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Life cycle and field abundance of the snail *Succinea costaricana* (Stylommatophora: Succineidae), a tropical agricultural pest

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Abstract: The neotropical terrestrial snail *Succinea costaricana* has become a quarantenary pest in ornamental plants (*Dracaena marginata*, Dracaenaceae). Specimens were collected in Guápiles, Limón, Costa Rica, where they reached a density of 282 900 individuals/ha. In the field, reproduction is continuous (as is rainfall) and eggs, young and copulating pairs are found mainly under moist litter. The population concentrated on plants rather than on the soil and greatly decreased after several control methods were applied. The life cycle was studied in the laboratory. The following are mean values: 7 eggs/cluster; 1.4 mm egg diameter; 0.25 and 0.84 mm embryo and newborn shell length, respectively; 11 days (embryo development at 24 °C); 16 mm/min locomotion speed (young). The animals can reproduce at 12 weeks (lifespan: 44 weeks). The pigmentation pattern is defined after seven weeks.

Key words: Land snail, reproduction, life cycle, growth, quarantenary pest, population, spatial distribution.

Most knowledge about the cosmopolitan terrestrial snail genus *Succinea* Draparnaud 1801 (Succineidae) is based on European or North American species. The few studies on tropical species are mostly local taxonomic papers (Lanzieri 1966, Hertlein and Allison 1968) or morphological studies (Patterson 1989).

Some species are agricultural pests, causing damage to cucumber, tomato, lettuce, chrysanthemus, carnations, roses and tulips. Sometimes they are carriers of diseases or intermediate hosts of parasites (Godan 1983). Taxa are particularly difficult to identify, in part because shell morphology is very similar in several species (von Martens 1892-1901, Godan 1983).

The neotropical species *Succinea costaricana* von Martens 1898 has been recorded from Costa Rica through Mexico. It was described from specimens collected in the XIX century at La Palma and Guácimo, near Guápiles, Limón Province, Costa Rica (von Martens 1892-1901).

This paper provides the first observations about the life cycle and field abundance of the species, which were studied taking advantage of an abnormal population increase of this species in a farm during 1992 (Monge-Nájera 1995).

MATERIAL AND METHODS

Study site: The study site was an ornamental plant farm (Fig. 1) located at La Roxana de Guápiles, Limón Province, Costa Rica (altitude 106 m a.s.l.). The region has a tropical rainy climate and the following yearly means: 24.5°C, 4440 mm rainfall and 87 % relative

Fig. 1. The study site: organization of plant rows in the farm that currently covers what was a tropical rain forest in Limón, Costa Rica.

humidity (Costa Rican Meteorological Institute). Soil pH is 4.6 and the mean calcium concentration is 122 ppm (A&L Southern Agricultural Laboratories, Florida, U.S.A.). The main crops of this farm are *Dracaena marginata* and *Dracaena deremensis* (Dracaenaceae).

In the three years previous to this study, leaf litter was normally abandoned on the plants and soil to reduce costs and as an organic fertilizer. *S. costaricana* and another snail species, became abundant under the litter. Pesticide applications, basically aimed at the control of thrips (Thysanoptera), caused some mortality among snails. The chemicals used include metamidofos OP, malation OP, metoMil C, protiofos OP, metiocarb C and endosulfan, but no detailed records were kept by the farmer regarding time, frequency and other application parameters.

Field methods: All counts mentioned in this section were done on individually numbered plant rows selected with a table of random numbers. The four observers participated in all types of counts to avoid individual bias.

An estimate of density was done the night of March 13, 1992 (20:30-24:30 hr) when the population reached pest proportions, by counting snails and shells in plants and in a 20 cm radius hemicircle of soil at the base of each plant. This was done with flashlights checking only the accesible side of each plant (they are planted in tight double rows, Fig. 1). A random procedure was also used to decide if the west or east side of each row was examined.

To assess changes in abundance throughout the year, visits were made to the field every two months from March 1992 through May 1993. Fixed time collections were done during mornings on plant rows (5 min) and the soil at their bases (5 min). This was done on the accessible side of plants and on the undisturbed soil below (workers crush shells while walking between rows). The animals were counted in the laboratory.

To assess the reliability of sampling, a random selection of plants and a 20 cm radius

hemicircle in their bases were sampled by the normal procedure and then taken in sealed bags to the laboratory, where plants were dissected and soil examined at ten magnifications to extract overlooked snails.

