ELSEVIER

Journal of Experimental Marine Biology and Ecology 335 (2006) 39–51

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland

William S. Rodney [a], Kennedy T. Paynter [a,b,*]

[a] *Marine, Estuarine, Environmental Sciences Program, Room 0105 Cole Field House, University of Maryland, College Park, Maryland 20742, United States*

[b] *Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, One Williams Street, Solomons, MD 20688, United States*

Received 2 May 2005; received in revised form 20 January 2006; accepted 25 February 2006

Abstract

Maryland's recently created oyster restored reefs provide us with a unique opportunity to observe the abundance and species composition of macrofauna assemblages on unexploited reefs with high concentrations of mature oysters and undisturbed reef architecture. They might thus be used to better understand the magnitude of losses to reef dwelling macrofauna communities, and the associated loss of ecological functions resulting from reef destruction. We sampled reef macrofaunal assemblages on restored plots at four restored oyster reefs and adjacent non-restored plots located outside restored boundaries. We then compared the effects of study site location, and habitat quality (restored versus non-restored) on macrofaunal density using thirteen response variables. Density of macrofauna was an order of magnitude higher on restored reefs, epifaunal density was more than twice as high on restored reefs and sessile macrofaunal density was two orders of magnitude higher on restored reefs. Three out of the five dominant taxonomic groups were much more abundant on restored plots. Mean amphipod density was 20 times higher on restored plots and densities of xanthid crabs and demersal fish were both four times greater on restored plots. Two out of four functional feeding groups: suspension feeders and carnivore/omnivores, were more abundant on restored plots. Since reef macrofauna include many important fish prey species, oyster reef restoration may have the potential to augment fish production by increasing fish prey densities and fish foraging efficiency.

Keywords: *Crassostrea virginica*; Functional feeding group; Macrofauna; Oyster reef; Restoration ecology

1. Introduction

Large complex reefs created by eastern oysters (*Crassostrea virginica*) were once a prominent feature of the Chesapeake Bay ecosystem. By the early 20th century, overfishing had decimated the Bay's oyster population (Kennedy and Breisch, 1981; Jackson et al., 2001). In the mid and late 20th century two diseases, MSX and Dermo, further reduced the Bay's struggling oyster population (Ford and Tripp, 1996). Today the Bay's oyster population is a small fraction of its historic levels, and this has likely had a profound effect on

* Corresponding author. Tel.: +1 301 405 6893; fax: +1 301 314 4139.

E-mail address: paynter@umd.edu (K.T. Paynter).

0022-0981/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2006.02.017

the ecological functions once provided by oyster reefs (Newell, 1988; Newell and Ott, 1999). Unfortunately, a paucity of data describing Chesapeake Bay oyster reef fauna prior to the mid 1900s exists. Maryland's recent oyster restoration effort provides us with an opportunity to analyze the composition of macrofaunal assemblages on restored reefs with high concentrations of large oysters and undisturbed reef architecture in upper Chesapeake Bay. Therefore, we have utilized them to assess the ecological roles of oyster reefs and reef dwelling macrofaunal communities.

We quantified the differences in benthic macrofaunal community composition between three to five year old restored plots on sanctuary oyster bars and nearby degraded non-restored plots in the mesohaline portion of Chesapeake Bay. Our goal was to assess whether reef restoration resulted in increased density and/or species richness of benthic macrofauna and a more complex trophic structure with more energy being transferred to higher trophic levels.

2. Materials and methods

2.1. Study sites

Benthic macrofaunal assemblages were sampled at four sanctuary oyster reefs in the mesohaline region of Chesapeake Bay: Chinks Point, Neal Addition, Spaniard Point and Howell Point. Each site was located in a different Chesapeake Bay subestuary: the Severn, Patuxent, Chester and Choptank Rivers respectively. For each restored (treatment) site a nearby, paired non-restored (control) site was also sampled. Restored reefs were defined as areas having been restored with fresh oyster shell and topped with a layer of shell that was seeded with live juvenile oysters. They were protected from oyster harvesting activities and were three to five years old at the time of sampling. These reefs had high densities (mean of 173 oysters m^{-2}) of adult oysters embedded in a thick matrix of living and dead oysters and oyster shell. A large scale, experimental, oyster restoration program established these areas to recreate subtidal oyster reefs similar to those that normally would have resulted from high densities of natural settlement. Non-restored reefs were defined as areas located on the same historic oyster bars, according to Maryland Department of Natural Resources maps (Smith, 1997), as the restored plots but not restored with new shell or oyster seed. Non-restored plots typically contained dead oyster shells buried beneath up to several centimeters of silt. Non-restored sites were between 0.16 and 0.8 km from their paired treatment sites and located in similar water depth (3 to 5 m). Criteria for our site definitions were verified visually for each sampling location by SCUBA divers. Water quality information for the four study sites was obtained from the Maryland Department of Natural Resources Water Quality Monitoring Program. Water temperature ranged from 0.9 to 28.8 °C with a mean of 22.3 °C. Salinity ranged from 5.3 to 18.5 with a mean of 10.3. Dissolved oxygen ranged from 0.2 to 13.0 mg l^{-1} with a mean of 5.9 mg l^{-1}.

2.2. Sampling procedures

Sampling units were plastic bakery trays (50 × 58 × 10 cm) lined with fiberglass window screen, and randomly assigned to sites and treatments. Three trays were deployed on each plot. Nylon ropes of randomly assigned length (≥ 2 m) linked the trays together and were attached to nearby buoy anchors or anchor screws. SCUBA divers excavated holes in the bottom substrate and placed the excavated material into the trays. These trays were then inserted into the holes created by excavation. Care was taken to transfer the restored reef materials into trays with as little disturbance as possible and to place reef materials in the trays without changing the orientation of the oysters relative to flow direction or the vertical dimension. This was done to preserve the reef structure created by the growing oysters and shell. Trays were allowed a minimum of 6 weeks colonization time. During tray retrieval, caps were placed over the trays by SCUBA divers. Caps were then secured with elastic cords. The trays were then lifted aboard a boat where trays and their contents were placed in plastic bags and taken to shore for field processing. To collect and sort the fauna, the retrieved trays were placed upright on a sieving apparatus that consisted of two sieves with large (1.6 cm^2 mesh size) and small (1 mm^2 mesh size) mesh stacked on a special sieving platform. All visible motile organisms were removed and placed in jars containing 70% ethanol. Clumps of oysters, single oysters and all loose shells were dunked and agitated in buckets of water to dislodge cryptic organisms. Buckets were then poured through a sieve (1 mm^2 mesh size) and organisms collected were preserved in 70% ethanol. Trays were then inverted onto the large sieve and gently rinsed with ambient bay water. Organisms attached to the trays were not included in the samples in order to minimize any tray effect. Materials retained on the large sieve were similarly rinsed and all live organisms were collected. Remaining materials on the large sieve were placed in plastic bags for further processing in the laboratory. Once cleared, the large sieve was removed and any visible organisms retained on the small sieve were collected. Any materials remaining on

the small sieve were retained in 70% ethanol for further processing. Organisms collected in the field and from preserved samples were identified, enumerated and weighed in the lab. High abundances of amphipods and polychaetes from Howell Point plots made it necessary to subsample these collections. Abundances for these species were estimated using simple random sampling without replacement (Thompson, 2002).

