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Reproductive Effort in Danish Mudsnails (Hydrobiidae)

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Summary. The four species of Hydrobiid mudsnails found in Danish brackish water habitats are ranked with respect to reproductive effort. The biology of the species indicate that *Hydrobia neglecta* and *Potamopyrgus jenkinsi*, showing the highest reproductive effort are also more r-selected than the other species, *H. ventrosa* and *H. ulvae*.

Introduction

In the mudsnails (Hydrobiidae) found in Danish brackish water habitats, a wide variety of life cycle traits are represented with respect to length of life, number of breeding seasons, clutch size, offspring size, larval development type and brood protection.

Recent works have tried to correlate such a variety of traits under the headings of different directions of selection in different ecological regimes, the theory of *r*-and *K-selection* (MacArthur and Wilson, 1967; Pianka, 1970, 1972). Various life cycle traits have been taken as indications of either r-or K-selection in a species. However, the position of an organism in the *r-K-continuum* (Pianka, 1970) cannot be judged from e.g. size and numbers of offspring alone. Christiansen and Fenchel (1977) find, under the assumption of r-selection that evolutionary optima may exist of both many small and fewer large offspring. Further it is demonstrated (Christiansen and Fenchel, 1979) that in the arctics – where to common thought conditions are unstable and populations density independently regulated – large larvae (with lecitotrophic or direct development) in the benthic, marine invertebrates are evolutionarily favoured over small (planktotrophic) larvae. Also, the inadequacy of single life cycle traits as r-K-measures is illustrated by Murphy (1968) and Schaffer (1974), whose results on the evolutionary advantages of iteroparity versus semelparity may be contrary to straight forward r-K-expectations, when survival probabilities in stable and fluctuating environments are considered for both juvenile and adult stages. Thus, with respect to r-K-theory, the above traits are to be viewed as correlates of various

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selective regimes, rather than direct measures as to whether a population is more or less r- or K-selected.

A better measure is the relative amount of energy spent for reproductive purposes (Gadgil and Solbrig, 1972) – no matter how this energy is parcelled – versus energy used for somatic growth. Ideally, the *reproductive effort* is the proportion of the total energy budget that is allocated into reproduction, but even in lack of entire energy budgets, which are tedious to obtain, simpler expressions of reproductive effort will suffice for comparative purposes. Indeed, the r-K-position of a species is a relative one, the concept being meaningful only in comparisons between species-populations or closely related species.

Material

Data on the fecundity of the *Hydrobia* species is obtained from Lassen and Clark (1979). Each month over a year 100 snails were collected at stations in the Limfjord and the Aarhus Bay, Denmark. The snails were sexed, incubated with sediment and water from the field localities and placed outdoors, and the number of egg capsules deposited during a week was noted. The annual growth and adult weight of snails was measured in the laboratory. *Potamopyrgus jenkinsi* was sampled at the outlets of Bjørnsholm Å into the Limfjord and Odder Å into Kysing Fjord. Ten individuals were incubated at a range of salinities and the number noted of young produced during a week. In some individuals the brood pouch was punctured and the number of eggs and young counted. The adult weight was determined. In all species the diameter of the yolk mass was measured with an ocular micrometer.

Results

The Danish brackish water fauna of Hydrobiid mudsnails holds three species of the genus *Hydrobia*, viz.: *H. ulvae* (Pennant), *H. ventrosa* (Montagu) and *H. neglecta* (Muus) and a closely related species, *Potamopyrgus jenkinsi* (Smith), which also penetrates into freshwater. Morphologically the species are very similar, envisioned by the fact that *H. neglecta* was not described until recently (Muus, 1963), but with respect to life cycle characteristica large differences are observed as outlined below:

Hydrobia ventrosa has an annual life cycle, and at the stations sampled the females deposit 24–105 (av. 50) sandcovered egg capsules, mainly in the period May-August. Each capsule contains one egg (164 ± 7 µm diam.) hatching with direct development into a crawling young. On rare occasions two eggs may be found in the capsules. The adult weight of the snails is about 5 mg.

Hydrobia neglecta like the former species has a life length of little more than a year. The annual fecundity is higher, 104–467 (av. 300) eggs (164 ± 7 µm diam.) are deposited singly in egg capsules and hatch with direct development. The annual growth is like that of the former species.

Hydrobia ulvae may live for several years and probably has more than one breeding season. Observations of the annual fecundity were 81–186 (av. 150) egg capsules, which contain 23 ± 6 eggs. The size of the egg is smaller than in the former species (78 ± 9 µm) and the eggs hatch into small planktonic young. The adult weight of the snails is about 15 mg.

Table 1. Reproductive effort in 4 species of mudsnails

	No capsules	Eggs/ caps.	No eggs	Egg diam. µm	Volume	Growth	Reproductive effort	
					(V) of eggs, mm^3	mg (W)	V/W	relative
Hydrobia ventrosa	50	1	50	164	0.116	5	0.023	1
Hydrobia ulvae	150	23	3450	78	0.856	15	0.057	2.48
Potamopyrgus jenkinsi			230	190	0.837	10	0.084	3.65
Hydrobia neglecta	290	1	290	164	0.670	5	0.134	5.83

Potamopyrgus jenkinsi is a parthenogenetic, viviparous species, with an annual life cycle. Adult snails carry about 50 eggs (190 ± 8 µm diam.) and embryos in all stages of development in the brood pouch, which is formed by the enlarged oviduct. The young are shed singly and production of young is highest in low-salinity brackish water; 2 (max 4) young may be produced per snail per day under summer conditions. Sexual maturity is attained at the size of about 3.5 mm and full reproductive activity at 5 mm (10 mg w.w.). From Real (1971) an estimate is obtained of an annual fecundity of 230 young per snail.

