

Predation on Encapsulated Larvae by Adults: Effects of Introduced Species on the Gastropod *Ilyanassa obsoleta*

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ABSTRACT: The abundant and ubiquitous marine snail *Ilyanassa obsoleta* is not known to be a major food item of any predator. Several species prey heavily upon its egg capsules, which spend 1 or more wk attached to solid objects in the intertidal zone. Predation losses in caging experiments conducted in Barnstable Harbor, Massachusetts (USA) averaged 52 %, but in 1 case exceeded 85 % in 10 d. Thus, predation on encapsulated larvae of this population equals or exceeds that on planktonic stages. Much of this mortality was associated with introduced species. Predation rates (egg capsules individual⁻¹ 2 d⁻¹) measured in the laboratory were: native hermit crabs *Pagurus longicarpus*, 141; introduced green crabs *Carcinus maenas*, 330; and introduced periwinkles *Littorina littorea*, 11. *L. littorea* was the most abundant egg consumer in the mid-intertidal zone where most egg capsules were laid. Capsules detached by the predators released larvae as did whole capsules defecated by *L. littorea*. Two native predators on molluscs, moonsnails (*Polinices duplicatus*) and juvenile horseshoe crabs (*Limulus polyphemus*), did not eat egg capsules.

INTRODUCTION

For species with planktonic larvae, maximum mortality is generally associated with the plankton (e. g. Bayne, 1976; Levinton, 1982). Emphasis has been placed on mortality at settlement due to adults or established individuals (Thorson, 1950; Mileikovsky, 1974; Woodin, 1976, 1979; Wilson, 1980; Hunt, 1981). Established individuals may also prey on eggs or larvae before they reach the plankton (MacKenzie, 1961; Hurst, 1965; Perron, 1975; Race, 1979; Tallmark, 1980). Many soft-bottom polychaetes and gastropods do not directly shed their eggs, sperm, or larvae into the water column, but rather deposit eggs on the bottom in capsules or gelatinous masses (Pechenik, 1979). The relative importance of mortality on encapsulated larvae is not generally known. In this paper, I examine the importance of predation on egg capsules of the common marine gastropod *Ilyanassa obsoleta*.

Ilyanassa obsoleta attaches its egg capsules to many 'solid' surfaces in the intertidal zone, including wood,

algae, shells, eel grass, and marsh peat (Tyron, 1882; Dimon, 1905; Scheltema, 1962; Pechenik, 1978). In Barnstable Harbor, Massachusetts (USA), surfaces suitable for egg capsule deposition are so rare (Pechenik, 1978) as to limit the reproductive output of some populations of *I. obsoleta* (Brenchley, 1981). Egg capsules protect developing embryos from low-salinity stress (Pechenik, 1982), but are not necessary for development and do protect from desiccation (Pechenik, 1978). The encapsulated larvae are then exposed to intertidal predators over the next 1 to 3 wk, depending on seawater temperatures which regulate development (Scheltema, 1967). After 1 to 2 wk in the plankton, the larvae return to creep and swim near the bottom for another 2 wk.

Juvenile and adult *Ilyanassa obsoleta* are preyed upon by the green crab *Carcinus maenas* (Stenzler and Atema, 1977; Ashkenas and Atema, 1978), the moonsnails *Polinices duplicatus* and *Lunatia heros* (Atema and Burd, 1975; Stenzler and Atema, 1977), and migratory birds (Recher, 1966; Anderson, 1970), but *I. obsoleta* is not believed to be one of their major food items. Survivorship of individuals attaining sexual

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maturity (ca. 2 yr) is high. The greatest source of adult mortality is associated with trematode parasites (Miller and Northup, 1926; Grodhaus and Keh, 1958; Gambino, 1959; Sindermann, 1960; Stunkard, 1961; Schaefer et al., 1968; Stambaugh and McDermott, 1969; Vernberg, 1969; Smith, 1980). These parasites can affect the locomotion, reproduction, sexuality, growth, and physiological tolerances in older snails in particular.

