15 Temperature Sensitivity, Rate of Development, and Time to Maturity: Geographic Variation in Laboratory-Reared *Nucella* and a Cross-Phyletic Overview

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ABSTRACT Unlike most other physiological processes, the rate of development generally shows little evidence of temperature compensation—the tendency, for example, for physiological processes at the same temperature to proceed more rapidly in cold-adapted than warm-adapted organisms. As a consequence, a substantial fraction of the variation in rate of development can be explained on the basis of taxonomic affinity and temperature. These patterns suggest rather strong taxon-dependent constraints on the duration of the prehatching period. I report here that the rate of development in the laboratory of a rocky-shore thaidine gastropod, "northern" *Nucella emarginata*, lies very near that predicted from other muricacean gastropods. In spite of this close agreement, however, at temperatures less than 10°C, *N. emarginata* from southeast Alaska hatched in significantly less time (up to 15 percent less at 8°C) than snails from Barkley Sound, British Columbia. Over a rather narrow temperature range (8°–11°C), seasonal variation in laying frequency was more pronounced in Alaskan snails. On the other hand, rate of development (1/days to hatch) was less sensitive to temperature in Alaskan than British Columbian snails (Q_{10} values of 2.63 versus 4.66, respectively). These data thus provide evidence for intraspecific latitudinal temperature compensation in the average rate of development, as well as evidence for geographic variation in the temperature sensitivity of development rate. A review of the literature suggests that, in spite of considerable variation in reproductive characteristics, direct-developing muricacean gastropods not only develop more slowly than many other marine organisms but also exhibit a more precise relationship between temperature and rate of development. This slower rate of development, coupled with more precise temperature dependence, suggests that encapsulation during the entire prejuvenile period may impose significant constraints on the rate of development.

Introduction

Temperature has a profound impact on the rates of many physiological processes (Cossins and Bowler, 1987). In addition, many species exhibit the phenomenon of temperature compensation, where at a given temperature the rate of a physiological process in cold-adapted organisms is higher than that of warm-adapted ones. In contrast to most other physiological processes, however, rate of development appears to show little if any temperature compensation (Patel and Crisp, 1960; Emlet et al., 1987; Johnston, 1990; but see McLaren et al., 1969). So pervasive is the effect

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of temperature on development that, to a reasonable approximation, one can predict the development time of species of meso- and neogastropods simply by knowing their taxonomic affinities and their temperature of development (Spight, 1975).

Many marine invertebrates lay their eggs as gelatinous masses or enclosed in egg capsules attached to the substratum (Strathmann, 1987). Unlike solitary pelagic eggs, eggs in masses or in capsules experience limited rates of diffusion of metabolites, respiratory gases, and ions because of the medium by which they are surrounded and because of their proximity to other developing embryos (Strathmann and Strathmann, 1989). Encapsulation of embryos is particularly common among meso- and neogastropods (Strathmann, 1987), yet surprisingly little is known about its costs in terms of reduced fecundity or rate of development (Grahame and Branch, 1985; but see Perron, 1981b).

Species with limited gene flow should be more likely to exhibit geographic differentiation in response to different climatic regimes than species with greater dispersal potential. Prior studies on temperature compensation of development rate have examined species with moderate to high dispersal potential, including barnacles (Patel and Crisp, 1960), copepods (McLaren et al., 1969), echinoderms (Emlet et al., 1987), and fishes (Johnston, 1990). To assess the extent of latitudinal physiological adaptation of development rate in a species with limited dispersal capability, I examined data from the rocky-shore thaidine gastropod "northern" *Nucella emarginata* that were collected as part of a long-term study of the genetic basis of shell variation (Palmer, 1984a, 1985a,b). Successive generations of snails were reared in the laboratory for over ten years, and sea water temperature was recorded throughout this time. Because *N. emarginata* spawn throughout the year, and because ambient sea water temperature varied seasonally in the laboratory, the effect of temperature on rate of development and time to maturity could be assessed. In addition, because genetic studies were being conducted on snails from geographically widespread populations, I could test for temperature compensation in these traits. Finally, because snails were reared from laying to maturity in the laboratory, the prejuvenile period as a fraction of total time to maturity could be computed. To place these values in context, I compared development rate, the temperature sensitivity of development rate, and the prejuvenile period as a fraction of the total time to maturity, to published values for a wide variety of other organisms.

Methods

Taxonomic Concerns

The taxonomic status of "*Nucella emarginata*" (Deshayes, 1839) on the Pacific Coast of North America remains unsettled (Palmer et al., 1990). I have inspected Deshayes' syntypes, and they are clearly of the "southern" species. Hence the "northern" species, the focus of this chapter, requires a new name. Several varietal names are eligible (Dall, 1915), but shells alone are ambiguous and locality data are notoriously unreliable. More important, I have been unable to inspect one of Middendorf's specimens synonymized with *emarginata* by Dall (1915). Until these taxonomic problems can be resolved, I shall follow earlier recommendations (Palmer et al., 1990) and refer to the species studied here as the *northern* species of *N. emarginata*. For convenience, I have omitted *northern* from the frequent references to this species in the text, but in all instances I mean to refer only to the northern species, as the southern species is not found north of San Francisco Bay (Palmer et al., 1990).

