*Limnol. Oceanogr.*, 41(4), 1996, 672–679

# Recruitment in a temperate demersal fish: Does larval supply matter?

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## *Abstract*

The importance of larval supply to spatial patterns of larval settlement and recruitment was determined for a common Gulf of Maine fish (the cunner *Tautogolabrus adspersus*). The number of presettlement pelagic fish differed among the four sites sampled. Inshore sites had significantly greater densities than offshore sites, and this difference was consistent over time. The average size of presettlement fish also differed; fish at inshore sites averaged ~2 mm less in standard length than those at offshore sites. Settlement was quantified by using artificial substrata suspended above the benthos, and a nonsignificant trend for greater settlement at offshore vs. inshore sites was revealed. Recruitment surveys after the settlement season showed that densities of recruits were significantly greater offshore than inshore. Correlation analyses showed either significant inverse or nonsignificant relationships between densities of presettlement fish and settlement depending on the size of presettlement fish. The relationship between recruitment and densities of presettlement fish was not significant with each of the size classes of presettlement fish analyzed, but there was a strong positive relationship between settlement and recruitment.

Variable replenishment is a hallmark of populations of marine species that have pelagic, widely dispersed larvae (Doherty and Williams 1988; Roughgarden et al. 1988; Ólafsson et al. 1994). Determining the causes and consequences of variability in recruitment has become a central problem in marine ecology and fisheries biology. Recruitment refers to the addition of young-of-the-year individuals from the pelagic habitat to the adult habitat measured at some arbitrary time after larval settlement (Connell 1985). As such, recruitment represents the end product of a series of dynamic physical and biological processes that vary spatially and temporally. Thus, factors influencing such processes as fertilization of eggs (e.g. Petersen et al. 1992), growth and survivorship of larvae (Cushing 1973), dispersal or retention of larvae (Gaines and Bertness 1992), habitat selection by settling larvae (Sweatman 1985), and postsettlement growth and survival (Forrester 1990; Hixon and Beets 1993) can act separately or in concert to produce variability in recruitment.

Experimental ecologists working primarily on benthic invertebrates and coral-reef fish have focused on the hypothesis that variation in the return of larvae to appropriate habitat is a common cause of recruitment variability (e.g. Doherty 1983; Hughes 1990; Karlson and Levitan 1990). Until recently, the relationship between recruitment and larval supply was based largely on inferences from the distribution of newly settled individuals. The use of plankton pumps (e.g. Gaines et al. 1985) and tube traps (Yund et al. 1991) has allowed workers to test the hypothesis that variability in larval supply is reflected as subsequent variation in settlement (the movement of larvae or postlarvae from the water column to the adult habitat), recruitment, and adult abundance at small spatial scales. Similarly, light traps have become useful tools for quantifying abundances of larvae of coral-reef fish, thereby allowing tests of the effects of larval supply on population dynamics of reef fish (Milicich et al. 1992; Meekan et al. 1993; Milicich and Doherty 1994). For barnacles and some species of reef fish, there is support for the hypothesis that larval supply can influence variability in recruitment (Gaines et al. 1985; Milicich et al. 1992; Milicich and Doherty 1994).

Processes that control population dynamics on temperate rocky reefs and outcroppings can differ markedly from those affecting benthic invertebrate or coral-reef fish populations (Ebeling and Hixon 1991); consequently, extrapolation from results of rocky shore or coral-reef habitats must be explicitly tested. Although fisheries ecologists have emphasized the importance of the larval life-history stage in temperate waters, most studies have focused on large, often basin-scale, relationships between larval supply and recruitment (Sissenwine 1984). Additionally, fisheries ecologists tend to investigate large, highly mobile species rather than smaller, relatively site-attached reef fish.

Few studies in temperate or tropical habitats have examined local variability in the supply of presettlement

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*Acknowledgments*

The work of numerous field assistants is much appreciated. I especially thank D. Lockett, J. Cobbler Maret, E. Wright, M. Ganger, K. Gestring, and M. Armstrong. Thanks also to Capt. Pelletier and the crew of the RV *Jere Chase* and the staff of the Shoals Marine Lab for logistical support. I thank C. H. Peterson, J. A. Coyer, and two anonymous reviewers for comments on the manuscript. The advice, support, and criticism of P. F. Sale greatly improved this project.

The financial support of NSF grant OCE 91-02927 and National Geographic Society grant 4625-91 to P. F. Sale and P. S. Levin is gratefully acknowledged. I also thank M. E. Hay for support as a postdoc from NSF grant OCE 92-02847 while this manuscript was composed.

fish and subsequent settlement and recruitment to specific sites (*but see* Milicich et al. 1992; Milicich and Doherty 1994; Schultz and Cowen 1994). My goal was to quantify the supply of presettlement fish at a relatively small spatial scale (100s of meters to kilometers) and to ask whether among-site variability in the supply of presettlement fish explained subsequent variation in settlement and recruitment in a temperate demersal fish.

## Methods

*Study species*—The cunner, *Tautogolabrus adspersus,* is the northernmost member of the labrid family in the western North Atlantic (Scott and Scott 1991). Cunner are common from Newfoundland to New Jersey and occasionally are found as far south as Chesapeake Bay (Bigelow and Schroeder 1953). They occur from depths >90 m (Bigelow and Schroeder 1953) to intertidal zones (Ojeda and Dearborn 1990). Throughout their range, cunner are associated with reefs, sheltered rock substrata, or manmade structures (e.g. piers, wrecks, etc.).

