Oecologia (Berl.) 24, 283–294 (1976)

Oecologia

Ecology of Hatching Size for Marine Snails

Tom M. Spight

Woodward-Clyde Consultants, 2 Embarcadero Center, Suite 700, San Francisco, California 94111, USA

Summary. Chances for survival increase as a snail grows, and the resulting size-specific survival curve dictates hatching size. Related species tend to hatch at the same size, reflecting similarities in ecological roles. Hatching size depends upon macrohabitat and microhabitat among the Muricidae. *Thais emarginata* hatches large enough to escape from a major predator (the hermit crab) of newly hatched *T. lamellosa*. However, *Thais* hatching sizes reflect a general trend for upper shore muricids to hatch larger than lower shore ones, rather than a response to predators. A given volume of yolk will yield the same volume of hatchlings (regardless of hatching type or number of hatchlings) for all prosobranchs, including those whose embryos feed on nurse eggs. Therefore, no hatchlings are inflated more than others to make them less attractive to predators.

A. Introduction

Some prosobranch gastropods hatch as small as 80 μm (*Caledoniella montrouzieri;* Amio, 1963), while others attain fully 35 mm before hatching (*Syrinx aruanus;* Murray, 1964). Many of the smaller hatchlings are planktonic; however, individuals as small as 160 μm may metamorphose prior to hatching (*Cingulopsis fulgida;* Lebour, 1936). The objective of the present paper is to determine why prosobranch snails, and particularly snails that metamorphose before hatching, reach so many different sizes before hatching.

A parent can make vast numbers of small offspring or a few larger ones. If fecundity is adjusted to environmental stress level or other factors, then hatching size will be determined by fecundity. However, small hatchings are less likely to survive than larger ones (Thorson, 1950). If chances for survival increase with size, then there will be one size (the "optimum") at which the largest number of offspring will survive through the immediate post-hatching period (Smith and Fretwell, 1974), and hatching size will be determined by the survival characteristics of the hatchling.

If a hatchling's size depends on its survival characteristics, then (1) hatching size should depend upon habitat (snails will run more risks in harsher environments); (2) related species should tend to have similar hatching sizes (they will have similar physiological tolerances, diets, and predators), and (3) parents may attain both high fecundity and large hatching size by decreasing tissue density (analogous to the postecdysis expansion of a typical arthropod), or increasing apparent size (for instance, many adults add spines to discourage predators; Carter, 1967; Spight and Lyons, 1974).

To evaluate these hypotheses, I have examined available data on hatching sizes and habitats, and have evaluated survival characteristics for the rocky shore snails, *Thais lamellosa* and *T. emarginata* (Muricidae). Hatching sizes for most groups were obtained from Amio (1963) and Fioroni (1966), but an attempt has been made to locate all data for members of the family Muricidae.

B. Methods

1. Size-Selection Experiment

To determine how large snails must be to avoid being eaten by hermit crabs, I offered snails of several sizes to 4 *Pagurus granosimanus*, 2 *P. beringanus*, and 3 *P. hirsutiusculus*. *P. beringanus* and *P. granosimanus* occupied *Thais* shells 20–35 mm long while *P. hirsutiusculus* occupied *Littorina* and *Lirularia* shells only 4–9 mm long. The 3 small *P. hirsutiusculus* were kept together in a culture dish; each of the other crabs had a dish to itself. Several *T. lamellosa* hatchlings (1.2 mm), larger *T. lamellosa* (1.6–2.0 mm), *T. emarginata* veligers (0.5–1.2 mm; late, yolky, non-swimming veligers removed from capsules), and one *T. emarginata* hatchling (1.6 mm) were placed in each dish. All *T. emarginata* hatchlings and larger *T. lamellosa* had thicker shells than did *T. lamellosa* hatchlings or veligers.

Crabs and snails were left together overnight to observe size selection. One *Pagurus granosimanus* molted shortly after being isolated and can serve as a control. In its bowl, only 2 of 9 *Thais lamellosa* were killed, and all 3 *T. emarginata* veligers survived intact. Therefore, snail deaths can be attributed to the crabs rather than to unfavorable physical conditions.

2. Volume Estimations

Volumes were estimated using egg diameters and hatching shell lengths (Tables 1–2 and Table 39 of Fioroni, 1966; except the hatching size of *Volutopsis norwegica* is 20 mm, as given by Thorson, 1940b) as diameters of spheres. Since measured values are usually maximum dimensions, calculated volumes will overestimate actual volumes. Many gastropod eggs are off-round (for example, a *Thais emarginata* egg is 210 × 180 μm). Egg volumes are not greatly overestimated by using maximum dimensions. Hatchling volumes are more greatly overestimated because shell width is only about 60% to 80% of shell length (Table 14 of Amio, 1963). Therefore, the hatchling volumes used here must be regarded as "indices" rather than true volumes. If shell length is proportional to other shell dimensions, then estimated volumes will be proportional to true volumes by some constant. The "volume indices" calculated here can be used to compare taxa and to estimate missing egg or hatching sizes, even though the absolute volume change during development may be greatly overestimated.

