Group living and the effects of spatial position in aggregations of *Mytilus edulis**

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Summary. The mussel *Mytilus edulis* typically occurs in aggregations and several consequences of living in groups were studied. Isolated individuals and individuals associated in relatively small groups (6–9 mussels/group) grew more and therefore had greater reproductive output than mussels associated with relatively large groups of 21–28 individuals. Mussels located in the centers of groups exhibited reduced growth and thus lower reproduction relative to mussels located on the edges of groups whose growth and reproduction was similar to that of isolated individuals. Sampling from natural populations indicated that most mussels grow within the matrix of very large groups and hence will experience reduced growth and reproduction. Patterns of growth exhibited by mussels in association with living and model mussels showed that the adverse effects on growth exhibited by mussels in relatively large groups are not a function of the mere physical relief of a mussel clump, but are caused by some property of living neighbors.

Laboratory experiments on mussel predation by the crab *Pachygrapsus crassipes* indicated that crabs prey disproportionately on mussels growing on the edges of groups.

The consequences of group living in mobile and non-mobile organisms are considered, and it is suggested that a greater number of negative effects will arise in groups as mobility decreases. In addition, the noted ecological similarity between groups of sessile organisms and spreading clones and its evolutionary implications are discussed.

The mussel *Mytilus edulis* is characteristically found in aggregations that can form dense beds of conspecifics (Seed 1969; Kautsky 1982; Thompson 1984). Distinct larval settlement preferences and adult behavior lead to the formation of such mussel aggregations (Maas Geesteranus 1942; Seed 1969; Young 1983). A number of investigations of mussel beds have made important contributions to a growing appreciation of the ways in which disturbance, competition, and predation can operate to structure communities (Dayton 1971; Paine 1974; Menge 1976), however there has been little investigation of the dynamics within mussel beds (for exception see Bertness and Grosholz 1985). In addition, consequences of group living that arise in aggrega-

tions of mobile organisms have been the focus of many studies, but there are few such investigations of groups of sessile organisms.

This paper describes an experimental investigation of some of the consequences of group living for a sessile invertebrate, the bay mussel, *Mytilus edulis*. Variation in the patterns of growth and reproductive effort of mussels associated in groups of different sizes and composition, and for mussels located in particular positions within groups is discussed. Results for these experiments led to the further investigation of: 1) whether mussels move to positions in groups where growth and reproduction are not inhibited; and 2) whether mussels that occupy certain positions within groups are more vulnerable to predation.

Methods

Measurements of natural mussel groups

Mussels in all experiments were collected from natural populations in the mid to low intertidal at Point Richmond, CA, a site on the north-eastern shore of San Francisco Bay. In July 1983 these populations were sampled to obtain information on natural group sizes and lengths of individual mussels.

The effect of group size on mussel growth

Experiments on the growth rates of mussels in groups of different sizes were performed over the summers of 1981 and 1982 at the laboratories of the National Marine Fisheries Southwest Center in Tiburon, CA using mussels measuring 15–20 mm in length (shell tip to umbo). Mussels were individually marked and their lengths to the nearest 0.5 mm were recorded. Marked mussels placed on formica tiles (7.5 by 7.5 cm) in a seawater table produced a byssal attachment in several days. The number of mussels placed on each tile varied depending on the experimental treatment. During the attachment phase each tile was covered with a wire cage to keep mussels from crawling off the tiles and attaching to other surfaces.

After mussels had produced a firm byssal attachment tiles were fastened in random order to the undersides of a series of panels. Panels were then submerged into the San Francisco Bay from a float located beneath the pier of the National Marine Fisheries Southwest Center. On July 10, 1981 ten replicates of 1 mussel/tile, eight replicates of 3 mussels/tile, and nine replicates of 10 mussels/tile were submerged and sampled after 33 days. In 1982 twenty-five

replicates of 1 mussel/tile, five replicates of 10 mussels/tile, and five replicates of 30 mussels/tile were intially created, however a breakdown in the seawater system resulted in some mortality during the attachment phase. As a result, original groups of 10 and 30 mussels were reduced to ranges of 6–9 and 21–28 mussels respectively. Groups were submerged on July 16, 1982 and sampled after 38 days. In both summers loss of mussel identification marks as well as whole tiles occurred, therefore not all mussels originally put out in the field are accounted for in the results.

