Density-Dependent Dynamics of Soft Coral Aggregations: The Significance of Clonal Growth and Form

Ronald H. Karlson; Terence P. Hughes; Susan R. Karlson

Ecology, Vol. 77, No. 5. (Jul., 1996), pp. 1592-1599.

Stable URL:

http://links.jstor.org/sici?sici=0012-9658%28199607%2977%3A5%3C1592%3ADDOSCA%3E2.0.CO%3B2-2

Ecology is currently published by Ecological Society of America.

DENSITY-DEPENDENT DYNAMICS OF SOFT CORAL AGGREGATIONS: THE SIGNIFICANCE OF CLONAL GROWTH AND FORM[1]

RONALD H. KARLSON

*Ecology and Evolutionary Biology Program, Department of Biology, University of Delaware,
Newark, Delaware 19716 USA*

TERENCE P. HUGHES

Department of Marine Biology, James Cook University of North Queensland, Townsville, Queensland 4811 Australia

SUSAN R. KARLSON

266 Carters Mill Road, Elkton, Maryland 21921 USA

Abstract. In clonal plants and animals, stolons and runners often promote rapid directional growth and escape from crowded microhabitats. Here we evaluate the effects of density on clonal growth and dispersal by stolons, on colony mortality, and on recruitment in the soft coral *Efflatounaria* sp. This colonial organism forms dense aggregations on mid-shelf and outer reefs of the Great Barrier Reef, Australia, where it is subjected to frequent physical and biological disturbances. Stolonal growth and asexual recruitment of new colonies (by budding) were enhanced by experimentally reducing local density. Within unmanipulated aggregations of *Efflatounaria,* per-capita rates of asexual recruitment were higher at low density, but colony survivorship was lower. Furthermore, the effect of density on stolonal growth and dispersal of daughter colonies varied as a function of a colony's history of disturbance. Disturbance was simulated by detaching from the substrate a newly budded colony that was still connected by a stolon to the parent colony. At low density, these pairs of partially detached colonies moved apart, while at high density, stolonally connected colonies moved closer together.

Our results suggest that *Efflatounaria* employs a plastic life-history strategy that promotes recovery from injuries and the formation of dense aggregations. At low density, stolons facilitate rapid directional growth, asexual recruitment, and aggregation. At high density, clonal growth is inhibited, and mortality rates are greatly reduced. Enhanced survival within aggregations provides the adaptive context for interpreting the influence of density and disturbance history on the population dynamics of this clonal organism.

Key words: clonal growth form; density dependence; dispersal; disturbance; Efflatounaria; *genets; ramets; soft corals; stolons.*

INTRODUCTION

Clonality and modular growth in sessile organisms promote local exploitation of resources, facilitate dispersal of successful genotypes through adjacent microhabitats, and spread the risk of genet mortality (e.g., Harper and White 1974, Hughes and Jackson 1980, Highsmith 1982, Bell and Tomlinson 1980, Harper 1985, Jackson et al. 1985). Furthermore, the magnitude of these effects varies as a function of clonal growth form. For example, in clonal plants with a "guerilla" strategy, vegetative propagation of rhizomes, stolons, and adventitious roots is interpreted as a mechanism promoting rapid growth, spatial exploration, resource acquisition, and escape from competition (Lovett Doust 1981, Harper 1985, Fahrig et al. 1994). In contrast, plants with a "phalanx" strategy are characterized by a more compact growth form, slower growth, and a greater commitment to the initial site of establishment. Similarly, in clonal animals, a stoloniferous or runner-like morphology has been interpreted as a fugitive, refuge-seeking strategy relative to that of other growth forms, such as mounds, trees, sheets, or plates (Winston 1976, Buss 1979, Jackson 1979).

The morphological strategies of clonal organisms are predicted to have a number of important life-history correlates (e.g., review by Jackson 1979). For example, the consequences of stoloniferous growth include the potential for rapid clonal expansion, enhanced colonization by vegetative processes, the formation of loosely organized aggregations, indeterminant growth, early age of first reproduction, high fecundity, and high mortality rates among modules, as well as a strong association with disturbed or ephemeral environments (e.g., Jackson 1979, Coates and Jackson 1985, Sackville Hamilton et al. 1987). In both terrestrial and marine habitats, clonal aggregations often reach high densities (e.g., Lovett Doust 1981, Ayre 1984, Karlson 1988*a*) and commonly experience catastrophic mortality associated with disturbance events (e.g., Hanes 1971, Heinselmann 1973, Karlson and Hurd 1993, Hughes 1994). In shallow seas, turbulence associated

with storms frequently results in fragmentation and dispersal of ramets (daughter colonies) as connections between parts of a colony are broken, thereby dispersing the genet (genetic individual) across local spatial scales [animal examples include staghorn corals (Highsmith 1982, Hughes et al. 1992), gorgonians (Lasker 1984, 1990), zoanthids (Karlson 1986, 1988b), encrusting tunicates (Bak et al. 1981), and vine-like sponges (Wulff 1991)]. Hence, clonal organisms are likely to be exposed to selection pressures associated with both crowding and catastrophes.

