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SETTLEMENT AND POPULATION DYNAMICS OF ABUDEFDUF SAXATILIS ON PATCH REEFS IN CARIBBEAN PANAMA

D. ROSS ROBERTSON

Smithsonian Tropical Research Institute
APO Miami 34002-0011 USA

ABSTRACT

Studies of the dynamics of reef fish communities have focused on small, short-lived, highly sentary species on small (< .015 ha) isolated patch reefs. They have concluded that, apart from larval settlement, patch-reef populations are independent, and that very small-scale spatial variation in larval settlement controls community dynamics. To provide a contrast to such studies, I monitored larval settlement and adult populations of a medium-sized, mobile, moderately long-lived planktivorous damselfish, on larger (.08-.45 ha), more isolated (by 20-200 m) patch reefs in a low visibility environment (normally 8-12 m) over 6 y. Patch-reef populations were not independent in terms of their dynamics: planktonic juveniles settled only in reefs that sustained adult populations over 6 y. Change in adult population size was unrelated to settlement on each reef, and there were frequent major migrations of adults between reefs. Both the adult population and settlement varied little (by ≈ 10% annually) on an aggregate of reefs, i.e. on scales that relate to adult mobility (>0.5 km^2) and time to maturity (≈ 1 y).

INTRODUCTION

What processes determine the sizes of local populations of reef fishes and how those populations vary over time? How important are deterministic mechanisms, i.e. resource limitation, intra- and interspecific competition, and partitioning due to specialization? How important are processes which might prevent populations reaching levels at which resources are limiting, reduce the importance of deterministic mechanisms, and keep communities in a non-equilibrial state? These questions have stimulated much field research into the dynamics of reef fish communities over the past decade or so, especially in the South-Western Pacific (Sale and Dybdahl 1975, Sale 1980, Williams & Sale 1981, Doherty 1983, Doherty & Williams in press, Talbot et al. 1978, Russell et al. 1977, Jones 1987), and the Caribbean (Gladfelter et al. 1980, Ogden and Ebersole 1981, Bohnsack 1983, Warner & Chesson 1985, Victor 1986, Shulman and Ogden 1987, Robertson 1988).

In the "independent-mosaic" view, small scale spatial and temporal variation in settlement of planktonic larvae produces fluctuating local populations and, except for larval settlement, local populations (in areas of 1-200 m^2) are closed, i.e. events occurring in one small habitat patch have no real impact on the adult population in another patch. Population "stability" or constancy that is observed on larger spatial scales (i.e. ha or km^2) arises because different local populations change in different ways and a mosaic of their positive and negative numerical changes simply cancel out (Talbot et al. 1978, Sale 1980, Williams 1980, Sale and Steele 1986, and Doherty and Williams in press). Most studies of relationships between settlement and adult populations have been on small, short-lived, sedentary and often territorial species whose larvae settle where their adults live. Many of them also have used very small (1-150 m^2) habitat patches isolated from each other by distances of 10-20 m. Those studies have emphasized the possible effects of high variation in settlement that occurs on various temporal scales (days, months and years) and among habitat patches (Sale and Dybdahl 1978, Williams 1983, Sale and Steele 1986, Sale and Douglas 1984). Studies of non-territorial, less sedentary, longer-lived reef fishes, particularly those which show age/size specific differences in habitat use (c.f. Robertson 1988) are needed for two reasons. First, if the abundances and spatial distributions of juvenile and adult habitats differ, they may affect the abundances and distributions of adults in a complex manner. Second, the effects of temporal variation in settlement on variation in adult population size is likely to be less in longer-lived species than in short-lived ones (Murphy 1968, Chesson 1984, Warner and Hughes, in press).

The objectives of this study were (i) to determine if the "independent mosaic" view is applicable to the population dynamics of a common, mobile, longer-lived Caribbean reef fish, on large discrete, well isolated patch reefs, and (ii) to assess the magnitude of variation in its population size and larval settlement on different temporal and spatial scales, and determine how it varies on scales that are relevant to the dynamics of an independent local population.

I gathered field data aimed at answering the following questions: Is adult abundance (and patterns of change in such) on isolated habitat patches correlated with settlement of larvae? Except for larval settlement, are populations on isolated habitat patches independent, closed units or does between-patch migration influence population size in individual patches? How much between-reef migration of adults is there on different temporal scales? How does larval settlement vary on different spatial and temporal scales?

I consider the spatial scale relevant to the dynamics of an independent population to be set by the lifetime range after settlement. Appropriate temporal scales for such a population would be (a) turn-over time for the adult population, and (b) the time taken for settler to mature, and thus be able to influence the adult population size (Connell and Sousa 1983). Since I did not estimate turn-over time, only the maturational time scale will be considered here.

