BURROWING AND CRAWLING BEHAVIOUR OF THREE SPECIES OF UNIONIDAE IN FINLAND

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ABSTRACT

The aim of this study was to examine the burrowing and crawling behaviour of three unionid clam species in the field. Of the four study lakes in southern Finland, *Anodonta piscinalis* occurred in all, *Pseudanodonta complanata* in three and *Unio pictorum* in only one. In all three species, there was a positive correlation between the height of the above-sediment part of the shell and the burrowing angle (deviation from the horizontal position). When surfacing, the position of the clam became more vertical. *Anodonta piscinalis* was more visible in June than in August in one population, while in other populations monthly differences were not found. The result suggests that *A. piscinalis* may be more visible during its spawning period in early summer (June) than in late summer. This behaviour could have a reproductive function, ensuring external fertilization. Monthly differences in crawling activity of *A. piscinalis* were also found in one population: in Lake Alvajärvi, *A. piscinalis* crawled more in August than in June. No monthly differences in the burrowing or crawling of *P. complanata* were found. In *Unio pictorum*, no differences were observed in crawling, but the clams were more visible in August than in June. When compared with *P. complanata*, *A. piscinalis* and *U. pictorum* were more visible and in a more vertical position. In *A. piscinalis*, the bigger individuals were more visible than the smaller individuals, but this was not the case in *P. complanata* and *U. pictorum*.

INTRODUCTION

Many freshwater bivalves have relatively short siphons, so they usually burrow to depths where they are just beneath the sediment surface or are extended a little above it (McMahon, 1991). Some adult unionoid bivalves display surface locomotion behaviour and it is a fairly common phenomenon among unionoids (Imlay, 1982), despite the fact that the capacity for surface crawling is greatly reduced in most adult bivalves (McMahon, 1991). Crawling is achieved by using the same movements that are used for burrowing, with movement being horizontal instead of being vertical. Trueman (1968, 1983) described burrowing mechanisms in detail. Studies examining burrowing and crawling in freshwater mussels have generally focused on locomotion mechanisms, and the functions of vertical and horizontal movements have remained largely unexplained.

The ecology of some North American freshwater unionid clams has been studied in detail, including the function of the horizontal locomotion of *Elliptio complanata* Lightfoot, 1786 (Amyot & Downing, 1997, 1998). However, the crawling and burrowing behaviour of European freshwater unionid bivalves has not so far received attention.

The crawling behaviour of bivalves is hypothesized as being a response to unfavourable environmental conditions, for example scarcity of food (Brafield & Newell, 1961), oxygen deficiency (Brafield, 1963) or spatial competition (Kat, 1982), or of having a reproductive function in lentic systems, bringing mussels closer to each other during spawning (Amyot & Downing, 1998). It may also be involved with pedal feeding on organic sediment deposits (McMahon, 1991). Surfacing and crawling have also been suggested to be a behavioural abnormality induced by parasites, particularly trematodes, the larvae or eggs of which are taken in by the clam via inhaled water (e.g. Swennen, 1969,

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1974; Hulscher, 1973; Lim & Green, 1991). In marine environments, individuals infected by trematode metacercariae have been reported to remain closer to the sediment surface (Bartoli, 1974), and to have a reduced ability to burrow (Laukner, 1984; Thomas & Poulin, 1998), making clams more vulnerable to predation by final hosts and predators.

The proportion of trematode-infected individuals among mature individuals of *Anodonta piscinalis* (Nilsson, 1823) can be very high; for example, in Lake Saravesi the prevalence of infection by *Rhipidocotyle fennica* Gibson, Valtonen & Taskinen, 1992 was found to be 46.6% (Taskinen & Valtonen, 1995). In order to further understand the effect of parasites on host behaviour, the normal behaviour of non-infected clams must be established.

It can be hypothesized that during spawning the clams would burrow less deeply in order to be able to release and receive sperm more effectively. Furthermore, it can be hypothesized that during spawning the clams would be more active in crawling to bring individuals closer to each other to ensure fertilization, as suggested by Amyot & Downing (1998). Watters, O'Dee & Chordas (2001) observed several North American freshwater clam species to surface during spawning in spring.

