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SIGNIFICANCE OF LITTER SIZE IN *MUSCULIUM SECURIS* (BIVALVIA: SPHAERIIDAE)¹

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Abstract. Experiments were carried out to determine the effects of population density on the natality of *Musculium securis* (Prime). Laboratory studies showed that: (1) total recruitment increased with increasing densities of parental stock, to an asymptotic value, (2) that recruitment was greater than the reproductive carrying capacity, and (3) that the total litter size per average reproductive adult decreased with increasing densities of parental stock, to an asymptotic value. It is suggested that surplus recruitment may be an important mechanism in population control. Field studies supported these findings and showed that interspecific competition between *Musculium securis* and *Musculium transversum* resulted in lower natalities for both species. Also, competition among individuals of the predominant species is primarily intraspecific and the presence of the subdominant species has little effect on their reproductive capacities. Temporary coexistence is possible for the 2 species but *Musculium transversum* has a higher natality and probably would eventually exclude *Musculium securis* when they were complete competitors.

Key words: competitive exclusion; interspecific competition; intraspecific competition; litter size; *Musculium securis*; *Musculium transversum*; Ottawa; population density; recruitment.

INTRODUCTION

Sphaeriids are small, freshwater bivalves with a cosmopolitan distribution. They are hermaphroditic and ovoviviparous with 4 arbitrarily defined stages of larval development (Heard 1977). Embryos are contained within single-walled primary sacs and include all stages from the zygote through gastrulation. When the shell begins to form in the fetal larvae, the enveloping brood sac forms a second wall to become a secondary brood sac. The prodissoconch larva is the third developmental stage, including formation of the shell up to but not including escape from the tertiary sacs in which they are incubating. The shelled larvae that have escaped from the tertiary sacs are known as extramarsupial larvae and are contained within the marsupium prior to birth. This orderly development of larval stages facilitates enumeration of larvae in life history studies and in studies assessing the effects of environmental factors on fecundity and mortality rates.

The purpose of the present study is to determine the effects of population density and interspecific competition on the natality of *Musculium securis* (Prime). The significance of the findings are discussed in relation to existing schools of thought on significance of litter size (e.g., Lack 1954; Wynn-Edwards 1962; Mountford 1968), and competitive exclusion (Hardin 1960). Other life history aspects (e.g., age at first reproduction, reproductive tactics, etc.) were not investigated and readers are referred to Stearns (1976) for a review of the most current ideas about such life-

history tactics. Cole (1954) postulated several mechanisms by which semelparous and iteroparous animals could increase their biotic potential through an increase in the total litter size; Heard (1965, 1977) considered these postulates with regard to sphaeriids and concluded that biotic potential among different species was obtained by increasing the litter size in the same life-span or by increasing the number of litters in a longer life-span.

Musculium securis was chosen because it is easy to maintain, grows rapidly and reproduces in the laboratory within 60–80 days. In nature larvae are formed in the summer, newborn estivate and/or hibernate with little or no growth during the fall and winter, grow and reproduce the following spring, then die after producing 2–10 newborn. The extent of interpopulation variation in growth, birth periods, reproductive habits, and longevity is given in Mackie et al. (1975, 1976).

MATERIALS AND METHODS

Litter size is defined here as the number of young at birth and can be determined from natality data. Natality is realized natality—the amount of successful reproduction that occurs over a period of time (Smith 1974) and is determined by 1 of the 2 methods described below.

With the first method, newborn are grown in containers (glass dishes, plastic tubes, etc.) in the laboratory and/or field until they produce a litter of newborn. Natality is then expressed as a crude birth rate in terms of population size (e.g., 20 newborn/container/mo). For *M. securis* the parents usually die after producing a litter of newborn and it is necessary only to count the number of newborn shells (dead and living) in the container at the end of the experiment. The average litter size is determined by dividing the total

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number of newborn in the container by the number of parents that reproduced.

The second method is to dissect adult clams in greater length classes and count the number of extra-marsupial larvae in each parent. Care must be taken to ensure that none of the clams in a litter have been born (i.e., by noting that newborn are not present in a sample of the population).