Crowding is commonly associated with competition for depleted resources, resulting in density-dependent fecundity and mortality, and selection for a number of characteristic life-history traits (e.g., Roff 1992, Stearns, 1992). In contrast, catastrophic mortality from disturbances is generally density independent, and selects for a very different suite of traits. Consequently, it is not clear from current life-history theory how the effects of intermittent crowding might be manifested in clonal organisms living in a highly disturbed habitat. Interference between plants grown at high density typically results in high mortality of modules (i.e., buds and shoots), low "birth" rates of buds, and severely limited growth of branches (Schmid and Harper 1985, Jones and Harper 1987a, b, Solangaarachchi and Harper 1989). Under crowded conditions, plants with a "phalanx" growth habit should be favored over the "guerilla" form, although disturbances can facilitate coexistence among plant species (e.g., Platt 1975, Platt and Weiss 1977, Connell 1978).

Here, we focus on the consequences of stoloniferous growth on the dynamics of a common soft coral, *Efflatounaria* sp., on the Great Barrier Reef, Australia. The growth habit of this organism is analogous to that described for "guerilla" plants (Lovett Doust 1981, Harper 1985, Schmid and Harper 1985) and "runners" (Jackson 1979). The primary objective of this study is to determine how survival and growth by stolons in *Efflatounaria* respond to crowding and physical disturbance. In addition, we evaluate the contribution of this form of clonal growth to substrate colonization, the recruitment of new colonies, and the density-dependent dynamics of *Efflatounaria* aggregations. We will provide evidence that both physical disturbance and density influence stolonal growth, and that the effects of each of these factors can be conditional on the other. Furthermore, our results indicate that this species exhibits a plastic demographic response that facilitates rapid clonal growth at low density and enhances survival within aggregations at high density.

The organism

At least three species of *Efflatounaria* (Alcyonacea: Xeniidae) have been described (Gohar 1939, Verseveldt 1977), although a thorough systematic treatment of the genus has been hampered by the absence of well-differentiated spicules. Consequently, the stolon-bearing form described here remains unnamed. Stoloniferous *Efflatounaria* is particularly common on mid-shelf and outer barrier reefs of the Great Barrier Reef, Australia (Dinesen 1983, 1985, Lasker 1988).

Colonies of *Efflatounaria* usually consist of small clumps of polyp-bearing branches, typically 5 cm tall and often connected by stolons to nearby daughter colonies. Colonies cannot actively crawl across the substrate, so stolons represent an important form of local dispersal and are an essential component of the clonal processes affecting local population dynamics (see *Results*). *Efflatounaria* is a dioecious brooder, but the overwhelming majority of new colonies are derived asexually by fission (Dinesen 1985). Stolons in *Efflatounaria* are highly variable in shape, size, and location on the colony. They may be greatly elongated (up to 40–50 cm, Fig. 1A), elevated over the substrate or attached, and are sometimes broad and flattened where they come in contact with the substrate (Fig. 1B). They may be located basally on the stalk of a colony or apically at the end of branches (Fig. 1C). Stolons may be terminally bifurcated (Gohar 1939; R. H. Karlson, *personal observation*) and may possess "sucker-like" attachment sites (Macfadyen 1936, Gohar 1939). Stolons sometimes link different regions of a single colony undergoing repair (Fig. 1D). More typically, stolons connect incipient daughter colonies with the parent colony as it undergoes fission (Dinesen 1985, Fig. 1E). Frequently, most of the surface of an actively growing stolon is devoid of polyps.

As well as facilitating the local spread of genets, stolons play an important role in regeneration following injury and the redeployment of tissue following physical disturbance or an attack by a predator. Storms can injure and dislodge colonies and stolons from the substrate; recently attached stolons and small colonies are particularly susceptible (R. H. Karlson, *personal observation*). Complete dislodgement from the substrate may result in dispersal or death. Stolons connecting partially detached colonies may stretch or grow rapidly, further facilitating local dispersal.

METHODS

Stolonal growth

In order to determine how quickly stolonal growth changes occur in *Efflatounaria,* we followed the dynamics of 39 colonies (which initially bore 53 stolons) within 5 large aggregations of this species at Granite Head, Lizard Island (145°27′ E, 14°39′ S) on the northern Great Barrier Reef. These aggregations were one to several square metres in size and were located on inclined granitic substrate at depths of 1–5 m. The density of *Efflatounaria* within these aggregations was 2.01 ± 0.12 colonies/100 cm² (mean ± 1 SE). The height of the selected colonies was 46.7 ± 1.8 mm, and their initial stolon length was 19.1 ± 3.1 mm (means ± 1 SE) with a range of 2–180 mm. Growth was estimated
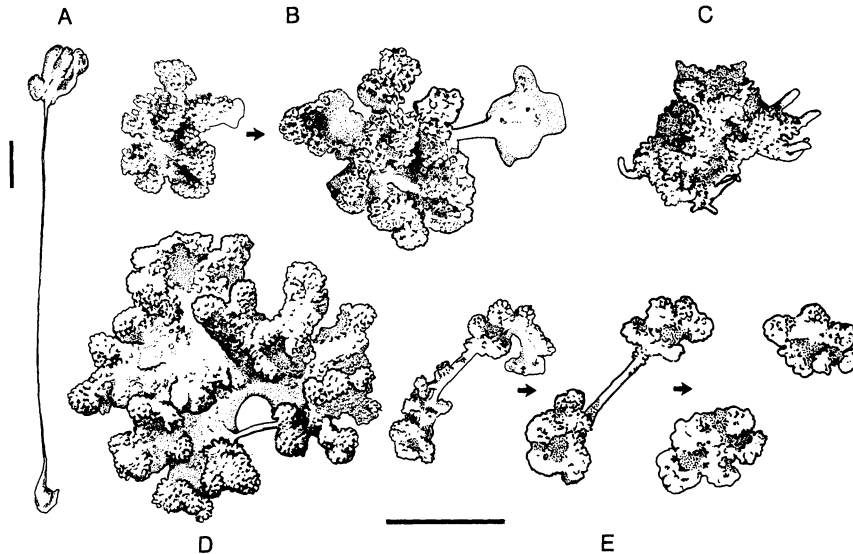
FIG. 1. Schematic, top-view illustrations drawn from photographs of stolon-bearing *Efflatounaria* colonies taken in the study area at Lizard Island during 1993–1994. Extensive morphological variation is exhibited by (A) a greatly elongated stolon; (B) a developing broad, flattened stolon photographed in August and September; (C) a colony bearing several apical stolons; and injured colonies with (D) a stolon connected at both ends to the same colony and (E) a degenerating stolon photographed in August, September, and January. Arrows indicate the time sequence; 5-cm scale bars are indicated for colonies in A and B–E.

