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ESTIMATES OF NAKED GOBY (*GOBIOSOMA BOSCA*), STRIPED BLENNY (*CHASMODES BOSQUIANUS*) AND EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) LARVAL PRODUCTION AROUND A RESTORED CHESAPEAKE BAY OYSTER REEF

Juliana M. Harding and Roger Mann

ABSTRACT

Naked gobies (*Gobiosoma bosc*) and striped blennies (*Chasmodes bosquianus*) rely on oyster reefs for nesting sites, feeding grounds, and refugia from predation by upper level piscivores. Seasonal densities of Eastern oysters (*Crassostrea virginica*), naked gobies, and striped blennies on Palace Bar Reef, Piankatank River, Virginia were quantified and used to develop species-specific larval production estimates. Densities of oyster adults, juveniles, and articulated shell valves (the result of recent mortality) did not significantly change from November 1995 to November 1996. Naked goby and striped blenny densities varied with substrate type and season; peak fish densities for both species were observed in August 1996. Areas where shell substrate dominated the bottom supported fish densities up to 14 times greater than those observed in habitat areas lacking shell. Larval production and recruitment estimates for Palace Bar Reef oysters are of the same order of magnitude as observed field densities. Benthic fish production estimates are within an order of magnitude of adult densities and are similar to previous recruitment estimates for Chesapeake Bay naked gobies. Species-specific production estimates for both oysters and fishes are sufficient to sustain observed adult densities on Palace Bar Reef, Piankatank River, Virginia.

Oyster reefs were physical and biological cornerstones for shallow water communities in the Chesapeake Bay until the early 20th Century. The physical reef structures created by Eastern oyster (*Crassostrea virginica*) shells created both navigational hazards and highly heterogeneous three dimensional habitats for benthic estuarine fauna. The living oysters helped maintain shallow water quality by filtering (Newell, 1988) and were central in the complex trophic structure that supported nursery and feeding grounds for both recreational and commercial finfishes, e.g., striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), spotted seatrout (*Cynoscion nebulosus*), Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and Atlantic menhaden (*Brevoortia tyrannus*); (Harding and Mann, 1999; Coen et al., 1999; see also Luckenbach et al., 1998 and references therein). As oyster populations have declined because of overfishing, disease, and habitat degradation, the associated shallow water communities and the fisheries that they supported have suffered. Current oyster reef restoration activities are examining the trophic networks centered on oyster reefs as an index of oyster restoration success and potential associated fishery rehabilitation (Coen et al., 1997; Luckenbach et al., 1998, Mann and Harding, 1997, 1998; Coen et al., 1999).

The life history of the Eastern oyster has been described (Kennedy et al., 1996 and references therein). Adult oysters increase metabolic activity as water temperatures rise in the spring. Oysters reach sexual maturity after one year or at approximately 18 to 23 mm shell length. Spawning activity begins when water temperatures are above 12 to 15°C (e.g., in Virginia: May–June), and continues until late summer. The veliger larvae

are planktonic for 14 to 21 d after which they settle onto hard substrate and metamorphose. Continued growth as sessile bivalves creates and maintains three dimensional reef habitats.

Several benthic fish species including naked gobies (*Gobiosoma bosc*) and striped blennies (*Chasmodes bosquianus*) commonly inhabit oyster reef interstices and rely on oyster reefs for nest sites, feeding grounds, and shelter (Wells, 1961; Dahlberg and Conyers, 1973). Habitat use by these fishes is not restricted to the three-dimensional shell reefs exclusively, but habitat availability and heterogeneity are increased by living oyster matrix much as the heterogeneity of coral reefs is facilitated by living corals (Ebeling and Hixon, 1991). These small (<65 mm) benthic fishes are intermediate in the oyster reef trophic structure. Adult gobies and blennies graze on infaunal and epibenthic invertebrates (Dahlberg and Conyers, 1973; Nero, 1976) and are prey items for apex pelagic predators (e.g., striped bass (*M. saxatilis*), bluefish (*P. saltatrix*), weakfish (*C. regalis*)) associated with reef communities (Markle and Grant, 1970; Nero, 1976; Mann and Harding, 1997; Breitburg, 1998; Harding and Mann, 1999).

Seasonal abundance estimates for benthic reef fishes (i.e., naked gobies and striped blennies) must consider overwintering and spawning patterns. During the winter months when temperatures are low (<10°C), adult fishes move into deeper water and burrow into mud (Hildebrand and Cable, 1938; Dahlberg and Conyers, 1973; Fritzsche, 1978) or simply reduce activity and become more cryptic (Nero, 1976). As temperatures rise, fish activity increases and both naked goby and striped blenny adults are more visible within the reef matrix (Dahlberg and Conyers, 1973).

The life histories of striped blennies and naked gobies have been previously described (Nero, 1976; Fritzsche, 1978; Breitburg, 1988, 1989, 1991, 1998; Harding, 1999). Naked gobies reach sexual maturity at the beginning of their second year (total length (TL) approximately 24 mm, Nero, 1976). Gobies spawned early in the spawning season (e.g., May–June) grow to approximately 16 mm TL by the end of September or October (Nero, 1976). By the beginning of the following spawning season, these same fishes are at least 22 to 26 mm TL and sexually mature (Nero, 1976). Adult gobies and blennies build nests in clean, articulated empty oyster shells (commonly referred to as “boxes”) in early to mid-summer after water temperatures increase above 19 to 20°C (Dahlberg and Conyers, 1973). The adhesive eggs hatch after 1 to 2 wks (Nero, 1976). Nests are maintained and defended by male fishes. Gobies and blennies are polygamous; multiple females may visit a male’s nest during the course of a spawning season. Naked goby and striped blenny larvae begin feeding within 2 h after hatching (J. Harding, unpubl. data) and are planktonic for 2 to 3 wks (Breitburg, 1989, 1991; Harding, 1999). Seasonally, goby larvae may dominate ichthyoplankton collections within the Chesapeake Bay (Shenker et al., 1983; Cowan and Birdsong, 1985; Olney, 1983, 1996). Laboratory experiments have shown that larval naked gobies and striped blennies preferentially prey on oyster veligers and may be a significant source of veliger mortality (Harding, 1999). Selective consumption of bivalve veligers by larval gobies has been demonstrated in Biscayne Bay by Houde and Lovdal (Gobiidae, 1984) and the Chesapeake Bay by Olney (*Gobiosoma ginsburgi*, 1996).