In Barnstable Harbor, *Carcinus maenas*, *Pagurus longicarpus*, *Littorina littorea*, and 2 molluscan predators – *Polinices duplicatus* (Edwards, 1974) and *Limulus polyphemus* (Green and Hobson, 1970) – were commonly found near surfaces where egg capsules were laid. Other predators in the Harbor such as *Lunatia heros* and *Natica clausa*, were not common in the study site. This research, part of a study on the migration and aggregation of mud snails, was undertaken to determine (1) which, if any, of these species prey on eggs of *Ilyanassa obsoleta* and (2) the extent of such predation in nature.

METHODS AND MATERIALS

The study was conducted during May and June, 1981 on a sandy intertidal flat between Indian Trail and Bone Hill Road in Barnstable Harbor, Massachusetts (41°43'N; 70°20'W). Laboratory experiments were done at the Marine Biological Laboratory.

Laboratory Experiments

The 5 suspected predators (Table 1) were collected in the mid-intertidal zone. Except for *Littorina littorea*, each specimen was placed in a glass finger bowl (bottom area, 70 cm²) with a 5 to 10 mm layer of sand collected from the Harbor, and a 1 to 2 cm strand of *Codium* or *Zostera* bearing approximately 500 intact *Ilyanassa obsoleta* egg capsules, collected the same day. These capsules contained early embryos with no velum pigmentation or shell visible. The bowls were covered with mesh and submerged in large tables with running seawater. The number of broken and empty egg capsules was counted every 1 to 2 d for the next 4 to 5 d.

Two sets of experiments were designed for *Littorina littorea* which migrated upwards in the submerged laboratory containers. In the first, 4 adult *Ilyanassa obsoleta* (18 to 22 mm in shell length) were added to each of 12 glass bowls and given several substrates on which to lay egg capsules (rock, shell, and *Codium* or peat). After 10 d, the mudsnails were removed, and 6 littorines added to each bowl. The number of intact

egg capsules remaining on each surface was recorded every 2 d for the next 8 d. In the second experiment, 4 adult mud snails were added to each of 24 compartments (4 × 4 × 4 cm) of a plastic storage box and again given several substrates for egg laying. The walls of the box were perforated and fitted with 4 seawater hoses to ensure adequate circulation. The water level was maintained 1 cm below the top of the box. After 10 d, egg capsules were counted, the mud snails removed, and 2 littorines added. As before, the number of egg capsules remaining on each surface was recorded every 2 d for 8 d.

Seawater temperatures rose from 14 °C to 18 °C in mid-June. At these temperatures, *Ilyanassa obsoleta* embryos emerge from capsules in 2 to several wk (Scheltema, 1967). Egg capsules from which larvae have naturally emerged can be identified by the absence of the opercular plug (Pechenik, 1975). To ensure that empty capsules found in the containers did not reflect natural emergence, experiments were terminated when larval within the capsules had acquired a purple velar pigmentation.

The successful completion of development in egg capsules defecated by *Littorina littorea* and broken by *Carcinus maenas* and *Pagurus longicarpus* was also examined. For 24 h *L. littorea* were fed mud snails egg capsules held in abundance within bowls. The periwinkles often trapped uneaten capsules behind their opercula when moved from one bowl to another. Therefore, the snails were examined for adhering capsules before they were transferred to a second clean bowl of seawater. Capsules collected the following day from their feces were moved to room temperature (24 °C) to accelerate development and examined periodically until all control capsules had hatched. *C. maenas* and *P. longicarpus* did not ingest the capsule itself. Broken and detached capsules were collected from bowls containing each predator species, moved to room temperature, and examined periodically for larval emergence.

Field Experiments

Censuses of *Ilyanassa obsoleta* and the suspected predators were conducted on the Barnstable Harbor sand flat in June 1981. Numbers of *I. obsoleta*, *Littorina littorea*, and *Pagurus longicarpus* on the surface or buried 2 to 3 cm in the sand were counted in 24 to 60 replicate 0.25 m² quadrats, (1) at the marsh edge and adjacent flat of the upper tidal zone, (2) in tide pools and exposed flats of the mid-intertidal zone, and (3) in the low intertidal *Zostera* bed. The abundance of *Carcinus maenas* was determined during flood tides with the aid of mask and snorkel. Counts were made in the

mid-intertidal zone on the exposed ends of 156 *Diopatra cuprea* tubes (= tube-caps) which had egg capsules already attached, or *I. obsoleta* actively depositing egg capsules, or no egg capsules or mud snails present.

