

# Coarse woody debris as a refuge from predation in aquatic communities

## An experimental test

R.A. Everett, G.M. Ruiz

Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, USA

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**Abstract.** This study demonstrates experimentally that coarse woody debris (CWD) can provide refuge from predation in aquatic habitats. In the Rhode River subestuary of Chesapeake Bay, Maryland, (USA), we (1) measured the abundance of CWD, (2) examined the utilization of CWD by mobile epibenthic fish and crustaceans, and (3) tested experimentally the value of CWD as a refuge from predation. CWD was the dominant above-bottom physical structure in shallow water, ranging in size from small branches (<2 cm diameter) to fallen trees (>50 cm diameter). In response to experimental additions of CWD, densities of common epibenthic species (*Callinectes sapidus*, *Fundulus heteroclitus*, *Fundulus majalis*, *Gobiosoma bosc*, *Gobiox strumosus*, *Palaemonetes pugio*, and *Rithropanopeus harrisi*) increased significantly compared to control sites without CWD. In laboratory experiments, grass shrimp (*P. pugio*) responded to predatory fish (*F. heteroclitus* and *Micropogonias undulatus*) by utilizing shelter at CWD more frequently than in the absence of fish. Access to CWD increased survivorship of grass shrimp in laboratory and field experiments. These experimental results (1) support the hypothesis, commonly proposed but untested for freshwater habitats, that CWD can provide a refuge from predation for epibenthic fish and invertebrates and (2) extend the recognized functional importance of CWD in freshwater to estuarine and marine communities. We hypothesize that CWD is an especially important refuge habitat in the many estuarine and freshwater systems for which alternative physical structure (e.g., vegetation or oyster reefs) are absent or in low abundance.

**Key words:** Coarse woody debris · Habitat structure · *Palaemonetes* · Refuge · Risk of predation

The quantity and quality of physical structure in aquatic habitats can strongly influence the structure (abundance

and species composition) and dynamics of faunal communities (e.g., Petersen 1918; Nord and Schulmbach 1973; Orth 1973; Peterson 1979; Carpenter and Lodge 1986; Sale and Douglas 1984; Smock et al. 1985). The potential roles of physical structure in population and community processes are well illustrated by studies of submerged aquatic vegetation (SAV) (see reviews in Cooper and Crowder 1979; Stoner 1980; Orth et al. 1984; Heck and Crowder 1991). While the mechanisms by which SAV can affect animal communities are numerous (e.g., Scoffin 1970; Burrell and Schubel 1977; Orth et al. 1984; Orth and Van Montfrans 1984; Peterson et al. 1984; Fonseca and Fisher 1986; Eckman 1987), its role as a refuge from predation has received the most attention and experimental support in freshwater (e.g., Crowder and Cooper 1982; Savino and Stein 1982), estuarine (e.g., Coen et al. 1981; Heck and Thoman 1981; Wilson et al. 1987, 1990), and marine (e.g., Reise 1977; Menge and Lubchenco 1981; Peterson 1982; Summer-son and Peterson 1984) habitats (but see also Robertson and Lenanton 1984 and Lenanton and Caputi 1989 for evidence of the importance of SAV as a foraging habitat).

In many freshwater lentic and lotic ecosystems, an important component of physical structure is coarse woody debris (CWD), which usually includes all pieces of wood >2 cm diameter and is thought to play a significant role in structuring animal communities (see reviews in Triska and Cromack 1980; Harmon et al. 1986; Bisson et al. 1987). Both animal abundance and diversity have shown positive correlations with the abundance of CWD (Dudley and Anderson 1982; Benke et al. 1984; Murphy et al. 1984; Smock et al. 1985, 1989, 1992), and additions of CWD to streams have resulted in increased abundances of fish (Saunders and Smith 1962; Burgess and Bider 1980; House and Boehne 1985, 1986). As with other types of structure, refuge from predation has been suggested as a primary mechanism by which CWD affects animal communities (Hall and Baker 1975, 1982; Triska and Cromack 1980). While Ware (1972) demonstrated that rates of attack and total food consumption

for trout (*Salmo gairdneri*), preying on freshwater amphipods in laboratory aquaria, were inversely correlated with the abundance of small (1 cm dia.) woody debris; experimental tests of this hypothesis in the field are lacking (Bisson et al. 1987).

Despite its perceived importance in freshwater communities, CWD has received relatively little attention in marine and estuarine systems. CWD is presently abundant in some nearshore (Flores-Verdugo et al. 1987; Gonor et al. 1988; Daniel and Robertson 1990) and deep ocean (Knudsen 1961) habitats, where it may have been even more pervasive historically (Sedell and Froggatt 1984; Triska 1984; Gonor et al. 1988). The role of CWD in marine and estuarine communities has received some attention both as an important agent of disturbance (e.g., Dayton 1971) and as an important habitat. However, studies of CWD as habitat focus primarily on utilization by assemblages of specialized wood-boring fauna (Turner and Johnson 1971; Becker 1971; Turner 1977, 1981, 1984; Gonor et al. 1988) or by birds and seals (e.g., Bayer 1978, 1981, 1983). Only one study (Daniel and Robertson 1990) has examined the utilization of CWD by epibenthic invertebrate and fish fauna in saline (brackish or marine) waters. As in freshwater, Daniel and Robertson (1990) found greatest abundances of estuarine epibenthic fauna where CWD was most abundant, and attributed this to the possible refuge from predation provided by CWD.

In this study we examined the utilization of CWD by epibenthic species and tested experimentally the refuge value of CWD in a temperate estuary of North America. The abundances of common species were compared between sites with and without CWD. In addition, laboratory and field experiments were designed to explicitly test the hypothesis that CWD provides a refuge from predation for an aquatic species. The grass shrimp *Palaemonetes pugio* (Decapoda: Palaemonidae) was chosen as a model species for these experiments due not only to its association with CWD, but also its numerical and functional importance in estuaries of Eastern North America (e.g., Darnell 1958; Odum and Heald 1972; Nixon and Oviatt 1973; Welsh 1975; Morgan 1980; Kneib 1985, 1987; Smith and Coull 1987; Posey and Hines 1991).

## Methods

### Study site

This study was conducted at the Rhode and West Rivers, two small subestuaries which share a connection to the mesohaline central Chesapeake Bay, MD, USA (Fig. 1). Average water temperature in the Rhode River peaks in July, at 27–28° C, and falls to lows of 2–4° C in January (Hines et al. 1987), summer temperatures can exceed 30° C along the shore, where ice often forms in winter. Salinity varies seasonally in the river from 3–17 ppt (Hines et al. 1987). Mean tidal amplitude in the river is 0.3 m, and mean low tide level is 0.2 m above mllw (Anonymous 1990). However, day-to-day tidal action in the Rhode River is highly influenced by winds, and fluxes greater than predicted can occur. Turbidity in the Rhode and West Rivers is very great in summer, with secchi depths under 0.5 m measured in the vicinity of our study site (Gallegos et al.

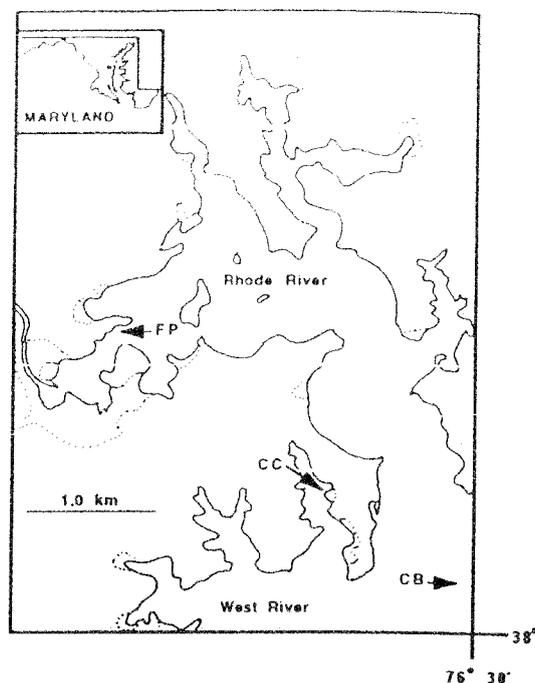


Fig. 1. Map of the Rhode River, Maryland. *Inset*: location of Rhode River along western shore of Chesapeake Bay. *Main figure*: FP, Fox Point; CC, Cheston Creek; CB: arrow points to connection with mainstem of Chesapeake Bay. *Dotted lines* delimit area of tidal marsh

1990). Further description of the Rhode River area can be found elsewhere (e.g., Correll 1975; Hines et al. 1987).