While oyster densities are fundamental to the maintenance of living oyster reef communities, ichthyoplankton densities are partially driven by the presence of appropriate habitat (feeding and nesting) for adult fishes. Densities of naked gobies and striped blennies are dependent upon the presence of oyster shells for nesting habitat. In this sense, reef communities are dependent on larval production of both veligers and fishes being

sufficient to sustain recruitment levels necessary to yield observed adult densities; i.e., the community is at equilibrium with respect to lower trophic levels. The objectives of this study were to describe adult naked goby, striped blenny, and oyster density patterns on Palace Bar Reef, Piankatank River, Virginia, and relate observed adult densities to larval production and recruitment estimates for all three species.

METHODS

STUDY SITE.—Palace Bar Reef, Piankatank River, Virginia was the study site for benthic fish and oyster reef surveys. Palace Bar Reef is an intertidal oyster reef (300 × 30 m, reef depth range of 0.5 m above MLW to 3 m below MLW) adjacent to the historic Palace Bar oyster grounds (Bartol and Mann, 1997; Fig. 1). The reef was built in 1993 by the Virginia Marine Resources Commission (VMRC) Shellfish Replenishment program as a series of shell mounds centered on and around an east-west centerline 300 m long (Mann et al., 1996). Approximately 70% of the reef (0.63 ha) is composed of oyster shell, while the remaining area (0.27 ha) is crushed clam shell (Fig. 2). Since its construction in 1993, Palace Bar Reef has received annual oyster spat settlement (Bartol and Mann, 1997; J. Wesson, Virginia Marine Resources Commission, Newport News, VA; unpubl. data) and all oysters on the reef originate from natural settlement and recruitment, i.e., the reef was not initially seeded with oysters. Mature oysters greater than 30 mm (maximum dimension) were first observed on the reef during fall, 1995.

The area delineated by the reef buoys was divided into 32 grid squares for the benthic fish surveys described herein; substrate within these grid squares spans a range of conditions including mud (at the edge of the reef area) sand, shell, and various mixtures (Fig. 2). Mean tidal range in the Piankatank River is approximately 0.4 m. Water temperature and salinity were recorded at the reef once a week in conjunction with benthic fish surveys and other monitoring studies from May to October during 1996 (Fig. 3). Water samples were taken at the surface and just above the bottom with a Niskin bottle. Temperature was measured immediately with a thermometer and salinity was measured with a refractometer.

Palace Bar, a natural shell bar, is immediately adjacent (within 200 m) to Palace Bar Reef. The bar is surveyed annually by the Virginia Institute of Marine Science (VIMS) Molluscan Ecology stock assessment program; stock assessment data from Palace Bar were used to conservatively

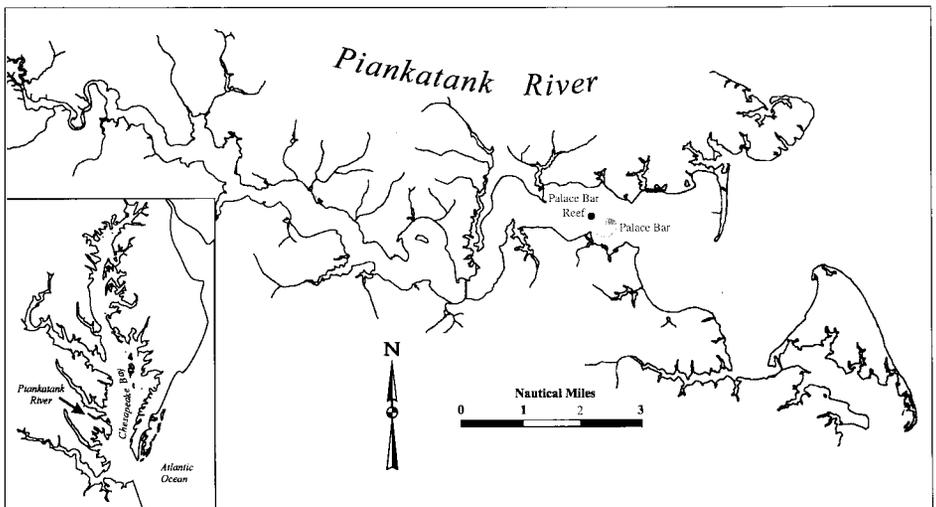


Figure 1. Map of the Virginia portion of Chesapeake Bay highlighting the Piankatank River and locating Palace Bar Reef (N 37°31'41.69", W 76°22'25.98") adjacent to Palace Bar oyster grounds.

