

Are Three-Dimensional Structure and Healthy Oyster Populations the Keys to an Ecologically Interesting and Important Fish Community?

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Abstract

Oyster reefs provide important habitat for a fish assemblage that is both ecologically interesting and important to the estuarine food web. These fishes are dependent on oyster reefs to varying degrees for feeding, reproduction and shelter from predators. Among the most dependent are the small resident fishes that attach their eggs to unfouled, articulated oyster shells. This resident oyster reef fish assemblage is unusual in the high degree of similarity of both the temporal patterns of recruitment and the diets of newly recruited juveniles. Larvae of the naked goby, the most abundant benthic fish in many mesohaline Chesapeake Bay oyster reefs, occur in sufficiently high densities during summer to be important grazers of zooplankton. The naked goby also has the highest recruitment rate recorded for any reef fish world-wide. In addition to the resident fishes, oyster reefs are extensively utilized by more widely ranging fish species. However, limited research involving visual observation in Chesapeake Bay and many other estuaries, and the difficulty of sampling this habitat with traditional nets, has likely led to our underestimating the importance of oyster reefs to many of these highly mobile fishes. For example, counts and observations conducted with scuba indicate that striped bass, especially juveniles, are very abundant on oyster reefs. Some individuals appear to remain in limited areas within reefs and forage on oyster reef fishes, especially on naked goby larvae aggregating near structures.

Oyster reef restoration and construction efforts have the potential to enhance local abundances of reef fishes. Reefs that develop "healthy" oyster populations will provide a continual supply of nest sites for resident fishes. Reefs that support large populations of mobile invertebrate infauna and epifauna will provide prey for both resident fishes and larger, more transient, bottom-feeding species. Enhancing topographical relief within reefs will attract oyster reef fish larvae by creating downcurrent low flow zones that allow larvae to remain on reefs and settle to the benthos. Reefs that extend to near the water surface and into shallow nearshore areas will also provide refuges for fish when oxygen concentrations in deeper areas of reefs decline to lethal levels. It is important that the requirements of fish populations and oysters on reefs are not likely to be in conflict; many of the same strategies proposed to enhance oyster populations will also improve the habitat for fishes.

Introduction

A wide variety of fishes utilize estuarine oyster reefs for feeding, shelter from predators, and for reproduction. The most abundant of these fishes are small benthic species that are cryptic in both coloration and behavior, and use oyster shells for nest sites. However, oyster reefs are also utilized by more widely ranging fish like spot (*Leiostomus xanthurus*) and black drum (*Pogonias cromis*), which feed on benthic invertebrates, and by some of the top predators in estuarine systems such as striped bass (*Morone saxatilis*), which feed on the benthic fishes and crabs found in and among the shell substrate.

Although the degree of dependence on oyster reefs varies widely among fish species, both the decline of oyster reefs in many estuaries and oyster reef restoration efforts have the potential to influence populations of many estuarine fishes. These fishes will potentially be

affected by oyster reef management and restoration efforts regardless of whether the consequences to fishes are implicitly considered (e.g. Chesapeake Bay Program: CBP 1993, 1994), or the reefs are managed only to maximize oyster production. The goals of programs designed to create complete oyster reef communities, and those designed to maximize oyster production are not necessarily in conflict; however, many of the factors that are likely to enhance oyster recruitment, survival and growth should also enhance fish populations.

The goal of this paper is to suggest some of the reasons that oyster reef fishes should be considered in restoration efforts, and to discuss how various methods for oyster reef restoration may affect oyster reef fish populations. To do this I draw on visual observations and field experiments conducted during 1985-1994 in mesohaline reefs in Chesapeake Bay. Because most of the fish species discussed have broad geographic ranges and the factors that affect their abundance deal with the general health and physical configuration of oyster reefs, the information in this paper should be relevant to reef management and restoration in many of the Atlantic and Gulf of Mexico estuaries of the United States.

Oyster Reef Fish Ecology And The Structure of Oyster Reefs

FLAG POND OYSTER REEF

Many of the observations and field experiments described in this paper were conducted on the Flag Pond oyster reef, located 7 km north of Cove Point, MD on the western shore of the Chesapeake Bay (approximately 38°25'N, 76°25'W; Fig. 1). During the summers of 1985-1994, research assistants and I dove extensively to sample fishes and monitor dissolved oxygen and flow at Flag Pond. The Flag Pond oyster reef consists of approximately 81 ha of extant oyster bar and rock substrate extending from the shore for approximately 0.3-1.0 km at water

