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LIFE-HISTORY STRATEGIES IN CONTRASTING POPULATIONS OF THE COASTAL GASTROPOD HYDROBIA III. LAGOONAL VERSUS INTERTIDAL-MARINE H. NEGLECTA

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ABSTRACT - The expected lifetime investments in reproduction (ELIR) of two populations of the directly-developing coastal mudsnail Hydrobia neglecta, one in its typical lagoonal habitat (in Suffolk, U.K.) and the other the only known intertidal marine population (in Finistère, France), are compared with each other and with previous data on equivalent populations of the larviparous H. ulvae. In lagoonal H. neglecta, there are two annual periods of egg production each year, and each of the two cohorts resulting can breed in both periods – the spring one both before and after their first winter, and the late summer one only after overwintering but then twice in the same calendar year. Adult mortality rates, however, are such that individuals of each cohort have an average expectation of surviving through only a single breeding period, although their differing densities ensure that the small percentage of spring cohort individuals that do survive to breed twice contribute half the eggs of the following spring. The strategy of a cohort that breeds before overwintering, not previously recorded in H. neglecta, has a marked pay-off in terms of increased survival through to adulthood, but at the cost of a reduced production of eggs per individual adult, relative to the typical summer cohort. The intertidal marine population displays a single short annual period of egg laying contributed solely by overwintered pre-reproductive mudsnails that do not survive through the next winter. In marked contrast to the position in H. ulvae although still conforming to the predicted relationship between breeding strategy and expectation of reproductive life, the intertidal and lagoonal cohorts of H. neglecta that overwinter before breeding had an identical ELIR, corresponding to their effectively identical expectations of adult survival. In contrast to the finding of Lassen (1979) that the annual reproductive effort of H. neglecta was more than twice that of H. ulvae, here the ELIR of H. neglecta was less than that of H. ulvae: only 16-89% of the investment of H. ulvae when both are lagoonal and 71% of it when intertidal. The large eggs/direct development strategy of H. neglecta appears markedly to reduce juvenile mortality, in both lagoonal and intertidal marine habitats, in comparison to that experienced by the larviparous H. ulvae.
INTRODUCTION

In earlier papers on reproduction in intertidal marine versus lagoon populations of the prosobranch mudsnail *Hydrobia* (Barnes, 1988 a; 1990), it was shown that in *H. ulvae* (Pennant) the contrasting patterns of numbers of eggs produced per unit time in the two environments were consonant with the different expectations of adult survival, although egg size, number of eggs per capsule and larval characteristics remained the same. The intertidal females with a low probability of adult survival produced in their 2.75 months of expected reproductive life more eggs than did the longer-lived lagoonal females in their entire first year of breeding. Some 15 % of lagoonal adults, however, live through 5 breeding seasons (equivalent to 2.5 years) (Barnes, 1990, updated by more recent data), whereas only 10 % of intertidal adults survive even for one year after reaching maturity. These data must be somewhere near maximum values because many cohorts in both the studied habitats failed to survive through to adulthood.

Two related species, *H. ventrosa* (Montagu) and *H. neglecta* Muus, differ from *H. ulvae* in several important life-history characteristics. They lack a free-living larval stage, for example, and each deposited capsule usually contains but a single large egg (Lassen & Clark, 1979; Fish & Fish, 1981); they are also generally supposed to live through a single breeding season and to achieve a maximum size of only some 4 mm (shell height) (Lassen, 1979; Lassen & Clark, 1979; Siegismund, 1982). Like *H. ulvae*, however, the habitat range of *H. ventrosa* includes both lagoonal and (very much less commonly) intertidal localities (Cherrill & James, 1985; Heide, 1960 under the name *H. stagnorum*), although until recently *H. neglecta* has solely been recorded permanently submerged in coastal lagoons or equivalent shallow, protected, brackish, non-tidal localities (Muus, 1967; Bishop, 1976; Cherrill & James, 1985; Hylleberg, 1986; and personal observations). The discovery in 1989 of an intertidal marine population in northwestern Finistère, France (Barnes, 1991 a), means that, like the two other *Hydrobia* spp., *H. neglecta* is now known to occur in both lagoonal and intertidal sites, inviting comparison between the directly developing *Hydrobia* species and the larviparous *H. ulvae* in terms of the effect of the different mortality patterns associated with the two differing habitat types on their life-history patterns. This paper refers solely to *H. neglecta*; the smallest of the northwest European *Hydrobia*, the most restricted in its food and habitat requirements (Hylleberg, 1976, 1986), and the most local, with a recorded range only from Galway Bay (Eire) to the Kattegat and Belt Sea (Denmark) and from Orkney (Scotland) to Finistère (France).

