

## Effects of *Lunatia heros* Predation on the Population Dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA

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### Abstract

The interaction between the naticid snail predator *Lunatia heros* and 2 iteroparous, infaunal, intertidal bivalves was investigated in Lubec, Maine, USA. The *Mya arenaria* population consists primarily of young, small individuals. *M. arenaria* survivorship is low when young ( $3.5\% \text{ yr}^{-1}$  for the first 5 yr), then increases. *M. arenaria* can attain a length of 60 mm, but it is susceptible to *L. heros* attack only until it is 30 mm long. It delays reproduction until it is 20 mm long (3.8 yr) and diverts its resources instead into rapid early growth ( $4.9 \text{ mm yr}^{-1}$  for the first 5 yr). The *Macoma balthica* population has a larger proportion of older individuals than does that of *M. arenaria*. Survivorship is higher for *M. balthica* than for *M. arenaria* ( $76.3\% \text{ yr}^{-1}$  for the first 5 yr). Unlike *M. arenaria*, *M. balthica* attains a final length of only 25 mm and all sizes are susceptible to *L. heros* attack. *M. balthica* grows slowly ( $2.7 \text{ mm yr}^{-1}$  for the first 5 yr) and diverts its resources into earlier reproduction at a length of 10 mm (2.9 yr). These contrasting life-history patterns and the possible relationship between bivalve resource allocation and refuges from predation are discussed.

### Introduction

Several marine organisms, including bivalves (Paine, 1976; Franz, 1977; Edwards and Huebner, 1977), gastropods (Paine, 1965; Vince *et al.*, 1976), barnacles (Dayton, 1971), and tunicates (Sutherland, 1974), can escape predation by reaching a size refuge. Seed and Brown (1978) have hypothesized that under conditions of intense size-selective predation on younger, smaller individuals, rapid growth would be advantageous for species which can reach a refuge. If food were limiting, then the allocation of

resources to growth might delay the onset of reproduction. On the other hand, early reproduction would be advantageous for species too small to ever reach a size refuge. In species of this type, growth would be slow. Seed and Brown (1978) studied populations of the cockle *Cerastoderma edule* and the mussel *Modiolus modiolus* in Northern Ireland to support their hypothesis. Unfortunately they had little data to substantiate their claim that crabs and starfish are important size-selective predators on cockles and mussels. In addition, the cockles they studied were infaunal and intertidal while the mussels were epifaunal and subtidal. The growth and reproduction patterns they observed may have resulted from differences between the two habitats.

The purpose of this study was to compare the populations dynamics of 2 New England bivalve species exposed to predation by the naticid snail *Lunatia heros*. The 2 bivalves, *Mya arenaria* and *Macoma balthica*, are infaunal and found together on the same intertidal flats. Several aspects of the basic ecology of *M. arenaria* (Brousseau, 1978 a, b, 1979) and *M. balthica* (Gilbert, 1973, 1977, 1978) in New England have recently been reviewed. Although naticid predation has been investigated in the field and laboratory, little is known about the effects which size-selective predation by naticids may have on the population dynamics of bivalves (Edwards and Huebner, 1977).

### Materials and Methods

Populations of *Mya arenaria* and *Macoma balthica* were investigated at Federal Harbor, an intertidal flat of sandy mud in Cobscook Bay near Lubec, Maine, USA (Lat.  $44^{\circ}52'N$ ; Long.  $67^{\circ}04'W$ ). Air temperature at Federal Harbor varies from a winter low of approximately  $-35^{\circ}C$  to a summer high of about  $35^{\circ}C$ . Water temperature is also seasonal and ranges from  $0^{\circ}C$  to about  $10^{\circ}C$ , but shallow water moving onto or off the flat with the tide can reach  $24^{\circ}C$  in the summer. Salinity is usually around

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**Table 1.** *Mya arenaria* and *Macoma balthica*. Number per 0.02 m<sup>2</sup>. Values are sample means  $\pm$  standard error. Sample size = 20 in 1977, 40 in 1978, 20 in 1979. Columns may not add up to totals because some individuals could not be aged and were included in totals only

Age	<i>Mya arenaria</i>			<i>Macoma balthica</i>		
	1977	1978	1979	1977	1978	1979
$\leq$ 1-yr old	13.15 $\pm$ 2.04	3.48 $\pm$ 0.56	14.50 $\pm$ 1.86	0.80 $\pm$ 0.36	0.80 $\pm$ 0.18	1.35 $\pm$ 0.33
> 1-yr old	7.70 $\pm$ 0.78	9.13 $\pm$ 1.32	4.85 $\pm$ 0.82	8.55 $\pm$ 0.57	6.10 $\pm$ 0.39	3.70 $\pm$ 0.35
Total	21.10 $\pm$ 0.21	13.58 $\pm$ 1.86	19.35 $\pm$ 1.97	9.45 $\pm$ 0.66	7.50 $\pm$ 0.64	5.05 $\pm$ 0.48

30‰ S but is as low as 15‰ S in the early spring and as high as 32‰ S in the early fall (Commito, unpublished data).

