DETERMINING THE ECOLOGICAL ROLE OF *EUSPIRA LEWISII*:
PART I: FEEDING ECOLOGY

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ABSTRACT The predatory naticid snail *Euspira lewisii*, Lewis' moon snail, native to the west coast of North America, is stated to be an economic threat to the shellfish aquaculture industry in British Columbia (BC). This species is being manually removed from the intertidal ecosystem, yet little is known about the ecology of this species. Enclosures and beach shell assemblages were used to determine the prey preference, feeding rates, and community impacts of *E. lewisii*. In the enclosures, *Protothaca staminea*, the native little neck clam, was found to be the preferred prey, whereas the commercially valuable Manila clam, *Venerupis philippinarum*, was avoided when *E. lewisii* was offered other clam prey choices. Drilled shells collected from the intertidal revealed similar feeding preferences. The feeding rate averaged for a variety of clam species was found to be 0.09 clams/day or 1 clam every 14 days. The feeding rate was dependent on prey species, and was highest for the preferred species and significantly lower on avoided species. The overall impact of *E. lewisii* to the bivalve community was found to be low. Based on these results, *E. lewisii* consumed only approximately 3% of the clam population over 1 y, assuming maximal feeding rates and typical population densities found on the west coast of BC. *E. lewisii* has minimal impacts to the Manila clam industry in BC and control measures are not necessary for this species. Baseline ecological field studies are important for gaining an understanding of poorly understood species, especially those considered threats to industry.

KEY WORDS: British Columbia, community impacts, gastropod, *Euspira lewisii*, feeding ecology, shellfish aquaculture

INTRODUCTION

Predation is one of the most important factors affecting community structure in intertidal communities. It can affect the distribution pattern, size and age composition, and abundance of prey species (Peitso et al. 1994, Beal 2006). Recent studies have stressed the importance of a full understanding of predation such that we can evaluate the ecological impact a predator has on a community (Savini & Occhipinti-Ambrogi 2006). The key to understanding the role a predator plays in a community includes knowing its prey preferences and feeding rates with respect to the densities of both the predator and the prey (Moran 1985, Thiel et al. 2001). From an applied aspect, without a full understanding of predation, it is difficult to manage intertidal communities or know whether antipredator practices, such as predator removal, are effective (Miron et al. 2005).

Many intertidal predators demonstrate prey preferences and select prey that maximize net energy intake by having a caloric value higher than the energy costs of capturing, handling, and consuming that prey item (Savini & Occhipinti-Ambrogi 2006). The effects of selective predation on community structure vary with relative abundance of prey species (Moran 1985), the escape abilities of the prey species and the nature of the habitat. Selective feeding on nondominant species can have adverse effects on unstable communities, such as decreasing species diversity by removing rare species (Wiltse 1980a).

Feeding rates of predators depend on a number of biotic and abiotic factors. Biotic factors include prey biomass, density, life cycle, species, quality, and predator and prey size (Wiltse 1980b, Commito 1982, Moran 1985, Thiel et al. 2001, DeGraaf & Tyrrell 2004). Time spent on other activities such as mating, competition, or predator avoidance also influences feeding rates (Thiel et al. 2001, DeGraaf & Tyrrell 2004). Abiotic factors such as temperature, season, wave action, and duration of sub-

mersion (Moran 1985, Weissberger 1999) also affect feeding rates. Greater feeding rates can lead to greater impacts on the prey community, such as reduced abundance of the prey species (DeGraaf & Tyrrell 2004, Savini & Occhipinti-Ambrogi 2006).

Euspira lewisii is a gastropod in the family Naticidae, a group commonly known as moon snails, which are infaunal, predatory snails that feed on bivalves. This species can be found crawling at the surface of intertidal sediments or within the sediments to depths up to 20cm (Bernard 1967). Several species of moon snails have shown both size and species preferences while feeding (Bernard 1967, Wiltse 1980a; Commito 1982, Rodrigues et al. 1987, Peitso et al. 1994, Dietl & Alexander 1997). Through drilling activities, very clear evidence of the predation of these species is left in intertidal habitats, most commonly on the Pacific littleneck clam (*Protothaca staminea*), the butter clam (*Saxidomus gigantea*), and the Pacific horse clam (*Tresus nuttallii*). For this reason, they are considered pest species, especially to Manila clam shellfish aquaculture (Bernard 1967, Peitso et al. 1994, British Columbia Shellfish Growers Association 2002, Beal 2006). However, little is known about the predation pressure of the moon snail on bivalve populations. A review of the literature suggests that bivalve mortality attributed to moon snails may, in fact, be overestimated (Wiltse 1980b, Peitso et al. 1994, Beal et al. 2001, Miron et al. 2005).

Manila clams, *Venerupis philippinarum,* is the primary cultured clam species in British Columbia (BC) and makes up 46% of BC shellfish aquaculture by value (BC Ministry of the Environment, Oceans and Marine Fisheries Branch 2008). The Manila clam industry brings in a total revenue of $192 million per year (Department of Fisheries and Oceans 2006).

On the west coast of BC, the native moon snail *E. lewisii* is being destroyed and eliminated from Manila clam shellfish farms, based on the assumption that they are effective predators. Hence, the objectives of this study are to assess the impacts of predation by *E. lewisii* on bivalve communities with special emphasis on the commercially valuable Manila clam, *V.*

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philippinarum. We use both field experiments and the collection of drilled bivalve shells to determine moon snail prey preference, feeding rates, and impacts on the prey community. Based on previous studies, we predict that *E. lewisii* will show distinct prey preferences, their feeding rate will be lower than previously thought, and thus their overall impact on bivalve communities will be relatively low.

MATERIALS AND METHODS

Study Areas

Field research was conducted intertidally in southern BC at Fillongley Provincial Park, on Denman Island (49°31′59″N, 124°49′0″W) and Shingle Spit, on Hornby Island (49°31′0″N, 124°37′59″W). The sites were selected because they were adjacent to Manila clam aquaculture leases and so were similar in terms of sediment characteristics and species composition (Whiteley & Bendell-Young 2007). Both sites are home to known populations of *E. lewisii* where they were found buried at depths from directly beneath the surface to approximately 10 cm, some actively drilling bivalve prey (pers. obs.) *V. philippinarum*, the commercially valuable Manila clam, and *P. staminea*, the native Pacific littleneck clam, dominate the bivalve community at these sites. *Nuttallia obscurata*, the varnish clam, a recent introduction to southern BC, as well as several other clam species are also found at these sites.

