Is recruitment of the temperate sand goby, *Sagamia geneionema*, affected by habitat patch characteristics?

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Abstract The temperate annual goby, *Sagamia geneionema*, showed pronounced spatial variation in recruitment among 8 isolated sand patches within a 1-ha area at Aburatsubo, Miura Peninsula, central Japan. Investigations were conducted to determine if such among-patch variation stemmed from differences in patch attributes, including patch size, sediment grain size, food availability, and densities of predators and heterospecific residents. No relationship between recruit density and each of the 5 attributes measured was found, although among-patch variability in patch attributes was apparent. This result suggests that recruitment was not influenced by patch characteristics. The mechanisms that produce among-patch variation in recruitment may be explained in part, by the aggregating behavior of presettlement individuals in the water column above the sand patches.

Key words. — Recruitment variation; *Sagamia geneionema*; sand patch attributes; settlement.

Most demersal marine fishes have open life cycles involving a dispersive pelagic larval phase and a site-attached juvenile and adult phase (Booth and Brosnan, 1995). In these species, a great deal of variation in recruitment from pelagic larvae to demersal populations occurs over a range of spatial and temporal scales (e.g., Doherty and Williams, 1988; van der Veer et al., 1990; Doherty, 1991; Booth and Brosnan, 1995). Several recent studies have emphasized that such variation can exert a profound influence on the sizes of adult populations (e.g., Victor, 1986; Doherty and Williams, 1988; Doherty and Fowler, 1994), although postrecruitment processes, such as predation and competition, have also been known to be important in determining adult population densities (e.g., Hixon, 1991; Jones, 1991; Caley et al., 1996). It is, therefore, critical to elucidate factors contributing to recruitment variation.

The benthic goby, *Sagamia geneionema*, is an annual species with discrete generations, inhabiting exposed sand and sandy mud areas in temperate shallow waters along the coasts of Japan and the Korean Peninsula (Akihito et al., 1984). Almost all adults die after spawning (January to March) in their first year (Shiobara et al., 1990; Sano, 1997). The larval life of the goby is unknown, but presettlement individuals (about 20–40 mm in total length, TL), which hover individually or in groups within 1 m of the sand substrate (see also Breitburg, 1989, 1991), appear in late April to June. Such individuals are translucent with some pigmentation. They settle onto sand habitats when they reach ca. 40 mm TL, in mid-May through to early July (Sano, 1997). In this paper, to clearly distinguish larval behavior in near-bottom water from benthic perching of settled juveniles, all individuals found in the water column are referred to as larvae (Breitburg, 1991; Victor, 1991). Recruits are defined as settled juveniles surviving until the end of the settlement period (early July), and recruitment as the density of recruits (Jones, 1990; Levin, 1994a). Settlers and recruits feed mainly on epi- and infaunal gammaridean amphipods, accounting for 66% of the total diet by volume (M. Sano, unpubl. data). Older juveniles and adults also prey heavily on the same (Shiobara et al., 1990).

Sano (1997) found considerable spatial variation in the recruitment of *S. geneionema* among sand patches sampled over a 1-ha area. This patch-to-patch variation may be explained by one or a combination of the following 3 factors (see Sano, 1997): 1) among-patch differences in larval supply (Kingsford et al., 1991; Milicich et al., 1992), 2) active patch choice arising from responses by settling fish to prey availability (Jones, 1984; Levin, 1994b), sediment grain size (Burke et al., 1991; Rogers, 1992), patch size (Levin, 1993), or agonistic interactions with resident fishes

(Sweatman, 1985; Jones, 1987; Sweatman and St John, 1990), or 3) differential postsettlement mortality through predation (e.g., Pihl and van der Veer, 1992; Hixon and Beets, 1993; Carr and Hixon, 1995). The first factor is affected by the hydrodynamics of the water column above the sand patches, whereas the latter 2 are associated with abiotic and biotic characteristics of the demersal environment. If these demersal characteristics contribute significantly to variation in goby recruitment, recruit densities should be positively related to prey availability (e.g., Levin, 1994b) or patch size (Levin, 1993) and negatively to the density of predators (e.g., Hixon and Beets, 1993) or resident fishes (e.g., Sweatman, 1985) across the patches. The relationship of recruitment to sediment grain size may be more complex (Burke et al., 1991; Rogers, 1992).