A field experiment was conducted to measure rates of predation on egg capsules in a tide pool near Indian Trail. The population of *Ilyanassa obsoleta*, about 20 000 individuals, remained within that pool all summer as it did the previous year (Brenchley, 1980). Most egg capsules were laid on 9 small clumps of eel grass and a few were laid on the stalks of the cord grass *Spartina alterniflora*, low in the rank of preferred substrates (Brenchley, 1981). Masses of egg capsules laid on *Codium*, a highly preferred substrate, were collected from the mid-intertidal zone. *Codium*, obtained from a pile of actively reproducing mud snails, was selected because variability in numbers of egg capsules per unit length was found to be small in the laboratory experiments. One strand was cut into 10, 1-cm lengths so that initial numbers of egg capsules per unit length could be estimated. The remaining was cut into 5-cm lengths, and tied to wooden stakes in the tide pool. Eight pieces were left uncaged and 6 strands were enclosed within two 0.1 m² × 15 cm high cages constructed of plastic mesh (0.6 mm openings). Each strand was collected and preserved on Day 10 (June 20) in alcohol. The number of egg capsules on each strand was counted.

RESULTS

Laboratory Results

Carcinus maenas and *Pagurus longicarpus* were voracious predators on mud snail eggs, ingesting the contents of an average of 330 and 141 capsules every 2 d (Table 1). These rates of predation are exaggerated

Table 1 *Ilyanassa obsoleta*. Rates of consumption on egg capsules in laboratory studies. Mean number of eggs individual⁻¹ 2 d⁻¹; SD: standard deviation. Brackets indicate number of specimens used; N: counts of predation rates

Species	Size (mm)	Consumption rate		
		N	Mean	SD
<i>Pagurus longicarpus</i>	(21) 5.0–6.9 ¹	35	141	46
<i>Carcinus maenas</i>	(9) 20–23 ²	10	330	103
<i>Littorina littorea</i>	(96) 9–18 ³	65	11	10
<i>Limulus polyphemus</i>	(4) 19–23 ²	12	0	
<i>Polinices duplicatus</i>	(6) 9–50 ³	12	0	

¹ Anterior shield length
² Carapace width
³ Shell length

by the lack of alternative prey. No depression in *C. maenas*' rate occurred when 200 *Gemma gemma* were added (ANOVA, $F_{1,10} = 0.048$, $P = 0.989$) even though 95 % of the clams were eaten within 2 d. Alternative prey were not provided to *P. longicarpus*. The feces of both species were the color of the embryos and did not contain empty capsules nor recognizable fragments of capsule walls. Living larvae emerged from most of those capsules which were detached or broken by these 2 species (Table 2).

Table 2. *Ilyanassa obsoleta*. Percent of intact and broken egg capsules from which larvae successfully emerged. N: number of capsules examined; %: percent with larvae emerging

Capsule condition	Intact		Broken	
	N	%	N	%
Undisturbed	106	97.1		
<i>Carcinus</i> detached	25	93.1	25	72.7
<i>Pagurus</i> detached	25	94.0	25	64.3
<i>Littorina</i> defecated	16	56.2	87	0

Littorina littorea destroyed an average of 11 capsules every 2 d (Table 1). The periwinkles attempted to engorge the capsules, usually breaking the wall and consuming the eggs. On occasion the entire capsule was swallowed. Most defecated capsules were broken and did not contain embryos. Larvae emerged from half of those defecated capsules which did not appear to be broken (Table 2).

Adult and juvenile *Polinices duplicatus* and juvenile *Limulus polyphemus* did not prey on egg capsules in the laboratory (Table 1). Few capsules were detached during numerous contacts by either of these species.

