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Invertebrate community responses to recreational clam digging

Received: 27 April 2005 / Accepted: 10 January 2006 / Published online: 5 May 2006
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Abstract Marine reserves can help in maintaining biodiversity and potentially be useful as a fishery management tool by removing human-mediated impacts. Intertidal, soft-sediment habitats can often support robust recreational and commercial shellfish harvests, especially for clams; however, there is limited research on the effects of reserves in these habitats. In San Juan County, Washington, several reserves prohibit recreational clam digging. We examined the effects of these reserves on infaunal community composition through comparison with non-reserve beaches during a 6-week period. Clam abundance, overall species richness and total polychaete family richness were greater on reserve beaches compared to non-reserve beaches. Additionally, an experiment within a reserve demonstrated negative impacts of digging on non-target infauna. These effects probably resulted from local disruption and disturbance of the sediment habitat and not from increased post-digging predation, which was controlled. Intertidal reserves could play an important role in sustaining local and potentially regional biodiversity.

Introduction

Marine reserves have the potential to help preserve biodiversity, boost and sustain overexploited fisheries, and

serve as benchmarks for undisturbed ecosystems (Pauly et al. 2002; Thrush and Dayton 2002; Gell and Roberts 2003). Empirical research on subtidal reserves strongly support the prediction that protected areas enhance biodiversity as well as the abundance and size structure of some fishery target species (Babcock et al. 1999; Halpern and Warner 2002). Less attention is paid to intertidal areas, popular not only for non-extractive recreational use but also for recreational and commercial shellfish harvest (e.g. clams and oysters).

Limited research on intertidal harvesting effects has focused primarily on target clam species and abiotic responses, but little on non-target species and non-mechanical (i.e. human powered) harvesting practices. The implications of reserves for target species were demonstrated by Byers (2005) for the primary harvest species, the non-native clam *Venerupis philippinarum*, which had higher abundances within reserves. Abiotic responses to digging disturbance include sediment shifts to coarser surface deposits that are deficient in organic and bioaggregated particles (Anderson and Meyer 1986). Dernie et al. (2003) also found that the sediment composition and hydrodynamic regime of an area can alter the effects of harvesting disturbance; disturbed plots in muddier sites took longer to infill than in sandier sites. Their study did not explore the effects of any specific harvesting practice, but showed that digging disturbances do affect overall community composition, with both the number of individuals and the species decreasing immediately after harvest. Lenihan and Micheli (2000) showed that hand raking of oysters and hand digging for clams caused relatively high rates of mortality and reduced abundance of non-target shellfish on intertidal oyster reef habitat. Bait-worm digging also negatively affected the non-target clam *Mya arenaria* through shell damage and increased exposure to predation (Brown and Wilson 1997); even low-intensity commercial digging for clams and bait worms affects benthic community structure in a short period of time by reducing species richness and abundance. However, this study was conducted on a heavily dug beach, and pre-experiment baselines were

Communicated by P.W. Sammarco, Chauvin

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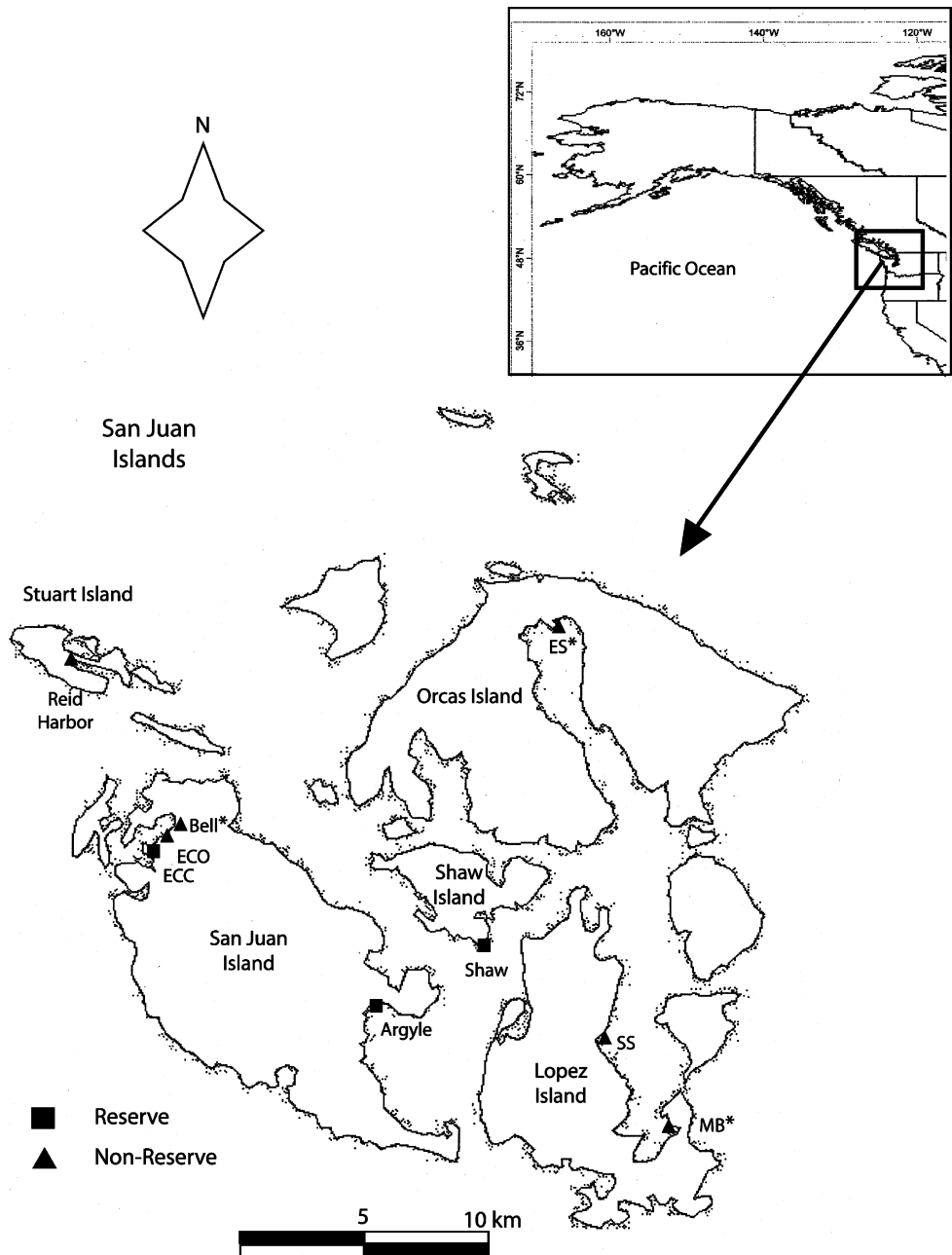
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not non-disturbance baselines. Most recently, Skilleter et al. (2005) showed in a three-tiered study that the recreational and commercial harvesting of callinassid shrimp increases polychaete spatial patchiness and causes declines in abundance of polychaetes, soldier crabs, and amphipods.