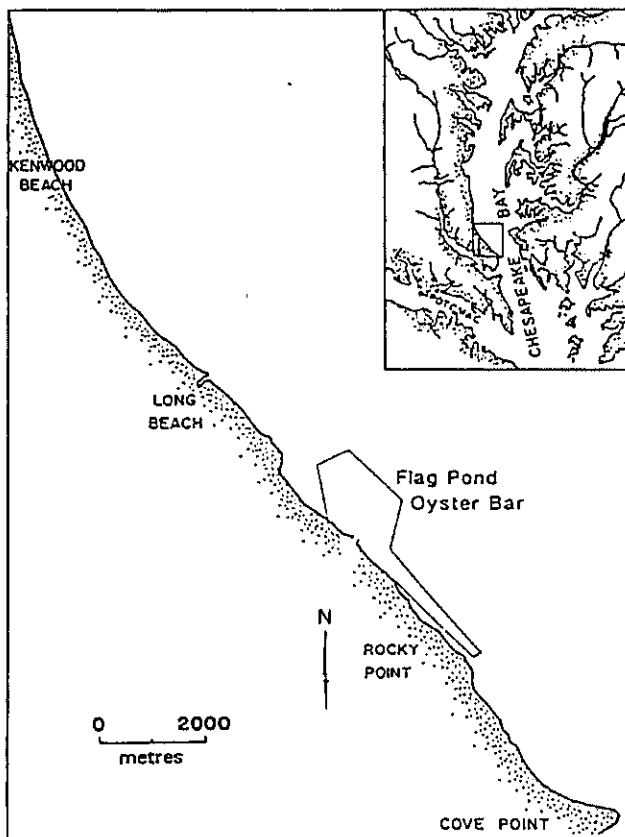


Figure 1. Flag Pond oyster reef. Physical conditions and biota are not significantly affected by the nearby Calvert Cliffs Nuclear Power Plant (Heck 1987).

Table 1. Fishes at Flag Pond oyster reef. Species listed as facultative residents appear to be represented by at least some individuals that remain on the oyster reef for several months. Some species listed as transients may actually be facultative residents. However, they are highly mobile within the reefs, and the duration of residency of individuals has not been studied.

Oyster Reef Resident Fishes	Facultative Residents	Transients
naked goby (<i>Gobiosoma bosc</i>)	black sea bass (<i>Centropristis striata</i>)	striped bass (<i>Morone saxatilis</i>)
skilletfish (<i>Gobiesox strumosus</i>)	northern pipefish (<i>Syngnathus fuscus</i>)	summer flounder (juv.) (<i>Paralichthys dentatus</i>)
striped blenny (<i>Chasmodes bosquianus</i>)	Atlantic spadefish (<i>Chaetodipterus faber</i>)	winter flounder (juv.) (<i>Pleuronectes americanus</i>)
feather blenny (<i>Hypsoblennius hentz</i>)		spot (<i>Leiostomus xanthurus</i>)
oyster toadfish (<i>Opsanus tau</i>)		pinfish (<i>Lagodon rhomboides</i>)
		inshore lizardfish (<i>Synodus foetens</i>)
		American eel (<i>Anguilla rostrata</i>)
		striped burrfish (<i>Chilomycterus schoepfi</i>)
		Atlantic silverside (<i>Menidia menidia</i>)

depths of 1-6 m. Oyster (*Crassostrea virginica*) shell provide fairly continuous bottom cover, interspersed with patches of sand and sediment, as well as low consolidated sandstone outcroppings and rocks (mostly <1 m diameter and <0.5 m high). Outcroppings and rocks, which are generally covered with oysters and other sessile invertebrates, provide three-dimensional physical structure within the oyster reefs and alter near-bottom flow. These structures become more prevalent shoreward, with continuous shell and sediment seaward. Flow at Flag Pond is bidirectional with predominant flood tides towards the NNW (ca 334°; Browne & Fisher 1988) and ebb tides towards the SSE. Salinity, temperature, and oxygen fluctuations, as well as the oyster reef fish community are described in Breitburg (1990, 1992). Bottom temperatures and biota at the study site are not affected by operation of the nearby Calvert Cliffs Nuclear Power Plant (Heck 1987).

Densities of oyster reef fishes described below were estimated in one of three ways. Numbers of demersal larvae of the naked goby were estimated visually. Densities of small

oyster reef fishes were estimated from collections made by suctioning fish isolated within 0.26 m² metal cylinders, or by allowing fish to colonize 0.35 m² fiberglass trays filled with 1 l of sand and 4 l of oyster shell (Breitburg 1992).

OYSTER REEF FISH ASSEMBLAGE AT FLAG POND

The fish assemblage found in the Flag Pond oyster reef during late spring through early autumn includes species that vary widely in their dependence on oyster reef habitat. These fishes comprise three general categories: (1) resident oyster reef fishes, which are dependent on oyster reefs as their primary habitat, (2) facultative residents that are generally not wide ranging, but utilize a variety of structured habitats, and (3) transients that can be quite abundant at times but are wide ranging at least as adults (Table 1).

The "resident oyster reef assemblage" at Flag Pond includes four small species – the naked goby, skilletfish, striped blenny and feather blenny – as well as the larger oyster

toadfish. All of these species are highly dependent on oyster reefs, and utilize this habitat for feeding, shelter and reproduction. Resident oyster reef fishes feed primarily on benthic invertebrates, but also prey on benthic fishes. They are cryptic in their behavior, tending to shelter under and among oyster shells, especially when predatory fish are present.