Field Studies

Carcinus maenas and *Pagurus longicarpus* were most numerous in the low intertidal *Zostera* bed and in the tide pools of the mid-intertidal zone (Table 3). Both species were active in the tide pools at low tide, and during high tides. Counts of *C. maenas* from a fixed location in the eelgrass beds during one flood tide ranged from 3 to 12 min⁻¹. Few could be seen when swimming over the sand flat, and many remained within the perimeter of the tide pools. Both species were attracted to egg capsules, being more abundant on tube-caps with capsules attached than on tube-caps with *Ilyanassa obsoleta* or without capsules (Table 4). *Littorina littorea* was most numerous in and along the marsh, but also abundant throughout the intertidal zone, particularly on drift algae, wood, rocks, and tube-caps lacking adult *Ilyanassa* (Tables 3 and 4).

Table 3. *Ilyanassa obsoleta*. Densities and egg predators 0.25 m⁻² (mean \pm 1 standard error) in Barnstable Harbor, June, 1981. N: number of quadrats censused. Relative abundance of *Carcinus maenas* determined from observations made at flood tide

Location	N	<i>Ilyanassa</i>	<i>Littorina</i>	<i>Pagurus</i>	<i>Carcinus</i>
Upper tidal zone					
Marsh edge	49	0.1 \pm 0.1	46 \pm 3.0	0.2 \pm 0.1	common
2-35 m from edge	39	3.3 \pm 1.0	2.8 \pm 1.0	0.1 \pm 0.1	rare
Mid tidal zone					
Tide pools	40	37 \pm 5.4	2.3 \pm 0.4	0.7 \pm 0.2	0.3 \pm 0.1*
Exposed flats	60	31 \pm 5.3	1.7 \pm 0.4	0.1 \pm 0.1	rare
Low <i>Zostera</i> bed	24	0	9.4 \pm 1.8	4.3 \pm 1.8	common

* Estimated from tide pools of known size

Table 4. Densities of egg predators on, or immediately adjacent to, tube-caps of *Diopatra cuprea* which either lacked egg capsules, had *Ilyanassa obsoleta* actively depositing capsules, or had egg capsules but no *I. obsoleta* (mean \pm 1 standard error). N: number of tube-caps examined

Condition	N	<i>Ilyanassa</i>	<i>Littorina</i>	<i>Pagurus</i>	<i>Carcinus</i> *
Without capsules	24	1.2 \pm 0.2	2.8 \pm 0.6	0.8 \pm 0.3	17 %
With <i>Ilyanassa</i>	62	97 \pm 6	0.7 \pm 0.2	0.5 \pm 0.1	12 %
With capsules only	70	0	2.5 \pm 0.3	1.9 \pm 0.2	36 %

* Percentage with *Carcinus maenas* present within 0.25 m²

The high rates of egg predation measured in the laboratory raise the question as to whether these predators have similar effects in nature where alternative, and possibly more preferable prey items are available. The initial number of egg capsules on 5-cm strands of *Codium* used in field caging experiments was determined to be approximately 1215 (243 \pm 12 capsules cm⁻¹; n = 10). After 10 d, caged strands averaged 1103

Littorina littorea was the most abundant egg predator in the mid-intertidal zone where most egg capsules were laid by *Ilyanassa obsoleta*. Two-week long photographic studies documented a decline in egg capsules from 80 % to 30 % by cover on the end of a log occupied by *L. littorea*. The other end, from which *L. littorea* were removed every 3 to 4 d, increased capsule cover from 75 % to 80 % over this period.

Table 5. *Ilyanassa obsoleta*. Number of egg capsules (mean \pm 1 standard deviation) remaining on caged and uncaged strands of *Codium fragile* after 10 d in a tide pool (June, 1981). F ratio from Analysis of Variance

Condition	N	Capsules	Range	F _(1,12)
Caged	6	1103 \pm 32	989-1172	16.72**
Uncaged	8	572 \pm 108	146-1040	

** p = .0015

egg capsules (Table 5), an unexplained loss of 9 % Strings binding the strands were probably responsible for this loss. Variability was small and no predators were seen within the cages. In contrast, variability among uncaged strands was large (Table 5). On the average, uncaged strands had 52 % fewer egg capsules than caged strands. One uncaged strand lost 85 %, while another was not attacked by predators.

