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Reproductive tactics in *Anodonta* clams: parental host recognition

JUKKA JOKELA & PÄIVI PALOKANGAS
**Laboratory of Ecological Zoology, Department of Biology, University of Turku, SF-20500 Turku, Finland*
and
Konnevesi Research Station, SF-44300 Konnevesi, Finland

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Freshwater unionacean clam larvae are parasitic on fish. Finding a suitable host is the most critical stage in the clam's life cycle. European clam species are believed to release their larvae more or less passively, although in some North American clams adaptations to finding the host have been reported (Kraemer 1970). We studied the reproductive behaviour of a common European freshwater clam, *Anodonta piscinalis* Nills., a generalist with respect to habitat (Haukioja & Hakala 1978) and range of hosts (Jokela et al. 1991). In a laboratory experiment, we found that female clams released more glochidia when in the presence of a fish, suggesting that they recognized its presence. In a second ex periment clams responded positively but nonspecifically to tactile, chemical and visual stimuli that might indicate the presence of a fish.

We collected the clams for the first experiment in December 1990, 3 months before they start releasing their larvae naturally (Jokela et al. 1991), from four populations in central Finland (Siikakoski, 62°37′N, 26°25′E; Pesiäissalmi 62°35′N, 26°15′E; Vuontee, 62°20′N, 25°55′E; and Kymönkoski, 63°07′N, 25°55′E). In the laboratory, the clams were pried slightly open to identify the glochidia-carrying females. Brooding females ($N=96$) were assigned randomly to three treatments (32 per treatment) for 6 days: (1) control (no fish), (2) perch, *Perca fluviatilis* (L.) and (3) roach, *Rutilus rutilus* (L.). The clams were kept individually in aerated 8-litre, sand-bottomed, glass aquaria in lake water (17–18°C), with indirect dim light (14:10 h light:dark). The fish treatments were set up by placing a fish (10–20 cm) caught from Lake Peurunka, central Finland, in the aquarium together with each clam. If a fish died during the experiment it was replaced by a similar one.

We observed all aquaria for 30–60 s nine times per 24 h (at 0730, 1000, 1200, 1400, 1600, 1800, 2000, 2200 and 0300 hours). We recorded the movement of clams since the last observation, their water-filtering activity and the conspicuous rapid closure of valves that clams use to release glochidia. The occurrence of free glochidia in the water was also monitored.

Indices of clam movement, filtering activity and glochidia-releasing activity were calculated by coding each observation as 1 if activity was observed and 0 if not, and dividing the sum by the number of observations. Square-root-transformed values of the indices were used as response variables in a two-way (treatment, population) multivariate analysis of variance model.

After 53 observation rounds, the clams were dissected. We excluded cases where the water was spoiled by a dead fish (20 cases), the clam died during the experiment (two cases) or the clam was castrated by a trematode parasite (one case). The remaining data are from 73 clams.

To count the number of glochidia released during the experiment, the water of each aquarium was thoroughly mixed and 3 litres of it was sieved through a plankton net (125 μm). The glochidia were then counted under a dissection microscope. Data of clams that released at least one glochidium (53 cases) was ln-transformed and analysed with two-way (treatment, population) ANCOVA using clam length as the covariate.

The clams in the fish treatments were more active than those in the control treatment (MANOVA, Wilks $\Lambda=0{\cdot}231$, $F_{6,118}=21{\cdot}28$, $P<0{\cdot}001$, Fig. 1a), whether measured as filtration, movement or glochidia-releasing activity. Differences in activity between populations were also statistically significant (Wilks $\Lambda=0{\cdot}645$, $F_{9,118}=3{\cdot}15$, $P=0{\cdot}002$).

A higher percentage of clams released glochidia in the fish treatments (81%) than in the control

*Address for correspondence.

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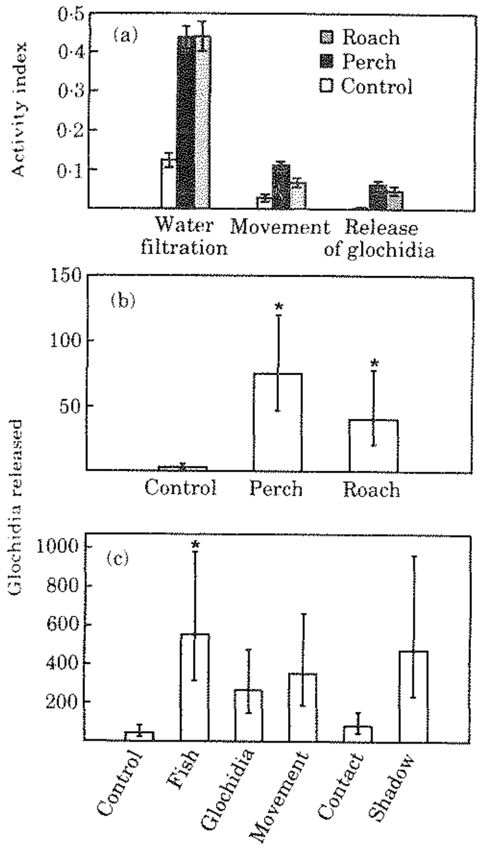

