Proceedings of the 6th International Coral Reef Symposium, Australia, 1988, Vol. 2

FATES OF STAGHORN CORAL ISOLATES ON HURRICANE-DAMAGED REEFS IN JAMAICA: THE ROLE OF PREDATORS

N. KNOWLTON[1], J.C. LANG[2] AND B.D. KELLER[1]

[1]Smithsonian Tropical Research Institute,
APO Miami, USA 34002-0011 or Box 2072, Balboa, Republic of Panama
[2]Department of Zoology, University of Texas,
Austin, TX, USA 78712

ABSTRACT

Caribbean corallivores have been poorly studied and their importance downplayed. They have, however, played a critical role in the failure of Acropora cervicornis to recover from hurricane damage in 1980 along the north coast of Jamaica. Here we analyze the influence of the snail Coralliophila abbreviata and the damselfish Stegastes planifrons on coral growth, division and survival from 1982 through 1985. Isolated segments from colonies with either of these predators were more likely to die and less likely to show net growth than predator-free isolates. The two predators acting individually had similar effects, but isolates from colonies with both predators were at substantially higher risk of subsequent reduction or death.

INTRODUCTION

In August of 1980, Hurricane Allen passed within 50 km of the north coast of Jamaica, causing extensive damage to shallow reefs (Woodley et al. 1981). Populations of the staghorn coral, Acropora cervicornis, were particularly hard hit (Knowlton et al. 1981). Despite predictions of relatively rapid recovery (Graus et al. 1984), many populations have subsequently collapsed (Knowlton et al. in press).

The high concentration of predators on surviving colonies has played a critical role in preventing recovery of staghorn (Knowlton et al. in press). Here we present a detailed analysis of the fates of isolates from marked colonies at three sites along the north coast of Jamaica, using methods developed by Hughes (1984). We contrast the patterns of growth, division, and death of isolates from colonies with and without two associated predators.

We focus our attention on the effects of the snail Coralliophila abbreviata and the damselfish Stegastes planifrons. The former is an obligatory cnidarivore which is most often associated with scleractinian corals (Miller 1981). The latter kills coral and defends the algal gardens which grow in the cleared areas (Kaufman 1977). Although the damselfish apparently does not kill corals for their direct food value, it is clearly a predatory relationship in a broader ecological sense, because the damselfish benefits from the interaction while the coral suffers (Taylor 1984). For adults of both of these predators, staghorn coral is a preferred prey, at least among scleractinians (Itzkowitz 1977, Kaufman 1977, Williams 1978, Waldner & Robertson 1980, Rylaarsdam 1983).

We do not consider here the effects of two other species known to prey upon A. cervicornis, the polychaete Hermodice carunculata and the urchin Diadema antillarum. Neither forms readily identifiable associations with particular staghorn colonies. The former was probably an important predator at some of our studied sites (Knowlton et al. in press), while the latter suffered catastrophic mortality one year after our study began, in July, 1983 (Lessios et al. 1984, Hughes et al. 1985).

METHODS

More detailed descriptions of the methods used in this study are presented in Knowlton et al. (in press).

Study sites

We pool here the results from three study sites located 1) near the airport just east of Montego Bay, 2) off the mouth of the Pear Tree River between Discovery Bay and Runaway Bay, and 3) between Priory and St. Ann's Bay. These sites showed a gradient of increasing hurricane damage to A. cervicornis from west to east, as reflected in colony density and size in 1982 (Knowlton et al. in press). We limited our study to depths between -8 and -13 m, with the majority of work at all sites between -9 and -12 m. Here we present analyses of censuses which took place in August, 1982; February, 1983; July-August, 1983; January, 1984; June, 1984; February, 1985; and July, 1985.

Marked colonies

We haphazardly chose healthy colonies of A. cervicornis which spanned the range of locally available sizes within each of the studied areas. By colony we mean an expanse of skeleton continuously covered by living tissue at the time of the first census; colonies so defined are physiological but not necessarily genetic individuals, in the sense of Jackson et al. (1985). Because we wanted to start our census with healthy colonies, to minimize recent historical effects on subsequent growth and mortality, we excluded any specimens with 1) evidence of recent mortality (indicated by recently bared, white skeleton), or 2) associated C. abbreviata or S. planifrons.