All the field work was done at Fox Point (Rhode River) or Cheston Creek (West River, see Fig. 1). The shoreline at both sites has a narrow fringe of emergent vegetation, primarily *Spartina alterniflora* and *S. cynosuroides*, and an abrupt rise (2–3 m) to a heavily wooded flood plain. CWD is abundant in the nearshore shallows at Cheston Creek, consisting of both single pieces and complex accumulations. As is common in tributaries of the upper Chesapeake Bay (pers. obs.), neither study site has SAV or any other above-bottom physical structure except CWD.

### Size, distribution, and abundance of CWD

The abundance and distribution of woody debris (>1 cm dia. and 10 cm long) in the nearshore zone was quantified at Cheston Creek (27 June 1991) and Fox Point (14 May 1991). At six locations for each site, line-transects (10 m length) were run parallel to shore at distances of 1, 2, 3, and 4 meters from the waters edge. All pieces of CWD intercepted by these lines were counted and measured for diameter to the nearest centimeter.

### Density of grass shrimp at naturally occurring CWD

Qualitative observations indicated that densities of grass shrimp were usually much greater around CWD than in areas lacking debris. To quantitatively test for this relationship, we measured densities of grass shrimp near and away from naturally occurring CWD at Fox Point in September 1990. Shrimp densities were estimated with a net (40 × 25 cm, 3 mm mesh) using a single sweep along 12 pieces of CWD (fallen trees and limbs, 0.1–0.2 m dia., 1–3 m long); adjacent to each CWD sample, another sample of identical length was taken from a location lacking CWD. In this and all other sampling efforts described below, shrimp (and other

epibenthic species) were counted and returned to their original site of collection. Data were standardized to number of shrimp per square meter, square-root transformed ( $\sqrt{x+0.5}$ ) and checked for homoscedasticity using Cochran's test (Winer 1971), then used to compare shrimp density in the presence and absence of CWD using *t*-test (Sokal and Rohlf 1981).

#### Density of mobile epibenthos at experimental CWD

To measure directly the effect of manipulating CWD on animal density, we used a standardized CWD unit, which controlled for variation due to the heterogeneous length, diameter, shape (i.e., number and size of branches, architectural complexity), species composition, age, and location of naturally occurring CWD. Ten replicate logs (1.5 m long  $\times$  10–15 cm dia.) were obtained by cutting sweet gum, *Liquidamber styraciflora*, saplings of similar age and size. The logs, anchored perpendicular to shore with steel stakes, were placed at approximately 10 m intervals along the shore at Fox Point in early June.

The experimental CWD units were first sampled for epibenthic fauna during both low and high tides in late July-early August 1991, after at least 2 weeks since previous disturbance (movement and/or sampling). At low tide (15–30 cm), shrimp had no access to the fringing emergent vegetation, and at high tide (30–50 cm) the water level was well into the vegetation. We sampled epibenthic fauna by dropping a rectangular sheet-metal caisson (2 m long  $\times$  0.5 m wide  $\times$  0.5 m high) over the experimental logs. For sampling, two people carrying the caisson with 1 m handles, slowly approached a site and deployed the trap from a distance of 0.5–1.0 m away from the sample sites. Upon deployment, the lower edges of the caisson became embedded in the bottom sediments, which prevented any escape of trapped fauna. After removing the logs, the interior of the trap was swept with nets until no fish, shrimp, or blue crabs were caught in 3 successive passes. In the same depth zone, adjacent control sites without debris (a minimum distance of 5 m away from experimental CWD sites) were sampled in a similar fashion, alternating the sampling sequence. All shrimp, fish and crabs caught were identified to species and counted. For blue crabs, molt stage was determined by carapace hardness and degree of epidermal retraction in the modified fifth walking legs (Van Engel 1958; Johnson 1980).

For shrimp, which were abundant in both high and low tide samples, differences in density between CWD and non-CWD treatments were compared with a 2-way ANOVA, using square-root transformed data checked for homoscedasticity as above, with tide height and CWD as main factors. Other epibenthic fauna were abundant only at high tide, and the data were highly heteroscedastic. Consequently, densities with and without CWD were compared using Mann-Whitney *U* or Wilcoxon signed-ranks tests.

Our results from the experimental CWD indicated that densities of several species were significantly greater at sites with than at sites without CWD. While these data demonstrated intense utilization of CWD by epibenthic fauna in the field, this pattern may have resulted to some extent from our presence. For example, animals may have responded to our sampling efforts by concentrating primarily at CWD. To test for this possibility, we repeated the experiment at a single depth zone (36–50 cm) in October 1992, including a third treatment—a short-term CWD treatment in which an experimental log was placed at a site otherwise lacking debris, then sampled within 5 min. For the short-term treatments, long-term logs were moved to new sites, with efforts to minimize disturbance, especially along the route of subsequent approach during sampling. All treatments were present in each of nine blocks, and the relative positions and sampling sequences were varied among blocks. If disturbance from our sampling method caused higher densities of fauna at CWD, then densities at long-term CWD (in place since June 1991) and short-term CWD (in place 5 min) would be similar, and higher than at no CWD sites. Alternatively, if our original hypothesis that faunal densities are naturally higher at

CWD is true, then densities at short-term and no CWD sites would be similar, and lower than at long-term CWD.

#### Abundance of potential shrimp predators

We sampled the nearshore zone at Fox Point for the abundance and composition of potential predators of grass shrimp in mid-July and mid-August 1991. In each month, 3 replicate seine samples were collected at non-overlapping sites along the shore over a 1–2 day period. The nets (10-m mouth opening, 0.63 cm mesh) were set parallel to shore at 1 m depth (approximately 15-m from shore) and pulled directly on to the beach, thus sampling an area of approximately 150 m<sup>2</sup>. All fauna caught, except for grass shrimp, were counted, identified to species, and measured to the nearest mm; blue crabs were molt-staged as above.

#### Field predation experiment

To test the hypothesis that CWD serves as a refuge from predation, we performed a field experiment that measured the relative intensity (risk) of predation near and away from CWD. Grass shrimp (30–35 mm total length) were tethered at a single depth zone (30 cm), either with or without access to a log (sweet gum, 30 cm long  $\times$  10 cm dia.). Only intermolt shrimp, as indicated by degree of tissue retraction in the uropods (Nicol and Stolp 1990), were used in the experiment. Shrimp were tethered to large nails with monofilament fishing line. A halter of 1 lb-test line was tied around the shrimp at the juncture of the thorax and abdomen, without restricting, the movement of pereopods or pleopods. A 30 cm leader of 4 lb-test line, bearing an attached hook (#20 size, barbed) at the shrimp end, was then tied to the halter and to a nail (16 d). After being tied to tether lines, shrimp were held individually in plastic cups with water, pending deployment in the field. Shrimp with halters tied too tight were rare, and were easily identifiable within 30 min after tying by a curled posture and an opaque white band around the body at the halter. Shrimp exhibiting either characteristic were not used in the experiment. Preliminary trials revealed 100% retention of tethered shrimp ( $n=10$ ) after 2 h. Shrimp were collected in the morning (0900–1000 h), tied to leaders in the late morning (1000–1300 h), then tethered in the field in the early afternoon (1400–1500 h).

The tether experiments were run at Fox Point on six days from late July to early August 1991. Twenty sites were selected at approximately 2 m intervals. Each site (60 cm dia.) was cleared of any natural CWD, and experimental logs (30 cm long  $\times$  10 cm dia.) were placed at the center of every other site. Logs of this diameter were used because of their utilization by shrimp in the field (see results). Nails bearing tethered shrimp were buried at the center of each site (and beneath logs when present), restricting shrimp movement to the cleared areas. Survivorship was measured after 15 min, and the size and species of any fish caught on the hooks, as well as the condition of surviving shrimp, were recorded. The data for shrimp survivorship were used to test for dependence of survivorship on presence/absence of CWD with a 2  $\times$  2 *G*-test (Model II, dead/alive vs CWD/no CWD) using data pooled over the six days. Data on the species of fish caught on the tethered shrimp were analyzed similarly for the dependence of predator species on habitat (CWD/no CWD).

#### Laboratory predation experiments

To examine more closely the utilization of CWD by grass shrimp under risk of predation, we performed two experiments in laboratory aquaria. The first experiment was designed to determine if access to CWD increased shrimp survivorship in the presence of known predators within a controlled laboratory environment. All experiments were run in aquaria (208 l) containing sand (3 cm depth)

and water from the Rhode River that was continuously filtered and aerated. The aquaria were shrouded with black plastic sheeting, to minimize visual disturbance by observers, and illuminated from above with a single, full-spectrum fluorescent light (20 w). Aquaria either contained a log (identical to those used in the tethering experiment) or had no structure at all. Each log was held 1 cm above the sediment surface by screws fastened to a buried plexiglass sheet.