In the present study, we examined burrowing and crawling behaviour of three unionid clam species, *Anodonta piscinalis*, *Pseudanodonta complanata* (Rössmässler, 1835), and *Unio pictorum* (Linnaeus, 1758) in mature individuals that were free of digenean trematodes. Spawning of *A. piscinalis* takes place in June (Jokela, Valtonen & Lappalainen, 1991; Taskinen, Mäkelä & Valtonen, 1997) and that of *P. complanata* from May to July (Aldridge, 1999). Our prediction was that *A. piscinalis* and *P. complanata* should be less deeply buried and more active in crawling during their spawning period in early summer (June) than in late summer (August). Two broods per summer have reported for *Unio pictorum* (Dudgeon & Morton, 1983; Pekkarinen, 1992). We predicted that the behavioural patterns of *U. pictorum* should differ from those of *A. piscinalis* and *P. complanata*, which have only one brood and spawn in early summer.

MATERIAL AND METHODS

Study areas

A total of 185 mature clams were collected using SCUBA from the littoral/sublittoral zones of Lake Alvajärvi, Lake Palokkajärvi, Lake Saravesi and Lake Tuomiojärvi, close to the city of Jyväskylä, Finland during June and August 1996. Sampling periods of June and August were chosen, because mid-June is the time of spawning of *A. piscinalis* in the present study area and by August spawning is clearly over. By choosing these months to study burrowing and crawling behaviour it might be possible to reveal short-term changes in behaviour, which would not be influenced by seasonal changes in the environment. The number of individuals of different species, the mean length and age (see Haukioja & Hakala, 1978a), and range of sizes and ages of the clams used in the analyses are given in Table 1. The size and mean depth of Lake Alvajärvi (62°19′N, 25°43′E), Lake Palokkajärvi (62°16′N, 25°45′E), Lake Saravesi (62°25′N, 26°00′E) and Lake Tuomiojärvi (62°15′N, 25°44′E) were 2.0 km² and 3.6 m, 2.7 km² and 2.7 m, 7.8 km² and 5.5 m, and 3.1 km² and 3.7 m, respectively.

In each lake, a sampling site was chosen based on accessibility, and on availability of clams. The sampling site in Lake Alvajärvi was situated 20–50 m from the shore, and the clams were collected from the zone of emergent macrophytes at depths of 1–2 m. The bottom sediment was firm clay and sand. In Lake Palokkajärvi the sampling site was situated 40–70 m offshore, and the clams were collected from clayey bottom sediments covered with organic material and with some sandy patches, at depth of 2–4 m. No emergent macrophytes were present at the sampling site. In Lake Saravesi the sampling site was situated 100–150 m from the shore, in the zone of submerged vegetation at depths of 2–3 m. The bottom sediment was clay covered with organic material. In Lake Tuomiojärvi the sampling site was situated in the city recreation area, 5–30 m from the shore, and the bottom was sandy in shallow water, but muddier with increasing depth. Clams were collected from the zone free of emergent macrophytes at depths of 1–3 m. Ice covers the lakes from late November until early May. The highest water temperatures (20–24°C) are reached at the end of July or beginning of August.

Natural history of the clams

Unionid clams mature at 2–4 years of age and reproduce annually (Haukioja & Hakala, 1978b; Bauer, 1994), reaching a maximum life span of more than 15 years (Ökland, 1963; Negus, 1966; Haukioja & Hakala, 1978b). Spawning takes place in early summer and fertilized eggs are stored in the outer gill blades of females, where they develop into glochidia larvae (Jirka & Neves, 1992). In the present study area, the development of new broods begins in the mid-June when the fertilization of eggs takes place. The development of glochidia of *Anodonta piscinalis* takes place in August in Finland, and they are fully developed by autumn (Jokela et al., 1991; Jokela, 1996), whereas the glochidia of *Pseudanodonta complanata* may sometimes mature during winter (Pekkarinen & Englund, 1995). Glochidia of *A. piscinalis* and *P. complanata* are stored in the gills over winter (Ökland, 1963; Negus, 1966; Pekkarinen, 1993; Bauer, 1994). The development of glochidia of *Unio pictorum* lasts about one month (Tudorancea, 1969; Pekkarinen, 1992, 1993). Dudgeon & Morton (1983) concluded that many broods per year are possible in *Unio* species in temperate zones. After release, unionoid glochidia attach to a fish host for a few weeks before benthic life begins.

