OIKOS 55: 349–355. Copenhagen 1989

Size hierarchies in Membranipora membranacea: do colonial animals follow the same rules as plants?

Aaron M. Ellison and C. Drew Harvell

Ellison, A. M. and Harvell, C. D. 1989. Size hierarchies in *Membranipora membranacea:* do colonial animals follow the same rules as plants? – Oikos 55: 349–355.

The relative importance of mode of intraspecific competition, growth rate, and recruitment time on size structure of populations of the bryozoan *Membranipora membranacea* was examined experimentally. Size distributions of populations of solitary colonies (1/225 cm^2), low density colonies ($<15/225$ cm^2), and high density colonies ($>25/225$ cm^2) were compared to determine if mechanisms that generate size hierarchies in plant populations also operate on populations of sessile invertebrates. Degree of inequality increased from solitary to low density populations, indicating that colony growth rate alone does not determine inequality. However, no difference in inequality was observed between low and high density populations, and degree of inequality neither increased nor decreased through time, indicating that the dominant mode of competition in these populations was resource depletion. Late-recruiting colonies were smaller than early recruits, but did not suffer disproportionately from competition relative to their size or recruitment time. This latter result lends further support to the hypothesis that resource depletion is the major determinant of size distributions in these populations. We conclude that processes similar to those that produce hierarchical size distributions in plant populations also structure populations of colonial invertebrates.

A. M. Ellison and C. D. Harvell, Section of Ecology and Systematics, Corson Hall, Cornell Univ., Ithaca, NY 14853-2701, USA (present address of AME and all correspondence: Dept of Biology, Swarthmore College, Swarthmore, PA 19081, USA).

Introduction

Within populations of animals and plants, individuals can vary greatly in size. Larger individuals may have (for example) higher life expectancies or reproductive success (Hiroi and Monsi 1966, Cook 1979, Leverich and Levin 1979, Solbrig 1981, Grosberg 1982, Highsmith 1982, Watkinson et al. 1983, Hughes 1984, Hughes and Cancino 1985, Hughes and Jackson 1985), and if large individuals differ in genetic composition from other population members, the former may contribute a disproportionate share of alleles to future generations (Heywood 1986). Elucidating mechanisms that generate size inequality in populations of animals and plants is, therefore, necessary to further our understanding of population dynamics and evolutionary change. However, while investigators have long recognized the importance of the consequences of size variation among individuals (reviewed by Łomnicki 1988), there remains considerable debate among population biologists as to the mechanisms causing this variation (reviewed by Benjamin and Hardwick 1986, Weiner and Thomas 1986).

In the last thirty years, plant population biologists have carefully studied patterns of size distributions and uncovered several potential mechanisms for generating hierarchical (sensu Weiner and Solbrig 1984) size distributions (Ford 1975, Hara 1984a, b, 1986a, b, Uchmanski 1985, Benjamin and Hardwick 1986, Weiner and Thomas 1986). Weiner and Solbrig (1984) define size hierarchies in economic terms. A strongly hierarchical population is one in which most of the biomass or resources is concentrated in one or a few individuals. In contrast, a more equitable population is one in which no

Accepted 22 February 1989

one individual has a disproportionate share of the total populations's biomass or resources.