MATERIALS AND METHODS

The lagoonal populations of *H. neglecta* studied were those in the Reedland Marshes lagoon system, Dunwich, Suffolk, U.K. (the 150 m² lagoon at TM 484722), with supplementary sampling from the nearby Shingle Street/Bawdsey lagoon complex, Suffolk (“Lagoon 6 – South”, TM 373437) which was used as a check on cohort heights. Both these lagoons are currently separated from the sea only by some 70 m of porous shingle and their salinity is that of the local sea water (34.5 %c), with minor variation caused by the prevailing evaporation/precipitation ratio. In each of the lagoons sampled, *H. neglecta* was the only hydrobid present although *H. ventrosa* occurs in other lagoons within each of the two lagoonal complexes. The intertidal marine population was in an isolated 20 m² patch of *Zostera noltii* Hornem, in the Anse Lostrouc’h, at Lilai, near Plouguerneau, Finistère, France, where it occurs together with a few (c. 500.m⁻²) *H. ulvae* – an otherwise very uncommon sympatric combination (Barnes, 1988 b, 1991 a). Barnes (1987, 1989,
In the earlier studies of *H. ulvae* (Barnes, 1988 a; 1990) it was possible to select the lagoonal and marine study sites so as to be geographically extremely close to each other, to minimise any influence of latitude/temperature on the breeding system. Such was not possible in respect of *H. neglecta*. Even though the Suffolk lagoonal systems selected are the nearest ones, latitudinally, to Finistère that support flourishing populations of *H. neglecta*, they are still 600 km away to the northeast; mean sea surface temperatures are not likely to differ between the two sites in summer, but those in winter are liable to be some 5°C warmer in Finistère (Lee & Ramster, 1981; Gohin & Langlois, 1991).

The only locality of this species nearer to Lostrouc’h than the Suffolk sites is the Vale Pond lagoon, Guernsey (Barrett, 1976; Anon, 1977); although no living individuals could be found there in 1976 (Stiva, 1983) nor in 1992 (Barnes, unpubl.) when the lagoon contained only *H. ventrosa*. Because of the geographical distance between the intertidal population of *H. neglecta* and Cambridge, material from it for analysis of reproductive output also had to be maintained in the laboratory, rather than being replenished at frequent intervals (the same procedure was adopted for the lagoonal *H. neglecta*), and neither it was possible so frequently to monitor its dynamics. Present procedures therefore differed in these respects from those used earlier (Barnes, 1988 a, 1990), with the result that whereas the data on *H. ulvae* were based on average reproductive output over time, those on *H. neglecta* were derived by following the same cohorts of individuals through the breeding seasons.