2.3. Habitat characteristics

Three estimates of physical habitat quality were measured: an index of surface complexity, the number of oysters per sample, and the number of oyster "boxes" per sample. The surface complexity index, essentially a chain-length measure, was calculated for each sample by taking a plastic coated copper wire and, starting at one side of the tray, forcing the wire down into the spaces between shells until the wire reached the other end of the tray. The wire was then removed, straightened and measured. The measurement was then divided by the straight line length of the tray to give a dimensionless index of surface roughness. This method, adapted from the sinuosity index used in freshwater stream ecology (Allan, 1995), returns a value of 1 for a flat surface and grows larger as surface complexity increases. Since oysters provide the physical substrate for the reef community, the density of oysters is a direct measure of habitat quality. Therefore, we counted all live oysters in each sample. We also counted the number of intact shells of recently deceased oysters in each sample. These intact (still articulated by the hinge ligament) shells, commonly called "boxes," provide nesting sites and shelter for several species of resident fishes and xanthid crabs and are therefore considered to be an important component of reef habitat quality. For a variety of reasons, physical habitat data were not collected from the Neal Addition site.

2.4. Fouling community

All dominant fouling organisms were counted in samples from the Neal Addition site. In subsequent samples, abundances of the dominant fouling organisms (*Ischadium recurvum*, *Balanus* sp., and *Diadumene leucolena*) were estimated by subsampling using the methods described above. Colonial and/or encrusting organisms such as bryozoans and hydroids were recorded as being present or absent. Fouling community data were not included in analyses of faunal density between restored and non-restored plots because these organisms are sessile and thus obligate hard substrate dwellers. Differences in abundance of fouling organisms between restored and non-restored plots were large and, in our opinion, did not warrant statistical analysis. Fouling community data were used in comparisons of functional feeding group densities and mean number of macrofauna species per sample and was included in our species list (Table 1).

2.5. Faunal group density comparisons

We compared the effects of study site and habitat quality (restored versus non-restored) on macrofauna density using eight response variables. Three of these eight response variables were broadly inclusive groups including: (1) total free living macrofauna; (2) epifaunal organisms; and (3) infaunal organisms. The other five response variables were groups of taxonomically related organisms. [(1) xanthid crabs; (2) polychaetes; (3) clams; (4) amphipods; and (5) demersal fish]. Only free living organisms were used for density comparisons because these organisms could, in theory, move between habitat types and are thus capable of demonstrating habitat preferences. We defined "free living macrofauna" as any species that regulates its position on or in the substrate. Free living organisms included xanthid crabs, amphipods, errant polychaetes, demersal fish, clams, gastropods, isopods, caridean shrimp, nemerteans, and flatworms. We defined "epifaunal organisms" as any species that lives part of the time on the upper surface of the substrate. Epifaunal organisms included xanthid crabs, amphipods, demersal fish, gastropods, isopods, caridean shrimp, and flatworms. "Infaunal organisms" were defined as any species that lives most of its life below the upper surface of the substrate. Infaunal organisms included polychaetes, nemerteans, and clams. Counts of organisms per sample were converted to density (organisms m^{-2}) by dividing counts by the area of the settlement trays (0.28 m^2).

The differences between treatments to each response variable were analyzed using a 2-way ANOVA model in a randomized complete block design. Sites were treated as random blocks and treatments (restored and non-restored) were treated as fixed effects. Before any analyses were performed, the ANOVA assumptions of homoscedasticity and normality were evaluated using Levene's test and the Shapiro–Wilkes test respectively. When either test indicated that ANOVA assumptions were violated, graphical analysis of residuals was employed to examine the distribution of the residuals. Either a $\log(x+1)$ transformation or a square root$(x)+0.5$ transformation was used to correct for heteroscedasticity.

When variability in faunal density attributed to site effects was not significant, differences in density

Table 1
Cumulative macrofauna collected on restored and non-restored portions of four historic Maryland natural oyster bars

Latin name	Common name	Totals	
Fish		Restored	Non-restored
Gobiosoma bosci	Naked goby	452	113
Opsanus tau	Oyster toadfish	6	0
Chasmoides bosquianus	Striped blenny	19	0
Mud crabs			
Panopeus herbstii	Black-clawed mud crab	484	12
Eurypanopeus depressus	Flat mud crab	316	4
Rhithropanopeus harrisii	White-fingered mud crab	917	432
Grass shrimp			
Palaemonetes pugio	Grass shrimp	205	17
Amphipods			
Gammarus tigrinus	Scud	329	8
Gammarus mucronatus	Spined-back scud	88	6
Corophium lacustre	Slender tube builder	1230	1018
Leptocheirus plumulosus	Common burrower	0	641
Melita nitida	Scud	4464	24
Clams			
Mya arenaria	Soft shell clam	431	410
Macoma sp.	Hard clam	450	542
Gemma gemma	Gem clam	0	7
Mulinia lateralis	Little surf clam	0	63
Polychaetes			
Neanthes succinea	Common clam worm	4226	1562
Steblospio benedicti		0	2
Heteromastis filiformis	Capitelid thread worm	2	50
Arabella iricolor	Opal worm	0	5
Pectinaria gouldii	Trumpet worm	14	445
Other motile taxa			
Stylochus ellipticus	Oyster flatworm	10	3
Micrura leidyi	Red ribbon worm	0	4
Calinectes sapidus	Blue crab	0	1
Urosalpinx cinerea	Oyster drill	0	4
Cyathura polita	Slender isopod	0	1
Unidentified snail	Snail	3	1
Idotea sp.	Isopod	6	11
Edotea sp.	Isopod	1	0
Total motile organisms		13,653	5386
Fouling organisms			
Mogula manhatenensis	Sea squirt	179	45
Ischadium recurvum	Recurved mussel	11,456	52
Balanus sp.	Barnacle	11,129	339
Diadumene leucolena	White anenome	259	83
Garveia franciscana	Rope grass	Present	Present
Membranipora sp.	Encrusting bryozoan	Present	Present
Total fouling organisms*		23,023	519
Total macrofauna*		36,676	5905

Totals represent fauna collected from a cumulative area of approximately 3.5 m^{-2}.

attributed to treatments were compared using data pooled among sites. In certain cases, single species that were numerically dominant within groups were analyzed separately to determine if life history differences among species confounded the results of the group analysis.