Table 15.1. Approximate schedule for monitoring various aspects of reproduction and growth in laboratory-reared northern *Nucella emarginata*

Aspect of rearing procedure	Period of study		
	1982–84	1985–86	1987–92
Check for egg capsules produced by parents	1 week	2 weeks	3 weeks
Duration of capsules in mesh bags	80 days	70 days	70 days
Check cages for hatching and replenish small barnacles for hatchling snails	2 weeks	3 weeks	4 weeks
Size at which hatchlings were transferred to cages with larger mesh and larger barnacles	3–8 mm	3–10 mm	3–15 mm
Replenish barnacles for juvenile snails	3 weeks	4 weeks	6 weeks
Size at which male and female juveniles were isolated into separate cages	15–22 mm	15–22 mm	15–22 mm
Replenish barnacles for adult snails and check for production of capsules	3 weeks	4 weeks	6 weeks

Sources of Snails and Rearing Procedure

Snails were collected from several localities on the Pacific coast of North America, but extensive data were only available for two: (1) Torch Bay, southeast Alaska (58°19′41″ N, 136°47′56″ W), in July 1980 and July 1982, and (2) Barkley Sound, Vancouver Island, British Columbia (two sites: Wizard Island 48°51′30″ N, 125°09′33″ W; Cape Beale 48°47′05″ N, 125°12′54″ W), in August 1980 and July 1982. All snails from subsequent years were reared as successive generations from these initial collections.

Snails were reared following the general protocol outlined in Palmer (1985b). In brief, snails were sexed based on relative penis size, and single pairs of snails were placed in individual cages and provided with their preferred prey (Palmer, 1984b), the barnacle *Balanus glandula*, on small stones. Food was replenished and cages were monitored for egg-capsules at regular intervals (Table 15.1). Capsules were removed from the rock with fine forceps and placed in 3 cm × 3 cm plastic screen bags (2-mm mesh) with Velcro closures and suspended from fishing line in gently running sea water until shortly before hatching (Table 15.1). Before they began to hatch, capsules were transferred to freezer containers (10 × 10 × 15 cm) with 500-μm Nitex mesh sides that contained stones with small barnacles for food (*B. glandula* and *Chthamalus dalli*, 3–5-mm basal diam). After snails had begun to hatch, barnacles were replenished on a regular basis (Table 15.1). When juveniles reached an adequate size, they were transferred to larger freezer container cages with larger mesh and provided with larger barnacles on a regular basis (Table 15.1). Prior to maturity, male and female offspring were assigned to separate cages based on a visual inspection of relative penis size. Mature progeny were monitored for the production of egg capsules and provided with fresh barnacles at regular intervals (Table 15.1). To avoid introducing unwanted snails from the field, barnacle stones were collected only from quiet-water shores where *N. emarginata* were absent.

Cages and egg capsules were held continuously immersed in running sea water and under a natural photoperiod maintained by fluorescent lighting in the main aquarium room at the Bamfield Marine Station, British Columbia.

Sea Water Temperature

Sea water temperature varied seasonally and annually. All cages were held under ambient conditions in flow-through aquaria. Temperature was monitored periodically with a mercury thermometer (± 0.1°C) in the aquaria where the snails were held, usually every 2–4 days but sometimes less frequently. At least one temperature measurement was available for all but 14 of the 120 months of detailed records. Because temperature sometimes varied by up to 1°C over the course of each day and more so throughout the month, and because some months were sampled more intensively than others, the raw temperature data were rather noisy (Fig. 15.1). I attempted to remove the effects of short-term variability and the effects of gaps in the data by fitting a smooth curve via polynomial regression and moving averages. The final "best fit" to the regular seasonal variation was determined by eye. This best fit curve was then used to generate the expected daily temperature for each day of each month over the full 10 year period (Fig. 15.1). These best fit estimates of average temperature for a given day were probably accurate to within 0.1°C.

The effect of temperature on development time was determined by computing the average temperature over the roughly 3-month period from laying to hatching for each individual clutch based on the data from the best fit curve through the relevant time interval. Because snails spawned throughout the year (see Fig. 15.2), development time could be monitored over a natural range of temperature (8°–11°C).

Duration of Life History Stages

Although key life history events (laying, hatching, and maturity) were monitored on a regular basis, the uncertainty associated with each varied from inspection to inspection, and over the duration of the study (Table 15.1). The estimated time and the associated uncertainty of each event were determined in the same fashion for each clutch (Fig. 15.3). For example, laying date was estimated as the average of the date capsules were first observed and the previous date on which that cage had been checked. The maximum possible error in the estimated laying date for that clutch was thus the number of days between those two dates (e.g., $E1$, Fig. 15.3). The actual uncertainty associated with a given laying date would, of course, be half the value of $E1$ in days. Dates of hatching (first hatchlings observed in a cage) and maturity (first capsules produced by any mature offspring, whether in holding cages or as individual snails used in subsequent crosses) and their uncertainties were estimated in the same manner (Fig. 15.3). The mean (±SE) maximum uncertainty associated with each life history event over the entire period of study was: laying, 13.0 days (±0.23, $N = 591$), hatching, 28.7 days (±0.56, $N = 607$), and maturity, 23.7 days (±1.19, $N = 279$).

By chance the uncertainties for certain stages for some clutches were large, and for others small. To avoid introducing unnecessary errors, some observations with large uncertainties were excluded from the analyses. All analyses were restricted to clutches whose uncertainties were less than a predefined threshold: time to hatch ≤ 50 days (i.e., $E1 + E2$, Fig. 15.3), juvenile period ≤ 60 days ($E2 + E3$); and total time to maturity ≤ 50 days ($E1 + E3$). The average maximum uncertainties after removing observations above these threshold levels were 30.2 days ($N = 357$), 39.0 days ($N = 166$), and 24.6 days ($N = 169$) for time to hatch, juvenile period, and total time to maturity, respectively. Note that these thresholds yielded maximum possible uncertainties and that actual uncertainties would be half of these values (see preceding paragraph). Sample sizes varied for the estimates of different life history events and stages because reliable dates for all three events (laying, hatching, and maturity) were not available for all clutches.

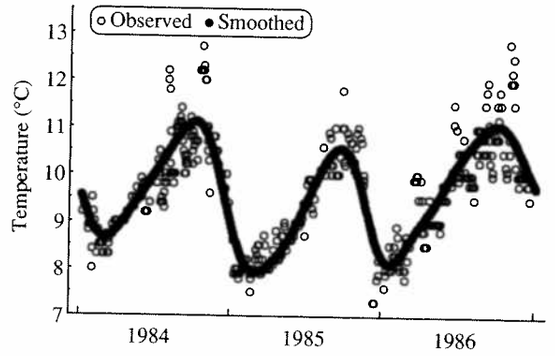

FIGURE 15.1. Observed and smoothed (best fit) daily sea water temperatures at the Bamfield Marine Station main aquarium room for the period 1 January 1984 to 31 December 1986.