Plastic tags with an engraved number were tied to the reef substratum near the selected colonies, and each was marked basally, on a dead portion, with plastic cord or a cable tie. During later censuses, additional markers were placed as basal death, and skeletal and tissue fragmentation occurred.

At each census, we relocated the tags and colonies and sketched the colonies which were still alive. After the first census (when by design there were no predators), we noted the presence of any C. abbreviata on the colony and whether the colony was part of the territory of the damselfish S. planifrons (the center of activity of a fish defined its territory). We measured the length of all living portions, and noted where intervening dead sections separated living portions, creating physiological isolates. From the drawings and the positions of the cable ties, we were usually able to follow unambiguously the growth, division and death of the original colonies through time.

Analysis

For the first census the number of colonies equalled the number of physiological isolates, by definition. This was not necessarily true for subsequent censuses because of medial tissue death and skeletal breakage. Thus the history of any colony could involve the creation of numbers of physiological isolates, each of which was in turn capable of further subdivision.

Fusions involving neighboring colonies or rejoining previously separated isolates were much rarer (11 cases, vs. 652 cases of fission) and typically transient. Consequently, fusion was ignored in the following analyses.

The analyses are based on the fates of living isolates through time. We divided the isolates into six size classes (I-VI) based on the following total lengths of living tissue: 1-5, 6-10, 11-20, 21-40, 41-80 and >80 cm (note that the upper bound doubles between intervals for all but the final, open-ended class). The number and size of classes reflect a compromise between potential for fine-grained analysis and the need for adequate sample sizes. For each isolate present during the first six censuses, we determined whether it had survived until the next census (i.e. using data from censuses 2-7), and if so what number and size isolates were derived from it. This process allows calculation of transition probabilities for each size class at each census (e.g. the probability of an isolate of class II in census 3 being produced per isolate of class I in census 2). Note that probabilities can sum to more than one, because a single isolate can have more than one descendent. The methods are summarized in more detail by Hughes (1984) and Hughes & Jackson (1985).

Both C. abbreviata and S. planifrons move readily within colonies of the sizes we were monitoring. Thus an isolate was considered to be influenced by predators if it was part of a colony with an associated predator, as defined above.

For statistical summaries of transition probabilities, each size class at each census was treated as a single datum. When comparisons were made (e.g. with vs. without predators or among the different types of predators) we only used those size class/census categories which were common to all groups being compared. Two-tailed sign tests were used for all statistical comparisons because they make relatively few assumptions about the character of the data.

For this paper we focus on two broad types of transition probabilities: the probability of death and the probability of isolate production. The latter is further divided into two categories. The first is the probability of isolate generation of all sizes. The second, the probability of generation of isolates of the same size class or larger, is a subset of the first. The second measure gives a more accurate picture of isolate production associated with stability of size or growth (e.g. for size class II, the sum of the transition probabilities for size classes II-VI).

RESULTS

The transition probabilities for all size classes and censuses are presented in Figure 1; data for isolates without predators are presented separately from data for isolates with predators. Table 1 summarizes many of the trends present in Figure 1 by 1) dividing the original size classes into two groups, and 2) condensing the patterns of isolate production into the two categories described above. Table 2 draws on a more limited data set (see above) than Table 1, allowing a direct comparison of the performance of isolates differing in the kinds of predators associated with the parent colony. We first discuss the fates of isolates without predators, and then show how these patterns changed when predators were present.

Table 1. Transition probabilities for death, production of all isolates, and production of isolates as large or larger than the progenitor. Data are presented for isolates with no predators (NP) or with predators (P). Data are further divided by census and isolate size class. Sample size is indicated by N.

Census Size	N		Death		Isolates: All		Isolates: Equal or larger	
	NP	P	NP	P	NP	P	NP	P
Census 1								
I-III	54	0	.30	-	.75	-	.71	-
IV-VI	106	0	.06	-	1.71	-	.87	-
Census 2								
I-III	75	13	.48	.79	.58	.38	.46	.00
IV-VI	133	18	.07	.44	2.11	1.71	.67	.36
Census 3								
I-III	138	56	.63	.81	.39	.19	.32	.19
IV-VI	117	57	.18	.37	1.67	1.74	.53	.40
Census 4								
I-III	122	81	.62	.68	.39	.34	.33	.29
IV-VI	118	40	.23	.47	1.83	1.98	.48	.14
Census 5								
I-III	77	129	.87	.94	.17	.10	.07	.04
IV-VI	39	84	.61	.73	.89	.63	.13	.11
Census 6								
I-III	30	39	.66	.87	.41	.13	.14	.13
IV-VI	12	21	.42	.62	.67	.92	.46	.06