After trying several methods, we found that a combination of soil (from a willow–elm forest), leaves, and water was the best medium for maintaining *M. securis* in the laboratory. Newborn *M. securis* were obtained from Carp Pond (Mackie et al. 1976) and grown in 100 mm diam \times 50 mm high Pyrex® dishes [=growth dish] containing 50 g (ovendry basis) of air-dried soil, (from Carp Pond), 2 g of air-dried black willow or white elm leaves, and enough distilled or deionized H₂O to fill each dish. The dishes with soil, leaves and water were allowed to stand 1 day before adding newborn *M. securis*. These were allowed to grow, reproduce, and die (60–80 days). Dishes were topped daily with distilled or deionized H₂O and examined every 2 weeks to determine how many adults were bearing larvae (shells are transparent enough to see if larvae are present). Dishes were otherwise left undisturbed (e.g., without aeration). At the end of the experiment, when at least 75% of the parents (usually 100%) were dead, the numbers of newborn produced within each dish were determined.

To determine the effect of population density on natality of *M. securis*, dishes were prepared as above but either 5, 10, 20, 30, or 40 newborn were added with 3 replicates per density treatment.

Field experiments were carried out to determine the effects of interspecific competition on natalities of *M. securis* and *M. transversum* in the shore and deep water zones of Britannia Bay of the Ottawa River near Ottawa. Growth tubes, made of 35 mm diam \times 60 mm high plastic vials with snap-on caps and with 2, 1 cm \times 4 cm rectangular holes cut from the lower sides and covered with nylon mesh (Mackie 1973), were used to hold each species. It was assumed that the nylon mesh permitted constant renewal of nutrients and removal of metabolites and that competition probably was for space. The density of adults used in the tubes was based on the observation that *M. transversum* occurred in densities of up to 1700/m² in the shore zones of Britannia Bay. Because clams were frequently found on the inside walls of the growth tubes, the area of a tube was taken to be the total inside area (i.e., 123.5 cm²). Therefore, a total of 20 clams was added to each growth tube to make the density of clams approximately equal to that in the natural habitat. The ratios of *M. transversum* to *M. securis* used were 19:1, 18:2, 16:4, 10:10, 4:16, 2:18, and 1:19. (Six replicates were made of each combination of clams, 3 of which were placed in the 0.3 m depth and the other 3 in the 3 m depth. In addition, 5 newborn of each species

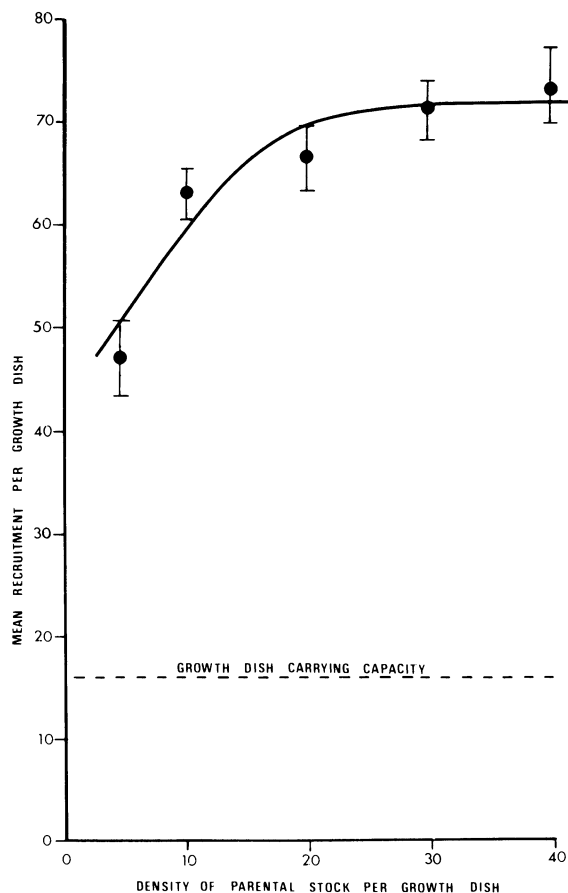


FIG. 1. Relation between recruitment and density of parental stock of *Musculium securis* in laboratory growth dishes. Vertical lines are standard deviations of the means. Curve was fitted by eye.

were isolated in growth tubes at each depth). Two additional tubes were prepared as controls with 20 *M. transversum* in one and 20 *M. securis* in the other. To determine the effects of smaller densities, ratios of 9:1 and 1:9 were prepared with controls of 10 *M. transversum* and 10 *M. securis* in 4 separate tubes. The number of young produced in each growth tube were enumerated at approximately 2-week intervals.