Mummichog (*Fundulus heteroclitus*) and Atlantic croaker (*Micropogonius undulatus*) were used as predators, because these were the only species of fish caught in the field-tethering experiment and were very abundant in the seine samples. Mummichogs were restricted in size to 85–110 mm total length, since smaller fish have not been observed by us to prey on shrimp in aquaria and were not caught with tethered shrimp in the field; croaker sizes ranged from 130–150 mm total length, the size range of fish present at the mouth of Muddy Creek.

To begin an experiment, 15 shrimp (30–35 mm) were allowed to acclimate overnight (12 h) in the aquaria. Three fish (either croaker or mummichogs), which had been starved for 24 h, were introduced into each aquarium at approximately 0900 h. After 24 h, the fish were removed and the number of shrimp remaining in each aquarium was recorded. Six aquaria were used, 3 with and 3 without CWD, and a total of 12 replicate runs of each of the 4 treatments (mummichog+CWD, mummichog–CWD, croaker+CWD, croaker–CWD) were conducted over the period August–October 1991. At least one replicate of each treatment was run on each date during the course of the experiment. The remaining data were analyzed for the effect of CWD presence on shrimp survival. Percent of shrimp surviving was first calculated for each replicate, then arcsin square-root transformed (Sokal and Rohlf 1981), tested for homoscedasticity, and analyzed with a 2-way ANOVA, with CWD and predator species as main factors.

In a second experiment, we examined the behavioral response of shrimp to predatory fish when CWD was present. Aquaria, shrimp, and fish were as described above, except all aquaria contained a log. Eight replicates were run for each of 3 experimental treatments: control (no fish), mummichog, and croaker. Small flaps cut in the plastic sheeting which covered the aquaria permitted observation of shrimp and fish. The distribution of shrimp in relation to a log was recorded just prior to introduction, and at intervals of 30, 60, 120, and 240 min after ward. The number of shrimp present a) under, b) on, c) within 3 cm, d) 3–13 cm, or e) >13 cm from the log was recorded at each time. The positions of fish in the aquaria were noted at each time as well.

To test for differences between treatments in the distribution of shrimp relative to CWD, the data from each replicate were first used to calculate the percent of surviving shrimp in each location. After testing for homoscedasticity, the arcsin square-root transformed percentages were analyzed for differences among treatments in the percent of surviving shrimp under logs at 30 min with a 1-way ANOVA, followed by a Ryan's  $Q$  test (Day and Quinn 1989) for comparisons between treatment means.

## Results

### Size, distribution, and abundance of CWD

CWD was common at both Cheston Creek and Fox Point in May–June 1991, although the characteristics of CWD appeared to differ between sites (Fig. 2). At Cheston Creek CWD declined in abundance with increasing distance from shore, while at Fox Point the opposite pattern was observed. Overall, CWD was more abundant at Cheston Creek and consisted of more large pieces (>4 cm dia.) than at Fox Point. This variation in characteristics of CWD between sites may reflect different degrees of disturbance historically, with Fox Point

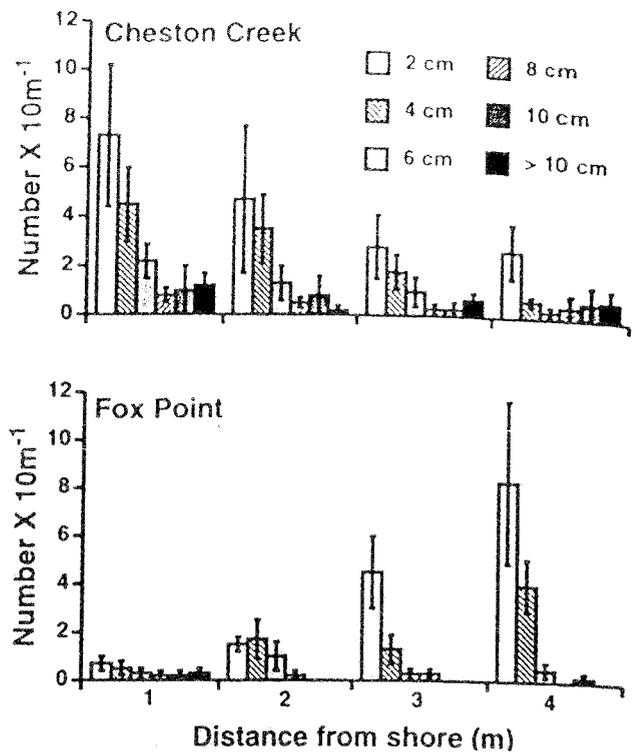


Fig. 2. Abundance and size distribution of natural CWD by distance from shore at Cheston Creek and Fox Point. Shown are mean numbers ( $\pm 1$  SE) for six replicate 10 m line-transects at each distance from shore, May–June 1991. Legend identifies size classes (diameters)

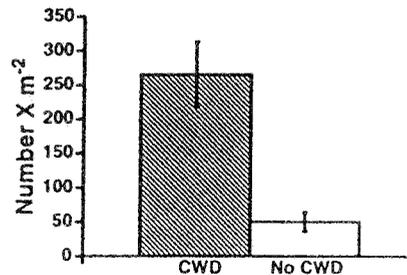


Fig. 3. Density of grass shrimp (mean  $\pm 1$  SE) at 12 sites with and 12 sites without natural CWD (individual logs), September 1990

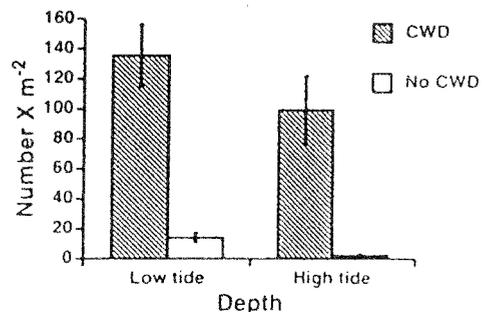


Fig. 4. Density of grass shrimp (mean  $\pm 1$  SE) at 10 sites with and 10 sites without experimental CWD (in place approx. 1 month), July–August 1991. Depth at low tide = 15–30 cm, depth at high tide = 30–60 cm

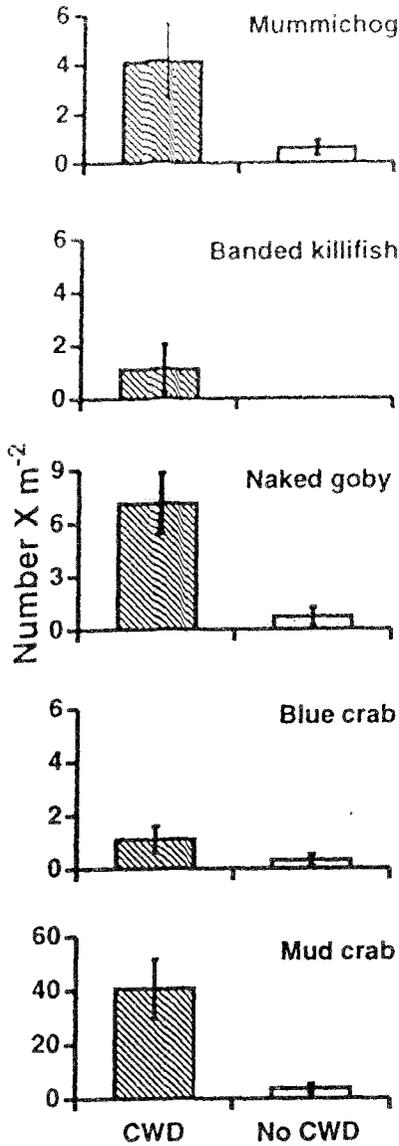


Fig. 5. Density of mobile epibenthic fauna other than shrimp (mean  $\pm$  1 SE) at 10 sites with and 10 sites without experimental CWD, during high tide, July–August 1991