C. Results

1. Size and Survival

A large hatchling will survive more environmental stresses than will a small one of the same type because the large hatchling (1) tolerates physical stresses

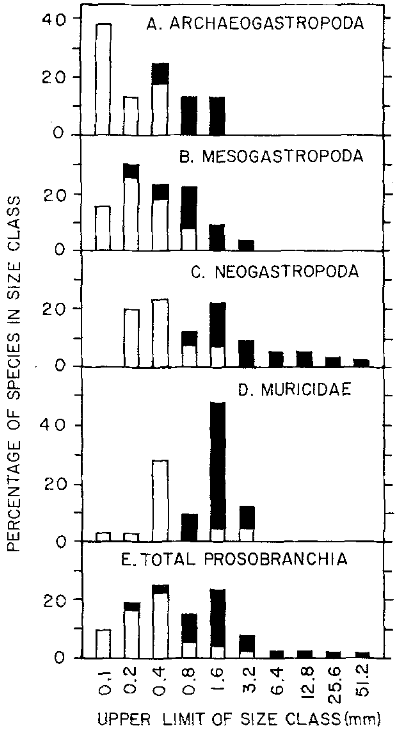

Fig. 1A–E. Sizes of newly hatched prosobranch gastropods (shell length, mm). Clear bars, swimming forms; dark bars, metamorphosed forms. **A** Archaeogastropoda, 16 species. **B** Mesogastropoda, 66 species. **C** Neogastropoda other than Muricidae, 56 species. **D** Muricidae, 44 species. **E** Total Prosobranchia, 182 species. Data from Fioroni (1966, 97 species, world-wide), Amio (1963, 50 species, Japanese) and Tables 1 and 2

such as dehydration more readily; (2) is susceptible to fewer predators (as a snail grows, progressively fewer predators will be able to eat it); (3) can withstand starvation longer (large and small snails should have equally large food reserves relative to their body masses; since large snails respire more slowly per gram of body weight, their food reserves will last longer); (4) can travel further to find food or shelter (for organisms travelling equal numbers of body lengths per unit time, the larger will cover more ground than the smaller one); and (5) has a larger food supply (large prey are taken in addition to the smaller prey captured by small predators; e.g., Wilson, 1974).

Survival rates increase rapidly as *Thais lamellosa* grows. A newly hatched *T. lamellosa* has a 1–2% chance to survive its first 3 months. A snail reaching 3 months has a 35% chance to reach age 1, and older snails have a 40–60% chance to survive through subsequent years (Spight, 1975). With this rapid increase in survival rates, a 2 mm snail should have much better prospects than a newly hatched 1 mm snail.

Hermit crabs are among the many predators that threaten newly hatched snails. These abundant crabs move readily throughout the shore and often comb through *Thais lamellosa* capsule masses to obtain hatching snails. Large shells are too thick for hermit crabs to crack (algae and detritus scraped from rock surfaces are the most frequent foods of these crabs; Roberts, 1968; Greenwood, 1972; Caine, 1975). Therefore, a small snail can lower its risk of capture by growing rapidly.

In the laboratory experiment, hermit crabs selected small snails with delicate shells. Small, thin-shelled *T. emarginata* veligers could neither crawl nor swim and none of 27 survived. Half (24 of 50) of the thin-shelled *T. lamellosa* hatchlings, 3 of 4 newly hatched *T. emarginata* and 8 of 11 older *T. lamellosa* survived. The crabs did not discriminate between species among either thin or thick-shelled snails and consumed *Thais emarginata* veligers readily. Larger snails must have escaped more often because crabs could not crack their shells.

A snail should evade hermit crabs after reaching 1.4 mm. A 1 mm *T. lamellosa* could reach 1.4 mm in a week if it grew as rapidly as 10 mm snails do (Spight, 1972). Many *T. emarginata* are 1.6 mm when they hatch, and are not susceptible to crabs although these predators kill many, if not most, young *T. lamellosa.*

Few hatchlings starve to death. Many newly hatched *Thais lamellosa* were kept without food for a month, and, other than those broken while handling the culture dishes, none died. Physical stresses and predation probably threaten a newly hatched snail more than starvation does.

A hatchling will always find it advantageous to be larger than its fellows. If hatching size increased from 1.0–1.6 mm, many more *T. lamellosa* would survive through their first year. Large size is least advantageous when mortality rates are the same for all size classes. However, the advantage is still positive; a small hatchling must still reach the larger sizes and may die before succeeding. Small size can be a disadvantage; the snail can be too small to avoid stresses, or catch prey, or, as the *Thais* data show, escape a predator.