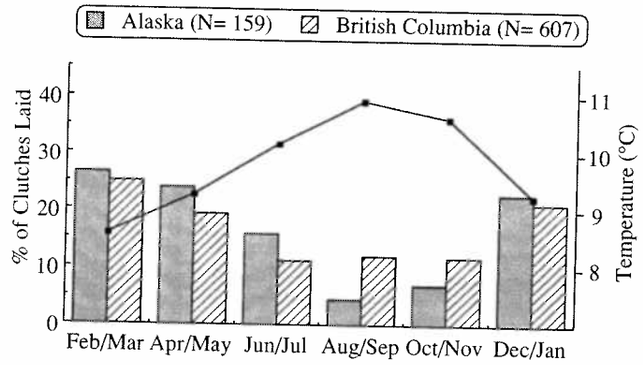

FIGURE 15.2. Seasonal variation in the frequency of clutch initiation for "northern" *Nucella emarginata* from two geographically distant populations held continuously immersed in the laboratory: Torch Bay, Southeast Alaska, and Barkley Sound, British Columbia. Temperatures are mean monthly sea water temperature over the duration of the study (1982–1992).

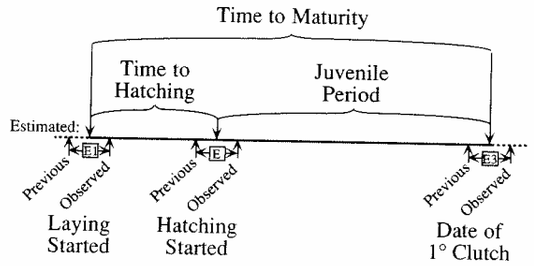

FIGURE 15.3. The procedure for estimating the duration and uncertainty of various life history stages. The horizontal line indicates time moving from left to right for an individual clutch. Vertical arrows below the line indicate actual dates, whereas those above it indicate estimated dates. E1, E2, E3 the maximum error or uncertainty associated with estimated dates used in the analyses.

Time to hatch as a fraction of total time to maturity was computed separately for each clutch for which both time to hatch and juvenile period were available. The average value was computed as the average for all clutches from each of the two geographic regions.

Comparisons with Other Species

To place the results obtained for *Nucella emarginata* in context, similar data were obtained from the literature for other species. Where data on time to hatch or juvenile period were expressed as a range of values at a given temperature, I used only the minimum for each. If data were given for a range of temperatures, I estimated time to maturity only for one temperature near the "normal" temperature range experienced by the species. Where graphical data were available describing the dependence of time to hatch on temperature, these data were digitized from the published figures and used to compute Q_{10} values.

Q_{10} Computations

Q_{10} values were computed from the slope (A) of the least-squares linear regression: X = temperature (°C), Y = log(1/days to hatch). Hence, for a given species $Q_{10} = 10^{(10 \cdot A)}$. Least-squares linear regression seemed more appropriate here than reduced major axis regression (LaBarbera, 1989) because errors in the estimate of time to hatch were probably considerably larger than those for temperature.

With two exceptions, Q_{10} values for time to hatch were estimated using all the available data published for a species. First, where data departed significantly from a linear relationship of log(1/days to hatch) versus temperature at extreme high temperature, observations near the stressful limits were not included. Second, for one species of snail upon which several studies had been conducted (*Urosalpinx cinerea*), one author's results differed from all the others and were excluded (see Spight, 1975).

Statistical analyses

Data manipulation, editing, and computation of uncertainties were conducted with Excel (Ver. 3.0a, Microsoft). Descriptive statistics, least-squares linear regressions, contingency table analyses, and analysis of variance (ANOVA) were computed with Statview II (Ver. 1.03, Abacus Concepts). Analysis of covariance (ANCOVA) was conducted with SuperAnova (Ver. 1.1, Abacus Concepts).

Results

Although both British Columbian and southeast Alaskan populations of *Nucella emarginata* produced egg capsules throughout the year, both spawned more frequently during the winter months (December–May) when laboratory water temperatures were lowest (Fig. 15.2). Alaskan snails, however, were significantly more sensitive to seasonal cues and spawned less frequently than those from British Columbia during the late summer and fall (August–November; $p = .04$, contingency table analysis).

Over the temperature range examined (8°–11°C), time to hatch decreased significantly with increasing temperature for capsules from both British Columbia and southeast Alaska (Fig. 15.4). The effect of temperature on hatching time was significantly more pronounced for capsules from the more southern region (see Fig. 15.4 legend). For British Columbian capsules, the Q_{10} for development rate (1/time to hatch) was 4.93 (±1.05 SE) whereas for those from southeast Alaska the Q_{10} was 2.63 (±0.69, see Table 15.2). Based on the slopes of the regressions in Figure 15.4,