Cunner spawn during early and midsummer (Pottle and Green 1979). After a pelagic presettlement stage averaging from 18 to >37 d (Victor 1986*a*; Malchoff 1993), fish settle to the demersal habitat. In the Gulf of Maine, cunner settle during a single pulse lasting ~3–4 weeks (Levin 1993, 1994*a*). Because cunner reproduce and settle in a discrete, single pulse, it is possible to sample a single demographic cohort from the larval stage through recruitment. In this paper, I refer to pelagic larval and postlarval individuals as "presettlement" fish (Kingsford 1988). At settlement, cunner are associated with macroalgal habitats (Levin 1991, 1993, 1994*b*) and seem to be very site attached (Levin 1994*a*).

*Study sites*—This study was conducted at four sites in the central Gulf of Maine. Two sites (Ft. Point and Whaleback) are along the New England coast near Portsmouth, New Hampshire (43°05′N, 70°44′W), and the other two (Appledore and Duck) are ~10 km offshore of Portsmouth at the Isles of Shoals, Maine (42°59′N, 70°37′W). The inshore sites are characterized by cobbles and large boulders covered with macroalgae (mostly *Chondrus crispus* and *Laminaria* spp.). Patches of sand, often with eel grass (*Zostera marina*), occur among the rocky substrata at the two inshore sites. The offshore sites are characterized by rock ledges with dense macroalgal cover. Macroalgal assemblages are similar between inshore and offshore sites, except that the green algal, *Codium fragile,* is far more abundant offshore.

*Sampling of presettlement fish*—Preliminary sampling with light traps (Doherty 1987) proved inefficient, probably due to the relatively high turbidity of the water. In addition, turbidity varied predictably among sites and over time, potentially biasing catch results from light traps (Milicich et al. 1992). Consequently, I quantified the supply of presettlement fish by performing surface ichthyoplankton tows with a 1,000-$\mu$m-mesh plankton net fitted with a General Oceanic flowmeter.

Presettlement cunner undergo diel vertical migrations with higher densities of fish of all size classes occurring higher in the water column at night (Malchoff 1993); therefore, all sampling was done at night. Plankton nets were 1 m in diameter. Three replicate 10-min tows were conducted on eight occasions that encompassed the entire 1991 settlement season (1, 5, 7, 8, 12, 13, 15, and 26 August) (Levin 1993). All tows were conducted adjacent to study sites in water 25–30 m deep. To prevent spatial trends from being confounded with temporal patterns, I sampled concurrently at two sites, immediately followed by sampling concurrently at the other two sites. The order of sampling was randomized.

Only the density of presettlement fish competent to settle is meaningful in the context of this study. I used two methods to determine size at competency. Gleason (1988) analyzed otolith microstructure and reported the age at settlement for cunner as well as the length-age relationship for pre- and early postsettlement cunner. His results indicated that the smallest length at settlement was 6.2-mm standard length (hereafter SL), and the mean size at settlement was 8.6-mm SL. I collected and measured the length of 659 newly recruited cunner (Fig. 1). Their minimum size was 7.0-mm SL and the modal length was 10.1-mm SL (Levin 1993). Because the size of fish considered competent to settle could greatly influence my conclusions, I repeated all analyses with three different size classes of presettlement fish: 7.0-, 8.6-, and 10.1-mm SL. All measurements of larval fish were performed with an image analysis system. Standard length was measured from the tip of the upper jaw to the end of the caudal peduncle.

*Quantifying settlement*—Settlement was quantified by deploying artificial settlement substrata at dusk on four dates on which presettlement fish were sampled. Each settlement substratum consisted of four cotton mopheads attached at 75-cm intervals to a 3.1-m length of PVC pipe (3.81-cm diam). Mopheads were soaked for 2 weeks in filtered seawater before deployment. The mophead array was suspended from the surface so that it was above the substratum by 1.85–2.46 m, depending on the tidal state. Two settlement substrata, separated by at least 20 m, were deployed at each of the four sites.

Mophead arrays were examined 24 h after deployment. Divers slowly approached mop arrays and enclosed each mop in a plastic bag. As divers approached, fish were observed to dart into the mop; fish were never observed swimming away from the array. Plastic bags were removed from individual mops. Mops were carefully searched visually, and the fish were enumerated. After sampling, mophead arrays were removed from the water, rinsed thoroughly with freshwater, and stored on land until the next sampling date.

*Quantifying recruitment*—Densities of recruits were estimated in late August at the end of the settlement season (2 weeks after the last new settler was observed in the natural habitat, Levin 1993). Replicate 15 × 1-m transects ($n$ = 10 per site) were randomly placed at each site using