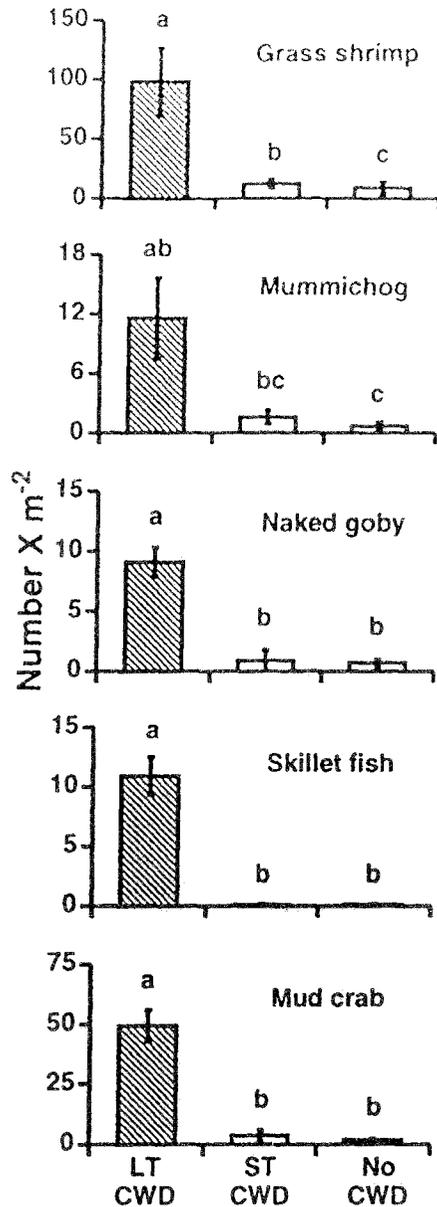


Fig. 6. Density of mobile epibenthic fauna (mean  $\pm$  1-SE) at sites with long-term (LT: in place since June 1991), short-term (ST: in place 5 minutes) and no CWD, October 1992.  $n=9$  in all treatments; treatments sharing letters not significantly different ( $p < 0.05$ ) according to nonparametric comparison among means test

being a site of more human activity that includes (1) a younger forest due to more recent clearing compared to Cheston Creek and (2) removal of CWD from shallow waters by previous investigators to facilitate seining efforts.

Abundance of mobile epibenthic fauna at CWD

Grass shrimp at Fox Point were 5X as abundant at naturally occurring CWD compared to sites without debris in September 1990 ( $t = 5.34$ ,  $df = 22$ ,  $p < 0.001$ , Fig. 3). After about 1 month of exposure, shrimp were also sig-

nificantly more abundant at experimental CWD than at sites lacking debris during both low and high tides in July–August 1991 (Fig. 4, Table 1). Shrimp were significantly more abundant at logs at low tide than at high tide (Table 1).

Five other species were caught in high tide samples at the experimental CWD in 1991 (Fig. 5), 4 of which were significantly more abundant at CWD than at sites lacking debris: Mummichogs (*F. heterochitus*;  $U = 87$ ,  $p < 0.005$ ), naked gobies (*Gobiosoma bosc*;  $U = 86$ ,  $p < 0.005$ ), blue crabs (*Callinectes sapidus*;  $U = 75.5$ ,  $p < 0.05$ ), and mud crabs (*Rhithropanopeus harrisi*; signed-rank test,  $p < 0.05$ ). Abundances of a fifth species, the

**Table 1.** Comparison of grass shrimp densities in samples from experimental CWD and control sites, July–August 1991. Shown are results of ANOVA on square-root transformed data (ns = not significant at  $p < 0.05$ )

ANOVA					
Source	SS	df	MS	F-ratio	<i>p</i>
CWD treatment (A)	577.57	1	577.57	71.67	$p < 0.001$
Depth (B)	54.55	1	54.55	6.77	$p < 0.025$
A × B	0.34	1	0.34	0.04	ns
Error	290.11	36	8.06		

**Table 2.** Summary of Kruskal-Wallis tests comparing densities among treatments for each species commonly captured during second sampling of experimental CWD October 1992. K-W: Kruskal-Wallis statistic. *p*: significance value ( $p <$ )

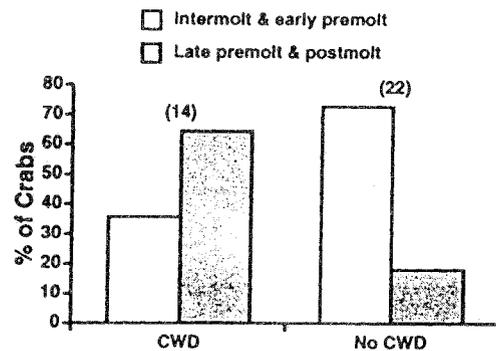
	Grass shrimp	Mummichog	Naked goby	Skillet fish	Mud crab
K-W	16.55	10.78	17.79	21.93	17.20
<i>p</i>	0.001	0.005	0.001	0.001	0.001

banded killifish (*Fundulus majalis*), were not significantly different between treatments, although there was a trend toward greater abundances at CWD.

Five species of mobile epifauna (grass shrimp, mummichogs, naked gobies, skillet fish *Gobiesox strumosus*, and mud crabs) were caught in the drop-trap samples in October 1992. Because most of the species had heterogeneous variances among treatments, Kruskal-Wallis tests were used to compare among treatment for differences in the densities of each species. There were significant treatment effects for all five species (Table 2), and subsequent nonparametric multiple comparison tests (Sokal and Rohlf 1981) revealed that densities of 4 of the 5 species were significantly greater at resident CWD than at either short-term or no CWD treatment sites, with no significant differences between the latter two treatments (Fig. 6). One species, mummichog, had densities at resident and short-term CWD treatments which were not significantly different according to the multiple comparison test; however, the comparison results (long-

term = short-term = no CWD, but long-term > no CWD) probably resulted from the low power of this multiple comparison procedure. By comparison, a single Mann-Whitney *U* test of the difference between the densities of mummichog at resident and short-term treatments revealed a significant difference ( $U = 65$ ,  $p = 0.027$ ). Together, our results indicated higher abundances of fauna at CWD, independent of sampling artifacts (see methods for discussion).

Although we did not quantify their occurrence, several species of sessile invertebrates also colonized the experimental CWD. The barnacle *Balanus improvisus* was abundant on every piece of experimental CWD, and en-



**Fig. 7.** Distributions of molt-stages for blue crabs caught with drop-traps at experimental CWD, and for blue crabs caught with seine nets in areas without CWD. Numbers in parentheses indicate number of crabs in each sample, July–August 1991

**Table 3.** Mean number and length in mm ( $\pm 1$  SE) of fish and crabs caught in seines ( $n = 3$ ) at Fox Point in July and August 1991

Species	July 1991		August 1991	
	Number	Size	Number	Size
Atlantic croaker ( <i>Micropogonias undulatus</i> )	24.3 $\pm$ 5.9	107.8 $\pm$ 3.6	15.0 $\pm$ 6.4	139.2 $\pm$ 1.9
Mummichog ( <i>Fundulus heteroclitus</i> )	17.3 $\pm$ 7.9	77.9 $\pm$ 1.5	7.0 $\pm$ 1.0	53.6 $\pm$ 2.4
Banded killifish ( <i>Fundulus majalis</i> )	11.7 $\pm$ 1.4	52.8 $\pm$ 4.3	18.0 $\pm$ 4.7	49.9 $\pm$ 1.9
Atlantic silversides ( <i>Menidia</i> spp.)	6.3 $\pm$ 2.9	69.1 $\pm$ 2.4	26.7 $\pm$ 0.3	68.3 $\pm$ 1.3
Bay anchovy ( <i>Anchoa mitchilli</i> )	5.7 $\pm$ 4.3	44.0 $\pm$ 1.6	6.0 $\pm$ 3.2	50.3 $\pm$ 2.6
Menhaden ( <i>Brevoortia tyrannus</i> )	5.0 $\pm$ 5.0	88.7 $\pm$ 4.1	103.3 $\pm$ 92.6	116.9 $\pm$ 0.6
Blue crab ( <i>Callinectes sapidus</i> )	4.7 $\pm$ 2.0	50.1 $\pm$ 7.5	3.0 $\pm$ 0.6	108.6 $\pm$ 12.4
Striped bass ( <i>Morone saxatilis</i> )	1.0 $\pm$ 1.0	80.3 $\pm$ 4.1	3.0 $\pm$ 1.0	123.4 $\pm$ 18.3
Bluegill ( <i>Lepomis macrochirus</i> )	0.3 $\pm$ 0.3	70.0	0	0
Hog choker ( <i>Trinectes maculatus</i> )	0.3 $\pm$ 0.3	69.0 $\pm$ 1.0	0.7 $\pm$ 0.3	120.5 $\pm$ 8.5
Lizard fish ( <i>Synodus foetens</i> )	0.3 $\pm$ 0.3	110.0	0	0
Naked goby ( <i>Gobiosoma bosc</i> )	0.3 $\pm$ 0.3	35.0	2.3 $\pm$ 0.9	38.7 $\pm$ 1.5
Spot ( <i>Leiostomus xanthurus</i> )	0.3 $\pm$ 0.3	92.0	3.0 $\pm$ 1.5	126.3 $\pm$ 2.2
Sheephead minnow ( <i>Cyprinodon variegatus</i> )	0	0	0.7 $\pm$ 0.3	50.5 $\pm$ 0.5