The four smaller resident oyster reef species attach their benthic eggs to the insides of unfouled, articulated oyster shells. Naked gobies, striped blennies and skillettfish appear to be particularly dependent on this resource. It is important to consider that a "healthy" population of oysters would be expected to have a continual, low level of mortality of a variety of sizes of individuals, and thereby provide a continual supply of nest sites for these fishes. In contrast, shell plants, reefs where disease kills oysters before they are large enough to be used by fish, and artificial structures not colonized by large bivalves, may not provide adequate reproductive habitat for these species. Furthermore, addition of shell or dredging the reef during the spring through late summer-to-early autumn breeding season could disrupt reproduction of these fish by burying nests, breaking apart articulated shells or scaring off males guarding their eggs.

Unlike the smaller species, oyster toadfish attach their eggs to the undersides of larger substrates including rocks and consolidated oyster shells. Oyster toadfish do not have planktonic larvae, and males guard their offspring until they leave the nest at 20 mm standard length (SL). Because they do not produce widely dispersing larvae, oyster toadfish may be more useful as indicators of local contaminant conditions than other estuarine fish species. No studies of which I am aware have tagged young-of-year oyster toadfish and returned them to the reefs from which they were caught. However, it would not be surprising if the egg through juvenile stages remained within a single oyster reef at least until water temperatures decline in autumn. Adults appear to have a strong tendency to return to their home reef when removed and relocated (Schwartz 1974).

ECOLOGICAL IMPORTANCE OF A RESIDENT OYSTER-REEF FISH TO ESTUARINE DYNAMICS

Some members of the resident oyster reef assemblage may be ecologically important because they are sufficiently abundant to play significant roles in estuarine trophic interactions. Naked goby larvae are typically either the first or second most abundant fish larvae in mesohaline areas of Chesapeake Bay tributaries during summer, and rank second only to bay anchovy larvae in the mainstem Bay. Densities above the pycnocline in the Patuxent River typically average 5 to 10 ind m^{-3} during late June through mid-August, with peak densities on the order of 50 to 60 larvae m^{-3} (e.g. Shenker et al. 1983, Keister et al. unpubl). Average densities of over 200 naked goby larvae m^{-3} have been reported from the North Inlet estuary in South Carolina (Allen and Barker 1990).

Perhaps because of their abundance, naked goby larvae are, at times, the most important prey of juvenile striped bass (Markle and Grant 1970). Also because of their abundance, naked goby larvae may crop a nontrivial portion of copepod production in Chesapeake Bay tributaries. Feeding rates vary among species of larval fishes. For example, yellow perch (*Perca flavescens*) larvae consume approximately 21% of their body weight each day (Mills and Forney 1983). In contrast, 200 μg dry wt. bay anchovy (*Anchoa mitchilli*) larvae consume approximately 50 *Artemia* sp. nauplii $\cdot h^{-1}$ or 6 μg nauplii $\cdot h^{-1}$ at prey densities of 50 nauplii $\cdot l^{-1}$ (Houde and Schekter 1980). If larvae feed 14 $h \cdot d^{-1}$, this would equal 42% of body weight $\cdot d^{-1}$. Personal experience rearing both species suggests that feeding rates of bay anchovy are greater than that for naked goby larvae. Assuming an intermediate feeding rate of 30% of body weight $\cdot d^{-1}$, and using an estimate of 6 μg dry weight for *Acartia tonsa* (Heinle 1969), an 8 mm SL, 2000 μg dry weight naked goby larva would consume approximately 100 copepods $\cdot ind^{-1} \cdot d^{-1}$. This is similar to the feeding rate of 17 dph striped bass larvae feeding on copepods at prey densities of 50 $ind \cdot l^{-1}$ (Chesney 1986). If

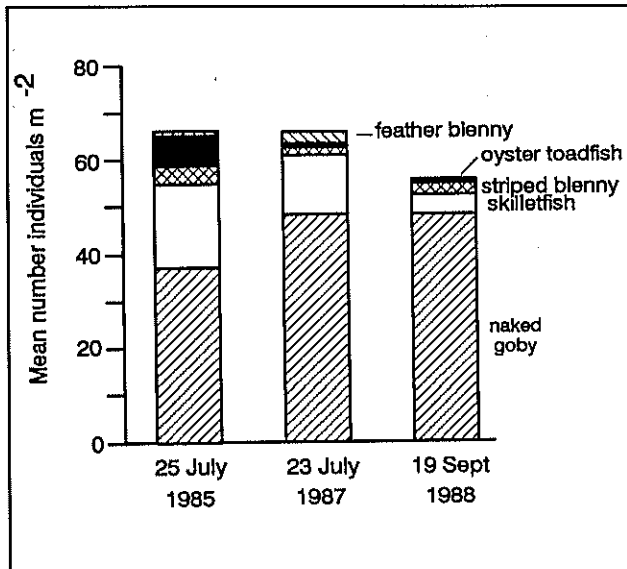


Figure 2. Mean densities of oyster reef resident fishes during peak sampled density in three years. Data are means of 5-10 samples per sample date.

summer densities of naked goby larvae sufficiently large to feed on mesozooplankton are approximately 2 ind·m⁻³, and these larvae range in size from 6-10 mm SL, consumption of copepods and copepodites would be on the order of 50-400 ind·m⁻³·d⁻¹.