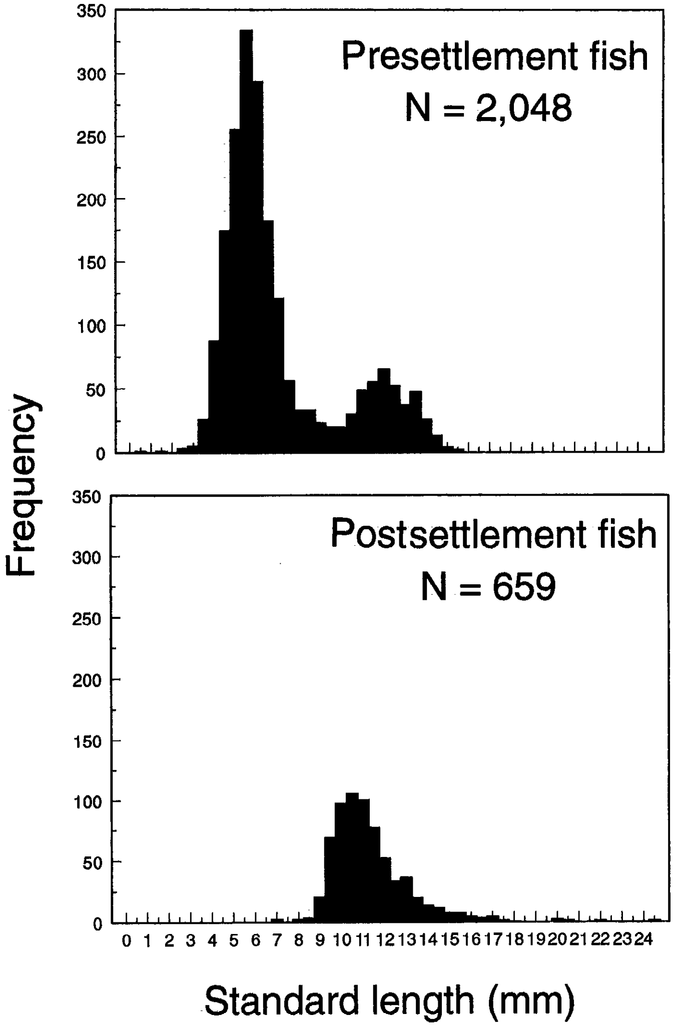

Fig. 1. The standard length of pre- and postsettlement cunner from Maine. Comparison of the size frequency distribution of pre- and postsettlement fish indicates that many of the presettlement fish sampled were similar in size to postsettlement fish.

triplets of random numbers. The first two numbers indicated a compass direction and distance from a haphazard starting point, and the third number indicated the compass direction in which the transect was extended. Five minutes after a transect line was extended, a diver swimming at a rate of ~3 m $\mathrm{min}^{-1}$ carefully counted all recruits within a meter-wide band along the length of the transect. Details of this sampling method are provided by Lincoln-Smith (1989).

*Data analysis*—Two-factor ANOVA was used to test the null hypothesis that no differences in the mean number of presettlement cunner captured (per $m^3$) were present among sampling dates or among sites. Similarly, a two-factor ANOVA was used to test the hypothesis that no differences existed in the number of settlers at each site or among sampling dates. In this analysis, each settlement sampler was considered a replicate because individual mops within a sampler are not independent replicates. A one-factor ANOVA was used to test the hypothesis that recruitment varied among sites.

Correlation analyses were used to examine the association among the supply of presettlement fish and settlement or recruitment. The total number of larvae collected at each site and the mean number of settlers or recruits observed at that site were used as data points in the analyses. I chose to use the product-moment correlation rather than regression analysis because the latter requires that the independent variable be measured without error (Zar 1984). Both variables were random factors in these analyses: thus, correlation analyses were appropriate for establishing and estimating the degree of association between variables (Sokal and Rohlf 1981). I used regression analysis to examine the relationship between settlement and recruitment. Because my estimate of settlement was subject to only minor measurement error (regression statistics are known to be robust to minor violations of the measurement error of the independent variable, Zar 1984) and because I wanted to describe the functional relationship between settlement and recruitment, regression analysis was appropriate.

## Results

*The distribution and abundance of presettlement fish*—The abundance of presettlement cunner differed significantly among sites. The mean number of presettlement fish (including all size classes) per 100 $m^3$ averaged 78.7 (SE = 24.6) at Ft. Point and 38.7 (SE = 15.9) at Whaleback. These numbers were significantly greater than the mean number of fish at Appledore (2.25, SE = 0.74) or Duck (1.21, SE = 0.43) ($F_{3,48} = 3.451$, $P = 0.04$). There were significant differences in the abundance of presettlement fish among sampling dates ($F_{5,48} = 4.663$; $P = 0.002$), and the magnitude of these differences was not consistent over time, as evidenced by a significant date × site interaction in the analysis of variance ($F_{15,48} = 4.554$; $P < 0.001$). However, when sites were ranked according to the density of presettlement fish on each sampling date and the ranks compared among dates, there was higher agreement than expected by chance (Kendall's coefficient of concordance = 3.367, $\chi^2 = 60.6$, $P < 0.001$). Thus, despite temporal changes in the magnitude of among-site differences in presettlement cunner, differences in the rank order of sites were consistent throughout the settlement season.

The average size of presettlement cunner, including precompetent size classes, also varied among sites (Fig. 2). Fish captured at the offshore sites (Appledore and Duck) averaged >9-mm SL. This was significantly greater than the 6.5-mm SL of fish from the inshore sites (Ft. Point and Whaleback; $F_{3,2060} = 39.81$; $P < 0.001$).