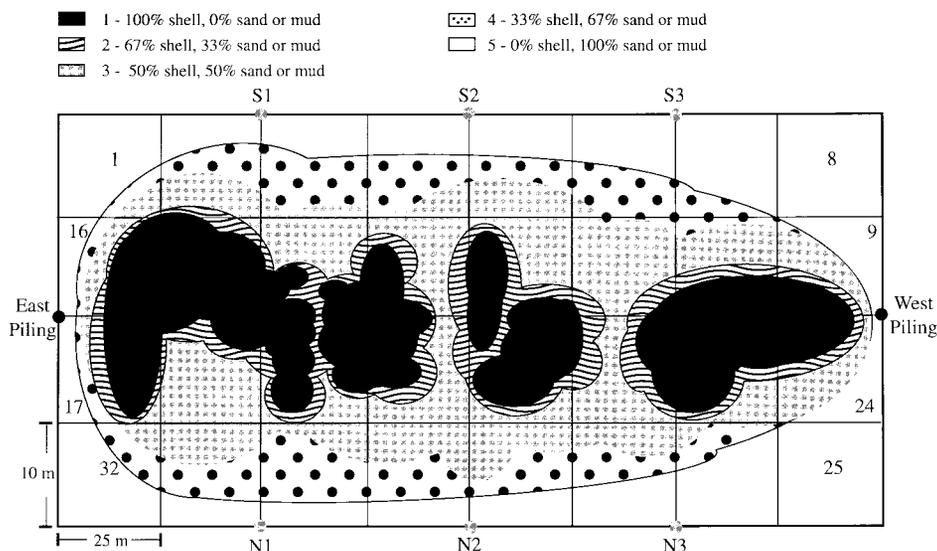


Figure 2. Schematic diagram of Palace Bar Reef, Piankatank River, Virginia, showing substrate composition and sampling grid layout. The East and West marker pilings and North (N1–N3) and South (S1–S3) lines of marker buoys form the boundaries for the reef perimeter. The grid within the reef perimeter forming squares (1 to 32) was used as a reference for randomly selecting sites for diver surveys of benthic fishes.

estimate length-frequency relationships for Palace Bar Reef oysters (see Oyster length-frequency distribution, below). Water depth at Palace Bar ranges from 1 to 4 m; water temperatures and salinities at Palace Bar are similar to those observed at Palace Bar Reef (R. Mann, unpubl. data).

OYSTER POPULATION ESTIMATES.—Adult oyster, spat, and box density.—Diver surveys of Palace Bar Reef were conducted in November 1995, June 1996, and October 1996 through a joint effort by the VIMS Molluscan Ecology program and the VMRC Shellfish Replenishment program (Mann and Wesson, 1996a). Divers removed all oysters and shell from within randomly selected squares 0.25 m² across by 0.15 m deep. The material was sorted and oyster adults (oysters >30 mm (maximum dimension)), juveniles (“spat” or oysters <30 mm (maximum dimension)), and clean, empty articulated shells without oysters (“boxes”) were counted.

Oyster length-frequency distribution.—Patent tong surveys were conducted on Palace Bar oyster grounds, immediately adjacent to Palace Bar Reef (Fig. 1) in November 1996 as part of the annual VIMS Molluscan Ecology stock assessment program. Standard hydraulic patent tongs were used to collect 1 m² bottom samples. Oysters were counted (adults, spat, boxes as in the diver surveys, above) and measured to the nearest 1.0 mm and length-frequency distribution was constructed for the population using 5 mm shell length intervals (Mann and Wesson, 1996b). This length frequency distribution was used for Palace Bar Reef oyster population production estimates (see Oyster production estimates, below).

FISH POPULATION ESTIMATES.—Adult fish density.—Density estimates for adult naked gobies and striped blennies at Palace Bar Reef were determined from May through September 1996 with a second, distinct set of diver surveys. The bi-monthly benthic fish survey schedule was disrupted on 25 July and 6 September 1996 by the presence of hurricane or tropical storm remnants. On each sampling date, 12 grid squares were randomly chosen out of the 32 grid squares available on the reef (Fig. 2). Within each target grid square divers placed a 0.25 m² square frame on the bottom, waited until visibility was >1 m, and then counted all adult fishes visible on or within the substrate. “Adult” fish were >40 mm long and displayed breeding coloration from May through late July. Two divers began facing each other over the square frame and then slowly worked around all four sides

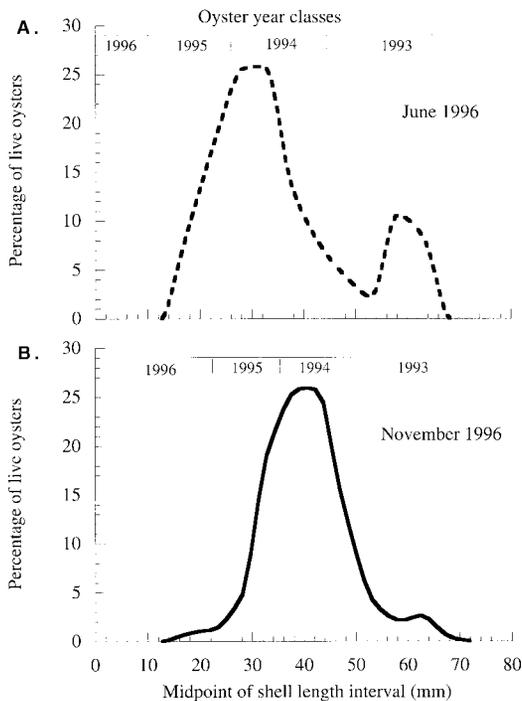


Figure 3. Length-frequency diagrams with midpoint of the shell length class (mm) plotted against the percentage of the population within a shell length class for the Palace Bar Reef oyster population. Patent tong data from November 1996 (b) were used to estimate a length-frequency distribution for the same population in June 1996 (a) in the absence of spring patent tong data.

of the frame in a clockwise fashion counting fishes in the interior of the frame as well as along the edges. Substrate composition and water depth were recorded within each square. Substrate was classified into five categories by its percentage composition of shell: 100% shell, 67% shell/33% sand or mud, 50% shell/50% sand or mud, 33% shell/67% sand or mud, or 100% sand or mud. Water depths were considered either deep (>1.5 m) or shallow (<1.5 m).

DATA ANALYSES.—Significance levels for all analyses were established a priori at $P = 0.05$. Assumptions of homogeneity of variance were tested with Bartlett's test and assumptions of normality were tested using the Ryan-Joiner test for normality. Unless otherwise noted, all data met both assumptions without transformation or were transformed to meet these assumptions. Fisher's test was used for post-hoc multiple comparisons when appropriate (Zar, 1996). All statistical tests were completed using Minitab software (ver. 10x; Minitab, 1995).