In the clearest exposition of the underlying causes of size hierarchy formation in even-aged monocultures, Weiner and Thomas (1986) distinguished two models for the effects of competition on size distributions, the resource depletion model (symmetric competition) and the resource pre-emption model (asymmetric competition). In the resource depletion, or two-sided competition model, competition acts on all individuals in the population equally or in proportion to their size, and degree of inequality should show little change through time and/or with increasing density. In the resource pre-emption, or one-sided competition model, large individuals suppress the growth of small ones and expropriate a disproportionate share of resources, and degree of inequality should increase dramatically through time and with increasing density (a detailed explanation of these models is given by Weiner and Thomas (1986)). The latter model is often referred to as the dominance and suppression model (Harper 1977, Turner and Rabinowitz 1983). Turner and Rabinowitz (1983), Ellison (1987a), and Petersen (1988) found evidence for a third mechanism responsible for size hierarchy formation in even-aged monocultures. These investigators found that variation in growth rate, acting on a population of individuals whose size distribution was initially normal, was sufficient to account for development of hierarchial size distributions (see also Koyama and Kira 1956, Koch 1966, Uchmanski 1985). Although Turner and Rabinowitz's study has been critized (Weiner and Thomas 1986), and dominance and suppression is by far the most common determinant of size hierarchies in even-aged monocultures (Benjamin and Hardwick 1986, Weiner and Thomas 1986), the growth rate model should serve as a null hypothesis for size hierarchy formation before assuming a priori that competition for resources determines size hierarchy formation.

In populations where individuals are of different ages, a fourth factor, recruitment time, also affects size distributions. There are far fewer studies of uneven-aged monocultures than there are studies of even-aged monocultures, even though very few natural populations are composed of individuals of identical ages. Different investigators have defined 'even-aged' or 'uneven-aged' in different ways; 'even-aged' had been used to describe populations whose individuals recruit in a period of as few as 3 to as many as 90 d (Mithen et al. 1984, Matlack and Harper 1986, Schmitt et al. 1986, Shaw and Antonovics 1986), while 'uneven-aged' has been used for populations whose individuals recruit in a period of as few as 1 to as many as 42 d (Ross and Harper 1972, Dolan 1984, Dolan and Sharitz 1984, Fowler 1984, Ellison 1987b, Ellison and Rabinowitz 1989). These latter studies have shown that the time of recruitment into the population can significantly affect final size. Delayed recruitment results in smaller size, fewer offspring, and higher probability of mortality.

Determining the relative contributions of recruitment time, growth rate, resource depletion and resource pre-emption to size hierarchy formation in plant populations has proven to be difficult (Donald 1958, Litav and Wolovitch 1971, Snaydon 1971, 1979, Willey and Reddy 1981, Cook and Ratcliff 1984, Weiner 1986, Wilson 1988). While it is generally agreed that competition for light is asymmetric (Weiner and Thomas 1986), whether competition for nutrients is primarily due to depletion or pre-emption remains contested (Weiner and Thomas 1986). Variation in growth rate can affect a plant's ability to compete for either resource. Similarly, late recruits would be expected to fare poorly in assymmetric competitive interactions, but might fare better if competition for needed resources was symmetric.

The best demonstration of the effects of recruitment time, growth rate, and mode of competition would use an organism that forms easily-aged monocultures (i.e. recruitment can be easily observed) and has only one major limiting resource. This experiment would clearly delineate the effects of recruitment time and mode of competition for a single resource on size hierarchy formation.

Sessile, colonial benthic invertebrates are good candidates for such a study. There are numerous parallels in growth form (modularity, sensu Harper 1981) and population dynamics between plants and sessile animals (e.g. Harper and Bell 1979, Wethey 1983, White 1984, Jackson et al. 1985, Harper et al. 1986). Like plants, sessile animals often form monospecific populations, but unlike plants, these animals have no hidden structures (e.g. roots), and for many benthic invertebrates, two-dimensional space available for growth is the dominant resource limiting growth (Wethey 1983, 1984, Connell 1983, Connell and Keogh 1985, Jackson et al. 1985, Roughgarden et al. 1985). There is evidence that competition for food among adjacent colonies occurs (e.g. Buss 1981, Buss and Jackson 1981, Okamura 1984, 1985), but these interactions are strongly dependent on available space. Limitations in available space for growth can limit colony size and reproduction; as with plants, timing and amount of reproduction in sessile invertebrates is often highly correlated with size (Grosberg 1982, Highsmith 1982, Hughes 1984, Hughes and Cancino 1985, Hughes and Jackson 1985, Harvell and Grosberg 1988, Harvell et al., in press). Although numerous studies of competitive interactions among sessile invertebrates have been done (Wethey 1983, 1984, reviewed by Connell 1983, Buss 1985, Connell and Keogh 1985, Jackson et al. 1985, Roughgarden et al. 1985), monoculture studies are not as common and a detailed examination of size hierarchies in these animals has not been reported.