The number of fish settling on the artificial settlement substrata at Appledore and Duck averaged >1 fish per settlement collector; at Ft. Point and Whaleback, settlement averaged <0.1 fish per settlement collector. However, this difference was not statistically significant ($F_{2,25}$

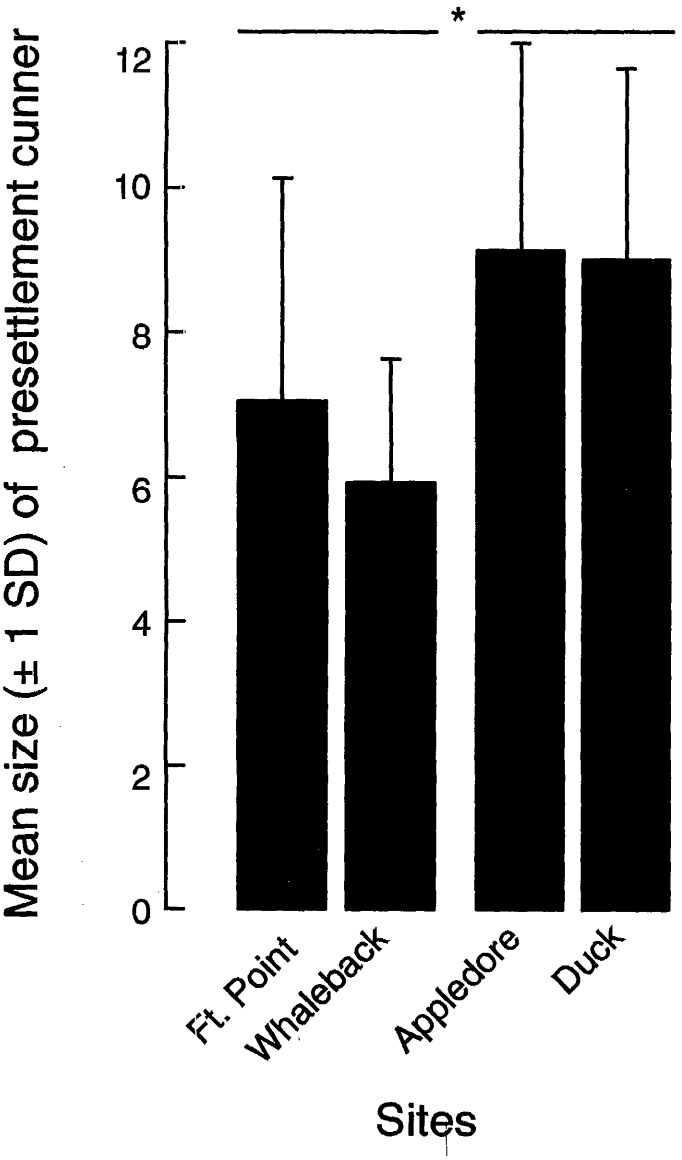

Fig. 2. The average size (standard length) of presettlement fish differed among sites. Larger fish were observed at the offshore sites (Appledore and Duck), while smaller fish were observed at the inshore sites (Ft. Point and Whaleback).

= 2.092; $P = 0.13$) due to the large variability within sites and the small sample size.

Recruit density also differed significantly among sites. Appledore received an average of 37.8 (SE = 7.65) recruits per 15 $m^2$ transect, which was significantly greater than the other three sites (Tukey's HSD, $P < 0.03$). Duck averaged 14.85 (SE = 5.1) recruits per transect, which was significantly greater than the recruit density at Whaleback (mean = 3.45 per transect, SE = 0.84, Tukey's HSD, $P = 0.03$) but not statistically distinguishable from Ft. Point (mean = 4.8 per transect, SE = 1.2, Tukey's HSD, $P = 0.21$). Recruit densities at Whaleback and Ft. Point did not differ significantly from each other (Tukey's HSD, $P = 0.80$).

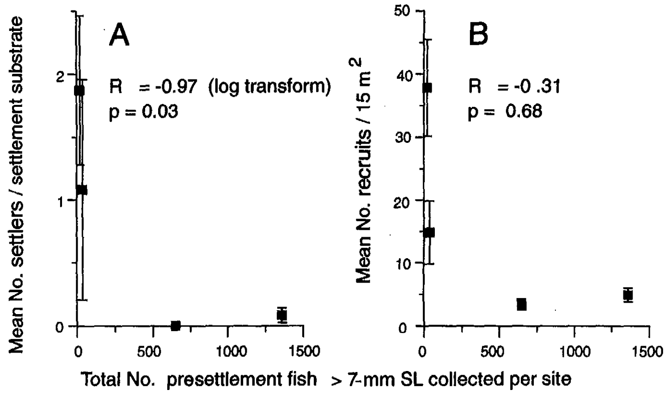

Fig. 3. A. A significant negative relationship existed between the total number of presettlement fish >7-mm SL collected at a site and the mean number of settlers sampled at that site. B. A similar relationship existed between the mean number of recruits sampled at a site and the total number of presettlement fish >7-mm SL sampled; however, this relationship was not significant. All error bars are ±1 SE.

*The relationships among the density of presettlement fish, settlement, and recruitment*—Plankton tows appeared to adequately sample presettlement fish that were competent to settle. An examination of the size frequency distribution of presettlement fish reveals that although many fish captured were probably too small to settle, a large number of presettlement fish were captured that were similar in size to postsettlement fish (Fig. 1).

A significant negative relationship existed between the density of presettlement fish >7.0-mm SL and settlement (Fig. 3A). The log $(x+1)$ of the total number of presettlement fish captured at each site and the log $(x+1)$ of the mean number of settlers collected from artificial settlement substrata at each site were highly inversely correlated. Similarly, there was an apparent inverse relationship between the supply of presettlement fish and recruitment (Fig. 3B); however, this relationship was significant only at the $P = 0.095$ level.