Feeding Experiments

Cage Design

We used enclosure experiments (12 cages) to determine the prey preferences of *E. lewisii*. Each cage was made of a PVC pipe frame measuring $1 \times 1 \times 0.3$ m and was enclosed in an area of 1 m^2. All sides of the frame were covered with plastic mesh with an aperture of 1 cm^2. The cages were dug into the sediment to a depth of 0.2 m, leaving 0.1 m exposed at the surface. Sediment was returned to the cage after all bivalves and drilled shells were removed. A 4×3 grid was created, using 12 cages, oriented parallel to the water line (Fig. 1). The cages in the grid were spaced approximately 2 m apart and were located between 1.7 m and 1.4 m above chart datum to incorporate the distributions of all the species and were placed at tidal height where shellfish tenures are located, which is between 1.5 m and 2.5 m above chart datum (Department of Fisheries and Oceans 2006).

Prey Preference

Three clam species collected from Fillongley were used in the experiments to analyze the prey preferences of *E. lewisii*: *P. staminea*, *V. philippinarum,* and *N. obscurata*. Twenty clams of each species were buried in each cage, with 5 individuals of each species in each corner. The clams were selected to be more than 38 mm, the legal size of *P. staminea* and *V. philippinarum,* and within the preferred prey size of *E. lewisii* based on the findings of Peitso (1980). *N. obscurata* was also selected in this size range to eliminate the possibility of prey preference resulting from size. This led to 60 clams in each cage (60/m^2) and 720 clams in all 12 cages. This density was selected because, in the area, the clam density was found to be 70 clams/m^2 and it is easiest to divide 60 into the three species of interest. This density is less than on aquaculture leases, but Peitso (1980) found that clam
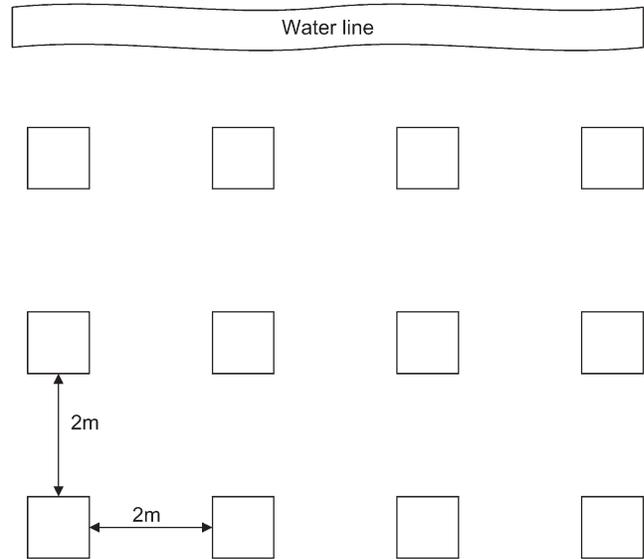

Figure 1. Diagram of the feeding experiment cage layout in the intertidal.

density did not have a significant effect of *E. lewisii* feeding rates. Two cages, selected at random and containing clams and no moon snails, served as controls that tested for clam transplant survivorship. In the 10 remaining cages, a single moon snail, collected from the site, was measured and buried into the center of the cage. Peitso et al. (1994) found that *E. lewisii* between 72.4 mm and 95 mm in length fed preferentially on clams between 35 mm and 50 mm shell length. Therefore, the snails we selected were between these sizes. The *E. lewisii* density was representative of the study areas. All cages were sealed and left.

The cages were checked every other tide cycle, approximately once every 3 wk throughout the course of 4 mo, and all drilled and dead clams were removed and replaced with live individuals of the appropriate species and size. Only completely drilled shells were used in the prey preference analyses. Very few ($n = 6$) clams died without drill marks, and those that were not drilled died of exposure at the surface so were not included in calculations. The prey preference experiments were run from May through September, summer 2005 and 2006.

Manly's α was used as an index of preference for constant prey populations (see Krebs 1999):

$$\alpha_i = r_i/n_i(1/\sum (r_j/n_j))$$

where α_i is Manly's α (preference index) for prey type *i*; r_i, r_j is the proportion of prey type *i* or *j* in the diet (*i* and *j* = 1,2,3, … *m*); n_i, n_j is the proportion of prey type *i* or *j* in the environment; and *m* is the number of prey types possible.

Similar preference experiments have used this index (Dudas et al. 2005), and it is well established in the feeding preference literature (Manly et al. 1972, Manly 1974, Krebs 1999). The interpretation of the α values for this index are

$$\alpha_i = 1/m = \text{no preference for species } i$$

$$\alpha_i > 1/m = \text{preference for species } i$$

$$\alpha_i < 1/m = \text{avoidance of species } i$$

where m = number of prey species.

For these experiments, 3 species were used; therefore, an α value of 0.33 indicates no preference, more than 0.33 is an indication of preference, and less than 0.33 is an indication of avoidance. These α values are considered significant if the 95% confidence intervals does not overlap the 0.33 prey types. A log-likelihood chi-square analysis was performed to substantiate these results.

Feeding Rates

Feeding rates were determined in tandem with the prey preference data. Feeding rates were calculated as the number of clams consumed divided by the number of days the moon snail was contained within the cage, and as the number of days the moon snail was contained within the cage divided by the number of clams consumed. An average of each of these measures was then taken.

By-species feeding rates were also determined. In summer 2006, a trial was carried out in which the 12 cages were randomly selected to contain one of each of the 3 species. Fifteen individuals of each species were buried in each of the 4 corners of the cage (i.e., 4 cages per species, 240 clams per species, for a total of 720 clams). Snails were added as described above and the cages were sealed for approximately 3 wk. After the 3 wk, all the cages were checked, and any drilled shells were removed and tallied. This design was representative of a mono-culture situation similar to those observed on the nearby clam tenures, thus observations could be made on how *E. lewisii* might feed under the conditions observed on the leases.

The Kruskal-Wallis test was applied to determine significant differences among species feeding rates on these 3 clam species because the data were not normally distributed.

Density and Drill Collection

Density surveys of all bivalve species and moon snails were conducted at both the Fillongley Provincial Park site and at Shingle Spit. To account for tidal influences, a 60-m-wide strip parallel to the shoreline representative of the intertidal communities was stratified into tide heights by dividing it into high, mid, and low zones (Table 1). The zones were different in size as a result of the geomorphology of the beach at each site.