from repeated measurements of each stolon, taken with calipers every 2–3 d from 16 to 26 September 1993.

Recruitment and mortality: effects of density

In order to monitor background changes in the abundance of *Efflatounaria* and to test for significant effects of density on recruitment and mortality, we established semi-permanent belt transects through nine additional aggregations of *Efflatounaria*. We used hard-coral heads to map. the end-points of the transects, which were 1–3 m long. During August and September 1993 and January 1994, we photographed 109–122 quadrats (16.4 × 10.9 cm each, the size of a close-up frame for a Nikonos underwater camera) along a total transect length of 14.5 m. Using sets of photographs, we estimated density (number of colonies per unit area) and recorded recruitment and mortality events. Subsequently we used regression analysis to test for any significant changes in per-capita vital rates as a function of density.

Clearing experiment

We experimentally evaluated the ability of *Efflatounaria* to colonize adjacent bare areas through clonal processes by removing colonies from selected quadrats within five additional aggregations. We hypothesized that crowding may inhibit stolonal growth and asexual fission through lack of resources, such as space and food. Within each of the five aggregations, we located three 396 cm² quadrats (24.0 × 16.5 cm, 15 cm apart) along semi-permanent transects. We randomly assigned treatments in each set of quadrats to control, total clear-

ing, and partial clearing groups; one central colony was left in quadrats designated for the partial clearing treatment. This design ensured that colonies at the periphery of the partial and total clearings (and the remaining central colony in the partial clearing treatment) experienced a local reduction in density, and thus may have been released from density-dependent competition within aggregations. The experiment was initiated in September 1993, when 109 colonies were removed from the 10 quadrats comprising the total and partial clearing treatments. Quadrats were sampled photographically in September and again 16 wk later in January 1994. One-way analysis of variance on the final density and percentage cover of *Efflatounaria* was used to evaluate the outcome.

Density-disturbance experiment

We hypothesized that dispersal by stolons might be affected by physical disturbance during storms. In January 1994, we located 40 pairs of stolonally connected colonies that were undergoing fission. Larger parent colonies were 48.6 ± 1.8 mm high, while smaller incipient daughter colonies were 37.4 ± 1.7 mm (means ± 1 SE). The initial length of the stolons between colonies was 35.1 ± 1.7 mm, while the total length of the stolons including the smaller daughter colonies was 56.9 ± 2.2 mm (means ± 1 SE). Each pair was randomly assigned to treatment groups in a two-factor experimental design; the treatments comprised a density reduction and a disturbance simulation in which the smaller colony in each pair was detached from the substrate using a putty knife. This partial detachment of
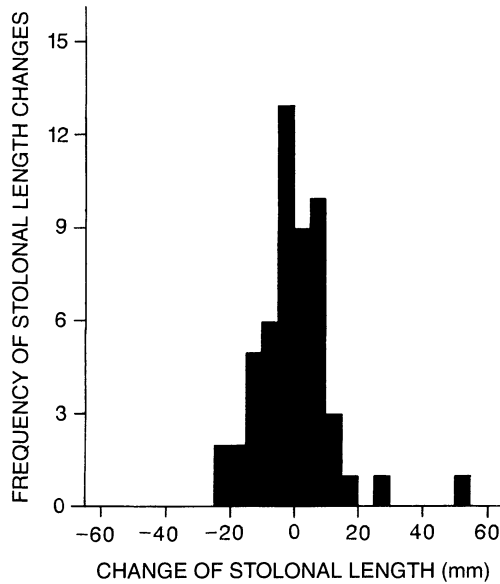
FIG. 2. Frequency distribution of the change in the length of 53 *Efflatounaria* stolons measured over a 10-d period during September 1993. See *Methods: Stolonal growth.*

the pair of colonies was designed to simulate one effect of disturbance from storms. Low-density areas were created by removing adjacent colonies within 15 cm of the parent colonies. The number of colonies within high-density areas was 3.03 ± 0.11 colonies/100 cm² (mean ± 1 SE). After 4–5 d, the total length of each stolon (the distance between each attached parent colony and the distal end of the detached smaller colony) was remeasured. The net change in total stolon length was evaluated using two-way analysis of variance. Homogeneity of variances was tested in all ANOVAs using F_{max} tests, and transformations were used where appropriate.