Temperature and salinity data.—Water temperature and salinity data collected weekly from May to October 1996 at Palace Bar Reef were transformed (natural logarithm) prior to analyses and satisfied assumptions of both homogeneity of variance and normality. Temperature and salinity data taken at the surface and just above the substrate (within 0.25 m) adjacent to the reef (within 5 m) were each compared with an ANOVA.

Adult Oyster, Spat, and Oyster Box Density.—Density estimates (animals m^{-2}) from diver surveys of Palace Bar Reef for adult oysters and oyster spat were available for November 1995, June 1996 and October 1996; oyster box data were available only for November 1995 and June 1996. Reef oyster density data were evaluated with 2-factor ANOVAs (year \times month). Adult oyster density data were transformed prior to analyses with the reciprocal transformation (Zar, 1996). While both spat and box density data satisfied the assumption of homogeneity of variance with the recip-

Table 1. Summary of density data from diver counts (fish $m^{-2} \pm$ standard error of the mean) for naked gobies and striped blennies from Palace Bar Reef, Piankatank River, Virginia made bi-monthly from May through September, 1996. Few (<1%) fishes were observed in areas with 100% sand substrate. Twelve total counts were made on every sampling day; the n values represent the number of counts on substrate with shell.

Date	n	Mean naked goby density fish m^{-2} (\pm SE)	Mean striped blenny density fish m^{-2} (\pm SE)
17 May 96	6	18.0 (4.47)	6.0 (2.87)
31 May 96	3	18.0 (8.0)	8.0 (6.11)
14 Jun 96	8	6.5 (1.67)	4.0 (1.51)
28 Jun 96	4	7.0 (2.51)	6.0 (2.0)
11 Jul 96	7	18.3 (2.11)	10.3 (3.47)
9 Aug 96	8	33.5 (8.68)	9.0 (3.91)
23 Aug 96	5	40.8 (9.1)	20.0 (7.26)
20 Sep 96	5	30.4 (5.15)	11.2 (4.08)

rocal transformation, neither data type met the assumption of normality regardless of the transformation ($\sqrt{x+1}$, $\ln+1$, reciprocal, arcsin).

Oyster density estimates (animals m^{-2}) for adult oysters and oyster spat from patent tong surveys of Palace Bar were transformed with the reciprocal transformation and compared with Palace Bar Reef density estimates using an ANOVA with site as a factor.

Oyster Production Estimates.—Size-specific fecundity estimates (F_{ind}) for June 1996 were made with the oyster length frequency data from the Palace Bar patent tong survey conducted in November 1996. The Palace Bar oyster length-frequency data (Fig. 5) were adjusted for year-class size distinctions (Mann and Evans, 1998; Evans and Mann, In review), growth rates (Evans and Mann, in review), growing season (Evans and Mann, in review), senescence mortality for oysters >55 mm (Mann et al., 1995), and larval mortality (Table 2) according to Mann and Evans (1998). Evans and Mann (in review) apply a growth burst function model using the positive half cycle of a sinusoid to James River, Virginia oyster data. This model describes a temperature dependent growth pattern that follows seasonal variation and ceases when temperatures go below a critical value and is common among sessile marine invertebrates (Evans and Mann, in review). This growth model gives a residual sum of squares value equal to 19.98 when applied to James River oyster data as in Evans and Mann (In review).

Size-specific individual fecundities were calculated using the relationship:

$$\text{Fecundity } (F_{ind}) = 39.06 \times (0.000423 \times \text{Length (mm)}^{1.75})^{2.36}; (r^2 = 0.89)$$

where F_{ind} is millions of gametes per individual oyster. This equation is modified from Cox and Mann (1992), Thompson et al. (1996), and Mann and Evans (1998) by substituting the weight to length conversion recommended by Mann and Evans (1998) for oyster weight (mg of dry tissue). Total oyster fecundity (F_{tot}) within a size class was calculated by summing the product of F_{ind} and the number of individuals within each size class across size classes for June 1996 (Table 2).

Mann and Evans (1998) describe a modifier for salinity effects (F_s), propose 13.5‰ as a threshold for salinity effects on oyster fecundity, and report 8.5‰ as the lowest salinity level where viable eggs have been found; i.e., F_s equals 0 when salinities are <8.5‰ and equals 1 when salinities are <13.5‰. Since Piankatank River salinities ranged from 11 to 15‰ during 1996, but were <13‰, the sex ratio for this oyster population was assumed to be 1:1 (per Cox and Mann, 1992), and the sex-related fecundity factor (F_q) was set at 0.5. Oyster fertilization efficiency (F_f) is dependent on the total oyster density (oysters m^{-2}). Mann and Evans (1998) apply a correction factor based on Levitan (1991) to estimate F_f :

Table 2. Summary of oyster length frequency estimates at Palace Bar Reef, Piankatank River, Virginia for June 1996 from November 1996 length-frequency data. June 1996 length-frequency distributions were used to estimate individual oyster fecundities (F_{ind}) and total oyster fecundity per m^2 (F_{tot}) per Mann and Evans (1998). All calculations are detailed in the text. Oyster daily growth rates were estimated with the positive half of the sinusoidal oyster growth model developed by Evans and Mann (in review); a summary of the model is provided in the text. The mortality estimate used is for senescence mortality per Mann et al. (1995).