Life cycle in the laboratory: Specimens for the laboratory were collected in March, 1992. In the University of Costa Rica (San José City) they were kept in plastic containers (diameter 7.0 cm; height 5.8 cm) with holes on the lid. A soil layer 1 cm deep, from the original location, covered the container's bottom. The animals were fed 2 X 4 cm pieces of lettuce twice a week. Eighteen individuals isolated since their eclosion were selected to determine age at first reproduction. From these, twelve were used to study egg production. Shell length of embryos with a maximum age of 24 hr was measured with a millimetric ruler and a estereomicroscope. In neonates (aged 12 hr or less) shell length was obtained at ten magnifications with a vernier caliper (0.05 mm precision). For establishing growth rate the shell lenght of 26 individuals was measured weekly. Illustrations are based on *camera lucida* drawings and represent specimens which contracted to some extent during fixation. Voucher specimens are deposited in INBio (Heredia, Costa Rica, catalogue numbers INBIOCRI001464008, INBIOCRI001464010 and INBIOCRI001464012). Additional vouchers will be deposited in the Universities of Costa Rica (San José) and Florida (Gainesville).

RESULTS

All descriptive statistics are presented as mean ± standard deviation (minimum-maximum).

Sampling procedure: Diurnal counts did not differ significantly from the real number of snails on the soil (Table 1, Mann-Whitney U, $p>0.05$) but underestimated populations on the plants by a factor of 17 in living animals and of 4.6 in shells (Mann-Whitney U tests, $p<0.05$). In contrast, nocturnal counts underestimated the population in all cases (Table 2, Mann-Whitney U tests, $p<0.05$). The amount of underestimation is unknown for shells on plants and alive animals on soil because the sampling test count was zero, but the number alive on plants and dead on soil must be multiplied by 3.7 and 2.3, respectively.

TABLE 1

Evaluation of the diurnal sampling procedure (individuals collected per 5 min interval by each collector): descriptive statistics of counted and real number of Succinea costaricana *in a Costa Rican farm (n=6 replications of each count)*

	$\bar{x}$	SD	Min	Max
Plant				
Alive				
Counted	0.3	0.5	0	1
Total	5.2	3.1	1	9
Dead				
Counted	0.8	1.3	0	3
Total	3.7	2.8	1	9
Soil				
Alive				
Counted	0.2	0.4	0	1
Total	0.2	0.4	0	1
Dead				
Counted	4.2	2.1	2	7
Total	7.0	5.5	0	14

$\bar{x}$ Mean, SD standard deviation, Min minimum, Max maximum

Density: The number of living *S. costaricana* in the farm can be estimated from the night count, which was made by plant and not

TABLE 2

Evaluation of the nocturnal sampling procedure (individuals per plant or soil at plant base): descriptive statistics of counted and real number of Succinea costaricana *in a Costa Rican farm (n=6 replications of each count)*

	x	SD	Min	Max
Plants				
Alive				
Counted	0.6	1.3	0	6
Total	2.2	1.7	0	8
Dead				
Counted	0	0	0	0
Total	1.1	1.0	0	0
Soil				
Alive				
Counted	0	0	0	0
Total	0.5	0.9	0	3
Dead				
Counted	2.4	2.3	0	8
Total	5.5	3.0	1	12

x Mean, SD standard deviation, Min minimum, Max maximum

TABLE 3

Number of Succinea costaricana *snails per plant half according to a nocturnal visual count on 314 plants*

	x	SD	Min	Max
Soil	0.242	0.558	0	5
Stems	0.799	1.314	0	8
Leaves	0.236	0.905	0	10

x Mean, SD standard deviation, Min minimum, Max maximum.

