With Compliments.
N. Stone

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THE DISTRIBUTIONS OF THREE SYMPATRIC MUSSEL SPECIES (BIVALVIA: UNIONIDAE) IN BUDWORTH MERE, CHESHIRE

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Many freshwater bivalve molluscs show an apparent preference for particular water depths within lake ecosystems. Morton (1969) observed that the zebra mussel, *Dreissena polymorpha* Pall., is most common at depths of 2 – 3 m, and he commented that this is "reminiscent of the zonation commonly observed on the sea shore". Similar restricted distributions have also been noted for some of the large unionid bivalves. For example, in Lake Borrevann, Norway, *Anodonta piscinalis* Nilsson (= *A. anatina* (Linné)) is most common at depths of 3 – 5 m (Ökland, 1963), and in lake Pocotopaug, Connecticut, U.S.A., Fisher & Tevesz (1976) found *Elliptio complanata* Solander to be largely restricted to depths of 1 – 3 m.

In the few detailed studies of freshwater bivalve distribution, the species investigated is by far the most numerous large bivalve in the lake and little information is presented regarding the distribution of a number of closely related species within the same lake. Budworth Mere (Cheshire, England) is, therefore, of considerable interest as three species of unionid mussel *(Unio tumidus* Philipsson, *Anodonta anatina* (Linné), *Anodonta cygnea* (Linné) co-exist here in large numbers. The distributions of the three species are compared in this paper.

We have also examined the most pronounced morphological difference between the three species which might be related to the differences in their distributions. The unionids present in Budworth Mere are typical filter-feeding bivalves and initial examination of their internal anatomy indicates that they are very similar. The shell of each species shows similar construction, consisting of a thin outer prismatic layer (30 – 100 μm thick) overlying middle and inner nacreous layers (Stone, 1980). However, the three species show marked differences in the thickness of this shell nacre. These observations suggest that shell thickness and strength might be important factors in determining the distribution of unionids and a comparison of these factors for *U. tumidus*, *A. anatina* and *A. cygnea* is presented.

BUDWORTH MERE

Budworth Mere (Grid ref. SJ 661 770) is approximately 1.2 km long and 0.4 km wide, with a maximum water depth of about 7 m (Fig. 1). Deciduous woodland and agricultural land surround the lake and extend to the water's edge. Water enters the mere as ground water drainage and also through two small streams entering from the east and north west. A third stream on the southern shore of the mere acts as an overflow and helps maintain the water level nearly constant (± 15 cm) throughout the year. The lake water is high in calcium (2.5 $mM.1^{-1}$) and supports an animal and plant community typical of eutrophic freshwater (Stone, 1980 – Appendix 4).

MATERIALS AND METHODS

Five stations were established at approximately equal intervals around the lake shore. Stations 1 – 4 (Fig. 1) were sampled over a period of 4 days during 18 – 22 July 1977, and the remaining station (5 in Fig. 1) was sampled two years later on 15 August 1979.

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Figure 1.

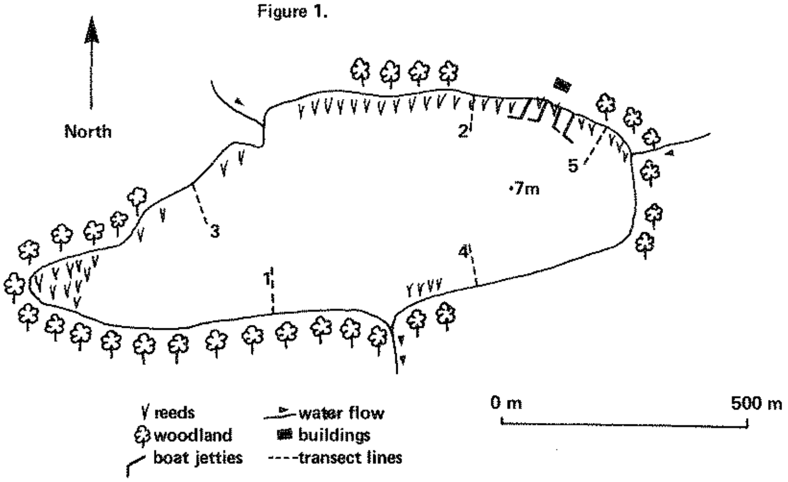

Fig. 1. Budworth Mere.