Shell length (SL) interval midpoint (mm)	% of population within SL interval 11/96	Daily growth rate (G) (mm)	Growth estimate from 6-11/96 (mm)	Estimated SL interval 6/96 (mm)	Portion of SL interval useful for 6/96 fecundity estimates (mm)	Mortality estimate for 6-11/96 (%)	% of population within SL interval 11/96	% of population within SL interval 6/96	Oyster density SL interval 6/96 (animal m^{-2})	Individual fecundity estimates (F_{ind})
18	0.8658	0.0932	13.9726	4.0274	none					
23	1.2987	0.0959	14.3836	8.6164	none					
28	4.7619	0.0986	14.7945	13.2055	none					
33	19.4805	0.0986	14.7945	18.2055	0.5	0.5	19.4805	9.7403	3.4091	33.4572
38	25.5411	0.0658	9.8630	28.1370	all		25.5411	25.5411	8.9394	528.3541
43	25.5411	0.0658	9.8630	33.1370	all		25.5411	25.5411	8.9394	1,037.2473
48	12.9870	0.0493	7.3973	40.6027	all		12.9870	12.9870	4.5455	1,219.1910
53	4.3290	0.0329	4.9315	48.0685	all		4.3290	4.3290	1.5152	815.2078
63	2.5974	0.0219	3.2877	59.7123	all	8	2.5974	10.5974	3.7091	4,881.8497
68	0.4329	0.0169	2.5377	65.4623	all	8	0.4329	8.4329	2.9515	5,675.7951

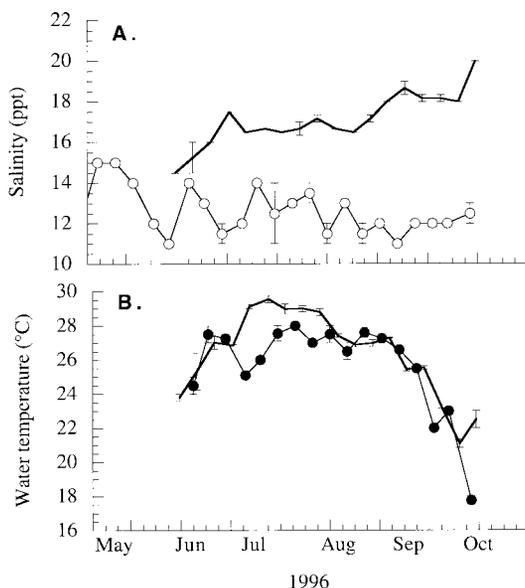


Figure 4. Mean salinity (‰, A) and water temperature (°C, B) patterns observed at Palace Bar Reef, Piankatank River, Virginia, during May–September 1996. Data from surface and bottom measurements were averaged since there was no significant difference in temperature or salinity between depths (ANOVA, $P < 0.05$). Reference mean values for temperature and salinity data from Palace Bar Reef during 1993–95 are plotted with a solid line (\pm SE). Data from 1996 are indicated by lines with symbols (\pm SE).

$$F_f = 0.0049 \times \text{Oyster density}^{0.72}$$

These F factors are combined to yield a total oyster production estimate for a given area in units of oyster embryos m^{-2} in the relationship:

$$\text{Oyster Embryo Production (F)} = F_{\text{tot}} \times F_q \times F_s \times F_f$$

This oyster embryo production estimate was combined with oyster density data from diver surveys to yield estimates of fecundity or larval production m^{-2} and then converted to larval production per reef assuming 0.63 ha of reef are available for settlement and production (Table 4). A time-stepped larval mortality function (L_{mort}) describing the daily larval mortality rate (Mann and Evans,

Table 3. Average densities of oyster adult, spat, and boxes m^{-2} from diver surveys of Palace Bar Reef in November 1995, and June and October 1996. Data are presented with standard error (SE); n refers to the number of samples collected. "Adult" oysters are oysters >30 mm (maximum dimension); "spat" refers to oysters <30 mm (maximum dimension); "boxes" are pairs of clean, articulated oyster valves. "NA" indicates data that were not available.

Date	n	Mean adult Oyster density (oyster m^{-2})	Mean spat density (spat m^{-2})	Mean box density (boxes m^{-2})
Nov 95	30	36.14 (5.84)	32.33 (5.73)	80.86 (11.84)
Jun 96	30	34.46 (4.72)	53.33 (8.34)	61.80 (0.31)
Oct 96	30	54.66 (4.27)	23.45 (2.87)	NA

1998) was used to make predictions regarding production of oyster spat (settled larvae) or the proportion of larval oyster survivorship on Palace Bar Reef (Table 4):

$$\text{Larval oyster survivorship} = (1 - L_{\text{mort}})^t$$

where L_{mort} or the larval mortality function may range from 0.0 (all living) to 1.0 (all dead). A value of 0.07 was used for L_{mort} (per hatchery data from the VIMS Aquaculture Breeding and Technology center as in Mann and Evans, 1998) and the time to oyster settlement (t) was set at 21 d following Mann and Evans (1998) for James River, Virginia oysters. Effects of physical transport of eggs and larvae onto and off of the reef were unknown.

FISH POPULATION DATA.—Adult Fish Density.—Density estimates of adults (fish m^{-2}) for both fish species were transformed with the reciprocal transformation (Zar, 1996) to meet assumptions of homogeneity of variance and normality and were analyzed with species-specific ANOVAs. Day of the year, depth, and substrate conditions were factors in both analyses.

Larval Fish Production Estimates.—Larval production estimates for naked gobies or striped blennies relying on numbers of eggs per nest must be differentiated from published fecundity estimates for these fishes using numbers of eggs per female; e.g., Nero (1976) for a Virginia population of naked gobies. Fecundity estimates for female naked gobies range from 250 to 1977 eggs per female (Deary Cove, Virginia; Nero, 1976). A value of 1200 eggs per nest (per Hildebrand and Cable, 1938 (North Carolina); Massmann et al., 1963 (Virginia); Dahlberg and Conyers, 1973 (Georgia); Nero, 1976 (Virginia)) was used to estimate naked goby nest production (Fi_{nest}). Striped blenny nests collected from Palace Bar Reef during 1995 and 1996 contained between 1000 and 1600 eggs per nest (J. Harding, unpub. data); a value of 1300 eggs per nest was used to estimate striped blenny nest production (Fi_{nest}).