RESULTS

Population density

Figure 1 shows that total recruitment per growth dish increased with increasing densities of the parental stock, to an asymptotic value (≈ 72). All adults in densities of 5 individuals per dish matured to produce young but where densities exceeded 10 the range of adults maturing to produce young was from 9 to 19 individuals. On the basis of the number of individuals which successfully reproduced, the carrying capacity of each dish was estimated to be 16 adults. Because as many as 40 to 86 newborn were produced in the growth dishes, the reproductive adults produced a sur-

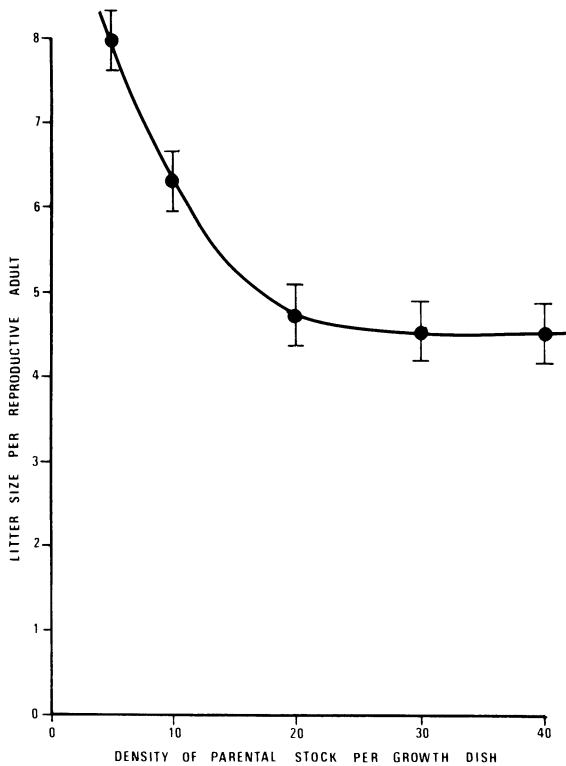


FIG. 2. Relation between the mean litter size per reproductive adult and the density of parental stock of *Musculium securis* in laboratory growth dishes. Vertical lines are standard deviations of the means. Curve was fitted by eye.

plus of 24 to 70 young. Figure 2 shows that the average number of young released per reproductive parent decreased with increased densities until the carrying capacity was reached and then remained constant.

Mortality rates increased with increased density. No adults died prematurely in dishes with densities of 5 individuals. The number of premature mortalities ranged from 1–2, 2–3, 3–4, and 4–8 in dishes with densities of 10, 20, 30, and 40 adults, respectively. Most of the adults that died prematurely were <3.00 mm in length (compared to 6–7 mm for reproductive adults). The remaining nonreproductive adults had completed growth after 67 days, and many of the reproductive adults had produced their young and died by this time.

Competition

The natalities of *M. securis* and *M. transversum* as they competed between and among themselves in different densities in the shore zone of Britannia Bay are given in Fig. 3. On the basis of the number of reproductive individuals, the carrying capacity of the growth tubes was ≈6 individuals. In general, intraspecific competition favored greater natalities than did interspecific competition (compare r & q, g & a, e & c, f & b, u & v, n & j, Fig. 3). When *M. securis* was

TABLE 1. Total litter sizes per average parent in 4 populations of *Musculium securis*. (Data calculated from Mackie et al. 1976.) See text for explanation

Parameter	Carp Pond			Greely Pond	Britannia Bay			Lac Bourgeois
Year	1970	1971	1972	1972	1970	1971	1972	1971
Total litter size per average parent	3.76	5.70	4.83	4.70	2.43	3.12	2.44	5.72

more numerous than *M. transversum* in the same growth tube, the former produced more young per reproductive adult than the latter (compare r & v, g & i, f & j, e & k, Fig. 3). When the numbers of the 2 species were equal, *M. transversum* had slightly greater natalities than did *M. securis* (compare l & d, Fig. 3). As the dominant species, *M. transversum* had higher average natalities than it had as a subdominant species (compare u & v, m & k, n & j, o & i, Fig. 3), and produced more young per reproductive individual than did *M. securis* under similar conditions (compare q & r, a & g, c & e, b & f with u & v, m & k, n & j, and o & i, Fig. 3). The greatest natalities occurred when each species was isolated: *M. securis* produced a mean of 9.8 newborn (SD = 2.4) per parent and *M. transversum* produced a mean of 11.8 newborn (SD = 3.2) per parent.

Evidently, interspecific competition between *M. securis* and *M. transversum* was not prevalent in the deeper waters of Britannia Bay. Even as isolate-controls, *M. transversum* did not grow to sufficient size to produce young and *M. securis* attained smaller average lengths (4.85 mm, SD = 0.34) and had smaller litter sizes (3.2 mm, SD = 0.8) in the 3 m depth than in the shore zone, as isolate controls.

