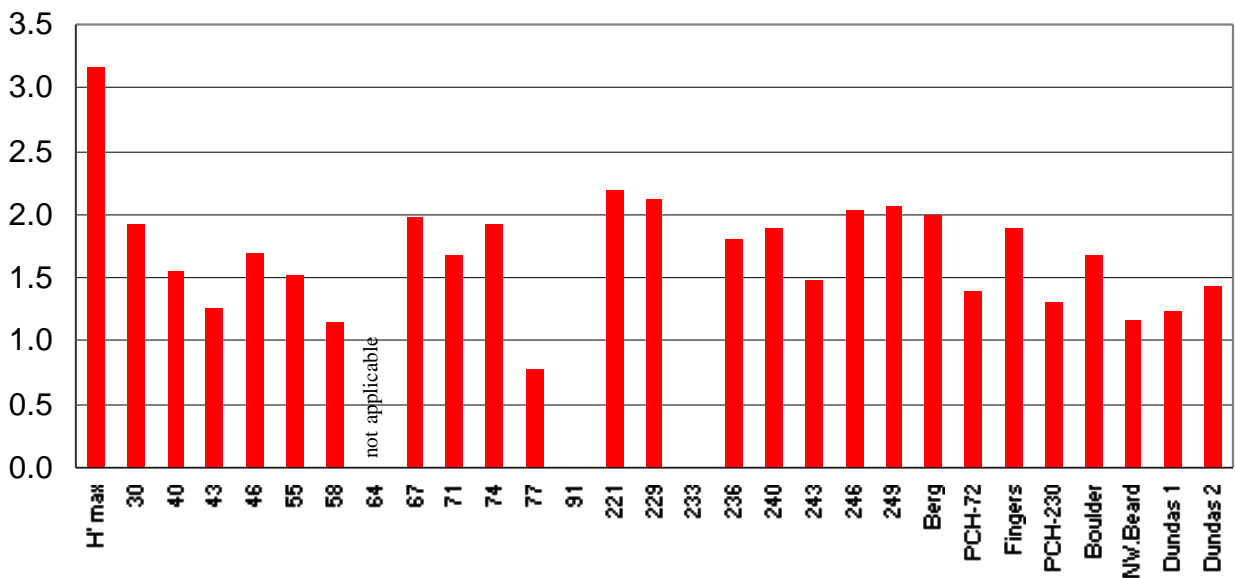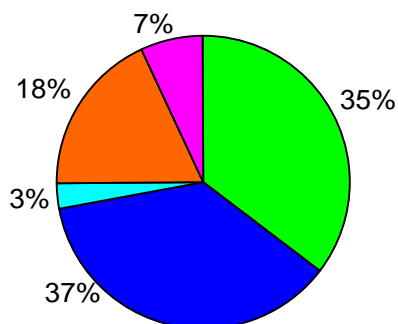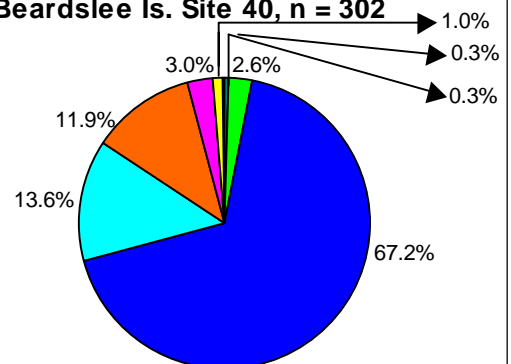

Figure 5. Proportion, by number, of each species of intertidal clam per sampling site. Unless otherwise noted, ten quadrats were sampled at each site. The n-value following each site number is the total number of clams for that site. Other = Unknown clams and *Gari californica,* however for calculating H' *Gari* was in its own category.

Other clam; *Clinocardium nuttali*; *Hiatella arcticus*; *Macoma* species; *Mya* species; *Protothaca staminea*; *Pseudophythina compressa*; *Saxidomus gigantea*.