2. *Size and Taxon*

Hatching sizes differ from one prosobranch order to another. The average mesogastropod hatches larger than most archaeogastropods and smaller than most neogastropods (Fig. 1). Nearly 40% of the archeogastropods hatch smaller than 155 μm, while only 2% of the neogastropods do, and all hatchlings larger than 3.2 mm are neogastropods. This trend holds for both planktonic and benthic hatchlings (Fig. 1); neogastropod veligers are about the same size as mesogastropod conchs.

Newly hatched Muricidae tend to be small relative to other Neogastropoda (Tables 1 and 2). The smallest neogastropod hatchlings are muricids (*Thais floridana,* 130 μm) while no muricid larger than 2.5 mm has been reported. Many neogastropods hatch larger than 7 mm, shell length (Table 3). All of these belong to three families: Buccinidae, Volutidae, and Melongenidae.

Muricids of some genera hatch larger than those of other genera. Among metamorphosed hatchlings, the average *Murex* (1.0–2.5 mm) is larger than the average *Thais* (0.7–1.3 mm) or *Acanthina* (0.6–0.8 mm) (Tables 1 and 2). The smallest veligers are all Thaidids (Table 2).

3. *Size and Environment*

Hatchlings of different species will often have quite different chances for survival when they are the same size. The risks facing a hatchling will reflect the kind

Table 1. Muricidae: sizes of eggs and newly hatched snails for species whose embryos consume nurse eggs during the developmental period. Data for *Thais emarginata* and *Acanthina spirata* are typical measurements of greatest egg diameter, for eggs from Friday Harbor, Washington, and Tomales Bay, California

Species	Egg diameter (µm)	Shell length at hatching (mm)	Nurse eggs per embryo[a]	Source
Embryos hatch as veligers:				
Murex incarnatus	180–200	1.8–1.9 × 1.1–1.2	49.2	Gohar and Eisawy (1967)
Murex virgineus	200–217	0.54–1.83 (mostly 1.18–1.75)	29.1	Natarajan (1957)
Murex ramosus	243–250	1.6–1.8 × 1–1.1	16.1	Gohar and Eisawy (1967)
Murex trapa	267	1.00–1.27	9.2	Natarajan (1957)
Embryos hatch as crawling snails:				
Thais lapillus	187	1.0	16.1[b]	Pelseneer (1911)
Murex quadrifrons	200	1.5–1.7	91.4	Knudsen (1950)
Murex senegalensis	200	2	35.0	Knudsen (1950)
Ocenebra japonica[c]	170[d]	1.76	481.2	Chapman and Banner (1949)
Ocenebra japonica	200	1.4–1.6	68.2	Amio (1963)
Thais emarginata[c]	180	>1.15	30.2	LeBœuf (1971)
Thais emarginata	210	1.19	30.2[e]	Spight (1976)
Ocenebra sp.	225–250	0.775–2.025 (most 1.0–1.5)	19.5	Fioroni (1966)
Bedeva hanleyi	250	0.90	3.0	Anderson (1967)
Acanthina spirata	275	0.67	1.7	Spight (1976)
Murex brandaris	240–330	0.660–1.840 ($\bar{X}=0.976$)	23.0	Fioroni (1966)
Murex trunculus	240–330	–	23.0	Fioroni (1966)
Ceratostoma burnetti	300 × 250	–	–	Amio (1963)
Thais calcar	300	>1.0	9.0	Gallardo (1973)
Murex torrefactus	480–520	1.8–2.0	5.9	Cernohorsky (1965)
Thais dubia	–	1.32	–	Bokenham and Neugebauer (1938)
Thais hippocastaneum	–	>0.7	27.8	Thorson (1940a)
Acanthina lapilloides	–	0.8	–	Hewatt (1934)

[a] (Total eggs – fertile eggs)/(fertile eggs)
[b] Fioroni (1966)
[c] Data not used
[d] Given as 1.7 mm
[e] Le Bœuf (1971)

of food it is searching for, the kind of predators likely to feed on it, and the kind of hiding places it requires to weather adverse conditions. A snail searching for barnacles and mussels on a rocky shore must tolerate exposure to air once or twice a day or, particularly when small, must find refuges for low-tide periods. Another snail of the same size that scrapes algae from submerged surfaces or scavenges on a mud bottom will have substantially different requirements and will face a very different suite of threats to its existence. If chances for survival are as different as in these examples, and if the species

Table 2. Muricidae: sizes of eggs and newly hatched snails for species whose embryos develop without nurse eggs. Original data are typical measurements of greatest egg diameter and hatching shell length for eggs from Friday Harbor, Washington (except *Thais lima*, from Amchitka Island, Alaska)

