Abundances of surgeonfishes on patch-reefs in Caribbean Panamá: due to settlement, or post-settlement events?

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Abstract

I examined whether patterns of settlement of planktonic juveniles determined the size and composition of adult populations of three Caribbean surgeonfishes (*Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*) on six isolated patch-reefs in Panamá. I monitored settlement monthly on six reefs (0.14 to 0.67 ha) for 8 yr (1978–1986), and censused adults on those reefs annually. Year-to-year fluctuations in the absolute and relative abundances of settlers arriving on each reef were not extreme. Densities of adults in 1986 were not correlated with the densities of settlers that arrived between 1979 and 1984. Survival of settlers, although apparently unrelated to the density of adults, was negatively related to the density of settlers per unit of adult habitat (but not per unit of settlement habitat) for each species. Changes in adult populations of each species between 1978 and 1986 were not correlated with the abundance of settlers relative to the initial number of adults. The relative abundances of adults of each species in 1986 did not reflect the relative abundances of settlers (1979–1984); these abundances were due to both spatial variation and interspecific variation in survival. In some cases, relocation of adults between isolated patch-reefs (as much as 100 m from other reefs) substantially altered the size and composition of surgeonfish populations. Thus, either post-settlement mortality or relocation overrode effects of settlement patterns in determining adult abundances on the six reefs. Relocation is important in organizing reef-fish communities and must be further examined, particularly in large habitat mosaics.

Introduction

What determines the densities, relative abundances and spatial distributions of adults of ecologically similar fishes within a small area of a coral reef? The numbers and spa-tial distributions of adults could be controlled by predict-able or random variation in when, where and how many settlers arrive on a reef. Alternatively, post-settlement pro-cesses (competition, disease, predation, relocation) could exert sufficient influence to override effects of settlement patterns. Settlement variation can profoundly affect the age-structure, densities, relative abundances and spatial distributions of some adult reef fishes (Williams 1981, Do-herty 1982, 1983, Munro 1983, Victor 1983, 1986, Cowen 1985, Munro and Williams 1985, Wellington and Victor 1985). However, interactions between residents and arriv-ing settlers can affect the settlement process itself (Shulman et al. 1983, Sweatman 1985) and interspecific interactions between fishes after settlement can also affect their spatial distributions (Ebersole 1985, Robertson and Gaines 1986).

Here I present the results of a field study that was de-signed to test whether settlement patterns or post-settle-ment processes determined the abundances of adults of three ecologically similar, congeneric fishes on large patch reefs. These post-settlement processes included mortality and adult relocation, i.e., a long-term change in the lo-cation of an animal's daily living area, as opposed to tem-porary migrations (e.g. diel feeding, resting or spawning migrations: Johannes 1978, Robertson 1983, Ogden and Quinn 1984). This test involved examining five predictions that derive from the hypothesis that settlement controls patterns of adult abundances.

(1) For each species, the density of adults should corre-late positively with the density of conspecific settlers that produced those adults.

(2) For each species, settler survival to adulthood should be independent of the density of both (i) settlers of all species (separately and combined) and (ii) adults of all species (separately and combined).

(3) Changes in adult populations should correlate posi-tively with the abundance of settlers relative to the number of adults initially present.

(4) If the proportional abundances of adults of different species on reefs do not correlate positively with the pro-

portional abundances of settlers that produced them, the lack of correlation should be due to interspecific differences in settler survival rather than spatial differences in settler survival.

(5) If there is post-settlement relocation of juveniles or adults between reefs, such relocation should have no net effect on either the size or species composition of the total assemblage population on a reef.

This study also tests the validity of extrapolating from studies of the population dynamics of highly sedentary species living on very small, isolated patch-reefs to reef-fish communities in general. Many studies of community dynamics have used patch-reefs as model systems (e.g. Russell et al. 1974, Nolan 1975, Smith and Tyler 1975, Sale and Dybdahl 1978, Sale 1980, Williams 1981, Bohnsack 1983, Doherty 1983, Thresher 1983, Sweatman 1985). Extrapolations from such studies to general community patterns make three major assumptions. First, apart from larval settlement, patch-reefs, and patches in habitat mosaics, are closed systems. Second, large-scale spatial patterns represent the sum of sets of randomly varying, independent events occurring in different patch-reefs on habitat patches in a large habitat mosaic, rather than the sum of sets of compensatory, non-independent events occurring in different patches. Third, patterns observed in highly sedentary species that operate on the spatial microscale are representative of patterns that affect species which operate on large scales, e.g. well beyond the size of small patch-reefs.

