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Fission and the dynamics of genets and ramets in clonal cnidarian populations

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Abstract

The dynamics of clonal populations involve a range of biological processes controlling 'birth' and 'death' rates of genets (i.e., clones) and ramets (i.e., the modular subunits of clones). These two levels of organization were examined for open, fissiparous, resource-limited populations using a modified Leslie matrix. Population projections were used to illustrate the method of predicting equilibrium population sizes and clonal structure for hypothetical populations with a range of recruitment, mortality, and fission rates; and to predict these parameters for natural populations of two common, coral reef zoanthids *Zoanthus sociatus* and *Z. solanderi.* Fission had the largest impact on population structure when recruitment rates were low and survivorship high. High recruitment rates resulted in the inhibition of density-dependent fission. Low survivorship precluded fission by restricting the number of ramets reaching a size large enough for fission to occur. In projections for zoanthid populations, undisturbed populations reached equilibrium sizes in 2–3 decades, but genet numbers within these populations continued to change over much longer time periods. This result indicates that the clonal structure of natural populations may not be at or near equilibrium and that realistic predictions about this structure will require extensive knowledge of past history.

Introduction

Fission is one of the major modes of asexual reproduction (amixis) in cnidarians. In two common, colonial zoanthids (*Zoanthus sociatus* (Ellis) and *Z. solanderi* Lesueur), fission results from endogenous processes controlling stolonal elongation, budding of new polyps, and stolonal degeneration (Karlson, 1986). As a result of exogenous disturbances which disrupt these fission products and the substrate on which they grow, clonal fragments are dispersed locally through zoanthid populations (Karlson, 1988). Here, two questions regarding the population consequences of fission are addressed: 1) In general, how does fission affect population size and clonal structure? 2) How do known life history differences between the two zoanthid species identified above affect population size and clonal structure?

These questions arise from consideration of the dynamics of clonal populations in which the processes affecting 'births' and 'deaths' of clones differ from those governing individuals. This distinction has been emphasized by Harper and his co-workers and it has influenced much recent work on clonal plant populations (Harper, 1981; Silander, 1985). Their terminology is used here in designating clones as genets and clonal fragments as ramets.

Methods

In order to predict the population consequences of fission, a modified Leslie matrix model for size-structured populations was used. This approach is appropriate for dealing with zoanthid populations because these tropical cnidarians are long-lived, fission is common, survivorship is size-dependent, and age and size are decoupled as determinants of life history (Karlson, 1988). The general model for closed populations has been used extensively (see Caswell, 1989) and is stated as: $X_{t+1} = A X_t$, where X is a column vector describing population age or stage structure and A is the transition matrix. Populations of most marine invertebrates, however, are open rather than closed. Most species have widely dispersed larval stages and there is little feedback between local production of larvae and local recruitment rates. The model describing the dynamics of a single, open population is: $X_{t+1} = A X_t + R$, where X and A are as described above and R is the column vector describing a recruitment process independent of local reproductive output (e.g., Hughes, 1984, 1990).

The effects of fission on hypothetical, resource-limited populations with the above characteristics were determined using a range of recruitment, survivorship and fission rates. Recruitment occurred at 10, 100 or 1000 recruits per time interval. Each recruit represented a unique genet, was assigned a unique identification code at the time of recruitment, and was monitored from recruitment through the time required for the population to reach equilibrium. This null model was used to generate a set of predictions regarding the clonal structure of fissiparous populations without discriminating among genets (i.e., there was no selection). Resource-limitation of population size (N) was achieved by multiplying the probability of fission (F_3) by $(K - N)/K$, where $K = 1000$ ramets. This made fission density-dependent (as it decreased with increasing density) and set an upper limit to population size. It was assumed that fission resulted only in transitions from the largest size class to the intermediate size class and that each fission event produced only two ramets. No distinction was made between ramets produced by fission and those that grew from the smallest size class.

