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Extreme Variation in Settlement of the Caribbean Triggerfish *Balistes vetula* in Panama

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In Spring 1985 a mass settlement of pelagic juveniles of the triggerfish *Balistes vetula* occurred in the eastern half of the southwest Caribbean, but not elsewhere in the tropical western Atlantic. This distribution of recruitment is correlated with major surface water currents: the southwest Caribbean is partly isolated from the rest of the Caribbean and has separate eastern and western current eddies. Settlers were 4.9–7.0 cm long, and estimated to be 66–86 d old. At Punta de San Blas (Panama) the abundance of settlers that arrived in 1985 was at least 50–100 times greater than in any other year since at least 1979. The mass settlement produced a 1.5 fold increase in the adult population at that site, but *B. vetula* adults remained uncommon (at about 5% the density which can occur elsewhere).

VARIATION in settlement of planktonic juveniles of reef fishes often is thought to have a more dominant role than post-settlement processes in determining the abundances of adults (Williams, 1980; Doherty, 1983; Cowen, 1985; Munro and Williams, 1985; Victor, 1986a). Moderate annual variation in the magnitude of larval settlement (i.e., <one order of magnitude) is known for various species of coral reef fishes (Williams and Sale, 1981; Williams, 1983; Sale et al., 1984). The frequency of occurrence of more extreme variation in settlement and its effects on reef fish populations remains to be determined. Although unusual mass-settlement events can establish a large population of adults of a previously rare species (Pillai et al., 1983), recruits that settle in such events may experience heavy mortality, due to starvation, soon after they arrive (Kami and Ikehara, 1978; Murakami-Walker, 1985). Here I document an unusual mass settlement by pelagic juveniles of the Caribbean reef balistid, *Balistes vetula,* that occurred in Panama in 1985, and discuss its effect on the adult population at one site in Panama.

Materials and Methods

Balistes vetula is widely distributed throughout the tropical Atlantic (Randall, 1983). Although it is not clear whether this fish produces demersal or pelagic eggs (Thresher, 1984), development includes a pelagic juvenile phase (Aiken, 1975). My observations on growth of members of the mass-settlement cohort indicate that maturity (about 17.5 cm fork length (FL), Aiken, 1975) can occur within a year after settlement. Randall's (1962) data indicate that maximum size (56 cm FL Randall 1983) could be achieved at about 8 yr.

I estimated the age of newly settled *B. vetula* by analyzing growth increments in the sagittal otoliths of fish that were collected on the day of their arrival on a small isolated patch reef. I used methods of Brothers (1984), Campana and Neilsen (1985) and Victor (1986b). I took the