Insofar as was previously known, breeding in *H. neglecta* begins in April and may last through the summer (Lassen, 1979); stocks for analysis of output of eggs per female were therefore obtained in late February 1991 (to guard against possible earlier breeding, especially in the French population), 10°C being both the temperature threshold for reproduction (Lassen, 1979) and the minimum temperature for 90 % embryo survival (Fish & Fish, 1981). Some 80 pre-reproductive mudsnails (i.e. from the overwintering juvenile age class) from each of the Dunwich and Lostrouc’h sites were then maintained in the laboratory under the same conditions as described earlier for *H. ulvae* (Barnes, 1990); significant numbers of overwintering post-reproductive adults were present at Dunwich (but not in the Anse Lostrouc’h) in February and approx. 80 of these were also kept under the same regime. Similar laboratory populations of Dunwich and Lostrouc’h mudsnails were set up in July (Dunwich) and August (Lostrouc’h) 1991 containing members of the pre-reproductive cohort that entered the populations in that summer. The numbers of eggs laid by members of the different cohorts were thereafter assessed at intervals of 14 days until egg laying stopped (in December); empty egg capsules being scored as hatched eggs. The number of female mudsnails in the captive Dunwich populations was assumed to be 50 % of the total individuals since surveys indicated a 1 ♀ : 1 ♂ sex ratio ($\chi^2 = 0.05; p > 0.7$); the sex ratio at Lostrouc’h, however, departed significantly from equality ($\chi^2 = 13.7; p < 0.001$), with more than twice as many females as males, and the number of females in the captive population was determined directly. After each assessment, egg capsules were removed from the dishes, as were any dead mudsnails which were replaced by individuals from reserve stocks maintained under the same experimental conditions (this was only necessary for the over-wintered Dunwich adults). The animals were kept in glass dishes, containing natural alga-rich sediment near Wells, Norfolk, and laboratory sea water both of which were changed after every assessment; the dishes were positioned under a 12 hours on/off 'growlux' tube to encourage the growth of algal food supplies, including added pieces of *Enteromorpha*. All other procedures and conditions were as described previously (Barnes, 1988 a, 1990), including the one constant-temperature regime under which both sets of mudsnails were maintained in an attempt to achieve comparability of performance, and the absence of any reason to believe that the quantity and quality of food available to the various test mudsnails were not identical throughout the experimental period (McKILp & Butler, 1979; Fletcher, 1984). Samples of 25 newly laid eggs of the Dunwich and Lostrouc’h mudsnails were measured, yielding mean egg diameters of 200 and 185 μm (somewhat larger than those recorded by Lassen, 1979 and Fish & Fish, 1981); equivalent to egg volumes of 0.0042 and 0.0033 mm³, respectively. The ash-free dry weight (AFDW) of one egg plus secreted capsular material was therefore assumed to approximate 15 μg (Dunwich) and 13 μg (Lostrouc’h) on the basis of their size relative to that of *H. ulvae* (Barnes, 1988 a; 1990) and of other small gastropods.

The population density and size structure of the Suffolk mudsnails were assessed at 4-weekly intervals from February 1991 until September 1992, and those of the French population were assessed on 10 occasions between February 1991 and August 1992; procedures were those described previously (Barnes, 1990) except as follows. (i) Because both the Dunwich and Lostrouc’h populations inhabited coarse sediments [Dunwich 86 % medium sand and coarser particles by weight; Lostrouc’h 84 % gravel and coarse sand], a 710 μm mesh sieve had to be used to extract the mud-
(ii) Adult AFDW was estimated from measured shell heights using the regression equation of Siegismund (1982) [that yields weight in mg, not μg as stated by that author]. (iii) The density of an age class was calculated as the product of total density and the proportion of the given age class in the population, the estimates of the latter, together with mean heights of the various age classes, being checked where appropriate by the computer programme distinguishing overlapping normal distributions contained in Press et al. (1989: 521-528).

RESULTS

The same intraspecific difference in behaviour between intertidal and permanently submerged populations noted by Barnes (1988 a) in respect of H. ulvae, namely that the intertidal marine mudsnails crawled above the water level in dishes whereas the lagoonal ones did not, was observed in the two laboratory stocks of H. neglecta, and as also noted in H. ulvae shell morphology differed in the two habitat types (Fig. 1). In contrast to the findings of Fish & Fish (1981), however, that H. neglecta never deposited its egg capsules on the shells of conspecific individuals, early and very late in the breeding season in the laboratory a small proportion of the Suffolk capsules (< 10 %) and up to 50 % of those of the Finistère mudsnails were so deposited, and capsules were also frequently observed on mudsnails in the field.

Intertidal population

The mudsnails from Lostrouc’h showed a single, very short, late spring – summer period of reproduction, peaking in May (Fig. 2A; 3A). All eggs were contributed by animals that first entered the censused population in the summer of the previous year but which overwintered without having bred. By December of their first calendar year, this cohort has achieved a mean height of 2 mm, increasing to 2.6 mm at the start of the breeding season and with a maximum height in the order of 4.3 mm (Fig. 4 A). Survival of these pre-and post-reproductive individuals is shown in Fig. 5A: there was an average expectation of reproductive life of 11 weeks. Mortality between egg (as
estimated from Fig. 6 A) and breeding adult (an interval of 1 year) was 87 % and no adult survived through the following winter. Translated into units of egg production, this means that although capable of producing only some 14 eggs during their single breeding episode, a female that survived to maturity on average succeeded in producing 11 eggs before dying, equivalent to some 37.5 % of her own AFDW at the time of death.