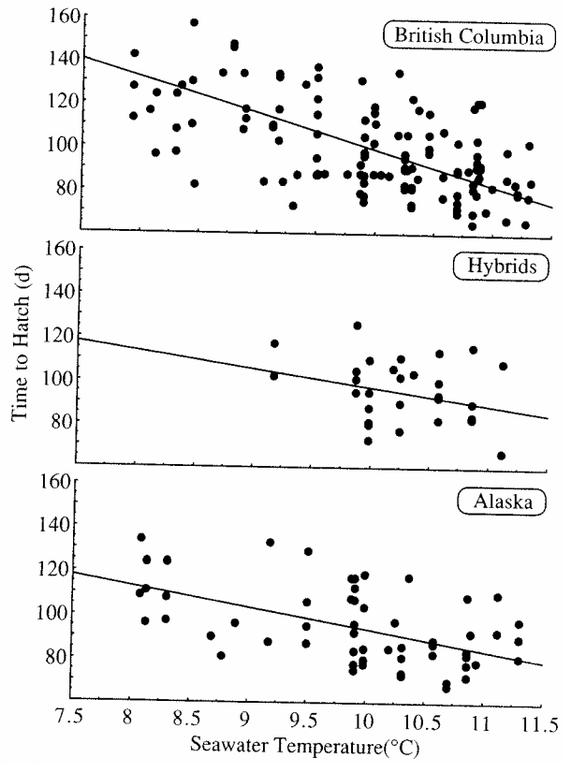

FIGURE 15.4. Time to hatch as a function of seawater temperature in laboratory-reared "northern" *Nucella emarginata* from two geographically distant populations, and in hybrid crosses between them. Only development times with uncertainties ≤ 50 days were included (see "Duration of Life History Stages" in Methods). Lines correspond to least-squares linear regression equations (slope ± S.E., intercept ± S.E.): BC, −16.3 ± 1.40, 262.5 ± 1.16 ($N = 203$, $r = 0.634$); hybrids, −8.2 ± 5.26, 179.0 ± 2.55 ($N = 32$, $r = 0.272$); AK, −9.5 ± 1.91, 188.5 ± 1.62 ($N = 81$, $r = 0.488$). The slopes for BC and AK differed signlficantly from each other ($p = .013$, ANCOVA). No further analysis was attempted for hybrids because the data spanned too narrow a range of temperature to be useful and because the slope for this group by itself did not differ significantly from zero. The data are included here only for completeness.

time to hatch increased 16.3 days for each degree drop in temperature for capsules from British Columbia and 9.5 days per degree for capsules from southeast Alaska. These would correspond to an impact on development time per degree of approximately 16 percent and 10 percent, respectively, of the total time to hatch at 10°C. No analyses were conducted for hybrid snails since the small sample size and limited temperature range yielded no significant association between development time and temperature.

Because of the different slopes for these two regions, capsules from British Columbia took significantly longer to hatch than those from southeast Alaska only at temperatures below about 10°C. For example, at 8°C British Columbian capsules took 17 percent longer to hatch than Alaskan capsules (140 versus 120 days), whereas at 10°C they differed by only about 5 percent (99 versus 94 days). The regression lines crossed at approximately 10.7°C. Because of the generally inverse exponential dependence of hatching time on temperature (Johnston, 1990), these linear regressions cannot be extrapolated reliably to higher temperatures.

Average juvenile period did not differ significantly between British Columbian and southeast Alaskan populations ($p = .80$, one-way ANOVA). For both, the juvenile period in the laboratory was approximately 430 days (Table 15.3). Similarly, the average time to maturity, measured as the

Table 15.2. Q_{10} values of rate of development (1/time to hatch) for selected fish and invertebrates

Species	N^a	Temperatures tested (°C) Min.	Max.	Mean	$Q_{10}{}^b$	Source
Teleost fishes						
Clupea harengus (Atl. herring)	9	5.3	14.2	9.0	4.18	Johnston, 1990
Cyprinodon macularis (pupfish)[c]	19	15.0	28.4	22.6	3.72	Kinne, 1963
Enchelyopus cimbrius (rockling)	12	5.3	23.1	13.4	2.80	Johnston, 1990
Gadus macrocephalus (Pac. cod)	11	2.5	13.2	7.4	4.18	Johnston, 1990
G. morhua (Atl. cod)	9	−1.0	14	6.8	2.84	Kinne, 1963
Harpagifer spp.	8	−0.4	0.6	0.1	3.89	Johnston, 1990
Morone saxatilis (striped bass)	8	15.3	22.5	18.8	3.61	Johnston, 1990
Mugil cephalus (grey mullet)	11	10.4	29.1	19.4	2.15	Johnston, 1990
Osmerus eperlanus (smelt)	11	4.9	17.8	10.3	5.77	Johnston, 1990
Pleuronectes platessa (plaice)	11	2.4	14.3	7.7	3.06	Johnston, 1990
Scomber scombrus (mackerel)	10	10.3	21	15.5	3.77	Johnston, 1990
Prosobranch gastropods						
Eupleura caudata	13	21.1	26.6	24.9	2.89	MacKenzie, 1961
Ilyanassa obsoleta	7	11.0	28.2	20.0	2.81	Scheltema, 1967
Urosalpinx cinerea	12	10.2	29.7	19.1	1.71	Spight, 1975
Nucella emarginata, AK	81	8.1	11.3	10.0	2.63	This study
N. emarginata, BC	203	7.9	11.3	9.9	4.93	This study
Opisthobranch gastropod						
Onchidoris bilamellata	7	5.0	15.0	10.7	2.17	Todd, 1991
Cephalopod						
Octopus vulgaris	13	15.8	24.7	20.2	2.23	Spight, 1975
Marine copepods						
Acartia clausi	3	0	10.8	5.2	4.73	McLaren et al., 1969
A. tonsa	5	10	25.4	15.5	4.13	McLaren et al., 1969
Calanus finmarchicus	4	0	20	9.9	2.41	McLaren et al., 1969
C. glacialis	4	0	8	4	2.94	McLaren et al., 1969
C. hyperboreas	3	0	7	3.4	3.06	McLaren et al., 1969
Centropages furcatus	5	16	30	21.8	3.24	McLaren et al., 1969
Eurytemora hurundoides	3	0	12	4.9	3.50	McLaren et al., 1969
Metridia longa	5	0	12	5.3	3.08	McLaren et al., 1969
Pseudocalanus minutus	5	0	12	5.9	2.86	McLaren et al., 1969
Temora longicornis	4	0	12	5.6	3.64	McLaren et al., 1969
Tortanus discaudatus	3	0	10.8	5.2	4.34	McLaren et al., 1969

time from the date of laying to the date upon which the first capsules were produced by progeny of a particular cross (see Fig. 15.3), did not differ between these populations either $p = .83$, one-way ANOVA), and was approximately 540 days for both (Table 15.3).