2.6. Functional feeding group density comparisons

Organisms were aggregated into functional feeding groups in order to assess the community level effects of restoration on ecosystem structure and function. We used the USEPA Chesapeake Bay Program's classification system (Ranasinghe et al., 1994) to assign functional feeding groups to specific taxa. In some cases functional feeding group membership was determined from other published sources. Four functional feeding groups were used in our analysis. These groups were: deep deposit feeders, surface deposit feeders, suspension feeders, and carnivore/omnivores. "Deep deposit feeders" are those organisms that feed on biodeposits below the sediment surface. "Surface deposit feeders" are organisms that feed on biodeposits at the sediment–water interface. "Suspension feeders" are organisms that filter plankton from the overlying water column. "Carnivore/omnivores" feed on other organisms but may also ingest significant amounts of non-living materials (biodeposits) either intentionally or while foraging for live prey. Differences in functional feeding group densities between restored and non-restored plots were compared using the same statistical procedures used for the other faunal groups.

3. Results

3.1. Physical habitat quality

Structural heterogeneity, as measured by our surface complexity index, was much greater on restored plots compared to non-restored control plots. Mean surface complexity index values were 1.84 (+/−0.15, SEM) versus 1.15 (+/−0.05) for restored and non-restored plots respectively. Mean oyster density on restored plots was 173 m^{-2} (+/−25.5). Mean density of oyster boxes on

restored plots was 70.6 m^{-2} (+/− 10.0). Oysters and oyster boxes were absent from samples of non-restored plots.

3.2. General description of faunal assemblages

We collected more than 19,000 free living macrofaunal organisms during the course of this study. Of these, 70% were collected from restored plots. If we include sessile or "fouling" organisms (barnacles, mussels, anemones and tunicates) in the total, then more than 40,000 organisms were collected with 86% from restored plots (Table 1). Thirty five species from twelve taxonomic groups were represented. Five taxonomic groups accounted for more than ninety five percent of all organisms: xanthid crabs (Xanthidae), polychaete worms (Polychaeta), clams (Bivalvia), amphipods (Amphipoda), and demersal fish (Teleostei). The other seven groups included portunid crabs (Portunidae), caridean shrimp (Caridea), isopods (Isopoda), nemerteans (Nemertea), flatworms (Platyhelminthes), gastropods (Gastropoda), and cnidarians (Scyphozoa). These seven groups were sparsely represented in the samples and made up less than five percent of all organisms. Free living macrofauna were more than twice as abundant on restored habitats compared to non-restored habitats (Table 1).

More than 23,000 fouling organisms were collected with 97% coming from restored plots. Fouling organisms were two orders of magnitude more abundant in restored plots compared to non-restored plots. The dominant fouling organisms were the recurved mussel (*Ischadium recurvum*) and balanoid barnacles (*Balanus* sp.). Mean mussel density was 3409.5 m^{-2} (+/− 1055.5) and 15.5 m^{-2} (+/− 7.0) on restored and unrestored plots

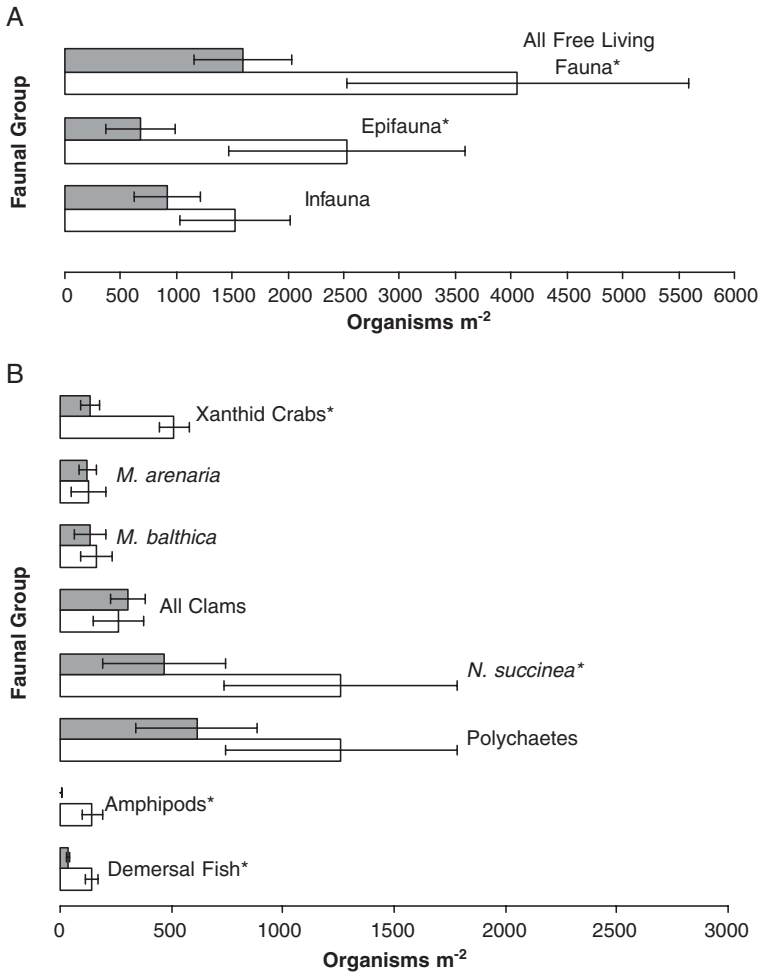

Fig. 1. Comparisons of mean faunal densities in restored (white bars) and non-restored (grey bars) plots for 3 broadly inclusive functional groups (A), and 8 taxonomic groups (B). Error bars represent +/− 1 SEM. Asterisks following group titles indicate statistically significant differences. Amphipod data for Howell Point is not included.

respectively. Mean barnacle density was 3312.3 m^{-2} (+/−1408.9) and 100.9 m^{-2} (+/−66.9) on restored and unrestored plots respectively. The white anemone (*Diadumene leucolena*) was also common. Colonies of encrusting bryozoans (*Membranipora* sp.) and hydroids (mostly *Garveia franciscana*) were extremely abundant on all restored plots but only occasionally observed in non-restored plots. Abundance of free living macrofauna and fouling organisms combined was an order of magnitude higher on restored plots compared to non-restored plots (Table 1). The average number of species per sample was significantly higher on restored plots (14.9) compared to non-restored plots (12.0) (paired *t* test, $p<0.05$).