Sources of egg mortality for both species include predation by xanthid crabs (Crabtree and Middaugh, 1982), cannibalism by guarding males (particularly for naked gobies; Dahlberg and Conyers, 1973), poor egg condition, and nest fungus (J. Harding, unpubl. data). Stage duration for incubation, determined from laboratory culture of both species (Harding, 1999) and field observations of naked gobies (Deary Cove, Virginia; Nero, 1976), was estimated at 9 d for both species. Total mortality of eggs in the nest (N_{nest}) for both species was estimated at 1% d^{-1} for 9 d of incubation (J. Harding, unpubl. data). The percentage nest survivorship was estimated using a general larval survivorship function for marine fishes modified from Houde (1989):

$$100 \text{N}_{\text{nest}} = e^{-0.01 \times 9}$$

Average adult fish densities (fish m^{-2}) for each species from Palace Bar Reef during 1996 were used to calculate species-specific larval fish production (larval fish m^{-2}) using the equation:

$$\text{Larval fish production } \text{m}^{-2} = \text{Fi}_{\text{nest}} \times \text{Fi}_q \times \text{N}_{\text{nest}} \times \text{Average number of adult fish } \text{m}^{-2}$$

where Fi_q is the sex-related fecundity factor. Nero (1976) reports a 1:1 sex ratio for adult naked gobies; striped blennies were assumed to have similar sex ratios, giving Fi_q a value of 0.5. The effects of salinity and temperature on naked goby and striped blenny nest production and success are unknown. Estimates of larval fish production m^{-2} for each species were combined with estimates of reef habitat suitable for nesting (0.63 ha) to yield species-specific larval fish production estimates for Palace Bar Reef (Tables 5,6).

An average daily growth rate (G) for striped blennies from laboratory cultured blennies was estimated by fitting a four parameter logistic regression to length-at-age data for pre-settlement and settlement stage fish using the equation:

Table 4. Eastern oyster larval production and recruitment estimates for Palace Bar Reef, Piankatank River, Virginia. Oyster densities are from diver surveys of Palace Bar reef in June, 1996. Symbols and calculations are described in the text; calculations for reef areas use 0.63 ha, the area of Palace Bar Reef with shell as a portion of the substrate.

	Mean density (oysters m ⁻²) - SE	Mean density (oysters m ⁻²)	Mean density (oysters m ⁻²) + SE
F _{out}	14,844	14,844	14,844
F ₀	0.50	0.50	0.50
F ₀ ⁰	0.75	0.75	0.75
F _s	0.0564	0.0627	0.0688
F _f	314.05	349.14	382.91
Oyster embryo production (embryos m ⁻²)	1,978,539	2,199,624	2,412,372
Oyster embryo production (embryos reef ⁻¹)	0.2178	0.2178	0.2178
Larval oyster survivorship	431,009	479,171	525,516
Larval oyster settlement (spat reef ⁻¹)	68	76	83
Larval oyster settlement (spat m ⁻²)			

Table 5. Naked goby larval production and recruitment estimates for Palace Bar Reef, Piankatank River, Virginia. Fish densities are from benthic fish surveys of Palace Bar Reef from May through September, 1996. Symbols and calculations are described in the text; calculations for reef areas use 0.63 ha, the area of Palace Bar Reef with shell as a portion of the substrate.

	Mean density (fish m ⁻²) - SE	Mean density (fish m ⁻²)	Mean density (fish m ⁻²) + SE
F_{i_q} (Nero, 1976)	0.5	0.5	0.5
$F_{i_{nest}^1}$	1,200	1,200	1,200
N_{nest}^2	0.9139	0.9139	0.9139
Mean fish density (fish m ⁻²)	18.86	21.47	24.08
Larval fish production (larvae m ⁻²)	10,342	11,773	13,204
Larval fish production (larvae reef ⁻¹)	65,154,885	74,171,547	83,188,209
G (mm day ⁻¹ ; Houde and Zastrow, 1993)	0.146	0.146	0.146
D (days) ³	18	18	18
Z (from G, per Houde, 1989)	0.2213	0.2213	0.2213
N_{set} (per Houde, 1989)	0.0186	0.0186	0.0186
Larval fish settlement (larvae reef ⁻¹)	1,212,433	1,380,220	1,548,006
Larval fish settlement (larvae m ⁻²)	192	219	246

¹ Hildebrand and Cable, 1938 (NC); Massmann et al., 1963 (VA); Dahlberg and Conyers, 1973 (GA); Nero, 1976 (VA).

² Per Houde (1989) based on laboratory culture of naked goby larvae from Harding (1999).

³ Per Breitburg (1989,1991) and Harding (1999).

Table 6. Striped blenny larval production and recruitment estimates for Palace Bar Reef, Piankatank River, Virginia. Fish densities are from benthic fish surveys of Palace Bar Reef from May through September, 1996. Symbols and calculations are described in the text; calculations for reef areas use 0.63 ha, the area of Palace Bar Reef with shell as a portion of the substrate.

	Mean density (fish m ⁻²) - SE	Mean density (fish m ⁻²)	Mean density (fish m ⁻²) + SE
F_{i_q} (per Nero, 1976)	0.5	0.5	0.5
$F_{i_{nest}^1}$	1,300	1,300	1,300
N_{nest}^2	0.9139	0.9139	0.9139
Mean fish density (fish m ⁻²)	7.58	9.03	10.48
Larval fish production (larvae m ⁻²)	4,503	5,364	6,226
Larval fish production (larvae reef ⁻¹)	28,368,515	33,795,210	39,221,905
G (mm day ⁻¹) ³	0.129	0.129	0.129
D (days) ⁴	18	18	18
Z (from G, per Houde, 1989)	0.1990	0.1990	0.1990
N_{set} (per Houde, 1989)	0.0278	0.0278	0.0278
Larval fish settlement (larvae reef ⁻¹)	787,842	938,551	1,089,260
Larval fish settlement (larvae m ⁻²)	125	149	173

¹ J. Harding, unpublished data.