Discussion

Temperature Compensation

That temperature should have an effect on the development rate of northern *Nucella emarginata* is not terribly surprising in light of the extensive effects of temperature on the rates of physiological

Table 15.2. Continued

Species	N^a	Temperatures tested (°C) Min.	Max.	Mean	$Q_{10}{}^b$	Source
Lepadomorph barnacle						
Lepas anatifera	2	19.7	24.8	22.2	3.05	Patel and Crisp, 1960
Balanomorph barnacles						
Balanus amphitrite[c]	5	17.6	31.7	24.2	1.91	Patel and Crisp, 1960
B. balanus	4	3.1	13.1	7.8	3.15	Patel and Crisp, 1960
B. crenatus[c]	5	3.1	18.1	10.3	2.92	Patel and Crisp, 1960
B. perforatus	7	9.1	27.4	19.9	2.56	Patel and Crisp, 1960
Chthamalus stellatus[c]	5	9.1	27.8	18.6	2.17	Patel and Crisp, 1960
Elminius modestus[c]	5	3.1	18.0	10.3	4.13	Patel and Crisp, 1960
Semibalanus balanoides	5	3.0	13.9	8.9	1.31	Patel and Crisp, 1960
Verruca stroemia[c]	6	3.0	18.1	10.8	2.99	Patel and Crisp, 1960
Echinoid echinoderms						
Sterechinus neumayeri	4	−1.9	−0.1	−0.8	9.58	Bosch et al., 1987
Strongylocentrotus droebachiensis	4	0.0	9.4	5.4	3.12	Bosch et al., 1987
S. franciscanus	2	10.2	12.7	11.5	2.13	Bosch et al., 1987

[a] N sample size.
[b] $Q_{10} = 10^{(10 \times A)}$, where A is the slope of log(1/days to hatch) as a function of temperature (°C).
[c] Data at stressful high temperature excluded.

Table 15.3. Juvenile period and time to maturity for laboratory-reared *Nucella emarginata* from two geographically distant populations

(No observations of juvenile period were obtained for hybrid clutches.)

	Juvenile period (d)			Time to Maturity (d)		
	N	Mean	SE	N	Mean	SE
Barkley Sound, British Columbia	126	429	7.8	126	541	8.7
Torch Bay, Alaska	30	434	18.1	32	545	17.7

processes (Kinne, 1963; Johnston, 1990). However, the discovery of latitudinal temperature compensation in *N. emarginata* is somewhat surprising given the apparently minimal or undetectable temperature compensation reported either within or among other species, including barnacles (Patel and Crisp, 1960), echinoderms (Emlet et al., 1987), and fishes (Johnston, 1990). Although temperature compensation has been reported in the short-term larval growth rates of several gastropods (Dehnel, 1955), Patel and Crisp (1960) note that short-term rates of size increase in larvae may not accurately reflect the impact of temperature on the entire process of growth and differentiation, a sentiment echoed by Johnston (1990).

N. emarginata may exhibit temperature compensation among distant populations because of the limited gene flow associated with direct development. The other species for which tempera-

ture compensation has been noted as lacking (barnacles, echinoids, and fishes) all have pelagic larval stages.

Questions persist about the proper analysis of temperature dependence of physiological processes (see the appendix in McLaren, 1963). For example, McLaren reports evidence of temperature compensation in rates of development of copepods both within (McLaren, 1966) and among species (McLaren et al., 1969) when using a different analytical approach that attempts to circumvent some of the inadequacies of conventional Q_{10} analyses. Hence the apparent lack of temperature compensation in rates of development reported by some may in part reflect a poor choice of analysis.

Q_{10} Values for Rate of Development in Northern *Nucella emarginata* and Other Taxa

Not only did Alaskan populations of *N. emarginata* develop more rapidly at temperatures less than 10°C (Fig. 15.4), but their rate of development was less sensitive to temperature variation than British Columbian snails over the temperature range examined (8°–11°C, Table 15.2). This difference in temperature sensitivity may have been due to the relative differences between lab and field sea water temperatures for these two populations. For British Columbia snails, although the range of monthly mean temperatures experienced in the laboratory was less than half that of surface sea water at nearby Cape Beale for the period November 1982 to August 1988 (laboratory range = 3.4°C [min.= 8.0, max. = 11.4] versus Beale range = 7.6°C [min. = 6.6, max. = 14.2]), the mean temperature experienced in the laboratory was 0.6°C less than that of surface sea water at Cape Beale over the same time period (9.9°C ± 0.11 SE versus 10.5°C ± 0.26, $N = 70$). For Alaskan snails, the mean laboratory sea water temperature was likely higher than those experienced in the field. Unfortunately, because I did not manipulate temperatures experimentally to try to mimic those experienced in air (i.e., up to 25°C during the summer months), I cannot be certain whether the rates of development of British Columbian snails would be faster than (as implied by the regressions of Fig. 15.4), or the same as, those for Alaskan snails at temperatures above 11°C.

The Q_{10} values reported here for rate of development (1/time to hatch) were comparable to those determined from a casual survey of published values for other marine taxa (Table 15.2, Fig. 15.5). At a Q_{10} of 2.6, rates of development of Alaskan *N. emarginata* were close to those of the majority of other species, which exhibited Q_{10} values in the range of 2 to 3. The Q_{10} of 4.9 for British Columbian snails seemed rather high in comparison since only two other species, one fish and one echinoid (Table 15.2), exhibited higher Q_{10} values for rate of development. Although Q_{10} values have been noted to increase at lower temperature in other taxa (Bosch et al., 1987), this is in part an artifact of Q_{10} analyses. Even for chemical reactions that behave precisely according to Arrhenius' function, Q_{10} is expected to increase with decreasing temperature (Schmidt-Nielsen, 1979: 537).