Human impacts on soft sediment intertidal areas, such as exacerbated erosion, nutrient input, beach nourishment, trampling, and harvest, have led to the establishment of marine reserves to protect some coastal habitats. The San Juan Islands in Washington State, USA (Fig. 1) contain several such reserves, closed to

shellfish harvesting within the last 2 decades to maintain biodiversity and pristine sites for ecological research. Because productivity on these beaches is high and local water quality is good, many surrounding sites outside of the reserves are subject to heavy recreational harvest for a variety of clam species. We examined the effects of reserves on community composition via a broad survey of reserve and non-reserve beaches. In addition, we initiated an experiment on one reserve beach to quantify the impact of recreational clam digging on non-target infaunal organisms, and the aspects of disturbance that impact the community most severely.

Fig. 1 Survey and experimental sites, San Juan Islands, Washington, USA (48°32.8'N, 123°0.6'W). All sites were surveyed for clams and other infauna except those denoted by *asterisks* which were only surveyed for clams. *Argyle* Argyle Creek, University of Washington Reserve, San Juan Island; *Bell** Bell Harbor, San Juan Island, *ECC* English Camp National Park Closed, San Juan Island, *ECO* English Camp National Park Open, San Juan Island, *ES** Eastsound, Orcas Island, *MB** Mud Bay, Lopez Island, *Reid Harbor* Reid Harbor, Stuart Island, *Shaw* Shaw University of Washington Reserve, Shaw Island, *SS* Spencer Spit State Park, Lopez Island



Methods

Survey methods

We conducted a quantitative survey of all macroscopic invertebrates at three reserve and three non-reserve sites in the San Juan Islands (Fig. 1). The three reserves included Argyle Creek and Shaw Reserve, both owned by the University of Washington and established as reserves in 1990, and a section of English Camp (previously British Camp, Byers 2005) National Park that has been closed to shellfish harvesting since ~1977. The three non-reserves were English Camp Open on San Juan Island, Spencer Spit State Park on Lopez Island, and Reid Harbor on Stuart Island. These non-reserve sites experience intense recreational shellfish harvesting pressure. Clam abundances but not other invertebrates were sampled at three additional non-reserve sites (Bell, East-sound, and Mud Bay, Fig. 1). Sites were chosen to correspond with previous clam surveys by Byers (2005) in 2000. Byers (2005) confirmed that general physical variables, such as primary productivity (i.e. chlorophyll), salinity, and temperature were similar across sites. Sites were on beaches with mixed mud–sand–pebble sediment, limited wave exposure, and a minimum combined density of *Protothaca staminea* (the native littleneck clam) and *Venerupis philippinarum* (the Japanese littleneck) of 16 individuals/m². This latter biological criterion directly ensured that the selected reserve and non-reserve sites were suitable habitat for the primary targets of clambers.

Survey sampling was completed during October and early November 2003. At each site, we dug test holes to establish the intertidal vertical distribution of *Protothaca*, which shares the same vertical range as *Venerupis*. Two transects running parallel to the water were then established between these vertical limits, at approximately 0.5 and 1.0 m above mean lower low water (MLLW). Tidal heights were measured using a hand level and meter stick and compared to NOAA tide predictions for Friday Harbor, San Juan Island.