The length of each mussel was recorded at the end of the experiments. In 1982 the initial and final maximum shell widths (measured along the dorsoventral axis) were recorded as was the position of mussels that could unambiguously be classified as growing on the edge or in the center of groups. A mussel on the edge of a group was defined as one that had no neighbors on one side, and a mussel in the center of a group as one that was surrounded by and in contact with neighboring mussels on all sides.

In the summer of 1982 experiments were performed to compare the growth of mussels in the presence of model vs. living mussel neighbors to test whether the activity of living neighbors might affect mussel growth. Groups of 7 and 27 model mussels were created using paired valves of dead mussels that were glued into approximately circular clusters with a mixture of Sea Goin' Poxy Putty (Permalite Plastics Corporation, Newport Beach, CA) and coarse sand. All mussel valves were clean and empty and measured between 15 and 20 mm in length. Three living mussels were induced to attach amongst the model mussels, and the growth of these mussels was compared with the growth of mussels growing in the presence of living mussels in groups of similar sizes.

The effect of group size on reproductive output and shell production

Reproductive effort of mussels associated in groups of differing sizes was assessed by dissecting out the gonad and associated mantle tissues from the other soft parts of the body. Both fractions were dried to a constant dry mass (80° C) and weighed. Shells of dissected mussels were also dried and weighed.

Movement of individual mussels within groups

Data collected in 1982 showed mussels within groups grew more slowly than mussels on the edges of groups (see results below). In the summer of 1983 a study was initiated to test whether mussels moved out of central areas to peripheral positions. Ten naturally occurring mussel groups at Point Richmond were monitored for six weeks beginning July 26 (mean group size = 55.23 mussels, SD = 14.81, range = 33–82). In each group the shells of approximately 10 edge and 10 central mussels (range = 9–13) were marked with a file. An outline of each group was drawn to show the approximate position of each marked mussel. Groups were searched for marked mussels in edge and central positions after two weeks and six weeks.

Effects of position within a group on the risk of predation by crabs

The potential risk of predation associated with relative positions in groups was investigated in a series of laboratory tests on five groups of mussels (range in group size = 39–66 mussels) on tiles that had been suspended in San Francisco Bay for several months. The crab *Pachygrapsus crassipes* was chosen for these experiments since it was readily available and is a common predator of *Mytilus edulis* (Harger 1972). Male crabs (31–40 mm at the widest point across the carapace) were collected from Bodega Bay Harbor, CA and maintained at 14° C in seawater-filled containers provided with emergent substrata.

Edge mussels and mussels inside groups were marked with monopoxy enamel paint. The groups were then mapped. Groups were exposed to crab predation for 24 h periods (one crab per group). After each predatory bout the positions of mussels that had been consumed were determined and the maps were revised. Crabs that had eaten mussels were offered groups of mussels again during the next 24 h period. Crabs that did not consume mussels were replaced with new crabs.

Results

Natural mussel groups

Group sizes measured in the field ranged from 1–648 individuals. While the median group size was 19.5 mussels, the mean was 92 (SD = 152, $n = 38$). Thus, although smaller groups (< 20 mussels) were relatively frequently encountered, more mussels were actually growing within the matrix of large groups.

82% of the mussels sampled were relatively small (≤ 20 mm in length, $n = 231$). In the previous two summers the mussel population at Point Richmond also appeared to be composed of relatively small individuals, although no quantitative data on mussel lengths were gathered during these years.