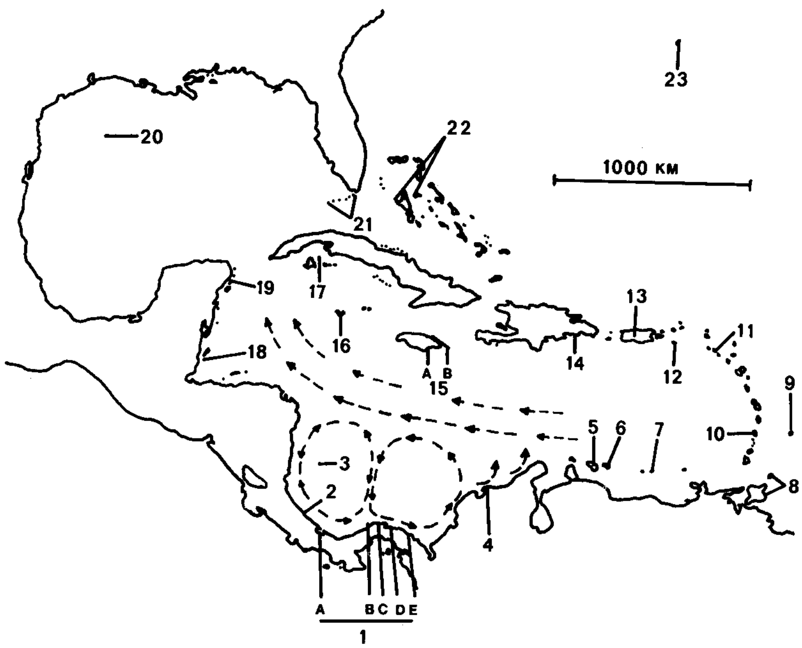

Fig. 1. Caribbean sites from which information was obtained on settlement by *Balistes vetula* in early 1985. 1. Panama (A—Bocas del Toro, B—Galeta, C—Isla Grande, D—Punta de San Blas, E—Achutupu); 2. Cahuita, Costa Rica; 3. Isla San Andres (Colombia); 4. Santa Marta (Colombia); 5. Curacao; 6. Bonaire; 7. Islas Los Roques (Venezuela); 8. Trinidad and Tobago; 9. Barbados; 10. St. Lucia; 11. St. Kitts; 12. St. Croix; 13. Puerto Rico; 14. Bahia Las Calderas (Dominican Republic); 15. Jamaica (A—Kingston and B—Discovery Bay); 16. Grand Cayman; 17. Golfo de Batabanó (Cuba); 18. Carrie Bow Cay (Belize); 19. Puerto Morales (Mexico); 20. Flower Gardens Bank; 21. Florida Keys, (Florida); 22. Nassau and Andros (Bahamas); 23. Bermuda. Dashed lines = major water currents in the southwest Caribbean, after Lessios et al., 1984.

mean of three counts of the numbers of increments in each sagitta of each fish to be the increment-age of that fish.

I have monitored settlement of *B. vetula* juveniles quantitatively at the Punta de San Blas (Figs. 1–2; Robertson, 1987) since 1982, by monthly counts of settlers in permanent backreef plots on five patch reefs. Nonquantitative observations in those plots began in late 1978, during monthly counts of settlers of other reef fishes.

Immediately after the mass settlement of *B. vetula* on Punta de San Blas (in late April) I visited 17 sites within a 12 km radius of Punta de San Blas (Fig. 2) and estimated densities of recently settled fish in settlement habitat: shallow back reef (1–3 m depth) composed of a mixture of sand, sparse seagrass and a few small coral growths on a rock base that contained numerous holes in which the triggerfish took shelter.

Subsequently I visited four other localities along the coast of Panama: Galeta and Buenaventura islands, between the Panama Canal and Punta de San Blas, in July 1985; 22 sites scattered over a 275 km^2 area at Bocas del Toro in western Panama, in Sept. 1985; and nine sites along 35 km of coast at Achutupu, in the eastern San Blas, in Oct. 1985 (Fig. 1). I also questioned indigenous, subsistence fisherman in the Achutupu area about the abundance of small *B. vetula,* which is a food fish. E. Weil provided further information on the abundance of *B. vetula* juveniles on about a dozen reef areas around Galeta and the Isla Grande area (between Punta de San Blas and Isla Buenaventura) in July 1985. He re-examined these sites in July of 1986 and 1987.

I also visited two localities outside Panama in the southwest Caribbean (four sites at Isla San Andres in July 1985, and two sites 15 km apart at Santa Marta, Colombia in Aug. 1985, Fig. 1), and two in the northwestern Caribbean (34 sites over a 450 km^2 area at Grand Cayman Island,