Survey Design

Within each stratum, four 60-m-long transects parallel to the shore were randomly selected at Fillongley and three 60-m-long transects were randomly selected at Shingle Spit. The beach at Shingle Spit was steeper than that at Fillongley. Along each transect, 6 quadrat locations were selected at random. This led

to 24 quadrats sampled in each stratum at Fillongley for a total of 72 quadrats, whereas 18 quadrats were sampled in each stratum at Shingle Spit for a total of 54 quadrats sampled. Random numbers were selected using a random number table. At each coordinate, a 0.5×0.5-m quadrat was dug (0.25 m^2) down to a depth of 0.2 m. All sediment dug from the quadrat was sifted through a 6-mm mesh, and all infaunal bivalves were identified and counted to determine community composition and densities. Whiteley (2005) found that only 10% of species and 25% of species count data were lost using 6-mm versus 1-mm sieve mesh. The larger aperture mesh also allowed for increased sampling, because field researchers were not limited by the lengthy sieving time using 1-mm mesh. This sampling was carried out from May until September for 2 summers, as tides allowed.

During the sifting process, any shells containing the distinct countersunk *E. lewisii* drill marks were removed and the clam species was identified (Peitso et al. 1994). All live organisms and drilled shells were replaced after sampling.

E. lewisii densities were determined using a mark–recapture technique carried out in May 2006. In an area of 660 m^2 at Shingle Spit and 2,010 m^2 at Fillongley that incorporated the high, mid, and low zones described previously, 50 individual snails were marked by scratching a number into their shell, then the snails were reburied in the sediment. After 3 wk, we returned and dug up 30 snails and determined the number of marked snails. This technique makes several assumptions: that the population is closed (no births, deaths, immigration, or emigration), the mark remains in place, all animals are equally likely to be captured in each sample and over time, and also that being trapped once does not make an individual more or less likely to be captured again. Assuming that the marked snails return homogeneously to the general population, the total *E. lewisii* population was calculated based on the work by Bernard (1967) as follows:

$$T = M/(R/C)$$

where T is the total population in the area, M is the number of marked animals in the 1st sample, R is the number of marked animals in the 2nd sample, and C is the total caught in the 2nd sample.

Prey Preferences from Beach Shell Assemblages

The density measurements and drills collected were used to determine whether *E. lewisii* prey preferences were also evident under natural conditions. Proportions of the clams were calculated based on a stratified multistage design (Krebs 2001, Schwarz 2005). The proportions of shells and species in the community were also used to calculate electivity coefficients (E) based on the work by Ivlev (1961):

$$E = (r - p)/(r + p)$$

where r is the proportion of a food item in the diet and p is the proportion of the food item in the environment. Preference is indicated by a positive value of E, avoidance is indicated by a negative value, and no preference is indicated by a value of 0.

Ivlev's electivity coefficient Ivlev (1961) was selected because of the variable nature of the bivalve communities in the intertidal. Manly's α is appropriate for constant prey populations or in experimental situations when the prey is being replaced, maintaining a constant supply of food (Krebs 1999).

TABLE 1.

Length of the 3 tide strata at each site.

Tide Zone	Tide Height (m above chart datum)	Zone Length (m) Fillongley	Shingle Spit
High	2.3–1.7	30	25
Mid	1.7–1.3	67	12
Low	1.3–0.7	80	20

It is not recommended that α values be calculated based on populations with different numbers of prey types (Krebs 1999).

It is also important to consider the assumptions of using a beach shell assemblage to describe prey preference. It is assumed that all clam species stand up equally to abiotic factors such as storms, currents, and dissolution. It must also be assumed that the observed prey preference is not a result of a size refuge in the prey species. The final assumption is that the shells originated in the same location as they were collected.

Community Impacts

Density measurements and average feeding rates were used to represent the effects of *E. lewisii* predation on these intertidal communities. The average feeding rate was used to calculate the number of clams consumed in a month, in 6 mo, and in 1 y based on

$$\text{Number of clams consumed} = (\text{feeding rate}) \times (\text{days}) \\ \times (\text{number of snails})$$

For these calculations we used the total number of snails in our study areas from mark–recapture estimates. Based on information from the Department of Fisheries and Oceans (2006), *V. philippinarum* are harvested at an average weight of 18 g and sell for $5.00/kg. This leads to the price of $0.09/clam. These values allow us to calculate the financial cost of *E. lewisii* predation to the Manila clam industry.

RESULTS

Prey Preference

When offered equal numbers of *P. staminea*, *V. philippinarum*, and *N. obscurata*, *E. lewisii* showed significant preference for *P. staminea* (α = 0.57, chi-square = 51.25, *P* < 0.0001; Fig. 2). *N. obscurata* was preferred although it was not statistically significant (Fig. 2). *V. philippinarum* was not a significantly selected prey item (α = 0.07, chi-square = 51.25, *P* < 0.0001; Fig. 2).

Feeding Rates

The average summer feeding rate of *E. lewisii* consuming a variety of prey species was found to be 0.09 ± 0.02 clams/day (±95% confidence interval), with 1 clam consumed every 14 days. This is the feeding rate determined for *E. lewisii*.

When the feeding rates were analyzed for each of the 3 species individually, the consumption rate on *P. staminea* was greater than that on *N. obscurata*, which was greater than the rate on *V. philippinarum* (Fig. 3).

The Kruskal-Wallis test showed that the feeding rates in clams per day were significantly different (H = 6.17, *P* < 0.05; Fig. 3). The feeding rate on *V. philippinarum* was significantly different from that of *P. staminea*. *N. obscurata* was not significantly different from either species (Wilcoxon, *P* < 0.05).

Bivalve and E. lewisii Density and Abundance

Based on the transect density surveys at both sites, the total density per square meter of bivalves decreased as the tide level decreased (Fig. 4). The density of *V. philippinarum* was greatest in the high tide zone and decreased through the other strata to the waterline. However, at both sites the density followed the same pattern of being highest in the mid-intertidal, followed by the high zone, and was the least dense in the low zone. *N. obscurata* was found in very low densities in the study areas and was only found in the high zone and to a lesser extent in the mid tide zone (Fig. 4). *Macoma* spp. was found in much higher densities at Shingle Spit, and at both sites it was at its highest densities in the mid and low strata (Fig. 4). The other species we found at both sites were *Mya arenaria*, *Saxidomus gigantea*, *Parvaleucina tenuisculpta*, and *Rhamphidonta retifera*. *Tellina carpenteri*, *Clinocardium nuttallii*, and *Lyonsia californica* were exclusively found at Fillongley whereas *T. nuttallii* and *Cryptomya californica* were only found at Shingle Spit. *Macoma* spp. was predominantly *Macoma nasuta*, but at smaller sizes it was difficult to distinguish it from *Macoma obliqua*, so both of these species were represented in these communities.