Growth experiments

There were no significant differences in the average length increment achieved by solitary mussels and mussels in group sizes of three and 10 mussels (see Table 1). Solitary mussels appeared to grow more slowly, but the sample size was small in this category. Experiments in 1982 were run to increase the sample size of solitary mussels as well as

Table 1. Analysis of covariance (covariate is initial length) of the adjusted mean length increments (mm) of mussels growing in small, moderate, and large groups (1, 3, and 10 mussels per group, respectively) during the summer of 1981

Source of variation	Sum of squares	d.f.	Mean square	F-value	Probability
Equality of adj. means	21.7603	2	10.8801	1.7614	0.1834
Equality of slopes	3.7271	2	1.8635	0.2922	0.7481
Error	274.2319	43	6.3775		
Zero slope	9.7061	1	9.7061	1.5714	0.2165
Error	277.9590	45	6.1769		

Group size:	Small	Moderate	Large
Adjusted mean length increment:	6.98	7.45	8.68

Table 2. Analysis of covariance (covariate is initial length) of the adjusted mean length increments (mm) of mussels growing in small, moderate, and large groups (1, 6–9, and 21–28 mussels per group, respectively) during the summer of 1982. Underlines indicate means which are not significantly different (Tukey-Kramer test, $P > 0.05$)

Source of variation	Sum of squares	d.f.	Mean square	F-value	Prob-ability
Equality of adj. means	97.0667	2	48.5333	11.7001	<0.001
Equality of slopes	7.4822	2	3.7411	0.9012	0.4074
Error	1054.4299	254	4.1513		
Zero slope	89.0530	1	89.0530	21.4684	<0.001
Error	1061.9121	254	4.1484		

Group size:	Small	Moderate	Large
Adjusted mean length increment:	8.02	8.24	6.71

Table 3. Analysis of covariance (covariate is initial length) of the adjusted mean length increments (mm) of mussels growing on the edges and in the centers of large groups (21–28 mussels per group) during the summer of 1982

Source of variation	Sum of squares	d.f.	Mean square	F-value	Prob-ability
Equality of adj. means	64.1395	1	64.1395	17.0964	0.0007
Equality of slopes	0.1297	1	0.1297	0.0326	0.8590
Error	63.6481	16	3.9780		
Zero slope	5.9040	1	5.9040	1.5737	0.2266
Error	63.7778	17	3.7516		

Group location:	Center	Edge
Adjusted mean length increment:	3.69	7.39

Table 4. Two-way analysis of covariance (covariate is initial length) of the length increment (mm) of mussels growing in association with living and model mussels in groups of moderate and large sizes (6–10 and 21–30 mussels per group, respectively). GS = group size; A = association with living and model mussels

Source of variation	Sum of squares	d.f.	Mean square	F-value	Prob-ability
Covariate	87.66912	1	87.66912	19.88	<0.0001
Main effects					
GS	3.78664	1	3.78664	0.86	0.3549
A	2.52521	1	2.52521	0.57	0.4499
Two-way interaction					
GS × A	30.16965	1	30.16965	6.84	0.0094
Error	1159.67544	263	4.40941		

GS:	Moderate	Moderate	High	High
A:	Living	Model	Living	Model
Adjusted mean length increment:	8.26	7.46	6.73	8.19

Table 5. Analysis of covariance of the % dry gonad weight of mussels growing in small, moderate, and large groups (1, 6–9, and 21–28 mussels per group, respectively). Covariate is dry body weight to control for differences in proportion of gonad at different body sizes. Per cent dry gonad weight values were arcsine transformed to normalize the data prior to analysis (Sokal and Rohlf 1981)

Source of variation	Sum of squares	d.f.	Mean square	F-value	Prob-ability
Equality of adj. means	6.6370	2	3.3185	0.0854	0.9184
Equality of slopes	12.8909	2	6.4454	0.1571	0.8553
Error	1230.9207	30	41.0307		
Zero slope	12.6980	1	12.6980	0.3267	0.5716
Error	1243.8115	32	38.8691		

Group size:	Small	Moderate	Large
Adjusted % dry gonad weights:	8.4506	9.5728	8.3232

to assess growth of mussels in larger groups than were studied in 1981.

In 1982 group size was found to significantly affect growth: mussels in larger groups (21–28 individuals) grew less than solitary individuals and mussels in groups of moderate size (6–9 individuals) (see Table 2). Parallel results were obtained in analysis of covariance (ANCOVA) of changes in mean width increments (Okamura 1984).

