Demersal schooling prior to settlement by larvae of the naked goby

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Synopsis

Field observations and collections indicate that the naked goby, *Gobiosoma bosci*, undergoes a near-bottom schooling phase prior to settlement. The size of these demersal larvae was intermediate between the sizes of larvae collected in plankton tows and of metamorphosed juveniles collected from the benthos. Two larvae that were captured unharmed quickly settled and metamorphosed. Otoliths of demersal larvae contained 20–41 daily increments. Most larvae were in schools made up of at least 25 individuals although single larvae were also seen. The dispersion pattern of demersal larvae was far more aggregated than that of recently settled juveniles indicating that larvae in schools probably do not settle to the benthos en masse.

Introduction

A major thrust of recent marine ecological research has been an attempt to understand the factors that influence the spatial and temporal patterns of recruitment of reef fishes. Unlike studies of marine invertebrates that have examined the behavior of larvae in the process of settling (e.g. Crisp 1974, Morse et al. 1979), studies of reef fish recruitment have generally focused on juveniles that have already settled (e.g. Williams 1980, Victor 1983, Doherty 1983, Shulman et al. 1983, Sale et al. 1984) or, on a large scale, factors influencing the transport of pelagic larvae towards suitable settlement sites (e.g. Johannes 1978, Lobel & Robinson 1983, Shanks 1983, Kingsford & Choat 1986). Except for a few notable exceptions, such as McFarland et al. (1985) and Marliave (1977), investigators have not examined the behavior of larval reef fishes during the transition from the planktonic to the demersal or benthic states, that is, the process of settlement itself. The paucity of such studies is undoubtedly due in part to the difficulty in making direct field observations on the extremely low densities of most fish larvae settling on coral reefs (e.g. Williams 1980, Doherty 1983, Victor 1983). Furthermore, the advanced development of the sensory and locomotory capabilities of fish larvae make the kinds of laboratory experiments that have been used to analyze invertebrate larval behavior difficult to perform with fish.

Here I describe field observations and collections of schooling demersal larvae of the naked goby, *Gobiosoma bosci,* from a Chesapeake Bay oyster bar. These larvae occur in much greater densities than do the larvae of most coral reef fishes and therefore can be more easily observed. The size and behavior of these larvae indicate that they represent a distinct interval in the life history of the species.

Methods

The naked goby, *Gobiosoma bosci,* is a small, benthic species that is abundant in estuaries and trib-

utaries along the east and Gulf coasts of the United States and Mexico. Naked gobies live in and among oyster shells, rock crevices, and other hard substrates, all of which they use for shelter and for egg attachment. The salient features of the ecology and life history of naked gobies, in the context of this paper, are: (1) adults are epibenthic and do not school and (2) embryos hatch into planktonic larvae which are dispersed throughout the water column (Nero 1976).

Observations of goby larvae swimming near the substrate (which I have designated demersal larvae), and collections of both larvae and recruits, were made in the Flag Pond oyster bar on the western shore of the mid-Chesapeake Bay near Camp Conoy, MD. This oyster bar occurs in water from approximately 2–6 m in depth and varies in bottom topography from low rock ledges and outcroppings to a nearly continuous cover of oyster shell with occasional patches of sand. During the period that larvae were observed, near-bottom temperatures ranged from 24.2 to 29.8° C, salinity from 10.9 to 17.5‰ and dissolved oxygen from 0.2 to 10.2 mg l^{-1} (D. Breitburg & B. Albright, unpublished data).

All field observations were made by divers using scuba. Larvae were collected on June 30, 1987 with diver-held 1 mm mesh bags that measured 32 cm across their opening and 50 cm in length. This method of capture may bias the size distribution toward smaller, weaker swimming larvae but it was our impression that the sample provided a good estimate of the range of sizes of larvae in the various schools. Larvae were preserved in reagent alcohol (95% denatured ethanol, 5% isopropanol by volume) immediately upon return to the dive boat and were later transferred to 70% reagent alcohol.

Five arbitrarily positioned, 30 × 2 m transects were run on 9 July 1987 to estimate the number of larvae in the schools. The two transects at 2 m depth traversed bottom with rock outcroppings, which were several cm to approximately 0.3 m in height, as well as stretches of oyster shell and patches of sand. In contrast, the two 5 m and one 6 m deep transects were made mostly across continuous cover of unconsolidated oyster shell except that one 5 m transect included a 1 m wide × 2 m

long × 0.6 m high metal frame structure with attached vexar trays used for growing oysters (an oyster platform). The number of larvae was counted for schools containing less than 10 individuals; larger schools were estimated to contain 10–24, 25–49, 50–99 or ≥100 individuals.