RESULTS

Stolonal growth

Growth, attachment, and morphology of stolons were extremely dynamic. After only 10 d, some stolons exhibited rapid extension (≤52 mm), while others underwent significant resorption (≤23 mm). The highly variable behavior of these stolons is indicated by the coefficient of variation in the change in stolon length; CV = 5800%, mean = −0.2 mm, standard deviation = 11.6 mm. Although the length of most stolons (38 of 53) changed <10 mm, six grew 10–52 mm, and nine shrank 10–23 mm (Fig. 2). Six of the nine rapidly shrinking stolons were initially unattached apical stolons, which were progressively resorbed over the brief interval. Among the six rapidly growing stolons, two that were initially unattached became fixed to the substrate, and three others developed polyps or a "sucker-like" attachment structure at the distal end. A similar

range of very rapid morphological changes also occurred among slow-growing stolons.

Recruitment and mortality: effects of density

Recruitment and mortality were sharply lower at high densities. The density of *Efflatounaria* within aggregations on Lizard Island was 2.13 ± 0.11 colonies/100 cm² (mean ± 1 SE), which did not vary significantly among sampling dates ($F = 0.39$, df = 2, 342, $P = 0.68$). A total of 39 new recruits was added to 34 quadrats, which initially included 177 colonies, over a period of 21 wk. Over all 122 quadrats, new individuals were added to aggregations at a rate of 0.11 recruits·m⁻²·day⁻¹. Thirty-six of the observed recruits were clearly products of fission following lateral growth and degeneration of stolonal connections between colonies (e.g., Fig. 1E). The origin of the three other recruits is uncertain, but only one of them appeared in summer, when sexually produced larvae are expected to settle following mass spawning in December (Dinesen 1985). Consequently, we estimate that at least 97% of all the recruits we recorded originated from clonal processes.

Density had a significant negative effect on the per-capita rate of recruitment in the 34 quadrats in which recruitment occurred (Fig. 3, $F = 13.10$, df = 1, 32, $P < 0.002$, $R^2 = 0.29$). [The linear relationship persists even after removing the unusually large value for an initially empty quadrat ($F = 7.89$, df = 1, 31, $P =$
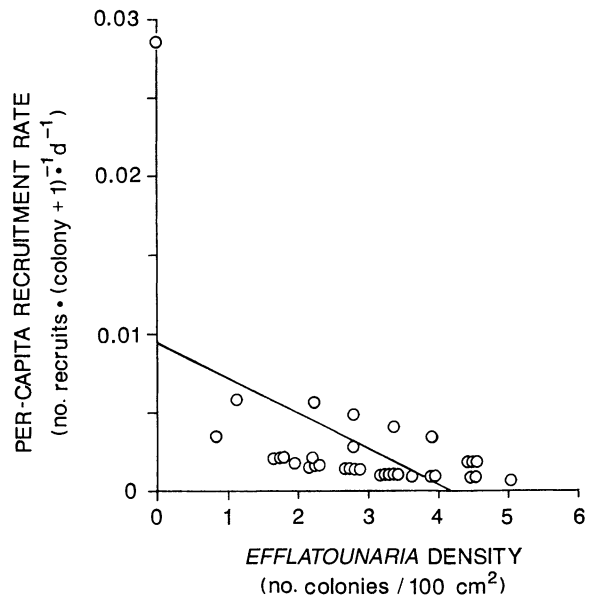

FIG. 3. Per-capita recruitment rate plotted against the density of *Efflatounaria* colonies in quadrats sampled within nine aggregations. The linear relationship from the regression analysis of 34 recruitment events is indicated. (See *Results: Recruitment and mortality: Effects of density* for further explanation regarding residuals and the single unusually large recruitment rate estimate.)
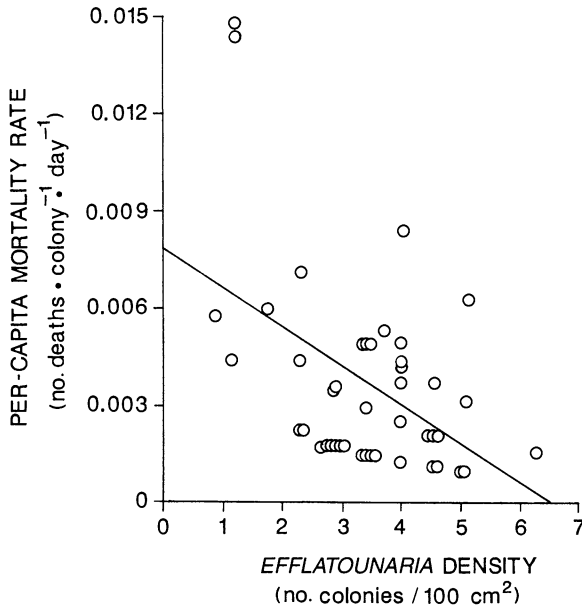
FIG. 4. Per-capita mortality rate plotted against the density of *Efflatounaria* colonies in quadrats sampled within nine aggregations. The linear relationship from the regression analysis of 44 mortality events is indicated.