Mussels located in central positions were found to grow more slowly in length relative to mussels located in edge positions (Table 3). Similar results were obtained for changes in width (Okamura 1984). Furthermore, the growth of mussels in edge positions did not differ significantly from that of solitary mussels. (ANCOVA indicated no difference in the mean increments in length ($F_{1, 29} = 0.974$, $P = 0.332$) and width ($F_{1, 29} = 0.063$, $P = 0.804$) of solitary mussels and mussels in edge positions.)

Two-way ANCOVA of the growth in length of mussels associated with living and model neighbors in groups of moderate and large size showed growth of mussels associated with *living* neighbors at *large* group sizes was much reduced (see Table 4). Similar results were obtained in AN-COVA of the changes in width (Okamura 1984). The

growth of mussels associated with *model* neighbors at *moderate* group sizes was also somewhat reduced relative to the other two treatments.

Reproductive output and shell production

ANCOVA showed no significant differences in the % dry "gonad weight"(GW) of solitary mussels and mussels growing in groups of moderate and large size (see Table 5). (A preliminary two-way ANCOVA indicated no significant differences in % dry GW between males and females growing in various group sizes, therefore sexes were pooled to increase sample size.) Since the ANCOVA corrected for differences in body weights (BW) between treatments the reproductive effort (defined here as % dry GW/total dry BW) was similar across treatments. However the absolute amount of gonad produced was actually different since

Table 6. Analysis of variance of the % dry shell weight of mussels growing in small, moderate, and large groups (1, 6–9, and 21–28 mussels per groups, respectively). Per cent dry shell weights were arcsine transformed to normalize the data prior to analysis (Sokal and Rohlf 1981)

Source of variation	Sum of squares	d.f.	Mean square	F-value	Prob-ability
Equality of cell means	8.4733	2	4.2366	2.8143	0.0748
Error	48.1723	32	1.5054		

Group size:	Small		Moderate	Large
Mean % dry gonad weight:	87.6096		87.1422	88.4728

mussels growing in the matrix of large groups grew more slowly than solitary mussels and mussels in groups of moderate size. This was reflected in the mean dry GW's of mussels in the three treatments. For solitary mussels the mean dry GW = 0.0054 g (SD = 0.0036, $n=9$); for mussels in groups of moderate size the mean dry GW = 0.0076 g (SD = 0.0055, $n=10$); for mussels in groups of large size the mean dry GW for mussels on the edges of groups = 0.0050 g (SD = 0.0044, $n=10$) and for mussels in the centers of groups = 0.0022 (SD = 0.0028, $n=9$). (These data include cases of no gonad development that were not included in ANCOVA because their dry BW's were not determined.) The higher value for the mean absolute GW of mussels in groups of moderate size is probably reflective of the slightly larger initial sizes of mussels sampled in this category. This initial discrepancy was adjusted for in ANCOVA of % dry GW vs. group size and hence no significant differences were detected.

The average % shell weights of mussels growing in different group sizes showed little variation (range = 87.14–88.47%), and analysis of variance (Table 6) indicated that mussels did not invest differentially in shell material when growing in groups of varying size.

Movement of mussels within groups

No mussels that were initially marked as "edge" individuals were ever recovered as "central" individuals and vice versa during the experiments on mussel movement in groups. All mussels were found in the vicinity of their original positions. It is unlikely that mussels moved away from and back to these positions during intervals between sampling. These results suggest that once groups are established mussels have little tendency to move.