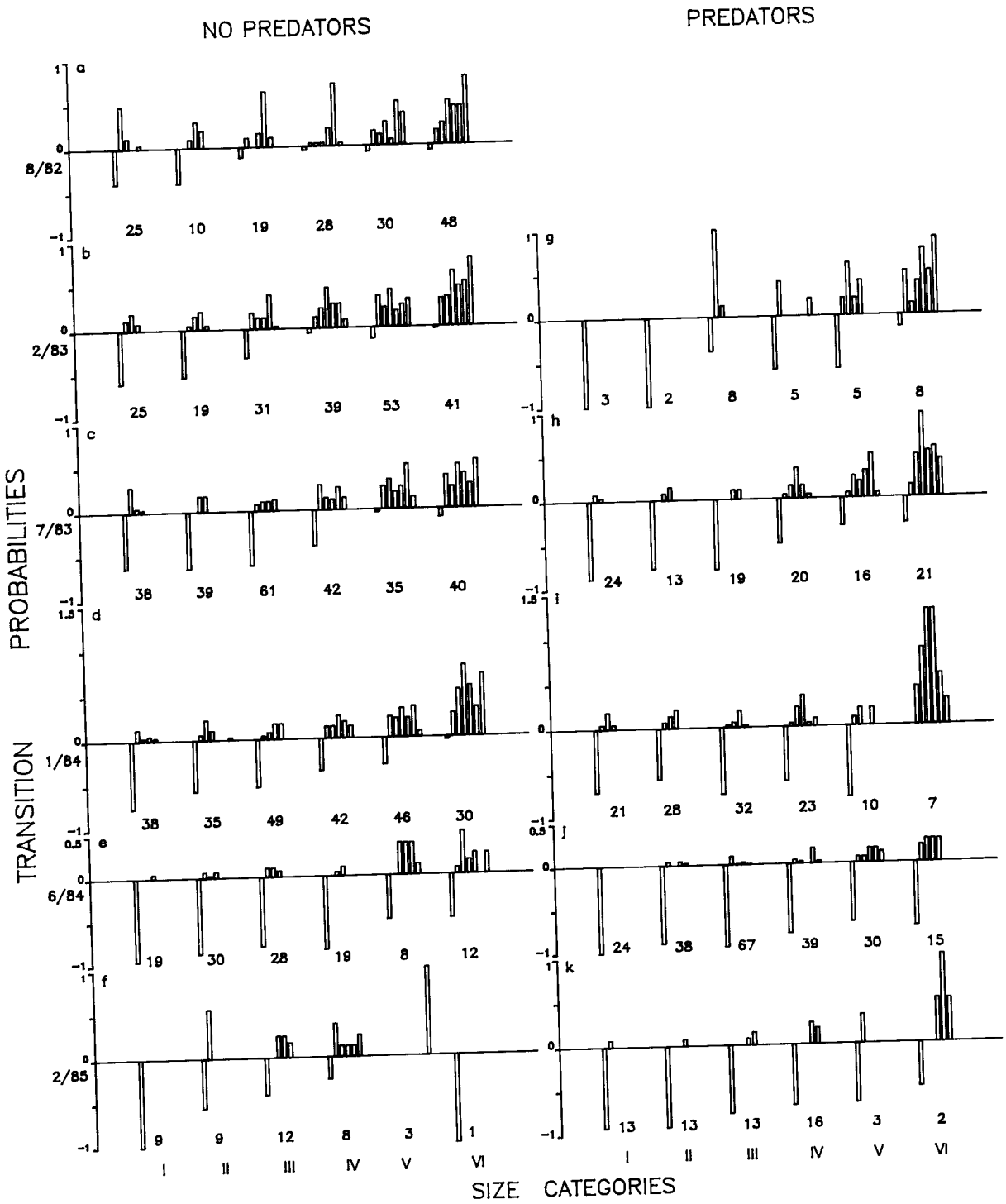

Figure 1. Transition probabilities for the six size classes at six censuses. Each pair of graphs presents the results for a single census (no predators vs. predators; all colonies were predator-free in 8/82). Each cluster within any graph shows the transition probabilities for a single size class (sample size shown below). The possible outcomes are death (below the horizontal axis) and the six size classes (I to VI from left to right above the horizontal axis). (See Hughes 1984).