At each station, a 60 m transect line was run towards the centre of the mere along a bearing normal to the lake shore. Mussels were sampled at several positions along each transect by clearing 0.25 m^2 quadrats. The quadrats were positioned using SCUBA techniques, the living and dead bivalves being removed from each quadrat and placed in a labelled bag. Underwater visibility was poor (0.15 – 0.30 m) throughout much of the experimental period so quadrats were cleared by touch. Water depth at each sampling position was measured using a floated plumb-line. This method was accurate to within 5 cm, a considerably greater accuracy than could be attained using a standard Bourdon depth gauge in shallow water. Substratum samples were obtained from each position and taken to the laboratory for subsequent composition analysis. Each sample was separated by particle size and the percentage volume of gravel, sand and mud was estimated.

The bivalve samples were taken to the laboratory at the University of Manchester and the length (greatest linear dimension parallel to the hinge), height (greatest linear dimension normal to length) and width (greatest linear dimension across both valves and normal to length and height) of each shell were measured using vernier calipers. The tissues were removed from living animals and were dried to constant weight at 80°C for biomass determinations. Shell weight was measured for all specimens.

Further collections of empty shells, still joined at the ligament, were made for each species at station 5 on 16 August 1979. The shells were kept in water prior to experimentation at Manchester, since it is known that shells tend to weaken due to drying (Taylor & Layman, 1972) and the thin shells of *Anodonta* spp. often split when dry. The length and weight (blotted dry) of each shell were determined. The strength of each shell was tested by crushing the closed valve pairs in a direction across the maximum width of the valves with a tensometer at the University of Manchester Department of Mechanical Engineering. Shell strength was defined as the maximum force (kN.m^{-2}) sustained prior to collapse of the valves.

RESULTS

In Budworth Mere the greatest unionid biomasses are found at depths below 1 m in sandy regions clear of macrophyte growth (e.g. 193.91 g dry wt.m^{-2} at 0.61 m depth on transect 1 & 157.50 g dry wt. m^{-2} at 0.70 m depth on transect 5). In deeper water (1 – 3 m) unionid biomass is usually greatest in sandy substrata and reduced in areas where mud predominates (e.g. 49.36 g dry wt.m^{-2} at 2.13 m depth, 93% sand on transect 1 & 31.48 g dry wt.m^{-2} at 2.13 m depth, 80% mud on transect 2). At depths below 3 m unionids are rare and benthic searches found few animals.

The live animal density of each species has been plotted against water depth and substratum composition (i.e. % mud) in Fig. 2. *U. tumidus* is the most numerous unionid bivalve in Budworth (max. observed density = 89 live animals.m^{-2}) and has a distribution restricted to shallow water (down to 1.5 m depth) and substrata low in mud. *A. cygnea* is present at lower densities (max. observed = 22 live animals.m^{-2}) than *U. tumidus* and is most frequently found