Sampling was carried out on 6 October 1977, 11 November 1978, and 29 October 1979. Repeated sampling at Federal Harbor at different times of the year has shown that annual recruitment is completed by early fall and the largest number of 0-year class individuals is found at this time (Commito, unpublished data). A round coring device with a cross-sectional area of 0.02 m<sup>2</sup> was pushed 20 cm into the sediment; organisms were never observed below that depth because of the presence of a clay hardpan layer. Twenty cores were taken in 1977 and 1979 and 40 cores were taken in 1978. Sieving was performed in the field, using a mesh size of 1.1 mm in 1977 and 0.5 mm in 1978 and 1979. Material retained on the sieves was immediately brought back to the laboratory, preserved with buffered formalin, stained with rose bengal, and later sorted in white enamel pans. All individuals of *Mya arenaria* and *Macoma balthica* were counted (as were *Lunatia heros* in 1978) and shell length was measured with Vernier calipers. All empty, disarticulated *M. arenaria* and *M. balthica* valves were counted and measured as well. In addition, all individuals of *M. arenaria* and *M. balthica* in 1978 and 1979 were aged by counting annual disturbance rings. Newcombe (1935) and Lammens (1967) have demonstrated the accuracy of this aging technique for *M. arenaria* in Maine and *M. balthica* in Europe where cold winter temperatures cause ring formation.

For each sampling date, the densities of 0-year class and older *Mya arenaria* and *Macoma balthica* were calculated, as were their spatial distributions using Morisita's index,  $I_{\delta}$  (Morisita, 1959, 1962). An  $I_{\delta}$  value of 1 indicates a random distribution, with values greater than 1 and less than 1 indicating aggregation and uniformity, respectively. Growth rates were calculated by regressing length versus number of annual rings for the 1978 clams; both linear and power exponential regressions were used. Size-class frequency histograms for all 3 yr were prepared for living *M. arenaria* and *M. balthica* as well as for total disarticulated valves and disarticulated valves with *Lunatia heros* bore holes. The percentages of valves which were bored in each size class were also calculated. Age-class frequency histograms for living *M. arenaria* and *M. balthica* were prepared for the 1978 samples.

On 24 April 1979, directly preceding the anticipated time of spawning (Battle, 1932; Coe and Turner, 1938;

Ropes and Stickney, 1965; Lammens, 1967), 15 cores were taken in order to collect individuals of all sizes from both species to determine age of sexual maturity. These samples were processed in the same manner as the others. The preserved specimens were measured, and the gonads were removed, sectioned, and analyzed histologically following the terminology and technique of Ropes and Stickney (1965) and Brousseau (1978 b).

## Results

### Density and Spatial Distribution

The density of *Mya arenaria* was variable from year to year, primarily as a result of annual differences in the abundance of 0-year class individuals (Table 1). Because sampling occurred at the end of the long summer settlement period, the density of first year individuals reflects both recruitment and early survivorship. Density of *Macoma balthica* was less variable (Table 1). First year individuals accounted for a much smaller proportion of total population size for *M. balthica* than for *M. arenaria*. Changing from a 1.1-mm to a 0.5-mm mesh size after the first year probably had little effect on the sampling efficiency for the smallest bivalves. By the time of the fall sampling date they were large enough to be retained by the 1.1-mm mesh. During the entire study only 1 *M. arenaria* and no *M. balthica* smaller than 1.5 mm were found.