When the size of presettlement fish considered competent to settle was increased to 8.6-mm SL, the relationship between density of presettlement fish and settlement was no longer significant (Fig. 4A) nor was the relationship between presettlement fish >8.6-mm SL and recruitment (Fig. 4B). In addition, when only fish >10.1-mm SL were considered competent to settle, the relationships between the density of presettlement fish and settlement (Fig. 5A) and recruitment (Fig. 5B) were not significant.

Despite the absence of a positive relationship between the density of presettlement fish and settlement or recruitment, there were significant relationships between the size of presettlement fish and settlement. Average settlement levels were highly correlated with the size of presettlement fish (Fig. 6A). Similarly, recruitment seemed correlated with the average length of presettlement fish. (Fig. 6B); however, this relationship was significant at the $P = 0.07$ level.

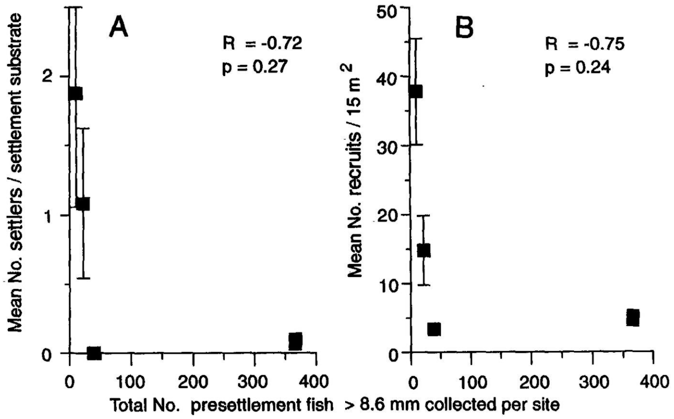

Fig. 4. A. The relationship between the density of presettlement fish >8.6-mm SL and the mean number of settlers sampled at a site was not significant. B. The relationship between the density of presettlement fish >8.6-mm SL and the mean number of recruits sampled at a site was also not significant. All error bars are ±1 SE.

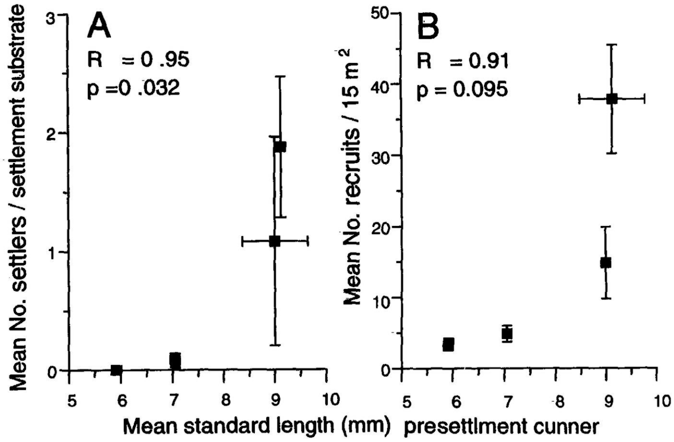

Fig. 6. A. A significant positive relationship was observed between the average size of presettlement cunner and the mean number of settlers sampled at a site. B. There was a nonsignificant trend for increasing recruitment with increasing average size of presettlement fish. All error bars are ±1 SE.

There was a strong positive relationship between settlement and recruitment (Fig. 7). A regression analysis with the mean number of settlers at each site as the predictor and the mean number of recruits as the response variable revealed that 93.3% of the variation in recruitment was explained by settlement ($P = 0.034$).

## Discussion

The assumption that small-scale variability in settlement or recruitment is related to variability in larval supply is frequently made but rarely tested (*but see* Milicich et al. 1992). For numerous fish and benthic invertebrates, adult abundances at various spatial scales are demonstrably related to the input of new recruits (e.g. Victor 1986*b*; Gaines and Bertness 1992; Doherty and Fowler 1994). By contrast, it is widely recognized by fisheries ecologists that year-class strength is not related to larval abundance for many exploited species (Sissenwine 1984). Determining when in the life history year-class strength is determined is thus critically important to our understanding the dynamics of marine populations. My

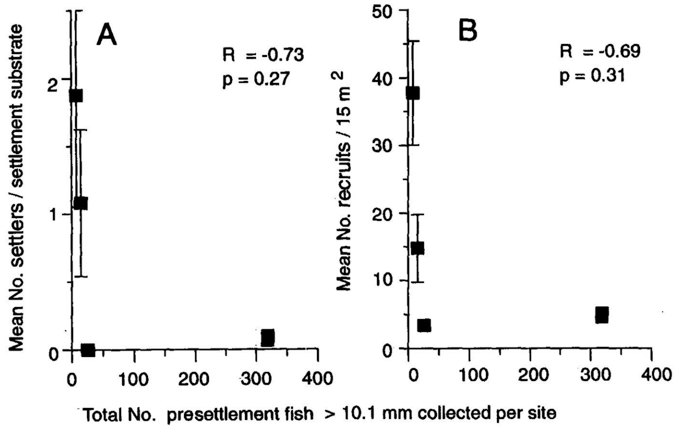

Fig. 5. A. The relationship between the density of presettlement fish >10.1-mm SL and the mean number of settlers sampled at a site was not significant. B. The relationship between the density of presettlement fish >10.1-mm SL and the mean number of recruits sampled at a site was also not significant. All error bars are ±1 SE.