Here, we report the results of a study that examined patterns of size inequality in the bryozoan, *Membranipora membranacea* L. *M. membranacea* grows as a sheet-like colony and two-dimensional space is the major resource limiting colony growth (Harvell et al., in

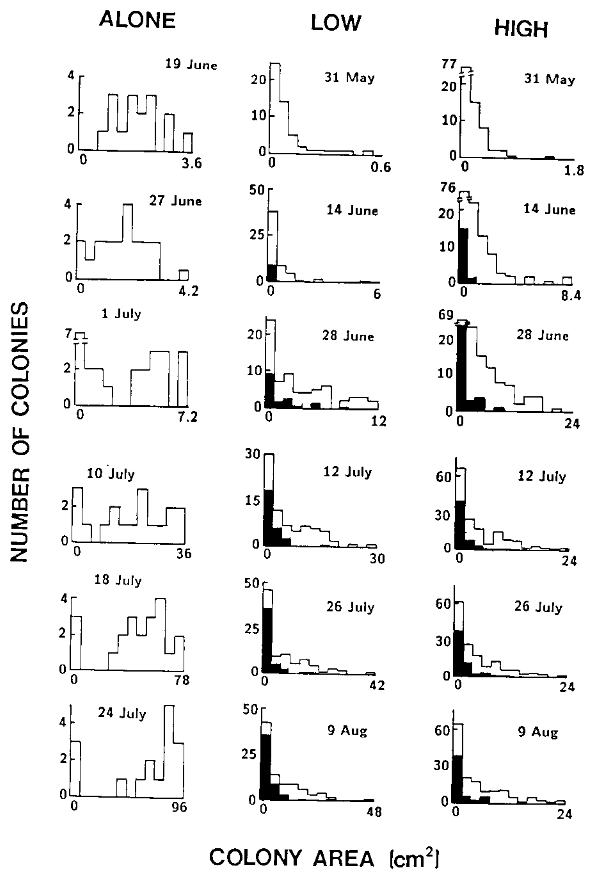

Fig. 1. Size distributions of *M. membranacea* colonies in the three treatments (Alone – 1 colony/panel; Low – <15 colonies/panel; High – >25 colonies/panel) throughout the summer. Each histogram presents size distributions in 12 equal size classes from 0 to the maximum size (Note change of scale on each histogram). Late-recruiting colonies are shaded. The sampling date is given for each histogram. Statistics for the histograms are given in Tabs 1–3.

press). In particular, we ask three questions: (1) do assemblages of *M. membranacea* exhibit size hierarchies, (2) do these size hierarchies increase or decrease with increasing density and how do these size hierarchies change through time, and (3) do these size hierarchies result from processes similar to those acting on plant populations?

Materials and methods

Membranipora membranacea is an encrusting cheilostome bryozoan that grows epiphytically on kelp blades throughout the world's temperate oceans (Osburn 1950). In the northeastern Pacific Ocean, thousands of individual colonies may occur on a single large kelp blade. In the San Juan Archipelago, Washington, larvae of *M. membranacea* settle onto kelp initially in May, and settlement continues for one-three weeks, with an occasional mid-season pulse. Growth and reproduction occur through the summer, and colonies senesce by September (Harvell et al., in press). By July, the colonies fill almost all their available space. When two colonies intersect, their growth stops at the zone of contact (Harvell and Padilla, in review, Harvell et al., in press). Unlike many other cheilostome bryozoans which overgrow one another when colonies intersect (e.g. Buss 1985), one colony of *M. membranacea* rarely overgrows another colony (Harvell et al., in press). Further details on the life history of *M. membranacea* are given in Harvell et al. (in press).