First year individuals of both species had significantly aggregated spatial distributions (Table 2). Although older *Mya arenaria* were usually clumped also, the older *Macoma balthica* were randomly distributed and showed a slight tendency towards a uniform spatial pattern. Adult

**Table 2.** *Mya arenaria* and *Macoma balthica*. Morisita's index of spatial dispersion,  $I_{\delta}$ . Each core = 0.02 m<sup>2</sup>. Sample size = 20 in 1977, 40 in 1978, 20 in 1979. Asterisk denotes  $I_{\delta}$  significantly different ( $P \leq 0.05$ ) from random

Age	<i>Mya arenaria</i>			<i>Macoma balthica</i>		
	1977	1978	1979	1977	1978	1979
$\leq$ 1-yr old	1.39*	1.75*	1.32*	3.83*	1.55*	1.43*
> 1-yr old	1.07	1.71*	1.20*	0.97	0.99	0.91
Total	1.14*	1.66*	1.15*	0.99	2.17*	0.98

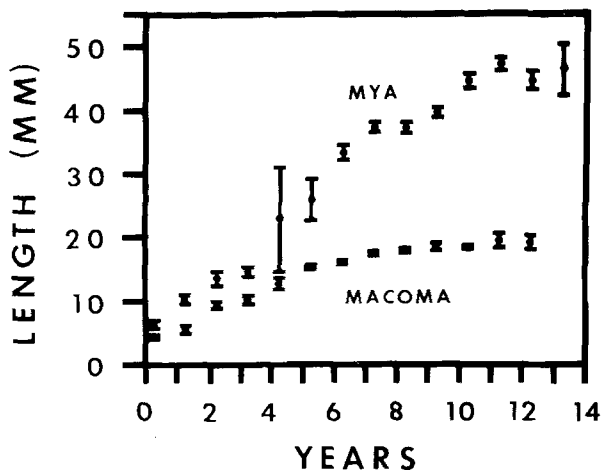


Fig. 1. *Mya arenaria* and *Macoma balthica*. Growth curves for *M. arenaria* (n=491) and *M. balthica* (n=277) where dots and vertical bars represent mean  $\pm$  standard error

*M. arenaria* are relatively stationary, but Levinton (1971) and Holme (1950) have demonstrated that adult tellinid bivalves can move horizontally and space themselves out at distances set by the length of the extensible siphons.

*Lunatia heros* individuals were abundant at Federal Harbor, with a 1978 density of  $0.38 \pm 0.12$  (SE) snail per  $0.02 \text{ m}^2$ . The large standard error and large Morisita's index value ( $I_d = 2.29$ ,  $P \leq 0.05$ ) indicate a clumped spatial distribution. The snails ranged in diameter from 7–20 mm. Although Abbott (1974) states that *L. heros* may attain a diameter of 100 mm, large snails are usually found subtidally (Franz, 1977). Medcof and Thurber (1958) found that most of the *L. heros* at an intertidal site in New Brunswick, Canada were 25–35 mm in diameter. No *L. heros* individuals larger than 20 mm have been found in over 2 yr of frequent sampling at 4 intertidal *Mya arenaria* flats in eastern Maine (Commito, unpublished data).

Growth Rates

Both the linear and power exponential regressions provide accurate descriptions of the growth of *Mya arenaria* and *Macoma balthica* at Federal Harbor (Table 3). *M. arenaria* grows more quickly than does *M. balthica*, about twice as rapidly over the first 5 yr of life. *M. arenaria* also reaches a larger size, approximately 2.5 times that of *M. balthica* when fully grown (Fig. 1).

*Mya arenaria* Size-Class Analysis

In 1977 most of the *Mya arenaria* population was comprised of small individuals 4–8 mm in length representing summer recruitment (Fig. 2). There were almost no individuals between the lengths of 8–30 mm, but larger clams from 30–60 mm were common. A similar pattern existed in 1978 except that there were fewer 0-class individuals (Table 1, Fig. 2) and the 1977 recruits, now 1-yr old, had grown in length and partially filled in the missing size classes. The 1979 population structure was similar to that in 1977. Most of the clams were new recruits and the year classes from 1977 and 1978 had largely disappeared (Fig. 2).