Species	Egg diameter (μm)	Shell length at hatching (mm)	Source
Hatch as young snails:			
Favartia cellulosa[a]	160	–	Lebour (1945)
Favartia cellulosa	–	1 × 0.66–1.25 × 1	Raeihle (1966)
Urosalpinx cinerea	300–400	1–2[b]	Hancock (1959)
Urosalpinx cinerea	240[b]	–	Lebour (1938)
Urosalpinx cinerea	–	0.8–1.0	Federighi (1931)
Eupleura caudata	340–390 ($\bar{X}=360$)	0.7–1.1 ($\bar{X}=0.9$)	MacKenzie (1961)
Trophon truncatus	400	1.2	Thorson (1946)
Ocenebra aciculata	450 × 390	–	Franc (1940)
Trophon muricatus	480	> 0.64	Lebour (1936)
Thais lamellosa	590	1.0	original
Thais canaliculata	620	1.3	original
Torvamurex territus	675	1.55 × 1.2	Murray and Goldsmith (1963)
Ceratostoma foliatum	720	–	original
Thais lima	920	1.3	original
Ocenebra erinacea	–	0.96	Lebour (1938)
Murex angularis[c]	–	2.5	Knudsen (1950)
Trophon clathratus	–	1.0	Thorson (1940b)
Hatch as veligers:			
Thais rustica	80	–	Lebour (1945)
Thais floridana	107	0.130	D'Asaro (1966)
Thais floridana	–	0.16	Lewis (1960)
Thais floridana	96	–	Fioroni (1966)
Acanthina angelica[a]	119	–	Wolfson (1970)
Thais coronata	125	–	Knudsen (1950)
Acanthina lugubris[a]	157	–	Wolfson (1970)
Murex turbinatus	150–170	–	Thorson (1940a)
Concholepas concholepas	158–169	0.260	Gallardo (1973)
Jopas francolinum	162–180	0.3	Gohar and Eisawy (1967)
Bedevina birileffi	190	0.30–0.32	Amio (1963)
Thais clavigera	190	0.30–0.32	Amio (1963)
Thais bronni	200	0.32–0.34	Amio (1963)
Thais carinifera	200–220	0.4	Thorson (1940a)
Morula marginalba	220	–	Anderson (1967)
Purpura patula	240	0.4	Lewis (1960)
Chicoreus asianus	250	–	Amio (1963)
Rapana thomasiana	260	0.41 × 0.29	Amio (1963)
Rapana bulbosa	280–320	0.42	Thorson (1940a)
Dicathais aegrota	–	0.24	Phillips (1969)
Thais deltoidea	–	0.36	Lewis (1960)
Thais bufo	–	0.283–0.367 (mostly 0.334–0.367)	Natarajan (1957)
Thais tissoti	–	0.317	Natarajan (1957)

[a] Hatching type not given by author

[b] Data not used in calculations

[c] Species may utilize nurse eggs

Table 3. Prosobranch gastropods with hatching sizes in excess of 5 mm, shell length

Species	Shell length (mm)	Location	Author
Melongenidae:			
Hemifusus ternatanus[a]	7–9	Japan	Amio (1963)
Syrinx aruanus	35	Australia	Murray (1964)
Volutidae:			
Melo melo	30	Japan	Amio (1963)
Cymbiola vespertilio	32	Malaya	Berry (1968)
Buccinidae:			
Sipho islandicus[a]	3.5–8.5	Arctic	Thorson (1935)
Colus stimpsoni[a]	5–8	North Atlantic	West (1973)
Troschelia berniciensis	8.75	Denmark	Thorson (1940b)
Neptunea cumingi	9	Japan	Amio (1963)
Neptunea antiqua[a]	6–12	Denmark	Pearce and Thorson (1967)
Beringius eyerdami	9–12	W. Canada	Cowan (1964)
Chrysodomus turtoni[a]	5–14	North Sea	Thorson (1940b)
Chrysodomus ossianus[a]	10–20	North Atlantic	Thorson (1940b)
Volutopsis norwegica	14–20	North Atlantic	Thorson (1940b)
Pyrulofusus deformis	17–18	Alaska	Gonor (1964)
Pyrulofusus harpa	19.5	Alaska	Cowan (1965)
Neptunea intersculpta[a]	25	Japan	Amio (1963)

[a] Nurse eggs observed

have similar stress tolerances, then hatching sizes should differ (see Smith and Fretwell, 1974).

Related species tend to have similar stress tolerances. When living in the same place they will face similar threats and therefore should have similar hatching sizes. Hatching size differences should correspond to habitat or microhabitat differences.