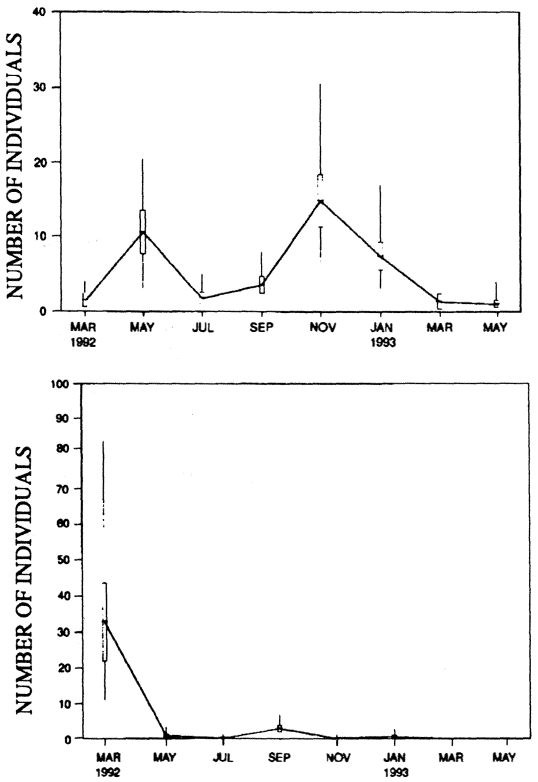

Fig. 2. Abundance of living *Succinea costaricana* on plants (above) and soil in Limón, Costa Rica.

by fixed time. If each plant had a mean of 2.55 snails (*i.e.* 1.277 X 2 sides) and correcting for overlooked animals by a factor of 3.7 (Table 2), the mean total associated with each plant was 9.43 snails. The farm administrator estimated that 210 000 plants (in 7 ha) were infected, thus the mean estimation is 1 980 300 snails or a density of 282 900 / ha. The animals were distributed as follows: soil 18.9 %, stems 63.4 % and leaves 17.7 % (N=314, Table 3). If the distribution in plant and soil is compared for day and night, the proportions in the plant are 81.1 % (night) and 77.4 % (day), which is not statistically different (Chi-square p>0.05, night N= 314, day N=297).

Abundance: In March of 1992 there were large numbers of dead animals on plants and of

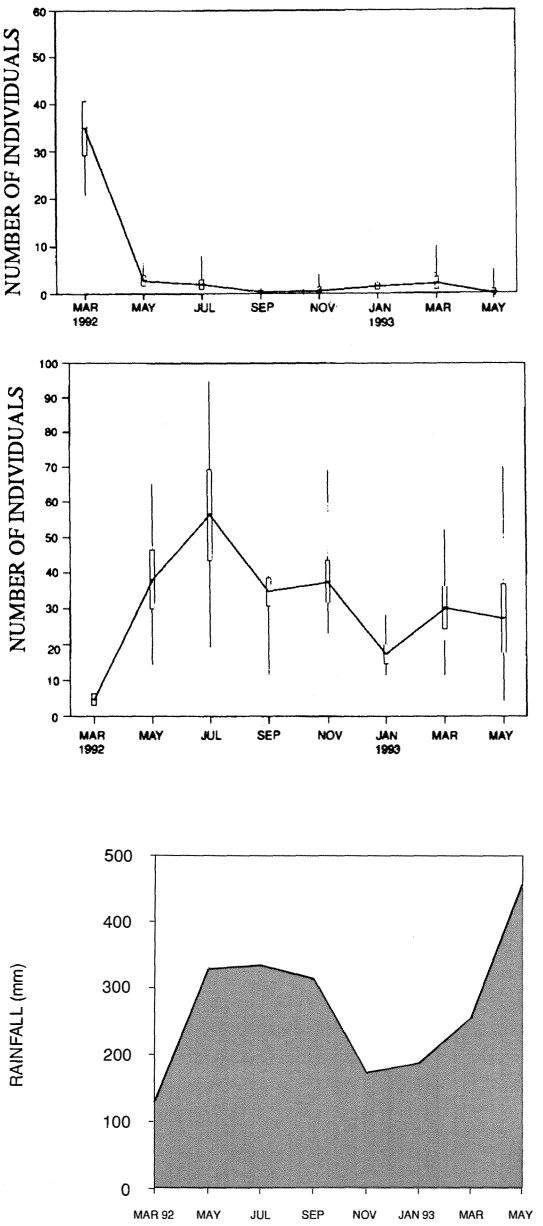

Fig. 3. Abundance of *Succinea costaricana* shells on plants (above) and soil (middle), and rainfall pattern during the study period in Guápiles, Limón, Costa Rica.

living animals on the soil. Correspondingly, there were few live snails on plants and few empty shells on the soil (Figs. 2 and 3). Two months later the situation was different: the number of shells had decreased in plants (never to recover) and increased in the soil, where it fluctuated greatly around relatively high numbers afterwards, until the end of the study in May 1993 (Figs. 2 and 3). The rainfall pattern (Fig. 3) does not correlate significantly with fluctuations in the total number of observed living animals (Spearman coefficient=0.11, $p>0.05$, N=8).