In each horizontal transect, clams were sampled in five or six 0.125 m² cores dug to 17 cm (beyond maximum clam burial depth, Byers 2005) and sieved in the field through 5 mm mesh. Other species were sampled with five or six 10 cm diameter cores to a depth of 15 cm and sieved on 4- and 1-mm nested sieves. All samples were taken 3–6 m apart; distances varied due to differences in beach length and permitting constraints at

English Camp National Park. Non-clam infaunal organisms were brought back to the lab, preserved, and identified to species if possible, using Kozloff (1987), Banse and Hobson (1974), Hobson and Banse (1981), and Blake et al. (1996).

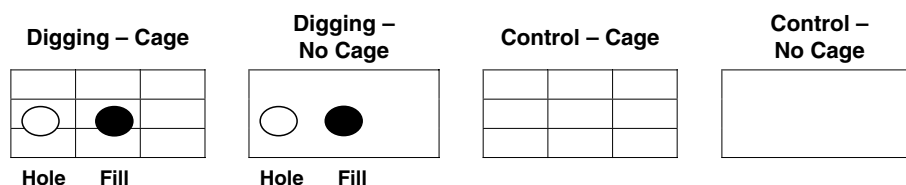
Because infaunal communities are known to be sensitive to sediment type, one core was taken up to 10 cm depth at each tidal height for sediment analysis using 2-cm diameter, 50-ml plastic centrifuge tubes. Samples were stored in a cold room at 12°C until analysis and protocol was guided by Folk (1974) and *Puget Sound Estuary Program* (1986). Samples were wet-sieved through a standard set of sieves (4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm) with fresh water. Fine sediments were collected in a bucket below the sieves and concentrated by air-vacuum filtering through pre-weighed 6- μ m filter paper. Filters with fine sediments were air-dried, and their weight calculated. Larger grains retained on the sieves were dried at 80°C for a minimum of 5 h and weighed.

Experimental methods

We quantified the impacts of digging on non-clam infauna at the English Camp reserve site (ECC, Fig. 1). At 0.5 m above MLLW we established 16 treatment plots in blocks of four (i.e. 4 treatments/block; Fig. 2). Each plot measured 1×0.6 m and was separated from the next by 1 m. A digging treatment simulated the disturbance created by recreational clambers; a no-digging treatment simulated a reserve where clamming is prohibited. Clammers are typically knowledgeable about the vertical range of target clams and dig holes in horizontal swaths across the beach within the clams' range. Our digging was done in half the plots; a 30×30 cm hole was dug to a depth of 20 cm, and the sediment from the hole ("fill") was deposited to one side of the plot. Holes were not refilled, following common clamming practices. Holes were initially dug during week 0 and the same points were re-dug during weeks 2 and 4. Infilling rates of holes will vary with wave activity and sediment type. We predicted our holes would refill and redug the holes to simulate the return of clambers to a dug and refilled beach. The no-digging controls were left undisturbed.

To test the role of predators in both digging and no-digging treatments, half of the plots were protected under cages made of 1/2 in. hardware cloth (Fig. 2) preventing access by any marine or terrestrial macropredators (e.g. crabs, raccoons). Cages were held in place at four corners by 3/8 in. rebar stakes, and the sides were buried 2-cm

Fig. 2 Experimental design at English Camp. Two factors with controls were each replicated four times on the beach in a horizontal line. Each plot is 1.0×0.6×0.01 m



into the sediment allowing easy migration of infaunal organisms. The height above the sediment was approximately 8-cm. Thus there were four treatments: (1) digging; (2) digging covered with a cage; (3) no-digging; and (4) no-digging covered with a cage. Treatments were blocked (one replicate of each of the four treatments per block) in space to account for any systematic spatial variation. Caged treatments alternated spatially with non-caged treatments to confer similar water circulation. A coin toss was used to assign digging and no-digging treatments within blocks to cage and no-cage treatments.

All experimental treatments were sampled for non-clam infauna at 1 and 5 weeks, using the same infaunal coring methods as described above. No-digging treatments were sampled with one core taken anywhere within the treatment plot. Digging treatments were sampled in the hole and also the fill. Hole samples were taken in the sediment infill not below the depth of the original hole. Samples were sieved and preserved as described above. Three sediment cores per treatment type (one core in three of four plots per treatment) were also taken during week 5 only for grain size analysis.

Additional sediment cores were taken during week 5 for the analysis of particulate organic carbon. One core was taken per disturbance type and frozen until analysis. Samples were thawed and wet-weighted on pre-weighed weighboats, then dried at 80°C for a minimum of 24 h and weighed again. They were then placed in a muffle furnace at 500°C for 4 h and re-weighed (Byers 2002). Loss on ignition was used as a proxy for organic content by comparing the portion of the sediment weight lost between the dry and combusted samples.

Statistical analysis

Statistical tests were performed with JMP 5.0.1 and initially tested for normality and homogeneity. Normality was determined by goodness of fit under the Shapiro–Wilk W test. Data were considered homogeneous when they were not significant (P value >0.05) under both the Brown–Forsythe and Bartlett tests.