3.3. Comparisons of faunal densities

The density of free living macrofaunal organisms (log $(x+1)$ transformed) was more than twice as high on restored plots compared to non-restored plots (Fig. 1A; $F=35.45$, $p<0.0001$). Epifaunal organisms were also found at more than twice the density in restored plots compared to non-restored plots ($F=50.77$, $p<0.0001$). No differences in infaunal density (square root $(x)+0.5$ transformed) between restored and non-restored plots were detected ($F=2.29$, $p=0.1469$). Amphipods were the most abundant taxonomic group in our samples and made up 41% of all organisms. A total of 7808 amphipods representing four genera in four families of the Suborder Gammaridea were collected. These four genera were *Melita* (Melitidae), *Corophium* (Corophiidae), *Leptocheirus* (Aoridae), and *Gammarus* (Gammaridae) made up 57.5%, 28.8%, 8.2%, and 5.5% of all amphipods respectively. 2 way ANOVA revealed a strong effect of Site on amphipod density ($F=7.12$, $p=0.0021$). Comparisons of least square means identified the Howell Point site as the source of this variability. Amphipod density was extremely high in both restored and non-restored plots at Howell Point compared to the other sites (Fig. 2B). Between sample variability in amphipod density was also extremely high in both restored and non-restored plots at Howell Point. For these reasons, we treated Howell Point as an outlier with respect to amphipod density. When Howell Point was excluded from the analysis, no significant differences in amphipod density were found among sites ($F=1.75$, $p=0.2103$). Amphipod density was 20 times higher in restored plots compared to non-restored plots ($F=10.59$, $p=0.0058$) (Fig. 1B). There was no difference in amphipod density between restored and non-restored plots from Howell Point (Fig. 2B).

Polychaetes were the second most abundant taxonomic group in our samples and accounted for 33% of all organisms. Two species dominated the counts, *Neanthes succinea* and *Pectinaria gouldii*, which made up 91% and 7% of all polychaetes respectively. Three other polychaete genera, *Heteromastus*, *Arabella*, and *Streblospio* were present in small numbers. Polychaete densities were on average twice as abundant on restored plots compared to non-restored plots ($F=6.64$, $p=0.0185$; Fig. 5). The 2 dominant polychaete species were clearly associated with different treatments. The tube building polychaete *Pectinaria gouldii* was found exclusively at the Neal Addition site and was found in greater densities in the non-restored plots at that site ($F=14.74$, $p=0.0185$). The errant polychaete, *Neanthes succinea*, was the most abundant polychaete in our samples and was present in every sample from every site. Density of *N. succinea* (log $(x+1)$ transformed) was

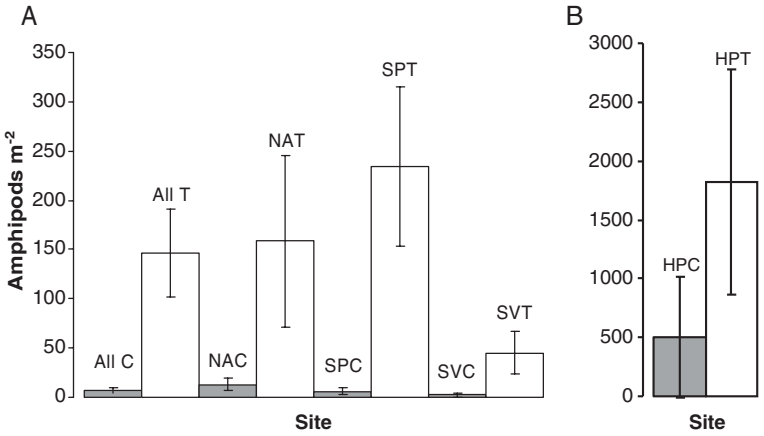

Fig. 2. Mean amphipod density for (A) all sites combined (All), Neal Addition (NA), Spaniard Point (SP), Severn (SV) and (B) Howell Point (HP). Site labels ending with 'C' (grey bars) are control (non-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/−1 SEM. See text for significance.

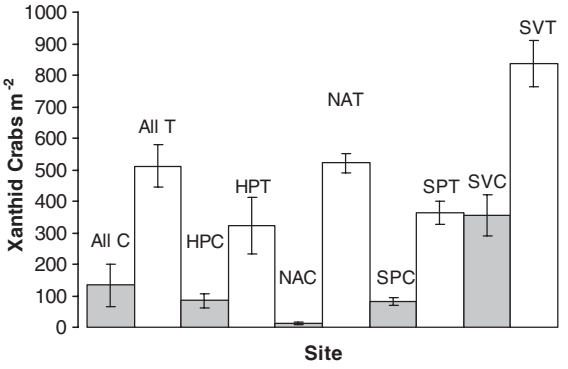

Fig. 3. Mean xanthid crab density for all sites combined (All), Howell Point (HP), Neal Addition (NA), Spaniard Point (SP), and Severn (SV). Site labels ending with 'C' (grey bars) are control (non-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/−1 SEM. See text for significance.

significantly higher in restored plots compared to non-restored plots ($F=24.2$, $p<0.0001$).

Xanthid crabs (mud crabs) were the third most abundant organisms in the samples and made up 11% of all individuals collected. Three species were represented, *Rhithropanopeus harrisi*, *Panopeus herbstii*, and *Eurypanopeus depressus*, which made up 62%, 22%, and 15% of all mud crabs respectively.

Mud crab density (square root $(x)+0.5$ transformed) was not significantly different when compared among sites (2-way ANOVA; $F=0.0$, $p>0.99$) (Fig. 3). Mud crab density was more than four times higher in restored plots compared to non-restored plots (2-way ANOVA; $F=85.64$, $p<0.0001$) (Fig. 1B).

Clams were the fourth most abundant group of organisms in our samples and made up 10% of all organisms. We collected 1903 clams representing four genera in four families. Of these four genera, three were identified to the species level: *Mya arenaria* (Myacidae), *Mulinia lateralis* (Mactridae), and *Gemma gemma* (Veneridae). The fourth genus, *Macoma* sp. (Tellinidae), was probably dominated by the Baltic clam (*M. balthica*). A close congener, *M. mitchelli*, may have also have been present but time constraints limited our ability to distinguish the species. Although both species occur in the study region, average density of the *M. balthica* is typically an order of magnitude greater than that of *M. mitchelli* in the mesohaline region of Chesapeake Bay (Gerritsen et al., 1994). Clams collections were dominated by *Macoma* sp. (52%) and *Mya arenaria* (44%). *Mulinia lateralis* and *Gemma gemma* were collected in small numbers. Tests of homoscedasticity and normality revealed that clam density data were not normally distributed. Graphical analysis did not suggest any particular pattern to the data and various transformations did not satisfy the normality assumption. Therefore, it was decided that densities of the two dominant clam species should be analyzed separately.

Macoma sp. densities did not satisfy tests of ANOVA assumptions. Tests of homoscedasticity and normality revealed that hard clam density data were not normally distributed. Graphical analysis did not suggest any particular pattern to the data and various transformations did not satisfy the normality assumption. Therefore, the nonparametric Wilcoxon rank sums test was used as an alternative method. No significant differences in *Macoma* sp. densities on restored versus non-restored plots were detected (Fig. 1B).