Sandy Cove Site 30, n = 71

35%
37%
3%
18%
7%

Beardslee Is. Site 40, n = 302

67.2%
13.6%
11.9%
3.0%
2.6%
1.0%
0.3%
0.3%

Beardeslee Is. Site 43, n = 592
1.7% 0.3%
0.3% 0.5%
36.5%
59.1%
1.5%

Beardslee Is. Site 46, n = 202
18.6% 0.5% 18.1%
3.4% 2.5%
56.9%

Young Is. Site 55, n = 1230, 9 quads
8.5% 4.1%
15.5%
5.1%
66.8%

Lester Is. Site 58, n = 134
8.2%
6.7%
8.2%
76.9%

Berg Bay Site 67, n = 410
3.2% 27.1%
23.7%
8.0%
38.0%

Berg Bay Site 71, n = 656
1.4% 0.5% 6.4%
22.1%
11.6%
58.1%

Fingers Bay Site 74, n = 10
20.0% 40.0%
20.0%
20.0%

Fingers Bay Site 77, n = 135
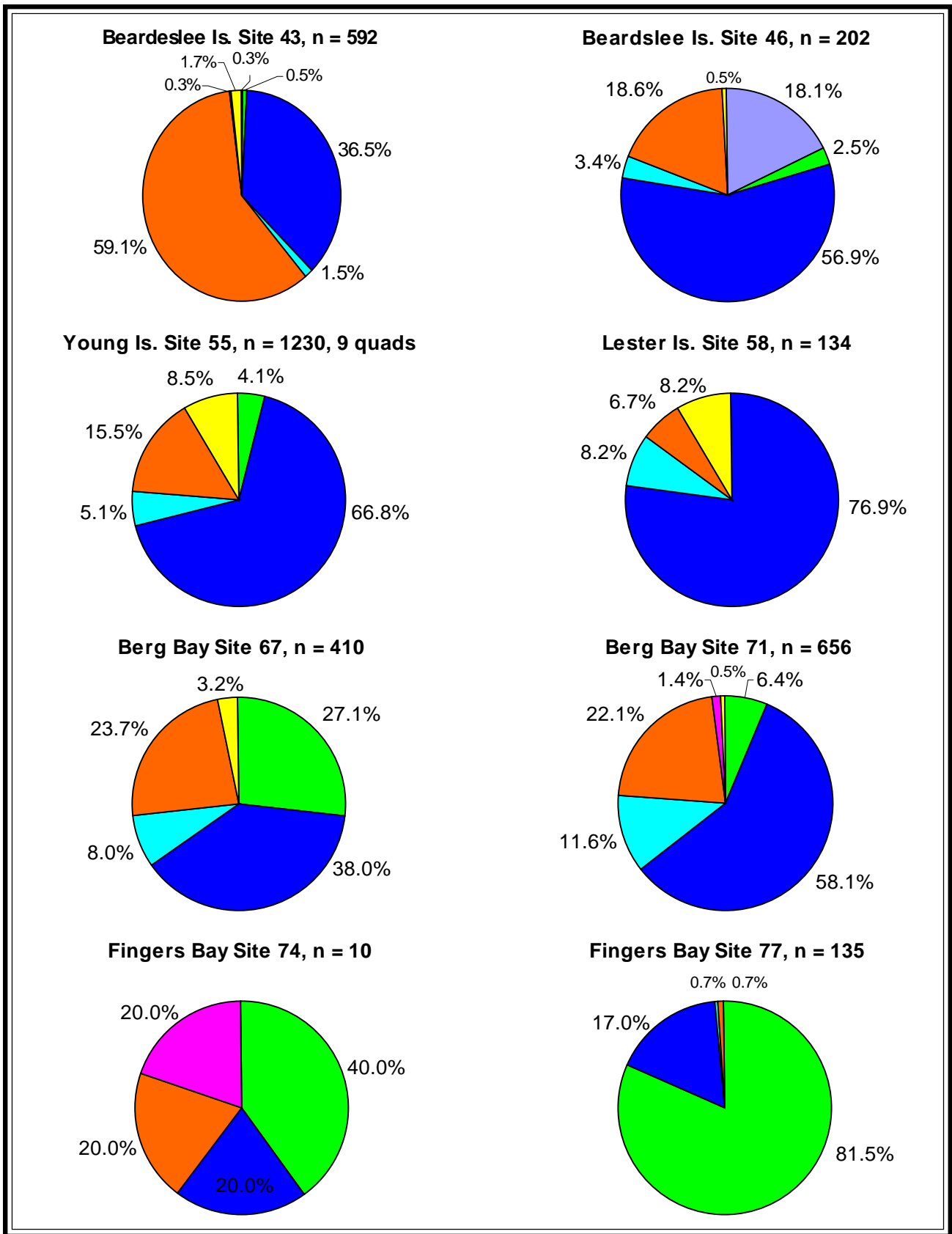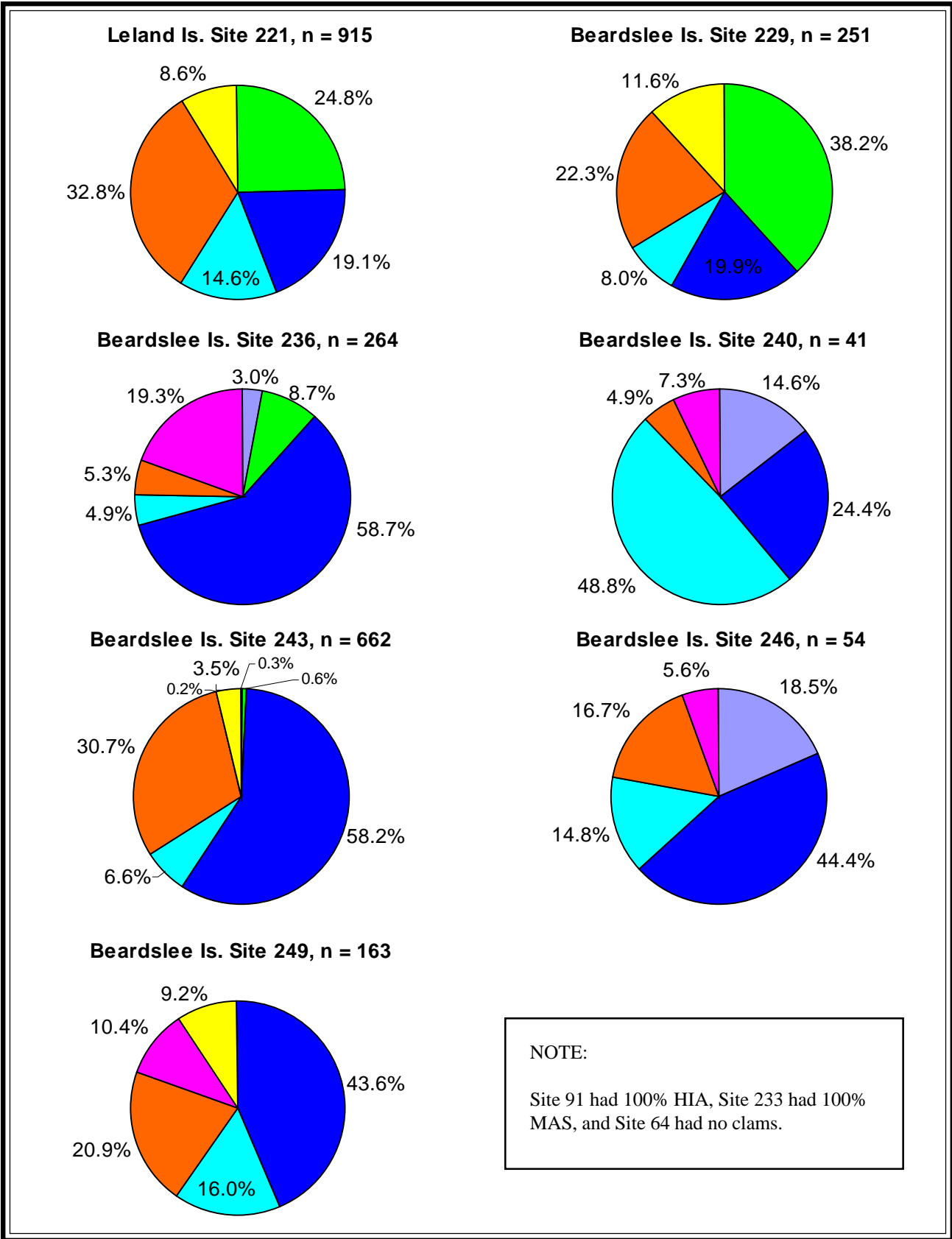0.7% 0.7%
17.0%
81.5%

Figure 5. Proportion, by number, of each species of intertidal clam per sampling site. Unless otherwise noted, ten quadrats were sampled at each site. See previous page for legend.

Leland Is. Site 221, n = 915
8.6% 24.8% 32.8% 19.1% 14.6%

Beardslee Is. Site 229, n = 251
11.6% 38.2% 22.3% 19.9% 8.0%

Beardslee Is. Site 236, n = 264
3.0% 8.7% 19.3% 5.3% 4.9% 58.7%

Beardslee Is. Site 240, n = 41
7.3% 14.6% 4.9% 24.4% 48.8%

Beardslee Is. Site 243, n = 662
3.5% 0.3% 0.6% 0.2% 30.7% 6.6% 58.2%

Beardslee Is. Site 246, n = 54
5.6% 18.5% 16.7% 44.4% 14.8%

Beardslee Is. Site 249, n = 163
9.2% 10.4% 43.6% 20.9% 16.0%

NOTE:

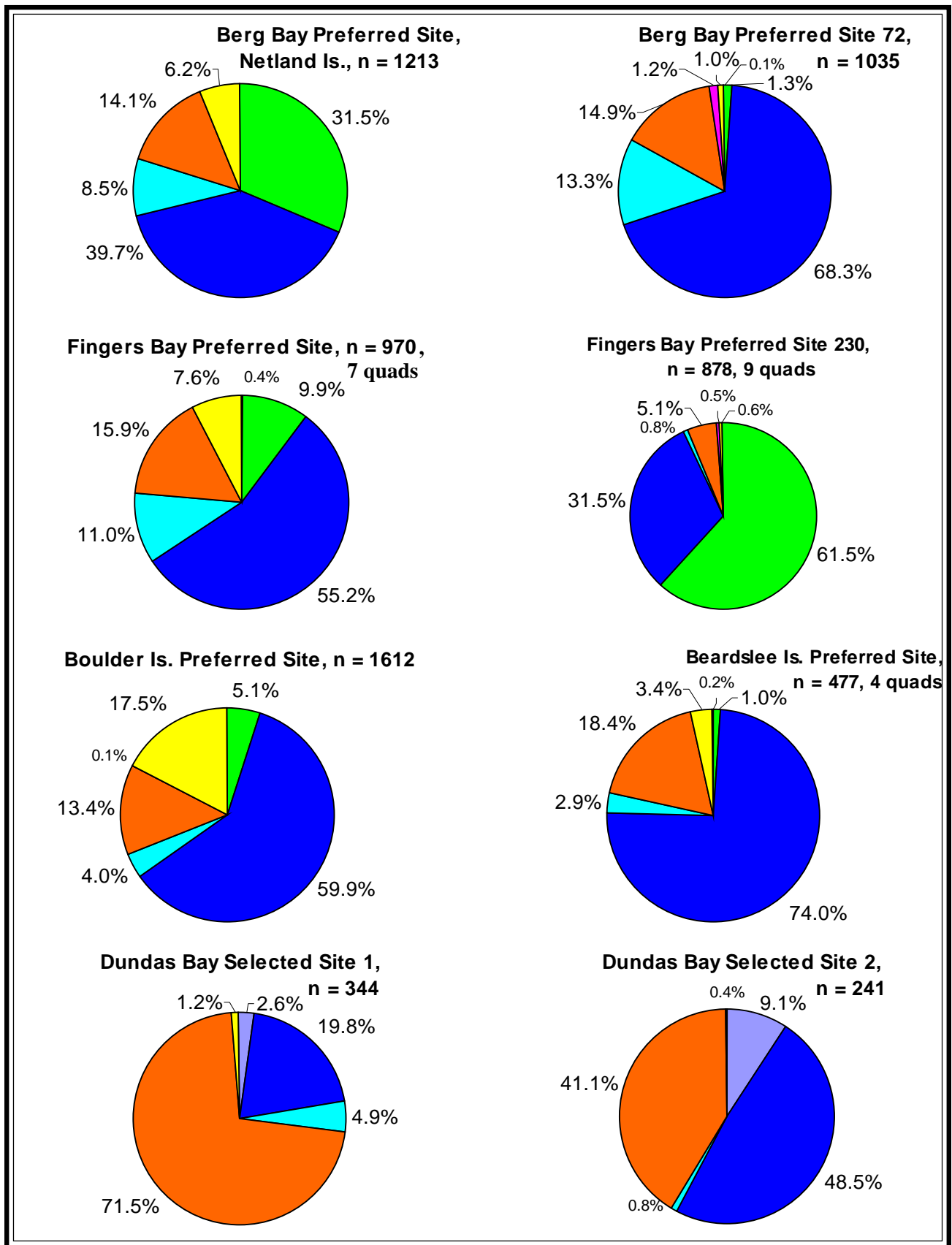Site 91 had 100% HIA, Site 233 had 100% MAS, and Site 64 had no clams.

Figure 5. Proportion, by number, of each species of intertidal clam per sampling site. Unless otherwise noted, ten quadrats were sampled at each site. See page 7 for legend.

Berg Bay Preferred Site, Netland Is., n = 1213
31.5%
39.7%
8.5%
14.1%
6.2%

Berg Bay Preferred Site 72, n = 1035
68.3%
13.3%
14.9%
1.2%
1.0%
0.1%
1.3%

Fingers Bay Preferred Site, n = 970, 7 quads
9.9%
0.4%
7.6%
15.9%
11.0%
55.2%

Fingers Bay Preferred Site 230, n = 878, 9 quads
61.5%
31.5%
0.8%
5.1%
0.5%
0.6%

Boulder Is. Preferred Site, n = 1612
5.1%
17.5%
0.1%
13.4%
4.0%
59.9%

Beardslee Is. Preferred Site, n = 477, 4 quads
3.4%
0.2%
1.0%
18.4%
2.9%
74.0%

Dundas Bay Selected Site 1, n = 344
1.2%
2.6%
19.8%
4.9%
71.5%

Dundas Bay Selected Site 2, n = 241
0.4%
9.1%
41.1%
48.5%
0.8%

Figure 5. Proportion, by number, of each species of intertidal clam per sampling site. Unless otherwise noted, ten quadrats were sampled at each site. See page 7 for legend.

Size

The overall means for clam size were 45, 26, 23.7, 40.2, 39, and 71 mm for CLN, HIA, MAS, MYS, PRS, and SAG, respectively. Clams, except MAS, appear to be larger in Fingers and Berg than in other areas sampled, however differences are slight and have not been statistically tested. Mean sizes of clams were not different between random and selected sites. See Figure 6 for sizes of clams per species per site.