M. membranacea larvae will readily settle onto artificial substrata (Harvell et al., in press). On 15 May 1984, 14 black plexiglass panels (15 × 15 cm) were suspended parallel to the water surface with nylon line at a depth of 2 m from the Friday Harbor Laboratories floating breakwater. The near opacity of the panels prevented light transmission and subsequent growth of diatoms on the bottoms of the panels. The horizontal undersurfaces of the panels were readily colonized and dominated by colonies of *M. membranacea*.

Panels were sampled non-destructively every two weeks from 31 May until 20 September 1984 by which time most colonies were dead. Fewer than 1% of the colonies recruited after 13 June 1984. The sampling areas on each 15 × 15 cm panel was 11 × 7 cm (77 cm^2) to minimize edge effects. Because the colonies are two-dimensional sheets, growth can be accurately measured as projected area, and the outlines of all colonies were traced onto transparent acetate sheets at each sampling date (details in Harvell et al., in press). Only colonies or portions of colonies completely within 11 × 7 cm rectangle were traced; sections of colonies that grew out of the area were not recorded. This sampling procedure underestimated the maximum size of some (particularly large) colonies and resulted in a conservative estimate of the magnitude of the size hierarchies on each panel. On 7 June, before all space on the panels was covered by *M. membranacea,* colonies were randomly thinned to two densities on seven panels each: <15 colonies/77 cm^2 (referred to as low density) and >25 colonies/77 cm^2 (referred to as high density).

A similar set of 25 panels was established in 1987 to examine variation among solitary colonies. These panels were thinned to 1 colony per panel (solitary treatment) and were sampled at irregular intervals between 19 June and 1 August 1987. After 1 August, solitary colonies completely covered their respective panels and further measurements of growth were impossible. The total area of each solitary colony was measured; thus, the measured area of solitary colonies can exceed 77 cm^2. Complete details on the culture methods used are given in Harvell et al. (in press).

The degree of size inequality among colonies in each treatment at each sampling date was determined using the Gini coefficient (G) (Weiner and Solbrig 1984).

Tab. 1. Values for G (with 95% confidence intervals) for the size distributions of solitary colonies shown in Fig. 1.

Date	G	95% confidence interval
19 June	0.248	0.164–0.297
27 June	0.331	0.227–0.424
1 July	0.454	0.327–0.566
10 July	0.385	0.260–0.494
18 July	0.269	0.165–0.372
24 July	0.269	0.135–0.407

Values of G increase from 0 to 1 with increasing inequality. If all of the individuals are the same size (no inequality), $G = 0$. The theoretical maximum of $G = 1$ would be obtained in a population where one individual was of size >0 and all other individuals were of size 0. Non-parametric bootstrapped 95% confidence intervals around G were calculated following the method of Efron (1982). Non-overlap of 95% confidence intervals among values of G indicated significant differences at the 0.05 level. The measure of size used was total colony area (cm^2), which is a good indicator of both competitive ability and reproductive potential (Highsmith 1982, Grosberg 1982, Hughes 1984, Hughes and Cancino 1985, Hughes and Jackson 1985, Harvell and Padilla, in review, Harvell et al., in press). To determine the contribution of recruitment time to degree of inequality in the low and high density populations, G was calculated for (1) the total population, regardless of settlement date, (2) for individuals settling on or before the first sampling date, 31 May (the 'early' cohort), and (3) for individuals settling between the first and second sampling dates (the 'late' cohort).

Results

Colonies growing alone were twice as large as the largest colonies grown at low densities, which, in turn, were twice as large as the largest colonies grown at high density (Fig. 1). Only data collected through 9 August are presented, as senescence (not-density-dependent mortality) set in after this date (Harvell et al., in press). The degree of inequality among solitary colonies was not significantly different from that of a normal distribution (Fig. 1, Tab. 1).