As a relative measure of the reproductive effort in the mudsnails is here adopted the ratio of yolk volume (V) to annual growth increment (W) or in the case of *Potamopyrgus jenkinsi* to adult weight. It is assumed that the energy per unit yolk mass is the same in all the species, since these are closely related. For *P. jenkinsi* especially, the assumption is made that brood protection does not cause any further energy expenditure on the female, than what is put into the yolk and fluid within the egg membrane. The calculation of the values of reproductive effort is shown in Table 1. The last column of the table gives the values of reproductive effort relative to the species with the lowest effort: *Hydrobia ventrosa*. A six-fold difference is noted between this species and the one with the highest reproductive effort. With respect to this measure the mudsnails are ranked as follows: *H. ventrosa, H. ulvae, P. jenkinsi* and *H. neglecta*. The fecundity data are considered valid estimates of agespecific fecundity in *H. ventrosa* and *H. neglecta*, since these species have an annual life cycle, but in *H. ulvae* the estimate is less accurate, since this species may have more than one breeding season. During the same time, however, energy is used for growth and maintenance, and among the *Hydrobia* species, *H. ulvae* has the highest standard metabolism (Hylleberg, pers. comm.); an exact value of reproductive effort therefore probably will not be higher than the one given here. Since not every detail of the life table parameters and energy budgets of the four Hydrobiid species is known, the values of reproductive effort can only be approximate, but the observed ranking of species will not change.

Discussion

The present findings support the assumption that single life cycle traits are not useful measures of whether a species is r-or K-selected (Menge, 1974; Graham, 1977) e.g. the species having the highest number of offspring (more than 3,000 in *H. ulvae*) is not the species yielding the highest reproductive effort.

The competitive relationships among the Hydrobiid species have not yet been fully elucidated by experimental observations, although Fenchel and Kofoed (1976) found evidence of exploitative, interspecific competition. The major obstacle to experimental work is that the larvae of *Hydrobia ulvae* cannot be reared beyond metamorphosis. Experiments, therefore, cannot run for more than a single generation, and the influence of population growth on the outcome of competition is out of reach. Evidence of competitive interactions, however, is found in the distribution patterns of the Hydrobiid species (Fenchel, 1975). *Hydrobia ventrosa*, which according to the present findings has the lowest reproductive effort, appears to be competitively superior in low-migration environments e.g. lagoons, especially where salinity is low. In open systems to which there is migratory access, this species may be displaced, most often by *Hydrobia ulvae*, which has pelagic larvae. The competitive relations of these species follow predictions of the migration-extinction model of Christiansen and Fenchel (1977).

Among the shallow-water habitats of the Hydrobiids many are characterized by drastic environmental fluctuations (salinity, desiccation, freshwater inundation, H_2S-production etc.) often leading to fluctuations in population density i.e. environments, where r-selection is to be expected. According to Fenchel (1975) the majority of localities in the Limfjord, where *Hydrobia neglecta* is found, is of this type, and it was conjectured that the species survives in this area as a fugitive species. A fugitive "strategy" is characterized by the ability of rapid population growth in an ecological vacuum – an r-selected feature, in the present case indicated by the high reproductive effort of *H. neglecta*. The fundamental trait of a fugitive species, however, is the ability of dispersal. In a heterogeneous environment a fugitive species may survive indefinitely (Christiansen and Fenchel, 1977) – even if it is competitively inferior in any single locality – provided that empty habitat patches recurrently appear and that the species is able to reach these before superior competitores colonize. In many species adopting a fugitive strategy (species of early successional stages, early colonizers of island biota etc.) dispersing stages or mechanisms are evolved, even at the sacrifice of reproductive effort. In *Hydrobia neglecta* no such stages are found, but in the adults the ability of floating may lead to dispersion. This habit, although it has not yet been quantified in the field, is more pronounced in *H. neglecta* than in the other Hydrobiid species. In experiments *H. neglecta* shows a much higher tendency of crawling and clinging to the surface film than *H. ventrosa* and due to higher mucus production the former species is able to stay in the water surface in spite of violent disturbance. Thus, in *Hydrobia neglecta* a potential way of dispersal is floating, driven by the wind. In *Potamopyrgus jenkinsi*, which also has a high reproductive effort, the mechanism of dispersal is unknown, but a high potential of migration is evidenced by the vast geographical distribution achieved by the species during the last century (Lassen, 1978). There is thus, biological evidence that the two species, *Hydrobia neglecta* and *Potamopyrgus jenkinsi*, showing the highest reproductive effort are also more r-selected compared to the other mudsnails, *H. ulvae* and *H. ventrosa*, and r-selection is an important component of a fugitive strategy, although the two concepts not necessarily are synonymous.

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