Life cycle in the laboratory

Fecundity and egg characteristics: Isolated animals were able to reproduce without mating. Oviposition usually occurred under litter, which provides both shelter and food for the young. A sample of 100 clutches from 12 individuals had 6.8 ± 4.5 (2-21) eggs/clutch. The mean number of eggs per individual varied little throughout lifetime but clearly decreased at old age, varying most when the animals were around 120 days old (Fig. 4). Total egg and clutch production were recorded in two individuals with the same lifespan: one produced six clutches (total 82 eggs) and the other 34 clutches (396 eggs).

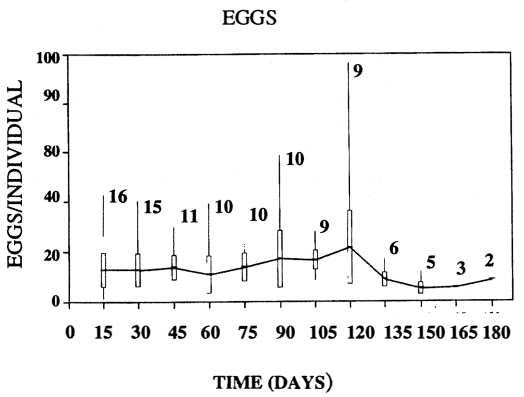

Fig. 4. Production of eggs in *Succinea costaricana* in relation with time after maturity; numbers close to each line: sample size.

The recently laid eggs, which are surrounded and cemented together by muscilaginous material, are spherical and translucid (solitary eggs were occasionally found). In an atmosphere with 100 % water saturation, eggs measure 1.367 ± 0.163 (0.99-1.67) mm in diameter, n=105. During the first months after the mother matures, the eggs have 95 % viability in the laboratory, a rate that decreases with time (pers. observ.).

Development: Embryos are white and oblonge and have a mean length of 0.246 ± 0.0128 (0.20-0.25) mm, n=57. They continuously rotate clockwise or counterclockwise on their body axes without other apparent displacement.

At around 24°C embryos develop in approximatelly 11 days (n=105).

Shell lenght of newborn individuals was 0.838 ± 0.044 (0.762-0.96) mm (n=52). Both shell and skin lack visible pigmentation, with the exception of two black spots (the eyes) located on the tips of the posterior tentacles. A general amber shell pigmentation becomes visible about 48 hr after hatching, starting in the upper rear end. Body pigmentation is apparent after seven weeks (Fig. 5).

Growth and lifespan: Shell lengh at two weeks is around 1.8 mm, and the body is clear amber by the third week. Dark spots become large by the seventh week (Fig. 5). As other Succineidae, *S. costaricana* retracts the tentacles by parcial invagination.

Shell length increases rapidly during the first 14 weeks (Fig. 6); then slows and stabilizes around week 22d. Most length variability is seen between the 6 th. and10 th. weeks. Reproduction begins at the 12th. week when shell length is 10.69 ± 0.98 mm (9.04-12.26), n=18. Regeneration of the shell, starting in the apex, was observed in one individual that had lost it for unknown reasons.

The maximum life span in the laboratory was 44 weeks, when shell lengh was 13.5 mm; 27 % of the lifespan is needed to reach maturity and there is a terminal reproductive diapause (Fig. 4).

General observations: In the field the animals are found mainly in dark moist microhabitats and are active day and night. In the laboratory, they tended to move toward light and moisture, but generally were less active under light than in darkness. Negative geotropism was frequent.