V. philippinarum was the most abundant species at both sites (Table 2). *P. staminea* was the second most abundant species at
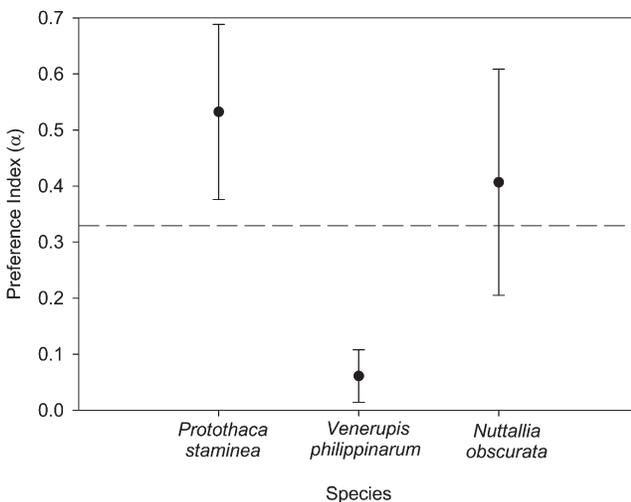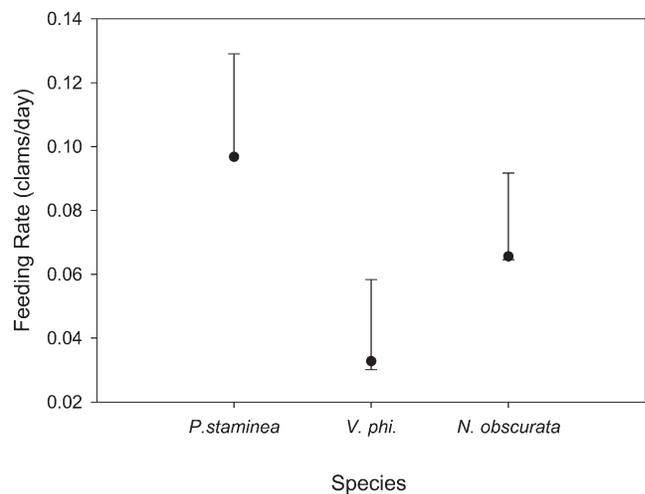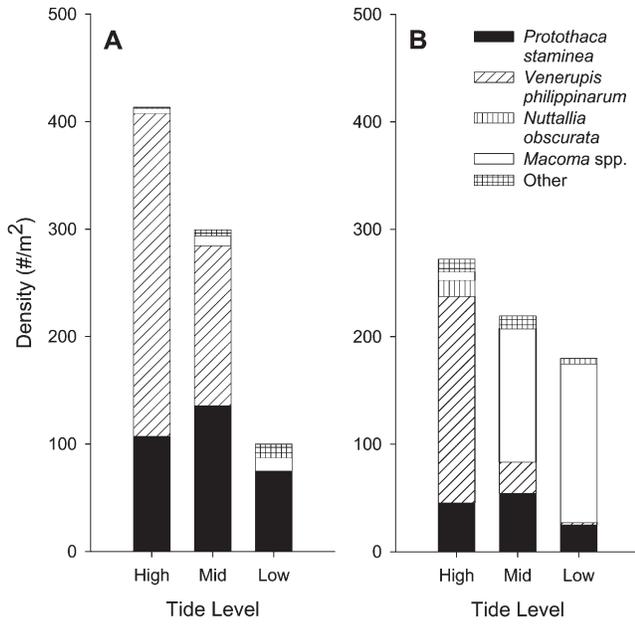

Figure 2. *E. lewisii* (●) prey preference (±95% confidence interval). The dashed line represents no preference (0.33). Values above the dashed line indicate prey preference; values below indicate avoidance.

Figure 3. Medians and interquartile ranges of the feeding rates of *E. lewisii* on *P. staminea*, *V. philippinarum*, and *N. obscurata* in clams per day per snail for each species.

Figure 4. (A, B) Density of clam species in number of individuals per square meter for Fillongley (A) and Shingle Spit (B).

Fillongley whereas *Macoma* spp. was the second most abundant species at Shingle Spit (Table 2). From the quadrat surveys, *E. lewisii* was found only in the lowest stratum at Fillongley at an abundance of 2,000 ± 3,000 individuals in a 60-m strip of the intertidal, although data variability for these measurements was very high (Table 3). *E. lewisii* was collected in both the mid and the low strata at Shingle Spit, and estimates suggested abundances of 200 ± 300 snails and 300 ± 500 snails in the mid and low stratums, respectively (Table 2). *E. lewisii* densities were more accurately estimated using the mark–recapture techniques and were found at all 3 tide heights. After recapturing 6 marked snails out of 50 at Fillongley and 10 out of 30 at Shingle Spit, the density of *E. lewisii* was 0.2 snails/m² at both sites (Table 3). Because of the shorter, steeper intertidal area at Shingle Spit, the total population was less than that of Fillongley, at 700 ± 500 individuals, compared with that at Fillongley of 2,000 ± 1,000 individuals.

Shell Assemblage Prey Preference

P. staminea was the most abundant of the drilled shells collected at Fillongley, followed by *Macoma* clams (Table 4). These were also the most common of the drilled shells collected at Shingle Spit, but the abundances were reversed, with *Macoma* spp. being the most abundant followed by *P. staminea*. The highest number of drilled shells were collected from the lowest tide stratum at both sites.

At Fillongley, 9 species were found with *E. lewisii* drill marks. The "other" group included *M. arenaria, S. gigantea, P. tenuisculpta, C. nuttallii,* and the wrinkled dogwinkle gastropod *Nucella lamellosa*. The diversity in the diet of *E. lewisii* was slightly lower at Shingle Spit, where 6 species were consumed. The "other" group was comprised of *M. arenaria* and *S. gigantea*.