**Lagoonal population**

The Suffolk lagoonal population, in contrast, displayed two peaks of reproduction during the year and consequently two annual cohorts (Fig. 2 B; 3 B). The cohort deriving from spring eggs ('spring cohort') first bred some two months later in late summer/autumn and then overwintered before breeding again in the spring. The cohort deriving from late summer/autumn eggs ('summer cohort') overwintered before breeding but then produced eggs both in the spring and again, after an interval of some 12 weeks, in the late summer/autumn. Both the annual cohorts could therefore potentially contribute to both the two peak egg-laying periods. The numbers of eggs produced per female by snails of the two cohorts were comparable during the spring laying season; during the late summer season, however, summer cohort females produced some 3-4 times as many eggs per female, as did the spring cohort females (which were then almost one and a half times the weight of the summer females). Nevertheless, in both of the survey years and during both of the breeding periods the spring cohort mudsnails were the more numerous group and comprised the majority of the *H. neglecta* population at any one time, even in the early spring when they were the older of the two cohorts (see below). As a result, they contributed 98 % of the total summer egg production and 52 % of that in the following spring. Why survival of young mudsnails produced early in the year should be so much better than of those hatching in the autumn is not obvious, although percentage survival through to adulthood must in part be a direct reflection of the intervening length of time (17 vs 35 weeks), and differential survival over autumn/winter may be related to individual size, being better for larger snails – the spring cohort certainly invested more in individual growth up to and during their first breeding episode than did the summer cohort, and therefore achieved large size by late autumn but at the apparent cost of a lesser output of eggs (see below and Table I).

The spring cohort had achieved a mean shell height of 2.1 mm by the time of first reproduction, of 3.6 mm by the start of the second breeding episode, and a maximum one of 5.9 mm. The comparable figures for the summer cohort were 2.1 mm, c. 3.2 mm and 3.8 mm respectively (Fig. 4 B). The survival of both is shown in Fig. 5 B. In respect of the spring cohort: 14 % of adults survived to breed twice and some 8 % survived through the whole of both breeding seasons; mean expectation of reproductive life was 13 weeks; and mortality between egg (as estimated from Fig. 6B) and breeding adult (an interval of only 17 weeks)
was 48%. Translated into units of egg production, this means that a spring-spawned lagoonal female that survived to maturity on average produced 13-15 eggs, equivalent to 62-65% of her own AFDW at the time of death; potential egg production over the two breeding episodes being 29.

In summary (Table I), therefore, (a) spring-spawned lagoonal H. neglecta experienced low juvenile mortality, high adult densities survived through to the start of their second breeding season although mortality was high thereafter, individual snails grew relatively large relatively rapidly, and on average adults survived to produce only some 19% of their potential annual total of eggs although significant numbers survived through two breeding seasons; (b) summer-spawned lagoonal mudsnails suffered very high juvenile mortality so that the cohort occurred at low density and the actual numbers surviving to breed twice were negligible, the snails were individually small but fecund, adults investing heavily in reproduction and succeeding in laying some 48% of their potential 29 annual eggs; and (c) marine H. neglecta experienced prolonged although low-level juvenile mortality, and adults lived through a single annual breeding season in which they survived to produce 79% of their potential egg total. Juvenile and adult mortality rates were comparable in the spring lagoonal cohort and in the marine population, although those of the summer lagoonal cohort were about twice those levels.

Table I. Summary of life-history and reproductive differences between intertidal-marine and lagoonal H. neglecta.