DISCUSSION

In this study, mortality of benthic, encapsulated *Ilyanassa obsoleta* larvae equalled or exceeded that during the planktonic phase: more than half of the larvae were eaten before the remaining emerged (Table 5). Spines on the capsules did not deter predation by *Pagurus longicarpus* and *Carcinus maenas*, but they may have interfered with egg consumption by *Littorina littorea*. Capsules protected embryos from digestion by *L. littorea* (Table 2). Pechenik (1979) suggests that encapsulation reduces mortality in the plankton since larvae spend less time at this vulnerable stage. However, selection did not appear to favor encapsulation in this study.

One explanation is that most of the predation was associated with introduced European species: *Car-*

cinus maenas, the most voracious predator, and *Littorina littorea*, the most abundant predator (Tables 1, 3 and 4). *C. maenas* may have been introduced by ships to the mid-Atlantic coast in the 18th century, from where it spread north into New England (Verrill et al., 1874; Bryant, 1906; Chilton, 1910; Scattergood, 1952; Carlton, pers. comm.). *L. littorea* first appeared in Nova Scotia around 1840 and rapidly spread south into New Jersey (Dexter, 1961; Kraeuter, 1974; Carlton, 1982). Less obvious is that the third major predator, the indigenous hermit crab *Pagurus longicarpus*, is probably more abundant now than before the arrival of *L. littorea* (Carlton, 1982). According to Say (1822), *P. longicarpus* most frequently utilized shells of *Ilyanassa obsoleta* in the early 19th century, but now *L. littorea* shells are commonly used (Scully, 1979; Carlton, 1982). Unlike other hermit crab populations (e. g. Childress, 1972; Vance, 1972; Fotheringham, 1976), populations of *P. longicarpus* in New England are not limited by shell availability (Scully, 1979).

Several lines of evidence suggest that *Pagurus longicarpus* and *Carcinus maenas* are attracted to egg capsules, but that *Littorina littorea* is not. *P. longicarpus*, a micro-herbivore and scavenger (Allee and Douglas, 1945; Roberts, 1968; Scully, 1978), and *C. maenas*, primarily a molluscan predator (Ebling et al., 1964; Ropes, 1969), detached many egg capsules under laboratory conditions and later ate them. Both species also devoured the egg collars of *Lunatia heros* and *Polinices duplicatus*. In the field, both crustacean species were more abundant near tube-caps with egg capsules than without capsules (Table 4). *L. littorea* in contrast, did not ingest unattached capsules or egg collars in the laboratory, and was as abundant on tube-caps with egg capsules as those without (Table 4). The lower density of littorines on tube-caps with *Ilyanassa obsoleta* present reflects the behavior of the adult mud snail, which actively avoids *L. littorea* (Brenchley, 1980, 1981). *L. littorea*, a herbivore (e. g. Lubchenko, 1978) incapable of digesting capsule walls (Table 2), inadvertently grazes upon the capsules because of their similarity to algal fronds or diatoms.

Ilyanassa obsoleta has not accomplished effective chemoreceptory responses in 30 generations to avoid the introduced predators, although its sense of chemoreception to prey and native predators is highly developed (Copeland, 1918; Carr, 1967; Brown, 1969; Crisp, 1969; Gurin and Carr, 1971; Atema and Burd, 1975; Stenzler and Atema, 1977). Unlike the European mud snail *Nassarius reticulatus*, the American species does not bury when the odor of *Carcinus* (European) is present (Atema and Stenzler, 1977; Crisp, 1978). *Littorina* also does not elicit an alarm response (Stenzler and Atema, 1977). In fact, *I. obsoleta* is somewhat attracted to crushed *Littorina littorea* (Snyder, 1967;

Atema and Burd, 1975). Laboratory studies show that physical contact, but not water soluble cues, cause *I. obsoleta* to delay egg laying when held with either *L. littorea* or *Pagurus longicarpus* (Brenchley, in prep.). The hermit crabs constantly handle the shells, and within 2 wk the shells are empty. Whether *P. longicarpus* eats *I. obsoleta* alive (Arnold, 1901) was not determined here, but the interaction probably occurs only in confinement.