0.009, $R^2 = 0.20$). Furthermore, there was no systematic bias in the residuals about the original linear regression (lack-of-fit test, $F = 3.71$, df $= 29, 3, P = 0.15$)]. Since almost all new colonies were generated asexually, it appears that crowding inhibits stolon formation and subsequent fission. Consequently, recruitment of asexually produced colonies was almost three times more likely to occur in quadrats with an isolated colony than in quadrats with colonies at average density (Fig. 3).

The number of deaths that occurred over the 21-wk period was twice the number of new recruits. There were 64 colony deaths in 44 quadrats, which initially included 265 colonies. Over all quadrats, colonies died at a rate of 0.21 individuals·m^{-2}·day^{-1}. A lower per-capita rate of mortality coincided with higher densities (Fig. 4, $F = 12.48$, df $= 1, 42, P = 0.001, R^2 = 0.23$). The linear relationship between mortality rate and density adequately described the data (lack-of-fit test, $F = 0.82$, df $= 28, 14, P = 0.68$). Based on these estimates, an isolated colony was twice as likely to die as one occurring in a group at average density.

Clearing experiment

The growth rate of stolons responded rapidly to the experimental reduction in density (Table 1). There was extensive stolonal growth from the edges of cleared areas and from the central colonies in the partial clearing treatments, which restored the original high densities (number of colonies) and percentage cover of *Efflatounaria* (Table 1). After 109 d, the final densities in cleared quadrats were not significantly different from the controls ($F = 1.508$, df $= 2, 12, P = 0.260$; Table 1). However, colonies recruiting to cleared quadrats were generally smaller, resulting in more free space available for growth than observed in controls at the end of the experiment ($F = 10.965$, df $= 2, 12, P = 0.002$, Table 1). Control quadrats exhibited no significant change in density or cover during the experiment (Table 1).

Density-disturbance experiment

Dispersal by stolons in this experiment was affected by density and by the simulated disturbance in which the smaller of the two colonies in each pair was detached from the substrate. In fact, the impact of this disturbance was conditional on density. Stolons connecting the detached colonies to the larger colonies were extremely dynamic, mostly growing at low density and shrinking at high density (Fig. 5). Of the original 40 stolons in this experiment, 16 extended or shrank at least 5 mm; 13 of these were in the disturbance treatments where total stolon length increased as much as 35 mm or decreased by up to 21 mm. At low density, 5 of 7 stolons bearing a detached colony extended ≥ 5 mm. In contrast, at high density, 6 of 9 stolons bearing a detached colony shrank ≥ 5 mm. Stolons (along with the smaller detached colony) broke off and disappeared in four replicates of the disturbance treatment. Stolons connecting attached control colonies did little regardless of density and none were lost (Fig. 5). Two-way analysis of variance on the change in total stolon length substantiates the significant interaction between density and the simulated disturbance (MSE $= 76.5$, $F = 4.154$, df $= 1, 32, P < 0.05$).

DISCUSSION

Our results support the conclusion that clonal growth, survivorship, and asexual recruitment of *Efflatounaria* are strongly density dependent. Clonal growth resulted in rapid directional movement, which promoted substrate colonization, asexual recruitment of new colonies by fission, and the formation of dense aggregations in which colonies experienced significantly higher survivorship. The dominance of *Efflatounaria* at our intermittently disturbed, shallow-water study site is consistent with the prediction that stolon-

TABLE 1. Results of clearing experiment after 109 d. Mean values $\pm$ 1 SE are given for initial and final densities (no. colonies/100 cm^2) and percentage cover.

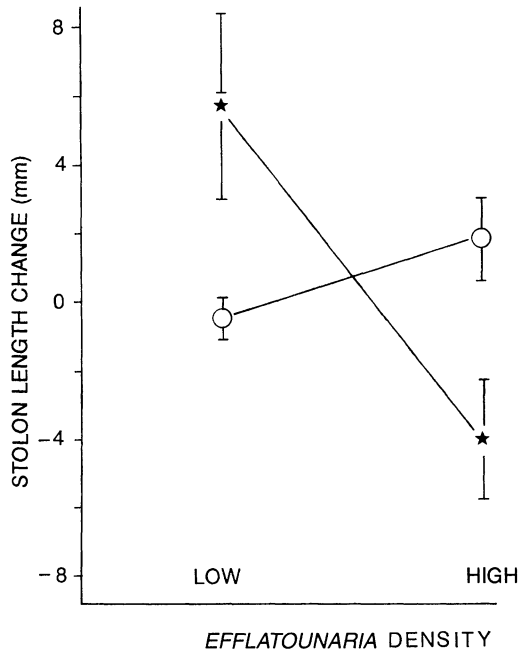|	Control (n = 5)	Total clearing (n = 5)	Partial clearing (n = 5)
Initial density	1.82 ± 0.15	0	1
Final density	2.02 ± 0.28	1.46 ± 0.26	1.36 ± 0.33
Initial percentage cover	75.7 ± 6.7	0	13.3 ± 5.0
Final percentage cover	66.6 ± 6.5	20.6 ± 8.0	34.5 ± 6.8