In the laboratory, total length (TL) of larvae with undamaged caudal fins and standard length (SL) of all larvae were measured to the nearest 0.25 mm with a dissecting microscope and stage micrometer. Gut contents were examined for the 21 undamaged individuals. Age of larvae was estimated from counts of otolith growth increments (Pannella 1971, Brothers et al. 1976), uncorrected for the age at which the first increment had been laid down. Sagittae and lapilli form during the second day of embryonic development at water temperatures of 24–26° C. Sagittae from each larva were removed and cleared in immersion oil for several days before increments were counted with a 40X oil immersion objective of a compound microscope. B. Victor kindly counted otolith increments for me.

Gobiosoma larvae collected by R. Gallagher in plankton tows (= planktonic larvae) conducted in the Patuxent River (the tributary of the Chesapeake Bay closest to the study site) were used to compare sizes of goby larvae in the water column (planktonic larvae) with sizes of demersal larvae and benthic juveniles. Optimally, planktonic larvae should have been collected in the same place and on the same dates as demersal larvae and recruited juveniles. However, no such collections were available to me. Planktonic larvae were collected with a 1 m Tucker trawl fitted with a 223 μm mesh plankton net towed for approximately 2 min. An average of 105.4 ± 3.1 l of water was filtered per tow. Larvae were collected during daylight on 17 July (1 surface and 2 mid-depth tows), 26 July (1 near-bottom tow) and 6 August 1985 (1 surface, 1 mid-depth, and 1 near-bottom tow). Benthic juveniles were collected at the study site in sand- and shell-filled trays and with a suction sampler (described in Breitburg 1988).

Results

Description of demersal larvae

Demersal naked goby larvae ranged in size from 6–9 mm SL and 7–11 mm TL. Total length and standard length were linearly correlated ($r^2 = 0.956$, TL = 0.003 + 1.21 SL). Total length is used for comparisons in this paper because only total lengths were measured for planktonic larvae.

The size range of demersal larvae was intermediate between the size of larvae collected in plankton tows and the size of the smallest recruited juveniles collected in tray and suction samples (Fig. 1). Larvae collected in plankton tows ranged from 2–12 mm TL with abundances declining sharply from 8 mm and larger. The smallest of the 88 juveniles ≤13.5 mm (recently settled juveniles) collected at Flag Pond during summer 1987 measured 9.0 mm TL. Thus, no benthic juveniles were collected that corresponded to the size of the smaller larvae in demersal schools. Settlement of larvae appears to generally occur at 9–12 mm TL.

Counts of growth increments indicated that age as well as size varied widely among demersal larvae (Fig. 2). Otoliths examined had 20–41 rings that appeared to be daily increments and showed no evidence of a settlement check. Total length was strongly and linearly correlated with number of daily otolith increments ($r^2 = 0.888$, Increments = −24.59 + 6.04 TL).

Gut contents of demersal larvae were examined because of the possibility that the observed schooling behavior was related to feeding. Of 21 larvae examined, only one had prey – a single copepodite – in the anterior half of its digestive tract. This larva measured 11 mm TL. Three of the nine 7–8 mm larvae and five of the 13 9–11 mm larvae examined had prey in the second half of their digestive tract. Most feeding larvae had consumed calanoid copepods. In addition, a single cladoceran, polychaete larva, and amphipod were found in larval guts.

Behavior
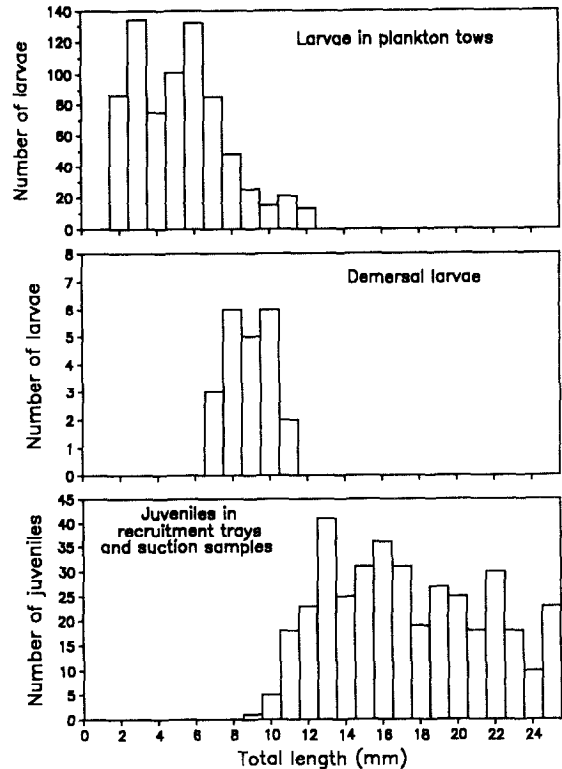
Demersal goby larvae were seen in the Flag Pond

Fig. 1. Size distribution of planktonic larvae of naked goby collected from the Patuxent River, and demersal larvae and benthic juveniles from the Flag Pond oyster bar. Note different scales of the vertical axes.

oyster bar on all but one field day (n = 14) from 30 June through 10 September 1987. On 29 July no larvae were seen at the study site and on 4 August only a single goby larva was seen. Dissolved oxygen levels on 25–27 July and 3–4 August fell to 0.2 mg l⁻¹, the lowest concentrations recorded in extensive monitoring throughout summer 1987 (Breitburg 1988).