A type III, size-dependent survivorship schedule was used in which the probability of death of a ramet (M_s) for each of three size classes (s = 1, 2 and 3) was defined using a constant exponential mortality rate (m); $M_s = \exp(-ms)$. At $M_1 = 0.9$, 0.7 and 0.5, this function yielded low size-dependent survivorship values of 0.100, 0.190 and 0.271, intermediate values of 0.300, 0.510 and 0.657, and high values of 0.500, 0.750 and 0.875 for small, medium, and large size classes, respectively. It was assumed that all surviving ramets in the two smaller size classes grew into the next larger class with a probability of $(1 - M_s)$. The probability of ramets remaining in the largest size class (i.e., looping as in Hughes, 1984) equalled $(1 - M_3)(1 - F_3)((K - N)/K)$. Population projections for hypothetical populations with the above growth, survivorship, and fission rates were run until both the number of ramets and genets stabilized, thus yielding estimates of equilibrium population size and clonal structure.

Fission in *Z. sociatus* and *Z. solanderi* occurs as the stolonal connections between polyps degenerate. The small clusters of connected polyps created by this process are defined here as ramets. These ramets remain together within large aggregations until they are dispersed locally during storms. Therefore, the growth in number of ramets is separate from the dispersal process and fission does not result in transitions between aggregation size classes. Furthermore, ramet survivorship and reproduction is dependent on the size of aggregations of ramets rather than on the size of the ramets (Karlson, 1986, 1988). Consequently, the appropriate size class states in the Leslie matrix model should indicate aggregation size rather than polyp cluster size.

These features of the zoanthid life history were incorporated into the Leslie matrix model as follows. It was assumed that the largest size class represented aggregations of ramets and that the transitions from the large to the intermediate size class represented storm-related, local dispersal of these ramets without any growth in their numbers. A net relative growth rate of 80% per annum for both species (Karlson, 1988) was used as a reasonable approximation of the growth in numbers of ramets within large aggregations and it was assumed that this growth rate would decrease as each population approached some carrying capacity (K). Therefore, the probability associated with the growth in the numbers of ramets within large aggregations was assumed to be $(1 - M_3)(1 - F_3)(1.8(K - N)/K)$.

The carrying capacity (i.e., the maximum number of ramets per unit area) for these sessile populations was estimated using polyp densities of 45000 polyps m^{-2} for *Zoanthus sociatus* and 16000 polyps m^{-2} for *Z. solanderi* (see Karlson, 1988) and estimates of ramet sizes of 2.3–4.5 polyps per cluster for *Z. sociatus* and 1.7–2.5 for *Z. solanderi* (see Karlson, 1986). Therefore, $K = 10000$ ramets for the former species and 6400 ramets for the latter.

Generally, *Z. sociatus* has lower survivorship rates than does *Z. solanderi* and these rates are highly dependent on aggregation size in both species (Karlson, 1986, 1988). The following approximations are given as probabilities that all polyps within an aggregation will die during one year: $M_1 = 0.60$, $M_2 = 0.60$ and $M_3 = 0.10$ for small, medium, and large aggregations of *Z. sociatus*; and $M_1 = 0.40$, $M_2 = 0.10$ and $M_3 = 0.01$ for *Z. solanderi*.

Finally, reasonable estimates of recruitment rates were required. As in so many other clonal organisms on coral reefs (see review in Jackson, 1985), recruitment rates in zoanthids appear to be extremely low (i.e., ≤ 10 recruits $m^2 y^{-1}$); far fewer ramets are produced by recruitment than by clonal growth and fission (Karlson, 1988). As a first approximation, 10 recruits per annum was used for both species. The assumption that these recruits come from regional sources, rather than from local populations, is compatible with our current understanding of zoanthid development. Ova are presumably broadcast spawned (Fadlallah *et al.*, 1984), externally fertilized, widely dispersed, and settling larvae are approximately an order of magnitude larger than the largest unfertilized ova (pers. obs.). Brooding is unknown among zoanthids.