The Soft Clam (*Mya arenaria*) was the second most abundant clam species in our samples. Tests of homoscedasticity and normality revealed that soft clam density data were not normally distributed. Visual inspection did not suggest any particular pattern to the data and various transformations did not satisfy the normality assumption. Therefore, the nonparametric Wilcoxon rank sums test was used as an alternative method. When treatments were compared using pooled data, densities of *M. arenaria* were significantly higher on non-restored plots (t approximation, $p<0.05$) (Fig. 1B).

Demersal fish were the fifth most abundant faunal group in our samples and made up 3% of all organisms. One species, the naked goby (*Gobiosoma bosci*), made up more than 95% of all demersal fish collected. Other species present in the samples included striped blennies (*Chasmoides bosquianus*) and oyster toadfish (*Opsanus tau*). Mean density of demersal fish ($\log(x+1)$ transformed) was not significantly higher in comparisons among sites ($F=0.00$, $p>0.99$). However, demersal fish

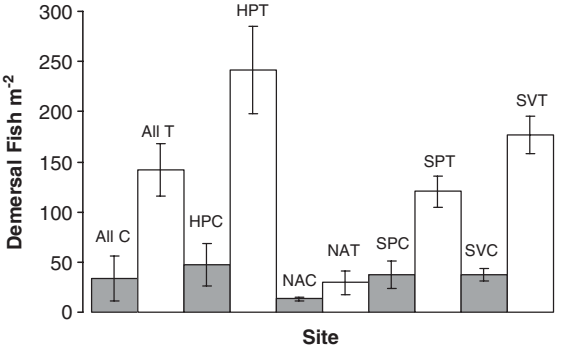

Fig. 4. Mean demersal fish density for all sites combined (All), Howell Point (HP), Neal Addition (NA), Spaniard Point (SP), and Severn (SV). Site labels ending with 'C' (grey bars) are control (non-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/−1 SEM. See text for significance.

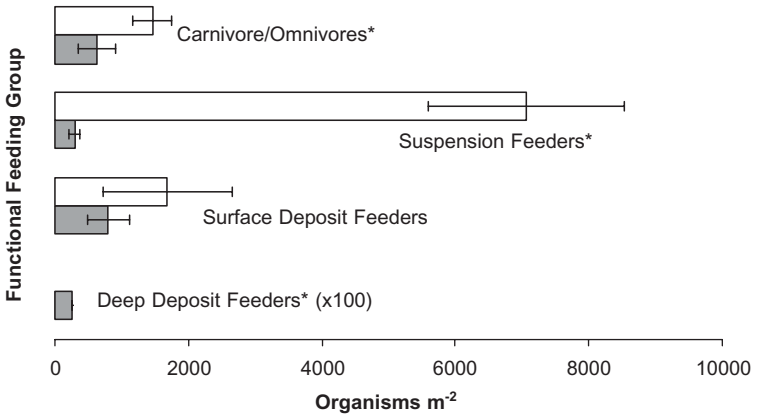

Fig. 5. Comparisons of mean functional feeding group densities in restored (white bars) and non-restored (grey bars) plots. Error bars represent +/− 1 SEM. Asterisks following group titles indicate statistically significant differences. Data from the Howell Point outlier site were omitted for the amphipods.

density was four times higher in restored plots compared to non-restored plots ($F=32.56$, $p<0.0001$) (Figs. 1B and 4).

3.4. Comparisons of functional feeding group densities

Analysis of functional feeding groups indicated that reef restoration resulted in a more complex trophic structure and increased energy sequestered in higher trophic levels. Two of the four functional feeding groups were found in significantly higher densities on restored plots. Only one group, deep deposit feeders, was found in higher densities on non-restored plots (Fig. 5). Deep deposit feeders were absent from samples from restored plots and occurred only sporadically in samples from non-restored plots. Mean density of deep deposit feeders on non-restored plots was 2.5 organisms m^{-2}. Data for deep deposit feeders did not satisfy ANOVA assumptions of normality and homoscedasticity so differences in density between habitats were assessed using the nonparametric Wilcoxon rank sums test. The difference in deep deposit feeder density between the two habitats was statistically significant (t approximation, $p<0.05$). There was no difference in density of surface deposit feeders between restored and non-restored plots ($F=0.98$, $p>0.05$). Density of suspension feeders was an order of magnitude greater on restored plots compared to non-restored plots ($F=127.5$, $p<0.0001$). Mussels (*I. recurvum*), barnacles (*Balanus* sp.), and soft shell clams (*M. arenaria*) were the numerically dominant suspension feeders and accounted for 46.5%, 46.4% and 3.4% of all suspension feeders respectively. Carnivore/omnivore density was twice as high on restored plots ($F=34.29$, $p<0.0001$) compared to unrestored plots.

4. Discussion

Our primary goal was to assess habitat value of structurally complex, undisturbed oyster reef habitat in the mesohaline portion of Chesapeake Bay. To do this we compared benthic faunal assemblages on mature, undisturbed, restored reefs (3 to 5 years old) to those on non-restored oyster reefs. Restored reefs exhibited greater structural complexity than non-restored reefs due to the presence of large numbers of live oysters and oyster boxes. Provision of habitat for a diverse community of benthic macrofauna is an important ecological function of oyster reefs. Undisturbed oyster reefs, naturally settled or restored, are comprised of hundreds of oysters m^{-2} most of which are oriented vertically from the bottom. This orientation and the structurally complex surface it creates provide a unique habitat to benthic organisms. The loss of this habitat through the destructive effects of fishing gear, and subsequent high rates of oyster mortality due to oyster disease has resulted in the loss of tens of thousands of acres of valuable benthic habitat in Chesapeake Bay. Our results show reef restoration can restore reef community structure to a certain degree. We found that the mean number of macrofauna species per sample was greater on restored plots (14.9) compared to non-restored plots (12.0) (paired t test, $p<0.05$). Total macrofauna abundance (free living + fouling organisms) was an order of magnitude higher on restored plots, free living macrofauna were twice as abundant on restored plots and fouling organisms were two orders of magnitude more abundant on restored plots. Also, three out of the five dominant taxonomic groups were much more abundant on restored plots. Mean amphipod density was 20 times

higher on restored plots and densities of xanthid crabs and demersal fish were both four times greater on restored plots. Furthermore, closer examination of infaunal community composition revealed that the numerically dominant polychaetes species (*Neanthes succinea*) was also significantly more abundant on restored reef habitats. Since many of the species that benefited from reef restoration are also important fish prey items, restoration clearly has the potential to increase the fish habitat value of the Bay's degraded oyster bars. By providing high quality habitat to a variety of ecologically important species, several other aspects of reef ecological function may be greatly improved thus further increasing the intrinsic value of reef systems in terms of ecosystem services.