Colonies without predators

We consider first the differences among the size classes and then the changes which occurred through time.

Small isolates (size classes I-III) were overall more than twice as likely to die than large isolates (size classes IV-VI), with average transition probabilities of .59 and .26 respectively. There were no exceptions among the six censuses (Table 1, column 4; sign test, p=.032). Large isolates were over three times more likely to generate descendent isolates than were small isolates, with average transition probabilities of 1.48 and .45 respectively (Table 1, column 6; sign test, p=.032). Although the difference between large and small isolates was not so marked in the generation of isolates of the same size or larger (average transition probabilities of .52 and .34 for large and small isolates respectively), there were again no exceptions for predator-free colonies in any census (Table 1, column 8; sign test, p=.032).

Through time, there was a general increase in the probability of death, and a decrease in the probabilities of isolate production, both of all sizes and sizes as large as or larger than the progenitor. For example, combining size classes in Table 1 and contrasting the average values for the first two, middle two, and final two censuses, one sees 1) an increase in the probability of death from .23 to .41 to .64 (Table 1, column 4), 2) a decrease in the overall probability of isolate production from 1.29 to 1.07 to .53 (Table 1, column 6), and 3) a decrease in the probability of production of isolates as large or larger from .68 to .42 to .20 (Table 1, column 8). Contrasting the average values for censuses 1+2 with those for censuses 5+6, there were no exceptions to these patterns for any of the six size classes (sign tests, p's=.032).

The effect of predators

Because there were no predators at census 1, we limit our summary comparisons to census 2 (before the die-off of D. antillarum), and censuses 3-6 (after the die-off).

Small isolates were consistently more likely to die when predators were present than when they were absent (averages of .82 vs. .65). The same pattern was even stronger for large isolates (.53 vs. .30). There were no exceptions among the censuses to this pattern for either small or large isolates (Table 1, column 4 vs. column 5 for censuses 2-6; sign test, p=.002).

Predators reduced the probability of isolate production for small isolates; their average transition probabilities with and without predators were .23 vs. .39, with no exceptions among the censuses (but p=.061 with only five contrasts in the sign test). For large isolates, however, there was no trend in this direction, with only two of five censuses showing this pattern and an insignificant average difference (1.40 with predators vs. 1.43 without). Thus there was no overall difference between isolates with and without predators in this characteristic (Table 1, column 6 vs. column 7 for censuses 2-6; sign test, p=.344).

For both small and large isolates the probability of isolates as large or larger being produced was clearly reduced by predators. In both cases the average transition probabilities in the presence of predators was half or less the average probability without predators (.13 vs. .26 for small isolates, .21 vs. .45 for large isolates). There were no exceptions among the censuses for either small or large isolates (Table 1, column 8 vs. column 9 for censuses 2-6; sign test, p=.002).

Comparisons among the predators

Our data (Table 2) allow us to compare three predator states: C. abbreviata only, S. planifrons only, and both predators present together, with the data for no predators also provided for comparison. Here we restrict ourselves to the 19 census/size class categories for which we have data for all four conditions (census 3, size classes I,II, IV; census 4, size classes I-V, census 5, all size classes; census 6, size classes I-V).

Table 2. Transition probabilities for death, all isolate production and production of isolates as large or larger than the progenitor. Data are limited to the 19 census/size class categories (N indicates the total number of isolates involved) for which examples of each of the following occurred: No predators, C. abbreviata present, S. planifrons present, and both predator species present.

			Isolates	
Condition	N	Death	All	Equal or Larger
No predators	486	.52	.61	.28
C. abbreviata	195	.69	.51	.19
S. planifrons	136	.71	.43	.16
Both predators	111	.94	.09	.03

We found no substantial difference between the effect of C. abbreviata alone and the effect of S. planifrons alone. Probabilities of death across all size class/census categories being compared were .69 and .71 for snails only and damselfish only respectively. Transition probabilities for production of all isolates were .51 vs. .43, while for the production of isolates as large or larger, the transition probabilities were .19 and .16 respectively (sign tests based on 19 size class/census categories, all p's >.5).