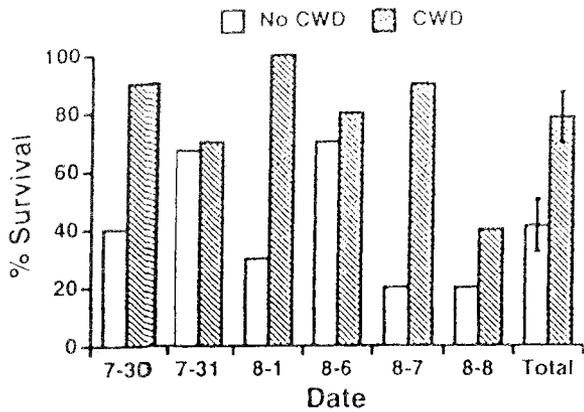


Fig. 8. Percent survivorship after 15 min of grass shrimp tethered in the field with and without access to experimental CWD. Ten shrimp tethered in each treatment on each of six days, during period of July 30–August 8, 1991. Survivorship is shown for each day, and for the total period (mean  $\pm$  1 SE over six days)

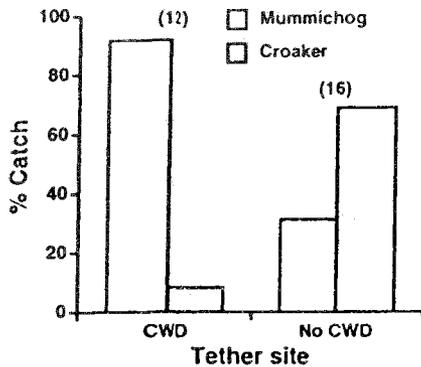


Fig. 9. Effect of presence or absence of CWD on species of fish caught with tethered shrimp. Total number of individual fish caught for each type of site indicated in parentheses

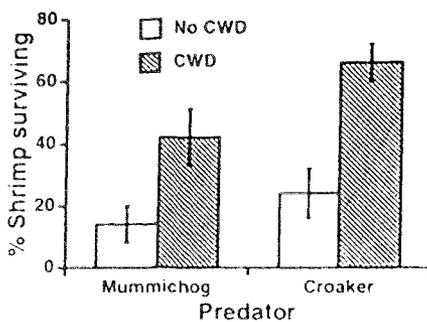


Fig. 10. Survivorship (mean  $\pm$  1 SE) of grass shrimp in laboratory predation experiments as a function of predator species and CWD presence. Each histogram shows survivorship ( $n = 12$ ) of 15 shrimp after 24 h exposure to 3 fish

crustacean bryozoans, mussels (*Ischadium recurvum*), and tunicates (*Molgula manhattensis*) were frequently present. These fouling organisms were observed only on the lower surfaces of the logs, usually in grooves formed by the rugose bark.

#### Abundance of potential shrimp predators

Atlantic croaker and mummichogs were the most abundant large species caught in seine samples from the near-shore zone at Fox Point in both July and August 1991 (Table 3). Banded killifish were also abundant in the samples, but their average size was relatively small (49.9–52.8 mm). Other potential predators of grass shrimp (blue crab, striped bass, bluegill, lizard fish, and spot) were caught in low numbers. Although silversides (*Menidia* spp.) and menhaden (*Brevoortia tyrannus*) were abundant in both months, they are planktivores rather than potential predators of juvenile and adult shrimp.

For blue crabs, there was a clear distinction in the distribution of molt-stages between the crabs caught in caisson samples of experimental CWD, and crabs caught in seine samples. Most of the crabs caught in seine samples, which were collected in areas lacking CWD, were either intermolt or early premolt (white line) stages, while crabs caught at logs were late premolt or early postmolt stages (Fig. 7;  $G_{adj.} = 7.604$ ,  $p < 0.01$ ).

#### Field predation experiment

Overall, the presence of CWD resulted in significantly greater survivorship of tethered grass shrimp, compared to shrimp without CWD ( $G_{adj.} = 17.81$ ,  $p < 0.001$ ; Fig. 8). Day-to-day variation in the effect of CWD was relatively high. Although the cause of this variation is unknown, it may reflect temporal changes in the abundance and composition of fish predators, as risk of predation varied according to fish species (see below).

Tethering experiments such as this are frequently used to measure the relative risk of predation in different locations or at different times (i.e., Shulman 1985; Heck and Wilson 1987; Barshaw and Able 1990). In using tethering techniques, it is important to acknowledge that the predation rates measured are not equal to actual rates in the natural prey population, and may only be compared among treatments within the experiment. Actual mortality rates in the grass shrimp population at Fox Point are undoubtedly much lower than those we observed for tethered shrimp.

Two species of fish, Atlantic croaker and mummichogs, were caught on the tethered shrimp. The species of fish caught was, however, significantly dependent on the treatment ( $G_{adj.} = 10.87$ ,  $p < 0.001$ ). Croaker were caught more often at sites lacking debris, and mummichogs were caught more often at logs (Fig. 9). Average size ranges of croaker and mummichogs caught were 115 mm (SE = 10.2) and 88.3 mm (SE = 8.2), respectively.

#### Laboratory predation experiments

As in the field, access to CWD greatly increased the survivorship of grass shrimp (Fig. 10, Table 4). In addition, the degree to which CWD constituted a refuge differed between the two fish species. In the presence of

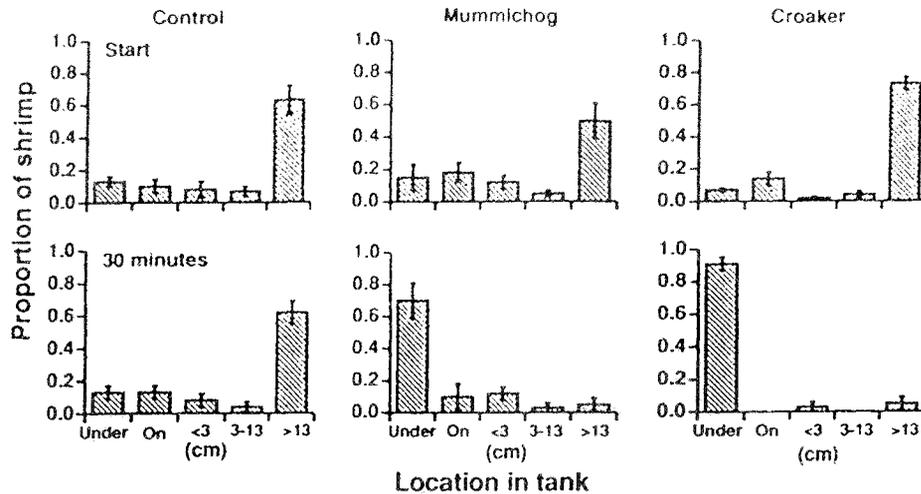


Fig. 11. Distribution of grass shrimp (mean proportion  $\pm$  1 SE), with reference to experimental CWD in laboratory experiments. *Upper row*: start = prior to addition of fish. *Lower row*: distribution of surviving shrimp 30 min after addition of fish. Control treatment received no fish. Eight replicate runs for each treatment, 3 fish/tank in mummichog and croaker treatments, 15 shrimp/tank in all treatments at time 0 and time 30 control;  $11.6 \pm 1.2$  and  $8.0 \pm 0.8$  surviving shrimp per tank at time 30 in mummichog and croaker treatments, respectively

Table 4. Survivorship of grass shrimp in laboratory aquaria experiments. Shown are results of ANOVA (arcsin square-root transformed data) examining the effects of predator species and debris presence (ns: not significant at  $p < 0.05$ )

ANOVA					
Source	SS	df	MS	F-ratio	<i>p</i>
Fish (A)	2813.47	1	2813.47	7.38	$p < 0.01$
CWD (B)	7901.83	1	7901.83	20.73	$p < 0.001$
A $\times$ B	182.96	1	182.96	0.48	ns
Error	16771.35	44	381.17		

Table 5. Proportion of grass shrimp under experimental CWD 30 min after addition of fish. A: results of ANOVA examining the effects of predator treatment on shrimp distribution. B: results of Ryan's *Q*-test of differences among means. Treatments ranked by means from high to low, those sharing letters were not significantly different ( $p < 0.05$ )

Source	SS	df	MS	F-ratio	<i>p</i>
A ANOVA					
Treatment	15736.22	2	7868.11	27.68	$p < 0.001$
Error	16771.35	44	381.17		
B Ryan's <i>Q</i> -test					
Rank	a	a	b		
Treatment	1 Croaker	2 Mummichog	3 No fish		

CWD, shrimp survivorship was significantly higher with croaker as predator than with mummichogs as predator (Table 4). There was no significant difference in shrimp survivorship between predator treatments in the absence of CWD.

