Dispersal of juveniles and variable recruitment in sessile marine species

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MARINE species commonly have broadly dispersing juveniles called larvae. Their return to the adult populations is highly variable[1-3], often generating large fluctuations in population size[4-6], yet the causes of the variation are poorly understood. Historically, attention has been focused on the roles of variable reproductive output by adults and variable mortality during larval development[7,8]. The limited success of these factors as general explanations prompted a more recent focus on the influence of variable transport of the larvae[9-13]. Here we show that nearly a decade of settlement variation of the barnacle, *Semibalanus balanoides* (L.), closely matched predictions based solely on a transport hypothesis: differences in transport generate recruitment variation by determining whether larvae complete development near a favourable habitat. The irregular nature of coastlines, particularly the presence of bays and estuaries, generates substantial regional variation in coastal transport that may generate correspondingly large variation in recruitment to marine populations.

The prediction that failure of larvae to return to shore is a common cause of variable recruitment in coastal species follows from numerous observations (such as location of fish spawning grounds[11], correlations between recruitment and shifts in wind direction[9,10,12,14,15], behaviour of larvae[16,17]). If the prediction is correct, then settlement ought to vary consistently with variation in transport. With this hypothesis in mind, we focused on a common feature of coastlines that predictably alters patterns of retention, bays. Rates of exchange between bays and nearby coastal waters vary because of differences in tidal amplitude, bay morphology, river input and winds[18]. The magnitude of variation among bays and among years is extensive and should provide strong tests of the significance of larval loss due to offshore transport.

Retention of larvae in bays has been studied for decades, but largely from the perspective of strictly estuarine species that must remain in or return to estuaries to survive[19-21]. The issue is changed substantially if we consider more cosmopolitan species that occur in bays and estuaries but are not restricted to them. For such species, failure to return to estuarine habitats is no longer synonymous with death. Rather, export merely. subjects larvae to the same physical conditions and transport processes as larvae released from coastal habitats. If transport of larvae away from the coastline is a major cause of settlement variation, then the potential retentive characteristics of bays should establish gradients of recruitment for bays versus open coast habitats. Similarly, recruitment rates should track the large variation in retention among years and bays.

To test these predictions we studied the intertidal barnacle, *Semibalanus balanoides,* at coastal and embayed sites in Rhode Island, **USA.** This species is ideally suited to addressing these problems because: (1) it is widely distributed both in bays and

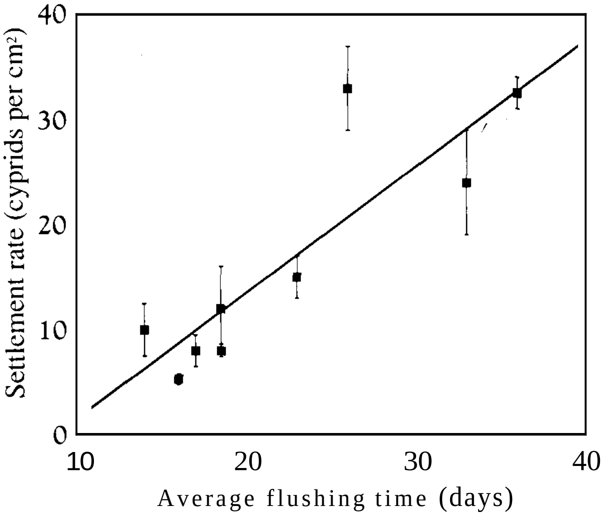

FIG. 1 Correlation between annual shoreline settlement of the barnacle Semibalanus balanoides and the estimated flushing time for Narragansett Bay, Rhode Island. Settlement rates were measured from photographs of 100-cm^2 quadrats ($n=16$ per year) taken at the end of the settlement season (that is they measure the total accumulation of settlers for a given year). Flushing times are estimates for the period January 15 to March 15, the normal interval of larval presence in Narragansett Bay. Error bars are 95% confidence limits. Flushing times are a measure of exchange rates between bay and coastal waters. They can be measured either by releasing a known quantity of material (such as dyes) into the bay and measuring the decline in concentration with time or by following the dynamics of natural constituents of the bay (such as fresh water). The volume of fresh water in a bay can be estimated from its salinity structure, and the source of fresh water is primarily river flow. Assuming that the fresh water content is in a steady state, the flushing time can be expressed simply as the time required for the river flow to equal the volume of fresh water in the bay. We use this latter measure for all quantitative estimates of flushing times. Estimates for Narragansett Bay, RI are based on the empirically derived relationship between fresh water input to the bay and flushing time[27]. River flow data were obtained from the Rhode Island Department of Water Resources.