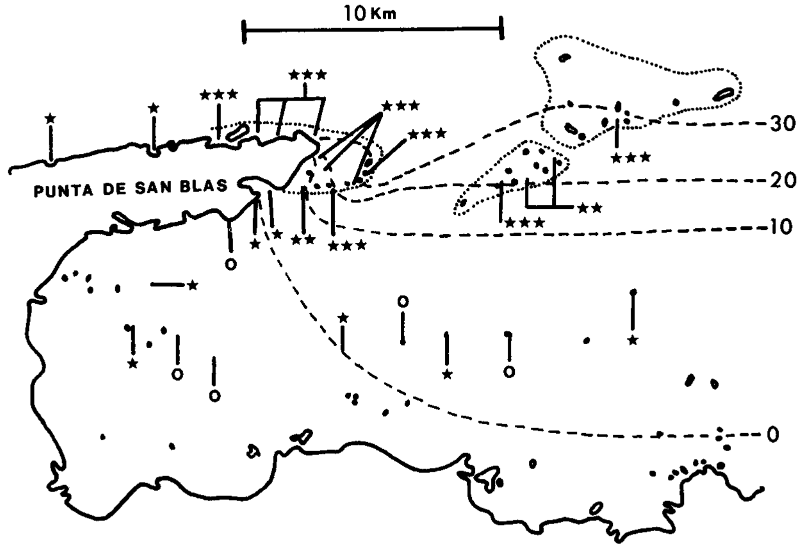

Fig. 2. The Punta de San Blas Study Area: dashed lines represent isopleths of densities of juveniles of a wrasse during 1983 (after Victor, 1986a). Densities of *Balistes vetula* settlers: 0 = not seen, * < 5/ha, ** ≈ 25–50/ha, *** ≫ 50/ha.

and 25 sites over a 60 km² area at Carrie Bow Cay, Belize, Fig. 1) in Aug. 1985. In late 1985 I requested information from biologists at other localities scattered around the tropical western Atlantic, using a questionnaire which included information on the size and habitat preference of *B. vetula* settlers.

Prior to the mass settlement no censuses of adults on Punta San Blas were made. However, since 1978 I have been making monthly visits to that site, monitoring larval settlement and fish populations on a variety of reefs scattered throughout a 15 km² area (Robertson, 1987). I began regular visits to Punta de San Blas reefs in 1974 and other reef fish biologists, students and research assistants have been working at that site since then. During May–Aug. 1985 adults were censused on 134 patch reefs (total ≈ 100 ha of reef), which included the full range of reef types available there. These reefs were recensused during June–Nov. 1986 to determine the effect of the mass settlement on the adult population.

Results

Based on my observations and those of biologists at 22 localities in the Caribbean outside Panama, *B. vetula* settled in unusually large numbers only along the eastern coast of Panama, at Santa Marta (Colombia) and at Discovery Bay (Jamaica) (Fig. 1). However, settlement at both the latter places seems to have been more localized than in Panama (see below). Although I saw many *B. vetula* juveniles in the Santa Marta harbor in Aug. 1985 I found none 15 km east, at Bahia Chengue. Resident biologists at INVEMAR in Santa Marta considered the 1985 recruitment at Santa Marta unusually large (A. Acero and J. Garzon, pers. comm.). The settlers arrived in Santa Marta harbor in the second week of April (Piedad Victoria, pers. comm.), i.e., immediately after the settlement in Panama. Although G. Bruno (pers. comm.) found small juveniles in one part of Discovery Bay (Jamaica) in May 1985, there is no evidence of an unusual settlement elsewhere on the coast of Jamaica (K. A. Aiken, pers. comm.).

On Punta de San Blas the mass settlement began in the last week of March, peaked at the start of April, and extended till mid-April. The number of settlers counted in the monitored plots in 1985 was over 50 times greater than numbers counted in any other year since 1982 (Table 1). Numbers of small *B. vetula* observed in those plots during 1979–81 were similar to those seen in years other than 1985. However, the 1985 counts probably were a substantial underestimate. I saw many settlers fighting for access to holes, which sometimes were crammed full of fish, and many fish were wounded and

TABLE 1. ANNUAL AND MONTHLY VARIATION IN SETTLEMENT BY *Balistes vetula* AT PUNTA DE SAN BLAS.