FIG. 5. Changes in total stolon length in response to the detachment of the daughter colony from the substrate (a simulated disturbance) at high and low densities of *Efflatounaria* colonies. Means ± 1 SE are indicated for 20 control (circles) and 20 disturbed (stars) pairs of stolonally connected colonies. Lines connecting mean values are indicative of the significant interaction between density and disturbance.

iferous or runner-like forms should be more successful than other growth forms in disturbed environments (Jackson 1979, Fahrig et al. 1994). The capacity to form stolons and reorganize colonies facilitated recovery from injuries and mortality caused by disturbance events. The inhibition of stolonal growth at high density in *Efflatounaria* is strikingly similar to the effects of competition in plants, where crowding also reduces modular "birth" rates, interferes with clonal growth processes (Schmid and Harper 1985, Jones and Harper 1987a, b, Solangaarachchi and Harper 1989), and diminishes the capacity of competing modules to exploit local resources (Harper 1985).

Virtually all of the recruits we observed during the study were of clonal origin, generated when stolonal connections between incipient daughter colonies were absorbed. Furthermore, the rate of (asexual) recruitment was sufficiently high to offset mortality, since the high density of colonies was maintained. The prevalence of asexual recruitment in *Efflatounaria* has been confirmed elsewhere from the Great Barrier Reef by Dinesen (1985) in a 19-mo study, and by Lasker (1988) who found that 92% of 60 colonies were undergoing fission. High rates of clonal fission appear to be the major source of aggregated colonies in this species. Clumped settlement of larvae or patchy mortality may also influence this dispersion pattern, but they are unlikely to be major contributors to the formation of dense

aggregations compared with the very rapid rates of directional growth and fission we have documented. The reduced risk of mortality to *Efflatounaria* colonies at high density represents a significant benefit of aggregation (see Buss 1981, Karlson 1988a for other examples) and is a plausible explanation for the selective advantage of stolonal growth. The observation that colonies moved closer together in response to the simulated disturbance only at high density (Fig. 5) also indicates the advantage of aggregation. If disturbed or injured colonies survive better under crowded conditions, then moving closer together should be adaptive (Fig. 4).

Some of our results are not consistent with the predicted life-history correlates of a stoloniferous growth form. We found that clonal processes dominated the dynamics of *Efflatounaria* aggregations, and that rates of sexual recruitment were very low. Therefore, it seems unlikely that colonies are highly fecund (as predicted for sessile animals employing "runners"; see Jackson 1979, Coates and Jackson 1985). Furthermore, the expectation that stoloniferous organisms should have relatively high mortality rates among modules (Coates and Jackson 1985, Schmid and Harper 1985, Jones and Harper 1987a, b) was also not realized. The mortality rates we measured were low, and became progressively lower with increasing density (Fig. 4). These inconsistencies may be indicative of a plastic life-history strategy in *Efflatounaria*, in which stolons are employed only intermittently in response to low density and to injuries associated with disturbance events. As density increases, *Efflatounaria* appears to switch from a fugitive strategy that promotes colony reorganization and clonal growth of stolons to one facilitating persistence of aggregations with greatly reduced mortality rates.

The "guerilla" growth habit of plants and the "runner" morphology of sessile animals has been viewed as a form of dispersal (Buss 1979, Sackville Hamilton et al. 1987, Fahrig et al. 1994) because they promote the movement of modules across local microhabitats. Although mobility in sessile organisms is generally confined to a juvenile dispersive phase, many attached clonal animals and plants have a considerable capacity for dispersal through rapid directional growth or by the production of asexual propagules by fission, fragmentation, or gemmulation. Theoretical explanations for the evolution of clonal dispersal mechanisms generally pose either density-dependent competition (Hamilton and May 1977, Comins et al. 1980) or the risks of density-independent catastrophes (Comins et al. 1980, Karlson and Taylor 1992, 1995) as the primary agents of selection on dispersal traits. Our recruitment observations and density manipulations both indicate that stolonal growth in *Efflatounaria* is promoted at low density and inhibited at high density. Thus, the theoretical notion that clonal dispersal represents some form of escape from the detrimental consequences of

high density is not supported by our results. Clearly, dense clonal aggregations provide considerable advantages to *Efflatounaria* which may involve important cooperative rather than competitive phenomena. Since clonal dispersal by stolons promotes the formation of these aggregations, we suggest that future developments in dispersal theory incorporate selection favoring aggregation and cooperative behavior.

LITERATURE CITED

Ayre, D. J. 1984. The effects of sexual and asexual reproduction on geographic variation in the sea anemone *Actinia tenebrosa*. Oecologia 62:222–229.

Bak, R. P. M., J. Sybesma, and F. C. van Duyl. 1981. The ecology of the tropical compound ascidian *Trididemnum solidum*. II. Abundance, growth and survival. Marine Ecology Progress Series 6:43–52.

Bell, A. D., and P. B. Tomlinson. 1980. Adaptive architecture of rhizomatous plants. Botanical Journal of the Linnean Society 80:125–160.

Buss, L. W. 1979. Habitat selection, directional growth, and spatial refuges: why colonial animals have more hiding places. Pages 459–497 *in* G. Larwood and B. R. Rosen, editors. Biology and systematics of colonial organisms. Academic Press, London, England.

———. 1981. Group living, competition, and the evolution of cooperation in a sessile invertebrate. Science 213:1012–1014.