The second laboratory experiment showed that shrimp actively utilized CWD in the presence of predatory fish. Prior to the introduction of fish, most shrimp in aquaria were distributed more than 13 cm from the

CWD. Within 30 min of fish introduction, however, most shrimp in the tanks with predators moved under the CWD, while the shrimp in control tanks had not changed position (Fig. 11). Significantly greater proportions of surviving shrimp were present under CWD in the predator treatment than in the no-predator treatment (Table 5). Although we observed that mummichogs (but not croaker) often chased shrimp out from under the CWD, there was no significant difference in the proportion of shrimp under CWD between tanks with mummichog and those with croaker (Table 5).

## Discussion

Our results demonstrate that CWD can play an important role in estuarine animal communities. In the Rhode River subestuary, CWD strongly influences the distribution of epibenthic fish and crustaceans along the shoreline. As in freshwater ecosystems (e.g., Hartman 1965; Bustard and Narver 1975a, b; Mortensen 1977; Lister and Genoe 1979; Tschaplinsky and Hartman 1983; Murphey et al. 1984; Fausch and Northcote 1992), the densities of epibenthic fauna at the Rhode River in July–August 1991 and October 1992 were higher at natural and experimental CWD compared to areas without large debris (Figs. 3–6). Our results also demonstrate that CWD provides an effective refuge from predation, supporting a common but previously untested hypothesis (e.g., Hall and Baker 1975, 1982; Triska and Cromack 1980; Moring et al. 1989; Daniel and Robertson 1990). In both laboratory and field experiments, the utilization of CWD significantly reduced the risk of predation for grass shrimp (Figs. 8 and 10). The extent of CWD utilization in laboratory aquaria was dependent upon risk of predation (Fig. 11), as observed for refuge use of other aquatic prey (Fraser and Cerri 1982; Petranka 1983; Werner et al. 1983; Power 1984; Bland and Temple 1990; Tonn et al. 1992). In addition, the pattern of CWD utilization by late premolt and early postmolt blue crabs (Fig. 7) may also result from changes in predation risk with molt stage

As reported for estuarine prey in other refuge habitats (e.g., Stone 1982; Minello and Zimmerman 1983; Minello et al. 1987), the degree of protection provided to grass shrimp by CWD was dependent upon the predator involved. Mummichogs consumed more shrimp than croaker in the presence of CWD, but fed at comparable rates in the absence of CWD (Fig. 10, Table 4). In addition, mummichogs appeared to remove a greater proportion of tethered shrimp at logs than croaker (Fig. 9). The effectiveness of CWD as a refuge was related to predator behavior. In the laboratory, we observed mummichogs actively driving shrimp out from underneath logs, whereas croaker were never observed to forage around logs; instead, croaker swam considerably above the bottom and struck at shrimp that ventured out away from logs. Despite these differences in feeding behavior of the fish, especially in the displacement of shrimp, the proportion of shrimp away from log refuges was not significantly different between predator species. Apparently, shrimp displaced by mummichogs either returned quickly to the protection of logs or were eaten.

The influence of CWD on relative mortality rates for grass shrimp, and probably other associated species, suggests that the presence of CWD can influence predator and prey population dynamics. Empirical studies have long suggested that refugia can result in increased persistence of prey populations (e.g., Gause et al. 1936; Huffaker 1958; Connell 1970; Menge and Lubchenco 1981). Although prey survivorship may benefit, predator-mediated refuge use can also produce indirect effects on prey fitness through costs to growth and reproduction (Werner et al. 1983; Skelly and Werner 1990; Fraser and Gilliam 1992; Tonn et al. 1992), and differential availability of refuge microhabitats can influence recruitment and structure of prey populations (Shulman 1984, 1985).

The importance of CWD in estuarine communities is almost certainly not limited to its refuge value. Food resources available at CWD may differ quantitatively or qualitatively from alternative sites, as for freshwater fish communities where the composition and abundance of invertebrate prey at sites with and without CWD are often quite different (Dudley and Anderson 1982; Benke et al. 1984; Moring et al. 1989; Smock et al. 1992). The increased habitat complexity provided by CWD is also likely to influence competitive interactions. For example, Dolloff (1983) has suggested that the visual barrier provided by CWD in streams reduces intraspecific aggression among juvenile coho salmon, and Mittelbach (1984, 1986) has argued that concentration of prey in refuge habitats results in increased interspecific competition. As a source of hard substratum, CWD in estuaries also provides a habitat for fouling organisms incapable of maintaining an existence on a sedimentary bottom. While community structure (species composition and diversity) can be fundamentally altered by the presence of CWD, these and other potential roles of CWD in estuarine communities, and their relative importance, remain unexplored.

A functional importance of CWD is well recognized in freshwater ecosystems but has rarely been suggested

for estuarine and marine habitats (but see Gonor et al. 1988). This disparity may be partially an artifact of anthropogenic alteration of estuaries. While CWD can be abundant presently in estuaries and bays (e.g., Boto and Bunt 1981; Jimenez et al. 1985; Flores-Verdugo et al. 1987; Robertson and Daniel 1989; Daniel and Robertson 1990; Robertson et al. 1991), it was probably much more abundant historically. Early explorers reported that North American estuaries and coastal beaches were choked with CWD (Gonor et al. 1988 and references therein), but snags and driftwood, which were so numerous to be considered hazards to navigation and impediments to commerce, have been actively removed from estuaries and coastal rivers (Sedell et al. 1982; Gonor et al. 1988). Furthermore, because estuaries are often sites of dense human habitation and deforestation, current input rates of CWD are probably small fractions of the historical rates.

Despite the probable decline in abundance of CWD among many estuaries, the relative importance of CWD may have increased recently in the Rhode River, and the Chesapeake Bay, due to the striking decline in abundance of submerged aquatic vegetation (SAV) during the past several decades (Bayley et al. 1968; Southwick and Pine 1975; Orth and Moore 1983, 1984). Although historically abundant in the Chesapeake Bay and providing an important refuge habitat (e.g., Heck and Thoman 1981; Wilson et al. 1987, 1990), SAV has been absent from the Rhode River since 1968 (Southwick and Pine 1975). Grass shrimp and other epibenthic animals previously common in offshore SAV meadows are now restricted primarily to shallow water (<70 cm depth), which provides a refuge from predation (Ruiz et al. in press). Currently, CWD constitutes the only natural above-bottom physical structure in the Rhode River, occurring mostly in shallow water (Fig. 2; pers. obs.), which appears similar to SAV in its refuge value. The relative importance of CWD in Chesapeake Bay may be further enhanced by a decline of oyster reefs or bars, another physical structure associated with elevated abundances of fauna and refuge from predation (Wells 1961; Bahr and Lanier 1981) that has declined over the last century (Sindermann 1968, 1990; Matthiessen 1969).

We suggest that the role of CWD in the Rhode River reflects generally its role in Chesapeake Bay and many other estuaries worldwide. Specifically, we propose that CWD is often an important structural habitat that provides refuge from predation for associated fauna. With declines in SAV observed throughout many estuaries (e.g., Den Hartog and Polderman 1975; Pères and Picard 1975; Cambridge and McComb 1984; Larkum and West 1990; Short et al. 1991), similar to those observed recently in Chesapeake Bay, other physical structure such as CWD would appear especially important as refuge.