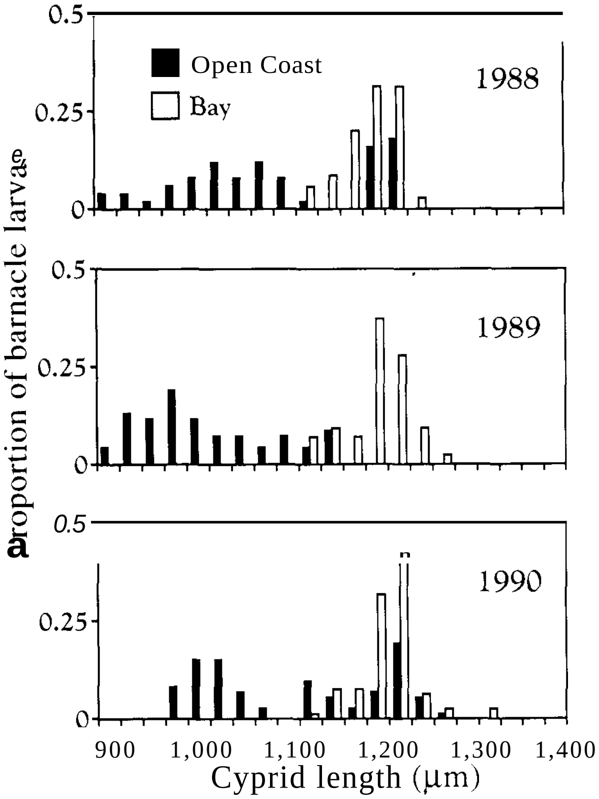

FIG. 2 Size frequency distributions for barnacle larvae collected at bay and coastal sites. Lengths were measured with an ocular micrometer on a dissecting microscope. Larvae were collected in passive tube collectors[24]. Sample sizes ranged from 162 to 200 larvae per site. Error bars are 95% confidence limits. Note that there is little overlap in the size distributions of coastal and bay larvae in 1989, a year with a long flushing time (36 days). In both 1988 and 1990, there is a bimodal distribution of larval sizes with substantial numbers of 'bay'-size larvae at coastal sites. Each of these two years had short bay flushing times (17 and 16 days, respectively).

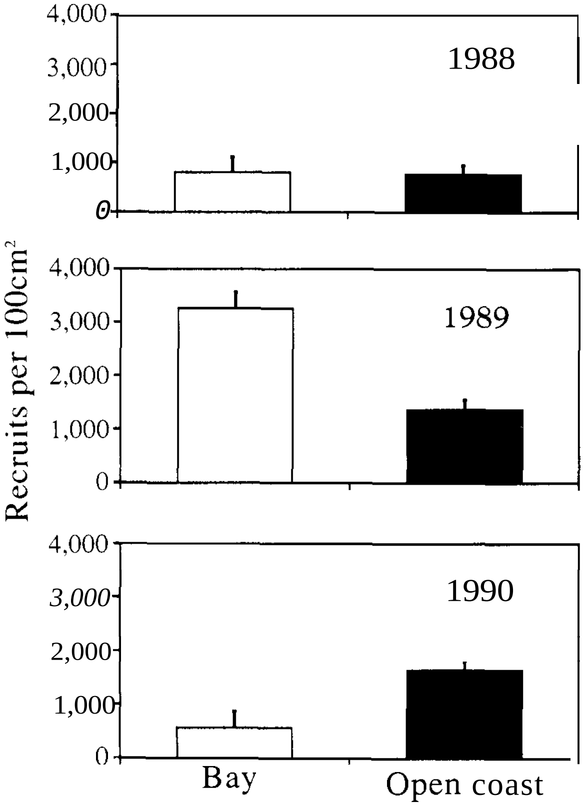

FIG. 3 Settlement rates of *Semibalanus balanoides* at bay and coastal sites. Settlement was monitored in 100-cm^2 quadrats ($n = 16$ per site per year) at the end of the settlement season (generally mid March). Error bars are 95% confidence limits.