Table 3. *Mya arenaria* and *Macoma balthica*. Regression equations of age on length, where y=length and x=age

<i>Mya arenaria</i>		
Linear	$y = 5.81 + 3.73x$	$r^2 = 0.93$
Power exponential	$y = 10.83x^{(0.547)}$	$r^2 = 0.84$
<i>Macoma balthica</i>		
Linear	$y = 5.49 + 1.57x$	$r^2 = 0.78$
Power exponential	$y = 6.61x^{(0.465)}$	$r^2 = 0.82$

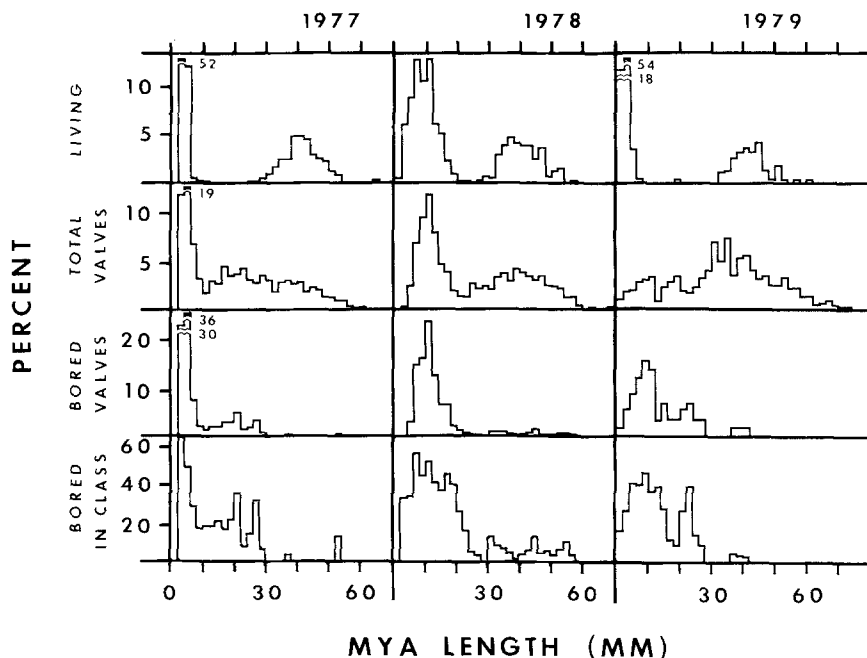


Fig. 2. *Mya arenaria*. Size-class frequency histograms from 3 yr for living *M. arenaria* (1977, n=417; 1978, n=492; 1979, n=380); total disarticulated valves (1977, n=913; 1978, n=1484; 1979, n=594); and disarticulated valves with *Lunatia heros* bore holes (1977, n=239; 1978, n=389; 1979, n=57). "Bored in class" refers to the percentage of disarticulated valves which were bored in each size class (1977, n=913; 1978, n=1484; 1979, n=594)

At least 2 reasons exist to explain the missing size classes from 8–30 mm. It is possible that poor larval recruitment occurred in the years corresponding to clams of those sizes. This hypothesis cannot fully explain the gap, however, because there was substantial recruitment during the years of this study but few of those clams survived long enough to reach 30 mm. A more feasible hypothesis is that size-selective predation by *Lunatia heros* removed clams smaller than 30 mm. Almost all of the disarticulated valves with bore holes (Fig. 2) were less than 30 mm in length. This pattern is also substantiated when the percentage of valves bored in each size class is considered (Fig. 2). It appears from the size-class histograms that *Mya arenaria* individuals were susceptible to predation by *L. heros* until the clams were about 30 mm long. Almost no bored *M. arenaria* valves longer than 30 mm were found, suggesting that *M. arenaria* can reach a size refuge from snail predation. Size-selective predation also explains why the 1977 and 1978 year classes were not able to persist into 1979. Edwards and Huebner (1977) have shown that the naticid snail *Polinices duplicatus*, which is closely related morphologically and ecologically to *L. heros*, captures and eats *M. arenaria* individuals which are about as long as the snail is wide. *L. heros* individuals at Federal Harbor were less than 20 mm in diameter and would thus be expected to prey selectively on the small *M. arenaria* individuals. Similar patterns of size-selective predation by naticids on bivalves have been discovered for *M. arenaria* and *P. duplicatus* in Massachusetts (Edwards and Huebner, 1977), for *Spisula solidissima* and *L. heros* off Long Island, New York (Franz, 1977), for *Mercenaria mercenaria* and both snails in New York and New Jersey (MacKenzie, 1977), and for 2 Miocene bivalves and *L.*

*heros* in a Chesapeake Bay fossil assemblage (Dudley and Dudley, 1980). Other predators such as oyster drills, whelks, decapod crabs, horseshoe crabs, and fish appear to feed in a similar size-selective manner on a variety of bivalve species (Smith and Chin, 1951; Walne and Dean, 1972; MacKenzie, 1977; Elner, 1978; Virnstein, 1979; Kelso, 1979).