Materials and methods

I monitored settlement of the planktonic juveniles of all three Caribbean surgeonfishes (*Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*) on six isolated patch-reefs in Panamá over a period of 8 yr (1978–1986), and examined relationships between settlement patterns and adult abundances on those reefs. In addition, I monitored patterns of changes in adult abundances on these and two other reefs to determine if such changes were due to adult relocation.

The study reefs

The study area was east of Punta de San Blas (9°34'N, 78°58'W) on the Caribbean coast of Panamá. Several hundred patch reefs from a few meters to about 1 km in diameter occur in an area of approximately 15 km² of shallow (< 15 m deep) water. Much of the sandy substrate between reefs is covered with dense beds of seagrasses and macroalgae. The six patch-reefs studied varied from 0.15 to 0.67 ha in area, and each was at least 25 m from neighboring reefs. The reefs examined were Smithsoniantupo 1 + 2, Aguadargana 3 and Wichubhuala 23, 24, 19 and 16 in figure 1 of Robertson (1987). Here they are referred to as ST1 + 2, Ag3, W23, W24, W19 and W16. Census data on the adult populations on two other reefs [Wichubhuala (W) 13–15, and Point (PT) 18] were used to examine effects of adult relocations.

Study species

The surgeonfishes *Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*, which are abundant inhabitants of reefs throughout the Caribbean Sea, are morphologically similar, and reach about the same maximum size (Randall 1983). All feed on a similar range of benthic algae, although *A. coeruleus* has a different gut structure and ingests less sediment and detritus than the other two species (Randall 1967, Clavijo 1974). In San Blas, all three often move together in feeding schools and occur in the same habitats, although *A. bahianus* ranges further from the shelter of the reef and is more prone to enter seagrass beds than are *A. chirurgus* and *A. coeruleus* (own personal observations). Reeson (1983) found that most *A. bahianus* and *A. coeruleus* mature at about 13 to 15 cm fork length (FL), and I took 14 cm FL to be the size at maturity for all three species. Based on Randall's (1962) limited growth data, and my own observations, I estimate that San Blas fish reach 14 cm FL within two years after settlement and that those fishes live up to about ten years.

Censuses

On small, emergent reefs of the type studied, adult surgeonfishes can be censused readily, since they generally restrict their movements to near the periphery of the reefs. They were censused on the study reefs in October 1978 and yearly from October 1981–September 1986. I used a life-sized, silhouette plastic model of a 14 cm FL surgeonfish to distinguish between adults and subadults.

Newly settled juveniles were easy to census, because they are large (3.0 to 3.5 cm FL) and morphologically and behaviorally conspicuous. Each reef comprises a central area that is semi-emergent at low tide plus subtidal, peripheral habitats that extended to depths between 0.5 and 15 m. The proportion of a reef that includes subtidal habitat and the depth to which such habitat extends varies among reefs. The habitat of adult *Acanthurus coeruleus* and *A. chirurgus* included all subtidal reef habitat below 1 m depth and 5 m laterally beyond the lower limit of hard substrate. The habitat of adult *A. bahianus* included the habitat of adult *A. coeruleus* and *A. chirurgus* plus any shallower habitat up to 5 m beyond the outer periphery of a reef. The settlement habitat of *A. bahianus* and *A. chirurgus* comprised the shallow (< 3 m deep) reef-seagrass interface, in which the substrate consisted of scattered corals and patches of bare rock mixed with sparse growths of seagrass. This settlement habitat was concentrated on the leeward side of the study reefs. The settlement habitat of *A. coeruleus* comprised the outer shallow periphery (about 10 m wide and < 2 m deep) of a reef plus areas in the emergent center that consist of rock substrate with sparse growths of live corals. For each reef, I estimated (to the nearest 100 m²) the areas of adult habitat and settlement habitat of each species, using an aerial photograph.