Clam abundances were compared separately between reserves and non-reserves with one-way Kruskal–Wallis tests. The non-parametric, one-way test was used because reserve and non-reserve sample sizes and variances were unequal, and because higher abundances for both species inside reserves than on harvested beaches were predicted (Byers 2005). A one-way Wilcoxon post hoc test was used to compare abundances among all sites. Non-clam data were analyzed for species richness, polychaete family richness, and biodiversity using a three-way, nested ANOVA design: reserve, site (reserve), and tidal height (reserve, site). A nested parametric analysis could not be used for epifaunal species richness or the Shannon Biodiversity Index due to lack of normality. The data were separated by high and low tidal heights and a Wilcoxon non-parametric test performed on each tidal height separately and combined. Multivariate analyses of the whole community (epifauna and infauna)

were performed using PRIMER software (Clarke and Gorley 2001). The data matrix of abundances was square-root transformed, and ordinations performed using non-metric multidimensional scaling (MDS). Analyses of similarity (ANOSIM) tested the significance of hypothesized differences in communities among treatments (reserve vs. non-reserve) and tidal heights, and the SIMPER routine analyzed the species most important in separating treatments. Correlations between community similarities and physical variables (grain sizes) were tested using the BEST procedure.

The percent gravel (retained on 4 and 2 mm sieves), sand (1, 0.5, 0.25, 0.125, and 0.063 mm sieves), and fines were calculated for all sediment samples. With two-way, crossed ANOVAs we tested the effect of reserve status and tidal height on grain size distribution between gravel, sand, and fines, with each grain size analyzed separately. Additional two-way, crossed ANOVAs tested for the effect of individual sites and tidal height on grain size distribution. Linear regressions were used to check for correlations between sediment size distributions and species richness and abundance.

Experimental data from English Camp were analyzed using a two-way, crossed MANOVA for species richness, with “Digging” and “Cages” as the fixed factors. A repeated measures response was used to test for differences between sampled times. Separate analyses were done for hole samples and fill samples. We also tested for the effect of the treatments on total polychaete abundance with a one-way MANOVA with only digging as a factor. Linear regressions were used to check for correlations between species richness and either percent fines or percent organic material at this finer spatial scale. Community-level analyses of infaunal abundances were done with PRIMER, as described above.

Results

Survey

The most common clam species in the sampled zones was the native littleneck, *Protothaca staminea* (38% of all individuals). The introduced Japanese littleneck, *Venerupis philippinarum*, a favored species for human consumption, made up 13% of sampled individuals. Other species found included mud clams (*Macoma* spp.), butter clams (*Saxidomus* sp.), the non-native softshell clam (*Mya arenaria*), and the non-native purple varnish clam (*Nuttalia obscurata*). Both littleneck species, which are largely targeted by recreational harvesters, were more abundant inside reserves than in areas where clam digging is allowed (Fig. 3, Table 1a). The post hoc test revealed that for each species, one site drove the difference between reserve and non-reserve sites: English Camp Closed for *Protothaca*, and Shaw Reserve for *Venerupis*. *Venerupis* was significantly less abundant than *Protothaca* at all sites. Site had a significant effect on the densities of both species.

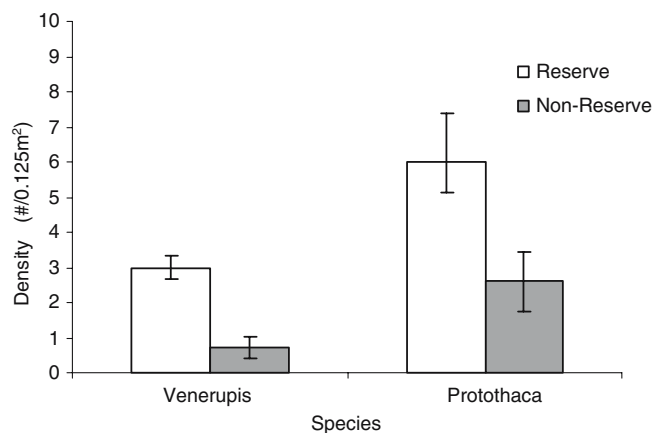


Fig. 3 *Protothaca* and *Venerupis* clam densities at reserve ($n=3$) and non-reserve ($n=6$) sites. Densities for each were averaged for both high and low tidal elevations. Bars represent ± 1 SE

The infauna at all surveyed sites consisted mostly of polychaetes, but also included nematodes and phoronids (*Phoronopsis harmeri*) and the epifauna included amphipods, *Hemigrapsus* spp. (shore crabs), and limpets. There was a significant, positive effect of reserve status on overall species richness (Fig. 4, Table 1a). Post hoc comparisons using the Tukey HSD procedure indicate that this effect was driven by the Shaw Reserve site, which differed significantly from all other sites (Table 1a). The low transects also had significantly higher species richness than the high transects (Fig. 4) in all sites. When infauna and epifauna were analyzed separately, reserves showed a significantly higher non-clam infaunal species richness (Fig. 4, Table 1a) and epifaunal richness (Fig. 4, Table 1a) than non-reserves.