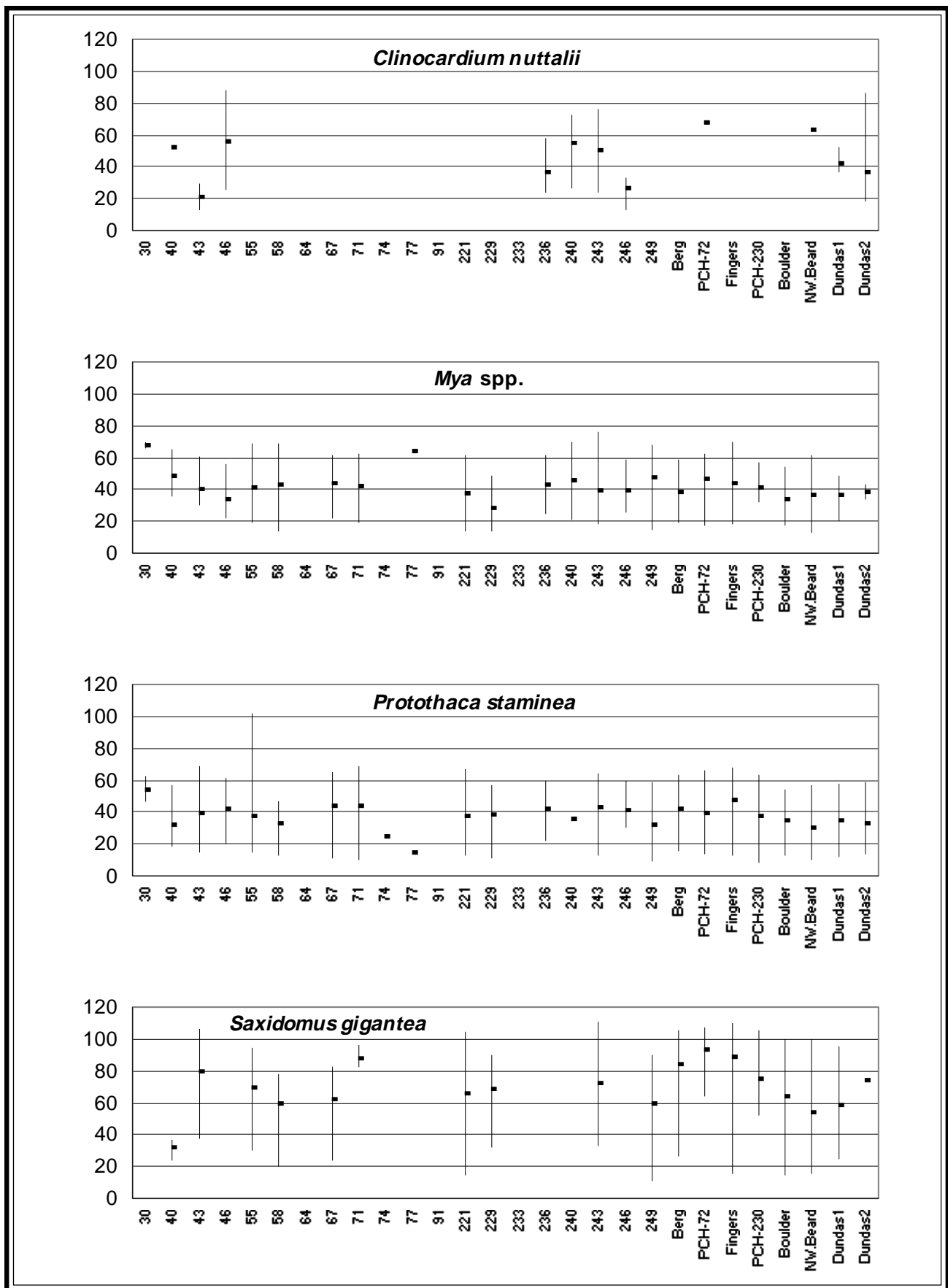Figure 6. Minimum, maximum, and mean size (in millimeters) of clams per 1/4 m^2 quadrat per site.
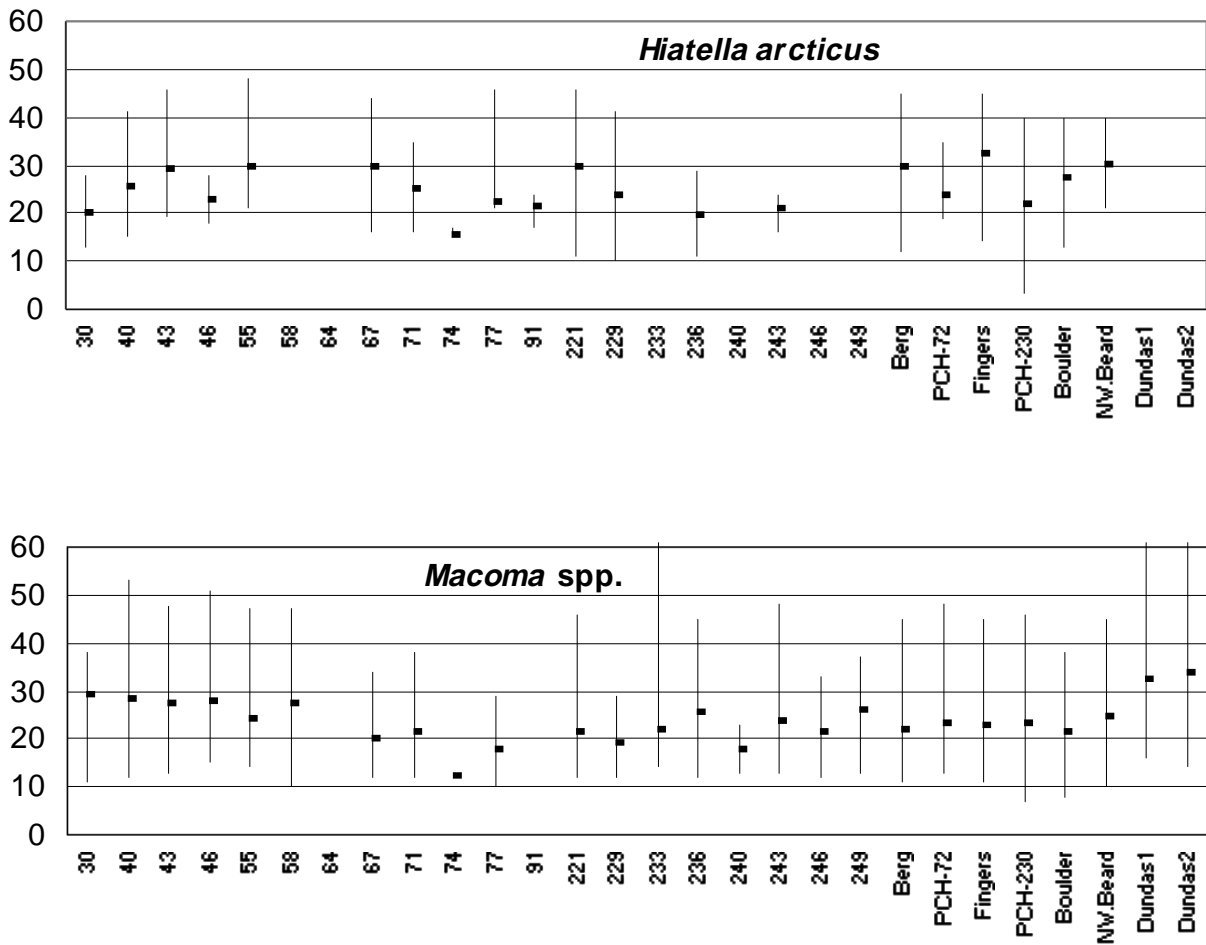
Figure 6. Minimum, maximum, and mean size (in millimeters) of clams per 1/4 m² quadrat per site.

Abundance and Biomass

The overall mean number of clams per quadrat ranged from 0 to 161.2 clams per 0.25 m² (mean ± sd: 50.94 ± 50.1) (Figure 7). There were no apparent relationships, based on visual examination of plots, between overall abundance and substrate type or location. There was no correlation between overall abundance and species diversity, H', (R = 0.188, P = 0.347). Mean number of clams per quadrat was statistically different between random and selected preferred sites (Mann-Whitney rank sum test, T = 137.00, P = <0.001). When looking at the abundance per quad of individual species of clams, MAS was the most abundant while CLN was the least (MAS > PRS > MYS = SAG = HIA > CLN) (Table 2). Field observations suggest CLN has a preference for smaller substrate sizes (e.g. coarse or fine sand) while HIA seems to prefer larger substrates (e.g. cobble or boulder). Sites with greater abundances of the other clam species had variable substrates (e.g. sands and/or pebble/gravel and/or cobble/boulder). Substrate alone is apparently not a good predictor of clam abundance. For example, random site 77 and selected preferred site Fingers had the same substrate classification (and are along the same stretch of beach) yet their mean number of clams per quadrat differed by an order of magnitude. See Figure 9 for abundance per site by species.

Figure 7. Mean numbers of clams per 1/4 m² quadrat per site.

Other clam; *Clinocardium nuttali*; *Hiatella arcticus*; *Macoma* species; *Mya* species; *Protothaca staminea*; *Pseudophythina compressa*; *Saxidomus gigantea*.
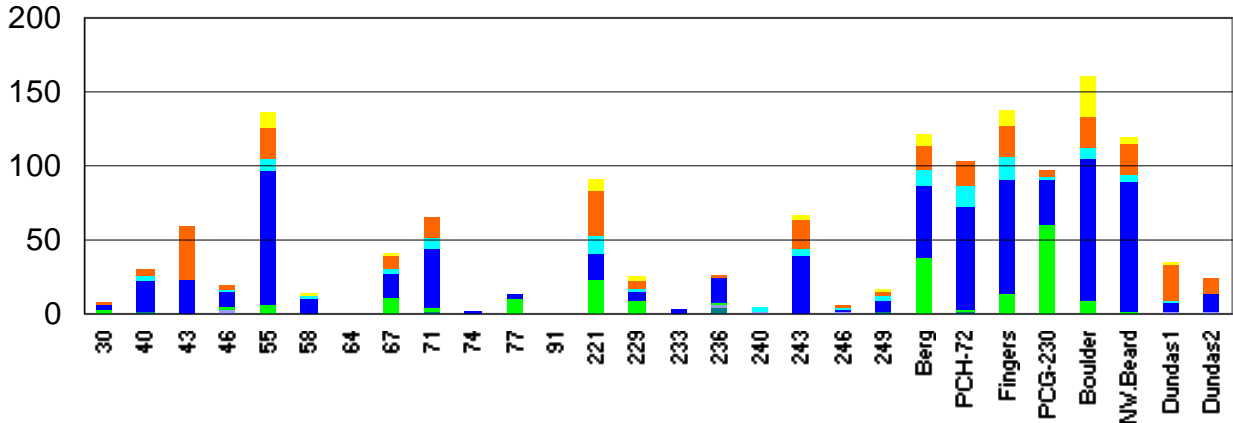
The overall mean biomass of clams per quadrat ranged from 0 to 193.0 grams dry weight (mean ± sd: 39.77 ± 49.5 grams dry weight). There were no apparent relationships, based on visual examination of plots, between overall biomass and substrate type or location (Figure 8). There was no significant correlation between H' and mean biomass (R = 0.188, P = 0.144). Mean biomass was significantly different between random and selected preferred sites (t-test, T = 129.00, P = <0.004). Not surprisingly, biomass correlates strongly with abundance (R = 0.883, P < 0.0000). When looking at the biomass of individual clam species: SAG = PRS = MYS = MAS > HIA = CLN (Table 2). See Figure 10 for biomass per site by species.