The rate of disappearance of marked mussels in these movement experiments also provided information on relative mortality of mussels in edge and central positions. There was no difference in mean disappearance rate of mussels from edge and central positions after two weeks (mean$_{edge}$ = 0.40, SD = 0.52, $n=10$; mean$_{center}$ = 0.50, SD = 0.53, $n=10$; Mann Whitney U = 55, $P>0.20$, two-tailed test) or after six weeks (mean$_{edge}$ = 1.20, SD = 0.63, $n=10$; mean$_{center}$ = 1.3, SD = 0.46, $n=10$; Mann Whitney U = 54.5, $P>0.20$, two-tailed test). There were, however, proportionately fewer mussels on the edges of groups than in the centers. Since marked mussels disappeared from both areas at the same rate, it would appear that the per capita
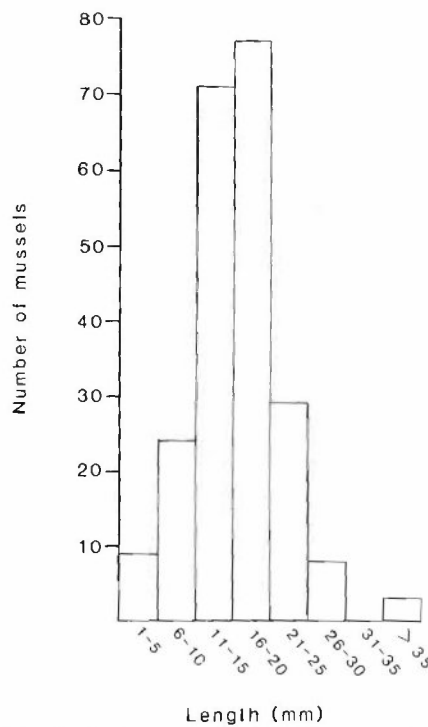

Fig. 1. The frequency distribution of the lengths (shell tip to umbo) of mussels sampled from natural populations at Point Richmond, CA in July 1983

risk of mortality is greater for mussels growing on the edges of groups. This could not be tested since the absolute number of mussels in each location was not determined.

Mussel predation by crabs

The mean rate of predation by crabs did not differ significantly for edge (mean = 1.6 mussels eaten/24 h, SD = 0.966, $n=10$) vs. central (mean = 1.18 mussels eaten/24 h, SD = 0.405, $n=11$) areas (Mann Whitney U = 68, $P>0.20$, two-tailed test). However, the proportion of mussels in edge and central areas varied from group to group and after each predatory act. Analysis of the mean proportion of mussels available in each area during each bout of predation indicated that more mussels were, on average, available in central areas (mean = 53.74%, SD = 3.67) than on the edges (mean = 49.06%, SD = 4.08) ($t=6.94$, $P<0.001$, df = 27; data normalized with an arcsine transformation prior to analysis).

Since crabs preyed upon mussels from both areas at the same rate, yet more mussels were available in the center, it can be concluded that crabs had the tendency to prey disproportionately more on mussels on the edges of groups. A t-test analyzing the differences in the mean per capita risk of predation over a 24 h period of edge and central mussels indicated that mussels on the edges of groups were preyed upon disproportionately (mean$_{edge}$ = 0.066, SD = 0.049; mean$_{center}$ = 0.037, SD = 0.011) ($t_s'=17.99$, $P<0.05$, df = 9; approximate t-test for the difference between two means with unequal variances, Sokal and Rohlf 1981). Per capita risks were calculated as the number of mussels eaten in an area divided by the total number of mussels present in that area.

Discussion

Reduction in growth and reproduction in groups

Mussels in groups of 21–28 individuals were found to suffer a reduction in growth and hence had a lower reproductive output relative to individuals living in smaller groups. The negative effect of large group size was exerted differentially on mussels located in different positions within groups. Mussels growing in the centers of these large groups suffered in growth and thus reproduction, whereas mussels living on the edges of groups did not. Nonetheless, mussels did not appear to change their position within groups. Field sampling showed that most mussels live in the matrix of large groups and are therefore likely to suffer from the negative effects demonstrated by these experiments.

Negative effects on the growth of *Mytilus edulis* have been demonstrated in studies of both intertidal and subtidal aggregations (Wilson and Hodgkin 1967; Seed 1969; Harger 1972; Kautsky 1982), however this is the first study to quantify reproduction at different densities. Reduction in growth at higher densities has also been demonstrated for other mussel species (Harger 1972; Bertness and Grosholz 1985) as well as for other sessile and slow-moving marine invertebrates including limpets (Frank 1965), snails (Underwood 1976), bryozoans (Buss 1981), and barnacles (Wethey 1983).