Data collection and statistical analyses

When a clam was encountered by the SCUBA diver, the trace of horizontal movement of the clam was measured. The clam was then gently removed and the line of the sediment surface was immediately marked on the shell using a sharp file. Each clam was put into an individually marked plastic bag. In the laboratory, the burrowing depth (measured as the distance from the surface line of the sediment to the highest part of the shell, in millimetres) and the burrowing angle (measured between the sediment surface line and longitudinal axis of the clam) were measured from the markings on the shell. For totally buried clams, it was not possible to determine burrowing angle. The clams were aged by counting the annual rings of the shell and their length was measured (see Haukioja & Hakala, 1978a). Gender was determined by pressing a piece of gonad between two large glass plates under a dissection microscope and transmitted light.

The effect of month on the burrowing depth of *A. piscinalis* was analysed using 2-way ANCOVA, with month (June *vs* August) and population (Lake Alvajärvi, Lake Tuomiojärvi and Lake Saravesi) as factors, and length as a covariate. Since the length and age of the clams are correlated, it is possible to control for the effect of both age and size by using clam length as a covariate. Length is usually included in models at first, but it is dropped off if its effect is not statistically significant. Lake Palokkajärvi was excluded from the analysis, because of a missing August sample. The effect of study month on the burrowing angle of *A. piscinalis* was analysed in the same manner. To determine the source of the significant interaction between study month and population (see Results), the effects of study month on the burrowing depth and burrowing angle were analysed separately in each population using one-way ANCOVA and one-way ANOVA, respectively, with Bonferroni-correction (critical level $\alpha = 0.017$).

The effect of month on the burrowing depth and angle of *P. complanata* and *U. pictorum* was analysed using one-way ANCOVA, with month (June *vs* August) as a factor and length as a covariate. Lake Palokkajärvi and Lake Tuomiojärvi were excluded from the analyses concerning *P. complanata*, because of a missing August and June samples, respectively.

The correlation between the burrowing depth and angle was analysed separately for each clam species and for each lake, using either partial correlation (controlling for study month) or bivariate correlation when only a one-month sample was available (in Lake Palokkajärvi).

The effect of a clam species on burrowing depth and burrowing angle was analysed using MANCOVA, with species and study month as factors, and length as a covariate. *Anodonta piscinalis* occurred in all of the four study lakes, *Pseudanodonta complanata* in three and *Unio pictorum* in one lake, only (Table 1). Therefore, differences between *A. piscinalis* and *P. complanata*, and between *A. piscinalis* and *U. pictorum* were analysed separately. An adequate sample size for a statistical test between *A. piscinalis* and *P. complanata* was from Lake Alvajärvi.

Logistic regression method was used to analyse the relationship between crawling activity and clam species, month, clam length and the interaction term 'species × month'. The test for *A. piscinalis* and *P. complanata* was performed including the data from Lake Alvajärvi, and the test for *A. piscinalis* and *U. pictorum* using the data from Lake Saravesi. Crawling (movement or no movement) was used as a dependent variable, clam species and month as categorical factors, and clam length as a continuous factor. Automated forward stepwise variable selection procedure was used to select the model that best fitted the data. By comparing hierarchical sets of regression models, the significance of interaction and main effects was calculated using likelihood ratio statistics (Forward LR). The variable selection was

Table 1. Number of individuals of different species and the mean length and age and range of sizes and ages of the clams used in the statistical analyses.

Population	Species	n	Age (yr)		Length (mm)	
			Mean	Range	Mean ± SE	Range
Lake Alvajärvi	*Anodonta piscinalis*	33	7	3–13	70 ± 2	46–96
	Pseudanodonta complanata	25	7	5–11	70 ± 2	47–95
Lake Palokkajärvi	*Anodonta piscinalis*	12	5	3–7	52 ± 3	40–66
	Pseudanodonta complanata	14	6	3–9	53 ± 2	32–67
Lake Saravesi	*Anodonta piscinalis*	23	6	4–11	61 ± 2	46–86
	Unio pictorum	22	7	3–11	66 ± 3	29–86
Lake Tuomiojärvi	*Anodonta piscinalis*	53	6	3–11	56 ± 1	33–74
	Pseudanodonta complanata	3	8	7–8	59 ± 4	51–66

then repeated using automated backward stepwise elimination procedure (Backward LR). If the two procedures did not result in the same model, then the terms that differed were tested for their significance using improvement χ^2 test. If the term was significant, it was included in the model.