	No. of settlers counted each month in five permanent plots												
Year	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
1982	ND	0	0	2	1	0	0	0	0	0	0	0	3
1983	0	0	1	3	1	0	0	0	0	0	0	0	5
1984	0	0	0	0	0	0	3	2	0	0	0	0	5
1985	0	0	130	105	9	16	0	0	0	0	0	0	260
1986	1	0	0	0	0	0	0	0	0	0	0	0	1
1987	0	0	0	2	1	0	0	0	0	0	0	0	3

ND = no data.

debilitated from such fights. The density of *B. vetula* juveniles observed in the monitored plots during the mass settlement ranged up to ≈800 individuals/ha, but may have been much higher, initially, since I collected 65 fish from a 63 m^2 reef on the day of their arrival, i.e., a density of 10,000/ha.

Settlement by 24 other species (of seven families) of reef fishes that were concurrently being monitored was not unusually large in March or April of 1985 (D. R. Robertson, unpubl.). Thus the 1985 mass settlement of *B. vetula* constituted a singular event for both the species and the fish community.

Fish settled in high density (i.e., ≫50/ha) on most of the shallow reefs on Punta de San Blas, and on offshore reefs along at least 15 km of the surrounding coastline. However, reefs to the south and inshore of this line had very few settlers (Fig. 2). Small juveniles of *B. vetula* were observed in densities ≫50/ha at all sites that contained settlement habitat along the Panama coast between the Panama Canal and Punta de San Blas (Fig. 1). However, juveniles were rare (≪5/ha) at Bocas del Toro in western Panama (Fig. 1). At Achutupu, about 110 km east of Punta de San Blas, I found moderate numbers (≈25/ha) of juveniles at several sites. However, poor weather and underwater visibility made surveys difficult, and I probably underestimated densities there. Local fishermen at Achutupu said that they had netted thousands of *B. vetula* about 5 cm long in shallow areas about the time of the mass settlement on Punta de San Blas. Local fisherman at Isla de Pinos (35 km east of Achutupu) volunteered that they had been catching unusually large numbers of small individuals in mid-1985. Thus, the *B. vetula* mass settlement extended along 225–260 km of the eastern coast of Panama.

During his visits to reefs around Galeta and Isla Grande in 1986 and 1987, E. Weil (pers. comm.) saw juvenile *B. vetula* only rarely. I also found them to be rare on reefs on San Blas point and on reefs to the east of that point (Fig. 2) in mid-1987. Thus settlement patterns on Punta de San Blas seem to be representative of what occurs along the coast between Galeta and Punta de San Blas.

I found many adults of *B. vetula* around Carrie Bow Cay, Belize (Fig. 2), in Aug. 1985 (average 11.3/ha in 20 ha of habitat between 0.5–20 m depth). However, juvenile densities averaged only 1.5/ha in 10.6 ha of shallow backreef habitat there, when the densities of juveniles at settlement sites at Punta de San Blas were still 25–50/ha (pers. obs.). Recruitment of *B. vetula* at Carrie Bow Cay during early 1985 does not seem to have been unusually large (S. M. Lewis and P. C. Wainwright, pers. comm.).

The fish I collected on the day of their arrival on a small isolated patch reef in 1985 ranged from 4.9–7.0 cm FL ($\bar{x} = 5.7$, standard deviation [SD] = 0.4, n = 72). Since six juveniles removed from the stomach of a 46 cm FL *Coryphaena hippuris*, collected 15 km from Santa Marta (Colombia) on 17 April 1985 by J. Garzon and A. Acero, were about this size (5.6–5.9 cm FL), it seems likely that the fish I collected were newly settled.

The number of growth increments in the sagittae of 70 newly settled juveniles ranged from 63–83 ($\bar{x} = 75$, SD = 4.7). The otoliths of eight post-settlement juveniles (6.6–9.2 cm TL) collected 5–8 wk after the mass settlement had 97–124 increments, i.e., numbers within a range expected if fish produced 1 increment/day and had 63–83 increments when they settled in early April. Consequently, if daily increment formation began several days after hatching (Jones, 1986) settlers would have been ≈66–86 d old upon arrival.