Multivariate analyses showed differences in overall community composition (clams and other infauna and epifauna). Communities differed between reserves and non-reserves (ANOSIM test, $P=0.013$); reserves had greater abundances of most clam species and a variety of polychaetes. Non-reserves had more *Macoma nasuta* (a non-harvested clam species), limpets, and *Nereis* polychaetes. Communities also differed among tidal heights ($P=0.002$).

Sediment composition varied greatly among sites (Table 2). For example, English Camp Closed had a very large proportion of fines compared to Argyle Creek, which had a high proportion of gravel. Tidal height did not consistently affect grain size distributions for gravel, sand or fines. While there was a difference in the proportion of gravel and sand between reserve and non-reserve sites, percent fines were similar. Abundances of *Protothaca* ($r^2=0.810$) but not *Venerupis* ($r^2<0.01$) were positively correlated with percent fines (Table 1). Non-clam species richness was not correlated with percent fines (linear regression, $r^2=0.0033$, $P=0.858$). Infaunal communities overall showed only weak correlations with grain sizes, with the strongest correlation ($\rho=0.29$) with fines alone.

Table 1 Results. (a) Survey results for clam abundance, non-clam species richness, and sediment composition and effects on clam abundance. (b) Experimental MANOVA results for species richness and polychaete abundance

	<i>df</i>	χ^2	<i>P</i> value	
(a) Survey results				
Clam abundance (one-way Kruskal–Wallis)				
<i>Protothaca</i>	1	5.507	0.019	
<i>Venerupis</i>	1	7.339	0.007	
<i>Venerupis</i> Abundance compared to <i>Protothaca</i>	1	30.675	<0.0001	
	<i>df</i>	χ^2	<i>P</i> value	
Site effect on density				
<i>Protothaca</i>	8	30.481	0.0002	
<i>Venerupis</i>	8	25.746	0.0012	
	<i>df</i>	Sum of squares	<i>F</i> ratio	Prob > <i>F</i>
Non-clam species richness (three-way, nested ANOVA)				
Reserve status	1	56.023	22.7306	<0.0001
Site [reserve status]	4	73.769	7.4826	<0.0001
Tidal height [reserve status, site]	6	55.083	3.7249	0.0039
		Least square mean	Standard error	
Post hoc Tukey test				
Shaw	6.10		0.49645	
ECC	3.70		0.49645	
Argyle	2.40		0.49645	
SS	2.60		0.49645	
ECO	2.08		0.45320	
Reid	1.8		0.49654	
	<i>df</i>	Sum of squares	<i>F</i> ratio	Prob > <i>F</i>
Infauna species richness (three-way, nested ANOVA)				
Reserve status	1	10.01195	7.4016	0.0089
Site [reserve status]	4	30.52500	5.6416	0.0008
Tide height [reserve status, site]	6	20.38333	2.5115	0.0334
	<i>S</i>	<i>Z</i>	Prob > <i>Z</i>	
Epifauna species richness (Wilcoxon non-parametric)				
		1,147.5	3.10	0.0019
	<i>df</i>	Sum of squares	<i>F</i> ratio	Prob > <i>F</i>
Gravel				
Sediment composition (two-way, crossed ANOVA)				
Reserve status	1	0.41275	14.2259	0.0023
Tidal height	1	0.03980	1.3684	0.2631
Reserve status \times tidal height	1	0.09461	3.2529	0.0945
Sand				
Reserve status	1	0.64760	21.8217	0.0004
Tidal height	1	0.00248	0.0836	0.7770
Reserve status \times tidal height	1	0.01189	0.4006	0.5377
Fines				
Reserve status	1	0.00086	0.0019	0.9662
Tidal height	1	0.04090	0.0886	0.7707
Reserve status \times tidal height	1	0.00908	0.0197	0.8906

Table 1 (Contd.)

	<i>df</i>	Sum of squares	<i>F</i> ratio	<i>P</i> value
Correlation with percent fines (ANOVA)				
<i>Protothaca</i>	1	67.58465	29.855	0.001
<i>Venerupis</i>	1	0.026355	0.007	0.94
	<i>df</i>	Value	Exact <i>F</i>	Prob > <i>F</i>
(b) Experimental results				
Species richness (two-way, crossed MANOVA)				
Holes				
Digging	1	1.18518	14.2222	0.0027
Caging	1	0.29629	3.5556	0.0838
Time	1	0.13298	1.5957	0.2305
Fill				
Digging	1	0.01342	0.1611	0.6952
Caging	1	0.27181	3.2617	0.0960
Time	1	0.00365	0.0438	0.8377
	<i>df</i>	Value	Exact <i>F</i>	Prob > <i>F</i>
Polychaete abundance (one-way MANOVA)				
Hole				
Digging	1	1.02819	14.3947	0.0020
Time	1	7.54067	105.5694	<0.0001
Digging×time	1	0.45954	6.4335	0.0237
Fill				
Digging	1	0.02301	0/3223	0.5792
Time	1	0.07891	1.1047	0.3110
Digging×time	1	0.34973	4.8962	0.0440

Interactions between all factors in the species richness two-way, crossed MANOVA were not significant and not included in the table

Experimental results

Experimental digging had a clear negative impact on the infauna in the English Camp reserve. “Hole” samples had significantly reduced species richness compared with control samples at both 1 week and 5 weeks (Fig. 5, Table 1b). The caging treatment had no significant impact on species richness and there was no difference over time among samples. There was also no difference between the “fill” samples and the controls due to digging (Fig. 5, Table 1b), caging, or time sampled.

