Levin, L. A. 1983. Drift tube studies of bay-ocean water exchange and implications for larval dispersal. Estuaries **6:** 364–371.

Meadows, P. S., and J. I. Campbell. 1972. Habitat selection by aquatic invertebrates. Adv. Mar. Biol. **10:** 271–382.

Oliver, J. S. 1979. Processes affecting the organization of marine soft-bottom communities in Monterey Bay, California and McMurdo Sound, Antarctica. Ph.D. thesis, Univ. Calif., San Diego. 300 p.

Palmer, M. A., and R. R. Brandt. 1981. Tidal variation in sediment densities of marine benthic copepods. Mar. Ecol. Prog. Ser. **4:** 207–212.

Sanders, H. L., and others. 1980. Anatomy of an oil spill: Long-term effects from the grounding of the barge *Florida* off West Falmouth, Massachusetts. J. Mar. Res. **38:** 265–380.

Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biol. Bull. **140:** 284–322.

———. 1974. Biological interactions determining larval settlement of marine invertebrates. Thalassia Jugosl. **10:** 263–296.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill.

Strathmann, R. R. 1978. Larval settlement in echinoderms, p. 235–245. *In* F. S. Chia and M. E. Rice [eds.], Settlement and metamorphosis of marine invertebrate larvae. Elsevier/North-Holland.

Williams, J. G. 1980. The influence of adults on the settlement of spat of the clams, *Tapes japonica.* J. Mar. Res. **38:** 729–741.

Wilson, D. P. 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornia* Savigny. Ann. Inst. Oceanogr. (Monaco) **27:** 49–156.

———. 1977. The distribution, development and settlement of the sabellarian polychaete *Lygdamis muratus* (Allen) near Plymouth. J. Mar. Biol. Assoc. U.K. **57:** 761–792.

Submitted: 18 July 1983
Accepted: 9 April 1984

Limnol. Oceanogr., 29(5), 1984, 1116–1119

Coral reef fish larvae: Patch size estimation and mixing in the plankton[1]

Abstract—The daily pattern of settlement of larvae of the bluehead wrasse, *Thalassoma bifasciatum,* onto a number of coral reefs was reconstructed with the daily otolith increment aging technique. Larvae settled simultaneously onto reefs within an area of about 1,000 km². The planktonic patch size of bluehead wrasse larvae is inferred to be at least 46 km wide. Larvae settling onto a reef at the same time were not the same age, indicating that planktonic dispersal results in mixing of cohorts of larvae.

It is notoriously difficult to directly measure the distribution and abundance of planktonic fish larvae, especially of species that are not particularly numerous. Unfortunately, most coral reef fish larvae fall into that category and, as a result, very little is known about their ecology. Around Hawaii the larvae of reef species with nonpelagic eggs are found close to shore while those with pelagic eggs are found offshore (Leis and Miller 1976). More precise information has not yet been obtained by direct sampling methods. It is, however, possible to extract detailed information about processes occurring in the plankton from individuals that have already settled by the use of the daily otolith increment technique. This aging method provides extremely precise estimates of the duration of the planktonic larval period and the date of settlement for any settled individual (Victor 1982).

Bluehead wrasse larvae settle in brief and sporadic episodes that have a major impact on the future population composition and size (Victor 1983*a*), but the question of what is controlling the timing and magnitude of these settlement peaks remains unresolved. Since planktonic organisms usually occur in patches (Haury et al. 1978), it may be that these episodes of settlement are the result of occasional dense patches of larvae passing over reefs. If bluehead wrasse larvae do occur in patches it would be possible to infer the planktonic patch size by documenting the concordance on a geographical scale of specific settlement peaks. In other words, if a patch of competent bluehead wrasse larvae moved inshore and settled on the reefs that they encountered, one would expect to see a peak of settlement on that particular day on only those reefs within the path of the patch. If the reefs are arrayed broadside to the prevailing current, the linear extent of reefs encountered would be a measure of the size of the patch. This approach presumes that peaks of settlement reflect peaks of availability of larvae in the plankton. Preliminary evidence (Victor in prep.) does indicate that in the San Blas Islands of Panama peaks of bluehead wrasse settlement closely correspond to peaks of planktonic fish larval abundance and diversity at a nightlight sampling station.