In 1985 I counted 15 adult *B. vetula* on 134 patch reefs at Punta de San Blas (i.e., 0.15/ha).

In 1986 there were 38 adults on those same reefs (0.38/ha).

Discussion

The 1985 mass settlement of *B. vetula* in San Blas was unusual. At least 50–100 times as many juveniles arrived during a single month as settled in any other year of a 9 yr period and the level of settlement during 1985 was over 200 times greater than during the worst year recorded. Mass settlement extended over 225–260 km of the Panama coastline and perhaps 450 km further eastwards at Santa Marta (Colombia). Although an unusually successful settlement of a central Pacific monacanthid may have occurred on a larger scale (i.e., 1500 km—Murakami-Walker, 1985) the *B. vetula* settlement event in Panama in 1985 covered a considerably larger area than recorded in other studies of other tropical reef fishes (Victor, 1984). Cowen (1985) recorded unusually successful recruitment of several temperate reef fishes along 400 km of the California coast, associated with current anomalies during the 1982–83 El Niño event. If major settlement events of *B. vetula* normally occur on such a large spatial scale then genetically well integrated populations of that species may cover many thousands of square kilometers.

My data on the mass settlement of *B. vetula* are consistent with the idea that spatial patterns of settlement of reef fishes are determined by water currents that deliver settlers (Eckert, 1984; Cowen, 1985; Victor, 1986a). First, the offshore-onshore gradient in the density of *B. vetula* settlers at Punta de San Blas (Fig. 2) was very similar to that described by Victor (1986a) for juveniles of a wrasse, and attributed by him to onshore currents encountering and depositing settlers on offshore reefs before onshore reefs. Second, the southwest Caribbean is partly isolated from the remainder of that region, and contains two large separate current eddies (Fig. 1). The mass settlement of *B. vetula* was restricted to and occurred along a large section of the coast influenced by the eastern eddy. However, because no other reef fish was observed to recruit in unusually large numbers during the 1985 *B. vetula* settlement event, it is difficult to attribute the cause of this *B. vetula* settlement event simply to (anomalous?) currents responsible for the final delivery of settlers (Cowen, 1985).

The degree of annual variation in settlement of *B. vetula* at Punta de San Blas is considerably greater than what has been recorded for most other tropical reef fishes. In response to the 50–100 fold increase in settlement during 1985 the local adult *B. vetula* population on Punta de San Blas increased by a factor of only 1.5, and the density of adults increased to only 5% of that which can occur in similar shallow habitat elsewhere in the Caribbean: average density < 0.5/ha at Punta de San Blas in 1986 vs ≈11/ha at Carrie Bow Cay, Belize, in 1985. Even allowing for recruitment over the preceding decade having contributed to the 1985 adult population at Punta de San Blas, the population increase in 1986 was disproportionately very small. This result has two implications. First, it means that assessing the degree of annual variation in juvenile recruitment by using the age structure of a population sampled at one point in time or by counting surviving juveniles at the end of breeding seasons (Jones, 1984; Sales et al., 1984; Cowen, 1985) is problematic. Although years of very low recruitment will be readily detectable, the magnitude of extraordinarily good years may be substantially underestimated. Second, it means that settlement patterns do not govern the sizes of all local populations of *B. vetula* in any simple manner. On the coast of Panama this long-lived species primarily may recruit infrequently in large pulses. The adult population at Punta de San Blas normally may be maintained below the carrying capacity by a combination of low average recruitment and high density-dependent mortality of juveniles during good recruitment years (as a result of competition for shelter or space among newly arrived recruits?). This is not to say that the reefs on Punta de San Blas could support adult populations as dense as occur elsewhere (e.g., Carrie Bow Cay). The poor response to a high level recruitment pulse could reflect the quality of the habitat for adults as well as factors affecting early survival of recruits.

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