Estimates of grazing by gelatinous predators indicate that predation by naked goby larvae on zooplankton may be comparable to that of sea nettles and ctenophores, which are recognized as important grazers in the Chesapeake Bay system (e.g. Purcell 1992, 1994a). Summer standing crops of planktonic copepods and other mesozooplankton in surface waters of tributaries and the mainstem Bay during July has been estimated at 1,000 to 55,000 ind·m⁻³ (e.g. MDE 1992, 1993). At copepod densities of 25,000 ind·m⁻³, a 60 mm bell diam individual sea nettle feeding at 27°C would be expected to consume approximately 200 copepods·d⁻¹ (from equation in Table 4 in Purcell 1992). At typical surface layer densities of 0.2 sea nettles m⁻³ (e.g. Purcell et al. 1994b, Keister et al. unpubl) sea nettles should therefore consume approximately 40 copepods·m⁻³·d⁻¹. At typical surface layer field densities of 1 ind·m⁻³ (Purcell et al. 1994b, Keister et al. unpubl) and copepod densities of 25,000 ind·m⁻³, ctenophores would consume approximately 1600 copepods·d⁻¹ (Purcell et al.

1994b). However, during mid-summer, ctenophore densities can be substantially lower than 1 ind·m⁻³.

Ultimately, naked gobies and other oyster reef fishes that survive the larval stage settle to the benthos, primarily to oyster reefs. By doing so, they transport carbon and nitrogen from the water column to the benthos. The result of these high recruitment rates is high densities of resident oyster reef fishes (Fig. 2), averaging as many as 60 or more ind·m⁻², with populations heavily skewed towards the young-of-year class.

Recruitment rates of naked gobies on Flag Pond are typically 1-2 orders of magnitude higher than maximum recruitment rates recorded for coral reef fishes or other temperate reef fish species. In field experiments conducted during 1994, we recorded 24-h recruitment rates averaging as high as 34.1±4.9 ind·m⁻²·d⁻¹ (n=16 0.35 m² recruitment trays), and an average of 9.1±2.9 ind·m⁻²·d⁻¹ during late July - late August (n=13 sample dates). This would result in an average recruitment rate of 272 ind·m⁻²·month⁻¹. Comparable experiments have not been conducted on other oyster reefs. However, these high rates are not likely to be unique to either Flag Pond or the Chesapeake Bay system because higher larval densities have been recorded elsewhere (e.g. Allen and Barker 1990).

REEF CONSTRUCTION AND THE SIMILARITY OF SPECIES

Resident oyster reef fishes are also interesting and unusual from an ecological standpoint because of the similarity in the temporal patterns of recruitment, and the diets of benthic juveniles of the four most abundant species. A consequence of this similarity, however, is that the timing of reef construction or rehabilitation efforts, and the degree to which reef restoration affects prey for newly settled fish, may strongly affect the resident oyster reef fish assemblage in its entirety. Three years of sampling at the Flag Pond oyster reef indicate that peak recruitment for all of the most abundant resident oyster reef fishes occurs within the same brief period