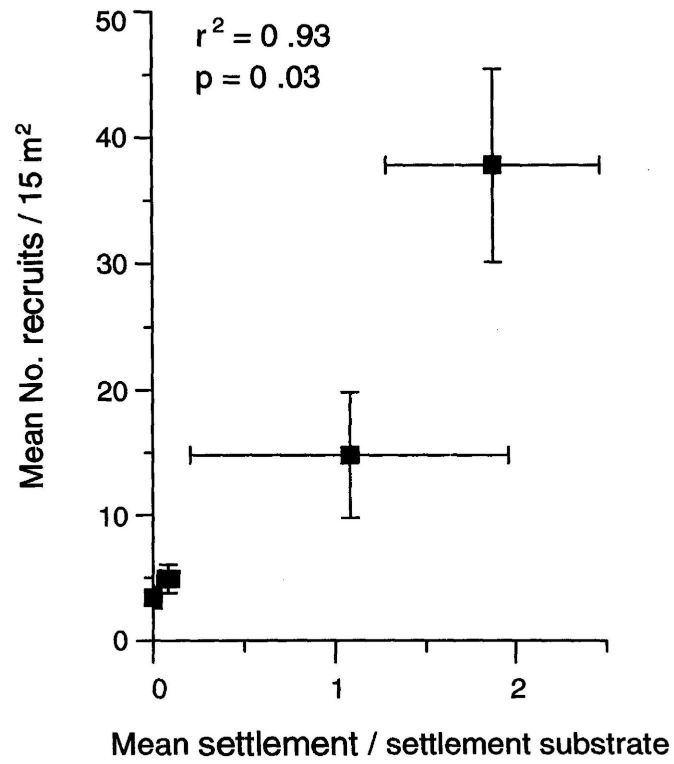

Fig. 7. Regression analysis revealed a significant relationship between the mean number of settlers sampled on artificial settlement substrates (mophead arrays) and the mean density of recruits at a site. Error bars are ±1 SE.

results suggest that the density of presettlement fish and consequently those processes directly or indirectly affecting larval density are not the leading determinants of recruitment variability for *T. adspersus* at the spatial scale examined. Rather, variability in the magnitude of settlement, which was correlated with the average size of presettlement fish, appears to drive patterns of recruitment.

Patterns of presettlement abundance can be decoupled from settlement patterns if settling fish select habitats at large spatial scales. Previous work on cunner indicates that branched (cf. Levin 1994*b*) and foliose algae are important habitats for newly recruited fish (Levin 1991, 1993) and that in some years as much as 80% of among-site variability in recruitment can be explained by variability in the cover of branched algae (Levin in prep.). My sites differed in their coverage of macrophytes. Appledore and Duck had high coverage (>50%) of branched algae (*C. fragile*), while the algal assemblage at Ft. Point and Whaleback had higher covers of the turflike *C. crispus*. Additionally, Ft. Point and Whaleback had patches of sand in which eelgrass was present. Although settlement was monitored on standardized artificial substrata in order to minimize the effects of habitat differences, it is possible that olfactory cues associated with the habitat resulted in higher levels of settlement to artificial substrata located in preferred habitat compared to settlement samplers located in low-preference habitats.

Patterns of presettlement abundance can also be decoupled from settlement patterns if differences in mortality alter patterns before settlement is quantified (Victor 1986*b*). Settlement samplers were suspended more than 1.85 m above the bottom to reduce early postsettlement predation by benthic fish, particularly sculpins such as *Myoxocephalus aenaeus*. However, settlement samplers were accessible to more pelagic species, such as pollock (*Pollachius virens*), which may be important predators of newly settled cunner (Levin 1994*a*). Thus, settlement samplers at sites with high densities of pollock may have experienced higher levels of early postsettlement mortality than sites with lower densities of pollock.

Although a comparison of the size frequency distributions of presettlement and postsettlement fish suggests that plankton nets did an adequate job of sampling presettlement fish competent to settle, plankton nets may not be the best way to quantify the larval supply. Plankton nets tend to capture smaller larvae (Choat et al. 1993) and by themselves cannot provide data on larval flux. Furthermore, although I was able to conduct plankton tows intensively throughout the brief settlement season, plankton tows can give only a snapshot of the water column. Light traps tend to capture larger larvae (Choat et al. 1993), measure larval flux, and integrate over time, but they were not used after preliminary sampling showed that water clarity was variable and often low. However, light traps could provide useful data in this system if sites distant from shore with low turbidity are examined.

The average level of settlement to artificial settlement substrata was correlated with the size of presettlement fish. Most fish at the two inshore sites were only slightly above the smallest size criteria (7-mm SL) used to determine whether fish were competent to settle. There are several reasons why sites receiving generally smaller presettlement fish can be expected to have lower settlement. Smaller settlers may be more susceptible to predation than larger individuals because of differences in escape ability or predator gape limitation (Zaret 1980; Blaxter 1986; Miller et al. 1988). Additionally, vulnerability to predation may be higher for smaller presettlement fish because small larvae are generally more vulnerable to starvation than larger larvae (Lasker 1981); consequently, smaller presettlement cunner may be under greater nutritional stress than larger fish (Miller et al. 1988).