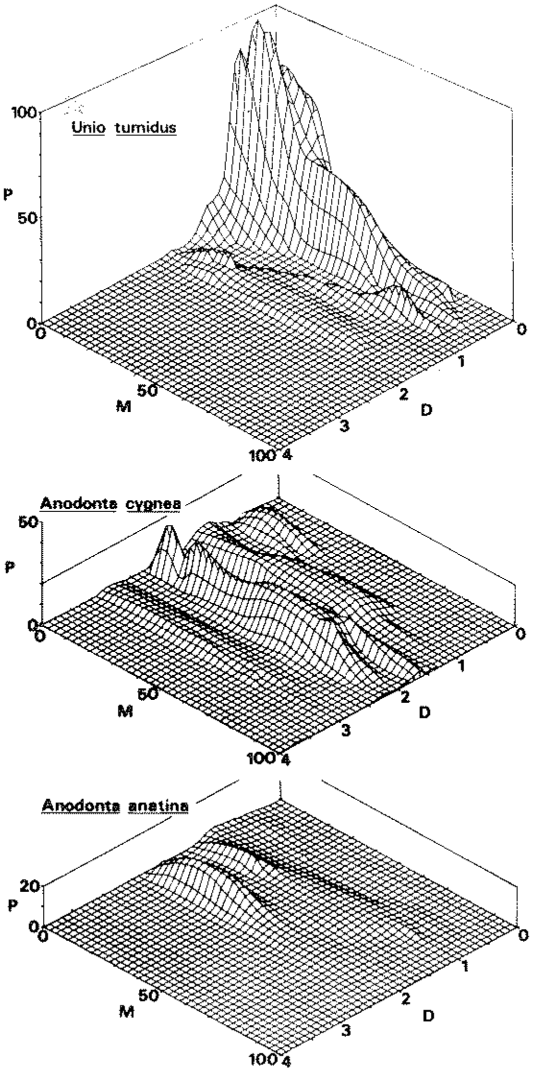

Fig. 2. Three dimensional graphs showing the observed population densities of living bivalves (P = No.m^{-2}) against water depth (D m) and substratum type (M = % mud by volume).

in deeper water (1 –3 m). *A. anatina* is uncommon, being found at low densities (max. observed = 6.m^{-2}) in most habitats occupied by the other two unionid species (Fig. 2). These distribution patterns appear to be very stable, being observed all around the mere and remaining substantially the same over the two-year period between sampling.

The data from all quadrat samples have been grouped into a number of frequency distributions in Table 1. Each quadrat was classified according to water depth (i.e. 0 – 1 m or 1 – 3 m) and sediment type (i.e. <30% mud or >30% mud) and the number of live specimens of each species in each quadrat was entered into the respective frequency distribution (note – there were no quadrats in water 0 – 1 m deep with >30% mud). The population density of *U. tumidus* is significantly greater in shallow water (0 – 1 m) with little mud (<30%) than in deeper water (1 – 3 m) with any type of substratum (<30% or >30% mud) (P <0.001). In

Table 1

Population densities of living bivalves in quadrats from different habitats. The habitats were classified according to depth (D = 0–1 or 1–3 m) and the mud content of the substratum (M = <30% or >30% by volume). Statistical test = Kolmogorov-Smirnov 2 sample test, one tailed (Siegel, 1956), the direction of the test is indicated, i being greater than ii.

Population density per quadrat ($N/0.25m^2$)	*U. tumidus*			*A. anatina*			*A. cygnea*		
	D = 0-1 M = <30%	1-3 <30%	1-3 ≥30%	D = 0-1 M = <30%	1-3 <30%	1-3 ≥30%	D = 0-1 M = <30%	1-3 <30%	1-3 ≥30%
0	2	10	17	33	8	23	33	6	6
1	5	4	8	14	6	5	9	4	12
2	6	1	1	3	1	2	6	1	4
3	3		0				2	1	4
4	8		3					1	2
5	4		1					0	2
6	5							1	
7	0							1	
8	1								
9	1								
10	2								
11	1								
12	1								
13	1								
14	1								
15	1								
20	1								
22	1								
23	1								
24	1								
25	2								
27	2								
N. of quadrats	50	15	30	50	15	30	50	15	30
Statistical test (one-tailed)	i——ii p <0.001			i——ii p >0.05			ii——i p >0.05		
		i——ii p >0.05			i——ii p >0.05			i——ii p >0.05	
	i————ii p <0.001			i————ii p >0.05			ii————i p <0.001		

deep water (1 – 3 m) *U. tumidus* shows no preference for sediment type. For *A. cygnea* the population density in shallow water with little mud (0 – 1 m depth & <30% mud) is significantly lower ($P < 0.001$) than in deep water with muddy substrata (1 – 3 m depth & >30% mud). *A. anatina* shows no obvious habitat preference, being present in most habitats at very low densities.