Figure 1. (a) Activity of clams ($\bar{X} \pm$ SE) in different treatments in experiment I and number of glochidia released (length adjusted back-transformed $\bar{X} \pm$ SE) in the different treatments in experiments (b) I and (c) II. $^*P<0.05$; Dunnett's test; treatment versus control. See text for details of calculation of activity indexes.

treatment (60%; Pearson $\chi^2=4.07$, $df=1$, $P=0.044$) and clams in the fish treatments also released more glochidia (Fig. 1b; $F_{2,40}=9.87$, $P<0.001$). Inter-population differences in the number of glochidia released were statistically significant ($F_{3,40}=4.91$, $P=0.005$), but the interaction between treatment and population was not ($F_{6,40}=0.771$, $P=0.597$, error mean square $=3.71$).

The clams released glochidia either by bursting out a group of free glochidia or by expelling strings of glochidia, which often tangled together as nets. The free glochidia remained in the water for several minutes before settling to the bottom. The clams in the fish treatments released strings of glochidia more often than the controls (63% of clams in the perch, 56% in the roach and 11% in the control treatment, Pearson $\chi^2=11.74$, $df=2$, $P=0.003$). A similar pattern was observed in the release of free glochidia; 63%, 44% and 6% of clams released glochidia in the perch, roach and control treatment, respectively (Pearson $\chi^2=13.41$, $df=2$, $P=0.001$). Both free glochidia and strings of glochidia were released by the same clams (Pearson $\chi^2=17.52$, $df=1$, $P<0.001$).

In the second experiment we set up six treatments to find out which stimuli produce the strongest response in terms of numbers of glochidia released. In January 1991, we collected female clams from the Pesiäissalmi and Vuontee populations and assigned them randomly to treatments. There were eight replicates in each treatment per population totalling 96 clams.

In treatment 2, 200 ml of water from a fish tank and in treatment 3, 100 ml of water that had contained glochidia (glochidia of two females in 2 litres of distilled water for 30 min), was added three times a day to the aquaria (at 0800, 1400 and 2000 hours). The same amount of distilled water was added to the control aquaria (treatment 1). Movement of fish (treatment 4) was simulated by dragging a small wooden spoon-bait, 20 times across the aquarium. Simulated contact of fish (treatment 5) was provided by touching the siphons of the clam gently with a water-colour brush. Treatments 4 and 5 were given seven times a day (at 0300, 0800, 1100, 1400, 1700, 2000 and 2300 hours). A shadow (treatment 6) was cast by covering the aquarium with a cardboard box (for 3 × 5 s) five times per day (as in treatments 4 and 5 except for 0300 and 2300 hours). After 6 days the clams were dissected and the number of glochidia released were counted as in experiment I. Of the original 96 clams, 18 were excluded because they started releasing glochidia during the 24-h acclimation period. The ln-transformed data were analysed with two-way ANCOVA. Each treatment was compared to the control using Dunnett's test.

During the experiment, 97% of the clams released glochidia. In the control treatment, the clams released fewer glochidia than in the other treatments ($F_{5,65}=2.51$, $P=0.039$, Fig. 1c). The highest number of glochidia was released in the aquaria treated with the smell of fish (Fig. 1c; Dunnett's $D=2.50$, $P=0.019$). The effect of population and the interaction between treatment and population were not significant (population: $F_{1,65}=0.62$, $P=0.436$; interaction: $F_{5,65}=0.34$, $P=0.890$, error mean square $=4.75$).

Our results indicate that the clams respond to fish. The probability of the glochidia attaching themselves successfully is further increased by releasing the glochidia in strings, forming net-like structures. The nets attach easily to the skin and fins of the fish, enabling simultaneous infection by several glochidia of the same female, thus increasing the intensity of infection (see also Wood 1974).

The clams also release free, solitary glochidia which are conspicuous and maintained in the water by even a slight water current. They may mimic planktonic food particles and be eaten by fish. The glochidia have larval threads, which may help them to attach themselves to the gills of fish when eaten (Wood 1974).

The non-specificity of the response to stimuli (Fig. 1c) may be beneficial in an unpredictable habitat. The ability to detect fish may substantially increase the clam's reproductive success since *Anodonta* clams are sedentary and cannot migrate to more favourable habitats as adults. Clams may release their glochidia over a period of several months (Jokela et al. 1991), and thus they may use sit-and-wait tactics in host finding, if they are able to detect the presence of fish nearby. The non-specific response is sufficient because of the wide range of hosts used.

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