Mechanisms of intraspecific competition

The negative effect on growth observed for individuals in large groups of living mussels was not observed for individuals associated with large groups of model mussels. Several properties of living mussels may explain these results. Living mussels may, by growing, exert physical pressure on their neighbors. Observations and experiments that show not only slower growth, but distortion, twisting, and thickening of shells of individuals in dense clumps lend support to this notion (Harger 1972; Bertness and Grosholz 1985). Shell deformation was not observed in this study, possibly due to the relatively short duration of the experiments. The active feeding of many mussels may reduce the absolute amount of food available to any one individual, thereby limiting growth (Fréchette and Bourget 1985). While it could be argued that competition for food may not be so important in intertidal mussel aggregations due to greater mixing by wave action, the reduced growth of intertidal individuals in dense clumps (Harger 1972; Bertness and Grosholz 1985) does not support this stand.

The growth of mussels associated with *model* neighbors at moderate group size was reduced relative to the growth of mussels associated with *living* neighbors at moderate group size. This pattern might be explained if coordinated pumping activity resulted in greater feeding by allowing individual mussels to feed from a larger volume of water as has been shown for encrusting bryozoans (Okamura 1985). Competition for food occurring at larger group sizes may reduce growth. However, the situation is somewhat confusing since the growth of mussels associated with *model* mussels at *large* group sizes was similar to the growth of mussels associated with *living* mussels at *moderate* group sizes. Perhaps the physical relief of the large model mussels altered water flow in such a way as to enhance feeding rates. There are many studies of suspension feeding by mussels (e.g. Jørgenson 1966, 1981 a, b), but none have determined how food capture per individual mussel is influenced by the presence of other feeding mussels.

Reproductive contribution of small mussels

Mussels that were used in these experiments were small, and it is possible that individuals of this size may contribute little to the pool of planktonic mussel larvae. However, mussels at Point Richmond were, on average, small. Suchanek (1981) similarly found that *Mytilus edulis* growing on the outer coast of Washington State never reached large sizes. Populations of *M. edulis* of the open coast of Britain have been observed to be composed of small individuals (Kitching et al. 1959; Ebling et al. 1964; Seed 1969). The total reproductive output of *M. edulis* in many habitats may therefore largely derive from many relatively small mussels (Seed 1969) although some populations in very sheltered habitats are dominated by very large individuals (Kitching et al. 1959).

Potential trade-offs associated with group position

Mussels located on the edges and in the centers of groups were found to remain in these positions. Paine (1974) similarly found little movement of *Mytilus californianus* within undisturbed mussel beds. This might seem surprising, given the effect of position within a group on the relative growth and reproduction of mussels. Movement in groups may be physically impossible when mussels are wedged inside groups, possibly entangled with the byssal attachments of other individuals. However, there may be costs of living on the edge of groups that might counteract the advantages associated with the edge. For instance, while mussels on the edges of groups are not inhibited in growth and reproduction, perhaps such edge individuals suffer a reduction in survivorship.

There were no differences in survivorship of marked mussels in different positions in groups in the intertidal over a six week period, however the disproportionately small number of mussels growing on the edges of groups suggests that the per capita risk of mortality may be greater for mussels in edge positions. Such individuals on the edge may be more vulnerable to attack by certain predators than mussels growing in the centers of groups. Witman and Suchanek (1984) found that edge individuals were more strongly attached than mussels in the centers of groups. They suggest that edge individuals may encounter large flow forces imparted by breaking waves and that individuals in central positions are hidden behind neighbors from such forces. The cost of producing a stronger byssal attachment may, in itself, represent a significant trade-off of living on the edges of groups. However their findings may also reflect responses to varying levels of predation. The results reported here on predation by crabs would suggest that this is so, however the relative importance of various kinds of predation on mussel populations is unclear and is probably variable.