Original values or length-adjusted means are used for interpretation of results. The means are given with ±1 standard error. Statistical analyses were performed using SPSS statistical package (SPSS Inc. Chicago, Illinois).

RESULTS

Burrowing depth

Neither the effect of study month (June *vs* August) nor the effect of population were significant with respect to the burrowing depth of *A. piscinalis* as suggested by the results of the 2-way ANCOVA ('month' $F = 0.883$, df = 1,102, $P > 0.1$; 'population' $F = 0.578$, df = 2,102, $P > 0.1$). However, there was a significant interaction between population and month ($F = 3.40$, df = 2,102, $P = 0.037$). One-way ANCOVA performed for each population revealed that the interaction was due to the significant difference between June and August in Lake Tuomiojärvi ($F = 22.303$, $P < 0.001$), while in other populations no such a difference was found. The length-adjusted mean height of the above-sediment part of the shell in Lake Tuomiojärvi was higher in June (28 ± 2 mm) than in August (14 ± 2 mm) (Table 2, Fig. 1). The covariate, clam length also had a positive effect on the height of the above-sediment part of the shell ($F = 35.466$, df = 1,102, $P < 0.001$), the bigger individuals being more visible than smaller ones.

The effect of the study month on the burrowing depth of *Pseudanodonta complanata* in Lake Alvajärvi was not statistically significant (one-way ANOVA, the main effect 'time' $F = 0.654$,

df = 1,23, $P > 0.1$), although it was in the case of *U. pictorum* (one-way ANOVA, $F = 9.922$, df = 1,20, $P = 0.005$). The mean height of the above-sediment part of the shell was 7 ± 3 mm in June and 22 ± 4 mm in August. Clam length did not have an effect on the height of the above-sediment part of the shell in either *P. complanata* or *U. pictorum*.
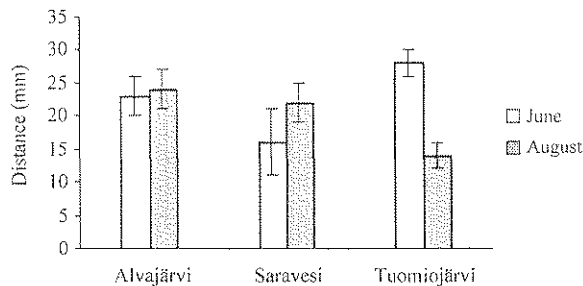
Burrowing angle

The effect of the study month on the burrowing angle of *A. piscinalis* was not significant (two-way ANOVA, the main effect 'time' $F = 3.482$, df = 1,94, $P > 0.05$). The effect of population was significant ($F = 3.516$, df = 2,95, $P = 0.034$), and there was a statistically significant interaction between population and month ($F = 15.792$, df = 2,95, $P < 0.001$). The effect of the study month on the burrowing angle was significant only in Lake Tuomiojärvi (one-way ANOVA, $F = 62.151$, df = 1,45, $P < 0.001$). In Lake Tuomiojärvi clams were more vertical in position in June ($61 \pm 3°$ in June and $28 \pm 4°$ in August; Table 2, Fig. 2).

The effect of the study month on the burrowing angle of *P. complanata* in Lake Alvajärvi was statistically significant ($F = 8.696$, df = 1,10, $P = 0.015$). Clams were in a more vertical position in August than in June ($34 \pm 6°$ and $11 \pm 5°$, respectively). The study month did not have any effect on the burrowing angle of *U. pictorum* ($F = 1.585$, df = 1,13, $P > 0.1$).

Correlation between the burrowing depth and burrowing angle

The correlation between the burrowing depth and angle was statistically significant in each population and in each species (Table 3, Figures 3–5). When the distance from the sediment surface to the siphons of the clam was larger (i.e. the position of the clam was more visible), then the orientation of the clam was more vertical.