When the proportions of the collected drilled shells were compared with the proportions of the species available in the community *E. lewisii* does not take clams in direct proportion to their availability (chi square = 1,739.74, $P < 0.0001$; Fig. 5). Even though *V. philippinarum* represented the species available in the highest proportion where the moon snails were found, the proportion of drilled shells collected for this species was very low.

When looking at each species individually, Ivlev's electivity coefficients (Ivlev 1961) showed that there was a preference for *P. staminea, N. obscurata, Macoma* spp., *M. arenaria, S. gigantea, P. tenuisculpta,* and *C. nuttallii* at Fillongley (Fig. 6D). *V. philippinarum, R. retifera, L. californica,* and *T. carpenteri* were avoided. At Shingle Spit, only *P. staminea, Macoma* spp., and *S. gigantea* were preferred, whereas all other species were avoided (chi square = 740.01, $P < 0.0001$; Fig. 7D). Differences in this feeding pattern were noted when each stratum was analyzed individually. *P. staminea* was a preferred prey item at both sites in every stratum with the exception of the low zone at Fillongley, where it was close to the no-preference line (Fig. 6A–C). *S. gigantea* was present only in the mid and low zones at both sites. Whenever it was present, it was a preferred prey species for *E. lewisii*. According to the Ivlev electivity coefficients (Ivlev 1961), *Macoma* clams were avoided at all tide heights at Shingle Spit, even though they were the most commonly collected drilled shell at that site (Fig. 7A–C). However, *E. lewisii* did show a preference for them when the study area was looked at as a whole. They were preferred prey in the mid and low zones at Fillongley.

TABLE 2.

Total clam abundance by species at Fillongley and Shingle Spit for each stratum ± 95% confidence interval.

	Site					
	Fillongley			**Shingle Spit**		
Species	**High Tide Zone**	**Mid Tide Zone**	**Low Tide Zone**	**High Tide Zone**	**Mid Tide Zone**	**Low Tide Zone**
Protothaca staminea	190,000 ± 40,000	600,000 ± 200,000	360,000 ± 60,000	70,000 ± 20,000	39,000 ± 9,000	30,000 ± 10,000
Venerupis philippinarum	540,000 ± 80,000	600,000 ± 50,0000	0	290,000 ± 80,000	20,960 ± 20,000	2,000 ± 3,000
Nuttallia obscurata	300 ± 600	1,000 ± 3,000	0	2,0000 ± 2,0000	0	0
Macoma spp.	8,000 ± 8,000	40,000 ± 20,000	60,000 ± 30,000	10,000 ± 10,000	90,000 ± 30,000	180,000 ± 30,000
Other	2,100 ± 2,000	20,000 ± 10,000	70,000 ± 20,000	20,000 ± 10,000	8,000 ± 4,000	6,000 ± 3,000
Total	750,000 ± 80,000	1,200,000 ± 600,000	500,000 ± 70,000	410,000 ± 60,000	160,000 ± 2,000	220,000 ± 40,000
Euspira lewisii	0	0	2,000 ± 3,000	0	200 ± 300	300 ± 500

Fillongley, $n = 72$; Shingle Spit $n = 54$.

TABLE 3.

Density of *E. lewisii* at Fillongley and Shingle Spit (measured in density per square meter ± 95% confidence interval) and total abundance in the survey area ± 95% confidence interval.

	Site	
Variable	**Fillongley**	**Shingle Spit**
Density (no./m²)	0.2 ± 0.2	0.2 ± 0.1
Total population	2,000 ± 1,000	700 ± 500

Fillongley, $n = 50$; Shingle Spit, $n = 50$.

Impacts of E. lewisii *Predation on Intertidal Clam Communities*

There were close to 3 million clams available in an area of 10,620 m² of beach at Fillongley within the range of *E. lewisii*. There was, on average, 228 clams/m². At an overall density of 0.22 snails/m² in this area, *E. lewisii*, feeding at a rate of 0.09 clams/day, in 1 mo approximately 5,400 clams would be consumed (Fig. 8). This is 0.22% of the clam population in the study area. If these values are then converted to 6 mo and 1 y of feeding in the area, *E. lewisii* consumes 1.35% and 2.70% of the clam population, respectively. This would cost $5,913/y in sales at Fillongley, plus the cost inputs of time and applying antipredator netting and manually removing *E. lewisii*. It must be said that this cost would be if *E. lewisii* consumed only *V. philippinarum* for the year, but the rate used is based on a variety of prey species. The year values should also be considered high estimates because *E. lewisii* decreases its feeding rate during the winter months and densities decrease (Peitso 1980, Huebner & Edwards 1981, Peitso et al. 1994).

The impacts were similar at Shingle Spit (Fig. 8). There were fewer clams total at Shingle Spit (close to 800,000 clams) and 228 clams/m². At the rate previously mentioned and a density of *E. lewisii* of 0.22 snails/m², 1,890 clams are consumed in 1 mo, which is 0.24% of the total clam population. Continuing at these feeding rates, *E. lewisii* consumes 1.47$ and 2.94% of the clam population in 6 and 12 mo, respectively, and costs the industry $2,069.55 in sales.

DISCUSSION

Prey Preference

The work described here found that *V. philippinarum* is avoided by *E. lewisii*, suggested by the results of both prey

TABLE 4.

Raw numbers of drilled shells collected in each stratum at each site with totals.