Juvenile Period and Time to Maturity in Northern *Nucella emarginata* and Other Taxa

In spite of significant differences in the rate of development reported above at temperatures less than 10°C, differences were not apparent in either juvenile period or total time to maturity between British Columbian and Alaskan snails (Table 15.3). Hence, differences in time to hatch over the majority of temperatures experienced in the laboratory did not translate into a longer overall time to maturity as, for example, reported for the nudibranch *Phestilla sibogae* with an increase in the larval period (Miller and Hadfield, 1990). In part this may be due to the cumulative effects of many small uncertainties affecting laboratory growth during the relatively long juvenile period for *N.*

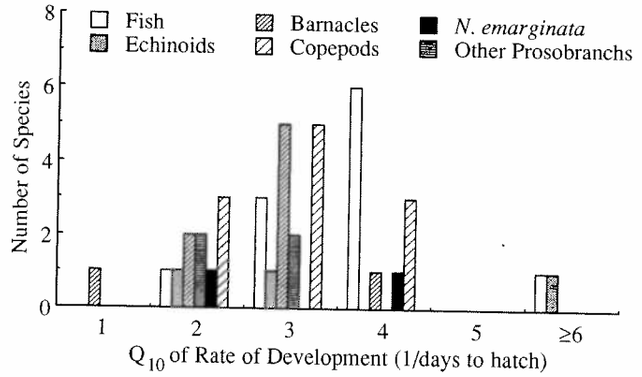

FIGURE 15.5. Temperature sensitivity of rate of development for a variety of marine organisms (see Table 15.2 for detailed data). The two values for *N. emarginata* correspond to separate estimates for the British Columbian and Alaskan populations.

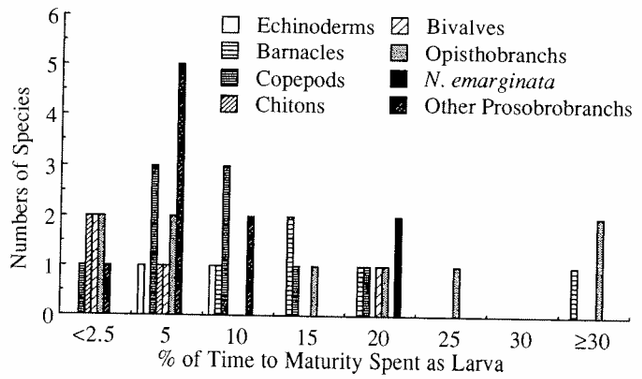

FIGURE 15.6. Percentage of time to maturity (see Fig. 15.3 for definition) spent as larvae or "prejuvenile" for a variety of marine organisms (see Table 15.4 for detailed data). The two values for *N. emarginata* correspond to separate estimates for the British Columbian and Alaskan populations.

emarginata compared to *P. sibogae* (430 versus 21 d). In further contrast to these results for *N emarginata*, Huntley and Lopez (1992) report dramatic effects of temperature on generation time (fertilization to maturity) in a broad survey of copepod growth: more than 90 percent of the variance in growth rate of thirty-three species over a temperature range from −1.7° to 30.7°C could be accounted for by temperature alone.

When compared to a selection of published values for other marine invertebrates, the time to hatch as a fraction of the total time to maturity for *N. emarginata* seemed high (Table 15.4, Fig. 15.6). This difference was apparent even though the prejuvenile period included time in the plankton for species with a pelagic stage. First, only six of thirty-one other species spent a longer fraction of their time to maturity as a larvae, and of these three were short-lived opisthobranch gastropods (time to maturity less than two months) and one was a short-lived balanomorph barnacle (time to maturity approximately three months). Second, of the eight species of meso- and neogastropods for which I could find comparable data, *N. emarginata* spent at least half again as long in the prejuvenile period compared to the next most similar species, *Strombus costatus* (17.7

Table 15.4. Time to juvenile, juvenile period, and time to maturity for selected marine invertebrates