Regression coefficients for shell length (L), height (H), width (W), weight (shell wt.), W/L ratio, W/H ratio, H/L ratio, shell wt./L ratio and tissue dry weight (Dry wt.) (dependent variables) against water depth (m) and sediment type (% mud) (independent variables) have been calculated from the data collected in 1977 in order to investigate any linear relationships between shell morphometry and environmental conditions (Table 2).

Highly significant increase in W/H ratio ($P < 0.001$) and decrease in H/L ratio ($P < 0.02$) with increasing water depth and mud in sediment indicate that specimens of *U. tumidus* from deeper water and muddy substrata have a broader shell shape than those from shallow water and sandy substrata. For *A. cygnea*, specimens from the most muddy substrates are generally larger than from other habitats and, consequently, shell length, height, width and weight show

Table 2

Regression constants for the equation $y = a + bx$ where y (the dependent variable) is a shell dimension and x (the independent variable) is a habitat parameter (water depth (m) or substratum type i.e. % mud). Symbols for shell dimensions as in text – p. 000, * $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$; **** $P < 0.005$; **** $P < 0.001$.

x→	*U. tumidus* (n = 356)				*A. anatina* (n = 36)				*A.cygnae* (n = 110)			
y	Depth (m)		Mud (%)		Depth (m)		Mud (%)		Depth (m)		Mud (%)	
↓	a	b	a	b	a	b	a	b	a	b	a	b
L (mm)	81.41	−1.525	80.63	−1.829	79.71	**** −7.015	71.86	−0.470	98.71	−0.979	91.38	***** 14.979
H (mm)	42.38	* −1.798	41.61	−5.874	42.30	* −2.425	39.29	−1.466	51.83	−0.966	47.62	***** 6.895
W (mm)	28.71	0.221	28.78	1.267	28.54	**** −2.907	25.38	−0.712	31.83	** −1.485	28.01	*** 3.662
Dry wt. (g)	2.09	−0.280	1.98	−1.091	2.81	** −0.562	2.17	0.040	4.02	***** −0.533	2.98	0.427
Shell wt. (g)	36.57	* −4.819	34.47	−14.666	17.94	*** −3.642	13.90	−0.417	18.43	−1.233	14.89	** 3.987
W/L	0.353	* 0.009	0.357	0.025	0.357	−0.005	0.352	−0.007	0.323	***** −0.014	0.305	−0.009
W/H	0.678	***** 0.036	0.693	***** 0.130	0.677	* −0.035	0.646	−0.043	0.617	*** −0.020	0.588	−0.009
H/L	0.521	** −0.012	0.516	**** −0.060	0.529	* 0.021	0.547	0.027	0.526	−0.006	0.520	−0.008
Shell wt.$^{-1}$	0.440	** −0.055	0.418	* −0.188	0.225	** −0.032	0.189	−0.001	0.187	** −0.015	0.159	0.012

significant increases with increasing mud in sediments. Conversely, the shells of *A. cygnea* show a trend towards decreasing size in deeper water with decreases in shell width ($P < 0.02$) and tissue dry weight ($P < 0.001$) with increasing depth. Shell width shows a relative increase in deeper water as W/L and W/H ratios decrease with depth ($P < 0.001$ and < 0.01 respectively).

A. anatina shows a trend towards decreased size in deeper water with shell length, height, width and weight, and tissue dry weight all showing negative relationships with depth ($P < 0.005, < 0.05, < 0.005, < 0.01$ and < 0.02 respectively).