The presence of both predators together, however, had a significantly larger detrimental effect than either predator alone (sign tests, all p's <.002). The probabilities of death for one (average of snail and damselfish) vs. both predators were .70 vs. .94. The probabilities for total isolate production were .47 vs. .09, and the probabilities for producing isolates as large or larger were .17 vs. .03. Thus the probability of death increased

by over one third, and isolate production dropped to less than 20% of average single-predator values. Indeed, the relative difference between no predators and the average for the two single predators is smaller that the difference between the average for a single predator and both predators. Although single predators do have significant effects on mortality and fragmentation when compared with predator-free colonies (Knowlton et al. in press), sign tests contrasting two vs. one predator yield consistently smaller p-values than sign tests contrasting one vs. no predators (all p's <.002 for one vs. two predators, in contrast to p's =.008 (death), .096 (production of isolates as large or larger), and .168 (production of all isolates) for one vs. no predators).

DISCUSSION

Comparison with other studies

The size specific patterns of death and division we documented are consistent with those previously described by Hughes & Jackson (1985). They too found that small colonies were more likely to die entirely, while large colonies more often suffered partial mortality which divided them into physiological isolates, even though the species they studied differed from staghorn coral in being foliaceous.

No analyses comparable to those presented here have been done at other sites for staghorn coral. Nevertheless, presentation of data by size category should facilitate comparisons of our results with those of other studies on this species as they appear.

Importance of predators

Our study probably underestimated the importance of predators for two reasons. First, we considered the effects of only two predators in this analysis (albeit important ones). Second, if a colony was free from predators during a particular census, it was assumed to be free from the influence of predators for the entire six-month interval which followed.

Neither C. abbreviata nor S. planifrons fundamentally changed the nature of the size-specific patterns of colony death; small isolates remained more vulnerable to total death than large isolates, with or without predators (Table 1, columns 4 and 5). Predators did, however, substantially increase the probability of death, and reduce the probability of isolates being produced of a size as large or larger than the progenitor.

Predators on Caribbean corals have received much less attention than their Pacific counterparts (including this mini-symposium), and perhaps for many species this neglect is more or less justified. But several earlier studies have pointed to the potential importance of C. abbreviata and S. planifrons as predators on Caribbean acroporids (e.g. Kaufman 1977, Brawley & Adey 1982), which we have confirmed. Elsewhere (Knowlton et al. in press) we suggest that the biological characteristics of staghorn and its predators make threshold effects (May 1977) more likely, such that predators have relatively little effect when this coral is abundant but can be of enormous importance when it is rare.

Importance of the die-off of Diadema antillarum

Some might argue that the effects of predators we observed were hopelessly confounded by and therefore perhaps dependent upon the effects of the die-off of D. antillarum. However, the predators had significant effects even during the interval between census 2 and census 3, when the urchin was present. Looking at just the census 2 transition probabilities for the six size classes, isolates from colonies with predators were consistently more likely to die than isolates from colonies without predators (sign test, p=.032). Indeed, the average strength of the predator effect was stronger in the presence of D. antillarum than in its absence for three of the five trends described above (Table 3). In the other two cases, the strength of the effect in the presence of the urchin was similar to the first of the two pairs of censuses following the die-off.

Table 3. Comparison of predator effects for five major trends (see text) for censuses prior to (urchins) and following (no urchins) the die-off of D. antillarum. Categories as in Table 1. The strength of the predator effect is measured by the ratio of the transition probability in the presence of predators to the transition probability in the absence of predators. For each category, the census(es) with the largest difference between predator-associated and predator-free isolates is indicated by an asterisk. For the transition probabilities for death, the larger the ratio, the greater the effect of predators (because transition probabilities were higher for death in the presence of predators). For transition probabilities for isolate production, the smaller the ratio the greater the effect of predators, because transition probabilities in the presence of predators were lower than in their absence.