Figure 1. The mean distance (±SE) from the sediment surface to the highest point of the shell of *Anodonta piscinalis* in Lake Alvajärvi, Lake Saravesi and Lake Tuomiojärvi in June and August 1996.
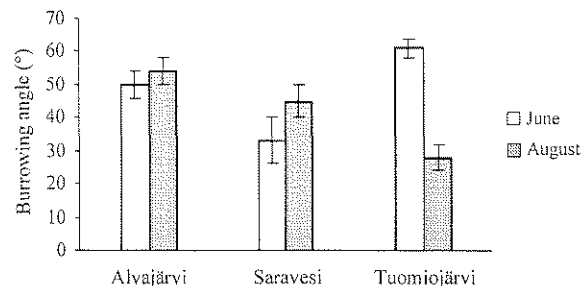
Figure 2. The mean burrowing angle (±SE) of *Anodonta piscinalis* in Lake Alvajärvi, Lake Saravesi and Lake Tuomiojärvi in June and August 1996.
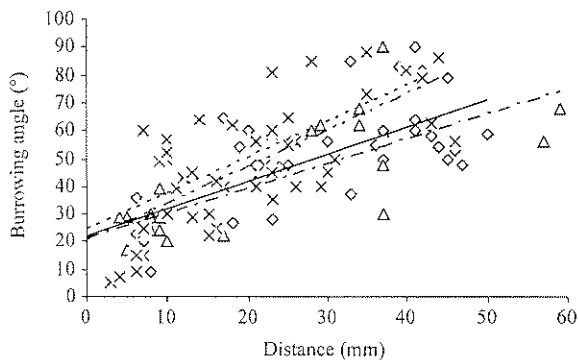
Table 2. Number of individuals of different clam species, the mean distance from the surface of the sediment to the highest point of the shell of the clam ± SE, the mean burrowing angle (°) ± SE, the portion of clams moved, and the mean length of crawling tracks ± SE in Lake Alvajärvi, Lake Palokkajärvi, Lake Saravesi and Lake Tuomiojärvi in June and August 1996.

Species	Population	Month	n	Highest point (mm)	Angle (°)	% moved	Mean crawling tracks (m)
A. piscinalis	Lake Alvajärvi	Jun	17	28 ± 4	50 ± 6	0	0.0
		Aug	16	31 ± 3	54 ± 4	38	1.5 ± 0.7
	Lake Palokkajärvi	Jun	12	19 ± 5	52 ± 7	17	0.3 ± 0.2
	Lake Saravesi	Jun	7	15 ± 4	33 ± 7	57	0.7 ± 0.1
		Aug	16	23 ± 5	45 ± 5	44	1.9 ± 0.5
	Lake Tuomiojärvi	Jun	29	22 ± 2	61 ± 3	0	0.0
		Aug	24	13 ± 2	28 ± 3	4	0.2
P. complanata	Lake Alvajärvi	Jun	12	3 ± 1	11 ± 5	8	0.1
		Aug	13	5 ± 2	34 ± 6	0	0.0
	Lake Palokkajärvi	Jun	14	3 ± 1	24 ± 5	0	0.0
	Lake Tuomiojärvi	Aug	3	13 ± 9	35 ± 5	0	0.0
U. pictorum	Lake Saravesi	Jun	14	7 ± 2	35 ± 6	36	0.5 ± 0.1
		Aug	8	22 ± 4	44 ± 3	38	0.9 ± 0.3

Table 3. Partial correlation (controlling for season) between the height of the above-sediment part of the shell and the burrowing angle.

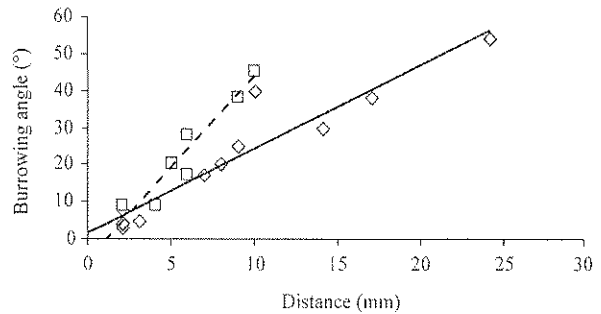| Species	Population	Correlation coefficient	P
A. piscinalis	Lake Alvajärvi	0.677	<0.001
	Lake Palokkajärvi*	0.865	0.001
	Lake Saravesi	0.741	<0.001
	Lake Tuomiojärvi	0.719	<0.001
P. complanata	Lake Alvajärvi	0.929	<0.001
	Lake Palokkajärvi*	0.949	0.001
U. pictorum	Lake Saravesi	0.796	0.001

*Bivariate correlation, significant at the 0.01 level (two-tailed), when only a one-month sample available.