To census adults, I swam slowly around the edge of a reef and counted all adults seen, a procedure that was re-

Table 1. *Acanthurus* spp. Between-year variation in settlement of three surgeonfishes on six patch-reefs in Panamá (total for all reefs). Data are number of settlers and (percentage they comprised of total). CV: coefficient of variation. Heterogeneity G_H: (null hypothesis, H_0 = relative abundances of three species do not differ between years) = 115.49, $P \ll 0.001$; partitioned G – all years contributed significantly to total G_H

Year	A. bahianus		A. chirurgus		A. coeruleus		Total
	No.	(%)	No.	(%)	No.	(%)	
1979	3 613	(56)	2 454	(38)	387	(6)	6 454
1980[a]	2 570	(66)	1 246	(32)	78	(2)	3 894
1981	1 693	(68)	672	(27)	125	(5)	2 490
1982	852	(49)	834	(48)	52	(3)	1 738
1983	837	(58)	426	(29)	206	(14)	1 469
1984	1 048	(51)	786	(39)	181	(9)	2 015
1985	1 336	(53)	958	(38)	227	(9)	2 521
1986	1 063	(52)	777	(38)	205	(10)	2 045
Total	13 012	(57)	8 153	(37)	1 461	(6)	22 626
$\bar{x}$(CV%)	1 627 (61)		1 019 (61)		183 (57)		2 829 (58)

[a] Estimated (see "Materials and methods – Censuses")

Table 2. *Acanthurus* spp. Between-year variation in abundance of settlers of three surgeonfishes on six patch reefs from 1979–1984. Absolute: number of settlers of that species counted each year; Relative: percent of all settlers represented by a particular species; total: total for all years

Reef	A. bahianus						A. chirurgus						A. coeruleus					
	Absolute			Relative (%)			Absolute			Relative (%)			Absolute			Relative (%)		
	$\bar{x}$	(CV)	total	$\bar{x}$	(CV)	total	$\bar{x}$	(CV)	total	$\bar{x}$	(CV)	total	$\bar{x}$	(CV)	total	$\bar{x}$	(CV)	total
W23	72	(111)	434	59	(23)	65	24	(85)	146	25	(38)	22	16	(84)	95	16	(67)	13
W24	264	(54)	1 581	60	(13)	67	96	(63)	577	25	(42)	24	35	(75)	207	9	(60)	9
W19	18	(54)	106	54	(29)	48	8	(96)	46	22	(47)	21	12	(130)	70	24	(66)	30
W16	127	(68)	764	62	(20)	63	51	(53)	308	28	(52)	26	18	(68)	106	10	(81)	11
ST1 + 2	610	(56)	3 658	53	(14)	52	507	(62)	3 041	43	(12)	44	49	(108)	294	4	(88)	2
Ag3	678	(78)	4 065	60	(18)	61	370	(83)	2 590	35	(34)	35	42	(58)	250	5	(49)	4

peated several times until consistent numbers were obtained. Reefs were censused on days in which water visibility was at least 12 m. All three species had lunar cycles of settlement, with minima around full moon (own unpublished data). Consequently, I estimated settlement each month by making a count on each reef during the five days preceding full moon. A 4 cm FL surgeonfish embedded in a block of clear plastic was used as an aid to distinguish recently arrived settlers from older juveniles. From November 1978 to October 1986, I censused newly settled fishes once per lunar month except from December 1979–April 1980. Annual recruitment for 1980 was estimated using the numbers of settlers censused during seven months of 1980 and the average monthly pattern for December–April observed in other years.

Results

Spatial and temporal patterning of recruitment

The total number of settlers that arrived annually on all reefs varied 4- to 7-fold between *Acanthurus bahianus*,

A. chirurgus and *A. coeruleus* (Table 1). Most settlers were *A. bahianus*, while *A. coeruleus* settlers were the least abundant in all years (Table 1) on all but one of the six reefs (Table 2). Levels of between-year variation in the magnitude of settlement by each species and in total settlement by all species were very similar (Table 1).

There were statistically significant differences between years in the relative numbers of settlers of each species that arrived (Table 1). However, in no year did settlement by any one species either fail or succeed in an extreme and disproportionate manner (Table 1). The best year, 1979, was the best for all species, while in 1982 and 1983 (the poorest settlement years), the relative abundances of the three species were not greatly different from those in other years (Table 1).