<table>
<thead>
<tr>
<th></th>
<th>Lagoonal population: spring cohort</th>
<th>Lagoonal population: summer cohort</th>
<th>Inter tidal marine population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean expectation of reproductive life (wk)</td>
<td>13</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>Mean nos. eggs produced</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Reproductive lifetime</td>
<td></td>
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<tr>
<td>Potential mean annual output eggs/female</td>
<td></td>
<td></td>
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<tr>
<td>Mean % adult resources devoted to eggs during reproductive lifetime</td>
<td></td>
<td></td>
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<tr>
<td>Max. cumulative ratio of egg weight to female body weight %</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Max. length of adult life (attained by 5% of adults minimum) (wk)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mortality between egg and adult (mean %.wk⁻¹)</td>
<td></td>
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</tr>
<tr>
<td>Adult mortality (mean %.wk⁻¹)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% adults surviving to breed twice</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. adult population density (m⁻²)</td>
<td>12,630</td>
<td>1,000</td>
<td>45,400</td>
</tr>
<tr>
<td>Size (mm shell height) at first breeding</td>
<td></td>
<td></td>
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</table>

Fig. 4. Growth curves of H. neglecta in the field, derived from the 1991-92 cohorts: A, intertidal-marine population; B, lagoonal population. Week 1 = 1st week of 1991; week 53 = 1st week of 1992.
DISCUSSION

As in H. ulvae (Barnes, 1990), considerable annual and intra-annual variation in strength and longevity of individual cohorts appears to occur in H. neglecta (see also the data on the 1977 and 1978 cohorts in Siegismund, 1982), and annual differences in growth rates were also evident. The extent to which the field data presented here for 1991 and 1992 are "typical" is therefore questionable, as it must be in all such short-term field studies; nevertheless useful comparisons including between habitat types are still possible.

In the laboratory, H. neglecta can survive for up to 3 years (Hylleberg, 1986), although in the field survival is clearly considerably less: average life expectancy of a 2 mm mudsnail [itself some 6-10 weeks (Dunwich) or 5.2 months (Lostrouc'h) old] was only a further 11-16 weeks. Growth rates in Suffolk and Finistère are equivalent to those recorded for this and other similar small hydrobiids elsewhere: a maximum juvenile growth rate of some 0.2 mm per week (Siegismund, 1982; Mandracchia & Ruber, 1990). The Dunwich (and Shingle Street) individuals, however, may attain a larger size than has otherwise been recorded (Siegismund, 1982; Hylleberg, 1986) in part by virtue of their longer life but also because growth occurs over a longer period and, in the spring cohort, at the expense of egg production. Thus Siegismund (1982) records that in Denmark re-
Different populations of *H. neglecta*

Hitherto, information on population dynamics and reproduction in *H. neglecta* has been available only from Danish waters and the present data from England and France show that marked regional differences in its reproductive strategy occur. On the east coast of Jutland, Denmark, *H. neglecta* displays a single annual period of reproduction peaking in late May and June (Lassen & Clark, 1979) that must be contributed solely by the overwintered mudsnails since they are the only cohort present at the time (Siegismund, 1982). Each breeding female produces 290 eggs on average during some 13 weeks of expected reproductive life, as estimated from data in Lassen (1979), Lassen & Clark (1979) and Siegismund (1982). In contrast, in Suffolk there are two periods of egg production each year, in April/May and in late August/September, and each of the two annual cohorts resulting can potentially breed twice. Average lifetime reproductive output of the overwintering and non-overwintering Suffolk cohorts were 4-5 eggs (over 13 weeks) and 14 eggs (over 10 weeks), respectively. The occurrence of a cohort of *H. neglecta* that does not overwinter before breeding is known only from the Suffolk populations described in this paper (although Muus, 1967, does briefly report that animals taken from Kysing Fjord, Denmark, in late August and late October produced eggs in the laboratory "a few days after capture"). It is therefore particularly notable that this atypical Suffolk cohort is also the one that is there numerically dominant and responsible for most (83.5%) of the annual egg production.