Results

The size and clonal structure of hypothetical populations were highly dependent on survivorship, recruitment and fission. Population projections clearly indicate that equilibrium population size increases with increasing survivorship and recruitment rates (Fig. 1). However, the largest number of ramets was produced by fission at the highest survivorship values, yet lowest recruitment rates (Fig. 1). Populations experiencing the lowest survivorship were composed only of recently recruited genets. Populations experiencing the highest recruitment rates exceeded carrying capacity thereby precluding fission.

Projections for zoanthid populations experiencing no physical disturbances reached equilibrium population sizes after 20–30 y (Fig. 2). This is an approximation of the time required for population size to fully recover from

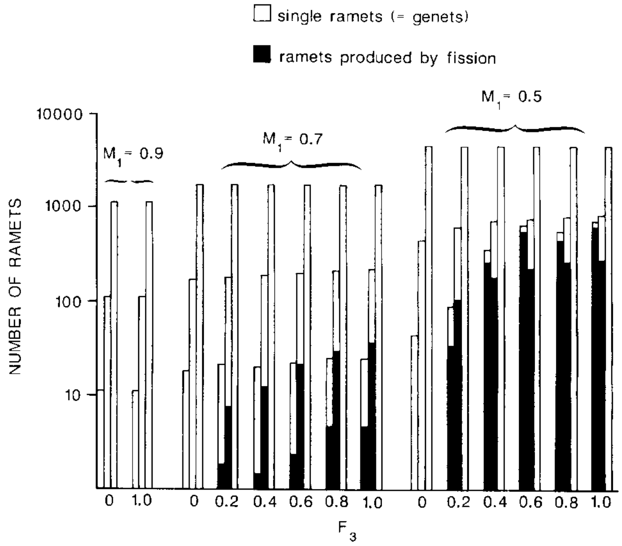

Fig. 1. Equilibrium population sizes (given as the total number of ramets) and mean number of ramets produced by fission (95% confidence limits were $< \pm 9.9$ ramets, $n = 10$) over a range of probabilities associated with fission (F_3) and mortality (M_i). Each triplet indicates the results when recruitment rates were 10, 100, and 1000 recruits (i.e., new genets) per time interval.

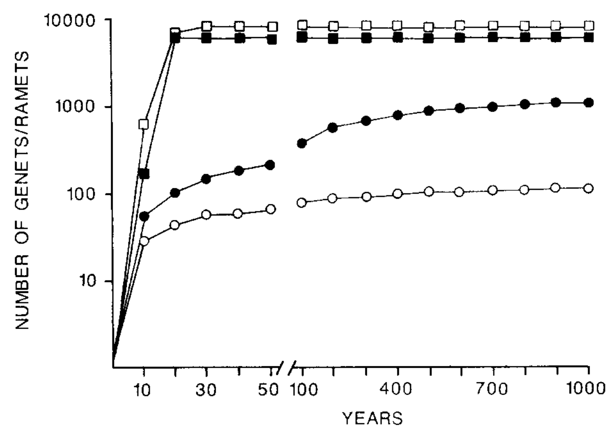

Fig. 2. Mean number of genets and ramets (circles and squares, respectively) versus time in population projections with no storm-related disturbances for *Z. sociatus* and *Z. solanderi* (open and closed symbols, respectively). 95% confidence limits for number of genets were < ± 6 genets for the former species and < ± 16 genets in the latter (n = 10).

catastrophic mortality associated with major storms. Because the number of new genets recruiting into these populations was low, the clonal structure of these populations did not begin to equilibrate for much longer time periods. For *Z. sociatus*, the number of genets in successive time periods began to repeat occasionally after 30–40 y; for *Z. solanderi*, after 50–120 y. These initial repetitions resulted from stochastic fluctuations in the numbers of genets dying or undergoing fission each year; these numbers depended on the frequency distribution of genet sizes with the smallest genets having the highest probability of dying (see May (1976) for a brief discussion of this type of variation). The zoanthid population projections indicate that centuries are required to reach a balance between the mean rate of genet death and the recruitment rate of new genets (Fig. 2). After reaching equilibrium, the number of genets in each population projection continued to fluctuate indefinitely in a stochastic manner.