Figure 8. Mean biomass of clams in grams dry weight per 1/4 m² quadrat per site. Legend is the same as figure 7.
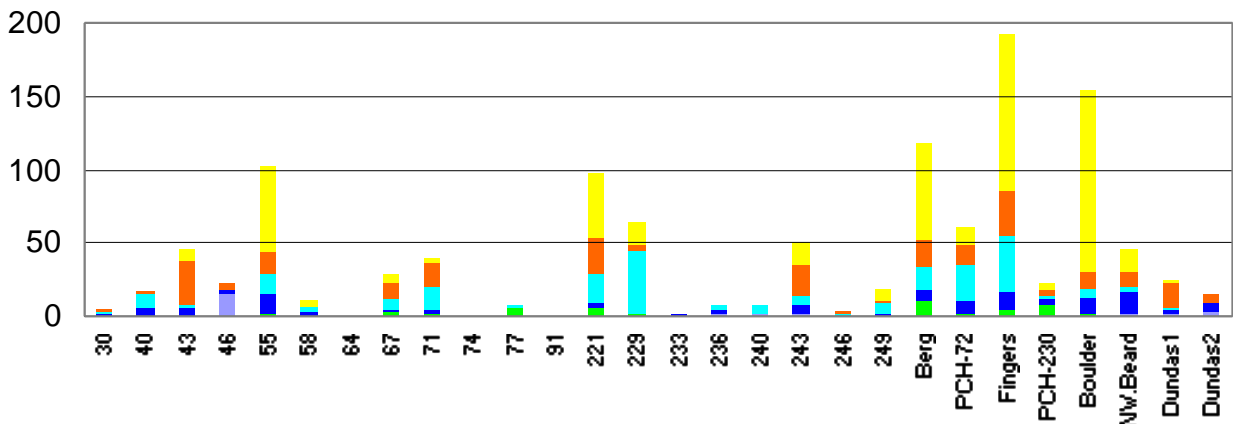
Table 2. Mann Whitney Rank Sum test results on mean number of clams (upper right half of table) and mean biomass (lower left half of table) per quadrat by species (ND = no difference):

(Mean Number) [Mean Biomass]	CLN (0.36)	HIA (6.94)	MAS (26.19)	MYS (3.70)	PRS (10.34)	SAG (2.95)
CLN [0.89]	****	P = 0.001	P < 0.001	P < 0.001	P < 0.001	P = 0.009
HIA [1.69]	ND	****	P < 0.001	ND	ND	ND
MAS [4.25]	P < 0.001	P = 0.005	****	P < 0.001	ND	P < 0.001
MYS [8.34]	P < 0.001	P = 0.001	ND	****	P = 0.035	ND
PRS [8.75]	P < 0.001	P = 0.001	ND	ND	****	P = 0.003
SAG [17.47]	P = 0.005	P = 0.099	ND	ND	ND	****

Figure 9. Minimum, maximum, and mean number of clams per 1/4 m^2 quadrat per site.