Density of settlers and density of adults

I measured the density of settlers both in relation to settlement habitat, SH (SH density = no. settlers/100 m² of settlement habitat) and in relation to habitat used by adult conspecifics, AH (AH density = no settlers/100 m² of adult

Table 3. *Acanthurus* spp. Survival and density of settlers, and density of adults. Survival is expressed as no. of adults present in 1986 as percentage of all fish that settled during 1979–1984. Density of settlers is no. fish/100 m². AH: density relative to adult habitat; SH: density relative to settlement habitat. Density of adults is no. fish/100 m² in 1978

Site	A. bahianus				A. chirurgus				A. coeruleus			
	Settlers			Adult density	Settlers			Adult density	Settlers			Adult density
	Survival	Density			Survival	Density			Survival	Density		
		AH	SH			AH	SH			AH	SH	
W23	4.6	33	121	1.5	6.2	13	41	0.8	11.6	9	15	0.9
W24	2.2	85	85	1.9	1.6	36	31	0.6	3.9	12.9	24	0.5
W19	71.4	4	16	2.6	6.5	2	7	0.1	83.3	3	11	0.03
W16	14.3	14	25	2.0	2.6	6	10	0.2	41.7	7	4	2.9
ST1+2	0.04	135	81	5	1.4	124	68	1.7	10.9	12	12	1.3
Ag3	0.01	203	226	2	0.01	130	144	0.05	5.0	12.5	16	0.3

Table 4. *Acanthurus* spp. Relative abundances of surgeonfish settlers and proportionate change in abundances of adults on six patch-reefs. Settler abundance: no. of settlers that arrived between 1979 and 1984 ÷ no. adults present in 1978; % adult change: no. adults in 1986 − no. in 1978 × 100: no. adults in 1978. (n) = no. of adults in 1978

Reef	A. bahianus			A. chirurgus			A. coeruleus		
	Settler abundance	% adult change	(n)	Settler abundance	% adult change	(n)	Settler abundance	% adult change	(n)
W23	15.0	− 31	(29)	16.2	0	(9)	14.3	+ 67	(6)
W24	31.6	− 30	(50)	82.4	+ 29	(7)	41.4	+ 60	(5)
W19	2.5	+ 74	(42)	46.0	+ 200	(1)	30.0	+ 2500	(2)
W16	10.5	+ 51	(71)	44.0	+ 14	(7)	6.6	+ 175	(16)
St1+2	35.9	− 85	(102)	86.9	+ 20	(35)	18.4	+ 100	(16)
Ag3	1 355	+ 25	(3)	1 163	− 50	(2)	125	+ 150	(2)

habitat). The densities of settlers of different species varied from 5- to 60-fold, while the densities of adults varied from 2- to 100-fold (Table 3). The local density of adults in 1986 was not correlated with the local density of settlers of any species (using either measure of settler density, Table 3).

Settler survival and densities of settlers and adults

Settler survival on different reefs varied by one to three orders of magnitude among the three species (Table 3). In each species, settler survival was negatively correlated with AH settler density (Kendal rank correlations, all $p < 0.05$). Survival of *Acanthurus bahianus* settlers was also negatively correlated with the AH density of *A. chirurgus* settlers and vice versa (Kendall rank correlations, both $p < 0.01$). This reflects complete overlap in use of settlement habitat by these two species and a positive correlation in their AH densities (Table 3, Kendall's rank correlation, $p < 0.01$). Settler survival of *A. coeruleus* was not correlated with AH density of either *A. bahianus* or *A. chirurgus* (Kendall rant correlations, $p > 0.05$). There were no significant correlations between settler survival of any species and either (a) the SH density of settlers of any or all species, or (b) the density of adults of any or all species combined (Table 3) (Kendall rank correlations, all $p > 0.05$).

Changes in adult abundances and abundances of settlers

There was large variation between reefs in the abundances of recruits that arrived between 1979 and 1984 relative to the abundances of adults present in 1978: as much as 20-fold for *Acanthurus coeruleus*, 70-fold for *A. chirurgus* and 500-fold for *A. bahianus* (Table 4). For none of the species was there a correlation between abundance of recruits in relation to the initial number of adults and the degree to which the adult population increased between 1978 and 1986 (Table 4, Kendall's rank correlations, NS in all cases). Thus, adult populations of each species did not tend to increase in association with high recruitment.