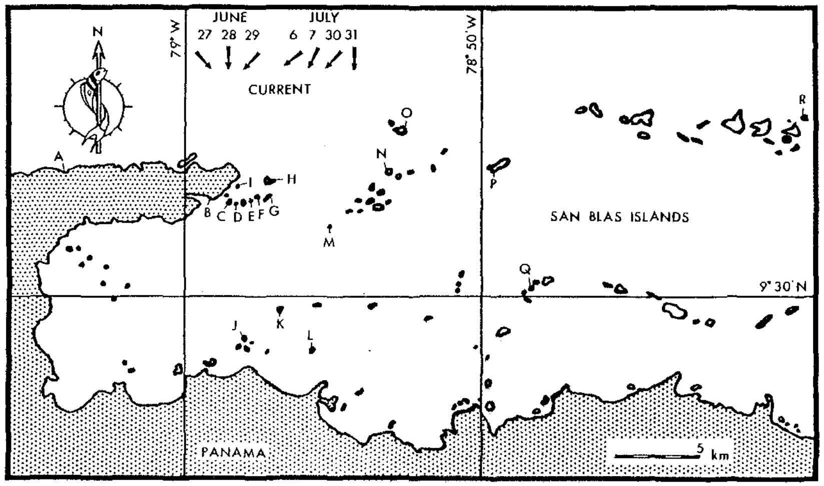

Fig. 1. Map of the San Blas Islands showing the position of the patch reefs on which bluehead wrasses were sampled. The current direction on days of peak settlement was measured near site I. The prevailing current in the area is from due north. The island between sites B and C is "Pico Feo where Fidel was born." A—Puerto Geladi; B—Ulugsukun; C—Guigalatupo; D—Taintupo; E—Ukubtupo; F—Wichubhuala; G—Aguadargana; H—Porvenir; I—Punta San Blas; J—Carti; K—Achuertupo; L—Naibetupo; M—Cayo Gallo; N—Helmet; O—Chichime; P—Masargantupo; Q—Salar; R—Holandes.

I used this method to estimate the patch size of bluehead wrasse larvae settling in the San Blas Islands, an archipelago of reefs extending along the Caribbean coast of Panama. I collected a sample of juvenile bluehead wrasses from 18 patch reefs in mid-1981 (Fig. 1). On each reef visited, I collected every juvenile I encountered during a several-hour survey. I calculated the date of settlement for each individual by subtracting the number of daily increments between the mark corresponding to settlement and the edge of the otolith from the date of capture (Victor 1982, 1983*b*). I also calculated the number of days each one had spent as a planktonic larva (the number of daily increments between the center and the settlement mark plus two: Victor 1982).

Most juvenile bluehead wrasses, 88% of the 654 captured, had settled during the 2 weeks around the new moon (Fig. 2). The largest peak of settlement occurred on 6 July, 5 days after the new moon, when 20% of all the juveniles captured had settled. The second largest peak of settlement, 12% of the total, took place on 29 June, 2 days before the new moon, and the peak the next month, 5% of the total, occurred on the night after the new moon. Fewer than 1% of the total settled during the week around the full moon.

---

[1] Supported by NSF grant DEB 81-09133 to Robert R. Warner.

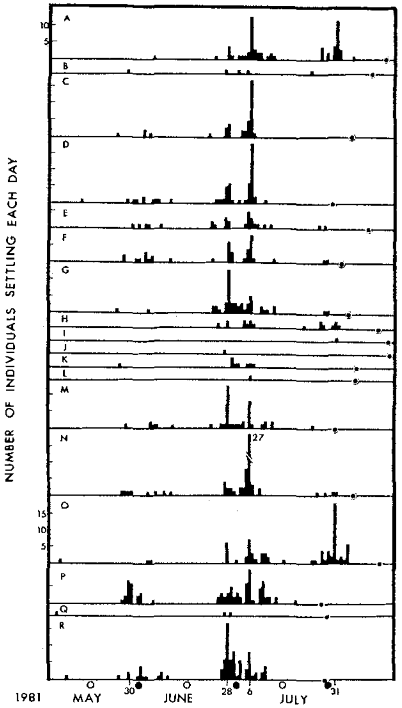

Fig. 2. The daily pattern of settlement of bluehead wrasses onto 18 reefs in the San Blas Islands. The letters correspond to the reefs in Fig. 1. Double circles—the day of collection; solid circles—new moon; open circles—full moon.

Recruitment was high during the June–July lunar month, permitting a detailed comparison of the daily settlement pattern between reefs. I did a three-way analysis of variance on the data in Fig. 2 (excluding settlement after 15 July). The effects of the date and the reef on the number of individuals settling per day were tested (the sample size for each reef was also tested to remove the variance accounted for by the unequal sample sizes from different reefs). The date had a highly significant effect on numbers settling per day ($P < 0.0001$), while the reef had no significant effect on the number of individuals settling per day ($P > 0.44$). On most reefs examined, the two highest peaks of settlement that month were on 29 June and 6 July, although which one was higher varied between reefs. With a single exception, all other reefs experienced peak settlement within a day of these two dates. For the exception only the second highest peak was on some other date. Since there is some small error associated with counting daily increments, it seems likely that larval recruits were settling simultaneously onto all of the reefs (an area 46 × 16 km, or 736 km^2). Since the prevailing current comes from the north in this area of Panama, it can therefore be inferred that the patch width of bluehead wrasse larvae was at least 46 km.