Analysis of functional feeding groups indicated that reef restoration improved two important reef ecological functions: increased grazing rates (water filtration) and subsequent transfer of energy from the plankton community to the benthos, and increased transfer of energy to the higher trophic levels of the reef community. The high density of suspension feeders on restored reefs clearly indicates that the water filtration/plankton grazing function of the reef system was restored. The vertical orientation, high oyster densities, and the ample hard substrate for other suspension feeders combine to maximize the density of suspension feeders per unit of benthic surface area. The loss of suspension feeding due to destruction of oyster reef cannot be replaced by the establishment of benthic infaunal suspension feeders in the same amount of space (Newell and Ott, 1999) and the ability of dense assemblages of suspension feeding organisms to influence phytoplankton dynamics has been demonstrated in several systems for several species (Cloern, 1982; Cohen et al., 1984; Newell, 1988; Dame et al., 1992; Roditi et al., 1996,). Such effects have also been predicted in modeling studies (Ulanowicz and Tuttle, 1992; Newell, 1988, 2004; Newell et al., 2004).

The higher densities of carnivore/omnivores that we observed on restored reefs is consistent with a scenario whereby energy is removed from the water column by suspension feeders and transferred to the benthic subsystem in the form of feces and psuedofeces. These biodeposits, in turn, are grazed by surface deposit feeders that are then preyed upon by carnivore/omnivores. Since the latter two categories are the highest trophic levels of the reef resident community, the net effect is a transfer of energy to higher trophic levels. The loss of dense suspension feeders from reef systems results in a simplified food web and a trophic bottleneck wherein energy from the plankton community is largely prevented from reaching the carnivore/omnivore component of the reef system. Such trophic bottlenecks have been predicted by modeling studies (Ulanowicz and Tuttle 1992, Newell, 1988) and have been implicated as a cause of decreased fish biomass production in polluted lakes (Sherwood et al., 2002).

Another important oyster reef ecological function may be that of providing foraging grounds for predatory fishes thus facilitating the transfer of energy from the benthos to higher trophic levels. Peterson et al. (2003) synthesized several studies of fish utilization of restored oyster reefs to estimate that restoration of 10 m^2 of reef in the Southeast United States results in an additional 2.57 kg 10 m^{-2} $year^{-1}$ of fish biomass. This relationship was derived from studies of reefs in the Southeast United States and may need to be adjusted to better fit our study area. However, our results suggest that reef restoration has the potential to increase the biomass of prey items available to fish predators. Many of the organisms that were significantly more abundant on restored reefs are also known to be important food items for several commercially and recreationally important finfish species. In mesohaline areas of Chesapeake Bay, these fishes include several species of the drum family (Sciaenidae) such as Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and weakfish (*Cynoscion regalis*); and two members of the temperate bass family: white perch (*Morone americana*) and striped bass (*Morone saxatilus*). Diets of adult spot, croaker, and white perch are primarily composed of benthic prey such as polychaetes, mollusks, small crustaceans, and small demersal fish (Homer and Boynton, 1978; Chao and Musick, 1977). Benthic prey also make up a large proportion of juvenile weakfish and striped bass diets (Stickney et al., 1975; Hartman and Brandt, 1995; Gardinier and Hoff, 1982) but these species become increasingly piscivorous as they grow larger. In the past several decades, commercial catches of all of these species have declined (Murdy et al., 1979). The destruction of oyster reefs has not received serious consideration as a contributing factor in Chesapeake Bay fisheries declines. However, modeling studies generally support a scenario where loss of benthic biomass production results in less biomass transferred up to fish predators. Szyrmer and Ulanowicz (1987) demonstrated how one can calculate the degree of importance to a species' diet for every other species in a given system through both direct and indirect pathways. When this method was applied to the seasonal trophic dynamics of the Chesapeake mesohaline system all of the aforementioned fish species, with the exception of striped bass, were found to depend heavily on the benthos as their energy source. Another estuarine fish predator, the

bluefish (*Pomatomus saltatrix*), was also found to be strongly linked to the benthos. Baird and Ulanowicz (1989) proposed that the current dominance of deposit feeders in the Chesapeake Bay benthos is a relatively recent phenomena and that the loss of dense communities of suspension feeders has likely caused a "trophic restructuring" in the estuary. A modeling study that compared the trophic functioning of three mid-Atlantic estuaries found that Chesapeake Bay was less efficient at producing carnivorous fish than both Delaware and Narragansett bays. Carnivorous fish in Chesapeake Bay relied more heavily on benthic deposit feeders than did their counterparts in the other two systems which relied more heavily on pelagic primary producers and parabenthic shrimp (Monaco and Ulanowicz, 1997).

Another function of oyster reefs is to provide nursery habitat for juvenile fish (Breitburg, 1991, 1999; Breitburg et al., 1995; Coen et al., 1999). Our results suggest that Maryland's restored reefs have ample prey for juvenile fish. However, our sites, though spatially complex, may have been in water too deep to afford juvenile fish much refuge from large predatory fish. The nursery habitat function of restored oyster reefs might be maximized by locating reefs in shallow (<2 m deep) waters where large fish predators are less abundant. This is especially true if reefs are located in areas where other refuge habitats (e.g., seagrass beds and tidal marshes) are scarce or absent (Grabowski, 2002). Shallow water oyster reefs, when located adjacent to deeper waters, can also provide alternative foraging habitats for fish and crabs that are displaced by anoxia/hypoxia below the pycnocline (Lenihan et al., 2001). This function can be optimized by designing reefs for maximum habitat complexity (Grabowski, 2004). Results of our study suggest that it may be possible to design reefs to maximize benthic primary and secondary production. This may facilitate recruitment of amphipods, polychaetes, and other species as we observed on our Howell Point plots.