In addition, *Ilyanassa obsoleta* has not evolved an obvious life history response. A 2 to 4 wk delay in the peak of activity during this study would have reduced the exposure of encapsulated larvae to predators by as much as 50 % to 75 %. This is because development was arrested in early May and remained slow into June, when seawater temperatures rose from 13°C to 18°C (Scheltema, 1967). Yet, the predators were active and egg capsules were laid at 13 °C in the laboratory (Table 1). Reproductive activity of *I. obsoleta* is triggered by rising seawater temperatures (Jenner, 1956; Scheltema, 1967; Sastry, 1971), and typically occurs early in the growing season. For example, egg laying begins in February in Beaufort, North Carolina (USA) and terminates there in May as it begins further north in Barnstable Harbor. Early reproduction prolongs only the encapsulated stage because, according to Scheltema (1967), by the time the larvae finally emerge, the sea will have warmed sufficiently to insure rapid development in the plankton. The emergence of the larvae would not be delayed, since development in capsules is slow or arrested during the period in question.

Co-evolutionary responses requiring genetic change will be slow to evolve in species like *Ilyanassa obsoleta* which are genetically homogeneous throughout their range (Gooch et al., 1972; Snyder and Gooch, 1973). Egg laying behavior of the marine gastropod *Aplysia* are genetically controlled (Scheller et al., 1982). A family of genes is responsible for both initiating egg laying and suppressing other activities, such as feeding and locomotion. Chemoreception is suppressed when *I. obsoleta* copulate (Stenzler and Atema, 1977). Thus, chemoreception, like egg laying, may be under genetic control and slow to evolve.

In contrast, avoidance behavior to introduced species evolves rapidly. *Ilyanassa obsoleta* was introduced to San Francisco Bay around 1905 (Carlton, 1979). The native gastropod *Cerithidea californica* now actively avoids *I. obsoleta* preying on its eggs and crawl-away larvae (Race, 1979). In New England, adult *I. obsoleta* actively migrate from tide pools where *Littorina littorea* are added, and migrate into marshes (Brenchley, 1980, 1982) and onto cobble beaches (Bertness, pers. comm.) when littorines are removed. The avoidance behavior is apparently ontogenetic, since

juvenile *I. obsoleta* do not avoid *L. littorea* (Brenchley, in prep).

The change in distribution of *Ilyanassa obsoleta* in response to *Littorina littorea* suggests that habitat or substrate preferences are quick to evolve and thus not genetically determined. In laboratory studies of egg laying, *I. obsoleta* prefers the branching green alga *Codium fragile* and the eel grass *Zostera marina* over *Spartina* shoots, marsh peat, and rocks (Brenchley, 1981). *C. fragile* is transient and often free of littorines which interfere with egg laying. Yet, *C. fragile* has only been present in the Harbor since 1975, having spread north from south of Cape Cod, where it was presumably introduced from Europe (Carlton and Scanlon, in prep.). *I. obsoleta* lays egg capsules often 10 layers thick on *C. fragile* (Table 5). While this may increase the reproductive output of *I. obsoleta* populations, these concentrations attract *Pagurus longicarpus* and *Carcinus maenas*. Together with *L. littorea*, these predators can destroy at least half of the egg capsules laid on *C. fragile* during the peak of reproductive activity (Table 5).

Acknowledgements. This research was made possible by the support of STEPS fellowships from M. B. L. as well as faculty research and travel grants from U. C. I. Jim Carlton and Judy Grassle raised timely questions which Merryll Alber helped me answer. I thank Jim Carlton for pointing out to me that *Littorina littorea*, *Carcinus maenas*, and *Codium fragile* are introduced species. I also thank Jim Carlton, Alex Yourke, Ami Scheltema, Rudi Scheltema, Nancy Marcus and anonymous reviewers for comments and suggestions.

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This paper was presented by Dr R. S. Scheltema; it was accepted for printing on June 16, 1982