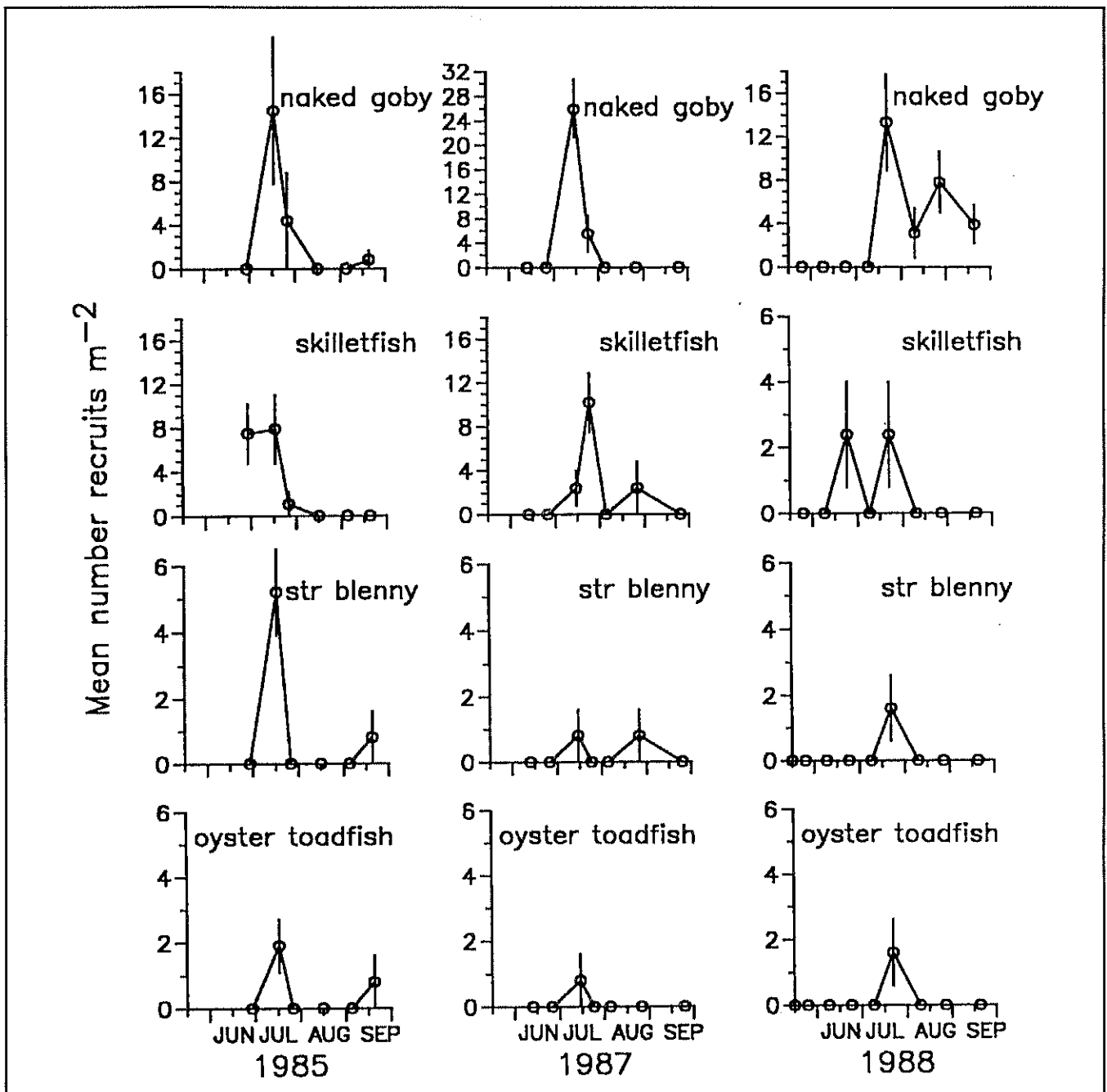


Figure 3. Mean number of recruits ≤ 2 weeks postsettlement m^{-2} in the Flag Pond oyster reef during 3 years of sampling. Sampling was conducted biweekly through most of the recruitment season. Numbers of recruits 2 weeks postsettlement for each species were calculated based on minimum sizes of individuals collected in samples and estimates of growth rates. For oyster toadfish these numbers represent individuals that have likely left their nest 2 weeks before being collected. Data are $\pm 1SE$ of 5-10 samples per date. str blenny = striped blenny.

during mid-summer (Fig. 3). If reefs are disturbed during this peak recruitment period, or if reef construction occurs after this peak, recruitment of the entire assemblage may be reduced for that year. In subsequent years, however, this initial timing will likely have little or no residual effect. Furthermore, until the overwintering behaviors of these fishes are better understood,

the consequences and benefits of disturbing oyster reef habitat at various times of the year will be difficult to predict.

The combination of high recruitment rates (described above) and the similarity in diets of the juvenile oyster reef resident species may make the way that reefs affect benthic invertebrate assemblages of more long-lived conse-

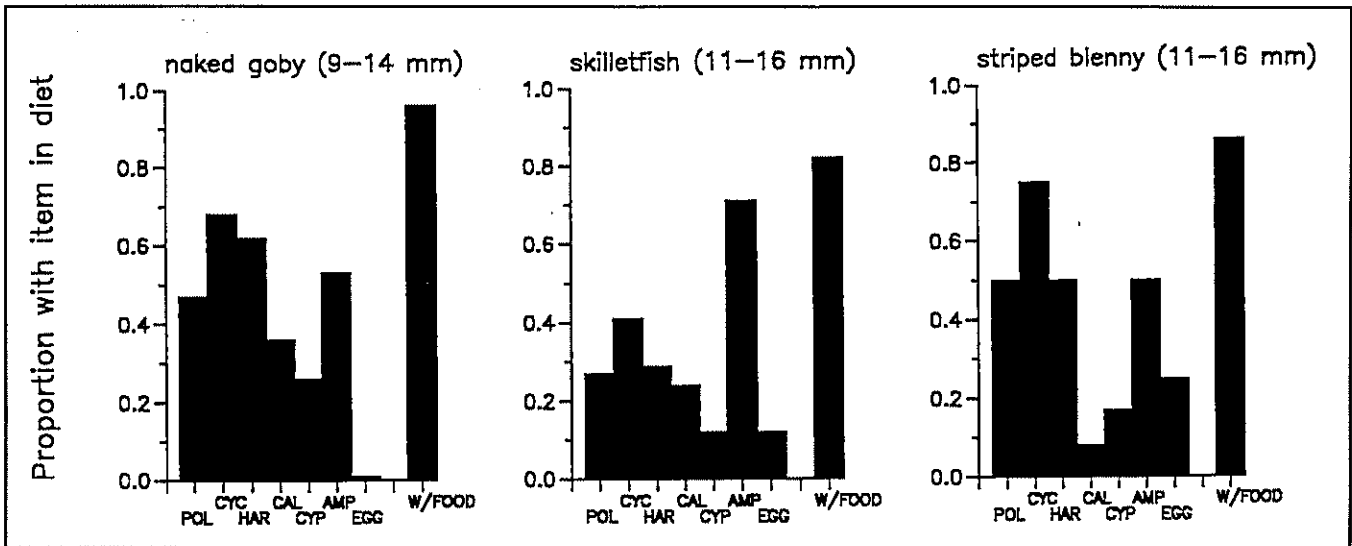


Figure 4. Diets of oyster reef fishes estimated to be 2 weeks postsettlement. *pol* = polychaetes, *cyc* = cyclopid copepods, *har* = harpacticoid copepods, *cal* = calanoid copepods, *cyp* = barnacle cyprids, *amp* = amphipods, *egg* = fish egg, *w/food* = proportion of fish with prey in their gut.