In the present study, a correlative approach was used to investigate whether or not the sand patch attributes (food availability, sediment grain size, patch size, and densities of predators and heterospecific residents) contributed to the recruitment pattern of *Sagamia geneionema* over nearshore sand patches.

Methods

Study site. — This study was carried out within a small shallow (<5 m deep) bay at Aburatsubo (35° 09′N, 139°37′E), situated on the south-western coast of the Miura Peninsula, central Japan. At this site, many sand patches are separated from one another by dense seagrass meadows and rocky reefs with bushy red and brown algae. Eight isolated sand patches within a 1-ha area were chosen for study, the two most widely separated being about 200 m apart and the two nearest 10 m apart. A map of the study site with the locations of the 8 sand patches appears in Sano (1997). The patches were similar to each other in surroundings and water depth (ca. 2 m at low tide). Patch size was measured using a scaled tape.

Fish censuses. — To examine spatial patterns in the recruitment of *Sagamia geneionema* over the patches, visual censuses were conducted on July 4 and 5, 1995, at the end of the settlement season. Five nonoverlapping transects 5 m long and 1 m wide were established in each patch using a scaled tape. Transect width was estimated visually. The tape was laid 5 min prior to censusing fish to reduce biases due to disturbance. After this recovery period, all recruits within the transect area (5 m^2) were counted using SCUBA. Each transect was censused once.

During the settlement period, the sand patches were commonly inhabited by adult residents of another benthic goby, *Favonigobius gymnauchen*. Other resident fish species were very rare. To assess the effect of prior residents on recruitment, this goby was also counted within the transect areas when *S. geneionema* recruits were censused. Densities of *S. geneionema* recruits and resident *F. gymnauchen* were expressed as the mean number of individuals per 5 m^2 in each patch ($n=5$ per patch).

Sagamia geneionema settlers on sand patches at the study site are consumed by resident piscivorous fishes, such as the sculpin, *Pseudoblennius percoides*, inhabiting rocky reefs and seagrass beds surrounding the sand patches (Sano, 1997). These potential predators were enumerated while swimming slowly along a nonoverlapping zigzag pattern around each sand patch for a 5-min period after the goby censuses. Piscivore density was represented as the number of fish counted per 5 min. All fish censuses were made between 1000 and 1500 h.

Sampling of primary prey. — To ascertain whether or not among-patch variation in recruitment was associated with prey abundance, epi- and infaunal gammaridean amphipods were collected after the fish censuses. Five replicate core samples were taken randomly from each sand patch between 1000 and 1500 h. A diver-held corer of 110-mm inside diameter (base area=95 cm^2) was pushed 5 cm into the sediment, resulting in 475 cm^3 of sediment being collected in each core. Core samples were then washed through a 0.5-mm mesh sieve and the contents retained preserved immediately in 5% buffered formalin. Gammarids remaining in the contents were sorted and counted under a binocular microscope in the laboratory.

Sediment analysis. — Approximately 100 g of surface sediment was taken from each sand patch at the time of gammarid sampling. A cumulative frequency curve of grain size diameters was determined by the wet-sieving method of Buchanan (1984) in the laboratory. The attribute of the sediment was expressed as mean grain size using the Ø value representing $-\log_2$ of the particle diameter in mm (Folk and Ward, 1957). Note that the larger the Ø value, the smaller the particle diameter.

Data analysis. — A one-way analysis of variance (ANOVA) was used to evaluate differences in mean recruit density among the patches. Prior to analysis data were transformed using $\log(x+1)$ to stabilize heterogeneous variances (Bartlett's test, $p>0.05$). A simple linear regression was performed to test the null hypothesis that no relationship existed between sand patch attributes and the mean density of recruits in each patch. Mean recruit density was the response variable, and patch size, sediment grain size, gammarid abundance, and resident and piscivore densities were independent variables.