DISCUSSION

Significance of Litter Size

The data in Table 1 and Figs. 1 and 2 show clearly that (1) the total recruitment increased with increasing densities of the parental stocks, to an asymptotic value (Fig. 1), (2) recruitment was greater than the reproductive carrying capacity (≈16 reproductive adults) of the growth dishes, (3) the total litter size per average reproductive adult decreased with increasing densities of the parental stock, to an asymptotic value (4.5, Fig. 2). These results support Mountford's (1968) hypothesis that "natural selection favors those genotypes that produce the greatest number of surviving descendants" (as opposed to Wynn-Edwards' [1962] hypothesis that animals maintain their reproductive rate below the maximum possible rate).

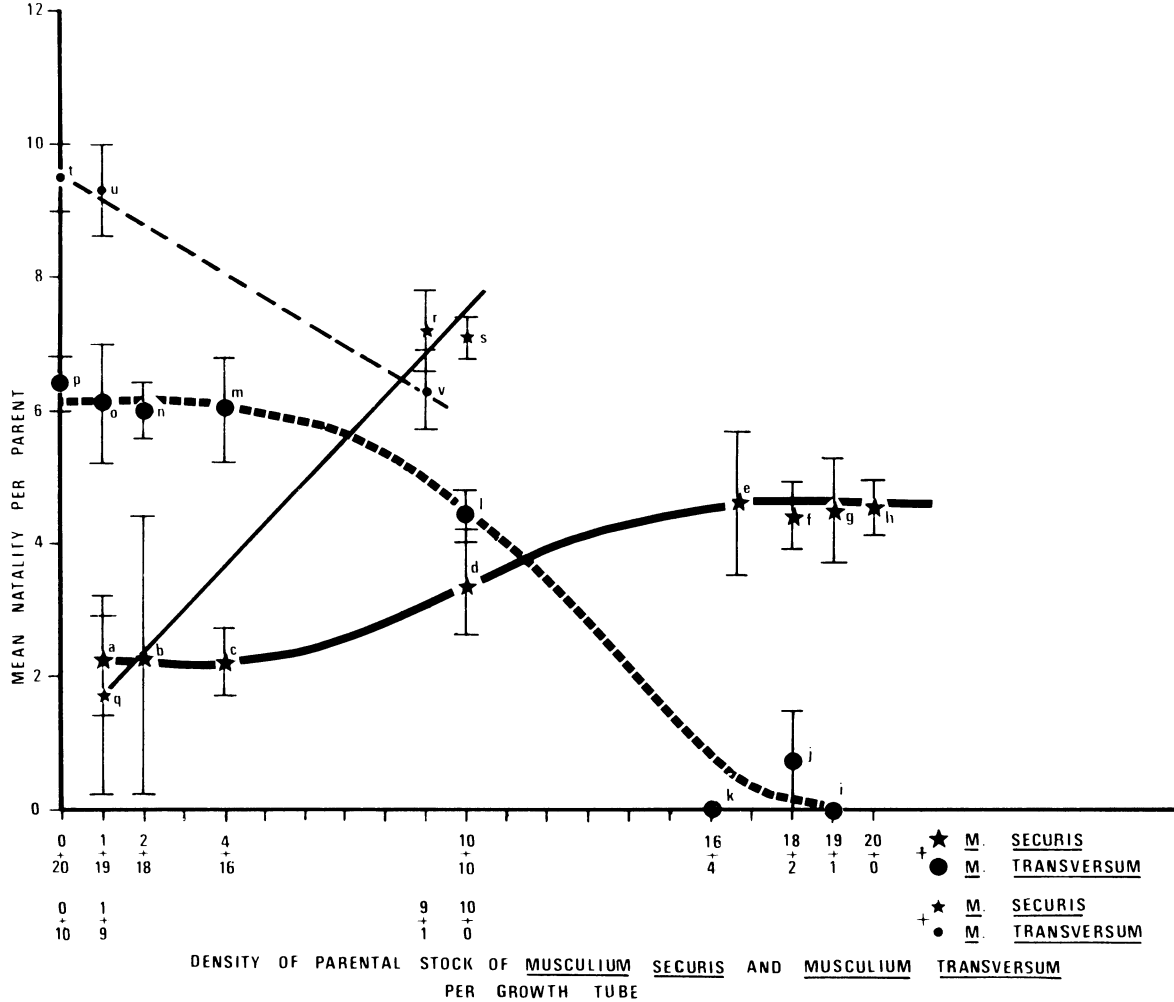


FIG. 3. Mean natalities per parent of *Musculium securis* and *Musculium transversum* showing effects of population density and competition in growth tubes placed in the shore zone of Britannia Bay. Vertical lines are standard deviations of the means. Curves were fitted by eye. See text for explanation of a-v.