All three species show some trend towards a decreased shell wt./L ratio in deeper water, indicating that the shells of deep water specimens are relatively thin.

Comparison of shell weight against length for the three unionid species (Fig. 3) shows that *U. tumidus* has a considerably heavier shell than either *Anodonta* species. *A. cygnea* has an extremely light, thin shell, while the shell of *A. anatina* is intermediate in mass. Fig. 4 shows that the increased thickness of shell in *U. tumidus* confers extra strength. *A. cygnea* shells are very much weaker than those of *Unio*, while *A. anatina* shells are intermediate in strength with the stronger specimens being as strong as the weakest *Unio* shells.

DISCUSSION

Budworth Mere presents a number of habitat types suitable for the survival of unionid bivalves. The distribution survey presented in this paper indicates that the shallow, sandy regions of the mere with little plant cover support the greatest unionid biomasses, suggesting that these regions offer the most favourable conditions for these bivalves. In these regions wind action at the water surface leads to good mixing of the water with the atmosphere, resulting in relatively high oxygen and low carbon dioxide levels. Summer temperatures are higher near the water surface and increased illumination probably increases the algal concentrations in these waters. Furthermore, the increased water movement usually observed above coarse sediments may directly facilitate the filtering activity of bivalves (Walne, 1972).

At greater depths (below 1 – 2 m at Budworth), water movement is reduced and mud takes over from sand as the dominant sediment. In these regions, oxygen levels are likely to be reduced and carbon dioxide levels increased by the respiration of benthic organisms, and maximum summer temperatures are lower than in shallower waters. In water overlying mud sedi-

Figure 3

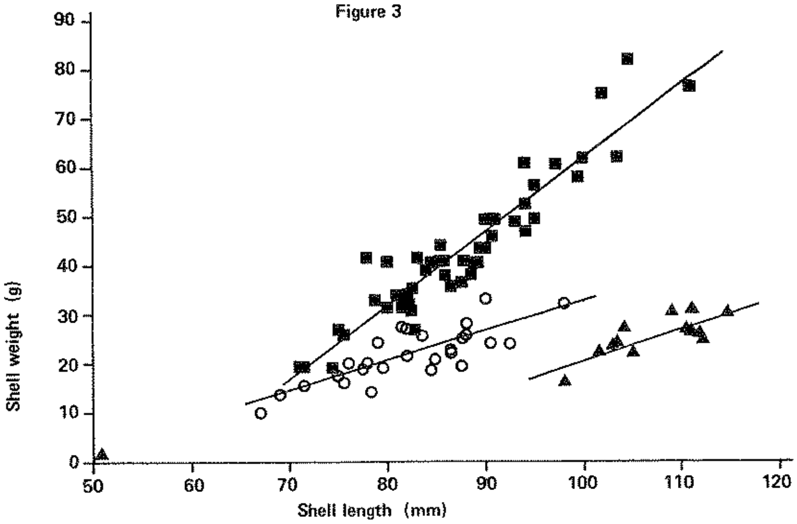

Fig. 3. Shell weight against shell length for the 3 unionid species found in Budworth Mere. ■ *Unio tumidus* – shell wt. = 89.67 + 1.52L, ○ *Anodonta anatina* – shell wt. = –28.20 + 0.61L, ▲ *Anodonta cygnea* – shell wt. = 43.97 + 0.65L.