	Transition Probability Ratios		
Categories	Urchins Census 2 P/NP	No Urchins Censuses 3-4 P/NP	No Urchins Censuses 5-6 P/NP
Death			
I-III	1.65*	1.19	1.18
IV-VI	6.29*	2.10	1.31
All Isolates			
I-III	.66	.67	.38*
Isolates as Large or Larger			
I-III	.00*	.75	.80
IV-VI	.54	.54	.28*

The mass mortality of D. antillarum has undoubtably had a detrimental effect on A. cervicornis, but even the increasing mortality rates for predator-associated and predator-free

colonies observed through time cannot automatically be attributed to this factor. An alternative explanation is that as staghorn densities and sizes decreased (Knowlton et al. in press), visitation rates of predators increased and the average duration of their stay decreased, so that both classes of colonies were more likely to have experienced unrecorded predator visits during the six month intervals which separated our censuses.

ACKNOWLEDGMENTS

G. Bruno, S. Greenwell, J. Hayes, L. Land, and B. Needleman assisted in the field; J. Brawn, G. Jacome, K. Kaufmann and I. Urreiztieta helped analyze and present the data; J. Hayes and J.B.C. Jackson commented upon the manuscript. The Discovery Bay Marine Laboratory and the Hofstra University Marine Laboratory provided essential logistic support. Financial aid came from the University of Texas at Austin (SRF-937 to JCL), as well as indirectly through support to other projects in Jamaica from the NSF (BSR-82-01172 to NK) and the National Geographic Society (2523-82 to NK). This is contribution no. 438 from the Discovery Bay Marine Laboratory, University of the West Indies, and publication no. N.S.-4 of the Texas Memorial Museum, University of Texas.

REFERENCES

Brawley, S.H. & Adey, W.H. 1982. Coralliophila abbreviata: a significant corallivore! **Bull. Mar. Sci.** 32:595-599.

Graus, R.R., Macintyre, I.G. & Herchenroder, B.E. 1984. Computer simulation of the reef zonation at Discovery Bay, Jamaica: hurricane disruption and long-term physical oceanographic controls. **Coral Reefs** 3:59-68.

Hughes, T.P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. **Amer. Natur.** 123:778-795.

Hughes, T.P. & Jackson, J.B.C. 1985. Population dynamics and life histories of foliaceous corals. **Ecol. Monogr.** 55:141-166.

Hughes, T.P., Keller, B.D., Jackson, J.B.C. & Boyle, M.J. 1985. Mass mortality of the echinoid Diadema antillarum Philippi in Jamaica. **Bull. Mar. Sci.** 36: 377-384.

Itzkowitz, M. 1977. Spatial organization of the Jamaican damselfish community. **J. Exp. Mar. Biol. Ecol.** 28: 217-241.

Jackson, J.B.C., Buss, L.W. & Cook, R.E. (eds.). 1985. **Population biology and evolution of clonal organisms.** Yale University Press, New Haven and London, 530 pp.

Kaufman, L. 1977. The threespot damselfish: effects on benthic biota of Caribbean coral reefs. **Proc. Third Intern. Coral Reef Symp.** 1:559-564.

Knowlton, N., Lang, J.C. & Keller, B.D. In press. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. **Smithson. Contr. Mar. Sci.**

Knowlton, N., Lang, J.C., Rooney, M.C. & Clifford, P. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. **Nature** 294:251-252.

Lessios, H.A., Robertson, D.R. & Cubit, J.D. 1984. Spread of Diadema mass mortality through the Caribbean. **Science** 226:335-337.

May, R.M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. **Nature** 269: 471-477.

Miller, A.C. 1981. Cnidarian prey of the snails Coralliophila abbreviata and C. caribaea (Gastropoda: Muricidae) in Discovery Bay, Jamaica. **Bull. Mar. Sci.** 31: 932-934.

Rylaarsdam, K.W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. **Mar. Ecol. Prog. Ser.** 13:249-260.

Taylor, R.J. 1984. **Predation.** Chapman and Hall, New York and London, 166 pp.

Waldner, R.E. & Robertson, D.R. 1980. Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). **Bull. Mar. Sci.** 30: 171-186.

Williams, A.H. 1978. Ecology of threespot damselfish: social organization, age structure, and population stability. **J. Exp. Mar. Biol. Ecol.** 34:197-213.

Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Knowlton, N., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J. & Sides, E.M. 1981. Hurricane Allen's impact on Jamaican coral reefs. **Science** 214:749-755.