Because recruitment exceeded the reproductive carrying capacity (defined here as the numbers that reproduce), it can be inferred that reproductive adults produced a surplus of young. This surplus, interpreted as representing mortality that can occur above carrying capacity and still maintain a balanced population, is shown in Fig. 1 to be a function of population density and increases as the litter size per parent decreases (cf. Figs. 1, 2) to an asymptotic value. Although it is true that in a balanced population, birth rate and mortality must be equal, Lack (1948, p. 46) maintains that this balance is primarily brought about by variations in the mortality and not the birth rate (litter size). The present study indicates that this is a valid hypothesis only for surplus recruitment and supports Skutch's (1967) suggestion that litter size is adjusted to balance mortality under saturation conditions. This implies that surplus recruitment acts as a buffer in

maintaining the carrying capacity. Under saturation conditions, the litter size per parent is at a minimum for *M. securis* and this minimum value (4.5) is sufficient to maintain saturation conditions. These results appear to contradict Lack's most-productive-clutch hypothesis but as pointed out by Fretwell (1969) and Stearns (1976) for birds, "wherever mortality selectively impinges on excess offspring through social dominance or other effects, then the birthrate can be adjusted downward, not in order to balance the death-rate, but to maximize the number of surviving progeny." If mortality exceeds surplus recruitment the balanced population is brought about by increased reproductive activity. Lack (1948) further contends that litter size does not vary sufficiently to achieve population balance; it is suggested here that marked variations in litter size may not be common due to the buffer effect of surplus recruitment. For example, for

M. securis in the present study, mortality of surplus adults can occur in growth dishes without affecting litter size per reproductive adult until carrying capacity is reached at which point any additional mortality would result in increased litter sizes. Although largely speculative, the buffer effect of surplus recruitment may be an important mechanism in population control. It is possible, although it remains to be shown, that the wide fluctuations in population densities that normally occur in nature (Nicholson 1933; Ehrlich and Birch 1967) are fluctuations in densities of surplus individuals and K (carrying capacity) tends to remain constant.

The life history studies of Mackie et al. (1976) tend to support the above conclusions; the total litter size per average reproductive parent in each of 4 different habitats is given in Table 1 and was calculated from the data in Table 2 and 4 of Mackie et al. (1976) by the formula: total litter size per average parent = (average number of extramarsupial larvae in first litter \times proportion of parents producing 1 litter) + (total number of extramarsupial larvae in 2 litters \times proportion of parents producing 2 litters). For example, the average parent in the 1970 Carp Pond population produced a total litter size of $(3.0 \times 0.64) + (5.1 \times 0.36) = 3.76$. The data from the Carp Pond population are particularly important because clams from this population were used in the present growth experiments to obtain the results in Table 2 and Figs. 1 and 2. As explained by Mackie et al. (1976), sampling itself in 1970 reduced the population size and this decrease in population size stimulated an increase in litter size in 1971. In this context, the 1971 data support the contention that the total litter size per average reproductive parent increases with decreasing densities.

The total litter sizes per average parent in Britannia Bay (Table 1) were much smaller than those in other habitats. This observation supports Lack's (1948) contention that litter size can be modified adaptively as do the transplant studies of Mackie et al. (1976) which indicate that the Britannia Bay population adapted to conditions in Britannia Bay and adults showed little reproductive capacity in other habitats. Greater numbers of young were achieved primarily by an increase in the number of litters produced (Mackie et al. 1976). However, the data also show that there may be an increase in the average litter size as well; this appears to be achieved by an increase in the viability of developing larvae rather than by an increase in egg production. Therefore, increased recruitment in *M. securis* is a function of both larval viability and of number of litters produced and supports Mountford's (1968) contention that maximum numbers of offspring are brought about by a combination of variation in litter sizes and the number of viable offspring per litter (rather than by number of viable offspring alone as proposed by Lack 1954).