All demersal larvae seen were within 0.5 m of the substrate or some other physical structure. Single individuals as well as schools of up to several hundred larvae were observed. The sites where the largest schools were found and where we found larvae most predictably appeared to be those with conspicuous three-dimensional structure, especially the oyster platform.

We saw no evidence of any coordinated group response when a diver approached a school or
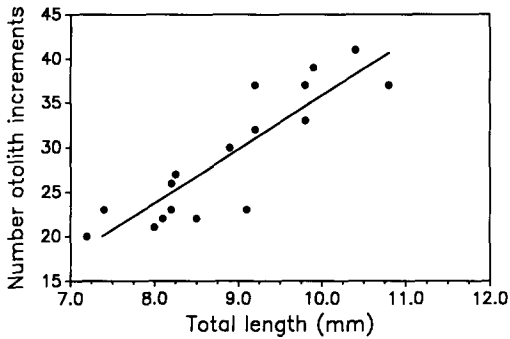
Fig.2. Total length vs. number of daily increments on sagittae of demersal naked goby larvae collected from the Flag Pond oyster bar.

thrust his/her arm in the midst of the larvae. Movement of individuals in schools was coordinated to some extent, however, in that individuals in groups of 2–3 larvae swimming along the oyster bar stayed within a few cm of one another during observations lasting several minutes each. Large schools could be seen moving as a group across the reef, but we did not attempt to track distances maintained between individual larvae in either large stationary or moving schools. For both moving and stationary schools individuals within schools were oriented in a uniform direction. When a noticeable current was present, individuals generally faced into the current.

We captured two transparent demersal larvae underwater in plastic bags. In <10 min the larvae were using their pelvic fins to perch on the sides of the bag in typical goby fashion and no longer swam in the water away from the surface of the bag. These larvae were brought back to the laboratory and by the next morning had acquired considerable pigmentation; their coloration and behavior were indistinguishable from those of small juveniles we collected from the substrate. In contrast, all demersal larvae seen and collected lacked pigmentation present in even the smallest benthic juveniles.

Dispersion of larvae compared with dispersion of recruits

Although most groups of larvae contained rela-

tively few individuals, most individuals were found in schools containing at least 25 larvae (Fig. 3). If larvae in schools settle as a group and do not disperse widely soon after settlement, the highly aggregated pattern of larvae should be reflected in the dispersion pattern of recently settled recruits. To compare the dispersion of larvae among schools with the degree of aggregation of benthic juveniles, I calculated a rough estimate of the coefficient of variation of the number of larvae per school and of Lloyd's index (Pielou 1977) by using the midpoint of ranges in each school-size category for those schools containing 10–99 idividuals, and by using 100 as the number of individuals in each of the largest schools. These estimates are very conservative in as much as the largest schools appeared to contain several hundred individuals rather than the 100 used for estimates. Because the variance estimates were rough, no statistical comparisons were made.

Demersal larvae were far more aggregated (CV = 143%) than juveniles ≤13.5 mm collected during the peak periods of recruitment of either 1985 (overall CV = 38.9%, n = 15) or 1987 (overall CV = 73.6%, n = 15) (Table 1). Lloyd's index indicated similar differences in dispersion patterns of demersal larvae and juveniles. Only 13 schools of larvae (or single individuals) were seen over the 300 m searched for the linear transects. These transects were run in the same areas of the reef and one week prior to the collection of the 1987 suction samples summarized in Table 1. Transects and suction collections therefore could have sampled some of the same individuals. Overall, the samples of benthic juveniles represent collections over two different spatial scales (trays were spaced 1 m during 1985 but trays and suction samples were 10 m apart during 1987) as well as two separate recruitment seasons. Notably, no trays in 1985 and only a single suction sample in 1987 were found to be devoid of recent recruits.

Discussion

Near-bottom schooling of larvae appears to be a distinct pre-settlement behavior of the naked goby.
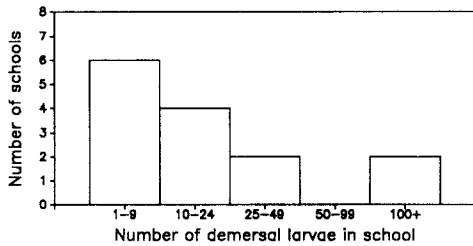
Fig. 3. Size distribution of schools of demersal larvae seen along transects. The two schools indicated as '100+' each appeared to contain several hundred larvae.