Figure 4

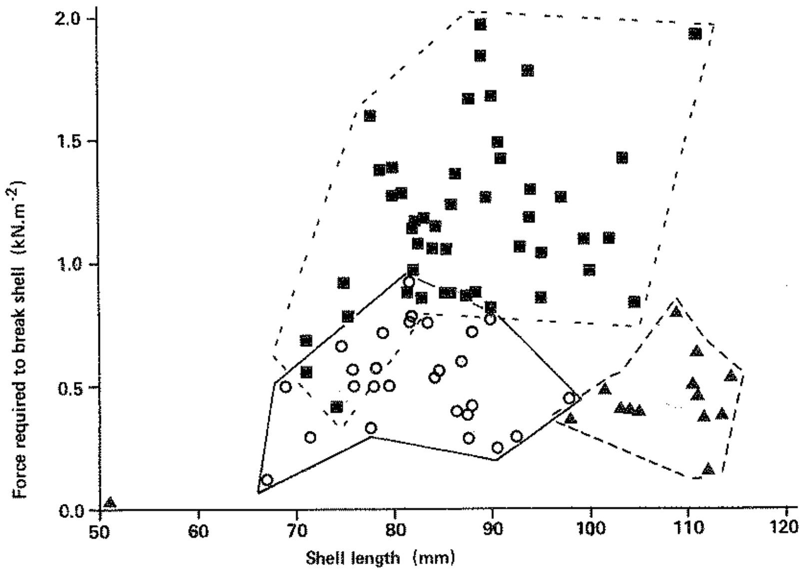

Fig. 4. Shell strength against shell length for the specimens in Fig. 3. Symbols as for Fig. 3.

ments, although food concentration may well be high in the form of organic detritus, useful food material will be mixed with inorganic particles also in suspension. The effect of high amounts of inorganic suspension is almost certainly to reduce the efficiency of filter feeding (Loosanoff & Tommers, 1948; Pratt & Campbell, 1956; Johnson, 1971; Foster-Smith, 1975) and hence reduce growth rates (Johnson, 1971). Field studies which have compared the growth of bivalves in sand and mud substrata have mostly shown faster growth in the sandy habitats (Swan, 1952; Rhoads & Young, 1970; Rosenberg, 1972; Peddicord, 1976, 1977).

Shallow regions of lakes would, therefore, appear to be most suitable for bivalves, although these regions present a number of hazards not found in deeper waters. These hazards include increased risk of exposure during drought conditions, increased risk from terrestrial predators (e.g. birds, otters and, perhaps, wading foxes), and risk of damage by large wading animals and storms.

Exposure during drought conditions is unlikely to constitute a major threat to British unionids inhabiting relatively undisturbed lakes (i.e. not reservoirs) as any decrease in water level will normally be slow allowing the bivalves sufficient time to change location and so avoid exposure (Isely, 1913; Trueman, 1968). Long periods of observation at Budworth failed to indicate any large predators of the bivalves. However, damage to bivalves caused by large wading animals is still a very real risk as land adjacent to the lake is grazed by cattle which frequently wade into the lake to depths of about 1.5 m. Also, occasionally, storms occur with sufficient force to move stones and lift bivalves from shallow water sediments thus rendering the molluscs vulnerable to damage.

The increased risk of predation, damage by wading animals and storms, and being washed from the substratum might all be mitigated by the development of a strong shell. *U. tumidus*, which inhabits the shallowest regions of Budworth, has a shell thicker and stronger than those of *A. cygnea* or *A. anatina*. Also, all three unionid species show a trend towards increased shell thickness (i.e. increased shell wt/L ratio) with decreasing water depth. A number of specimens of *U. tumidus* have been found with damage to the most vulnerable siphonal region of the shell