quence. All resident species are similarly dependent on benthic and demersal invertebrate prey. Diets of similar sized, 2 week postsettlement naked goby, skilletfish and striped blenny include the same array of polychaetes, copepods, barnacle cyprids, amphipods and fish eggs (Fig. 4). Diets of slightly larger, 20-25 mm SL, juveniles of these fishes are also similar and overlap with diets of similar-sized oyster toadfish (Fig. 5). Dissimilar-sized individuals of all of these species will eat each other, and naked gobies are also known to prey on smaller conspecifics (Nero 1976, Breitburg et al. 1994, Breitburg unpubl. data). Artificial reef structures and the height and dimensions of shell plants are sometimes purposefully designed to modify water flow, sedimentation and other physical properties that may influence the recruitment or growth of oysters. These same factors can affect the behavior, recruitment and abundance of prey of juvenile oyster reef fishes (e.g. Jumars and Nowell 1984, Palmer 1986, Butman 1989). Structures that are less readily colonized by invertebrate prey may thus decrease recruitment or growth rates, or increase cannibalism and predation within the resident oyster reef fish community.

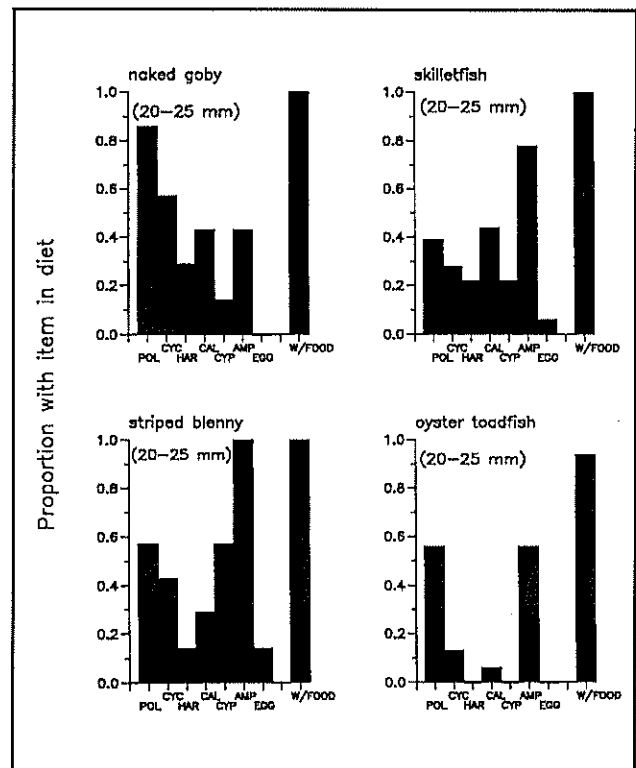


Figure 5. Diets of oyster reef fishes similar in size to that of oyster toadfish 2 weeks after leaving their nest. Abbreviations for diet items are the same as those used in Fig. 4.

RECRUITMENT AND SURVIVAL OF OYSTER REEF FISH AND THE THREE-DIMENSIONAL STRUCTURE OF OYSTER REEFS

The three dimensional structure of oyster reefs will affect the spatial distribution of demersal naked goby larvae on reefs, the spatial distribution of settlement of naked gobies (Fig. 6), and perhaps the overall abundance of this fish species (Breitburg et al. 1995). This structure can result from rehabilitation efforts or the natural relief that historically developed on unfished oyster habitat. Rocks and other structures create areas of reduced flow velocity on their downcurrent sides. Naked goby larvae aggregate in these downcurrent low-flow zones. For example, only 6% of the substrate measured on transects in the Flag Pond oyster reef consisted of structures that protrude more than 15 cm above the basal shell substrate, but over 90% of the schools of ≥ 10 larvae were located adjacent to these structures (Breitburg 1991). When the size and position of rocks were manipulated, larger numbers of larvae associated with larger rocks, which created larger downcurrent low-flow zones (Breitburg et al. 1995). Furthermore, larvae were nearly always within the downcurrent low-flow zone, and were never upcurrent of rocks even though planktonic prey

were more abundant in the upcurrent position. This attraction of larvae to low flow zones created by structure is reflected in the spatial distribution of settlement; most naked gobies settle adjacent to structures and in positions that during a portion of the tidal cycle would be within these downcurrent low flow zones (Breitburg et al. 1995). Other experiments designed to examine the response of naked goby larvae to flow and structure indicate that these structures may also create habitat that is heavily used by young-of-year striped bass (see below).