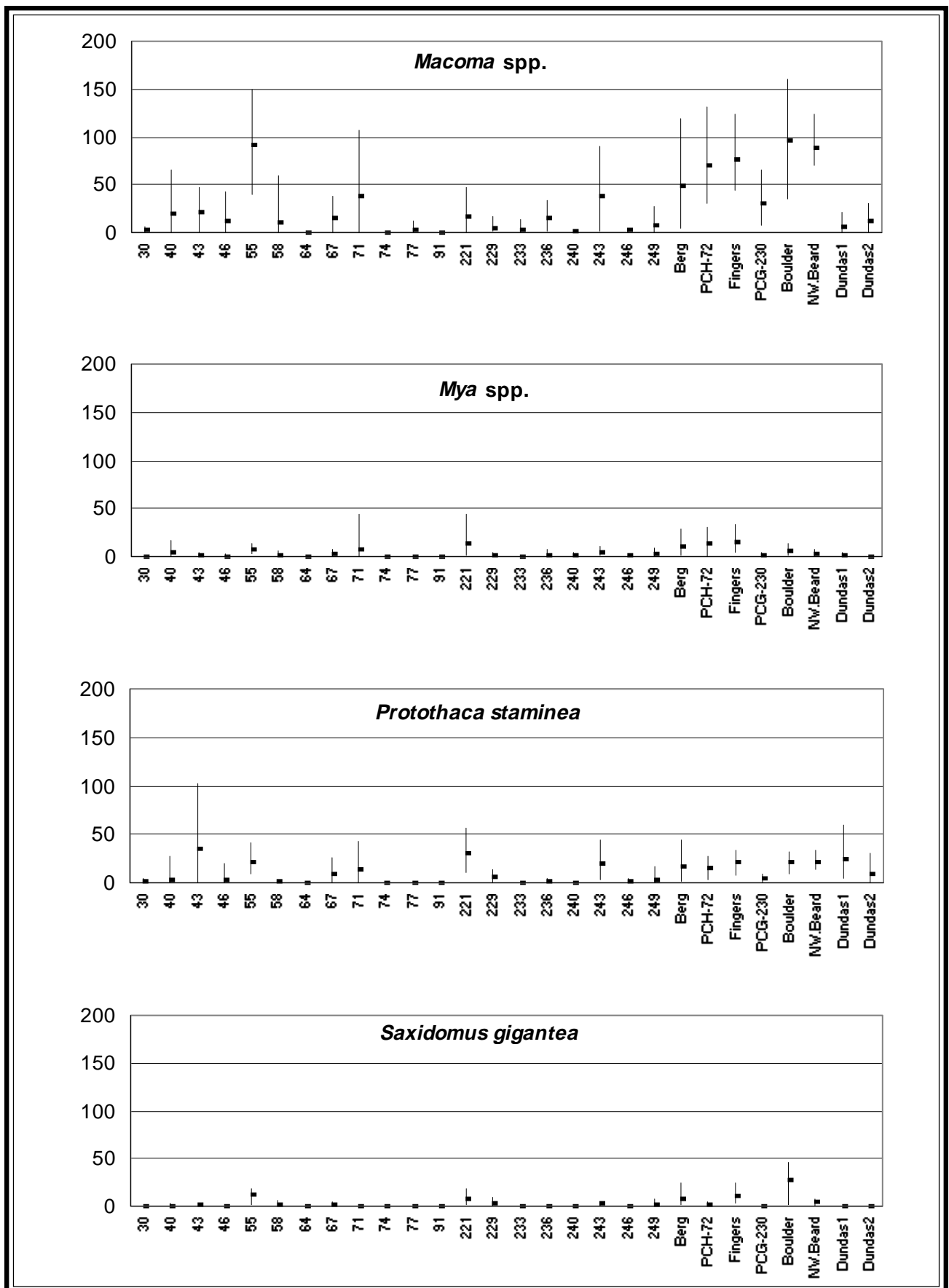*Clinocardium nuttallii*

Hiatella arcticus
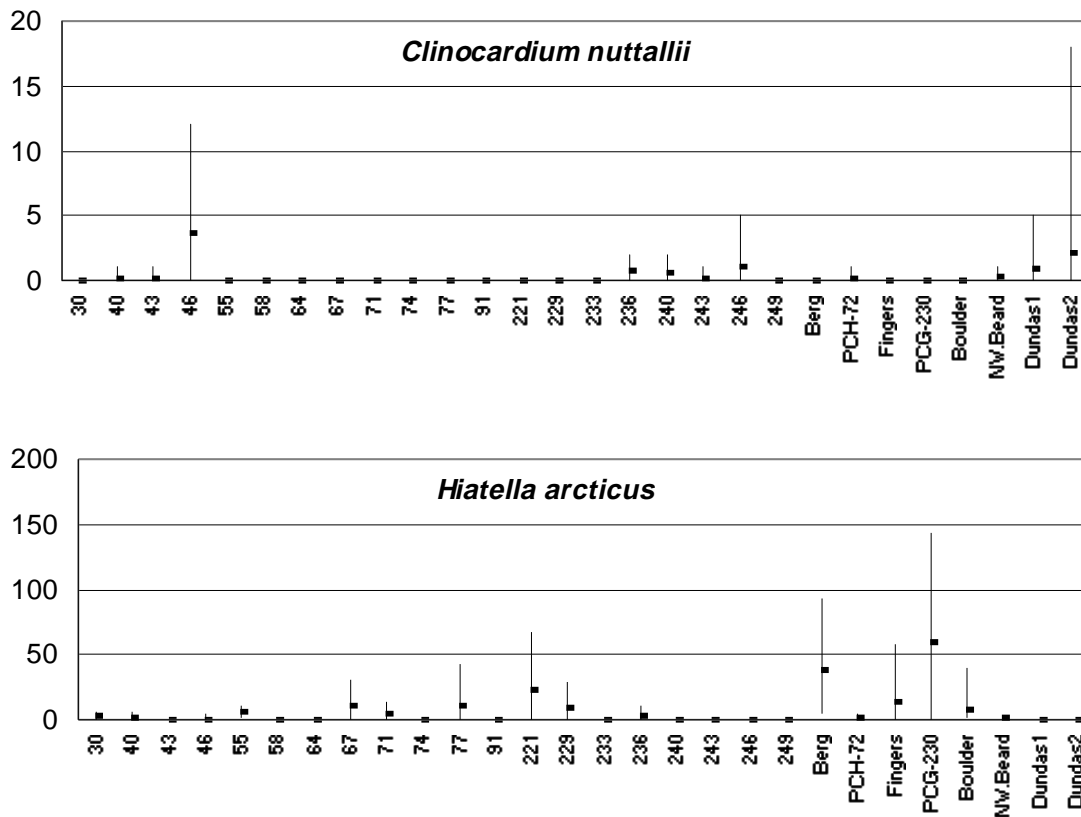
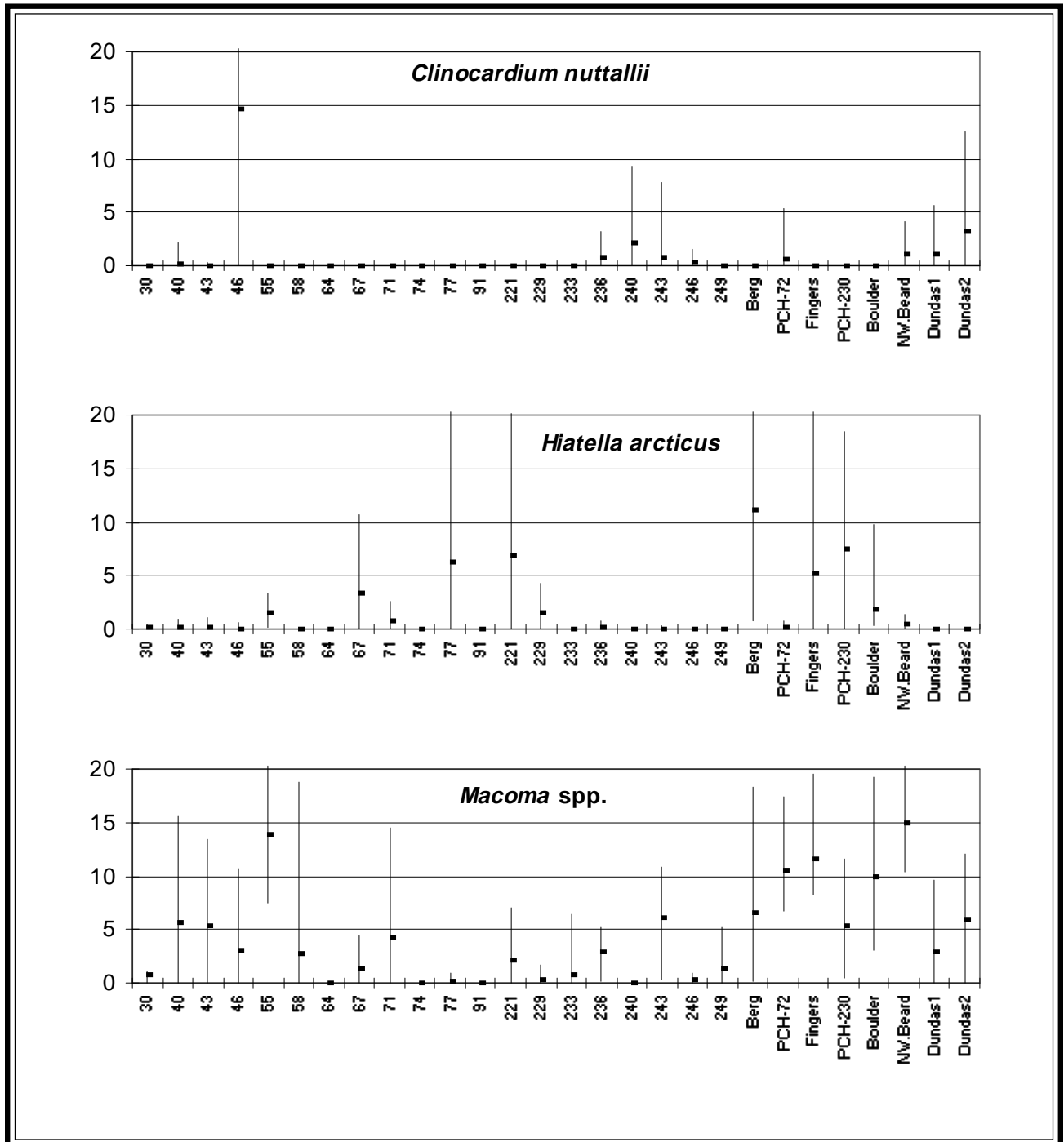Figure 9. Minimum, maximum, and mean number of clams per 1/4 m^2 quadrat per site.