in exposed coastal habitats[14,22,23]; (2) it has a short reproductive season and a single larval release, which simplifies the problems of measuring transport patterns; and (3) its larvae are accurately sampled by a new collector that integrates abundances over the entire settlement season, which makes it feasible to sample larvae at many widely separated sites simultaneously[24,25].

To examine the impact of larval retention on temporal variation in recruitment, we compiled a 9-year record (1982–1990) of settlement variation in Narragansett Bay, Rhode Island. The average flushing time of this bay varies substantially in response to variation in riverine input[26,27]. There was no correlation between the interannual variation in settlement and stocks of reproductive adults. The correspondence between settlement rates and flushing times, however, is striking (Fig. 1, $R^2 = 0.77$, $P < 0.001$). Most of the variation in nearly a decade of settlement is explained by a simple measure of the likelihood of export from the bay.

As with any conclusions based on correlation, this strong connection between settlement variation and residence times could be caused by other covarying factors. For example, here the pattern could reflect higher larval mortality in years with larger riverine inputs (and lower salinities) rather than greater losses by transport. Separating these two potential causes would typically be difficult because both larval mortality and transport would leave the same signature, declining larval densities in the bay. The solution lies in finding a marker that identifies larvae that are flushed from the bay.

Fortuitously, S. *balanoides* provides such a marker of origin, larval size. Larvae that develop within Narragansett Bay are substantially larger than larvae that develop over the continental shelf. For 3 years, we monitored larval abundance and size distributions in the water column. In a year with a long flushing time, such as 1989, there is little overlap in the size distribution of larvae collected in the bay compared with those from the open coast (Fig. 2). In years with short flushing times (1988 and 1990), there is a bimodal size distribution of larvae outside the bay. The large number of 'bay'-size larvae at coastal sites strongly supports the conclusion that the correlation of Fig. 1 is a consequence of losses due to transport. Genetic comparison of the coastal and bay larval pools further substantiate the causal role of larval transport. Transplant experiments suggest there is substantial genetic divergence of bay and coastal larval pools in retentive years, yet no divergence in years with greater transport[28].

Further support for the importance of retention comes from comparisons of open coast and embayed sites (Fig. 3). With long flushing times (1989), recruitment of barnacles within Narragansett Bay is significantly higher than recruitment to nearby open coast sites. In constrast, with shorter flushing times (1988 and 1990) recruitment in the bay is reduced to levels as low as or lower than those at the open coast.

The ability of retention alone to account for order of magnitude variation in settlement rates of this species poses the question of generality. Is the failure to reach favourable habitat a common source of fluctuations for other species or for other locations where patterns of local retention vary? The dynamics of herring in the North Sea[13] as well as hake' and barnacles[12] in the North Pacific all correlate with changes in transport and suggest that variable dispersal may indeed be a widespread source of recruitment variation. Beyond the obvious commercial benefits of knowing the causes of recruitment variation, the finding of a dominant role for variable dispersal would have important implications for the population biology of marine species. Variable transport, unlike variable reproductive output and variable mortality, implies that fluctuations in recruitment will covary with fluctuations in the exchange of individuals among sites. As a result, unravelling the causes of recruitment variation may be crucial to understanding the patterns of gene flow, genetic divergence and evolutionary dynamics of marine species. ☐

Received 17 July: accepted 19 October 1992

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ACKNOWLEDGEMENTS We thank D Bermudez. E Sanford, E. Stephens and P. Yund for field assistance and S. Hawkins for comments on the manuscript This work was supported by the National Science Foundation and a Brown University Research Support Grant to S D.G