In areas subject to low dissolved oxygen concentrations, reefs that extend to or near the surface, or along the bottom to shallow areas where oxygen concentrations remain suitable, potentially increase survival of oyster reef fishes and crabs (see also Lenihan et al., this volume). The behavioral response of oyster reef fishes to oxygen concentrations that approach lethal levels is to move upward onto rocks or other structures that protrude above the surrounding substrate and to migrate shoreward (Breitburg 1992). Xanthic crabs and blue crabs (*Callinectes sapidus*) climb upward onto rocks, buoy lines, and other structures. These behavioral responses can allow benthic fish and crabs to move into water depths with higher oxygen

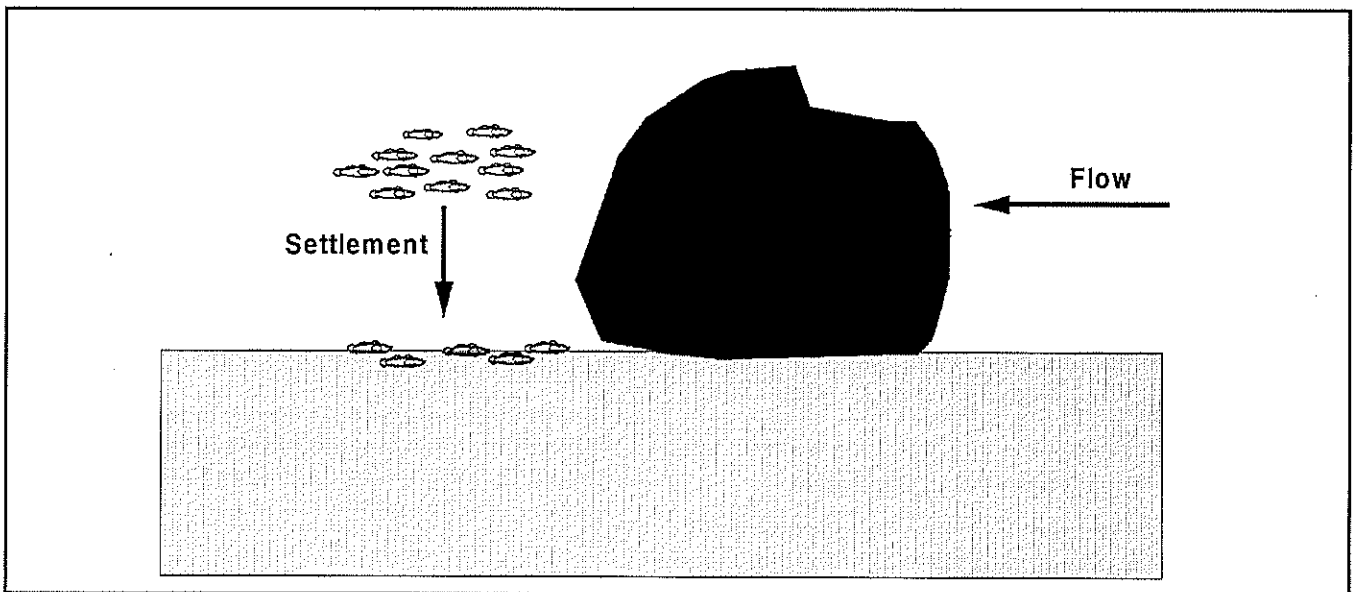


Figure 6. The spatial distribution of naked goby larvae and settlement of naked goby to the benthic oyster reef habitat. Demersal larvae aggregate downcurrent of structures that reduce flow velocity at least during portions of the tidal cycle when current velocities exceed the sustained swimming speed of larvae. Most larval settlement occurs in these downcurrent "flow shadows" created by three-dimensional structure within the oyster reef.