Colonies grown at both low and high densities (pooled over settlement cohorts) exhibited pronounced size hierarchies, but the degree of size inequality among all colonies did not change over the colonies' lifespan (Fig. 1, Tab. 2). Degree of size inequality was greater in dense populations than in populations of non-interacting individuals (cf. Tabs 1, 2), but there were no significant differences in degree of size inequality between low and high density populations (pooled over settlement cohorts) at any sampling date as determined by overlap of 95% confidence intervals (Tab. 2)

An examination of the degree of inequality among individuals within settlement cohorts revealed that for both density treatments, the late cohorts were significantly ($P<0.05$) more unequal in size distribution than early cohorts (Tab. 3) at all sampling dates after 14 June. However, within settlement cohorts, degree of inequality did not differ between density treatments at any sampling date. That is (for example), low density late recruits were no less hierarchical than high-density late recruits at any sampling date.

Discussion

The absence of size hierarchies in the solitary colonies, and the reduced size and high degree of inequality among the low and high density colonies indicate that variation in colony growth rate (Turner and Rabinowitz 1983, Uchmanski 1985) should be rejected as the mechanism generating size hierarchies in these bryozoan populations.

The results from the low and high density treatments (Fig. 1, Tabs 1, 2) are in complete agreement with the resource depletion model of Hara (1986b) and Weiner and Thomas (1986). *M. membranacea* colonies deplete available space in direct proportion to their size. The area covered by a single colony becomes unavailable to other colonies, as overgrowth does not occur among these bryozoans (Harvell et al., in press). The absence of overgrowth precludes an increase in degree of size inequality through time. Although colony size increases exponentially, growth stops when all available space is filled (Harvell et al., in press); hence, the degree of inequality found in early spring persists throughout the summer.

Recruitment time did affect colony size (Tab. 3); late recruits were consistently smaller than early recruits. Our examination of within-cohort patterns also further supported the resource depletion model (Tab. 3), as opposed to the resource pre-emption model. In uneven-

Tab. 2. Values for G (with 95% confidence intervals) for the size distributions of low and high density colonies shown in Fig. 1 (all ages pooled).

Date	Density	G	95% confidence interval
31 May	L	0.666	0.564–0.738
	H	0.656	0.574–0.723
14 June	L	0.687	0.569–0.749
	H	0.659	0.598–0.714
28 June	L	0.536	0.466–0.594
	H	0.571	0.523–0.612
12 July	L	0.538	0.470–0.594
	H	0.560	0.518–0.594
26 July	L	0.570	0.568–0.619
	H	0.552	0.507–0.587
9 August	L	0.557	0.493–0.610
	H	0.552	0.570–0.651

Tab. 3. Values for G (with 95% confidence intervals) for the size distributions of low and high density colonies shown in Fig. 1 (early and late recruitment cohort separated).

Date	Density	Early cohort		Late cohort	
		G	95% c.i.	G	95% c.i.
31 May	L	0.666	0.564–0.738	–	–
	H	0.656	0.574–0.723	–	–
14 June	L	0.642	0.529–0.696	0.616	0.365–0.817
	H	0.616	0.556–0.662	0.757	0.623–0.853
28 June	L	0.457	0.382–0.519	0.659	0.529–0.727
	H	0.497	0.455–0.536	0.639	0.556–0.685
12 July	L	0.404	0.329–0.469	0.661	0.491–0.718
	H	0.472	0.431–0.510	0.612	0.544–0.651
26 July	L	0.407	0.330–0.462	0.642	0.533–0.702
	H	0.470	0.426–0.504	0.589	0.521–0.627
9 August	L	0.404	0.330–0.461	0.644	0.537–0.700
	H	0.468	0.422–0.501	0.608	0.538–0.650

aged populations of peas where resource pre-emption occurred, Ellison and Rabinowitz (1989) showed that late-emerging plants displayed increasing inequality through time while the degree of inequality among early-emerging ones declined through time. Growth of late-emerging peas was suppressed by the early plants disproportionately to the former's size, and only those few plants that emerged surrounded by similar-aged individuals were able to grow large (Ellison and Rabinowitz 1989, see also Ross and Harper 1972). Thus, the late cohort of peas in Ellison and Rabinowitz's study consisted of a host of suppressed individuals and a few large ones, resulting in the classic pattern of inequality seen in populations undergoing dominance and suppression (e.g. Ford 1975, Harper 1977, Weiner and Thomas 1986).