Muricids do hatch larger in some habitats than others. Snails living on coral reef flats (*Murex incarnatus, M. ramosus, M. torrefactus,* and *Favartia cellulosa;* 1.1–1.9 mm) or in subtidal habitats (*M. quadrifrons, M. angularis, M. senegalensis, Trophon clathratus, T. muricatus,* and *Torvamurex territus:* 0.6–2.5 mm) generally hatch larger than those living on oyster reefs (*U. cinerea, O. japonica, E. caudata:* 0.9–1.5 mm) or on rocky intertidal surfaces (*Thais lapillus, T. dubia, T. hippocastaneum, T. lima, T. lamellosa, T. emarginata, T. canaliculata, Bedeva hanleyi, Acanthina spirata, A. lapilloides,* and *Ocenebra erinacea;* 0.6–1.3 mm, Tables 1 and 2).

An exact hatching size cannot be predicted for some particular muricid when only its macrohabitat is known. Each macrohabitat contains a whole range of microhabitats, and muricids that live in different microhabitats run somewhat different risks. Sufficient data are available to examine one microhabitat feature: shore level.

Several muricids are typically found at higher shore levels and these often coexist with other species typically found at lower shore levels. The high shore is exposed longer and more frequently to air than the lower shore, and therefore

Table 4. Relationships between egg size (X, mm × 100) and hatching shell length (Y, mm × 100) for various prosobranch taxa. Data of Fioroni (1966), Amino (1963), and Table 2. Neogastropoda, "Other", includes Buccinaeea, Volutacea, and Mitracea

Taxon	Relationship	N	r^2	MSE	$F_{1,n-2}$	$\bar{X}$
Archaeogastropoda	$Y=1.8150\ X-3.9182$	11	0.739	13.6184	25.5522	15.1818
Mesogastropoda	$Y=2.1777\ X-5.2662$	36	0.825	69.8802	159.8174	16.3472
Neogastropoda						
Muricidae	$Y=1.8021\ X-3.5043$	18	0.767	503.7323	52.7729	35.6667
Conacea	$Y=2.0861\ X-5.7606$	15	0.907	108.6332	126.9793	25.8667
Other	$Y=1.6514\ X+6.1762$	12	0.743	288.8136	28.8613	29.6667
Total	$Y=1.8419\ X+1.1589$	45	0.803	295.3199	174.8331	30.8000
All species	$Y=1.9085\ X-1.4128$	92	0.841	173.6537	475.6141	23.2772

Analysis of covariance:

Among Neogastropoda: MSE = 316.9252 $F_{2,39}=0.4918$
Among Prosobranchia: MSE = 176.7122 $F_{2,86}=0.6523$

N = number of species; MSE = mean square error

high shore species face a greater risk of death by dehydration or overheating. Low shore snails are submerged for long periods and during immersion are exposed to predators from the intertidal (such as hermit crabs) and from the adjacent subtidal. Hatchlings probably have substantially different chances to survive at the various tide levels, and I therefore expected to find a correlation between shore level and hatching size.

Tide levels do correspond to hatching sizes for the muricids. Muricidae that dwell chiefly at upper shore levels (*Thais emarginata, T. lima, T. canaliculata*) all hatch at about 1.3 mm shell length, while ones that dwell lower (and usually the adjacent subtidal as well), hatch at about 1.0 mm (*Urosalpinx cinerea, Eupleura caudata, Ocenebra erinacea, Thais lapillus, T. lamellosa;* Tables 1 and 2) with the exception of *Acanthina spirata* (0.67 mm) found on the shore below *T. emarginata* in Tomales Bay.

If hatching size is adjusted to the regime of stresses facing a species, then size should vary from locale to locale as the regime of stresses changes. Only a few examples of variations in hatching size have been documented. The opisthobranch *Brachystomia rissoides* hatches smaller in more saline waters, and clutches of small hatchlings contain many more snails (Rasmussen, 1951). Newly hatched *T. emarginata* are larger at Friday Harbor, Washington (mean 1.39 mm) than at Tomales Bay, California (mean 1.19 mm, Spight, 1976; the latter size is used in Table 1 with LeBoeuf's (1971) estimate of the number of nurse eggs per embryo for Bodega Bay snails).