Taxon	Time to juvenile: Lay to hatch (d)	Time to juvenile: Hatch to juvenile (d)	Time to juvenile: Lay to juvenile (d)	Time to juvenile: Temp. (°C)	Time to juvenile: Ref.[a]	Juvenile period: (days)	Juvenile period: Ref.[b]	Time to juvenile as % of time to maturity
Annelida								
Polychaeta								
Pseudopolydora kempi japonica	4	15	19	?	(13)	21	(13)	47.5
Mollusca								
Gastropoda								
Prosobranchia								
Mesogastropoda								
Polinices lewisi	42	1	43	?	(1)	915	(1)	4.5
Strombus costatus	6	36	42	27	(2)	300	(2)	12.3
S. gigas	4.5	27	31.5	28	(2)	1095	(2)	2.8
Neogastropoda								
Conus pennaceus	25	0	25	25	(9)	730	(10)	3.3
C. quercinus	15.5	30	45.5	25	(9)	2555	(10)	1.7
Eupleura caudata	18	0	18	25	(6)	710	(6)	2.5
Nucella canaliculata	90	0	90	?	(12)	915	(11)	9.0
N. emarginata "northern", BC	100.5	0	100.5	9.9	(15)	429	(15)	19.0
N. emarginata "northern", AK	93.7	0	93.7	9.9	(15)	434	(15)	17.7
N. lamellosa	67	0	67	?	(13)	1460	(11)	4.4
Opisthobranchia								
Nudibranchia								
Archidoris pseudoargus	?	?	37	10	(14)	730	(14)	4.8
Doridella obscura	?	?	9	25	(14)	26	(14)	25.7
D. steinbergae	?	?	25	14	(14)	24.5	(14)	50.5
Onchidoris bilamellata	?	?	53	10	(14)	270	(14)	16.4
O. muricata	?	?	58	10	(14)	270	(14)	17.7
Phestilla melanobranchia	?	?	8	23	(14)	135	(14)	5.6
P. sibogae	5	7	12	23	(8)	21	(8)	36.4
Tritonia hombergi	?	?	1.5	9	(14)	730	(14)	0.2
Adalaria proxima	?	?	2	9	(14)	300	(14)	0.7
Polyplacophora								
Katharina tunicata	?	?	7	14	(13)	730	(13)	0.9
Lepidochitona fernaldi	12	2	14	10	(13)	182	(13)	7.1
Mopalia muscosa	1	10.5	11.5	15	(13)	730	(13)	1.6
Bivalvia								
Heterodonta								
Bankia setacea	?	?	28	14	(13)	120	(13)	18.9
Panope abrupta	?	?	18	17	(13)	1275	(13)	1.4
Tapes philippinarum	?	?	24	15	(13)	365	(13)	6.2
Tresus capax	?	?	26	10	(13)	1095	(13)	2.3
Arthropoda								
Crustacea								
Copepoda								
Acartia clausi	8.2	?	8.2	5.2	(7)	31	(4)@10°C	20.9
A. tonsa	3.3	?	3.3	16	(7)	16	(4)@16°C	17.1
Calanus finmarchicus	2.4	?	2.4	9.9	(7)	45.2	(4)@10°C	5.1
C. glacialis	4.3	?	4.3	2.6	(7)	180	(4)@1.5°C	2.3
C. hyperboreas	6.64	?	6.64	0.0	(7)	185	(4)@0°C	3.5
Centropages furcatus	1.4	?	1.4	22	(7)	19.3[b]	(4)@15°C	6.8
Eurytemora hurundoides	7.81	?	7.81	3	(7)	75.1[c]	(4)@2°C	9.4
Pseudocalanus minutus	5.8	?	5.8	5.9	(7)	47.5	(4)@6.6°C	10.9
Temora longicornis	2.31	?	2.31	12	(7)	26.3	(4)@12°C	8.1
Cirripedia								
Lepadomorpha								
Pollicipes polymerus	25.4	30	55.4	14	(13)	365	(13)	13.2

Table 15.4. Continued

Taxon	Time to juvenile: Lay to hatch (d)	Hatch to juvenile (d)	Lay to juvenile (d)	Temp. (°C)	Ref.[a]	Juvenile period: (days)	Ref.[b]	Time to juvenile as % of time to maturity
Balanomorpha								
Balanus glandula	27	21	48	12	(3)	182	(3)	20.9
B. pacificus	8	14	22	15	(5)	105	(5)	17.3
Chthamalus fissus	14	21	35	12	(3)[d]	60	(3)	36.8
Tetraclita squamosa	40	30	70	12	(3)[d]	730	(3)	8.8
Echinodermata								
Asteroidea								
Pisaster ochraceus	1.25	76	77.3	12	(13)	1725	(13)	4.3
Echinoidea								
Strongylocentrotus purpuratus	1	74	75	10	(13)	730	(13)	9.3

[a](1) Bernard, 1967; (2) Brownell, 1977; (3) Hines, 1978; (4) Huntley and Lopez, 1992; (5) Hurley, 1973; (6) MacKenzie 1961; (7) McLaren, et al., 1969; (8) Miller and Hadfield, 1990; (9) Perron, 1981b; (10) Perron, 1986; (11) Spight, 1975; (12) Spight, 1976; (13) Strathmann, 1987; (14) Todd, 1991; (15) this study.

[b]For *Centropages hamatus*.

[c]For *Eurytemora herdmanni*.

[d]Estimated from settlement data.

percent versus 12.3 percent of total time to maturity; Table 15.4). Some of this difference may have to do with the relatively short juvenile period of *N. emarginata* in the laboratory. But even if this period were two years (Spight and Emlen, 1976), the fraction of time spent in the prejuvenile period would still be approximately 14 percent.

These data suggest that although natural selection has been able to reduce the time from hatching to maturity in *N. emarginata* compared to other meso- and neogastropods, it has had little impact on the time spent in the egg capsule. This implies that substantial constraints may limit the rate of intracapsular development, as suggested for gelatinous egg masses (Strathmann and Strathmann, 1989). Whether these constraints are related to rates of gas exchange, or metabolite or ion diffusion, across the capsule wall remains to be seen.

Some caution should be exercised when interpreting Figure 15.6 since apparent differences among taxa may have arisen due to a nonrandom selection of modes of development within particular taxa. A more systematic survey would be required to reject this possibility.

Is Development More Tightly Constrained in Muricacean Gastropods with Direct Development?

Spight (1975) was the first to observe that hatching time for meso- and neogastropods could be predicted with reasonable accuracy simply by knowing taxonomic affinity and temperature. An expanded search of the literature suggests this is largely true across an even broader range of taxa (Fig. 15.7). The results of this expanded search further suggest that direct-developing muricacean gastropods are unusual in two respects. First, relative to the total time to maturity, they take longer to hatch at a given temperature than many other marine organisms. Second, they exhibit an unusually precise dependence of time to hatch on temperature.

When compared at a given temperature (Fig. 15.7a), not only do direct-developing muricacean gastropods take among the longest times to develop of prosobranch gastropods, but prosobranch gastropods generally take longer to hatch than opisthobranch gastropods (Fig. 15.7b), and molluscs generally take longer than barnacles, echinoid echinoderms, and teleost fishes (Fig. 15.7c). All of these taxa exhibit a pronounced effect of temperature on rate of development, but what is striking about direct-developing muricaceans is the precision of this temperature dependence across species. Because this precision is even greater than that for muricaceans with a pelagic stage following their intracapsular period (compare solid versus open circles in Fig. 15.7a), constraints on the rate of development in direct-developing species would seem to be acting during the later stages of development, during the transformation from a veliger into a hatchling snail.