Results

The mean densities of newly-recruited goby at the end of the settlement season varied significantly among the sand patches (one-way ANOVA, $F_{7,32}=6.92$, $p<0.001$). There was a 2.9-fold difference in mean recruitment between the patches with maximum and minimum recruitment (Fig. 1).

Among-patch variability in patch attributes was apparent (Table 1). In particular, mean gammarid density at patch 8 was 9.2 times greater than that at patch 1. Nonetheless, the linear regression revealed no relationship between the mean density of recruits and each of the 5 patch attributes (Table 1).

Although the regression analysis showed neither a positive nor negative relationship between recruit density and sediment grain size, recruits may had have a preference for a medium grain size within the size range examined. Such a preference, however, was not found (Fig. 2).

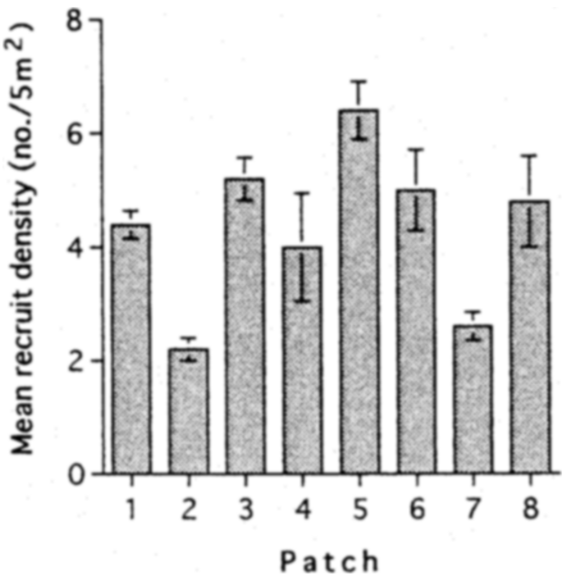

Fig. 1. Mean recruit density (±SE, $n=5$) of *Sagamia geneionema* in 8 isolated sand patches within the 1-ha study area at Aburatsubo.

Discussion

Sagamia geneionema showed pronounced spatial variation in recruitment among the sand patches sampled over a 1-ha area. This recruitment variation could not be explained by any of the 5 patch attributes quantified. Additionally, since goby recruitment was not associated with sediment grain size, which to a large extent is related to flow velocity over a patch (Gibson and Robb, 1992), flow velocity also may not

Table 1. Abiotic and biotic characteristics of 8 isolated sand patches (coefficients of determination [r^2] in the relationship between mean recruit density and each characteristic are also given, along with F- and p-values for the significance test in regression)

Patch*	Area (m^2)	Mean sediment grain size (Ø)	Mean gammarid density (no./95 cm^2±SE)	Mean Fg density (no./5 m^2±SE)	Piscivore density** (no./5 min observation)
1	101	2.33	12.4±4.67	3.0±0.32	0
2	180	1.86	28.8±7.31	2.4±0.24	1
3	180	1.18	14.0±1.48	1.6±0.24	2[a]
4	52	1.91	22.4±3.59	3.2±0.58	1
5	162	1.79	15.8±1.56	4.2±0.37	1
6	57	2.10	44.0±11.4	1.2±0.37	1[b]
7	90	2.35	13.4±1.57	3.0±0.71	3[a]
8	63	1.93	113.6±27.9	1.8±0.58	2
r^2	0.001	0.148	0.013	0.005	0.060
$F_{1,6}$	0.004	1.041	0.080	0.031	0.385
p	0.947	0.347	0.787	0.865	0.558

*Patch numbers as in Fig. 1. **Piscivores were mostly *Pseudoblennius percoides*; [a]includes one *Pseudoblennius cottoides*; [b]includes one *Antennarius striatus*. Fg, *Favonigobius gymnauchen*.