The impact of disturbance and the storm-related dispersal of ramets in these zoanthid populations was evaluated by varying the probability of ramet transitions from large to intermediate-sized aggregations. This transition exposed ramets to higher mortality rates and precluded the production of new fission products by stolonal degeneration. Therefore, equilibrium population size in both species was inversely related to the magnitude of this transition probability (Fig. 3). Since the number of genets in these zoanthid populations could fluctuate over very long periods without reaching a single equilibrium value, the mean effect of size-class transitions is reported using the number of genets in each population projection when this variable began to repeat. These repetitions occurred at time intervals equivalent to 1–8 y. At low disturbance levels, the number of genets was over 5 times greater in *Z. solanderi* than in *Z. sociatus* and, on average, each genet was represented by over 7 times more ramets in the latter species (Fig. 3). In general, the number of ramets produced endogenously by fission (i.e., clonal propagation of new ramets) diminished with increasing levels of disturbance (Fig. 3).

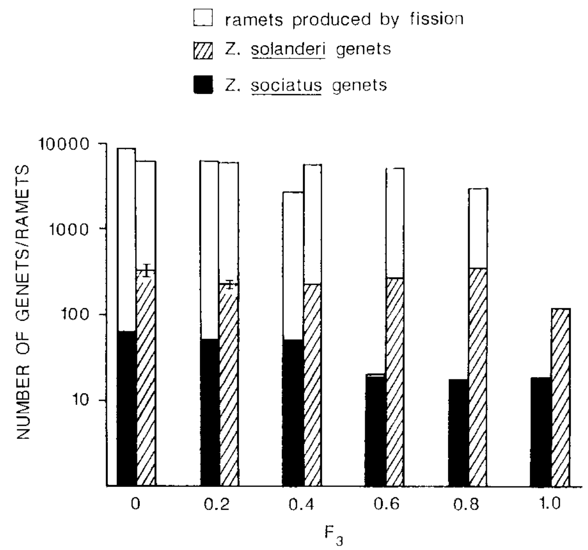

Fig. 3. Equilibrium population size (given as the total number of ramets) and mean number of genets plotted against a range of transition probabilities (F_3) representing disturbance. 95% confidence limits for number of genets were < ± 5 genets for *Z. sociatus* and < ± 14 genets for *Z. solanderi* except where indicated (n = 10).

Discussion

For resource-limited populations, fission had its greatest impact on population size and clonal structure when rates of recruitment and mortality were low. These two conditions appear to apply not only to zoanthids, but also to many other fissiparous invertebrates (Jackson, 1985). The population projections for fissiparous zoanthids indicate that the two species should differ considerably in terms of clonal structure, susceptibility of this structure to disturbance, and the recovery time following disturbance. However, given the long recovery times, the relative high frequency of disturbance events on coral reefs, and the unpredictable effects of these disturbances (e.g., Hughes, 1989), realistic predictions about clonal structure will require extensive knowledge of population history (e.g., the magnitude, frequency, and specific effects of past disturbances, variation in the biological and physical processes controlling normal recruitment rates, and the occurrence of episodic recruitment or mass mortality events). Since genet life spans can be extremely long, it is virtually impossible to know the complete history of such populations. Furthermore, the frequency of disturbance events is too high for clonal structure ever to equilibrate. These strong historical effects greatly diminish our ability to predict the clonal structure of these populations.