In contrast, although the late cohort of bryozoans were more unequal in their size distributions than the early cohort, no change in degree of inequality occurred through time within densities, or across densities within cohorts (Tab. 3). That the two cohorts of bryozoans studied here showed no changes in inequality through time (Tab 3), supports the notion (augmented by the pooled cohort analysis) that these animals are experiencing resource depletion, not resource pre-emption. The within-cohort patterns are identical to those observed when cohorts were pooled. Late-recruiting colonies settled into available space, and grew until that space was exhausted. Because most of that space was small (between already established colonies), there is a larger percentage of small colonies among the late recruits than among the early recruits, resulting in larger size hierarchies in the late-recruiting population. However, because late recruits were not overgrown by the early recruits, they maintained their position within their cohort's size distribution through time.

We conclude, therefore, that (1) size hierarchies do occur in populations of *M. membranacea,* (2) the magnitude of these size hierarchies do increase with increasing density, but do not change through time within density treatments, and (3) size hierarchies in *M. membranacea* result from resource (two-dimensional space) depletion in a fashion consistent with models developed for populations of plants.

We would predict that in populations of encrusting species where overgrowth is common (Buss 1985), the degree of size inequality among colonies would increase with increasing density and through time within densities, in accordance with the resource pre-emption model (Hara 1986b, Weiner and Thomas 1986). While experiments examining size hierarchy formation in other benthic invertebrates have yet to be done, the results described here support the notion that similar mechanisms determine size distributions in populations of colonial invertebrates and plants. These results should encourage the development of general theories applicable to all modular organisms, as opposed to theories limited to plants or animals (cf. Jackson et al. 1985, Harper et al. 1986).

Acknowledgements – We thank T. Hara, D. Padilla and J. Weiner for reviewing early versions of this manuscript. Supported by grant NSF OCE-8796230 to CDH.

References

Benjamin, L. R. and Hardwick, R. C. 1986. Sources of variation and measures of variability in even-aged stands of plants. – Ann. Bot. 58: 757–778.

Buss, L. W. 1981. Bryozoan overgrowth interactions – the independence of competition for space and food. – Nature, Lond. 281: 475–477.

– 1985. Competition and community organization on hard surfaces in the sea. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 517–537.

– and Jackson, J. B. C. 1981. Planktonic food availability and suspension feeder abundance: evidence of in situ depletion. – J. Exp. Mar. Biol. Ecol. 49: 151–161.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. – Am. Nat. 122: 661–696.

– and Keogh, M. 1985. Succession on marine hard substrata. – In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp. 125–151.

Cook, R. E. 1979. Asexual reproduction: a further consideration. – Am. Nat. 113: 769–772.

Cook, S. J. and Ratcliff, D. 1984. A study of the effects of root and shoot competition on the growth of green panic (*Panicum maximum* var. *trichoglume*) seedlings in an existing grassland using root exclusion tubes. – J. Appl. Ecol. 21: 971–982.

Dolan, R. W. 1984. The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa* (Onagraceae). – Am. J. Bot. 71: 1302–1307.

– and Sharitz, R. R. 1984. Population dynamics of *Ludwigia leptocarpa* (Onagraceae) and some factors affecting size hierarchies in natural populations. – J. Ecol. 72: 1031–1041.

Donald, C. M. 1958. The interactions of competition for light and nutrients. – Aust. J. Agric. Res. 9: 421–435.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. – SIAM monograph number 38.

Ellison, A. M. 1987a. Density-dependent dynamics of *Salicornia europaea* monocultures. – Ecology 68: 737–741.