Digging had a significant impact on the total abundance of polychaetes, which comprised a majority of the infaunal individuals. Polychaete abundance was greatly reduced in holes, and there was a change in effect over time (Table 1b). At week 1, abundances were reduced to such low levels that no further reduction could be observed in week 5. There was also a significant interaction between digging and time, indicating that these two factors are not independent of each other in their effect on polychaetes. Again, there was no difference in the fill areas versus the controls due to digging (Fig. 6, Table 1b) or time. Multivariate analyses of the whole infaunal community further illustrate these trends (Fig. 7). Each point represents the community in one sample, and closer points have more similar communities (both species and abundances). Control and Fill samples are similar, with no clear trend among the different weeks.

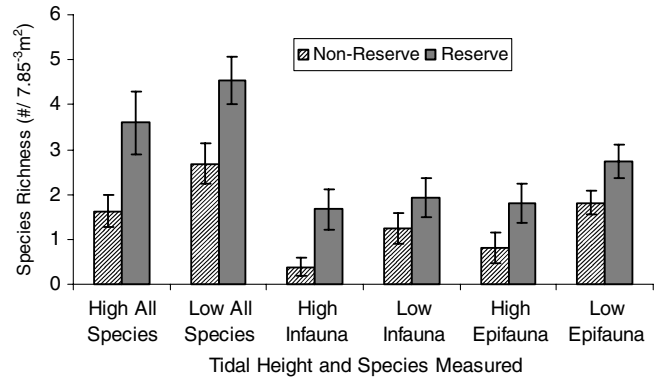


Fig. 4 Average non-clam species richness: reserves vs. non-reserve sites. Species density per core pooling all reserve sites and non-reserve sites by tidal height. Bars as in Fig. 3

The Hole samples, on the other hand, are all outside the ‘cloud’ of Control and Fill points, and they show very high variability both within and among times. ANOSIM analyses showed strong differences among treatments ($P=0.001$), but pairwise tests showed no differences between Fill and Control communities. The Fill and Control cores contained more of almost all families of polychaetes (capitellids, orbinids, lumbrinerids, and spionids) than the Holes, while the Holes contained more of only two taxa, the opheliid *Armandia brevis*, and the dorvilleid *Protodorvillea gracilis* (represented by very few individuals). Overall changes through time in the treatments were gradual, with communities differing between weeks 0 and 5 but not at intermediate times.

Both the sediment composition and the organic content were variable among samples, showing no clear pattern (Table 3). There was no correlation between

Table 2 Proportion of gravel, sand, and fines per tidal height by survey site

Site	Tidal height	Gravel	Sand	Fines
Argyle	Low	0.944	0.045	0.011
Argyle	High	0.619	0.380	0.002
ECC	Low	0.531	0.361	0.107
ECC	High	0.173	0.165	0.662
Shaw	Low	0.546	0.412	0.042
Shaw	High	0.456	0.516	0.028
ECO	Low	0.199	0.566	0.235
ECO	High	0.261	0.640	0.099
SS	Low	0.294	0.681	0.025
SS	High	0.290	0.704	0.006
Reid	Low	0.094	0.864	0.042
Reid	High	0.376	0.578	0.046
Bell	Low	0.363	0.589	0.049
Bell	High	0.299	0.605	0.096
MB	High	0.245	0.727	0.028
ES	Low	0.003	0.986	0.012
ES	High	0.001	0.990	0.009

Survey site abbreviations are the same as in Fig. 1 and reserve site names are in bold. Tidal height definitions are as follows: Low = approximately 0.5 m above MLLW; High = approximately 1.0 m above MLLW. $N = 1$ for all sites. There was no sample for M B Low

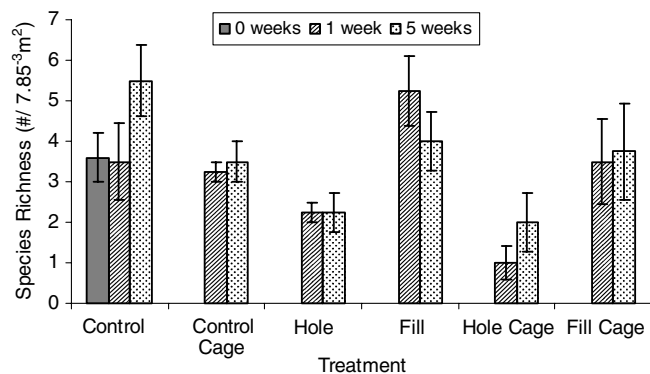


Fig. 5 Average non-clam species richness per treatment, English Camp Closed. Species density per core by treatment sampled. The unmanipulated control treatment was sampled only at time zero ($n=5$) and all experimental treatments were sampled in weeks 1 and 5 ($n=8$). Bars as in Fig. 3

percent fines and percent organic material ($r^2=0.0003$, $P=0.158$); however, sample sizes were extremely small.