4. *Investment per Hatchling*

Fioroni (1966) and Amio (1963) have both shown, with non-overlapping sets of data, that shell-length at hatching is closely related to egg diameter for

Table 5. Relationships between logarithms of egg volume in mm^3 (X) and logarithms of hatching volume (Y, in mm^3) for various Muricidae (Tables 1 and 2) and for other Prosobranchia with nurse eggs (Table 39 of Fioroni, 1966). Other Muricidae are species that hatch as snails and do not use nurse eggs

Group	Relationship	N	r^2	MSE	$F_{1,n-2}$	$\bar{X}$
Muricidae:						
With nurse eggs	$Y=0.7751\ X+0.7433$	14	0.54	0.0887	13.9355	−0.9011
With veligers	$Y=1.1487\ X+0.9646$	10	0.89	0.0245	67.4251	−2.4039
Other	$Y=0.4243\ X+0.2998$	8	0.26	0.1154	2.1367	−1.1287
Total	$Y=1.1197\ Y+1.0119$	32	0.88	0.1022	230.8196	−1.4276
Other Prosobranchia:						
With nurse eggs	$Y=1.2172\ X+0.7590$	10	0.96	0.0975	217.6178	0.0436

Analysis of covariance:

Among Muricidae: MSE $=0.0751$ $F_{2,26}=2.2867$ $P>0.10$

Among species with nurse eggs: MSE $=0.0922$ $F_{1,20}=3.8140$ $0.10>P>0.05$

N = number of species; MSE = mean square error

a variety of species. Fioroni (1966) plotted data for 29 species. Amio (1963) found hatching length to be on average 1.733 times egg diameter for 40 species. Amio excluded species with egg sizes over 200 µm (to eliminate nurse-egg feeders) and included opisthobranchs in his calculations. Neither author determined the significance of his overall relationship or of possible differences among prosobranch taxa.

To estimate an overall relationship (Table 4), I combined all of the data from these sources (again excluding nurse-egg feeders), and added the available data for the Muricidae (Tables 1 and 2). Variations in egg diameter account for 84% of the variations in hatching length among these 92 species ($r^2=0.84$), and the overall slope (1.908) is similar to that obtained by Amio. Relationships for the major taxa differ slightly, but none of the differences is significant (Table 4, Analysis of Covariance).

No consistent relationship between egg diameter and hatching size can be expected among species that utilize nurse eggs because some embryos consume only a few eggs, and others thousands (Table 39 of Fioroni, 1966). A size relationship for nurse egg feeders will, therefore, require another unit for the amount of egg material invested in each hatchling. Embryos feeding on a given volume of yolk should attain the same size whether the yolk is in the form of nurse eggs or is contained in the embryo's own egg, and therefore yolk volume is an appropriate unit.

To obtain a size relationship, logarithms of hatching volumes for the Muricidae of Table 1 and for nurse-egg feeders listed by Fioroni (1966) were regressed on logarithms of egg volumes. The data for the Muricidae span a fairly small range, and the egg volumes account for only 54% of the variation in hatching volumes (Table 5). Other prosobranchs that feed on nurse eggs form a much larger size range and the calculated relationship is correspondingly less variable (Table 5). The two relationships are marginally different; on average, muricid hatchlings are slightly larger than other prosobranch hatchlings with the same initial egg volume.

Egg volumes were also calculated for Muricidae without nurse eggs. Over a range of 0.0062 mm^3 (*Thais floridana*) to 0.436 mm^3 (*Murex quadrifrons*), variations in egg volume per embryo account for 88% of the variations in hatchling volume (Table 5). Differences among muricid groups are not significant (Table 5). Therefore, a volume of yolk will yield the same volume of hatchlings, regardless of hatching type, embryonic feeding mechanism, or number of hatchlings.

D. Discussion

A hatchling's chances for survival usually increase rapidly as it grows. When a species produces many small offspring, most die in the immediate post-hatching and/or post-settling period, and mortality rates for older individuals are usually much lower. Such a size-specific mortality curve has been outlined roughly for *Thais lamellosa,* and numerous size-specific mortality factors have been identified. It is always an advantage to an individual to hatch as large as possible.

The survival characteristics of offspring will limit fecundity options of parents. If chances for survival change at the same rate as cost per embryo for the parent, a given volume of yolk will yield the same number of offspring after the high-mortality, immediate posthatching period whether the parent initially produces many or few eggs. In this case, a parent can "choose" to emphasize number of offspring, individual quality, or some intermediate combination. However, other size-specific survival curves will have an optimum hatching size. Parents producing offspring of optimum size will have more surviving offspring at the end of the post-hatching period than will parents that produce larger or smaller offspring (Smith and Fretwell, 1974). The female with the most surviving offspring will be the most fit, and therefore fecundity will be determined by the size-specific survival characteristics of the offspring.

Fecundity can be changed to allow a variety of strategies if the survival characteristics of the hatchling change readily. However, survival characteristics depend on the ecological relationships of hatchlings. Major changes in hatchling ecology are likely to be associated with major structural modifications, and these would be in turn recognized as taxonomic-level changes. Available hatching sizes are consistent with this proposition (Tables 1 and 2). Hatchlings of one genus are generally about the same size (within either the planktonic or benthic types). Size ranges are largest in genera which have large hatchlings (Table 3), and no hatchlings from these genera are small. Type of hatchling (swimming or crawling) is a major strategy option open to most species. However, within each hatching type, hatching size is defined by the ecological role of the species.