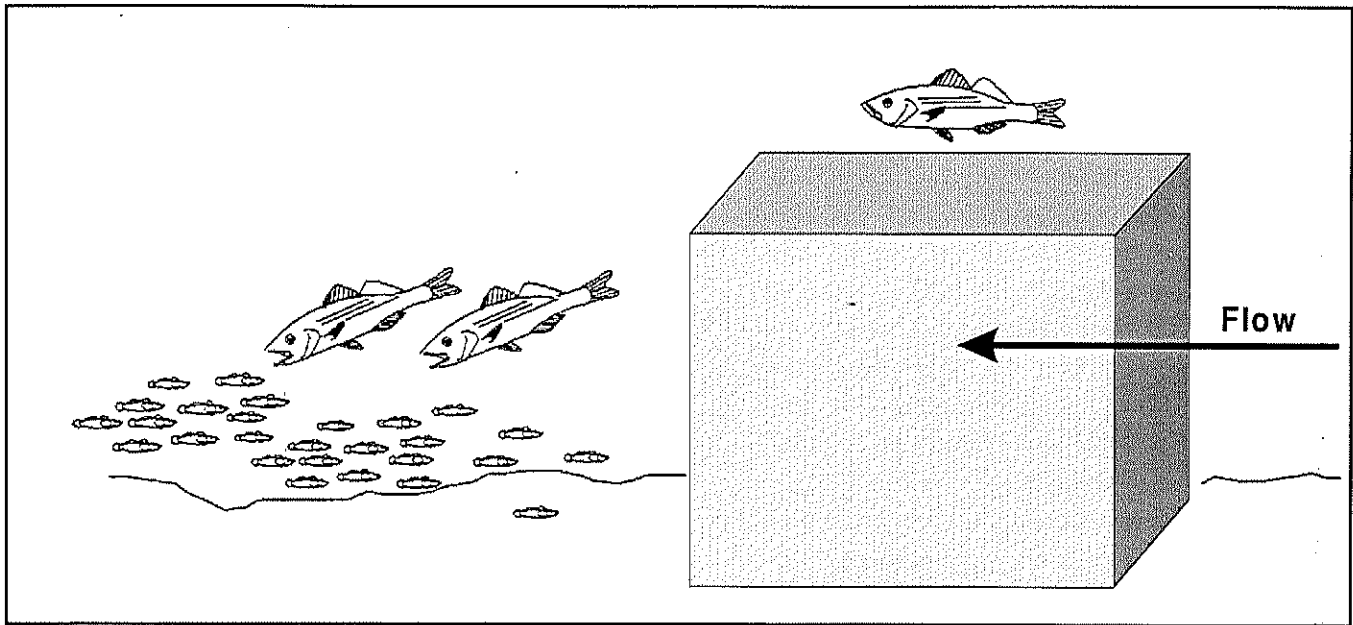


Figure 7. Illustration of cube experiment testing effects of flow on naked goby larvae. Young-of-year striped bass hovered above cubes and fed on larvae.

concentrations and can sometimes substantially increase survival (Breitburg 1992). Relatively flat oyster reefs that do not extend shoreward to shallow water depths will not provide a refuge during low dissolved oxygen events.

ARE OYSTER REEFS IMPORTANT HABITAT FOR STRIPED BASS?

The limited research involving visual observations on oyster reefs in the Chesapeake Bay and elsewhere, and the difficulty of sampling oyster reefs with bottom trawls, has likely led to our underestimating the importance of oyster reefs to many of the highly mobile fish species. For example, my observations while diving at Flag Pond indicate that densities of striped bass, especially juveniles, are extremely high on oyster reefs. Since Chesapeake Bay striped bass populations have begun to recover, I have often seen >50 individuals during a 1-hour dive covering an extremely limited area. Some individuals, especially young-of-year and age class 1+ fish, appear to remain in limited areas within reefs and forage on oyster reef fishes, especially on naked goby larvae aggregating near structures. Other striped bass, especially

larger fish, occur in schools of up to several hundred individuals.

None of my oyster reef research has focused specifically on striped bass. However, two instances when striped bass abundances were estimated illustrate their abundance on oyster reefs. Both of these counts were pre-planned, i.e. we did not initiate the count because of high densities on a particular date. First, during summer 1993, I conducted an experiment using 33 x 33 x 33 cm cubes designed to separate the effects of flow and structure on aggregating behavior of naked goby larvae (Breitburg unpublished data). Seven of the 12 cubes monitored on 26 July 1993 had young-of-year striped bass hovering within a few cm above the top of the cube, for a total of 20 striped bass per 1.3 m² of cube top area (Fig. 7). These young-of-year were actively feeding on the naked goby larvae that aggregated in large numbers along the downcurrent side of the complete cubes (some cubes had open sides to allow water to pass through unimpeded). In addition to the young-of-year that remained associated with the cubes, large numbers of larger juvenile and subadult striped bass actively swam above, beside and between the cubes.

Second, during 1994 research assistants and I did 5 min counts of numbers of striped bass and other piscivorous fishes swimming 50 cm above the substrate that passed over 0.35 m² recruitment trays adjacent to, and 2 m distant from, large rocks (approximately 80-100 cm in diameter perpendicular to the prevailing flow direction). Four trays (upcurrent/downcurrent, adjacent/distant) were counted simultaneously, each by a different diver. Averages of 4.4 and 1.9 observations of juvenile striped bass per 5 min were counted for trays distant from, and adjacent to rocks, respectively (n=8 trays per distance category). Most of the striped bass were probably 1+ year class individuals. Although it is impossible to estimate densities of striped bass from these counts because some individuals likely swam over the trays more than once, it is clear that the abundance of these fish is sometimes sufficiently high for them to be important predators within this oyster reef.

Conclusions

No studies of which I am aware have examined the direct or indirect effects of resident oyster reef fishes on oysters or mobile fauna in oyster reef communities (as of the submission date of this manuscript.) Similarly, although we know that many of the more transient fishes, including a number of commercially and recreationally valuable species, utilize oyster reefs, we do not know the importance of oyster reefs to these transient fishes on either the individual or population level. Excluding issues of water quality, we cannot answer the question: Would we have fewer or smaller striped bass, spot, pinfish, etc., if there were no oyster reefs in Chesapeake Bay? Nor do we know the type or magnitude of effects of these transient fishes on the oyster reef community. Clearly these are major gaps in our understanding of oyster reef communities that could have important management implications.

The part of the fish:oyster reef relationship that is evident, however, is that an ecologically interesting and important assemblage of resident

fishes is dependent on a healthy oyster population for habitat and reproduction. The methods used for reef enhancement and rehabilitation and for the construction of artificial reefs are likely to influence their suitability for these fish species. One important feature of reef construction, also singled out as important to oysters themselves (see Bartol and Mann 1999, Chapter 10, this volume) is likely to be the extent and type of three-dimensional structure created. In addition, reefs must provide shelter from predators, sites for egg attachment, and suitable habitat for prey.

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