Discussion

Prohibiting recreational clam digging in reserves has a significant effect on soft sediment community composition of protected beaches. Reserve effects are illustrated by increased diversity, abundance of harvested clam species (Fig. 3), non-clam species richness (including both epifauna and infauna, Fig. 4), and overall community composition inside reserves. Our survey characterized these beaches only during one 6-week time period, but because the sampling was done at a time of year with little digging (see below), it may be conservative in its estimation of an overall reserve effect.

Physical factors such as wave energy and temperature vary among sites and can affect community composition (Dethier and Schoch 2005), but using carefully selected sites minimized the influence of factors other than clam digging. There was no difference in sediment conditions among sites that corresponded with reserve status. Addi-

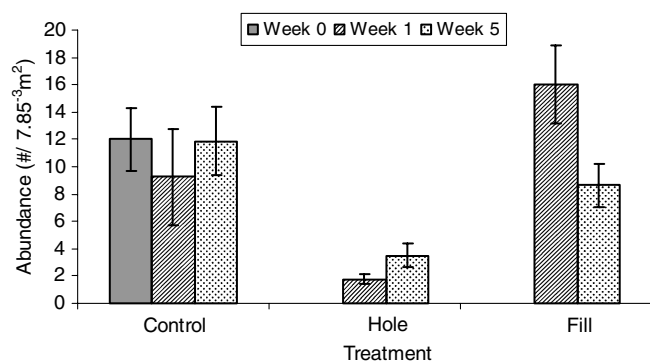


Fig. 6 Average abundance of polychaetes per treatment over time, shown as the density per core. Bars as in Fig. 3

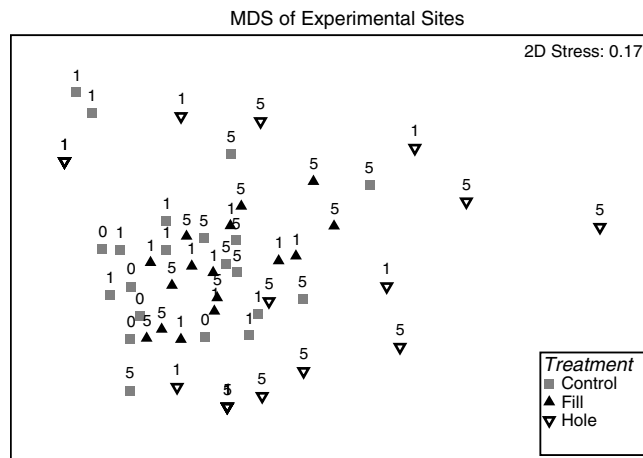


Fig. 7 Non-metric multidimensional scaling plot of community similarities (Bray-Curtis) for all cores in the digging experiment. Closer points indicate greater community similarity. Numbers by each point indicate the time of the sample (0, 1, or 5 weeks)

tionally, while other studies show species richness (especially for polychaetes) correlating positively with the percentage of fines in the beach sediment (Nichols 1970), we did not find this relationship at any of our sites.

The lack of correlation between species richness and physical factors underscores that human harvesters likely drive the observed differences among sites. Clam digging is a popular recreational activity on beaches in the San Juan Islands, and harvest weights generally fall between 1,000 and 60,000 lbs each year at sites throughout Washington State (WDFW 2000). In 2000, our survey sites had between 400 and 600 user trips (WDFW 2000). In the summer, accessible clam-rich zones of these popular beaches often appear to be entirely disturbed, suggesting that turnover of sediment may be rapid. This magnitude of harvest has the potential to decrease not only clam abundance, but also cause habitat changes that directly reduce the richness and abundance of other species within the affected area.

Our experimental results from disturbance experiments at the English Camp reserve indicate that digging and not refilling clamming holes reduces preferred habitat but does not cause direct mortality of infauna. The experimental clamming holes showed a significant negative effect of disturbance on species richness (Fig. 5), and

Table 3 Average proportion and standard error of gravel, sand, fines, and organic material per treatment

	Gravel	Sand	Fines	Organics
Control	0.478±0.052	0.303±0.019	0.218±0.045	0.031
Control Cage	0.209±0.069	0.368±0.043	0.422±0.107	0.041
Hole	0.590±0.037	0.230±0.020	0.181±0.050	0.021
Hole Cage	0.604±0.036	0.252±0.011	0.144±0.032	0.026
Fill	0.619±0.022	0.276±0.015	0.105±0.009	0.032
Fill Cage	0.543±0.039	0.267±0.042	0.190±0.002	0.019

$N=3$ for all gravel, sand, and fines samples except fill cage where $n=2$. For organic samples $n=1$

an overall change in the community (Fig. 7), while the fill areas were not significantly different from the controls. This suggests that most non-target infauna transferred by clam diggers from a hole to a fill area survive the process and do not migrate elsewhere. The majority of families found in the fill areas are classified by Fauchald and Jumars (1979) as discreetly motile or sessile, including Spionidae, Cirratulidae, Nereidae, Lumbrineridae, and Terebellidae. Discreetly motile organisms may move to forage for food, but are functionally sessile in between feeding bouts. Worms classified as motile, primarily Capitellidae and Orbiniidae, were also found in fill areas but apparently did not re-colonize the holes, corresponding to observations by Dernie et al. (2003) that opportunistic species did not immediately enter disturbed areas. Organism transfer therefore increased the patchiness of distributions in the sediment. This consequence of harvesting was also shown by Skilleter et al. (2005) for polychaetes and amphipods in areas of callinassid shrimp harvest.