Figure 10. Minimum, maximum, and mean biomass (in grams dry weight) per 1/4 m² quadrat per species per site.
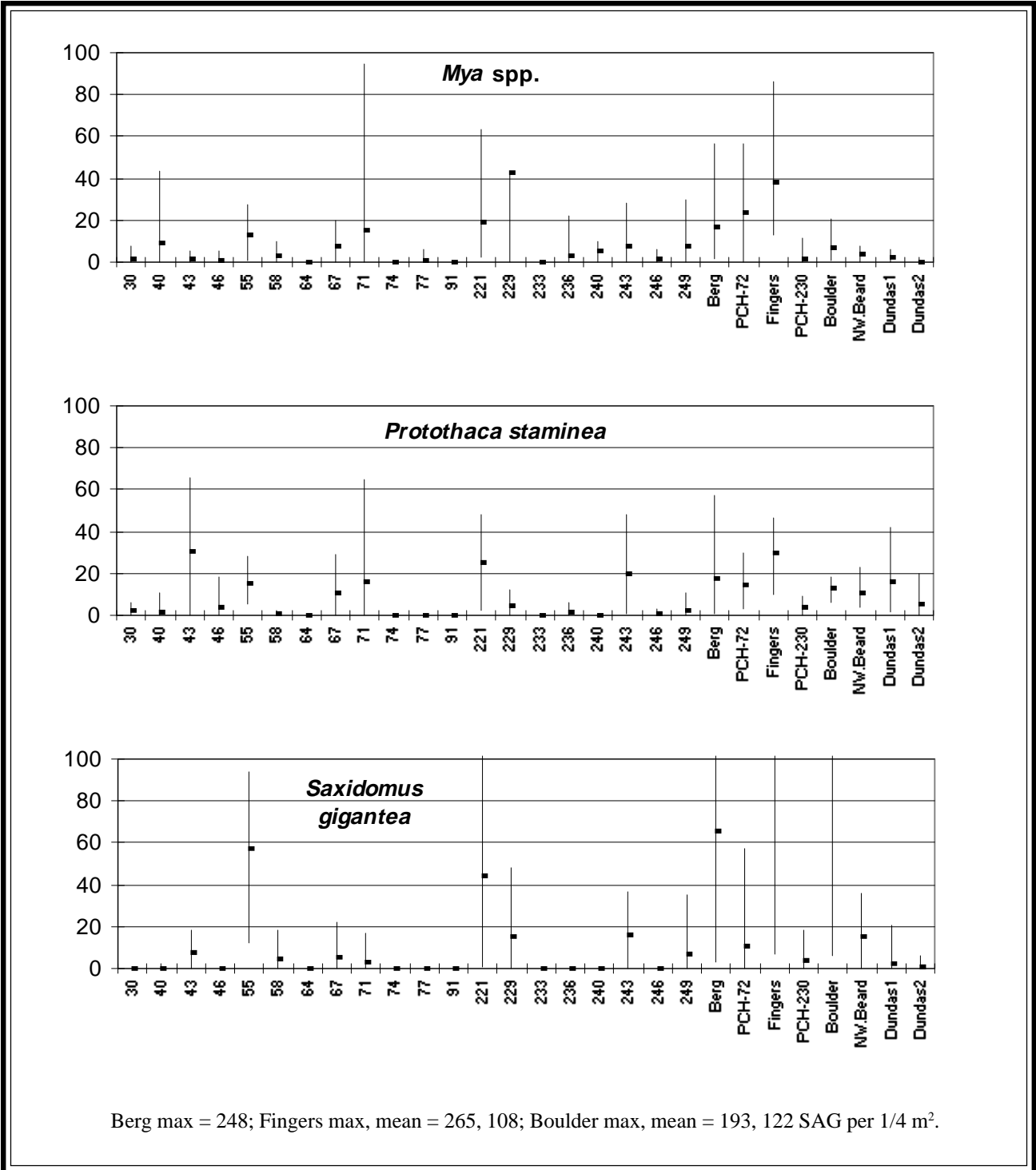
Figure 10. Minimum, maximum, and mean biomass (in grams dry weight) per 1/4 m^2 quadrat per species per site.

CONCLUSIONS

Diversity

We found eight different clam species/groups in our Glacier Bay sampling. Mueller (1973) found nine species in 1971 and seven in 1972. Assuming that the species found in the seventies still exist in the Park, a total of twelve species of clams exist (GAC, CLN, HIA, MAS, MYS, PRS, PSC, SAG, *Axinopsida serricata*, *Nuculana minuta*, *Panomya ampla*, and *Serripes groenlandicus*). This gives a theoretical H'max = 3.59. The highest H' in our sampling was 2.194. We would not expect to find *Axinopsida serricata* because its maximum size is 8 mm making it small enough to slip through our sieve screens (10 mm mesh, 14 mm diagonal). We have observed *Panomya ampla* in the intertidal near one of our sites and have found shell litter of *Serripes groenlandicus*, but haven't yet found either clam in our sampling. We expected to find *Serripes groenlandicus* and *Panomya ampla* as well as *Nuculana minuta* and may come across them during the remainder of our sampling. Sharman (1988) shows that species richness (S) for intertidal invertebrates increases linearly with increasing distance from tidewater glaciers. We have not observed this in our intertidal clam sampling, but perhaps this is because our samples have come from a relatively narrow band without much variation in distance from the glaciers. After sampling more sites along a broader range of the glacial chronosequence, we expect to see decreased clam diversity at sites closer to glaciers.

Abundance and Biomass

The analysis of intertidal clam abundance per site per species will be completed after our treatment (i.e. colonization of a number of sites by sea otters). When we began sampling in Glacier Bay we expected to find a greater abundance of clams than in areas we had studied that support sea otter populations. Sea otters are known to be effective at depletion of preferred prey species. Because otters have only been in Glacier Bay for a short time we expect that they have not yet exhausted prey resources.

We estimated abundances in Glacier Bay for *Macoma* species, *Protothaca staminea*, and *Saxidomus gigantea* at randomly selected sites of (mean ± standard error) 15.19 ± 4.78, 7.60 ± 2.42, 1.51 ± 0.67, respectively; while densities at preferred sites were 68.49 ± 10.14, 17.18 ± 2.69, 8.64 ± 4.21 clams per 0.25 m^2. Using sampling methods similar to this study, researchers in the Nearshore Vertebrate Project (Holland-Bartels et al. 1997, 1998) measured densities of *Macoma* species, *Protothaca staminea*, and *Saxidomus gigantea* at systematically selected and preferred sites in two areas of Prince William Sound (PWS). At systematically selected sites, *Macoma* species were 3 - 23 times more abundant in Glacier Bay than in PWS; *Protothaca staminea* was 4 - 7 times more abundant in Glacier Bay than in PWS; and *Saxidomus gigantea* was 38 - 188 times more abundant in Glacier Bay than in PWS. At preferred habitat sites, *Macoma* densities were 27 - 53 times higher; while *Protothaca* densities were only two times higher in Glacier Bay. Although the mean densities in PWS are lower than we calculated in Glacier Bay, they do fall within the range measured (See Figure 9 for minimum, maximum, and mean number of clams per 1/4 m^2 quadrat per site in Glacier Bay). Kvitek et al (1985) estimated *Saxidomus gigantea* abundances in Elkhorn Slough, California, of 0.8 ± 0.15 clams per 0.25 m^2. This is approximately 10

times lower than for the Glacier Bay PCH sites, however it is also within the range measured.   We expect that, as sea otters colonize Glacier Bay in greater numbers and for a longer duration, the overall abundance of preferred clams (SAG, PRS, MYS) will decrease and the size distributions of those clams will shift toward higher proportions of smaller individuals.