At least 2 reasons exist which explain the presence of relatively large numbers of *Mya arenaria* individuals longer than 30 mm. One hypothesis is that *Lunatia heros* population density may have been lower for several years before 1977, exposing the small *M. arenaria* to less predation pressure and allowing them to reach a large size. Another hypothesis is that the large clams are the survivors from exceptionally strong year classes which were abundant enough to swamp the predatory ability of *L. heros*.

#### *Macoma balthica* Size-Class Analysis

In 1977, 1979, and to a lesser degree 1978, the *Macoma balthica* population had a bimodal size-class distribution (Fig. 3). This type of distribution is found in marine molluscs which grow more slowly as they get older (Brown and Seed, 1977). It has been described in other *M. balthica* populations at latitudes similar to Maine's (Lammens, 1967; Gilbert, 1973). Unlike the *Mya arenaria* population, bored valves were found in all size classes (Fig. 3). *M. balthica* individuals never reached a length greater than 30 mm at Federal Harbor, indicating that all sizes were potentially susceptible to attack by *Lunatia heros*. Although all sizes were attacked, the percentage of valves

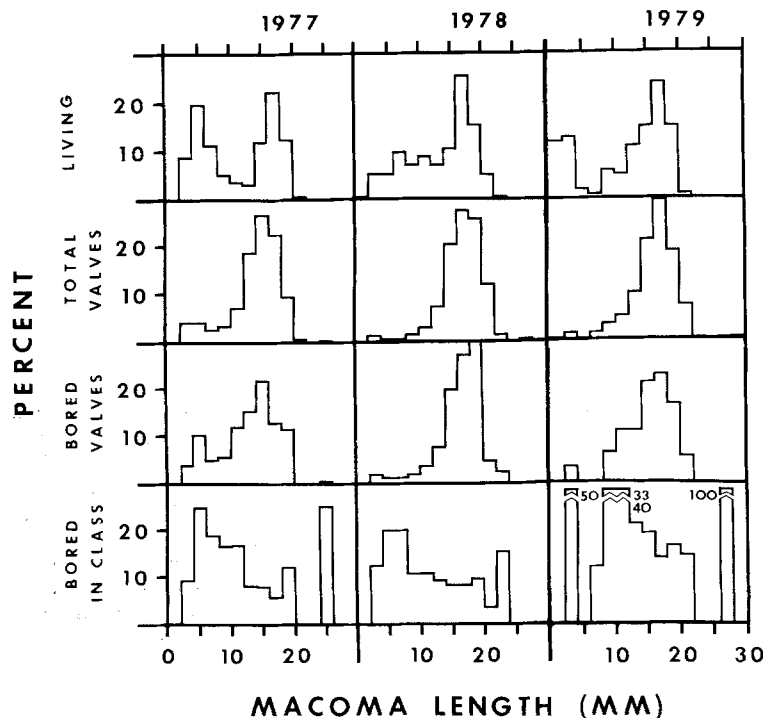


Fig. 3. *Macoma balthica*. Size-class frequency histograms from 3 yr for living *M. balthica* (1977,  $n=191$ ; 1978,  $n=274$ ; 1979,  $n=102$ ); total disarticulated valves (1977,  $n=789$ ; 1978,  $n=1046$ ; 1979,  $n=566$ ); and disarticulated valves with *Lunatia heros* bore holes (1977,  $n=155$ ; 1978,  $n=173$ ; 1979,  $n=109$ ). "Bored in class" refers to the percentage of disarticulated valves which were bored in each size class (1977,  $n=789$ ; 1978,  $n=1046$ ; 1979,  $n=566$ )

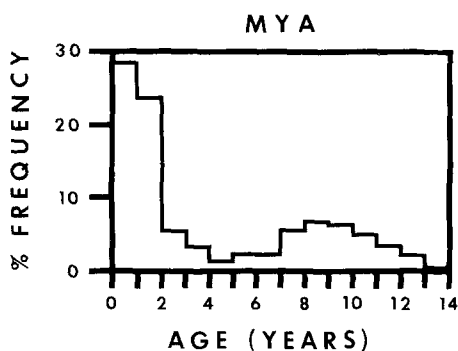


Fig. 4. *Mya arenaria*. Age-class frequency histogram for 1978 (n=491)