– 1987b. Effects of seed dimorphism on the density-dependent dynamics of experimental populations of *Atriplex triangularis* (Chenopodiaceae). – Am. J. Bot. 74: 1280–1288.

– and Rabinowitz, D. 1989. Effects of plant morphology and emergence time on size hierarchy formation in experimental populations of two varieties of cultivated peas (*Pisum sativum*). – Am. J. Bot. 76: 427–436.

Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. – J. Ecol. 53: 311–333.

Fowler, N. L. 1984. The role of germination date, spatial arrangement, and neighborhood effects in competitive interactions in *Linum*. – J. Ecol. 72: 307–318.

Grosberg, R. K. 1982. Ecological, genetical, and developmental factors regulating life-history variation within a population of the colonial ascidian *Botryllus schlosseri*. – Dissertation, Yale University, New Haven, CT.

Hara, T. 1984a. A stochastic model and the moment dynamics of the growth and distribution in plant populations. – J. theor. Biol. 109: 173–190.

– 1984b. Dynamics of stand structure in plant monocultures. – J. theor. Biol. 110: 223–239.

– 1986a. Growth of individuals in plant populations. – Ann. Bot. 57: 55–68.

– 1986b. Effects of density and extinction coefficient on size variability in plant populations. – Ann. Bot. 57: 885–892.

Harper, J. L. 1977. Population biology of plants. – Academic Press, London.

– 1981. The concept of population in modular organisms. – In: May, R. M. (ed.), Theoretical ecology, 2nd ed. Sinauer Associates, Sunderland, MA, pp. 53–77.

– and Bell, A. D. 1979. The population dynamics of growth and form in organisms with modular construction. – In: Anderson, R. L. (ed.), Population dynamics. Blackwell Scientific Publications, Oxford, pp. 29–53.

– , Rosen, B. R. and White, J. (eds). 1986. The growth and form of modular organisms. – Cambridge Univ. Press, Cambridge.

Harvell, C. D. and Grosberg, R. K. 1988. The timing of sexual maturity in clonal animals: an empirical study. – Ecology 69: 1855–1864.

– and Padilla, D. K. (in review). Inducible morphology, heterochrony and size hierarchies in a colonial monoculture. – Proc. Nat. Acad. Sci.

– , Simpson, P. and Caswell, H. (in press). Density dependence in clonal populations: experimental studies with a marine bryozoan (*Membranipora membranacea* L.). – Oecologia (Berl.).

Heywood, J. S. 1986. The effect of plant size variation on genetic drift in populations of annuals. – Am. Nat. 127: 851–861.

Highsmith, R. C. 1982. Reproduction by fragmentation in corals. – Mar. Ecol. Prog. Ser. 7: 207–226.

Hiroi, T. and Monsi, M. 1966. Dry-matter economy of *Helianthus annuus* communities grown at varying densities and light intensities. – J. Fac. Sci., Univ. of Tokyo 9: 241–285.

Hughes, R. N. and Cancino, J. M. 1985. An ecological overview of cloning in the Metazoa. – In: Jackson, J. B. C., Buss, L. W. and Cook, R. E. (eds), Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 153–186.

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.

– and Jackson, J. B. C. 1985. Population dynamics and life histories of foliaceous corals. – Ecol. Monogr. 55: 141–166.

Jackson, J. B. C., Buss, L. W. and Cook, R. E. (eds). 1985. Population biology and evolution of clonal organisms. – Yale Univ. Press, New Haven, CT.

Koch, A. L. 1966. The logarithm in biology. I. Mechanisms generating the lognormal distribution exactly. – J. theor. Biol. 12: 276–290.

Koyama, H. and Kira, T. 1956. Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. – J. Biol., Osaka Cy. Univ. 7: 467–485.

Leverich, W. J. and D. A. 1979. Age-specific survivorship and reproduction in *Phlox drummondii*. – Am. Nat. 113: 881–903.

Litav, M. and Wolovitch, S. 1971. Partial separation of roots as a means of reducing the effect of competition between two grass species. – Ann. Bot. 35: 1163–1178.