It is apparent from examining Figure 7 and 8 that, when present in a quadrat, *Saxidomus* and *Mya* contribute considerably to the biomass. Although *Macoma* was the most abundant clam, it only slightly influences biomass.

Size

We expected to see a broad range of size classes represented in our sample. Sea otters preferentially select larger prey items thus skewing size class distributions towards smaller individuals. An absence of smaller size classes can mean a lack of recruitment. The analysis of size class distribution per site per species will be completed after our treatment (i.e. colonization of a number of sites by sea otters). We pooled all of the randomly selected sites and all of the preferred habitat sites and examined size class distributions of several species of clams for comparison with other studies. The size class distributions of *Macoma* species for both random and preferred sites have bell shaped curves with larger proportions of clams in the middle size classes and fewer at the extremes (Figure 11). These distributions are similar to data collected in 1996 by the Nearshore Vertebrate Project in Prince William Sound (Holland-Bartels et al. 1997). However the 1997 distributions from the same study are skewed toward the lower size classes (Holland-Bartels et al. 1998). The size class distributions of *Protothaca staminea* show a striking difference from the Nearshore Vertebrate Project 1996 and 1997 distributions (Figure 11). Approximately 90 - 95% of the *Protothaca* from the Prince William sound study areas were < 35 mm, while in this study approximately 60% were > 35 mm.

Figure 11. Size class distributions (in mm) for *Macoma* and *Protothaca*.
Key:
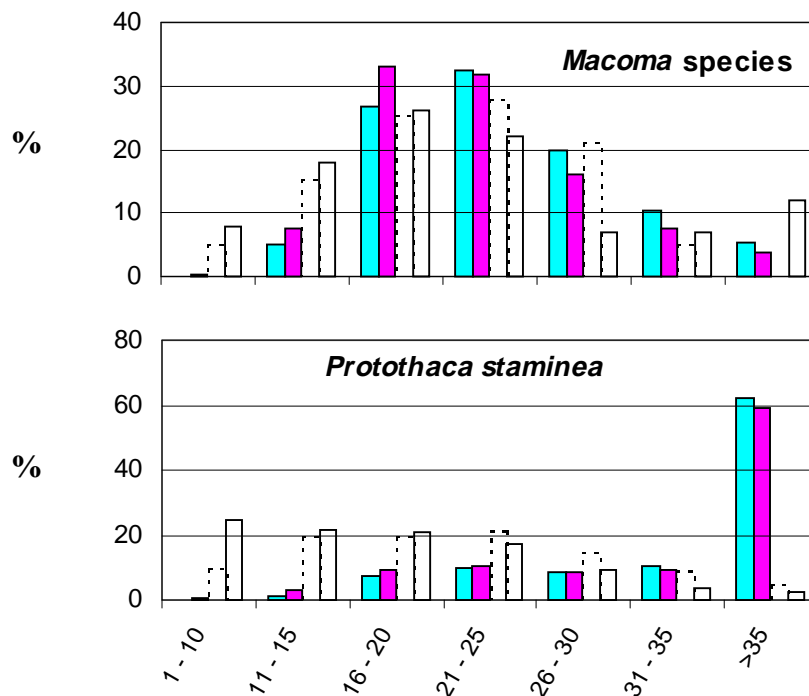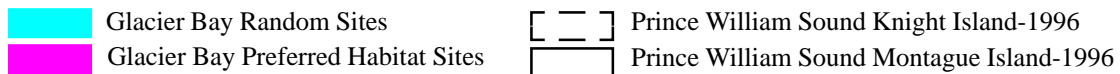
FUTURE WORK

Figures 1 - 3 show the sites that remain to be sampled in lower Glacier Bay as well as the proposed upper bay sites (sites with green stars). A complete set of lower bay sites and subsequent re-sampling after colonization by sea otters will allow the documentation of changes as well as inference to the cause. It is important to have adequate controls for both experimental rigor and power. A comprehensive sampling itinerary including both lower and upper bay will serve multiple purposes: characterization of the intertidal bivalve populations (species diversity, size class distribution, abundance, biomass, species distribution) of the entire bay, baseline data to examine intertidal successional changes along the glacial chronosequence, comparison between the east and west arms, data to perform power analyses to determine our ability to detect changes (either due to sea otters, humans, or natural bivalve life history variability), and information regarding the biological carrying capacity of different habitats for intertidal bivalves.

Baseline data is a valuable tool enhancing our ability to observe changes and assign cause as well as predict impacts (of sea otters or human activities) and design restoration programs in the event of a mishap. Intertidal clam data is a key component of the baseline library because clams are an important food resource for sea otters, sea ducks, octopus, starfish, snails, and subsistence gatherers. Bivalves also play an important role filtering particulate matter from the water column, filtering organic material from sediments and altering their physical environment by affecting water flow and substrate organization (Dame 1996).

REFERENCES

Bodkin, J. L., Esslinger, G. G., and Monson, D. H. 1999. Estimated sea otter population size in Glacier Bay, 8-13 May 1999. Unpublished report to Glacier Bay National Park and Preserve. U. S. G. S. Alaska Biological Science Center, Anchorage AK. 13 pp.

Dame, R. F. 1996. Ecology of Marine Bivalves: An Ecosystem Approach. Boca Raton, Florida: CRC Press.

Foster, N. R. 1991. Intertidal Bivalves: A guide to the Common Marine Bivalves of Alaska. University of Alaska Press.

Harbo, R. M. 1997. Shells and Shellfish of the Pacific Northwest, a field guide. Madeira Park, B. C., Canada: Harbour Publishing.

Holland-Bartels, L., et al. 1997. Mechanisms of Impact and Potential Recovery of Nearshore Vertebrate Predators, Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 97025), U. S. Geological Survey-Biological Resources Division, Anchorage, Alaska.

Holland-Bartels, L., et al. 1998. Mechanisms of Impact and Potential Recovery of Nearshore Vertebrate Predators, Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 97025), U. S. Geological Survey-Biological Resources Division, Anchorage, Alaska.

Irvine, G. 1998. Development of Coastal Monitoring Protocols and Process-Based Studies to Address Landscape-Scale Variation in Coastal Communities of Glacier Bay National Park and Preserve, Katmai National Park and Preserve, and Wrangell-St. Elias National Park and Preserve. Phase II: Development and Testing of Monitoring Protocols for Selected Intertidal Habitats and Assemblages. U. S. G. S. Biological Resources Division, Annual Report NRPP Project, 62 pp.

Kvitek, R. G., Fukuyama, A. K., Anderson, B. S., and Grimm, B. K. 1988. Sea otter foraging on deep-burrowing bivalves in a California coastal lagoon. Marine Biology 98, 157-167.

———, Oliver, J. S., DeGange, A. R., and Anderson, B. S. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology, 73(2): 413-428.

Mueller, G. J. 1973. Preliminary survey of intertidal fauna and flora of Glacier Bay National Monument: A final report. Unpublished Report, U.S. Department of the Interior, National Park Service, Glacier Bay National Monument, Juneau, AK.

Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. Journal of Theoretical Biology, 10: 370-383.

Sharman, L. 1988. Marine intertidal community development following glacial recession in Glacier Bay, Alaska. *In Proceedings of the 2nd Glacier Bay Science Symposium, September 19 - 22*. Milner, A. M. and J. D. Wood, ed.