Comparisons of our results with other published studies are complicated by differences in location, faunal groupings, sampling methods, and other factors. Our results are, however, qualitatively comparable to studies of oyster reef macrofauna in other systems. Lenihan et al. (2001) sampled macrofauna on natural reefs, restored reefs and sand bottom in the Neuse River estuary, North Carolina. They collected 15 species of amphipods, decapods, molluscs and resident fishes from restored and natural reefs combined and only three species from sand bottom. They did not report density of total macrofauna or the mean number of species on restored versus natural reefs. Also, their species list did not include any annelids. The methods of Lenihan et al. (2001) differed from ours in that they used defaunated oyster shells in 0.25 m^2 "traps" that were deployed for seven days whereas our 0.28 m^2 trays were filled on-site with benthic materials containing organisms at ambient densities and deployed for at least six weeks. Therefore, the data describe a very early successional community made up of animals that recently immigrated or recruited to their traps whereas our data describe populations that more closely resemble a mature, undisturbed community. Meyer and Townsend (2000) reported mean numbers of species of 17.3 and 9.6 for restored and natural reef habitats respectively on intertidal salt marsh edge reefs in coastal North Carolina. These results are similar to our mean numbers of species per sample. However, Meyer and Townsend (2000) did not report any annelids in their samples and only reported densities for four macroinvertebrate species. Zimmerman et al. (1989) compared winter and summer densities of infauna and epifauna on natural oyster reef, salt marsh and mud bottom habitats in West Bay, Texas. They found 63 macrofaunal species on oyster reefs in winter compared to 59 in summer. Macrofaunal densities for oyster reefs and salt marshes were similar (~ 430 versus ~ 375 organisms m^{-2} for oyster reefs and salt marshes respectively) and both were significantly greater than macrofaunal densities for mud bottom habitats (~ 100 organisms m^{-2}) (these densities are converted from organisms 0.785 m^{-2} to organisms m^{-2} and averaged across seasons). Bahr and Lanier (1981) combined the results of three earlier studies (Dame, 1979; Bahr, 1974; Lehman, 1974) to report a total of 42 species for natural intertidal reefs in the southeastern United States. Dame (1979) found 37 species and densities ranging from 2476 to 4077 organisms m^{-2} on natural intertidal reefs in South Carolina. Bahr (1974) reported 42 species and a mean density of 3800 organisms m^{-2} on natural intertidal reefs near Sapelo Island, Georgia. Similarly, Lehman (1974) reported 31 species and a mean faunal density of about 6200 organisms m^{-2} from Crystal River, Florida. Frey (1946) reported 41 species of free living epifaunal and infaunal organisms from natural reefs in the Potomac River, Maryland. These results are similar to our 35 species and mean densities of 4057 and 1596 organisms m^{-2} on restored and non-restored sites respectively. Wells (1961) reported 284 species from the Newport River, North Carolina. Wells' study sampled 5 reefs located along a salinity/intertidal–subtidal gradient. When mean number of species per collection was plotted against salinity, a steep drop (from 30 species to 16 species) was observed between 24 and 19 mg l^{-1}. This decline in species richness with decreasing salinity

is similar to that observed for soft bottom benthic fauna in Chesapeake Bay (Boesch, 1972) and probably accounts for much of the lower species counts in our study relative to Wells (1961).

Our study differed from the nine studies mentioned above in several important respects. We sampled mesohaline, subtidal reefs with high densities of mature oysters. Frey (1946) was the only other study we found that matched these conditions and he sampled natural reefs only and only reported presence/absence data for reef organisms (not to mention a time span of more than five decades between the two studies). Only two other studies (Lenihan et al., 2001; Meyer and Townsend, 2000) compared restored reefs to natural reefs and both of these studies were located in higher salinity areas than this study. Also, these two studies were located in coastal North Carolina near the boundary between the Virginian and Carolinian biogeographic provinces (Engle and Summers, 1999; Cerame-Vivas and Gray, 1966). The influence of the more subtropical Carolinian fauna is evident in their species lists. These salinity and biogeographic differences also mean that organisms in these two locations were subjected to a different suite of fish and invertebrate predators than our location. These two studies also used different restoration methods than this study. In Maryland, where natural oyster reproduction is unpredictable, reefs are topped with a layer of shell that is seeded with juvenile oysters in the hatchery. In North Carolina, where oyster spatfall is more predictable, reefs are created by depositing unseeded shell on a site and letting oysters recruit naturally. The remaining six studies (Wells, 1961; Bahr, 1974; Lehman, 1974; Dame, 1979; Bahr and Lanier, 1981; Zimmerman et al., 1989) were all conducted on natural reefs, in different tidal and salinity zones and were located either in or near different biogeographic provinces. Yet in spite of these many differences, a general pattern is evident. Oyster reefs typically support between 33 and 63 macrofaunal species at densities ranging from around 300 to around 6000 organisms m^{-2}.

5. Conclusions

The restored oyster reefs clearly supported higher densities of benthic organisms than their degraded "non-restored" counterparts. Analysis of faunal groups indicated that community structure was enhanced by restored reef creation. Analysis of functional feeding groups indicted that two important ecological functions were also enhanced. Since many of the benthic species that benefited from restoration are also important fish prey items, reef restoration clearly has the potential to increase the fish habitat value of the Bay's degraded oyster bars. By providing high quality habitat to a variety of ecologically important species, several other aspects of reef ecological function may also be greatly improved thus further increasing the intrinsic value of restored oyster reefs in terms of ecosystem services. The ongoing effort to restore oyster reef habitats in Maryland offers many opportunities for ecological insights. This is fortunate because many questions, both applied and theoretical, remain to be answered. Understanding the pathways and magnitudes of trophic energy flows through these systems will require carefully designed manipulative experiments. Many other questions regarding the relative importance of competitive versus facilitative interactions, predation, resource partitioning, and possible indirect effects also beg to be explored.

Acknowledgements

We wish to thank the Oyster Recovery Partnership, the Army Corps of Engineers Baltimore District, and Maryland Department of Natural Resources for financial support. Drs. David Secor and Roger Newell reviewed early drafts of the manuscript and provided advice that resulted in a much improved manuscript. Dr. Sandra Shumway and two anonymous reviewers also provided valuable input on the later draft of the manuscript. Jake Goodwin and Tim Koles provided logistical support. Claire Goldschmidt, Valerie Hagan, Stephanie Stottel, Ellison Alldredge, and numerous others provided field, lab and sample processing help. We also thank Wonderbread, Inc. for donation of trays. **[SS]**

References

Allan, J.D., 1995. Stream Ecology: Structure and Function of Running Waters. Kluwer Academic Publishers, Boston MA.

Bahr, Jr., L.M. 1974. Aspects of the structure and function of the intertidal oyster reef community in Georgia. Ph.D. Dissertation. University of Georgia, Athens.

Bahr, L.M., Lanier, W.P., 1981. The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-81/15. 105 pp.

Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59 (4), 329–364.

Boesch, D., 1972. Species diversity of marine macrobenthos in the Virginia area. Chesap. Sci. 13, 206–211.

Breitburg, D.L., 1991. Settlement patterns and presettlement behavior of the naked goby, *Gobiosoma bosci*, a temperate oyster reef fish. Mar. Biol. 109 (2), 213–221.

Breitburg, D.L., 1999. Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster reef habitat restoration: a synopsis and

synthesis of approaches. Virginia Inst. Mar. Sci. Press, Gloucester Point, VA, pp. 239–250.

Breitburg, D.L., Palmer, M.A., Loher, T., 1995. Larval distributions and spatial pattern of settlement of an oyster reef fish: response to flow and structure. Mar. Ecol. Prog. Ser. 125, 45–60.