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## References

- Anonymous (1990) Tide tables 1990. High and low water predictions for the East coast of North and South America (including Greenland). US Dep't of Commerce, National Oceanic and Atmospheric Administration, Washington, DC
- Bahr LM, Lanier WP (1981) The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. US Fish Wildl Serv
- Barshaw DE, Able KW (1990) Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters *Homarus americanus*. Fish Bull 88:415-417
- Bayer RD (1978) Aspects of Oregon estuarine great blue heron population. In: Sprunt A, Ogden JC, Winkler S (eds) Wading Birds. Res Rep 7, National Audubon Soc, New York, pp 213-217
- Bayer RD (1981) California sea lions in the Yaquina estuary. Oregon. Murrelet 62:56-59
- Bayer RD (1983) Nesting success of western gulls at Yaquina Head and on man-made structures in Yaquina estuary, Oregon. Murrelet 64:87-91
- Bayley S, Rabin H, Southwick CH (1968) Recent decline in the distribution and abundance of eurasian milfoil in Chesapeake Bay. Ches Sci 9:173-181
- Becker G (1971) On the biology, physiology, and ecology of marine wood-boring crustaceans. In: Jones EBG, Eltringham SK (eds) Marine borers, fungi and fouling organisms. Org Econ Co-oper Develop, Paris, pp 303-326
- Benke AC, Van Arsdall TC, Gillespie DM, Parrish FK (1984) Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol Monogr 54:25-63
- Bisson PA, Bilby RE, Bryant MD, Dolloff CA, Grette GB, House RA, Murphy ML, Koski KV, Sedell JR (1987) Large woody debris in forested streams in the Pacific Northwest: past, present and future. In: Salo EO, Cundy TW (eds) Streamside management: forestry and fishery interactions. College of Forest Resources, Univ of Washington, Seattle, WA, pp 143-190
- Bland JD, Temple SA (1990) Effects of predation-risk on habitat use by Himalayan Snowcocks. Oecologia 82:187-191
- Boto KG, Bunt JS (1981) Tidal export of particulate organic matter from a northern Australian mangrove system. Estuar Coastal Shelf Sci 13:247-255
- Burgess SA, Bider JR (1980) Effects of stream habitat improvements on invertebrates, trout populations, and mink activity. J Wildl Manag 44:871-880
- Burrell DC, Schubel JR (1977) Seagrass ecosystem oceanography. In: McRoy CP, Helfferich C (eds) Seagrass Ecosystems. Marcel Dekker, New York, pp 195-227
- Bustard DR, Narver DW (1975a) Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J Fish Res Board Can 32:667-680
- Bustard DR, Narver DW (1975b) Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. J Fish Res Board Can 32:681-687
- Cambridge ML, McComb AJ (1984) The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. Aquat Bot 20:229-243
- Carpenter SR, Lodge DM (1986) Effects of submersed macrophytes on ecosystem processes. Aquat Bot 26:341-370
- Coen LD, Heck KL, Jr, Abele LG (1981) Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62:1484-1493
- Connell JH (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol Monogr 40:49-78
- Cooper WE, Crowder LB (1979) Patterns of predation in simple and complex environments. In: Shoud RHL, Clopper H (eds) Predator-prey systems in fisheries management. Sport Fisheries Inst, Washington, DC
- Correll DL (1975) The Rhode River program. Estuarine pollution control and assessment, vol I. Pensacola, FL. US Env Prot Agency, pp 19-27
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-1813
- Daniel PA, Robertson AI (1990) Epibenthos of mangrove waterways and open embayments: community structure and the relationship between exported mangrove detritus and epifaunal standing stocks. Estuar Coast Shelf Sci 31:599-619
- Darnell RM (1958) Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ Inst Mar Sci Univ Texas 5:353-416
- Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. Ecol Monogr 59:433-463
- Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41:351-389
- Den Hartog C, Polderman PJG (1975) Changes in the seagrass populations of the Dutch Waddenzee. Aquat Bot 1:141-147
- Dolloff CA (1983) The relationships of wood debris to juvenile salmonid production and microhabitat selection in small southeast Alaska streams. Ph D thesis, Montana State Univ, Bozeman, 100 pp
- Dudley T, Anderson NH (1982) A survey of invertebrates associated with wood debris in aquatic habitats. Melanderia 39:1-21
- Eckman JE (1987) The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. J Exp Mar Biol Ecol 106:165-191
- Fausch KD, Northcote TG (1992) Large woody debris and salmonid habitat in a small coastal British Columbia stream. Can J Fish Aquat Sci 49:682-693
- Flores-Verdugo FJ, Day JW, Briseno-Duenas R (1987) Structure, litter fall, decomposition, and detritus dynamics of mangroves in a Mexican coastal lagoon with an ephemeral inlet. Mar Ecol Prog Ser 35:83-90
- Fonseca MS, Fisher JS (1986) A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Mar Ecol Prog Ser 29:15-22
- Fraser DF, Cerri RD (1982) Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. Ecology 63:307-313
- Fraser DF, Gilliam JF (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. Ecology 73:959-970
- Gallegos CL, Correll DL, Pierce JW (1990) Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. Limnol Oceanogr 35:1486-1502
- Gause GF, Smaragdova NP, Witt AA (1936) Further studies of interaction between predators and prey. J Anim Ecol 5:1-18
- Gonor JJ, Sedell JR, Benner PA (1988) Chapter 4. What we know about large trees in estuaries, in the sea, and on coastal beaches. In: Maser C, Tarrant RF, Trappe JM, Franklin JF (eds) From the forest to the sea: a story of fallen trees. Pac NW Res Sta, US Dep Agric, Forest Serv, Portland, Or
- Hall JD, Baker CO (1975) Biological impacts of organic debris in Pacific northwest streams. Logging debris in streams, workshop 2, Corvallis, OR, Oregon State Univ, pp 1-13
- Hall JD, Baker CO (1982) Rehabilitating and enhancing stream habitat. In: Meehan WR (ed) Influence of forest and rangeland management of anadromous fish habitat in western North America. USDA Forest Service Gen Tech Rep PNW-138. Pac NW For and Range Exp Stn, Portland, OR
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Chne SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack KJ, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. In: MacFadyen A, Ford ED (eds) Advances in Ecological Research. Academic Press, pp 133-302