METHODS

The damselfish Abudefduf saxatilis, which is a common, conspicuous inhabitant of Caribbean coral reefs, is a moderate sized (up to 18 cm total length, TL) schooling, planktivore (Emery 1973). When feeding in midwater, individuals usually remain within about 10 m of the coral bottom, but range many 10s of meters about a large reef, apparently in response to changes in food availability due to shifting water currents (cf. Bray 1981). Maturity (at 10 cm TL) can be reached within 1 y and adults can live at least 5 y (Cummings 1968).

The study area at Punta de San Blas, on the Caribbean coast of Panama consists of a complex of about 250-300 separate coral patch reefs scattered over a shallow (1-15 m deep) 15 km^2 area of sand, macroalgae and seagrasses. The environment is coastal. Water visibility is usually 8-12 m and rarely exceeds 20 m.

Because settlement by A. saxatilis is lunar periodic and minimal around full moon (D.R.R. unpublished data), I censused newly settled juveniles (<1.5 cm total length) once per lunar month (<5 days prior to full moon) at 11 sites between January 1983 and December 1987. These sites were Wichubhuala (W) 13+14, W19, W23, W24, W26, Aguadargana (Ag) 3, Ag-Island, Porvenir (PV) 17+18, PV26, PV27 and a patch of corals on West Barrier (WB)11.

Nine of the 11 sites used for settler censuses (i.e. all except Ag-Island and WB11), are distinct patch reefs that also were used for adult censuses. Adults on those 9 reefs and 1 other (Smithsoniantupo (ST) 1), which ranged in size from 0.08-0.45 ha, were censused annually, in July or August of the years 1982, and 1984-1987. Between July and December 1987 adults were censused monthly on the same 10 reefs censused annually and on 9 other reefs, each of which ranged from 0.02-0.08 ha in size. Those 19 reefs ranged from 20-200 m from their nearest neighboring reef ($\bar{x}$=50m). During each census adults were counted at least twice (until counts were within $\pm$5%), while the observer swam in 9 zig-zag fashion across an entire deep reef, or around the edge of an emergent reef. Annual and monthly censuses were conducted on days with relatively high water visibility.

Adults were censused daily at 14:00 h on PV25 (0.07 ha) for 92 days, beginning September 30, 1987. PV25 is 30 m south of a group of three other reefs. During each census the direction of current flow (from the North or the South) was noted. In addition, the prevailing direction of current in the channel on the west side of ST-Island (950 m from PV25) was noted in the morning and in the afternoon of each census day. Days were divided into three classes (a) North current at PV25 and all day at ST-I; (b) South current at PV25 and all day at SI-Island; (c) mixture of currents at both sites. The relationship between the number of adult A. saxatilis on reef PV25 during each day census, and the direction of current flow was analyzed using ANOVA.

RESULTS

Settlement Patterns

Annual levels of settlement varied considerably among the 9 reefs on which both settlement and adult populations were monitored over 5 y. Five reefs with large amounts of intertidal habitat consistently received settlers every year while 3 that lacked such habitat received none (Fig. 1). Settlers were commonly observed around intertidal rocky fringes of islands and the edges of mangroves as well as in intertidal habitat on patch reefs.

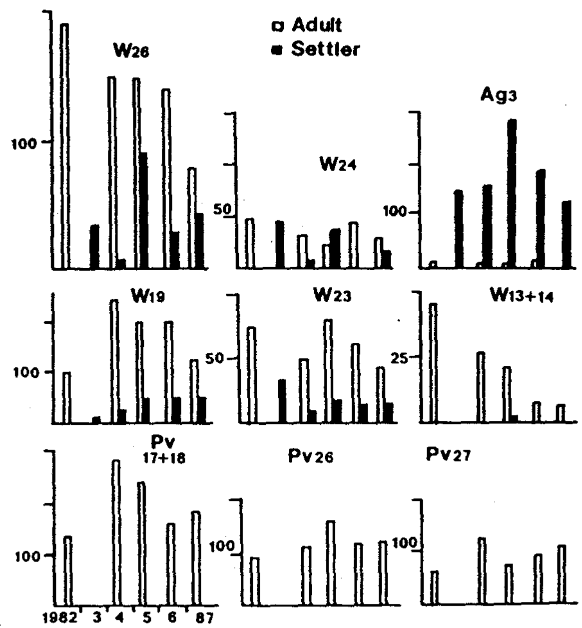

Figure 1: Numbers of A. saxatilis on nine reefs. Open bars: Numbers of adults counted during annual censuses. Solid bars: total number of settlers counted during monthly censuses each year. No adult censuses were made in 1983, and settlers were not counted in 1982. Reefs PV17+18, PV26 and PV27 lacked intertidal habitat, while reefs W24, W26 and Ag3 had an abundance of intertidal habitat.