Coates, A. G., and J. B. C. Jackson. 1985. Morphological themes in the evolution of clonal and aclonal marine invertebrates. Pages 67–106 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionary stable dispersal strategies. Journal of Theoretical Biology 82:205–230.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Dinesen, Z. D. 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. Coral Reefs 1:229–236.

———. 1985. Aspects of the life history of a stolon-bearing species of *Efflatounaria* (Octocorallia: Xeniidae). Proceedings of the 5th International Coral Reef Congress, Tahiti 6:89–94.

Fahrig, L., D. P. Coffin, W. K. Lauenroth, and H. H. Shugart. 1994. The advantage of long-distance clonal spreading in highly disturbed habitats. Evolutionary Ecology 8:172–187.

Gohar, H. A. F. 1939. On a new Xeniid genus *Efflatounaria*. Annals and Magazine of Natural History 11:32–36.

Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. Nature 269:578–581.

Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. Ecological Monographs 41:27–52.

Harper, J. L. 1985. Modules, branches, and the capture of resources. Pages 1–33 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Harper, J. L., and J. White. 1974. The demography of plants. Annual Review of Ecology and Systematics 5:419–463.

Heinselmann, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329–382.

Highsmith, R. C. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series 7:207–226.

Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551.

Hughes, T. P., D. Ayre, and J. H. Connell. 1992. The evolutionary ecology of corals. Trends in Ecology and Evolution 7:292–295.

Hughes, T. P., and J. B. C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209:713–715.

Jackson, J. B. C. 1979. Morphological strategies in sessile animals. Pages 499–555 *in* G. Larwood and B. R. Rosen, editors. Biology and systematics of colonial organisms. Academic Press, London, England.

Jackson, J. B. C., L. W. Buss, and R. E. Cook, editors. 1985. Population biology of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Jones, M., and J. L. Harper. 1987a. The influence of neighbours on the growth of trees. I. The demography of buds in *Betula pendula*. Proceedings of the Royal Society of London, Series B 232:1–18.

Jones, M., and J. L. Harper. 1987b. The influence of neighbours on the growth of trees. II. The fate of buds on long and short shoots in *Betula pendula*. Proceedings of the Royal Society of London, Series B 232:19–33.

Karlson, R. H. 1986. Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians. Marine Ecology Progress Series 28:245–249.

———. 1988a. Growth and survivorship of clonal fragments in *Zoanthus solanderi* Lesueur. Journal of Experimental Marine Biology and Ecology 123:31–39.

———. 1988b. Size-dependent growth in two zoanthid species: a contrast in clonal strategies. Ecology 69:1219–1232.

Karlson, R. H., and L. E. Hurd. 1993. Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs 12:117–125.

Karlson, R. H., and H. M. Taylor. 1992. Mixed dispersal strategies and clonal spreading of risk: predictions from a branching process model. Theoretical Population Biology 42:218–233.

Karlson, R. H., and H. M. Taylor. 1995. Alternative predictions for optimal dispersal in response to catastrophic mortality. Theoretical Population Biology 47:321–330.

Lasker, H. R. 1984. Asexual reproduction, fragmentation, and skeletal morphology of a plexaurid gorgonian. Marine Ecology Progress Series 19:261–268.

———. 1988. The incidence and rate of vegetative propagation among coral reef alcyonarians. Proceedings of the 6th International Coral Reef Symposium, Townsville 2:763–768.

———. 1990. Clonal propagation and population dynamics of a gorgonian coral. Ecology 71:1578–1589.

Lovett Doust, L. 1981. Population dynamics and specialization in a clonal perennial (*Ranunculus repens*). I. The dy-

namics of ramets in contrasting habitats. Journal of Ecology **69**:743–755.

Macfadyen, L. M. I. 1936. Alcyonaria (Stolonifera, Alcyonacea, Telestacea, and Gorgonacea). Scientific Reports of the Great Barrier Reef Expedition **2**:19–71.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs **45**:285–305.

Platt, W. J., and I. M. Weiss. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. American Naturalist **111**:479–513.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York, New York, USA.

Sackville Hamilton, N. R., B. Schmid, and J. L. Harper. 1987. Life-history concepts and the population biology of clonal organisms. Proceedings of the Royal Society of London, Series **B 232**:35–57.

Schmid, B., and J. L. Harper. 1985. Clonal growth in grass-

land perennials. I. Density and pattern-dependent competition between plants with different growth forms. Journal of Ecology **73**:793–808.

Solangaarachchi, S. M., and J. L. Harper. 1989. The growth and asymmetry of neighboring plants of white clover (*Trifolium repens* L.). Oecologia **78**:208–213.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Verseveldt, J. 1977. Australian Octocorallia (Coelenterata). Australian Journal of Marine and Freshwater Research **28**: 171–240.

Winston, J. E. 1976. Experimental culture of the estuarine ectoproct *Conopeum tenuissimum* from Chesapeake Bay. Biological Bulletin **150**:318–335.

Wulff, J. L. 1991. Asexual fragmentation, genotype success, and population dynamics of erect branching sponges. Journal of Experimental Marine Biology and Ecology **149**:227–247.