The schools of larvae are not incidental aggregations of individuals all attracted to the same structure. Rather, schools move en masse across the oyster bar. The larger larvae in schools are of the appropriate size to settle, and the two individuals that we captured live and in an undamaged condition quickly settled and metamorphosed. The fate of the smaller larvae in schools is unclear. These larvae may not successfully settle or may die shortly after settlement. It is also possible that the smaller larvae do not attempt to settle but rather re-enter the upper water column.

Our limited data do not suggest that goby larvae remain near the bottom in order to feed and grow rapidly until they are large enough to settle. Only one larva examined had food in the first half of its gut, a condition that would indicate recent feeding. However, all larvae were collected at about midday, and since about half the larvae had food in the rear half of their guts, it is possible that these larvae are primarily nocturnal and/or crepuscular feeders. Alternatively, feeding may have occurred prior to movement towards the bottom. Nearly all benthic juveniles collected during the day from the Flag Pond oyster bar had food in the front part of their guts (Breitburg, unpublished data). Furthermore, many of the 8–12 mm goby larvae collected in the Patuxent River had food in the first half of their guts. Thus, neither planktonic larvae nor benthic juveniles appear to avoid daytime feeding. If demersal larvae in schools never or rarely feed, the schooling phase may be brief, preparatory to searching the bottom for a proper site on which to settle. Additional collections of larvae are needed to support or refute the tentative conclusion that demersal schooling is unlikely to be a protracted growth phase.

The estimated 20 day age range of larvae in demersal schools does not preclude the possibility that all demersal naked goby larvae, including small individuals, are in the process of settling to the benthos. The competent settling period for many reef fishes may be quite long. For example, larvae of the bluehead wrasse, *Thalassoma bifasciatum*, can settle during a competent period spanning at least 40 days (Victor 1986). Various species of tropical gobies have been found to settle at ages of <20 to >42 d (Brothers et al. 1983, McFarland et al. 1985), a range that is similar to the ages of the demersal naked goby larvae we collected. The range of ages at settlement of individual tropical

Table 1. Dispersion of benthic juveniles (≤13.5 mm TL) and demersal larvae of the naked goby. A 'sample' for demersal larvae is a discrete group of larvae or a single individual. CM = middepth Conoy site, CD = deep Conoy site, CS = shallow Conoy site. Suction samples at CS are considered separately because the substrate sampled was markedly different from that at CM or CD. n.a. = not applicable.

Period	Data	Sample type	Area of sample (m²)	Site	No. of samples	Number of individuals per sample			
						X̄	SD	CV (%)	Lloyd's index (p)
juveniles	25 July 1985	tray	0.30	CM	5	7.8	4.3	55.4	1.118
juveniles	15 Aug. 1985	tray	0.30	CM	10	6.8	1.8	26.7	0.917
juveniles	14 July 1987	suction	0.26	CD + CM	10	3.6	2.3	63.1	1.080
juveniles	14 July 1987	suction	0.26	CS	5	1.8	1.6	91.3	1.111
demersal larvae	9 July 1987	visual	n.a.	CD + CM + CS	14	23.8	34.4	144.5	2.870

goby species cannot be estimated at this time because only a few individuals have been examined for each species.

The dispersion pattern of recent recruits is far more uniform than what would be expected from the aggregated pattern of the demersal larvae. Behaviors of larvae at the time of settlement (e.g. choice of settlement sites), behavioral interactions between larvae and animals in the benthos, and post-settlement mortality all could have modified the larval pattern. One key possibility to examine is whether the single and small groups of larvae frequently seen represent individuals that have broken away from larger schools in their search for suitable settlement sites. Schooling could provide some protection from predators until larvae disperse to settle.

Presettlement schooling may be a common behavior of temperate benthic fishes. Marliave (1986) observed schooling near the bottom by species representing five families of eastern Pacific reef and intertidal reef fishes (Gobiesocidae, Cottidae, Stichaeidae, Pholidae, Gasterosteidae), but larvae in these schools represented a wider range of developmental stages than those I observed. Hexagrammid and clinid larvae that appeared sufficiently large and mature to settle have been seen schooling near the substrate in southern California kelp beds (M. Carr, unpublished data). Presettlement schooling has also been observed for trypterygid larvae on Tasmanian reefs (R. Thresher, unpublished data). Larval behavior of coral reef fish species that do not school as adults is largely undescribed, but presettlement schooling by the pomacentrid *Pomacentrus wardi* has been predicted based on the distribution of recruits (Doherty 1987). For those temperate and tropical species in which presettlement larval schooling occurs, interactions among larvae may exert an important influence on the ultimate spatial and temporal patterns of recruitment.

Acknowledgements

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