Somewhat surprisingly considering its latitudinal position and the role of low temperature in curtailing reproduction (Lassen, 1979), the French population conforms to the pattern of the Danish population, rather than to the Suffolk one, with a single peak of reproduction contributed solely by overwintered pre-reproductive mudsnails, the single annual cohort producing 11 eggs in an expected 11 weeks of reproductive life. It may be significant here that *H. neglecta* appears to be essentially a northern species (although it has a low tolerance to freezing and is frequently severely reduced or rendered locally extinct by Danish winters; Hylleberg, 1986; Hylleberg & Siegismund, 1987), and that Lassen & Clark (1979) have shown that the duration of the breeding season in Danish material decreases as temperature increases under experimental regimes; at Lostrouc'h, the species is both at the southern limit of its known range and in an atypical habitat—this may be reflected in the unusual sex ratio there. Since it is particularly sensitive to high temperatures under conditions of low salinity (Lassen & Hylleberg Kristensen, 1978), it is prob-
ably also significant that at this relatively low latitude it occurs in full strength sea water.

Comparing the corresponding cohorts (those that overwinter before breeding), the lagoonal and intertidal populations had identical reproductive investments, in marked contrast to that previously shown in *H. ulvae* (Barnes, 1990). This clearly parallels the close similarity of expected adult life span at Dunwich and Lostrous’ch. Other features of the breeding and general biology of the *H. neglecta* populations do not so easily accord with postulated relationships between reproductive investment and expectation of adult survival. The short-lived summer lagoonal cohort did produce eggs at a faster rate than the longer-lived spring cohort, for example, but the few eggs of the latter and the more plentiful eggs of the former would appear to equate more with the differential adult densities. The unusual strategy of a cohort of *H. neglecta* that breeds before overwintering clearly has a pay-off in terms of increased survival through to adulthood, but at the cost of a reduced production of eggs per individual adult, relative to the typical summer cohort. Since, however, the adult survival rates are such that individuals of each cohort have an average expectation of surviving through only a single breeding period, it follows that in practice one cohort ought solely to be the direct descendent of the previous one, and the high survival/few eggs versus poor survival/more eggs system simply alternate through the generations. In fact, however, such is the numerical dominance of the spring cohort that the small percentage of those mudsnails that do survive to breed twice nevertheless comprise significant numbers of individuals and they account for half the spring egg production. The percentage of the summer cohort adults that survive to breed twice is the same as that of the spring cohort, but numbers of individuals are very small (some 100/g/m$^2$). The explanation of these contrasting lagoonal cohorts is presumably environmental rather than evolutionary, although shortage of resources for the spring cohort under conditions of high population density would seem unlikely to be responsible for the low output of eggs since mudsnail growth rates were then high, and higher than of the low-density summer-cohort individuals that devoted their resources to egg production.

Various authors (e.g. Hylleberg, 1986) have assumed, on the basis of Lassen’s (1979) estimates, that *H. neglecta* is an $r$-selected, fugitive species that can maintain its presence in an area only because of its especially high reproductive rate. The data presented here indicate that in several areas its rarity may be more a consequence of a low rate of reproduction, and its failure to persist in certain localities (Barnes, 1991 b) a consequence of recruitment problems.

**H. neglecta versus other Hydrobia species**

Adult mortality in *H. neglecta* was at a much higher rate (2-6 times) than that reported earlier for *H. ulvae* (Barnes, 1990). This is not unreasonable in that *H. neglecta* has generally been considered to be a small, short-lived, semelparous species in comparison to the larger, potentially iteroparous *H. ulvae*: some 14% of lagoonal *H. neglecta* may survive through two breeding seasons but nevertheless in the laboratory mortality was very high amongst the overwintered spring-cohort Dunwich adults, then one year old, even in the absence of predators (although not of nemertines that are present in the coastal sea but absent from lagoons, so that its main predators may be the infaunal polychaetes and nemertines that are equally represented in both the habitat types.