The smaller size of presettlement fish at Ft. Point and Whaleback also implies that these fish were younger than those at Appledore or Duck (Malchoff 1993). If the age-length relationship calculated by Malchoff (1993) for larval cunner in the New York Bight is applied to Gulf of Maine cunner, presettlement fish collected at Ft. Point and Whaleback were ~7 d younger than those collected at Appledore or Duck. The younger age of individuals at Ft. Point and Whaleback could indicate that their propensity to settle was lower than the older fish at Appledore and Duck.

Evidence that presettlement fish can prolong their pelagic lives in the absence of appropriate conditions for settlement (Victor 1986*b*; Cowen 1991) suggests that presettlement fish have some control over the timing of settlement. Older presettlement fish may be nearing the end of their ability to postpone settlement; thus at sites that receive older presettlement fish, the relationship between the supply of presettlement fish and settlement may be stronger than at sites where presettlement fish are generally younger.

The reason presettlement fish at the offshore sites were generally older than at the inshore sites is a matter of speculation. I did not examine differences in flow regime between sites; however, with a slight offshore component operating, older larvae may tend to accumulate at offshore sites. Additionally, in the absence of an offshore current, the generally southerly flow of the Gulf of Maine suggests that fish reaching offshore sites came from scattered islands far to the north. Thus, larvae would tend to be older and fewer in number than along the mainland shore where there is a more uniform distribution of adult fish. It is clear that work focusing on mesoscale current patterns is needed to identify the source of larvae as well as to determine the flux of larvae.

In the present study, variability in settlement measured by means of artificial settlement samplers explained >93% of the variance in cunner recruitment. Because settlement of fish has been difficult to quantify, most workers quantify only recruitment. The extent to which patterns of recruitment are indicative of patterns earlier in the life history is a matter of considerable debate. Similar to my results, recent work on several species in the Caribbean (Robertson 1992) and the Great Barrier Reef (Williams et al. 1994) suggests that patterns of recruitment are good indicators of earlier patterns of settlement.

However, in a previous study on cunner, Levin (1994*a*) showed that although there was an initial strong correlation between settlement and recruitment, this relationship disappeared over time. Differences in the spatial scale of interest may be the primary reason for the discrepancy between the results of this study and those of Levin (1994*a*). Here I focused on larger scale (100s of meters to kilometers) patterns of settlement and recruitment, while my previous work on settlement-recruitment relationships in cunner was conducted at scales of meters (Levin 1994*a*). Thus, postsettlement processes distorted initial patterns of settlement at small spatial scales so that initial patterns of settlement were not reflected as patterns of recruitment. However, this study revealed that at larger scales, settlement patterns did manifest themselves as patterns of recruitment.

Recent models of reef fish have focused on the relative contributions of recruitment and postrecruitment mortality or growth to the demography and abundance of populations. Empirical tests of these models have generally concluded that recruitment-limited populations (cf. Doherty 1983; Victor 1983) suffered from a shortage of pelagic propagules. This conclusion seems rooted in the findings of recruitment studies of benthic invertebrates (e.g. Gaines et al. 1985) and not on studies performed on exploited temperate fish, where egg and larval abundance are routinely quantified and generally are not correlated with densities of juvenile fish (Sissenwine 1984). My results suggest that processes occurring at or within the first 24 h of settlement can decouple the supply of presettlement fish from patterns of settlement. Although the empirical demonstration of recruitment limitation may indicate a scarcity of larvae (Milicich et al. 1992), without a direct examination of larval abundance it is imprudent to assume that this is the mechanism responsible for low levels of recruitment.

## *References*

BIGELOW, H. B., AND S. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. Fish. Bull. **53:** 577 p. U.S. Fish Wildl. Serv.

BLAXTER, J. H. S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. **115:** 98–114.

CHOAT, J. H., P. J. DOHERTY, B. A. KERRIGAN, AND J. M. LEIS. 1993. A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. Fish. Bull. **91:** 195–209.

CONNELL, J. H. 1985. The consequences of variation in initial vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. **93:** 11–45.

COWEN, R. K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. Mar. Ecol. Prog. Ser. **69:** 9–15.

CUSHING, D. H. 1973. The natural regulation of fish populations, p. 399–411. *In* F. R. Harden-Jones [ed.], Sea fisheries research. Elek Sci.

DOHERTY, P. J. 1983. Tropical territorial damselfishes: Is density limited by aggression or recruitment? Ecology **64:** 176–190.

———. 1987. Light-traps: Selective but useful devices for quantifying the distributions and abundances of larval fishes. Bull. Mar. Sci. **41:** 423–431.

———, AND T. FOWLER. 1994. An empirical test of recruitment limitation in a coral reef fish. Science **263:** 935–939.

———, AND D. MCB. WILLIAMS. 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. **26:** 487–551.

EBELING, A. W., AND M. A. HIXON. 1991. Tropical and temperate reef fishes: Comparison of community structure, p. 509–563. *In* P. F. Sale [ed.], The ecology of fishes on coral reefs. Academic.

FORRESTER, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish population. Ecology **71:** 1666–1681.

GAINES, S. D., AND M. D. BERTNESS. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature **360:** 579–580.

———, S. BROWN, AND J. ROUGHGARDEN. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle *Balanus glandula*. Oecologia **67:** 267–272.