Abundances of adults in relation to variation in settler survival

I considered settler survival to be the number of adults present in 1986 as a percentage of the numbers of settlers censused between 1979 and 1984.

For five of the six reefs, the proportional abundances of adults of the three species present on a reef in 1986 differed from the proportional abundances of settlers of each species that arrived on that reef between 1979 and 1984 (Data on adult abundances from Table 5 and on settler

Table 5. *Acanthurus* spp. Abrupt, substantial changes in abundances of adults on five patch-reefs. Values are nos. recorded at two time intervals

Species	Nos. present on Reef:				
	W23 (Sep./Oct. 1986)	W24 (Sep./Oct. 1986)	W19 Sep. 1983/ Oct. 1984)	PT18 (Sep./Oct. 1986)	W13–15 (June/Aug. 1986)
A. bahianus	20/6	35/52	35/45	39/8	2/12
A. chirurgus	9/2	9/16	6/3	4/4	1/1
A. coeruleus	10/10	8/8	3/55	4/4	1/4
Change in size of total population	−54%	+46%	+134%	−66%	+143%
Change in relative abundance of the 3 spp. (χ^2, null hypothesis = no change) (p)	(<0.05)	(NS)	(<0.001)	(<0.01)	(<0.01)

abundances from Table 2. G test: Reef W23, $p < 0.05$; Reef W24, NS; Reef W19, $p < 0.001$; Reef W16, $p < 0.001$; Reef ST1 + 2, $p < 0.001$; Reef Ag3, $p < 0.001$.

A two-way ANOVA of the data (arc-sine transformed) on settler survival of the three species at the six sites (Table 3) shows that there were both significant interspecific variation in survival ($F_{2,10} = 4.93$, $p < 0.05$) and significant spatial variation in survival ($F_{5,10} = 6.06$, $p < 0.01$).

Relocation of adults between reefs

The *Acanthurus coeruleus* population increased greatly from 1983 to 1984 on one of the six main study reefs – Reef W19 (Table 5). This change, which occurred after several years of low abundance, was maintained until the end of the study. Decreases in adult numbers on one reef (W23) from one month to the next were matched by concurrent increases in another reef (W24) 25 m away (Table 5). On one other small complex of reefs (W13–15), which was 45 m from the nearest neighboring reef, the population of *A. bahianus* increased substantially from one month to the next (Table 5), while on Reef PT18, which was 100 m from the nearest neighboring reef, it decreased sharply (Table 5). Those changes were maintained for 1 to 3 mo after their initial detection. The net effect of these abrupt changes was to alter the total adult population size on each reef by 46 to 143% and, on four of the five reefs, to significantly alter the proportional abundances of the three species (Table 5).

Discussion

Although annual levels of recruitment in *Acanthurus bahianus, A. chirurgus* and *A. coeruleus* fluctuated over the 8 yr monitoring period, such fluctuations were not extreme. No species failed to settle in any year or had an extreme and disproportionately successful year. The degree of annual variation in settlement success was much the same for each species, and the relative levels of settlement of each conformed to the same pattern each year. Consequently, it is possible to obtain a reasonable estimate of the effects of settlement patterns on abundances of adults of these relatively long-lived fishes using total or mean annual settlement, and it is unlikely that a particular year's settlement by a particular species has a disproportionate effect on its adult population.

The data do not support most predictions of the settlement-control hypothesis: the prediction that final adult densities should correlate with settler densities was not upheld. The prediction that settler survival should be independent of settler and adult densities was only partly upheld, since there is evidence that settler survival may have been negatively density-dependent. The prediction that changes in adult populations should correlate with settler abundances was not supported. Finally, differences between proportional abundances of adults of different species and their settlers seem due to both spatial variation in settler "survival" and interspecific variation in such "survival". Thus, if post-settlement relocation of fishes between reefs had no net effect on the adult populations of individual reefs, then density-dependent settler survival and spatial variation in settler survival were overriding effects of settlement patterns. Aldenhoven (1986) recognized the potential importance of spatial variation in post-settlement mortality, and estimated that longevity of one reef angelfish varied 10-fold between sites a few kilometers apart in one continuous reef complex.

Fishing undoubtedly caused some adult mortality in the study area, which is exposed to subsistence fishing by a population of 700 indigenous people. However, surgeonfishes are not preferred food fishes, and they constituted very small portions (<5%) of catches analysed by Stier (1977) and A. de Leon (personal communication 1986). I doubt that fishing could have significantly affected adult surgeonfish populations on the study reefs and offset effects of settlement patterns.