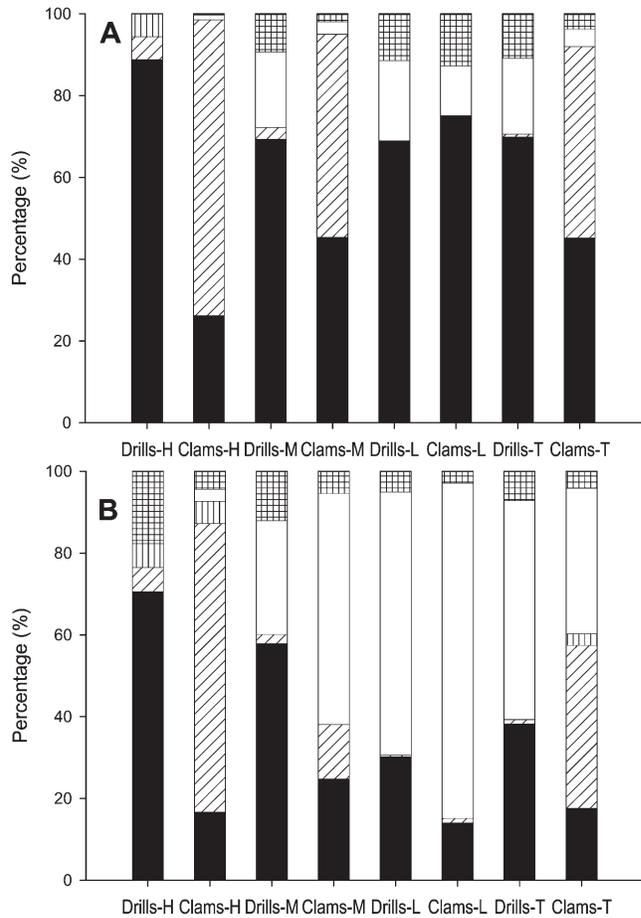|	Fillongley				Shingle Spit			
Species	**High**	**Mid**	**Low**	**Total**	**High**	**Mid**	**Low**	**Total**
Protothaca staminea	16	278	623	917	12	106	157	275
Venerupis philippinarum	1	6	2	9	1	4	2	7
Nuttallia obscurata	0	0	0	0	1	0	0	1
Macoma spp.	0	67	176	243	0	51	334	385
Other	1	38	103	142	3	22	26	51
Total	18	389	904	1,311	17	183	519	719

Figure 5. (A, B) The proportion of drilled shells collected from Fillongley (A) and Shingle Spit (B) compared with the proportion of clams available at each site (H, high; L, low; M, mid; T, total). ■ *Protothaca staminea*; ▨ *Venerupis philippinarum*; ⦚ *Nuttallia obscurata*; ☐ *Macoma* spp.; ⊞ Other.

preference experiments and observed shell assemblages. The only other study conducted on *E. lewisii* prey preferences found that only 0.4% of the drilled shells collected were *V. philippinarum*, indicating that this species is not favored (Bernard 1967). *P. staminea* was the preferred prey of *E. lewisii* based on our experiments. Bernard (1967), Harbo (2001), Peitso (1980), and Reid and Gustafson (1989) also found this preference. Beach shell assemblages also confirmed a preference for *P. staminea*. Despite the observed prey preference, the beach shell assemblages showed a diverse diet. At specific tide heights other prey were chosen, including *Macoma* spp., *P. tenuisculpta, M. arenaria, S. gigantea, N. obscurata,* and *C. nuttallii*. The beach shell assemblages gave important indications of the prey preferences of *E. lewisii*. The accuracy of this data is limited in that the drilled valves of thinner shelled prey species are not likely to persist as long in the habitat (Vignali & Galleni 1986).

Prey preference is common in naticid snails. Wiltse (1980a) found that *Polinices duplicatus*, an east coast naticid snail, ate 13 different species but showed preferences for *M. arenaria* and *Gemma gemma*. *Euspira heros* was shown to favor *Macoma balthica* and *M. arenaria* (Commito 1982). *Spisula solidissima* was preferentially consumed by *E. heros* (Weissberger 1999). Vignali and Galleni (1986) found that *Donax trunculus* was the
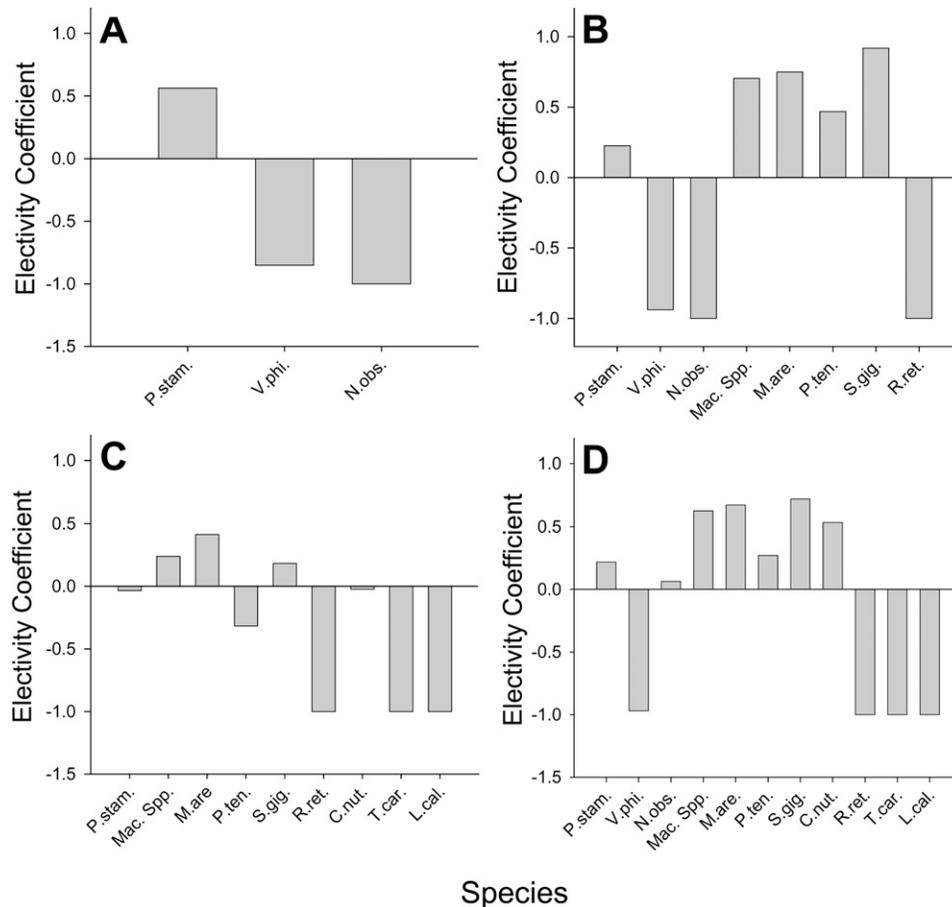
Figure 6. (A–D) Electivity coefficients for *E. lewisii* feeding on the clam populations in the high (A), mid (B), low (C), and all 3 zones (D) at Fillongley. Negative values indicate avoidance whereas positive values indicate preference.

species that was most attacked by the naticids from Piombino, Italy.

Preferences from the cage experiments may be attributed to the stratification of the 3 tested species within the sediment, because burial depth is a phenomenon that can affect prey preferences (Commito 1982). *V. philippinarum* lives very close to the sediment surface because of its short siphons (Meyer & Byers 2005). *E. lewisii* may burrow below *V. philippinarum* and therefore does not encounter it as readily as it does *P. staminea* and *N. obscurata*, species found deeper within the sediment.