GLEASON, T. R. 1988. A contribution to the early life history of the cunner *Tautogolabrus adspersus* (Walbaum), in Narragansett Bay, Rhode Island. M.S. thesis, Univ. Rhode Island. 98 p.

HIXON, M. A., AND J. P. BEETS. 1993. Predation, prey refuges and the structure of coral-reef fish assemblages. Ecol. Monogr. **63:** 77–101.

HUGHES, T. P. 1990. Recruitment limitation, mortality, and population regulation in open systems: A case study. Ecology **71:** 12–20.

KARLSON, R. H., AND D. R. LEVITAN. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: An evaluation. Oecologia **82:** 40–44.

KINGSFORD, M. J. 1988. The early life history of fish in coastal waters of northern New Zealand: A review. N.Z. J. Mar. Freshwater Res. **22:** 463–479.

LASKER, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting years, 1975 through 1978. Rapp. P.-V. Reun. Cons. Int. Explor. Mer **178:** 375–388.

LEVIN, P. S. 1991. Effects of microhabitat on small scale recruitment variation in a Gulf of Maine reef fish. Mar. Ecol. Prog. Ser. **75:** 183–186.

———. 1993. Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. Oecologia **94:** 176–185.

———. 1994*a*. Fine-scale temporal variation in recruitment of a temperate demersal fish; the importance of settlement versus post-settlement loss. Oecologia **97:** 124–133.

———. 1994*b*. Small-scale recruitment variation in a temperate fish: The roles of macrophytes and food supply. Environ. Biol. Fish **40:** 271–281.

LINCOLN-SMITH, M. P. 1989. Improving multispecies rocky reef censuses by counting different groups of species using different procedures. Environ. Biol. Fish **26:** 29–37.

MALCHOFF, M. H. 1993. Age, growth and distribution of cunner (*Tautogolabrus adspersus*) and tautog (*Tautoga onitis*) larvae in the New York Bight: A single season analysis. M.S. thesis, Bard College. 75 p.

MEEKAN, M. G., M. J. MILICICH, AND P. J. DOHERTY. 1993. Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. Mar. Ecol. Prog. Ser. **93:** 217–225.

MILICICH, M. J., AND P. J. DOHERTY. 1994. Larval supply of coral reef fish populations: Magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. Mar. Ecol. Prog. Ser. **110:** 121–134.

———, M. G. MEEKAN, AND P. J. DOHERTY. 1992. Larval supply: A good predictor of recruitment of three species of reef fish (Pomocentridae) Mar. Ecol. Prog. Ser. **86:** 153–166.

MILLER, T. J., L. B. CROWDER, J. A. RICE, AND E. A. MARSCHALL. 1988. Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45:** 1657–1670.

OJEDA, F. P., AND J. H. DEARBORN. 1990. Diversity, abundance and spatial distribution of fishes and crustaceans in the rocky subtidal zone of the Gulf of Maine. Fish. Bull. **88:** 403–410.

ÓLAFSSON, E. B., C. H. PETERSON, AND W. G. AMBROSE. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Annu. Rev. **32:** 65–109.

PETERSEN, C. W., R. R. WARNER, S. COHEN, H. C. HESS, AND A. T. SEWELL. 1992. Variable pelagic fertilization success: Implications for mate choice and spatial patterns of mating. Ecology **73:** 391–401.

POTTLE, R. A., AND J. M. GREEN. 1979. Territorial behavior of the north temperate labrid, *Tautogolabrus adspersus.* Can. J. Zool. **57:** 2337–2347.

ROBERTSON, D. R. 1992. Patterns of lunar settlement and early recruitment in Caribbean reef fishes at Panama. Mar. Biol. **114:** 527–537.

ROUGHGARDEN, J, S. D. GAINES, AND H. POSSINGHAM. 1988. Recruitment dynamics in complex life cycles. Science **241:** 1460–1466.

SCHULTZ, E. T., AND R. K. COWEN. 1994. Recruitment of coral-reef fishes to Bermuda: Local retention or long-distance transport? Mar. Ecol. Prog. Ser. **109:** 15–28.

SCOTT, W. B., AND M. G. SCOTT. 1991. Atlantic fishes of Canada. Univ. Toronto.

SISSENWINE, M. P. 1984. Why do fish populations vary? p. 59–94. *In* R. M. May [ed.], Exploitation of marine communities, Springer.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman.

SWEATMAN, H. P. A. 1985. The influence of adults of some coral reef fishes on larval recruitment. Ecol. Monogr. **55:** 469–485.

VICTOR, B. C. 1983. Recruitment and population dynamics of a coral reef fish. Science **219:** 419–420.

———. 1986*a*. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar. Biol. **90:** 317–326.

———. 1986*b*. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. **56:** 145–160.

WILLIAMS, D. McB., S. ENGLISH, AND M. J. MILICICH. 1994. Annual recruitment surveys of coral reef fishes are good indicators of patterns of settlement. Bull. Mar. Sci. **54:** 314–331.

YUND, P. O., S. D. GAINES, AND M. D. BERTNESS. 1991. Cylindrical tube traps for larval sampling. Limnol. Oceanogr. **36:** 1167–1177.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall.

ZARET, T. M. 1980. Predation and freshwater communities. Yale.

*Submitted: 9 September 1994*
*Accepted: 31 October 1995*
*Amended: 18 January 1996*