The results also support Cody (1966), who on the

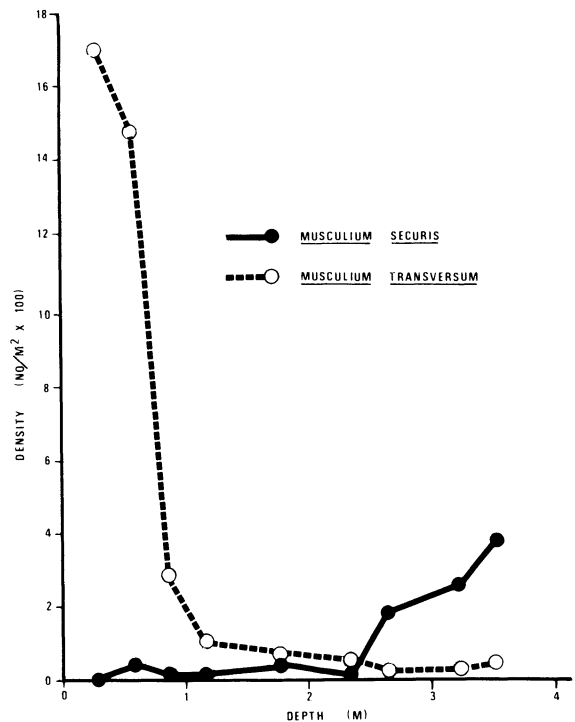


FIG. 4. Distributions of *Musculium securis* and *Musculium transversum* in Britannia Bay.

basis of environmental stability and utilization of food resources, predicted that birds favor reduced clutches in stable environments (e.g., the tropics, islands, and coasts) and increased clutch sizes in unstable environments (e.g., inland temperate regions). For example, Britannia Bay is a more stable environment (at least with respect to fluctuation of water levels and water quality) than the other habitats and favors reduced litter sizes; instability of conditions in the ponds favors increased litter sizes. In terms of r - and k -selections (MacArthur and Wilson 1967), the Carp Pond population of *M. securis* with a high natality in a comparatively unstable ephemeral habitat is an r -strategist; Britannia Bay is a more stable, perennial habitat and the population of *M. securis* is a k -strategist and has a low natality.

Competitive exclusion between

Musculium securis and *Musculium transversum*

The results of the competition experiments indicate that under overcrowded conditions and where 1 species predominates (e.g., greatly outnumbers the other) (1) competition among individuals of the predominant species is primarily intraspecific, and the presence of the subdominant species has little effect on their reproductive capacities, (2) interspecific competition results in reduced reproductive capacities of individuals of the subdominant species, and (3) *M. securis* is usually more prolific and therefore a better

competitor as a subdominant species than is *M. transversum* but when the numbers of individuals in each species become equal under overcrowded conditions, competition is primarily interspecific and *M. transversum* is more prolific and will eventually outnumber *M. securis*. Where less crowded conditions prevail, competition is primarily interspecific and *M. transversum* is again the better competitor since parents produced more young per clam than did *M. securis*.

The competitive exclusion principle (Hardin 1960) states that complete competitors cannot coexist. Although there is no definitive evidence that *M. securis* and *M. transversum* are complete competitors, the present study indicates that coexistence of the subordinate species is possible only in nominal numbers when one species greatly outnumbers the other. When populations are of similar size (as in h & u, Fig. 3), these species may coexist in moderate numbers but this probably is of short duration and may be found only as a transitory stage when 2 species (complete competitors) are colonizing a new habitat. However, populations of large and similar sizes will probably rarely, if ever, occur in nature when one species has a higher reproductive rate than the other (Hardin 1960). That is, the sequence of events that occur in the colonization of a suitable habitat where *M. securis* and *M. transversum* have just been introduced, would probably favor establishment of the latter. For example, *M. transversum* has a higher reproductive capacity than *M. securis* and population growth of the former species would be proportionately faster. The field experiments show that as the densities of the 2 species increased, interspecific competition also increased and the reproductive capacity of *M. securis* was depressed. In the absence of predation, competition, parasitism, etc., the carrying capacity of the habitat eventually would be filled, at which point the population of *M. securis* either would become extinct or be present in nominal numbers.

Support for the competitive exclusion principle is seen in the distribution patterns of *M. securis* and *M. transversum* in Britannia Bay (Fig. 4) in the 0.1 m depth. The 2 species may be found together but one usually greatly outnumbers the other in the deeper waters. However, experiments showed that *M. securis* grew much faster than *M. transversum* in the 3–4 m depths of Britannia Bay, even in the absence of interspecific competition (Mackie 1973). Therefore *M. se-*

curis was better adapted to conditions in the 3–4 m depths than was *M. transversum* and they were not complete competitors in the 3–4 m depth.

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