Alternatively, Richard Strathmann has suggested to me that the seemingly more precise temperature dependence of development rate in direct-developing muricaceans may have less to do with constraints imposed by encapsulation and more to do with variation in the stage, and hence time of development, at which species with pelagic veligers hatch. I cannot rule out this possibility for muricaceans. However, other prosobranchs with encapsulated direct development exhibit much less precise temperature dependence of development than do muricaceans (compare filled triangles to filled circles in Fig. 15.7a), which suggests that encapsulation per se is not the only constraint.

Taken together, the unusually long time to hatch, coupled with the rather precise temperature dependence of development rates, suggest that the rate of development is constrained at some very fundamental level in direct-developing muricacean gastropods, even though egg size, number of

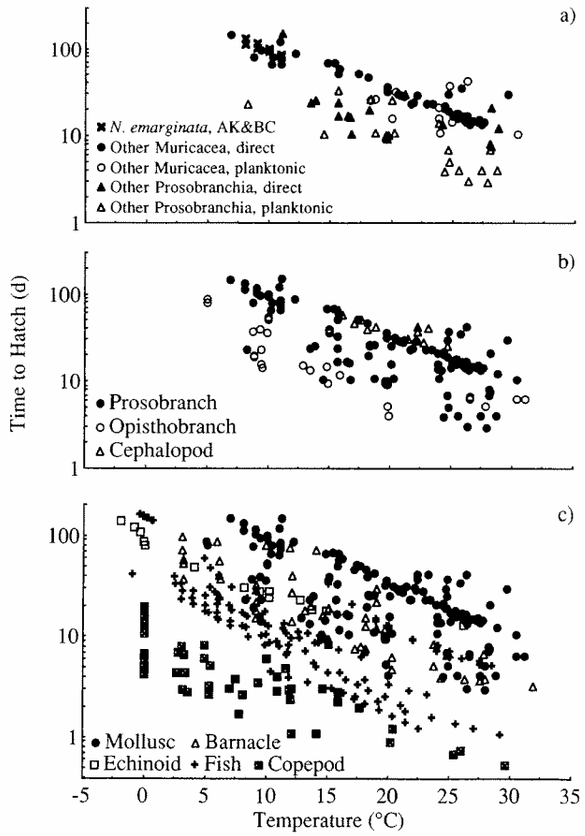

FIGURE 15.7. Time to hatch (in days) as a function of water temperature for a variety of marine organisms: (a) prosobranch gastropods, (b) various molluscs, (c) higher marine taxa. For some species, development time was measured over a range of temperatures; for others data are for only a single temperature. Direct: entire prejuvenile period spent within the egg capsule; planktonic: some fraction of the prejuvenile period spent in the plankton. Compiled from several sources: "northern" *Nucella emarginata* (this study); prosobranch gastropods (Fourteen species [MacKenzie, 1961; Scheltema, 1967; Spight, 1975]); opisthobranch gastropods (Twenty-three species [Spight, 1975; Todd, 1991]), cephalopods (one species [Spight, 1975]), barnacles (Twelve species [Patel and Crisp, 1960; Hines, 1978]), echinoid echinoderms (Seven species [Bosch et al., 1987]), fish (Eleven species [Kinne, 1963; Johnston, 1990]), and copepods (Eleven species [McLaren et al., 1969]).

embryos per capsule, nurse egg to embryo ratio, and egg capsule morphology all vary substantially among these species.

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16 Current Knowledge of Reproductive Biology in Two Taxa of Interstitial Molluscs (Class Gastropoda: Order Acochlidiacea and Class Aplacophora: Order Neomeniomorpha)

M. Patricia Morse

ABSTRACT Two taxa are important members of the molluscan assemblage in the interstitial environment, the well-represented gastropod order Acochlidiacea and the lesser known aplacophoran family, Meiomeniidae. Adaptations of the reproductive systems, discussed for representatives of these taxa, are consistent with a general reduction in the organ systems associated with minute species of molluscs. In the acochlidiaceans, four out of five families are interstitial; two of the families are composed of monoecious species and one of dioecious species. Spermatophores have evolved for sperm transfer with a subsequent reduction in accessory copulatory organs. In mature females, only a few large vitellogenic eggs are present at any one time, and where known, egg capsules with few developing embryos enclosed are reported. The aplacophorans, represented by the family Meiomeniidae, are monoecious, with small numbers of vitellogenic eggs and copulatory spicules.

Introduction

Adaptations have evolved for interstitial molluscs, ranging from 0.5 mm to 3.0 mm in length, to live in the pore spaces of sediments. Such adaptations are evident among representatives of the gastropod order Acochlidiacea and the aplacophoran order Neomeniomorpha, which constitute a major part of the molluscan assemblage characteristic of coarse sand habitats (Morse, 1987). These molluscs are cosmopolitan in distribution, occurring in subtidal and low intertidal habitats in both temperate and tropical waters. The reproductive biology of these interstitial species is poorly known. Swedmark (1959, 1964) was the first to consider adaptations of organisms living in the interstitial environment. He investigated the biological adaptations of interstitial molluscs and noted that they possess a small number of reproductive cells, reduced organ systems, and a tendency for encapsulated development of the larvae (Swedmark, 1968a).

Acochlidiaceans are shell-less opisthobranch gastropods, arranged in five families, Microhedylidae (*Unela*, *Microhedyle*), Asperspinidae (*Asperspina*), Ganitidae (*Ganitis*, *Paraganitis*), Hedylopsidae, (*Hedylopsis*, *Pseudunela*), and Acochlidiidae (*Acochlidium* and *Strubellia*) (Arnaud et al., 1986). The first four families of acochlidiaceans are minute (0.5 mm to 3 mm in length) and are known only from the interstitial environment. Members of the family Acochlidiidae are larger (30 mm in length) and are found mainly on Pacific Islands in freshwater streams where they live under rocks (Rankin, 1979). An interstitial freshwater form from the Caribbean

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Reproduction and Development of Marine Invertebrates

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