The relative importances of environmental stresses facing hatchlings are known only generally. *Thais emarginata* hatches larger (1.4 mm) than *T. lamellosa* (1.0 mm), and as a result most *T. emarginata* escape from a major predator (the hermit crab). However, *T. lamellosa* hatches on the lower shore and should be exposed much more often to hermit crabs than *T. emarginata* will be on the upper shore. The actual risks from predation, dehydration, and other environmental stresses at the two shore levels have yet to be quantified sufficiently to explain why *T. lamellosa* does not hatch larger than it does.

Acknowledgements. This work was supported by NSF Grants 6518X to the University of Washington, GB 3386 to Friday Harbor Laboratories, and GA 25349 to R.T. Paine. Publication was supported by Woodward-Clyde Consultants.

References

Amio, M.: A comparative embryology of marine gastropods, with ecological emphasis. J. Shimonoseki College Fisheries **12**, 229–253 (1963)

Anderson, D.T.: Further observations on the life histories of littoral gastropods in New South Wales. Proc. Linn. Soc. New South Wales **90**, 242–251 (1967)

Berry, A.J.: A gastropod and its spawn. Malayan Nature J. **21**, 223–224 (1968)

Bokenham, N.A.H., Neugebauer, F.L.M.: The vertical distribution of certain intertidal marine gastropods in False Bay, with notes on the development of two of them. Ann. Natal Museum **9**, 113–137 (1938)

Caine, E.A.: Feeding and masticatory structures of selected anomura (Crustacea). J. exp. mar. Biol. Ecol. **18**, 277–301 (1975)

Carter, R.M.: The shell ornament of *Hysteroconcha* and *Hecuba* (Bivalvia): a test case for inferential functional morphology. Veliger **10**, 59–71 (1967)

Cernohorsky, W.O.: The radula, egg capsules and young of *Murex (Chicoreus) torrefactus* Sowerby (Mollusca: Gastropoda). Veliger **8**, 231–233 (1965)

Chapman, W.M., Banner, A.H.: Contributions to the life history of the Japanese oyster drill (*Tritonalia japonica*) with notes on the other enemies of the Olympia oyster (*Ostrea lurida*). Wash. Dept. Fish. Biol. Rept. **49A**, 167–200 (1949)

Cowan, I.M.: The egg capsule and young of *Beringius eyerdami* Smith (Neptuneidae) (Mollusca: Gastropoda). Veliger **7**, 43–44 (1964)

Cowan, I.M.: The egg capsule and young of the gastropod *Pyrulofusus harpa* (Mörch) (Neptuneidae). Veliger **8**, 1–2 (1965)

D'Asaro, C.N.: The egg capsules, embryogenesis and early organogenesis of a common oyster predator, *Thais haemastoma floridana* (Gastropoda: Prosobranchia). Bull. Mar. Sci. **16**, 884–914 (1966)

Federighi, H.: Studies on the oyster drill (*Urosalpinx cinerea*, Say). Bull. U.S. Bur. Fish. **47**, 85–115 (1931)

Fioroni, P.: Zur Morphologie und Embryogenese des Darmtraktes und der transitorischen Organe bei Prosobranchiern (Mollusca: Gastropoda). Rev. suisse Zool. **73**, 621–876 (1966)

Franc, A.: Recherches sur le développement d'*Ocenebra aciculata*, Lamarck (Mollusque gastéropode). Bull. Biol. Fr. Belg. **74**, 327–345 (1940)

Gallardo, C.: Desarrollo intracapsular de *Concholepas concholepas* (Brugière). Publ. Ocas. 16, Museo Nacional de Historia Natural, Santiago, Chile, pp. 1–16 (1973)

Gohar, H.A.F., Eisawy, A.M.: The egg-masses and development of five rachiglossan prosobranchs (from the Red Sea). Publ. Mar. Biol. Sta. Al-Ghardaqa, Egypt **14**, 216–266 (1967)

Gonor, J.J.: Egg capsules and young of the gastropod *Pyrulofusus deformis* (Neptuneidae) at Barrow, Alaska. Arctic **17**, 48–51 (1964)

Greenwood, J.G.: The mouthparts and feeding behavior of two species of hermit crabs. J. nat. Hist. **6**, 325–337 (1972)

Hancock, D.A.: The biology and control of the American Whelk tingle *Urosalpinx cinerea* (Say) on English oyster beds. Fishery Invest., Lond. (Ser. II) **22** (10), 1–66 (1959)

Hewatt, W.G.: Ecological studies on selected marine intertidal communities of Monterey Bay. Ph.D. Thesis, Stanford University (1934)