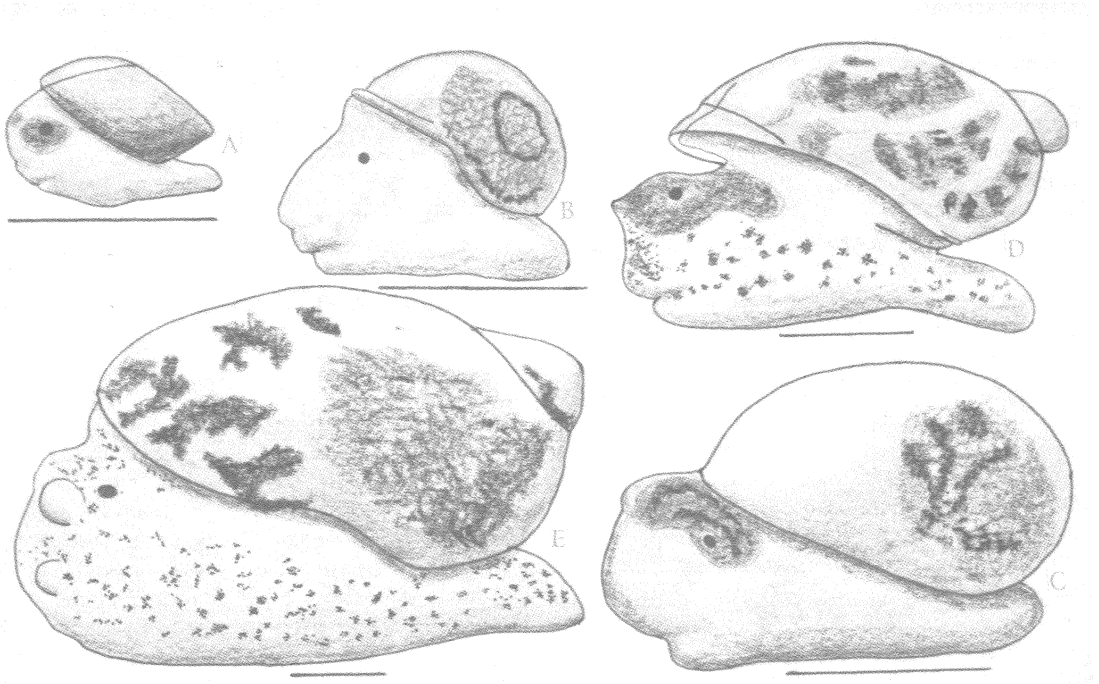

Fig. 5. Post-eclosion development of pigmentation in *Succinea costaricana* aged 24 hr (A), 48 hr (B), and two (C), seven (D) and eleven (E) weeks. Bar 1 mm.

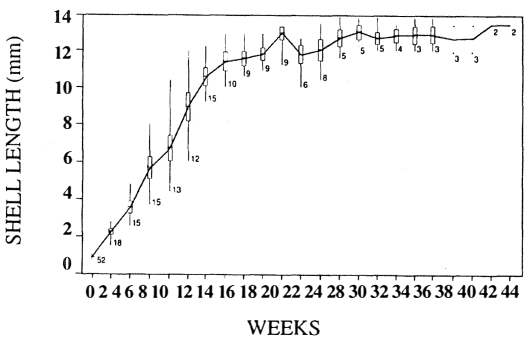

Fig. 6. Growth pattern of *Succinea costaricana*; numbers close to each line: sample size.

Two copulations, which had already begun when noticed, lasted 15 and 20 min and one individual positioned itself over the other's shell (one couple exchanged positions). Eggs, which in nature are produced year-round, were often found under moist litter and unfrequently on *Dracaena* plants, at the base of leaves.

The speed of eight individuals with a mean shell length of 4.15 ± 0.47 (5.00-3.50, *i.e.* juveniles) moving over horizontal moist filter paper was 16.2 ± 8.61 (4.25-33.5) mm/min, n=80.

The animals could be removed from the cropped plants by inmersion in tap water and if active at the time of inmersion they took 5.0 ± 4.9 (1.0 -18.4) min to emerge (by crawling or floating, n=24). Inactive snails required more time: 29.2 ± 28.6 (1.30-85.0) min, n=19 (Mann-Whitney U Test, $p<0.05$). The use of inverted plastic cups on stems to stop the ascending animals from moving toward the foliage was unsuccessful.

DISCUSION

The snail population: The density of 282 900 snails/ ha is a rough estimate and may be lower than the real value because only the soil closest to plant bases was considered. If there were any live individuals under the soil, they were not considered at all, although we suspect that this species is not as likely to occupy subterranean microhabitats as is *Opeas pumilum* (Pfeiffer, 1840) for example (Monge-Nájera 1995). There are more animals on stems than in other

parts of the plant or the soil surface, a finding that is of interest for collection and control but does not necessarily imply real density because the relative area of those substrates was not measured.