Figure 4. The burrowing angle in relation to the distance from the surface of the sediment to the highest point of the shell of *Pseudanodonta complanata* in Lake Alvajärvi (◇, —) and Lake Palokkajärvi (□, ——).
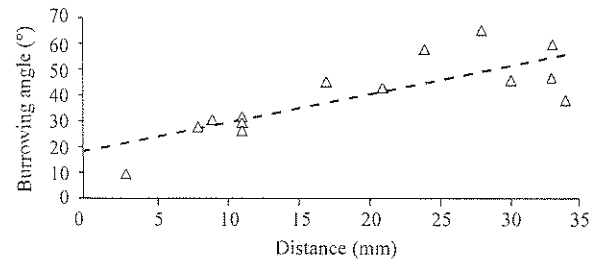

Figure 3. The burrowing angle in relation to the distance from the surface of the sediment to the highest point of the shell of *Anodonta piscinalis* in Lake Alvajärvi (◇, —) Lake Palokkajärvi (□ ——), Lake Saravesi (△ · · · ·) and Lake Tuomiojärvi (×, ······).

Figure 5. The burrowing angle in relation to the distance from the surface of the sediment to the highest point of the shell of *Unio pictorum* in Lake Saravesi.

Differences between the clam species in burrowing

The clam species *A. piscinalis* and *U. pictorum* co-occurred only in Lake Saravesi, and they did not differ from each other by their burrowing depth or by burrowing angle (Wilks' lambda $F = 0.159$, df $= 2,31$, $P > 0.1$). The study month did not have any

effect on burrowing behaviour (Wilks' lambda $F = 2.545$, df $= 2,31$, $P > 0.05$).

In Lake Palokkajärvi, *P. complanata* and *A. piscinalis* differed from each other (Wilks' lambda $F = 27.732$, df $= 2,38$, $P < 0.001$). *Pseudanodonta complanata* was less visible than *A. piscinalis* ($F = 56.83$, df $= 1,39$, $P < 0.001$). The mean distances ± SE from the surface of the sediment to the highest point of the shell were 8 ± 3 and 31 ± 2 mm (length-adjusted means), respectively (Fig. 6). *Pseudanodonta complanata* was in a more horizontal position than *A. piscinalis* ($F = 22.92$, df $= 1,39$, $P < 0.001$). The mean burrowing angles ± SE (deviation from a
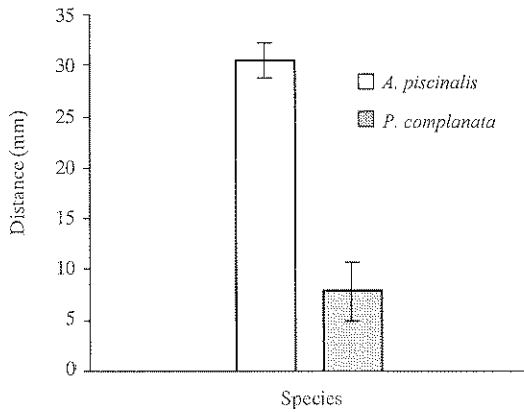
Figure 6. The length adjusted mean distances (± SE) from the surface of the sediment to the highest point of the shell of *A. piscinalis* and *P. complanata* in Lake Alvajärvi.

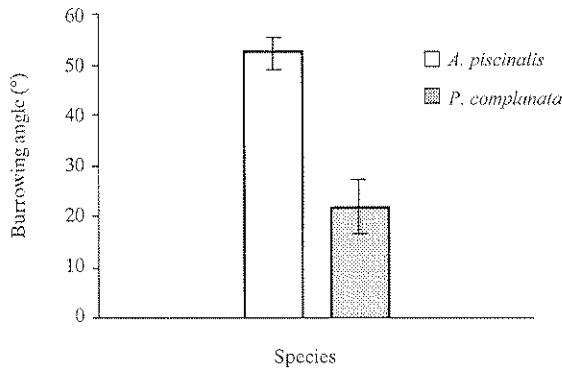**Figure 7.** The mean burrowing angle (±SE; deviation from a horizontal position) of *A. piscinalis* and *P. complanata* in Lake Alvajärvi.

totally horizontal position) were $22 \pm 5°$ and $52 \pm 3°$ (length-adjusted means; Fig. 7). The study month did not have any effect on burrowing behaviour (Wilks' lambda $F = 1.696$, df $= 2,38$, $P > 0.1$), but the effect of clam length on the burrowing depth was statistically significant (test of between-subjects effects $F = 28.17$, df $= 1,39$, $P < 0.001$).