The relocation of adult surgeonfishes between reefs (see also Randall 1962) can substantially and rapidly alter the size and composition of patch-reef populations, as my data show. Such relocations probably were an important source of recruits to at least two of the six study reefs, on which very few settlers arrived between 1979–1984 compared to the number of adults present in 1986 (Reef W19 for *Acanthurus bahianus*, and Reefs W19 and W16 for *A. coeruleus*.

These changes were gross and readily detectable, and the average net effects of such relocations on the patch-reefs of San Blas Point, and the relative importance of relocation and post-settlement mortality remain unknown. However, either or both of these processes overrode the effects of settlement patterns on the study reefs. Given the degree of variation in reef size, and in the absolute and relative abundances of settlement and adult habitat on the patch-reefs of San Blas Point, complex patterns of spatial variation in the actions and interactions of settlement, mortality and relocation in both time and space probably exist. Relocation may be the primary source of recruits on the many patch-reefs in the study area that lack high-quality settlement-habitat and that receive few settlers (own personal observation). Many patch-reefs in the more seaward parts of the San Blas Point reef complex are of this type and support large populations of adult surgeonfishes (own personal observations).

The general importance of relocation of reef fishes between patches of habitat or from juvenile to adult habitats remains unclear. Some previous studies have emphasized that the great majority of recruits to isolated patch-reefs are settlers (e.g. Russell et al. 1974, Nolan 1975, Williams 1981, Doherty 1983). However, other reports describe relocation between habitat patches by subadult and adult reef fishes (Randall 1962, 1963, Springer and McErlean 1962, Robertson 1974, Gundermann and Popper 1975, Robertson and Foster 1982, Doherty 1983, Choat and Bellwood 1985, Itzkowitz 1985). In one case, relocation of juveniles was evidently a major source of recruits to an isolated patch-reef (Brock et al. 1979). Even if few adults or subadults arrive in a habitat patch in comparison to the number of planktonic settlers, their relative contribution to the adult population may be as great as that of settlers if juvenile mortality rates are much higher than adult mortality rates (e.g. Doherty 1983, Victor 1986).

Although the detection of relocation and assessment of its contribution relative to that of settlement is easiest on isolated, small patch-reefs, their isolation may hinder relocation. As Doherty (1983) pointed out, relocation may be easiest when fish are provided with shelter as they move between habitat patches. Relocation probably is facilitated most on large reefs comprised of continuous mosaics of different types of habitats, less so between isolated small reefs separated by dense beds of seagrass or macroalgae, and least between isolated reefs separated by bare sand. Studies of patch-reefs surrounded by sand may have biased our perception of the relative contributions that settlement and relocation normally make, because the great bulk of the populations of most reef fishes live on large areas of complex habitat mosaics, not on small isolated patch-reefs. Sale (1979, and earlier papers cited therein) found that relocating juveniles and adults were a major source of recruits to habitat patches within a large reef mosaic, although it is not clear from his data how much of that relocation consisted of long-distance movements between habitat patches versus short movements within an immediate neighborhood.

The fact that relocation of adult surgeonfishes between moderately large habitat patches can substantially alter populations on different patches reduces our ability to generalize from studies that have used highly sedentary species that operate in microscale space on very small, isolated patch-reefs. Small patch-reefs may be entirely appropriate for the study of such species, because populations on different reefs are likely to be essentially independent. However, other species will relocate been habitat patches and many of them commonly live in situations that should facilitate relocation. In some species, relocation may be the norm, particularly if their settlers, juveniles and adults have different habitat requirements (cf. Choat and Bellwood 1985) and live their daily lives on very different spatial scales. In such situations, small habitat patches will not be independent entities and the abundances of fishes on both small and large spatial scales will be determined by the sum of a large set of compensatory small-scale events.

While there has been a tendency in the past to treat reef fishes as analogs of barnacles in terms of their attachment to their settlement sites, it should not really be surprising that, for some species, different life-history phases have different habitat requirements, that habitat quality varies, that these animals often relocate in response to such differences or to interactions with conspecifics, competitors and predators, and that such relocations affect community structure.

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