² Per Houde (1989) based on laboratory culture of stripped blenny larvae from Harding (1999).

³ Calculated from laboratory culture data (Harding, 1999; J. Harding, unpublished data).

⁴ Per Harding (1999).

$$L_t = L_0 + \frac{a}{1 + e^{-\frac{t-t_0}{b}}}$$

where L_0 is the fish length (mm) at hatch or $t = 0$, a is a coefficient describing the maximum length at settlement, t is time post-hatch or age in days, t_0 is the time corresponding to the midpoint of the rise, and b is a coefficient describing larval stage duration. The resulting average growth rate (G) of 0.129 mm d^{-1} (standard error = 0.06; $r^2 = 0.91$) is based on data from 312 blennies ranging in age from 1 to 22 d. Attempts to fit the same growth model to naked goby growth data from laboratory cultures were unsuccessful because data were only available for four fish ages. Alternatively, a larval naked goby growth rate of 0.146 mm d^{-1} from Houde and Zastrow (1993) for gobies held at 26°C in laboratory experiments was used (E. Houde, Univ. Maryland Center for Environmental Science, Chesapeake Biological Laboratory, Solomons, Maryland; pers. comm.).

Larval stage duration (D), or time from post-yolk sac to settlement, was set at 18 d given stage duration estimates of 15 to 21 d for laboratory cultured blennies (Harding, 1999) and approximately 18 to 20 d for field caught naked gobies (Breitburg, 1989, 1991). Instantaneous daily mortality (Z) was estimated from average G values using the relationship given by Houde (1989):

$$Z = 0.0303 + 1.3085 (G)$$

The percentage of larval fishes surviving to settlement was calculated using the relationship given in Houde (1989) for fishes surviving to metamorphosis (N_{met}):

$$100 N_{\text{met}} = e^{-ZD}$$

This survivorship function was used to adjust larval fish production estimates per reef for mortality prior to settlement. Adjusted estimates of larval fish production per reef were used to calculate species-specific settlement estimates per reef and per m^2 (Tables 5,6). Larval transport into and out of the reef system by physical forces was unknown.

RESULTS

TEMPERATURE AND SALINITY DATA.—There was no significant difference between surface and bottom water temperatures or salinities on any date (ANOVAs, both P values >0.05) indicating that the water column at Palace Bar Reef was well mixed. Therefore, surface and bottom temperature and salinity data for each day were pooled for presentation and discussion (Fig. 4). Recorded water temperatures in 1996 were similar to those observed during 1993–95 (Fig. 4, R. Mann, unpubl. data). Salinities observed in 1996 were the lowest observed from 1993–5.

OYSTER POPULATION DATA.—*Adult Oyster, Spat, and Oyster Box Density.*—There was no significant difference in adult oyster, spat, or box densities (Table 3) at Palace Bar Reef between 1995 and 1996 (ANOVA, $P > 0.05$) or months (ANOVA, $P > 0.05$); oyster density data from diver surveys of the reef were used for oyster production calculations and comparisons (Table 4). Winter mortality during 1995–96 was low. Increases in average adult oyster densities between June 1996 and October 1996 were most likely due to the development of June 1996 spat or juveniles into adults.

Oyster Production Estimates.—Estimates of larval oyster production and subsequent survival to settlement predict annual recruitment of 68 to 83 spat m^{-2} (Table 4) to the reef and are similar to actual observed densities (Table 3). Field estimates of spat abundance

range from 53.33 m⁻² in June 1996 to 23.45 m⁻² in November 1996 (Table 3). Densities of adult oysters were greater in October than in June 1996, as would be expected given the maturation of the 1996 year class throughout the growing season.

FISH POPULATION DATA.—Adult Fish Density.—In May 1996, densities of both naked gobies and striped blennies were approximately 18 to 20 fishes m⁻² (Table 1). Naked goby densities were significantly higher on substrate that was >33% shell (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$) while striped blenny densities were significantly higher in areas with >67% shell substrate (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$). Areas where shell substrate dominated the bottom supported fish densities up to 14 times greater than those observed in habitat areas lacking shell. Only one site of the 49 sites sampled in grid squares (Fig. 2) with substrate composition of less than 50% shell contained benthic fishes; naked gobies were present at a density of 4 m⁻². Goby densities 10 times higher occurred in concurrently surveyed grid squares with greater than 50% shell substrate. Goby and blenny densities declined during June 1996, but increased throughout July with maximum numbers of both fishes observed in August 1996 (Table 1). Densities of naked gobies were significantly higher in August than in May or June (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$). Striped blenny densities in late August were significantly higher than those observed in June (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$). The observed increase in both naked goby and striped blenny densities during August is probably due to seasonal recruitment of young-of-the-year fish.

Larval Fish Production Estimates.—Species-specific estimates of benthic larval fish production and survival to recruitment for Palace Bar Reef ranged from 192 to 246 juvenile naked gobies m⁻² (Table 5) and 125 to 173 juvenile striped blennies m⁻² (Table 6). These estimates of larval fish production are within an order of magnitude of field observations for adult fishes on Palace Bar Reef during 1996, i.e., 18 to 24 naked gobies m⁻² and 7 to 10 striped blennies m⁻² (Table 1) and are well within Breitburg's (1998) estimate of an average recruitment rate of 272 individual naked goby larvae m⁻² mo⁻¹ for Flag Pond oyster bar near Cape Conoy, Maryland. Similar goby abundance estimates (207 ± 29 goby larvae m⁻³) have been reported by Allen and Barker (1990) from tidal creeks in North Inlet Estuary, South Carolina.