LINKED CITATIONS

- Page 1 of 3 -

You have printed the following article:

Density-Dependent Dynamics of Soft Coral Aggregations: The Significance of Clonal Growth and Form
Ronald H. Karlson; Terence P. Hughes; Susan R. Karlson
Ecology, Vol. 77, No. 5. (Jul., 1996), pp. 1592-1599.
Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28199607%2977%3A5%3C1592%3ADDOSCA%3E2.0.CO%3B2-2

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

Group Living, Competition, and the Evolution of Cooperation in a Sessile Invertebrate
Leo W. Buss
Science, New Series, Vol. 213, No. 4511. (Aug. 28, 1981), pp. 1012-1014.
Stable URL:
http://links.jstor.org/sici?sici=0036-8075%2819810828%293%3A213%3A4511%3C1012%3AGLCATE%3E2.0.CO%3B2-R

Diversity in Tropical Rain Forests and Coral Reefs
Joseph H. Connell
Science, New Series, Vol. 199, No. 4335. (Mar. 24, 1978), pp. 1302-1310.
Stable URL:
http://links.jstor.org/sici?sici=0036-8075%2819780324%293%3A199%3A4335%3C1302%3ADITRFA%3E2.0.CO%3B2-2

Succession after Fire in the Chaparral of Southern California
Ted L. Hanes
Ecological Monographs, Vol. 41, No. 1. (Winter, 1971), pp. 27-52.
Stable URL:
http://links.jstor.org/sici?sici=0012-9615%28197124%2941%3A1%3C27%3ASAFITC%3E2.0.CO%3B2-G

The Demography of Plants
J. L. Harper; J. White
Annual Review of Ecology and Systematics, Vol. 5. (1974), pp. 419-463.
Stable URL:
http://links.jstor.org/sici?sici=0066-4162%281974%295%3C419%3ATDOP%3E2.0.CO%3B2-J

Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef
Terence P. Hughes
Science, New Series, Vol. 265, No. 5178. (Sep. 9, 1994), pp. 1547-1551.
Stable URL:
http://links.jstor.org/sici?sici=0036-8075%2819940909%293%3A265%3A5178%3C1547%3ACPSALD%3E2.0.CO%3B2-Y

Do Corals Lie about their Age? Some Demographic Consequences of Partial Mortality, Fission, and Fusion
T. P. Hughes; J. B. C. Jackson
Science, New Series, Vol. 209, No. 4457. (Aug. 8, 1980), pp. 713-715.
Stable URL:
http://links.jstor.org/sici?sici=0036-8075%2819800808%293%3A209%3A4457%3C713%3ADCLATA%3E2.0.CO%3B2-S

Size-Dependent Growth in Two Zoanthid Species: A Constrast in Clonal Strategies
Ronald H. Karlson
Ecology, Vol. 69, No. 4. (Aug., 1988), pp. 1219-1232.
Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28198808%2969%3A4%3C1219%3ASGITZS%3E2.0.CO%3B2-X

Clonal Propagation and Population Dynamics of a Gorgonian Coral
Howard R. Lasker
Ecology, Vol. 71, No. 4. (Aug., 1990), pp. 1578-1589.
Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28199008%2971%3A4%3C1578%3ACPAPDO%3E2.0.CO%3B2-A

Population Dynamics and Local Specialization in a Clonal Perennial (Ranunculus Repens): I. The Dynamics of Ramets in Contrasting Habitats
Lesley Lovett Doust
The Journal of Ecology, Vol. 69, No. 3. (Nov., 1981), pp. 743-755.
Stable URL:
http://links.jstor.org/sici?sici=0022-0477%28198111%2969%3A3%3C743%3APDALSI%3E2.0.CO%3B2-8

The Colonization and Formation of Equilibrium Plant Species Associations on Badger Disturbances in a Tall-Grass Prairie
William J. Platt
Ecological Monographs, Vol. 45, No. 3. (Summer, 1975), pp. 285-305.
Stable URL:
http://links.jstor.org/sici?sici=0012-9615%28197522%2945%3A3%3C285%3ATCAFOE%3E2.0.CO%3B2-J

LINKED CITATIONS

- Page 3 of 3 -

Resource Partitioning and Competition within a Guild of Fugitive Prairie Plants
William J. Platt; I. Michael Weis
The American Naturalist, Vol. 111, No. 979. (May - Jun., 1977), pp. 479-513.
Stable URL:
http://links.jstor.org/sici?sici=0003-0147%28197705%2F06%29111%3A979%3C479%3ARPACWA%3E2.0.CO%3B2-8

Clonal Growth in Grassland Perennials: I. Density and Pattern-Dependent Competition Between Plants with Different Growth Forms
Bernhard Schmid; John L. Harper
The Journal of Ecology, Vol. 73, No. 3. (Nov., 1985), pp. 793-808.
Stable URL:
http://links.jstor.org/sici?sici=0022-0477%28198511%2973%3A3%3C793%3ACGIGPI%3E2.0.CO%3B2-Z

Experimental Culture of the Estuarine Ectoproct Conopeum tenuissimum from Chesapeake Bay
Judith E. Winston
Biological Bulletin, Vol. 150, No. 2. (Apr., 1976), pp. 318-335.
Stable URL:
http://links.jstor.org/sici?sici=0006-3185%28197604%29150%3A2%3C318%3AECOTEE%3E2.0.CO%3B2-0