Settlement was seasonal, although some occurred in all months of the year. Considering those months of the year that provided more than 1/12 of the annual total in one or more years (i.e. April-December), monthly variation in settlement on individual reefs was very high, considerably higher than on all reefs combined. Annual variation in settlement was much less than monthly variation, both on individual reefs and on all reefs combined (Table 1). Settlement varied least on the annual time scale on all reefs combined (Table 1).

Table 1: Magnitude of variation in settlement on different temporal and spatial scales.

Time Scale	Mean (Std.Dev.) Percent deviation from Median: Individual Reefs	(n)	All reefs combined	(n)
Monthly	252(469)	(225)	71.6(67.6)	(45)
Annual	50.6(76.3)	(25)	10.3(9.7)	(5)

There was no correlation between annual settlement and adult numbers initially present on a reef, regardless of whether these were expressed as absolute numbers or as densities: Pearson r=-.40 to -0.49, p>.05 in all cases. That is, settlers did not occur more or less often on reefs depending on the number of adults already in residence on the reefs.

Adult Populations on Patch Reefs

Annual Variation: Mean numbers of adults present per reef per census ranged from 7 to 201, and their densities from 35-875/ha. Numbers counted per census varied among reefs by factors between 1.7 to 12.0. The mean percent deviation from the median (Fig. 1) Schultz 1985) ranged from 13.3 - 62.5% per reef (overall x=29.3%). The total population (all reefs combined) varied much less than populations on individual reefs - by 1.3 fold over all years, and by a mean of 9.1%.

Monthly Variation: The 19 reefs had mean populations of 1-195 fish (overall x=63). The mean percent deviation in numbers of fish per reef ranged from 6-150% among reefs (overall x=33%). Monthly variation in population size among the 19 reefs was not different from annual variation on 10 of them (Median values = 17 and 24% respectively, Mann Whitney U= 136.5, p>.05). Similarly, on the 10 reefs censused both annually and monthly, monthly variation did not differ from annual variation (medians = 19 and 25% respectively, Wilcoxon Paired Sample T = 12, p>0.05).

Partial correlation analyses detected no relationship between the mean level of monthly variation in population size on a reef and either its mean population size (r = 0.338, p>.05), or its distance from the nearest neighboring reef (r = -0.044, p>.05).

Table 2: Daily censuses of adult *A. saxatilis* on reef PV25 (October-December 1987).

Water Current Direction	Mean (±95%CI) No. Adults	n
From North all day	30.6 ± 4.55	47
Mixed	59.1 ± 14.60	17
From South all day	82.9 ± 10.04	28

Daily Variation: On reef PV25 the daily counts of adults ranged from 3-145 (median = 47). Changes in population size from one day to the next ranged up to 102 fish. The number of fish present was related to water current direction (Table 2). More fish were present on days with a south current than on days with a north current, while intermediate numbers were recorded on days with a mixture of currents.

ANOVA (log transformed data) F (2,89) = 131.7, p<.001. GT2 *a posteriori* comparison of means: all different at p<.05.

Population Size and Change in Relation to Settlement: Reefs with large abundances of adults in 1982 did not receive large numbers of settlers over the subsequent 5 yrs (see section on settlement patterns). There was no correlation between the change in the adult population density on a reef between 1982-1987, and the abundance of settlers that arrived on that reef relative to the number of adults present in 1982 (i.e. X annual number of settlers no. adults censused in 1982: Pearson r = -0.45, p>.05). Three of the reefs retained large adult populations over 6 y but received no settlers, and the reef that received the greatest numbers of settlers maintained a small adult population (Fig. 1).

DISCUSSION

The final size and the pattern of change in size between 1982 and 1987 of adult populations on isolated patch reefs were not related to larval settlement on those reefs over 5 y. Larger, or increasing numbers and densities of adults did not occur on reefs with higher levels of settlement. Some reefs that never had many adults received a continuing abundance of settlers, while others with large, non-decreasing adult populations never received any settlers.

Juveniles settle only in intertidal habitats while adults inhabit deeper water. This size-specific difference in habitat usage, and the migration of adults between reefs, has resulted in adult populations on individual isolated reefs being completely disconnected from settlement patterns on the same reefs.