Knudsen, J.: Egg capsules and development of some marine prosobranchs from tropical West Africa. Atlantide Rep. **1**, 85–130 (1950)

LeBoeuf, R.: *Thais emarginata* (Deshayes): Description of the veliger and egg capsule. Veliger **14**, 205–211 (1971)

Lebour, M.V.: Notes on the eggs and larvae of some Plymouth prosobranchs. J. Mar. Biol. Assn. U.K. **20**, 547–566 (1936)

Lebour, M.V.: The eggs and larvae of the British prosobranchs. J. Mar. Biol. Assn. U.K. **22**, 105–166 (1938)

Lebour, M.V.: The eggs and larvae of some prosobranchs from Bermuda. Proc. Zool. Soc. Lond. **114**, 462–489 (1945)

Lewis, J.B.: The fauna of the rocky shores of Barbados, West Indies. Canad. J. Zool. **38**, 391–435 (1960)

MacKenzie, C.L., Jr.: Growth and reproduction of the oyster crill *Eupleura caudata* in the York River, Virginia. Ecology **42**, 317–338 (1961)

Murray, F.V.: The spawn of some Australian marine prosobranch molluscs. Australian Nat. Hist. December, pp. 405–408 (1964)

Murray, F.V., Goldsmith, M.H.: Some observations on the egg capsules and embryos of *Torvamurex territus* (Reeve, 1845). J. Malac. Soc. Austr. **7**, 21–25 (1963)

Natarajan, A.V.: Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. Proc. Indian Acad. Sci. **46** (3), 170–228 (1957)

Pearce, J.B., Thorson, G.: The feeding and reproductive biology of the red whelk, *Neptunea antiqua* (L.) (Gastropoda: Prosobranchia). Ophelia **4**, 277–314 (1967)

Pelseneer, P.: Recherches sur l'embryologie des Gastéropodes. Mém. Acad. Roy. Belg. Cl. Sci. Sér. **2**, 3, 1–163 (1911)

Phillips, B.F.: The population ecology of the whelk *Dicathais aegrota* in Western Australia. Aust. J. Mar. Freshw. Res. **20**, 225–265 (1969)

Raeihle, D.: An observation of captive *Murex cellulosus* Conrad. Ann. Rept. Amer. Malacol. Union **1966**, 28 (1966)

Rasmussen, E.: Faunistic and biological notes on marine invertebrates. II. The eggs and larvae of some Danish marine gastropods. Vidensk. Meddr dansk naturh. Foren. **113**, 201–249 (1951)

Roberts, M.H.: Functional morphology of mouth parts of the hermit crabs, *Pagurus longicarpus* and *Pagurus pollicaris*. Chesapeake Science **9**, 9–20 (1968)

Smith, C.C., Fretwell, S.D.: The optimal balance between size and number of offspring. Amer. Natur. **108**, 499–506 (1974)

Spight, T.M.: Patterns of change in adjacent populations of an intertidal snail, *Thais lamellosa*. Thesis, Univ. Washington (1972)

Spight, T.M.: On a snail's chances of becoming a year old. Oikos **26**, 9–14 (1975)

Spight, T.M.: Hatching size and the distribution of nurse eggs among prosobranch embryos. Biol. Bull. (Woods Hole) **150**, (1976)

Spight, T.M., Lyons, A.: Development and functions of the shell sculpture of the marine snail *Ceratostoma foliatum*. Mar. Biol. **24**, 77–83 (1974)

Thorson, G.: Studies on the egg-capsues and development of arctic marine prosobranchs. Medd. Grønland **100**, 1–71 (1935)

Thorson, G.: Studies on the egg masses and larval development of gastropods from the Iranian Gulf. Danish Sci. Invest. Iran **2**, 159–238 (1940a)

Thorson, G.: Notes on the egg-capsules of some north-Atlantic prosobranchs of the genus *Troschelia, Chrysodomus, Volutopsis, Sipho* and *Trophon*. Vidensk. Meddr dansk naturh. Foren. **104**, 251–265 (1940b)

Thorson, G.: Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the sound (Øresund). Meddr Komm. Danm. Fisk.-og Havunders. (Ser. Plankton) **4** (1), 1–529 (1946)

Thorson, G.: Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. **25**, 1–45 (1950)

West, D.L.: Notes on the development of *Colus stimpsoni* (Prosobranchia: Buccinidae). Nautilus **87**, 1–4 (1973)

Wilson, D.S.: Prey capture and competition in the ant lion. Biotropica **6**, 187–193 (1974)

Wolfson, F.H.: Spawning notes V. *Acanthina angelica* I. Oldroyd, 1918 and *Acanthina lugubris* (Sowerby, 1821). Veliger **12**, 375–377 (1970)

Received December 17, 1975