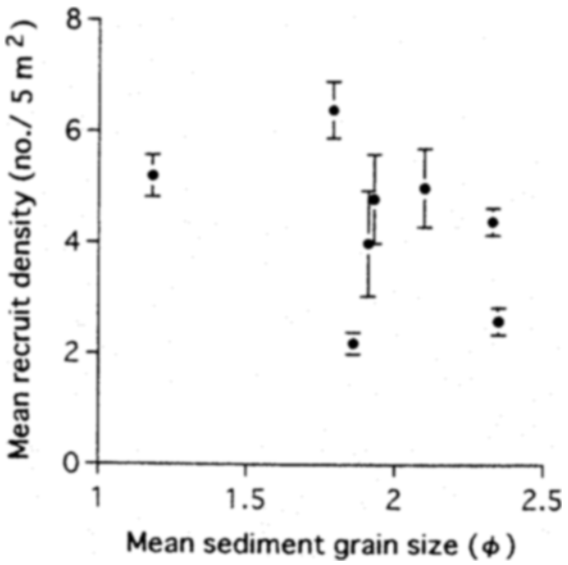

Fig. 2. Relationship between mean sediment grain size and mean recruit density (±SE, n=5) of *Sagamia geneionema* across 8 isolated sand patches.

have been a contributory factor in recruitment variation.

The density of potential predators did not influence recruitment. This result suggests that recruitment variation was set up during the act of settlement, rather than by differential postsettlement survival.

The goby settled exclusively on a sand habitat, indicating distinct habitat selection at settlement, as demonstrated for many other fishes (e.g., Eckert, 1985; Carr, 1991; Wellington, 1992; Caselle and Warner, 1996). Settling goby were frequently observed reentering the water column and swimming actively (see also Shiobara et al., 1990). These behaviors indicate the possibility of presettlement fish moving across sand patches before finally choosing a high quality patch. The data presented here, however, did not indicate such patch choice on the basis of at least 4 of the patch attributes: patch size, sediment grain size, prey availability, and resident density. Similar findings have been made for several temperate and tropical demersal fishes. Prey availability did not account for differences in recruitment among habitats for some flatfishes (Pihl and van der Veer, 1992; Rogers, 1992) and coral reef fishes (Shulman, 1984), and Tolimieri (1995) found no relationship between patch reef area and density of settlers in the tropical damselfish, *Stegastes planifrons*.

The density of resident *Favonigobius gymnauchen* had no effect on the recruitment of *Sagamia geneionema*, probably because the former is nonterritorial, with different feeding habits compared with *S. geneionema* settlers and recruits (Kikuchi and Yamashita, 1992; M. Sano, unpubl. data). I did not observe *F. gymnauchen* residents chasing newly-settled *S. geneionema*.

The present data did not provide information on how among-patch variation in the recruitment of *S. geneionema* is established. However, the mechanisms that produce such variation may be partly explained by the aggregating behavior of presettlement individuals. Most presettlement fish (ca. 20–40 mm TL), including small larvae not competent to settle, aggregated in shoals of up to 100 individuals (see also Shiobara et al., 1990), and maintained their position in the water column over sand patches by actively swimming counter to prevailing currents. If shoals remain over patches for periods of time sufficient to allow many larvae to settle, or if gregarious settlement occurs while shoals move en masse among patches, the distribution and degree of aggregation may produce large variation in settlement among patches. Larger aggregations may be formed by coalescence of small shoals and single larvae when they encounter (Breitburg, 1991). Highly variable recruitment resulting from such clumped larval distributions has been demonstrated in the temperate reef goby, *Gobiosoma bosci* (Breitburg, 1991; Breitburg et al., 1995), and some coral reef fishes (Shulman, 1985). These studies, in addition to the present one, indicated that it may not always be appropriate to assume that the spatial distribution and abundance of newly-settled fishes reflect preferences for more favorable microhabitats or patches within the overall settlement habitat.

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