The method of attack employed by a number of mussel predators may result in differential predation on mussels depending on their positions in groups. Edge mussels are probably easier to grab and firmly hold than central mussels, and may therefore suffer greater mortality from predators such as starfish, diving ducks, and fish (Brett 1979). Under natural conditions, however, several phenomena might complicate patterns of predation with respect to posi-

tion within groups: 1) constant predation will expose new edge individuals and may ultimately remove entire groups (unless new members recruit to the edge) and; 2) if predation is size-dependent, individuals in favorable conditions for growth on the edges of groups may reach invulnerable sizes faster than those in the center. The operation of these phenomena will depend on rates, timing, and local history of predation.

While the feeding mode of certain predators may constrain them to almost exclusively attack mussels on the edges of groups, other predators may show no such pattern. There is probably little reason to expect that predaceous gastropods will display any position-dependent tendency to drill mussels (unless, perhaps, they refuge outside the mussel bed). The results described here indicate that crabs are not constrained to feeding on mussels occupying particular positions in groups (see also Kitching et al. 1959) although they may have a greater tendency to feed on mussels on the edges of groups. In summary, it would appear that edge mussels may be subject to heavier predation than mussels within groups, and this may represent a potential cost incurred by individuals in this position. However, there are probably no positions within aggregations that confer invulnerability to predation.

Consequences of group living in perspective

While this study does not show any positive aspects associated with living in groups, it does not imply that all aspects are negative. For instance, group living in *Mytilus edulis* may allow for protection from desiccation to intertidal populations (Seed 1969) or may result in greater fertilization during spawning as has been shown for urchin aggregations (Pennington 1985). Bertness and Grosholz (1985) found a reduction in mortality by both crab predation and winter ice scour when the mussel *Geukensia demissa* grew at high density.

Most studies that have demonstrated negative effects imposed by group living have been on aggregations of "sessile" organisms such as colonies of nesting birds (Hoogland and Sherman 1976) and prairie dogs (Hoogland 1981), bryozoans (Buss 1981), and spiders (Buskirk 1975). In contrast, studies of group living in highly mobile organisms have mainly illustrated positive aspects of aggregation (in fish: Weihs 1973; Barlow 1974; Neill and Cullen 1974; Peterson 1976; Robertson et al. 1976; Hobson 1978; Major 1978; Gross and MacMillan 1981; Pitcher and Magurran 1983; in birds: Lissamen and Schollenberger 1970; Ward and Zahavi 1973; Powell 1974; Siegfried and Underhill 1975; Barnard 1980; Wiklund and Andersson 1980; Gochfeld and Burger 1981; in tadpoles: Beiswinger 1975). This pattern may reflect some basic differences between groups of mobile and non-mobile organisms.

Aggregating mobile organisms may not experience as many group-related negative effects as non-mobile organisms since mobility allows individuals to enter and leave groups and also allows groups themselves to move through and sample new habitats in the environment. Thus one would predict that groups of highly mobile organisms will fall into two categories: 1) short-lived groups that disband when negative effects are expressed, and 2) longer-lived groups whose continuous movement ensures resource renewal. It may be that negative consequences associated with group living diminish in frequency, strength, and duration

as the degree of mobility of individuals (or groups) increases. These considerations imply that group living will be more rare in sessile organisms and furthermore that sessile organisms that form groups will experience a complex suite of both costs and benefits.

Two commonly-encountered groups of sessile organisms are groups of non-clonal individuals (e.g. mussels, barnacles) and groups of clonal individuals (e.g. some anenomes, bryozoans, ascidians). The formation of groups of clonal organisms results from lack of movement after growth and asexual reproduction, thus group members are genetically identical and members can remain physically connected (e.g. zooids in colonies of bryozoans) or can be separate (e.g. some anenomes). Therefore, while members of both kinds of groups may experience similar ecological costs and benefits, the fitness of these organisms pertains to different scales or entities (the individual unit in groups of non-clonal organisms and the sum of the individual units that compose clones). The obvious similarity between groups of sessile organisms and spreading clones has been noted earlier. In both cases space-occupation results, and this may confer important ecological advantages in a number of habitats (Jackson 1977; Bertness and Grosholz 1985). However, while the ecological roles of clones and groups of sessile organisms may be similar, any selection that may have occurred to produce organisms with these life histories must have operated at very different levels.