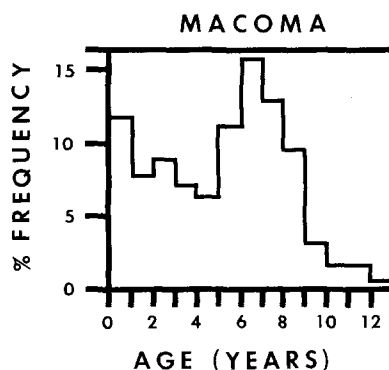


Fig. 5. *Macoma balthica*. Age-class frequency histogram for 1978 (n=277)

bored in each class (Fig. 3) was generally lower across classes for *M. balthica* than for *M. arenaria*. The chance of being preyed upon was smaller for *M. balthica* than for an *M. arenaria* individual of the same size. This pattern indicates that there may have been lower mortality due to *L. heros* in the *M. balthica* population than in the *M. arenaria* population.

Population Structure of *Mya arenaria* and *Macoma balthica*

The age-specific mortality patterns suggested by the size-class histograms are reflected in the 1978 age-class frequency histograms for *Mya arenaria* (Fig. 4) and *Macoma balthica* (Fig. 5). The *M. arenaria* population was comprised primarily of young individuals, even though 1978 had the smallest 0-year class of the 3 yr under investiga-

tion. Young individuals apparently suffered extremely high rates of mortality. A mean survivorship for *M. arenaria* of only 3.5% yr<sup>-1</sup> over the first 5 yr of life was obtained by comparing the number of clams of age x in 1978 with those of age (x + 1) in 1979 (Table 4). Although this method is crude because of the small numbers of individuals in some year classes, it demonstrates that survivorship is at least qualitatively much higher for *M. arenaria* after age 5. This age corresponds well to *M. arenaria*'s 30-mm size refuge from predation.

Unlike *Mya arenaria*, the *Macoma balthica* population had a large proportion of older individuals. The pattern of survivorship (Table 4) was different as well and indicated that predation by *Lunatia heros* was lower on *M. balthica* than on *M. arenaria*. Mean survivorship was 76.3% yr<sup>-1</sup> over the first 5 yr of life and was reduced rather than enhanced for older individuals.

Table 4. *Mya arenaria* and *Macoma balthica*. Estimated survivorship obtained by comparing the number of individuals of each age x in 1978 with number of each age (x + 1) in 1979. Numbers for 1979 were obtained by multiplying actual numbers by a factor of 2 because only half as many samples were taken in 1979 as in 1978

Age, x	<i>Mya arenaria</i>			<i>Macoma balthica</i>		
	No. of age x in 1978	No. of age (x + 1) in 1979	Percent survival	No of. age x in 1978	No. of age (x + 1) in 1979	Percent survival
0	141	8	5.7	33	10	30.3
1	118	0	0	22	14	63.6
2	28	0	0	25	26	104.0
3	17	2	11.8	20	14	70.0
4	9	0	0	18	26	144.4
5	12	14	116.7	31	26	83.9
6	12	30	250.0	44	26	59.1
7	29	64	220.7	36	14	38.9
8	34	32	94.1	26	4	15.4
9	31	24	77.4	9	4	44.4
10	25	10	40.0	5	0	0
11	19	2	10.5	5	0	0
12	12	2	16.7	2	0	0
13	4	0	0	0	0	0
14	0	0	-	-	-	-

### Gonad Analysis

Forty-five *Mya arenaria* specimens ranging in length from 3.6 to 63.6 mm and 20 *Macoma balthica* from 5.4 to 23.9 mm were analyzed for condition of the gonads. In both species sexual maturity was clearly related to size of the individuals. The 14 smallest *M. arenaria* (3.6–18.1 mm) had gonads in the indifferent stage, as did 3 individuals of length 20.3, 24.3, and 63.6 mm. The remaining 28 clams, which ranged in length from 19.4–62.7 mm, all had gonads in the developing, ripe, spawning, or spent stages. It appears that *M. arenaria* individuals became sexually mature at Federal Harbor at a length of about 20 mm. This length corresponds to an age of 3.8 yr.

The 5 smallest *Macoma balthica* (5.4–8.6 mm) had gonads in the indifferent stage, as did 1 individual of length 18.5 mm. The remaining 14 clams, which ranged in length from 10.1–23.9 mm, all had gonads in the developing, ripe, spawning, or spent stages. *M. balthica* apparently became sexually mature at a length of about 10 mm or an age of approximately 2.9 yr. These data suggest that *M. balthica* becomes sexually mature at a smaller size and younger age than does *Mya arenaria*.