Individual patch reef populations were in a state of short-term (daily and monthly) flux, with substantial percentages of adults frequently entering and leaving each reef's "populations". On one reef such relocations produced extreme variation in population size from one day to the next - up to 70% of maximum size and <200% of median size on one reef. Intensive study of that reef showed that daily variation was correlated with changes in water current direction, and probably represented migratory responses to short-term changes in the availability of current - borne planktonic food (c.f. Bray 1981). Changes in food-bearing currents, although important, is undoubtedly not the only factor influencing the short term flux in adult numbers on PV25. Reproductive activity would also have been involved since males of *A. saxatilis* guard nests containing demersal eggs for 4-5 days after spawning (Cummings 1968), and spawning activity in the PV25 population was weakly semi-lunar periodic (D.R.R. unpublished). Regardless of whether the degree of population flux observed on PV25 was typical for reefs in the study area, or what balance of factors determined the precise number of adults present at a particular time of a particular day, the data clearly demonstrate the level of flux that can occur in a single reef's population.

Monthly censuses showed that movements of large proportions of populations between reefs were common occurrences. However, the degree of monthly variation in adult populations on individual reefs, due to such migration was not related to either population size or distance between reefs, at least up to 200 m.

Adult populations on individual reefs varied by up to 12 fold over 6 yrs and by an overall average of 29% from year to year. An estimate of annual variation in the size of an independent or closed local population would take into account (a) the distances over which adults must have migrated between reefs, (b) the distributions of settlement habitat and adult habitat in the reef system of San Blas Point, and (c) the monthly flux in population size due to temporary migrations. Based on adult movement the minimum area for an independent population would be 0.5-1 km^2. On the 10 reefs censused both monthly and annually, which are spread over 0.5 km^2, the magnitude of monthly and annual variation (% about the median) in combined adult population size of that aggregate was small (mean = 9%). If a substantial part of that variation was due simply to temporary migration of adults between reefs then the size of that population was remarkably constant over the 6 y period. The potential openness of the population to migration means that many of the same individuals may not have remained in that area from year to the next, and that constant population size could have occurred even with considerable turnover of individuals present.

As has been described in studies of other reef fishes that have promoted the independent-mosaic view of reef fish communities (Williams 1980, Sale and Dybdahl 1978, Sale and Steele 1986, Victor 1986), settlement of A. saxatilis varied greatly on small temporal and spatial scales i.e. monthly settlement on individual patch reefs. However, such small scale variation is irrelevant to the population dynamics of A. saxatilis. Because this species takes about a year to mature (Cummings 1968), and moves hundreds of meters between reefs. The smallest relevant temporal and spatial scales on which to assess how settlement variation may affect an independent local adult population are annual variation on an aggregate of sites in 1 km^2. On that spatial scale annual levels of settlement varied little (mean = 10% about the median, maximum 23%). That level was about the same as annual variation in adult population size on that aggregate.

Although both adult population size on an aggregate of reefs and annual settlement of A. saxatilis into that population are fairly constant, this study provides no insights into what factors regulate the size of that population. In a mobile species that frequently redistributes substantial proportions of a local population in response to short-term variation in the availability of an externally generated food supply, even defining the carrying capacity of a large area would be extremely difficult. Experimental manipulation of such a population to test the importance of various potential limiting factors would be well nigh impossible. If larval recruitment shows more extreme variation over the long-term we may be able to learn whether that constancy of the adult population reflects the constancy of settlement.

This study shows that even on substantially larger patch reefs separated by larger distances (in a relatively low visibility environment) than those used in previous studies, the independent-mosaic hypothesis is untenable for a mobile, schooling fish that is very distinctly a part of the reef fish fauna. Is A. saxatilis in San Blas unusual, or is it typical of a suite of species or of particular localities or ecological situations? Post-settlement relocation probably has little or no impact in the dynamics of local populations of some small, sedentary (and often territorial) Australian reef fishes (Doherty 1983, Aldenhoven 1986, Russell et al. 1974, Williams 1983).

However, at San Blas Point, adults of three moderately mobile, non-territorial herbivorous surgeonfishes relocate between reefs in sufficient numbers to substantially alter the size and species composition of populations on individual reefs (Robertson, 1988). As in A. saxatilis, and some other reef fishes (Choat and Bellwood 1985), those surgeonfishes show size-specific differences in patterns of habitat use that probably contributed to the openness of patch-reef populations. A. saxatilis may lie towards one end of a spectrum of reef fishes which vary greatly in terms of the degree of adult mobility, the propensity to relocate after settlement, the degree of overlap in the habitat requirements of conspecific juveniles and adults and the degree of the temporal and spatial stability of their food resources. However, to assess the limits of the independent-mosaic view on the small spatial scale on which it previously has been applied more studies are needed of a variety of types of reef fishes, sedentary and otherwise, in a variety of localities and under a variety of population densities and degrees of population fragmentation due to habitat patchiness. Particular attention needs to be paid to populations on large reefs that contain continuous mosaics of large patches of different habitats. The bulk of the population of many (most?) species of reef fishes live in such situations, which are likely to favor post-settlement relocation and reduce the potential for the operation of an independent-mosaic (Robertson 1988).

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