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Population structure and thinning in natural stands of Atlantic White Cedar (*Chamaecyparis thyoides* (L.) BSP)

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Summary. Data from forestry yield tables were used to investigate the population structure of natural stands of Atlantic White Cedar (*Chamaecyparis thyoides*) in the mid-Atlantic states. The proportion of individuals in three size classes, 1–5 inch dbh, 5–8 inch dbh and >8 inch dbh was shown to depend on both site age since clearcutting and site quality. Site age and site quality also determined the degree to which cedar populations underwent density dependent mortality (self-thinning). On all sites, the smallest individuals were removed by self-thinning. Analyses of this type allow predictions to be made of forest stand dynamics and further an understanding of population processes in natural communities.

It is well established that the internal structure of a plant community is largely determined by the interaction between the component species populations. One of the best documented principles which governs the structure of plant populations are the density/yield relationships expressed by the $-3/2$ self-thinning law (Yoda et al. 1963; White and Harper 1970; White 1980, 1981). The self-thinning rule, that results from density-dependent mortality, expresses the relationship between the number of surviving plants in a population (i.e. density, p) and their level of performance in terms of mean yield per plant (w) according to the equation: $\log w = \log K - 1.5 \log p$ where K is a constant. The generality of this relationship is such that plant populations can occupy any position on a log density/log yield plot but have an upper bound according to the -1.5 self-thinning line (Gorham 1979; White 1980). Current understanding of this concept has largely come from experimental studies either in the greenhouse or under controlled field situations in monospecific stands (e.g. Lonsdale and Watkinson 1983). Due to the complexity of interspecific interactions, the demonstration of density/yield relationships have rarely been shown in natural systems (Yoda et al. 1963; Watkinson and Harper 1978; Jefferies et al. 1981). Forestry yield data, where appropriate, can provide a good test of these relationships in the field situation (see White 1980), but are often drawn from monospecific plantations (e.g. *Pinus radiata*, Drew and Flewelling 1977; *Pinus resinosa*, White 1981).

In this report, forestry yield data for North American Atlantic White Cedar swamps are used to study population structure and thinning in natural, unmanaged populations. Cedar swamps are unique in that the tree strata are almost pure cedar (*Chamaecyparis thyoides*). Woody competitors are largely limited to the understory (McCormick 1979). Stands of cedar are generally believed to be even-aged, representing a single or short period of recruitment following clear-cut harvesting (Korstian and Brush 1931; Little 1950). Recruitment is entirely by seed and not through root sprouting of existing stock (Little 1950). Cedar swamps thus represent relatively simple-structured, natural communities that are ideal for observing the natural processes of population structural development.

Methods

The data used in this report are drawn from yield tables presented by Korstian and Brush (1931). Their yield tables were prepared by L.H.T. Reineke and C.F. Korstian from field data collected by the Appalachian Forest Experimental Station in cooperation with the State foresters of the mid-Atlantic states. A total of 63 plots were measured, covering a large portion of the range of cedar (Little 1971), of which 47 were selected for yield table construction. The distribution of these sites was North Carolina, 11 sites; Virginia, 21 sites; New Jersey, 13 sites and Connecticut, 2 sites. Although the details of sampling are not given by the authors, it is stated that the yield tables are based on, and refer to, well-stocked stands grown under natural conditions without thinnings or other treatment. Their tables provide density and yield data for cedars in three size classes: >1 inch diameter at breast height (dbh), >5 inches dbh, and >8 inches dbh. These data can be used to calculate the proportion of individuals within the size class ranges 1–5 inches dbh, 5–8 inches and >8 inches. Yield data were not calculated within these size classes because cedars greater than 8 inches were measured between a stump height of 1 foot and a top diameter of 6 inches; whereas, in the smallest size class, >1 inch dbh, the entire stem volume was recorded. There are also problems in converting the units of yield used for each size class; Korstian and Brush used cubic feet per acre for individuals >1 inch, cords per acre for individuals >5 inches and board feet per acre for individuals >8 inches dbh. Whilst conversion factors exist for these different units (Husch et al. 1972) and were used here to calculate graph axes and in the calculation of log

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