The similar plant/soil distribution for day and night suggests the absence of daily vertical migrations.

The results showed that there was no need for night sampling because, contrary to expectations, the animals were also active during the day. The more reliable diurnal counts are recommended for future ecological work on this population.

It would be very interesting to discuss the possible role of rainfall and other natural factors on yearly population fluctuations but the lack of proper records about chemical spraying prevents that sort of analysis. Nevertheless, our impression is that sampling began when the population was at a peak but a recent pesticide application had left many dead animals on the plants. Before the second sampling, the elimination of leaf litter that was recommended to the farmer apparently was the cause that kept the population low (Monge-Nájera 1995).

Life cycle: The ability of animals isolated since eclosion to lay fertile eggs suggests parthenogenesis or self-fertilization, which would require elaborated studies to distinguish (Nicklas and Hoffmann 1981). Although we ignore which is the case in *S. costaricana,* this result suggests that the species adapted to low densities (in which mates can be impossible to find, Ghiselin 1975), or to very stable habitats in which adapted genotypes are conserved (Nicklas and Hoffmann 1981). If *S. costaricana* evolved in the tropical rainforest that 200 years ago covered the area where it is found today, we would favor the stable-habitat hypothesis, but the historical distribution of the species is unknown.

In comparison with temperate pulmonates such as the snail *Cepaea nemoralis* and the slug *Deroceras laeve* (Wolda and Kreulen 1973, Williamson and Cameron 1976), *S. costaricana* lays relatively few eggs per clutch, perhaps because its non-seasonal habitat allows continuous reproduction, while temperate species must concentrate reproduction in one part of the year. This might also be true for other tropical species *(e.g. Criptaegis pilsbry,* which lays 5-16 eggs per clutch, Peake 1968). Egg diameter is within the known range for eggs with little or no calcium in the shell (Peake 1978).

Usually, when proper laboratory conditions are available embryo survival is close to 100 % (Wolda and Kreulen 1973, Nicklas and Hoffmann 1981), as was the case with *S. costaricana,* but it must be very different from the field where climate, predators and parasites probably destroy most eggs.

D. laebe has a slighly slower embryo development but reaches maturity much faster (Williamson and Cameron 1976) than *S. costaricana,* which nevertheless is faster than the Cuban snail *Polymita picta,* which must survive a dry season (Bidart *et al.* 1989). However, if shell length is compared, *P. picta* grows five-fold before reproduction while *S. costaricana* must grow almost twelf-fold.

In the laboratory, *S. costaricana* lives three times longer than *D. laeve* (Nicklas and Hoffmann 1981), but fails to reproduce in its last weeks.

General observations: *S. costaricana* is associated with moist microhabitats. The same is true of *Succinea putris,* which lives on river banks and streams (Godan 1983), and of *Succinea oblonga,* a marsh dweller (Evans 1968, Godan 1983). Like the North American species *Succinea vaginacontorta, S. costaricana* often moves toward light (Franzen 1971). We suspect that in nature, the unpigmented young of *S. costaricana* find protection from light, as well as food and moisture, by staying under the soil litter, and that upward movement is an adult phenomenom associated perhaps with avoidance of ground-surface predators (Rollo 1983), dispersal, or overcrowding (see Dan and Bailey 1982, Rollo *et al.* 1983). Our observations were done with adults and a vertical distribution experiment comparing ages would be of interest. We ignore why the animals become less active when they reach an illuminated site, but it could reflect the lower relative humidity of such sites.

Locomotion is slow if compared with that of *Succinea amphibia* (60 mm/min Hyman 1967), but very little has been written on this subject for any elaboration.

The elimination of natural enemies by unproper pesticide application, and the use of *Dracaena* litter as fertilizer, apparently produced the population explosion that made *S. costaricana* a pest in Guápiles. As normal in terrestrial snails (Williamson and Cameron 1976), this species does not consume live foliage, but adults spend much time in leaves. Thus, the species became a quarantenary pest because plant shipments with snails are not allowed to cross international borders. The water extraction test showed that inactive animals take up to 1.5 hr to emerge: This method is not recomended to clean shipments because prolonged immerson may damage these plants, although it proved satisfactory in other cases of molluscan pests (Monge-Nájera 1995). Details of other control attempts which succesfully reduced the population to economically unimportant numbers are given by Monge-Nájera (1995).

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