Newly settled bluehead wrasses probably metamorphose in hiding for their first 5 days on the reef, as has been demonstrated for another coral reef wrasse, the slippery dick, *Halichoeres bivittatus* (Victor 1983*b*). Therefore I sampled only some of the reefs late enough to capture juveniles that settled during the July–August lunar peak of settlement (reefs ABEHIJKLNO). During this period peak settlement occurred on 30 and 31 July on most of the reefs with large samples (i.e. not on reefs BEJKL). Since the easternmost reefs (PQR) were not sampled late enough to include this settlement, the minimum patch width estimate for this settlement is only 20 km.

Since peaks of settlement tended to occur on all reefs simultaneously, the most parsimonious explanation would be that bluehead wrasse larvae occur in patches at least as wide as the area surveyed. Smaller patches of larvae could conceivably have moved through the area and happened to pass over all the reefs each time. However, as the prospective patch size gets smaller, this coincidence becomes progressively more unlikely. Since the reefs surveyed are arrayed broadside to both the prevailing onshore current in the area and the current measured during these settlement peaks (Fig. 1), a large patch size is much more likely. The patch of larvae moving in on a particular day was internally heterogeneous, since the magnitude of settlement peaks was not consistent between nearby reefs; for example, reef G received its largest settlement on 29 June and its second largest on 6 July, which was less than half the size of the 29 June peak, while reef D, <1 km away, received its largest settlement on 6 July and its second largest on 29 June, and the 29 June peak was only a third the size of the 6 July peak.

It is possible that rather than being passively delivered to the reef by circulating water masses, bluehead wrasse larvae are able to choose actively when to move inshore, either by swimming or by maneuvering themselves into favorable onshore currents. If this is true, the cues for such behavior must operate over an area of at least the size surveyed. This would suggest a different form of patch, as would the possibility of passive delivery by a front rather than a patch (for example by episodic internal wave trains: Shanks 1983), but both of these phenomena would still involve the simultaneous presence of larvae on a front at least as wide as the area surveyed. There is some lunar influence either on these cues or on passive delivery of patches of larvae, for the likelihood of any settlement during the week around full moon was very low. It is not, however, under precise celestial control, as days of settlement did not consistently fall on certain days of the lunar month. Gross weather and water conditions did not appear to trigger settlements, since peak settlements occurred on both clear and rainy days and generally at normal turbidity readings.

The bluehead wrasse larvae settling on any particular day were not of the same age. The variance in age for those larvae settling on a single day onto a single reef was not significantly different from the total variance known for the species [samples with settlement of more than 10 individuals onto a single reef on a single day vs. pooled sample; nine F-tests, only one significant ($P < 0.05$), range in age = 37–72 days]. Patches of larvae are therefore made up of many separate cohorts of individuals spawned over a number of weeks that somehow aggregate by active or passive means before settlement. As a result, the juveniles that settle together are probably not closely related.

This is the first demonstration that planktonic dispersion of eggs does indeed mix cohorts of larvae before settlement and has important ecological ramifications. If larvae are settling simultaneously over very large areas, then the cues for settlement cannot be localized to a single reef. The notion that individuals settle from a pool of superabundant larvae onto reefs in response to local changes in the supply of food or space (Smith and Tyler 1973; Sale 1978) is therefore inconsistent with my findings.

Benjamin C. Victor

Department of Biological Sciences
and Marine Science Institute
University of California
Santa Barbara 93106

References

Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions, p. 277–327. *In* J. H. Steele [ed.], Spatial patterns in plankton communities. Plenum.

Leis, J. M., and J. M. Miller. 1976. Offshore distributional patterns of Hawaiian fish larvae. Mar. Biol. **36:** 359–368.

Sale, P. F. 1978. Coexistence of coral reef fishes—a lottery for living space. Environ. Biol. Fishes **3:** 85–102.

Shanks, A. L. 1983. A mechanism for the onshore migration of crab larvae. Mar. Ecol. Prog. Ser. **13:** 311–315.

Smith, C. L., and J. C. Tyler. 1973. Population ecology of a Bahamian suprabenthic shore fish assemblage. Am. Mus. Novit. 2572. 38 p.

Victor, B. C. 1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. **71:** 203–208.

———. 1983*a*. Recruitment and population dynamics of a coral reef fish. Science **219:** 419–420.

———. 1983*b*. Settlement and larval metamorphosis produce distinct marks on the otoliths of the slippery dick, *Halichoeres bivittatus*, p. 47–52. *In* The ecology of deep and shallow coral reefs. Symp. Ser. Undersea Res., v. 1. Office of Undersea Research, NOAA.

Submitted: 27 October 1983
Accepted: 30 March 1984