Łomnicki, A. 1988. Population ecology of individuals. – Princeton Univ. Press, Princeton, NJ.

Matlack, G. R. and Harper, J. L. 1986. Spatial distribution and the performance of individual plants in a natural population of *Silene dioica*. – Oecologia (Berl.) 70: 121–127.

Mithen, R., Harper, J. L. and Weiner, J. 1984. Growth and mortality of individual plants as a function of "available area." – Oecologia (Berl.) 62: 57–60.

Okamura, B. 1984. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. I. *Bugula stolonifera* Ryland, an arborescent species. – J. Exp. Mar. Biol. Ecol. 83: 179–193.

– 1985. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. II. *Conopeum reticulatum* (Linneaus), an encrusting species. – J. Exp. Mar. Biol. Ecol. 89: 69–80.

Osburn, R. C. 1950. Bryozoa of the Pacific coast of America, volume 14. – Univ. of Southern California Press, Los Angeles, CA.

Petersen, T. D. 1988. Effects of interference from *Calamagrostis rubescens* on size distributions in stands of *Pinus ponderosa*. – J. Appl. Ecol. 25: 265–272.

Ross, M. A. and Harper, J. L. 1972. Occupation of biological space during seedling establisment. – J. Ecol. 60: 77–88.

Roughgarden, J., Iwasa, Y. and Baxter, C. 1985. Demographic theory for an open marine population with space-limited recruitment. – Ecology 66: 54–67.

Schmitt, J., Ehrhardt, D. J. and Cheo, M. 1986. Light-dependent dominance and suppression in experimental radish populations. – Ecology 67: 1502–1507.

Shaw, R. G. and Antonovics, J. 1986. Density-dependence in *Salvia lyrata*, a herbaceous perennial: the effects of experimental alteration of seed densities. – J. Ecol. 74: 797–813.

Snaydon, R. W. 1971. Influence of root competition in absence of competition for light. – J. Appl. Ecol. 8: 687–697.

– 1979. A new technique for studying plant interactions. – J. Appl. Ecol. 16: 281–286.

Solbrig, O. T. 1981. Studies on the population biology of the genus *Viola* II. The effect of plant size on fitness in *Viola sororia*. – Evolution 35: 1080–1093.

Turner, M. D. and Rabinowitz, D. 1983. Factors affecting frequency distributions of plant mass: the absence of dominance and suppression in competing monocultures of *Festuca paradoxa*. – Ecology 64: 469–475.

Uchmanski, J. 1985. Differentiation and frequency distributions of body weights in plants and animals. – Phil. Trans. R. Soc. London B310: 1–75.

Watkinson, A. R., Lonsdale, W. M. and Firbank, L. G. 1983. A neighborhood approach to self-thinning. – Oecologia (Berl.) 56: 381–384.

Weiner, J. 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. – Ecology 67: 1425–1427.

– and Solbrig, O. T. 1984. The meaning and measurements of size hierarchies in plant populations. – Oecologia (Berl.) 61: 334–336.

– and Thomas, S. C. 1986. Size variability and competition in plant monocultures. – Oikos 47: 211–222.

Wethey D. S. 1983. Intrapopulation variation in growth of sessile organisms: natural populations of the intertidal barnacle *Balanus balanoides*. – Oikos 40: 14–23.

– 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*. A field experiment. – Biol. Bull. 167: 176–185.

White, J. 1984. Plant metamerism. – In: Dirzo, R. and Sarukhán, J. (eds), Perspectives in plant population ecology. Sinauer Press, Sunderland, MA, pp. 15–47.

Willey, R. W. and Reddy, M. S. 1981. A technique for separating above- and below-ground interactions in intercropping: an experiment with pearl millet/groundnut. – Exp. Agric. 17: 257–264.

Wilson, J. B. 1988. Shoot competition and root competition. – J. Appl. Ecol. 25: 279–296.