Crawling activity

When analysing the crawling of *A. piscinalis* and *P. complanata* in Lake Alvajärvi, the logistic regression model included only the interaction term 'species × month' (change in log likelihood if term removed $= -21.361$, $P = 0.001$), but not the terms 'species', 'month' or 'length'. This result suggests that *A. piscinalis* and *P. complanata* did not differ in their total activity and that clam length had no effect on activity in these species. Logistic regression performed separately for the two species revealed that the interaction was due to the significant difference between June and August in the crawling activity of *A. piscinalis*, as the model included the term 'month' (change in log likelihood if term removed $= -10.123$, $P = 0.001$). *Anodonta piscinalis* moved more frequently in August than in June (38 and 0%, respectively; Table 2). In *P. complanata*, the monthly differ-

ence in moving was not significant (change in log likelihood if term removed $= 1.513$, $P > 0.1$)

In the case of *A. piscinalis* and *U. pictorum* in Lake Saravesi, the model included only the constant, indicating that activity was not affected by clam species, study month or clam length (Table 2).

DISCUSSION

The hypothesis that the clams would burrow less deeply during their spawning period in June as compared to late summer was supported only to a small degree. In *A. piscinalis*, the clams burrowed less deeply during spawning in one population, while no monthly differences were found in two other study populations. In *P. complanata*, no monthly differences in burrowing were found.

The hypothesis that the clams would be more active in crawling during spawning compared to late summer was not supported. In *P. complanata*, no monthly difference in crawling was observed. In *A. piscinalis*, difference was found, but in an opposite direction to that predicted; clams moved more actively in August than in June in one population, while no differences were found in other populations.

Unio pictorum differs from *A. piscinalis* and *P. complanata* in having two broods per summer (Dudgeon & Morton, 1983; Pekkarinen, 1992). Possibly due to this, the monthly behaviour patterns of *U. pictorum* differed from the other two species; no differences were found in crawling, but clams were more visible in August than in June.

Watters *et al.* (2001) studied the vertical migration of eight freshwater clam species, and discovered that some of them surfaced at spawning time in spring and remained exposed until autumn. Individuals of some other species re-burrowed after spring, but then surfaced again and remained there until autumn. The changes in burrowing depth during spring may be rapid. For example, Watters *et al.* (2001) noticed that most of a population of *Elliptio dilatata* (Rafinesque, 1820) surfaced over only two days in spring. Amyot & Downing (1998) suggested that the crawling behaviour has a reproductive function in lentic systems, aggregating clams closer to each other during spawning. Amyot & Downing (1997) reported that, unlike many poikilotherms, locomotion activity of *Elliptio complanata* is little influenced by water temperatures, but instead is linearly correlated with day length. In the present study area, maximal day length occurs in June. Therefore, the day length cannot explain the observed higher moving activity of *A. piscinalis* in August.

In *A. piscinalis* the bigger individuals were more visible than smaller ones. In some habitats the bigger clams may have hit a harder substrate beneath the looser top layer, which may contribute to this result.

Anodonta piscinalis and *U. pictorum* did not differ from each other in burrowing depth, burrowing angle or crawling activity. However, *P. complanata* was buried deeper than the other two species. The shell of *P. complanata* is much thinner (M. Saarinen, unpublished observation). Therefore, *P. complanata* may be more vulnerable to predation by muskrats (Convey, Hanson & MacKay, 1989) than the other two species. In the present study areas, the muskrat populations are dense (Jokela & Mutikainen, 1995), and *P. complanata* may burrow deeper than the other species to avoid predation.

Taskinen & Valtonen (1995) suggested that the risk of infection of *A. piscinalis* by the trematode parasite *Rhipidocotyle fennica* would increase with the increasing exposure of the shell. The possible costs, such as risk of predation or parasitism, and benefits, such as enhanced reproduction or feeding, related to clam burrowing and crawling behaviour remain to be explored in the future.

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