- Hartman GF (1965) The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *J Fish Res Board Can* 22:1035-1081
- Heck KL Jr, Crowder LB (1991) Habitat structure and predator-prey interactions in vegetated aquatic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, London, pp 281-299
- Heck KL Jr, Thoman TA (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. *J Exp Mar Biol Ecol* 53:125-134
- Heck KL Jr, Wilson KA (1987) Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *J Exp Mar Biol Ecol* 197:87-100
- Hines AH, Haddon PJ, Miklas JJ, Wiechert LA, Haddon AM (1987) Estuarine invertebrates and fish: sampling design and constraints for long-term measurements of population dynamics. In: Boyle TP (ed) *New Approaches to Monitoring Aquatic Ecosystems*. ASTM STP 940. American Society for Testing and Materials, Philadelphia, pp 104-164
- House RA, Boehne PL (1985) Evaluation of instream enhancement structures for salmonid spawning and rearing in a coastal Oregon stream. *N Am J Fish Manag* 5:283-295
- House RA, Boehne PL (1986) Effects of instream structure on salmonid habitat and populations in Tobe Creek, Oregon. *N. Amer J Fish Manag* 6:38-46
- Huffaker CB (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-383
- Jimenez JA, Lugo AE, Cintron G (1985) Tree mortality in mangrove forests. *Biotropica* 17:177-185
- Johnson PT (1980) Histology of the blue crab, *Callinectes sapidus*. A model for the Decapoda. Praeger Sci Publ Co, New York
- Kneib RT (1985) Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-substrate benthic invertebrate assemblages. *J Exp Mar Biol Ecol* 93:91-102
- Kneib RT (1987) Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68:379-386
- Knudsen J (1961) The bathyal and abyssal Xylophaga (Pholadidae, Bivalvia). In: Wolff T (ed) *Galathea report, scientific results of the Danish deep-sea expedition round the world 1950-52*. Danish Science Press, Ltd, Copenhagen, pp 163-209
- Larkum AWD, West RJ (1990) Long-term changes of seagrass meadows in Botany Bay, Australia. *Aquat Bot* 37:55-70
- Lenanton RCJ, Caputi N (1989) The role of food supply and shelter in the relationship between fishes, in particular *Cnidogobius macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. *J Exp Mar Biol Ecol* 128:165-176
- Lister DB, Genoe HS (1979) Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) in the Big Qualicum River, British Columbia. *J Fish Res Board Can* 27:1215-1224
- Matthiessen GC (1969) A review of oyster culture and the oyster industry in North America. *Woods Hole Oceanogr Inst Contrib No 2528:52pp*
- Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol Monogr* 51:429-450
- Minello TJ, Zimmerman RJ (1983) Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *J Exp Mar Biol Ecol* 72:211-231
- Minello TJ, Zimmerman RJ, Martinez EX (1987) Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: effects of turbidity and substratum on predation rates. *Fish Bull* 85:59-70
- Mittelbach GG (1984) Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* 65:499-513
- Mittelbach GG (1986) Predator-mediated habitat use: some consequences for species interactions. *Environ Biol Fishes* 16:159-169
- Morgan MD (1980) Grazing and predation of the grass shrimp *Palaemonetes pugio*. *Limnol Oceanogr* 25:896-902
- Moring JR, Negus MT, McCullough RD, Herke SW (1989) Large concentrations of submerged pulpwood logs as fish attraction structures in a reservoir. *Bull Mar Sci* 44:609-615
- Mortensen E (1977) Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams. *J Fish Biol* 11:613-617
- Murphy ML, Koski KV, Heifetz J, Johnson SW, Kirchhofer D, Thedinga JF (1984) Role of large organic debris as winter habitat for juvenile salmonids in Alaska streams. *Proc West Assoc Fish Wildl Agencies* 1984:251-262
- Nicol S, Stolp M (1990) A refinement of the moult-staging technique for Antarctic krill (*Euphasia superba*). *Mar Biol* 104:169-173
- Nixon SW, Oviatt CA (1973) Ecology of a New England salt marsh. *Ecol Monogr* 43:463-498
- Nord AE, Schmulbach JC (1973) A comparison of the macroinvertebrate aufwuchs in the unstabilized and stabilized Missouri River. *Proc S Dak Acad Sci* 52:127-138
- Odum WE, Heald EJ (1972) Trophic analyses of an estuarine mangrove community. *Bull Mar Sci* 22:671-738
- Orth RJ (1973) Benthic fauna of eelgrass, *Zostera marina*, beds. *Ches Sci* 14:258-269
- Orth RJ, Moore KA (1983) Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science* 222:51-53
- Orth RJ, Moore KA (1984) Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: an historical perspective. *Estuaries* 7:531-540
- Orth RJ, Van Montfrans J (1984) Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquat Bot* 18:43-69
- Orth RJ, Heck KL Jr, Montfrans JV (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7:339-350
- Péres JM, Picard J (1975) Causes of decrease and disappearance of the seagrass *Posidonia oceanica* on the French Mediterranean coast. *Aquat Biol* 1:133-139
- Peterson CGJ (1918) The sea bottom and its production of fish food. A survey of work done in connection with the valuation of the Danish waters from 1883-1917. *Rep Danish Biol Sta* 25:pp 1-62
- Peterson CH (1979) Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston RJ (ed) *Ecological Processes in Coastal and Marine Systems*. Plenum Press, New York, pp 233-264
- Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar Biol* 66:159-170
- Peterson CH, Summerson HC, Duncan PB (1984) The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. *J Mar Res* 42:123-138
- Petranka JW (1983) Fish predation: a factor affecting the spatial distribution of a stream-breeding salamander. *Copeia* 1983:624-628
- Posey MH, Hines AH (1991) Complex predator-prey interaction within an estuarine benthic community. *Ecology* 72:2155-2169
- Power ME (1984) Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* 65:523-528
- Reise K (1977) Predation pressure and community structure of an intertidal soft-bottom fauna. In: Keegan BF, Ceidigh PO, Boaden PJS (eds) *Biology of Benthic Organisms*. Pergamon Press, New York, pp 513-519
- Robertson AI, Daniel PA (1989) Decomposition and the annual flux of detritus from fallen timber in tropical mangrove forests. *Limnol Oceanogr* 34:640-646

- Robertson AI, Lenanton RCJ (1984) Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. *J Exp Mar Biol Ecol* 84:265-283
- Robertson AI, Daniel PA, Dixon P (1991) Mangrove forest structure and productivity in the Fly River estuary, Papua New Guinea. *Mar Biol* 111:147-155
- Ruiz GM, Hines AH, Posey MH (in press) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar Ecol Prog Ser*.
- Sale PF, Douglas WA (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65:409-422
- Saunders RL, Smith MW (1962) Physical alteration of stream habitat to improve brook trout production. *Trans Am Fish Soc* 91:185-188
- Savino J, Stein RA (1982) Predator-prey interaction between largemouth bass and blue gills as influenced by simulated, submerged vegetation. *Trans Am Fish Soc* 111:255-266
- Scoffin TP (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *J Sed Petrol* 40:249-273
- Sedell JR, Froggatt JL (1984) Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. *Verh Int Verein Limnol* 22:1824-1834
- Sedell JR, Everest FH, Swanson FJ (1982) Fish habitat and streamside management: past and present. *Soc Amer Foresters, Proc Ann Mtg* 1981, pp 244-255
- Short FT, Jones GE, Burdick DM (1991) Seagrass decline: problems and solutions. *Coastal Wetlands: Coastal Zone '91 Conference-ASCE, Long Beach, CA*, pp 439-453
- Shulman MJ (1984) Resource limitation and recruitment patterns in a coral reef fish assemblage. *J Exp Mar Biol Ecol* 74:85-109
- Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66:1056-1066
- Sindermann CJ (1968) Oyster mortalities, with particular reference to Chesapeake Bay and the Atlantic coast of North America. *US Fish & Wildl Serv Sci Rep*
- Sindermann CJ (1990) Principle diseases of marine fish and shellfish. Vol 2. *Diseases of marine shellfish*. Academic Press, San Diego, CA, 516 pp
- Skelly DK, Werner EE (1990) Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71:2313-2322
- Smith LD, Coull BC (1987) Juvenile spot (Pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrata. *J Exp Mar Biol Ecol* 105:123-136
- Smock LA, Gilinsky E, Stoneburner DL (1985) Macroinvertebrate production in a southeastern United States blackwater stream. *Ecology* 66:1491-1503
- Smock LA, Gladden JE, Rickenberg JL, Smith LC, Black CR (1992) Lotic macroinvertebrate production in three dimensions: channel surface, hyporheic, and floodplain environments. *Ecology* 73:876-886
- Smock LA, Metzler GL, Gladden JE (1989) Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70:764-775
- Sokal RR, Rohlf EF (1981) *Biometry*. Freeman, San Francisco, 859 pp
- Southwick CH, Pine FW (1975) Abundance of submerged vascular vegetation in the Rhode River from 1966 to 1973. *Ches Sci* 16:147-151
- Stoner AW (1980) The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull Mar Sci* 30:537-551
- Stoner AW (1982) The influence of benthic macrophytes on the foraging behavior of the pinfish, *Lagodon rhomboides* (Linnaeus). *J Exp Mar Biol Ecol* 58:271-284
- Summerson HC, Peterson CH (1984) The role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar Ecol Prog Ser* 15:63-77
- Tonn WM, Paszkowski CA, Holopainen IJ (1992) Piscivory and recruitment: mechanisms structuring prey populations in small lakes. *Ecology* 73:951-958
- Triska FJ (1984) Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. *Verhandl-Int Verein Theor Ang Limnol* 22:1876-1892
- Triska FJ, Cromack K (1980) The role of wood debris in forests and streams. In: Waring RH (ed) *Forests: fresh perspectives from ecosystem analysis. Proceedings 40th Biology Colloquium* (1979). Oregon State University Press, Corvallis, pp 171-190
- Tschaplinsky PJ, Hartman GF (1983) Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. *Can J Fish Aquat Sci* 40:452-461
- Turner RD (1977) Wood, mollusks and deepsea food chains. *Bull Am Malac Union* 1974:59-65
- Turner RD (1981) "Wood islands" and "thermal vents" as centers of diverse communities in the deep sea. *Sov J Mar Biol (Biologiya Morya)* 7:1-9
- Turner RD (1984) An overview of research on marine borers: past progress and future directions. In: Costlow JD, Tipper RC (eds) *Marine biodeterioration: an interdisciplinary study*. Naval Institute Press, Annapolis, MD, pp 3-16
- Turner RD, Johnson AC (1971) Biology of marine wood boring molluscs. In: Jones EBG, Eltringham SK (eds) *Marine borers, fungi and fouling organisms*. Org Econ Co-operat Develop, Paris, pp 259-301
- Van Engel WA (1958) The blue crab and its fishery in Chesapeake Bay: Part 1-Reproduction, early development, growth, and migration. *Comm Fish Res* 20:6-17
- Ware DM (1972) Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. *J Fish Res Bd Canada* 29:1193-1201
- Wells HW (1961) The fauna of oyster beds, with special reference to the salinity factor. *Ecol Monogr* 31:239-266
- Welsh BL (1975) The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. *Ecology* 56:513-530
- Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548
- Wilson KA, Able KW, Heck KL Jr (1990) Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Mar Ecol Prog Ser* 58:243-251
- Wilson KA, Heck KL Jr, Able KW (1987) Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fish Bull* 85:53-58
- Winer BJ (1971) *Statistical Principles in Experimental Design*. McGraw-Hill Kogakusha, Tokyo, Japan, 2nd edition, 907 pp