Potential long-term consequences of sediment transfer, however, include decreased water circulation to the sediment underneath "fill" piles and therefore reduced oxygen and nutrients. Post-digging mortality may be higher in the summer due to the exposure of disturbed organisms during daytime low tides, when higher temperatures also increase thermal stress (Woodin 1974). Additionally, infauna underneath the fill pile may be adversely affected as fill can increase their burial depth in the sediment. This may ultimately decrease their ability to get food and oxygen from the water column (e.g. for clams) and increase mortality.

Numerous families, for example Capitellids, were absent or in low abundance in the holes. These worms are frequently colonizers of disturbed areas (Fauchald 1977; Kozloff 1990), including the genus dominating these samples, *Mediomastus*. However, digging treatments completely altered the dug area; changes in sediment grain size, organic matter, and oxygen content within holes may have made this habitat unsuitable for these polychaetes, at least over the 5 weeks of this study. Holes collected standing water and partly filled with muddy, fine sediments. Fill areas and controls, by comparison, had much larger grain sizes and a large amount of shell hash, which are characteristic of these beaches.

The only species to occur in relatively high abundance in holes was *Armandia brevis*, an extremely mobile worm common in mixed sediments in the region. They appeared in the samples only from the fifth week, and were not found in either the controls or the fills. Therefore, in the short term, holes are suitable habitat for only a single species on a normally rich and productive beach.

Turning over sediment exposes invertebrates to predators. Previous work by Ferns et al. (2000) found that intertidal invertebrate harvesting frequently provides feeding opportunities for birds. Birds were unlikely to have affected our experiment because low tides during this period occurred after dark, and thus disturbed animals were exposed when few seabirds were foraging.

However, it is likely that during daytime low tides that occur during peak clamming season (spring and summer), bird predation could be a significant cause of infaunal mortality.

Although crab and fish predation on clams can be substantial in the San Juans (e.g., Byers 2005; Meyer and Byers 2005), the lack of a cage effect suggests that crab and fish predation had little effect on infaunal worms in the disturbed areas. Woodin (1974) found that *Cancer magister* is an important predator on polychaetes in the low intertidal zone in this region. Crab surveys at English Camp Closed concurrent with our study found very low abundances of *Cancer gracilis*, and no other cancer crabs (A. Glaub, unpublished), and Byers (unpublished data) found crabs to be more abundant in warmer months. During periods of intense clam digging, predatory crabs and birds are likely to be more abundant and could have a greater effect on infauna.

Our experimental results are consistent with those of Brown and Wilson (1997), who showed that commercial clam and bait-worm digging had a negative impact on several infaunal species after three months of digging treatments. Their experiment was conducted on a heavily dug mudflat, potentially only populated by organisms already adjusted to a high level of disturbance. Skilleter et al.'s (2005) much more intensive harvesting experiment also demonstrated negative effects on polychaete abundances and increased patchiness. Despite a less-intensive digging treatment in our experiment, there were still measurable effects on community composition, perhaps because of slow hole filling at English Camp. The holes had only partially refilled at the time of the second treatment (2 weeks) and not at all by the third treatment (4 weeks), despite periods of stormy weather. Thus, redigging non-filled holes resulted in deeper holes over time (intensifying the treatment) although species response did not increase after week 1. Fill areas continued to show control levels of richness and abundance. Limited clam digging could increase habitat heterogeneity and create a more patchy distribution of polychaetes without decreasing overall system diversity. However, high-intensity clam digging due to high yearly visitation rates could lead to more severe community impacts as entire beaches tend toward hole environments.

Clam digging has a substantial influence on the abundance of both target and non-target species in soft sediment communities. Digging disturbance increases community patchiness and has the potential to decrease community richness, as seen in the overall comparison of reserve versus non-reserve beaches. Year round monitoring of clamming beaches and reserve beaches would provide further insights on digging disturbance. Rotating closures, especially among intensely dug beaches that are already recreationally clammed may stimulate recovery of the whole community. Continuing research on the impacts of harvesting disturbance in soft sediment intertidal communities is essential, along with the application of that research to management plans.

Acknowledgements Assistance in the field of Amy Glaub, Courtney Lyons, Jessica Harm, Abby Lunstrum, Marcos Toran, and Jenny Selgrath was greatly appreciated. Craig Staude helped with the sediment analysis. Thank you to all the MPA apprentices and the Friday Harbor Labs community for encouragement and support, and to the National Park Service for access to the English Camp Historic Site and English Camp National Park. A grant from the Mary Gates Foundation made this research possible. The experiments performed in this research complied with all current laws of the United States.

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