Cerame-Vivas, M.J., Gray, I.E., 1966. The distributional pattern of benthic invertebrates of the continental shelf off of North Carolina. Ecology 47, 260–270.

Chao, L.N., Musick, J.A., 1977. Life history, feeding habits and functional morphology of juvenile Sciaenid fishes in the York River estuary, Virginia. U. S. Natl. Mar. Fish. Serv. Fish. Bull. 72, 657–702.

Cloern, J.E., 1982. Does benthos control phytoplankton biomass in South San Francisco Bay? Mar. Ecol. Prog. Ser. 9, 191–202.

Coen, L.D., Luckenbach, M.W., Breitburg, D.L., 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In: Benaka, L.R. (Ed.), Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society, Symposium, vol. 22, pp. 438–454. Bethesda, Maryland.

Cohen, R.R.H., Dressler, P.V., Philips, E.J.P., Cory, R.L., 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. Limnol. Oceanogr. 29, 170–180.

Dame, R.F., 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. Proc. Natl. Shellfish. Ass. 69, 6–10.

Dame, R.F., Spurrier, J.D., Zingmark, R.G., 1992. In situ metabolism of an oyster reef. J. Exp. Mar. Biol. Ecol. 164, 147–159.

Engle, V.D., Summers, J.K., 1999. Latitudinal gradients in benthic community composition in Western Atlantic estuaries. J. Biogeogr. 26, 1007–1023.

Ford, S.E., Tripp, M.R., 1996. Disease and defense mechanisms. In: Kennedy, V.S., Newell, R.I.E., Able, A.F. (Eds.), The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant Publications, College Park, MD, pp. 581–660.

Frey, D.G., 1946. Oyster bars of the Potomac River. U.S. Fish and Wildlife Service Special Report, vol. 32, pp. 1–93.

Gardinier, M.N., Hoff, T.B., 1982. Diet of striped bass in the Hudson River estuary. N. Y. Fish Game J. 29, 152–165.

Gerritsen, J., Holland, A.F., Irvine, D.E., 1994. Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. Estuaries 17 (2), 403–416.

Grabowski, J.H., 2002. The influence of trophic interactions, habitat complexity, and landscape setting on community dynamics and restoration of oyster reefs. Ph.D. Dissertation, University of North Carolina at Chapel Hill, NC.

Grabowski, J.H., 2004. Habitat complexity disrupts predator prey interactions but not the trophic cascade in oyster reef communities. Ecology 85, 995–1004.

Hartman, K.J., Brandt, S.B., 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Trans. Am. Fish. Soc. 124, 520–537.

Homer, M., and Boynton, W.R., 1978. Stomach analysis of fish collected in the Calvert Cliffs region, Chesapeake Bay — 1977. University of Maryland. UMCES 78-154-CBL, 1–363. Chesapeake Biological Laboratory, Solomons, Maryland, USA.

Jackson, B.C., Jeremy, Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637.

Kennedy, V.S., Breisch, L.L., 1981. Maryland's Oysters: Research and Management. Maryland Sea Grant Publication — UM-SG-TS-81-04, College Park, Maryland.

Lehman, M.E., 1974. Oyster reefs at Crystal River, Florida and their adaptation to thermal plumes. Doctoral Dissertation, University of Florida, Gainesville, Florida.

Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecol. Appl. 11, 764–782.

Meyer, D.L., Townsend, E.C., 2000. Faunal utilization of created intertidal eastern oyster (*Crassostrea virginica*) reefs in the southeastern United States. Estuaries 23 (1), 34–35.

Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Mar. Ecol. Prog. Ser. 161, 239–254.

Murdy, E.O., Birdsong, R.S., Musick, J.A., 1979. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington DC.

Newell, R.I.E., 1988. Ecological changes in Chesapeake Bay: Are they the result of over harvesting of the American oyster (*Crassostrea virginica*)? In: Lynch, M.P., Krome, E.C. (Eds.), Understanding the Estuary: Advances in Chesapeake Bay Research. Chesapeake Research Consortium, Solomons, Maryland, pp. 536–546.

Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J. Shellfish Res. 23 (1), 51–61.

Newell, R.I.E., Ott, J.A., 1999. Macrobenthic communities and eutrophication. In: Malone, T.C., Malej, A., Harding, L.W., Smodlaka, N., Turner, R.E. (Eds.), Ecosystems and the Land-Sea Margin: Drainage Basin to Coastal Sea, vol. 55. American Geophysical Union, Washington DC, pp. 265–293.

Newell, R.I.E., Fisher, T.R., Holyoke, R.R., Cornwell, J.C., 2004. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. P. In: Dame, R., Olenin, S. (Eds.), The Comparative Roles of Suspension Feeders in Ecosystems. NATO Science Series IV — Earth and Environmental Sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser. 264, 249–264.

Ranasinghe, J.A., Wiesberg, S.B., Dauer, D.M., Schaffner, L.C., Diaz, R.J., Frithsen, J.B., 1994. Chesapeake Bay benthic community restoration goals. United States Environmental Protection Agency Chesapeake Bay Program. CBP/TRS, Annapolis, MD. 107/94.

Roditi, H.A., Caraco, N.F., Cole, J.J., Strayer, D.L., 1996. Filtration of Hudson River water by the zebra mussel (*Dreissena polymorpha*). Estuaries 19 (4), 824–832.

Sherwood, G.D., Kovecses, J., Hontela, A., Rassmussen, J.B., 2002. Simplified food webs lead to energetic bottlenecks in polluted lakes. Can. J. Fish. Aquat. Sci. 59, 1–5.

Smith, G.S., 1997. Maryland's historic oyster bottoms: a geographic representation of the traditional named oyster bars. Maryland Department of Natural Resources, Fisheries Service, Cooperative Oxford Laboratory, Mapping and Analysis Project.

Stickney, R.R., Taylor, G.L., White, D.B., 1975. Food habits of five species of young southeastern United States estuarine Sciaenidae. Chesap. Sci. 16 (2), 104–114.

Szyrmer, J., Ulanowicz, R.E., 1987. Total flows in ecosystems. Ecol. Model. 53, 123–136.

Thompson, S.K., 2002. Sampling, 2nd ed. John Wiley & Sons Inc, New York NY.

Ulanowicz, R.E., Tuttle, J.H., 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. Estuaries 15, 298–306.

Wells, H.W., 1961. The fauna of oyster beds with special reference to the salinity factor. Ecol. Monogr. 31, 239–266.

Zimmerman, R., Minello, T., Baumer, T., Castiglione, M., 1989. Oyster reef as habitat for estuarine macrofauna. NOAA Technical Memorandum NMFS-SEFC-249. NOAA/NMFS Southeast Fisheries Science Center, Galveston Texas.