The distribution of clams throughout the intertidal could also result in the preferences. *V. philippinarum* lives at the higher end of the range of *E. lewisii*, and therefore there is limited overlap in their distributions in the intertidal. However, this does not explain the observed preferences, because *N. obscurata* lives even higher on the intertidal than *V. philippinarum* and was consumed to a greater extent by *E. lewisii*.

Feeding Rate

Prey species is known to affect feeding rates (Moran 1985, Vignali & Galleni 1986, Rodrigues et al. 1987, Thiel et al. 2001). Our by-species feeding rates show that *P. staminea* was preyed upon at the highest rate by *E. lewisii*. *N. obscurata*, a newly introduced species in the area, was consumed at the second fastest feeding rate. *V. philippinarum* was the avoided prey type

with the lowest feeding rate, even under monoculture type conditions. Bernard (1967) found that *E. lewisii* consumed *P. staminea* faster than it consumed *S. gigantea* and *T. nuttallii*, which supports the conclusions of this work.

The feeding rate of 0.09 clams per snail per day was determined for *E. lewisii* consuming a variety of available species. This is within the range found in previous studies (Peitso et al. 1994). An earlier study by Bernard (1967) found the feeding rate to be 0.25 clams per snail per day. However, in the study by Bernard (1967), snails were starved for 5 days prior to experimentation, placed in tanks with a limited amount of sediment, and all attempts and partially consumed clams were used in feeding rate calculations. Studies have shown that moon snails will not return to the same drill site to continue feeding on the prey item when they have been interrupted (Dietl & Alexander 1997, Kingsley-Smith et al. 2003). Thus, including drill attempts could have inflated the feeding rate. Peitso et al. (1994) found that the summer feeding rate was approximately 0.07 clams per snail per day, which is close to our 0.09 estimates. Our rate was determined to be 1 clam consumed every 14 days, a very slow feeding rate. Previous work on moon snail feeding rates has shown a wide range of feeding rates between snail species. *E. heros* had a maximum feeding rate of 1 clam per day (Weissberger 1999). *P. pulchellus* was found to consume 14.57 clams per snail per month at its maximum rate (Kingsley-Smith et al. 2003). Thus, feeding rates are not comparable between species.
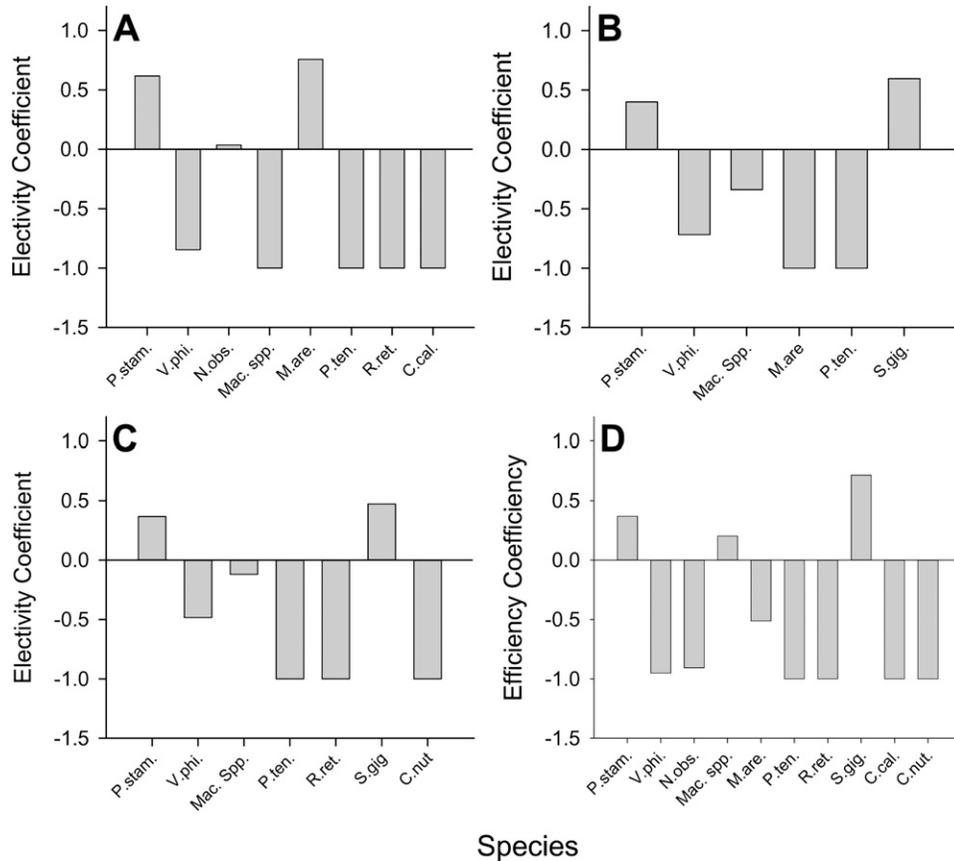
Figure 7. (A–D) Electivity coefficients for *E. lewisii* feeding on the clam populations in the high (A), mid (B), low (C), and all 3 zones (D) at Shingle Spit. Negative values indicate avoidance whereas positive values indicate preference.

Predator size, prey size, and temperature can all influence feeding rates. These factors must be considered when looking at feeding ecology because they can lead to an elevated feeding rate. Smaller snails have higher consumption rates (Edwards & Huebner 1977, Wiltse 1980b, Huebner & Edwards 1981, Peitso et al. 1994, Kingsley-Smith et al. 2003, Beal 2006). Prey size can be optimized for best grip by the moon snail, which facilitates drilling and increases feeding rates (Wiltse 1980b, Commito 1982, Vignali & Galleni 1986). Prey can also reach a size refuge making them

Figure 8. The number of clams consumed by *E. lewisii* at the rate of 0.09 clams/day at a density of 0.22 snails/m² in 1 mo, 6 mo, and more than 12 mo compared with the total number of clams available at Fillongley and Shingle Spit.

unavailable to predation (Rodrigues et al. 1987); however, we did not find any evidence to show that a size refuge was achieved at our study sites. Peitso (1980) found significant differences between the summer and winter feeding rate of *E. lewisii*, with the rate being highest during the summer. The rate determined in our study is a summer feeding rate over both years. The spring, fall, and winter rates are lower as a result of lower temperatures. Kingsley-Smith et al. (2003) and Weissberger (1999) found that moon snail feeding rates were dependent on temperature. Many naticid snails will actually stop feeding for 4 mo in the winter, as was seen in *P. duplicatus* (Huebner & Edwards 1981). This species stopped feeding completely at a temperature less than 5°C (Edwards & Huebner 1977). The density of *E. lewisii* in intertidal habitats decreases in the winter months, which would also lead to a decrease in impact (Peitso 1980). Therefore, the feeding rate determined in the current work is an upper limit, which must be considered when estimating the snail's impact on the community.