Recent studies on the genetic structure of some fissiparous cnidarian populations indicate higher levels of predictability than suggested above. Hunter (1988) reported an inverse relationship between clonal diversity and the time since major disturbances for populations of the coral *Porites compressa*. Since her genetic analysis indicated that recruits into these populations are locally derived, strong feedback within populations (associated with short dispersal distances and relatively high recruitment rates) may result in rapid equilibration of clonal structure in these coral populations. However, given the high frequency of corals which are broadcast spawners with external fertilization (Harrison *et al.*, 1984), many coral populations may disperse their larvae great distances, experience low rates of recruitment, and approach genetic equilibrium slowly.

Contrasting patterns have recently been reported for actinians. Clonal populations of *Anthopleura* spp. appear to be extremely diverse with many clones being represented by few ramets (Smith & Potts, 1987). Populations of *Metridium senile*, on the other hand, are composed of few clones represented by many ramets (Hoffmann, 1986). The relative rates of recruitment and clonal reproduction by pedal laceration appear to be critical determinants of clonal structure in these populations (Hoffmann, 1986, 1987).

In all of the above examples of clonal populations, the dynamics of genets and ramets are decoupled and operate on different time scales. In extreme cases with very low recruitment rates, the number of ramets in a population can be at equilibrium while the number of genets is far from equilibrium. In fact, the dynamics of genets in clonal populations with low genet 'birth' rates are probably so far from equilibrium that non-equilibrium models will be required to generate adequate null expectations of clonal structure.

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References

Caswell, H., 1989. Matrix population models. Sinauer Associates, Inc., Sunderland, 328 pp.

Fadlallah, Y. H., R. H. Karlson & K. P. Sebens, 1984. A comparative study of sexual reproduction in three species of Panamanian zoanthids (Coelenterata: Anthozoa). Bull. mar. Sci. 35: 80–89.

Harper, J. L., 1981. The concept of the modular organism. In R. M. May (ed.), Theoretical ecology: Principles and applications, 2nd edn. Sinauer, Sunderland: 53–77.

Harrison, P. L., R. C. Babcock, G. D. Bull, J. K. Oliver, C. C. Wallace & B. L. Willis, 1984. Mass spawning in tropical reef corals. Science, N.Y. 223: 1186–1189.

Hoffmann, R. J., 1986. Variation in contributions of asexual reproduction to the genetic structure of populations of the sea anemone *Metridium senile*. Evolution 40: 357–365.

Hoffmann, R. J., 1987. Short-term stability of genetic structure in populations of the sea anemone *Metridium senile*. Mar. Biol. 93: 499–507.

Hughes, T. P., 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. Am. Nat. 123: 778–795.

Hughes, T. P., 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70: 275–279.

Hughes, T. P., 1990. Recruitment limitation, mortality and population regulation in open systems: a case study. Ecology 71: 12–20.

Hunter, C. L., 1988. Genotypic diversity within and between Hawaiian *Porites compressa* populations with different disturbance histories. Am. Zool. 28: 111A.

Jackson, J. B. C., 1985. Distribution and ecology of clonal and aclonal benthic invertebrates. In J. B. C. Jackson, L. W. Buss & R. E. Cook (eds), Population Biology and Evolution in Clonal Organisms. Yale University Press, New Haven: 297–355.

Karlson, R. H., 1986. Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians. Mar. Ecol. Prog. Ser. 28: 245–249.

Karlson, R. H., 1988. Size-dependent growth in two zoanthid species: a contrast in clonal strategies. Ecology 69: 1219–1232.

May, R. M., 1976. Irreproducible results. Nature, Lond. 262: 646.

Silander, Jr, J. A., 1985. Microevolution in clonal plants. In J. B. C. Jackson, L. W. Buss & R. E. Cook (eds), Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven: 107–152.

Smith, B. L. & D. C. Potts, 1987. Clonal and solitary anemones (*Anthopleura*) of western North America: population genetics and systematics. Mar. Biol. 94: 537–546.