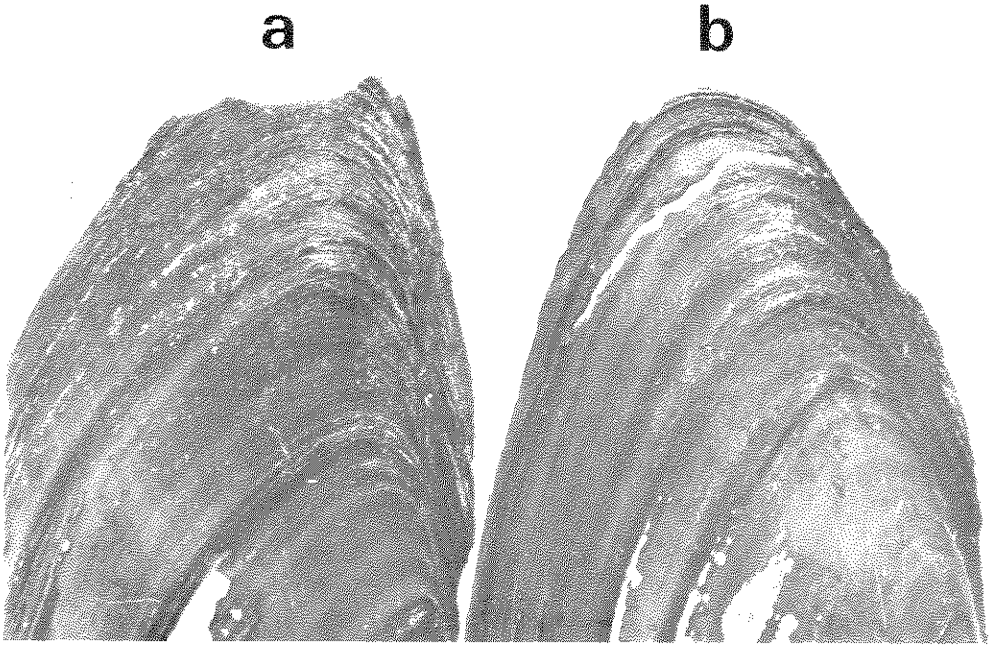

Fig. 5. Typical examples of damaged shells taken from Budworth Mere. (a) the posterior siphonal region of a shell showing damage to shell edge; (b) similar damage to that shown in (a) has been followed by repair and further shell growth.

(Fig. 5a) and some shells show signs of damage followed by repair (Fig. 5b). Similar forces applied to thinner shells might well have been more deleterious.

The heavy shell of *U. tumidus* may also aid the penetration of exposed animals into the sand and gravel sediments during the initial pedal probing period of the digging cycle (Trueman, Brand & Davis, 1966; Eagar, 1978). Many of the thin-shelled *A. cygnea* observed in shallow water were found to be lying on their sides on top of the sediment. Conversely, the heavy shell of *U. tumidus* would be a disadvantage in mud substrata as it would increase the rate at which the animal sinks below the sediment surface (Eagar, 1978). Specimens of *Unio* found in more muddy conditions have relatively wide shells which probably helps to retard sinking (Eager, 1978). *A. cygnea* is better adapted to fine sediments as it has a very light shell. Also, a light shell is probably energetically less expensive to produce, an advantage in the less favourable muddy habitats. *A. anatina* would seem less well adapted for any particular substrates as it has a shell intermediate in mass. This might account for the present low density of *A. anatina* living in Budworth, possibly through competition for the best habitats.

This investigation, therefore, suggests that differences in shell weight and strength are important factors relating to the distributions of the unionids in Budworth Mere. However, further work should be undertaken to determine other differences between the three species which may also be related to their different habitat preferences.

SUMMARY

Benthic surveys in Budworth Mere, Cheshire, revealed that 3 species of unionid bivalve inhabit the lake. Unionid biomass is highest in the shallow margins of the mere (0 – 1 m.) in regions of sand and gravel substrata, suggesting that these regions are most suitable for bivalves.

Unio tumidus Philipsson occurs in highest densities in shallow water and it is suggested that this species is able to colonise these regions by virtue of its stronger shell.

Anodonta cygnea (Linnaeus) is mainly found in deeper water (1 – 3 m.) and its thin, light shell may be an adaptation to the softer sediments which predominate in these regions.

Anodonta anatina (Linnaeus) has a shell intermediate in thickness and shows no habitat preference in water less than 3 m. deep. This species is uncommon and may have been partly excluded by interspecific competition for the most favourable habitats.

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