Other factors that can influence feeding rates include predator and prey density. Feeding rates in *E. lewisii* were not influenced by intraspecific density or by prey density, as was demonstrated by Peitso (1980). Although we did not test for this, we can assume that at higher prey densities on aquaculture leases, the feeding rates we determined would remain constant.
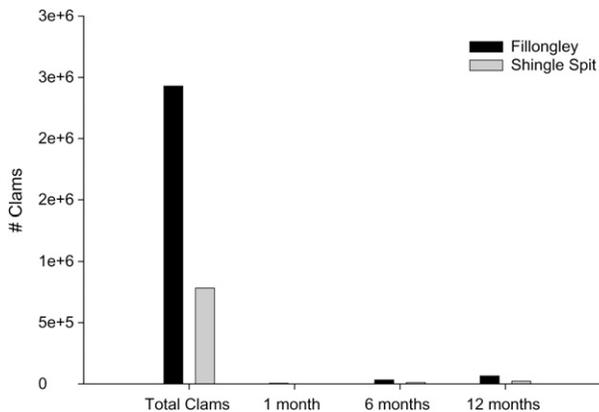
Foraging Behavior

Prey preferences and the resulting feeding rates can be explained using the optimal foraging theory in which predators

consume prey that leads to the highest energy gain in the least amount of time and energy input (Boggs et al. 1984). Naticid gastropod prey preference follows this hypothesis (Dietl & Alexander 1997). Savini and Occhipinti-Ambrogi (2006) found that moon snails maximize their energy intake by selecting a specific prey species that they can consume efficiently, rather than the immediately available species. *E. lewisii* followed this pattern, except where its preferred prey was not readily available. *V. philippinarum* is the numerically dominant species at both study sites, yet it was avoided in our experiments and the beach shell assemblages, where other species are available in lower numbers.

Feeding in *E. lewisii* is a large investment of energy, because they must spend quite a lot of time and energy drilling through the shell of its prey before feeding actually begins. Therefore, it needs to find prey that will facilitate these activities. Rodrigues et al. (1987) found that prey was selected based on a shell morphology that eases handling and reduces energy input. *P. staminea*'s round and inflated shell morphology facilitates drilling at the umbo (Vignali & Galleni 1986, Reid & Gustafson 1989). Variations in shell thickness lead to variations in feeding rates and handling time. Minor changes in shell thickness can lead to dramatic changes in feeding rate. In a slow-feeding organism, such as *E. lewisii*, fractions of millimeters can increase drilling time by at least 25 h (Dietl & Alexander 1997). It may take longer to drill *P. staminea* because of its relatively thick shell, but it contains more calories than the other 2 species (Kirk 2007). Although *N. obscurata* has the lowest energy content, it may be selected over *V. philippinarum* because it has a thinner shell and takes less time to drill. In *P. duplicatus*, drilling alone took approximately 36 h on its preferred prey species, *Mya arenaria* (Boggs et al. 1984). Finding exact feeding rates in burrowing snails such as *E. lewisii* is complicated as a result of not being able to measure drilling times directly.

Commercial Implications

In eastern Canada and the United States, moon snail predation on commercially valuable shellfish has been considered to be high enough to warrant the use of public funds to control their populations. Commito (1982) proposed that moon snails are responsible for 96.5% of the mortality of *M. arenaria*. Predation is stated to be the most important factor determining juvenile clam survival in Maine, where 77% of clam mortality is attributed to the moon snail *E. heros* (Beal 2006). In BC, the code of practice put out by the British Columbia Shellfish Growers Association (2002) listed *E. lewisii* as one of several species that can have significant economic impact to the *V. philippinarum* industry. To protect their crop, the shellfish growers are removing *E. lewisii* from the intertidal.

Recent work has shown that feeding rates and impacts may be exaggerated. Clam deaths by crabs and other predators have been attributed to moon snails in some studies, implying that moon snail predation was over emphasized (Beal et al. 2001).

Green (1968) estimated annual mortality rates of 28.2% from skate predation and other shell-destroying causes, 14.3% from crowding-related causes, and only 4% from naticid predation and this was by 2 different species. Predation by *P. duplicatus* was found to be only a minor source of mortality for *G. gemma*, one of its preferred prey species (Wiltse 1980b). Miron et al. (1985) found that the naticid *E. heros* was the predator that had the lowest feeding rate on all clam species tested compared with 2 sea star predators in eastern North America. Feeding rates in *P. duplicatus* were found to be less than previously believed (Huebner & Edwards 1981). Our work and the work performed by Peitso (1980) and Peitso et al. (1994), demonstrated that the feeding rates of *E. lewisii* are much lower than Bernard (1967) originally found. Our findings, as with those of Peitso et al. (1994) suggest that, over a year, about 3% of clam population mortality is the result of *E. lewisii* predation. This study stresses the importance of understanding the feeding ecology of a predator before suggesting antipredation measures.

E. lewisii's avoidance of *V. philippinarum*, low feeding rate, and low impact on the bivalve community can be applied to sustainable shellfish aquaculture practices. The results demonstrate that there is no longer a need to remove *E. lewisii* from intertidal lease areas, saving the time and energy of shellfish growers. The economic impact is limited, especially when the cost of antipredator netting and manual removal is considered. The impact to the intertidal ecosystem by aquaculture activities is thereby reduced and *E. lewisii* can be left in place to fulfill its ecological function.

CONCLUSION

Our study and the results of recent studies can lead to the general conclusion that moon snails have very low impacts on natural clam populations through predation activities. Biases with regard to the amount of moon snail prey could stem from the incriminating artifacts that are left behind, such as the bored shell, the number of which will accumulate over time, given a false impression of the numbers of clams actually preyed upon during a given period. Studies prior to 1990 have also been conducted under artificial conditions over short time periods, which lead to predation overestimates.

ACKNOWLEDGMENTS

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