### Discussion

*Macoma balthica* of all sizes and ages were preyed upon by *Lunatia heros* (Fig. 3), although survivorship was higher for *M. balthica* than for similarly sized *Mya arenaria* (Table 4). This difference may be due to the fact that *M. balthica* possesses much longer siphons than does *M. arenaria*. Blundon and Kennedy (unpublished manuscript) have found *M. arenaria* in the Choptank River, Maryland, as deep as 25 cm below the sediment surface and *M. balthica* as deep as 35 cm, despite their smaller body size. They showed that over all sediment depths *M. balthica* burrowed more deeply than did *M. arenaria* of the same size. The same pattern occurs at Federal Harbor in Maine. Perhaps the deep burrow of *M. balthica* pro-

vides a spatial refuge and affords it some protection from *Lunatia heros*. The experimental work of Smith and Chin (1951), Virnstein (1977, 1979), and Blundon and Kennedy (unpublished manuscript) has demonstrated that deeply burrowing bivalve species are less susceptible to predation by horseshoe crabs and decapod crabs than are those which live nearer the surface. Their results also showed that older, larger *M. arenaria* are safer from crab predation than are younger, smaller individuals close to the surface. The refuge commonly associated with size may have a spatial component in addition to greater resistance to attack due to a thicker, stronger shell (Walne and Dean, 1972; MacKenzie, 1977; Elner, 1978). It is difficult to separate these 2 factors because both depth in the sediment and shell strength may be correlated with size.

The selective advantage of a size refuge can occur only if a species reaches a large adult size. Since adult *Macoma balthica* never get large enough to escape from *Lunatia heros*, there would be no selective advantage for this species to adopt a rapid growth rate. Indeed *M. balthica* grows more slowly than does *Mya arenaria* despite the fact that it has a thinner shell and could apparently divert the resources thus saved in growth (Griffiths and King, 1979). In addition, intertidal *M. arenaria* can feed only at high tide whereas *M. balthica* has the ability to ingest food over the entire tidal cycle because it is a deposit feeder as well as a suspension feeder (Gilbert, 1977). Although no comparative estimates of reproductive effort exist for *M. arenaria* and *M. balthica*, the slower growth of the latter species may be due in part to its earlier diversion of resources into reproduction. Lammens (1967) has demonstrated that growth in *M. balthica* slows down and often stops during periods of gonad development.

A summary of life-history parameters for *Mya arenaria* and *Macoma balthica* (Table 5) shows that these 2 species are consistent with the model for resource allocation into growth and reproduction proposed by Seed and Brown (1978). Like the Seed and Brown *Modiolus modiolus* population, *M. arenaria* grows rapidly and delays reproduction until it reaches a size refuge from predation. Like

**Table 5.** *Mya arenaria* and *Macoma balthica*. Differences in life-history parameters between the 2 populations at Federal Harbor, Lubec, Maine, USA

Life-history parameter	<i>Macoma balthica</i>	<i>Mya arenaria</i>
<b>Reproduction</b>		
Age at first reproduction	2.9 yr	3.8 yr
Size at first reproduction	10 mm	20 mm
Recruitment pattern	low, less variable	high, more variable
<b>Growth</b>		
Rate for first 5 yr	2.7 mm yr <sup>-1</sup>	4.9 mm yr <sup>-1</sup>
Final size	25 mm	60 mm
<b>Population structure</b>		
Size classes	all sizes common	mostly small, few large
Age classes	all ages common	mostly young, few old
Survivorship	moderate for all ages	low when young, then high
Susceptibility to predation	moderate for all ages	high until 30 mm long, then low

the *Cerastoderma edule* population, *M. balthica* grows slowly, never reaches a size large enough to escape predation, and reproduces early. There is a difference, however, between the 2 systems. *C. edule* and *M. modiolus* both live close to or on the sediment surface and are exposed to intense predation pressure (Seed and Brown, 1978). *M. balthica*, on the other hand, may suffer less mortality due to predation than does *M. arenaria*, despite its small size and thin shell. It incorporates early reproduction with the possible attainment of a spatial refuge afforded by its deep burrow. The adaptive option of a similar spatial refuge is unavailable to *C. edule*. Seed and Brown (1978) have not considered spatial refuges and other modes of escaping predation. Thus the applicability of their model may be restricted to epifaunal bivalves and those infaunal bivalves which live close to the sediment surface.

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