DISCUSSION

Larval production and recruitment estimates for Palace Bar Reef oysters are of the same order of magnitude as observed field densities. Benthic fish production estimates are within an order of magnitude of adult densities and are similar to previous recruitment estimates for Chesapeake Bay naked gobies (Breitburg, 1998). Interactions between life history stages of oysters and benthic fishes are pivotal to reef community structure and form foundations for upper and apex trophic levels. Larval gobies (Houde and Lovdal, 1984; Olney, 1996; Harding, 1999) and blennies (Harding, 1999) selectively feed on bivalve veligers. Larval fish survival is enhanced by high growth rates (due to preferred prey availability) and subsequent reduction of the time period to settlement (Shepherd and Cushing, 1980; Houde, 1987). Post-settlement naked gobies and striped blennies are prey items for upper level predators (e.g., striped bass (Markle and Grant, 1970; Harding and Mann, 1999), bluefish (Mann and Harding, 1997, 1998)). Densities of adult reef fishes are driven by availability of suitable nesting habitat and predation shelters, as well as by the success of larval fish recruitment from the plankton. Adult oysters derive little

obvious benefit from the presence of small benthic fishes in reef interstices, yet the ecological community supported by the oyster reef depends on the success of these fishes.

The three-dimensional habitat created by the living oyster reef is highly heterogeneous and offers many habitat refugia. Complex reef habitats offer more shelter for benthic fishes than two dimensional shell or sand habitats where suitable cover and substrate are limiting factors. Nero (1976) reports densities of 8 naked goby adults m^{-2} in Deary Cove, Virginia where the dominant habitat type was sand bottom with sparse shell substrate and the primary nesting and habitat substrates available to gobies were discarded aluminum cans (Nero, 1976). Goby densities on Palace Bar Reef in 1996 ranged from 7 to 40 fish m^{-2} . Reef substrate heterogeneity and relief have been previously correlated with increased fish densities and species richness for coral reefs (Roberts and Ormond, 1987; Ebeling and Hixon, 1991; Friedlander and Parrish, 1998) and oyster reefs (e.g., Coen et al., 1999; Harding and Mann, 1999).

Naked gobies were more numerous than striped blennies on Palace Bar Reef. Fish size and morphology may influence selection of oyster shell nesting sites and habitat refugia by both species (Crabtree and Middaugh, 1982). Adult striped blennies are longer and of greater body depth than adult naked gobies and adult males of both species may occupy shells with the smallest gapes that would accommodate the fish's total length (Crabtree and Middaugh, 1982). Naked gobies occupied shells which had significantly smaller total shell lengths than shells occupied by striped blennies (Crabtree and Middaugh, 1982) and may avoid competition for suitable shell refugia and nesting sites by using the smallest shells available. Smaller shells would give gobies refuge from predation by piscivorous apex predators and egg predation by xanthid crabs (Crabtree and Middaugh, 1982). Given the low densities of large (>50 mm shell length) oysters on Palace Bar Reef and, consequently, potentially low availabilities of large intact boxes, suitable shell refugia may be a limiting factor for the Palace Bar Reef striped blenny population.

Shell size and morphology may not be the only determining factors in benthic fish selection of oyster boxes for nesting sites and refugia. Fouling may place an important role in nest site selection by these fishes. Dahlberg and Conyers (1973) describe "clean" oyster shell as suitable for attachment of adhesive goby and blenny eggs. Biofouling in relation to nest site selection and egg attachment has not been quantitatively investigated. Rheinhardt and Mann (1990) and Mann and Evans (1998) report a one third reduction of appropriate settlement surfaces for oyster spat at biofouling levels ranging from 14 to 37% biofouling of available oyster shell in the James River, Virginia. Adult benthic fishes are probably capable of reducing or eliminating oyster shell coverage by sediment or detritus (abiotic fouling); they may remove also remove or reduce biofouling and subsequently increase the availability of clean substrate necessary for oyster settlement by their foraging and nesting behavior. Similar selective grazing or "gardening" behavior by tropical damselfishes maintains coral reef algal communities at early successional stages precluding the development of encrusting algal mats (Lassuy, 1980; Montgomery, 1980).

Goby larvae seasonally dominate Chesapeake Bay ichthyoplankton (Dovel, 1971; Shenker et al., 1983; Cowan and Birdsong, 1985; Olney, 1996); 55% of all fish larvae collected by Dovel (1971) were naked gobies. Densities of up to 688 naked goby larvae per 100 m^3 were reported by Massmann et al. (1963) for the Pamunkey River, Virginia. Shenker et al. (1983) reports 22 to 6063 larval naked gobies per 100 m^3 in the Patuxent River, Maryland. Larval recruitment estimates for Palace Bar Reef, Virginia and Flag Pond, Maryland predict greater than 200 juvenile naked gobies m^{-2} ; similar larval goby recruitment estimates have been made for South Carolina estuaries (Allen and Barker, 1990).

The impacts of numerically dominant taxa on related trophic levels are potentially high. Sympatric ichthyoplankton with similar prey and settlement requirements (e.g., striped blennies) may be at a competitive disadvantage for resources, but may benefit from potential numeric "swamping" of predators (e.g., striped bass). Predation by larval gobies on bivalve veligers (Olney, 1996; Harding, 1999), may affect subsequent recruitment patterns of oysters. Historically, goby and oyster populations were well established throughout the intertidal areas of the Chesapeake Bay. Previous population levels of gobies and blennies are unknown, but it is likely that benthic fish densities have declined as suitable habitats, in the form of living oyster reefs, have disappeared (Luckenbach et al., 1988; Coen et al., 1999). In areas that currently support modest densities of adult benthic fishes and adult oysters, species-specific production by both oysters and fishes may be appropriate to sustain observed adult densities as observed on Palace Bar Reef, Piankatank River, Virginia.

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