Lassen (1979) estimated the annual reproductive effort of Danish *H. neglecta* to be more than twice that of local *H. ulvae*. That of *H. ulvae* is itself variable dependent on habitat (Barnes, 1990) but comparing like with like, expected reproductive effort (estimated as AFDW eggs + AFDW eggs plus growth increment) of lagoonal *H. neglecta* is 16 or 89% that of lagoonal *H. ulvae* (both from East Anglia, U.K.), dependent on cohort, and of intertidal marine *H. neglecta* is 71% that of *H. ulvae* from the same habitat type (a Finistère vs East Anglia comparison). That in this study *H. neglecta* should apparently invest less in reproduction than *H. ulvae* is in part a reflection of a smaller annual output of eggs than in Denmark. Lassen (1979) estimated a mean total of 290 eggs per female per year whereas annual output was here 14 (Finistère) to 24-29 (Suffolk). The extent to which this difference requires explanation is debatable, however, in that few adult mudsnails survive throughout the breeding season to produce their potential total, except at the Finistère site where the breeding season is very short. Nevertheless, the apparent decrease in output along the

**Suffolk Finistère gradient may again reflect the basic cool-water nature of *H. neglecta***.

The potential number of eggs that can be produced per annum by the Suffolk and Finistère *H. neglecta* also suggests that generally this species may be very much in the same league as the otherwise ecologically extremely similar lagoonal spe-
cies *H. ventrosa* (which can lay some 50 eggs in a year; Lassen, 1979). Hitherto, the two mudsnails have been regarded as being at opposite ends of the hydrobid reproductive-investment spectrum (Lassen, 1979), with an investment by *H. ventrosa* of only 17% that of *H. neglecta*. Although it is not yet possible to convert the published egg production data of *H. ventrosa* into those of lifetime reproductive investment, *H. ventrosa* and *H. neglecta*, which often occur sympatrically (Fenchel, 1975; Cherrill & James, 1985; Hylleberg, 1986), have similar life spans, body sizes and productivity (Siegismund, 1982), similar sized eggs and development patterns (Lassen, 1979; Fish & Fish, 1981) and now similar expected reproductive lifetimes (see above) and potential annual egg production, so that a similar investment in reproduction would not be unexpected.

In fact it would not be unexpected either that the essentially lagoonal species, including *H. neglecta*, should have a lesser investment in reproduction than the mainly intertidal marine and estuarine *H. ulvae* since lagoons are likely to be more stable than the intertidal zone and in them mortality rates of large individuals are generally lower and less variable than those of the young stages, favouring small reproductive effort and the production of few (large) young, as in *Littorina* (Hughes & Roberts, 1980; Hart & Begon 1982) and within *H. ulvae* (Barnes, 1990).

There remains the question of whether the contrasting breeding strategies of *H. neglecta* and *H. ulvae* influence juvenile mortality, as the equivalent ones do, for example, in the polychaete *Streblospio benedicti* Webster (Levin & Huggett, 1990). *H. neglecta* produces large young (hatching at some 300 µm; Fish & Fish, 1981) that develop directly, whereas *H. ulvae* is larviparous and its planktonic young hatch at some 150 µm (Fish & Fish 1977; Barnes 1988 a). Here any variation in juvenile mortality between the two mudsnails must relate solely to the difference between "egg mortality" (*H. neglecta*) and "egg + larval mortality" (*H. ulvae*), since in both species the young snails begin to lead an independent benthic existence at exactly the same size (Fish & Fish, 1981; Bachelet & Yacine-Kassab, 1987). Egg mortality in *H. neglecta* was not specifically assessed in this study, but whereas Barnes (1990) estimated minimum mortality between egg and adult in *H. ulvae* to be 99.85% (lagoonally) and 97% (intertidally), the comparable figures for *H. neglecta* were here 48.24% (lagoonally) and 87.2% (intertidally). This does at least indicate greater juvenile survival in *H. neglecta*, although the time intervals involved are not the same. The percentage mortalities stated for *H. ulvae* were over periods of some 39 weeks whereas those for *H. neglecta* were of 17 or 35 (dependent on cohort) and 52 weeks respectively, so that when the data are expressed as average mortality per week (the data being consistent with exponential declines), the figures for *H. ulvae* are 15.7% (lagoonally) and 8.8% (intertidally), and for *H. neglecta* are 3.4% (lagoonally) and 3.9% (intertidally). Hence rates of juvenile mortality of the directly-developing *H. neglecta* are only half — at most — those seen in *H. ulvae*, and indeed, in contrast to *H. ulvae*, juvenile mortality rates are less than those of the adult *H. neglecta* in both habitats and in both lagoonal cohorts.

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