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Relationship Between Growth Rate and Egg Production in the Copepod *Acartia clausi hudsonica*

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Abstract

Egg production by *Acartia clausi hudsonica* ceases at low concentrations of *Isochrysis galbana* as food and at high levels reaches a maximum that increases with temperatures in the natural range. This increase parallels the rate of production of fecal pellets. Females without males can produce about 400 eggs before entering a generally short postreproductive period. Weight increments between copepodite stages are exponential and, assuming isochronal durations of stages and that development time of older stages is the same mutiple of embryonic duration at all temperatures, a temperature-dependent rate is estimated for pre-adult growth. We demonstrate that this growth rate also predicts the observed maximal rate of egg production by the non-growing adult females. Published data for other copepod species (except *Pseudocalanus*) are inadequate for wider testing of this hypothesis, but available data do suggest that no such simple rule governs total output of eggs by females of different species.

Introduction

Three major reasons for the study of egg production by copepods can be found in the growing literature on the subject. 1) Eggs are the only form of production by non-growing adult females, and can be an important part of the total organic production by a copepod population (e.g. McLaren, 1969). 2) Egg production responds to food and physical-chemical variables, and may reflect environmental quality (Parrish and Wilson, 1978). 3) Ecological and evolutionary aspects of reproduction are of general interest, for example the variety of spawning schedules in relation to life-histories (Sekiguchi, 1976a), or the rate of reproduction as an adaptation to predation pressure (Sekiguchi, 1976b). The present paper describes egg production by *Acartia clausi* in greater detail than previously (cf. Iwasaki *et al.*, 1977), but its primary aim is to test a hypothesis that laying rates are predictable from growth rates.

Acartia clausi is clearly a species complex, and *A. clausi hudsonica* is probably specifically distinct (Bradford, 1976), but we give it subspecific status here to stress its comparability with other copepods that have been included under *A. clausi*.

Materials and Methods

Adult *Acartia clausi hudsonica* were taken from Bedford Basin, Halifax, N.S., Canada by horizontal tows at 5 to 10 m during September to November 1978, when water temperatures at these depths were 9 ° to 13 °C.

Single adult females or an adult pair were kept in 25 x 50 mm plastic vials. The copepods were given 5 d-old cultures of *Isochrysis galbana* diluted to the required concentration (with a Coulter Counter type B) in glass-filtered natural seawater. Each vial contained about 20 ml of culture and was changed every 3 d, when fecal pellets were also removed (though counted daily)

All vials were kept in temperature-controlled rooms (max. ranges ± 0.2 C°) with a subdued light cycle of 12 hL:12 hD. All eggs were counted and removed twice daily to lessen the chance of predation by the copepods. Nevertheless, some empty egg membranes were found and counted as eggs. Preliminary experiments showed that starved females lived 4 to 16 d at ca 10 °C and produced some eggs until the third day. Eggs produced on the first day under various conditions were excluded in estimating rates of production. Those females that failed to produce any eggs within the first 2 d were considered to be abnormal or injured, and were discarded.

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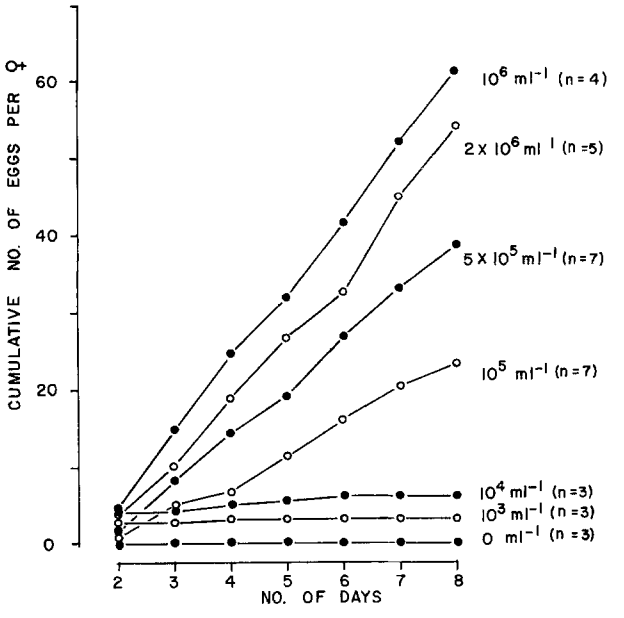

Fig. 1. *Acartia clausi hudsonica*. Cumulative production of eggs by females (with males) fed at various concentrations of *Isochrysis galbana* (changed every 3 d) at 10.4 °C

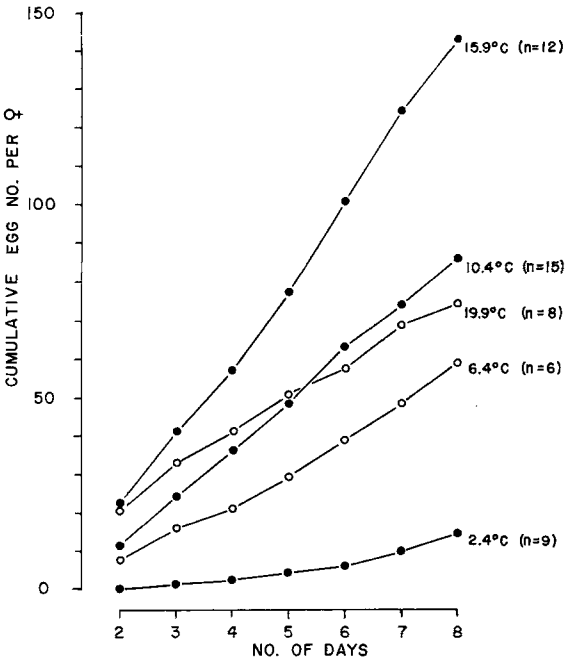

Fig. 2. *Acartia clausi hudsonica*. Cumulative production of eggs by females (without males) at various temperatures when fed 10^6 cells ml^{-1} *Isochrysis galbana* (changed every 3 d)

Table 1. *Acartie clausi hudsonica*. Effect of food concentration (*Isochrysis galbana*) on production of eggs and fecal pellets over a 7 d period at 10.4 °C

Food conc. cells ml^{-1}	No. ♀♀	No. d^{-1}, mean ± S.D. (range)			
		Eggs		Fecal pellets	
2 x 10^6	5	7.7 ± 1.72	(5.0–10.4)	16.6 ± 3.16	(4.2–20.1)
10^6	4	8.7 ± 3.07	(5.4–12.8)	16.9 ± 5.10	(10.4–24.7)
5 x 10^5	7	5.7 ± 1.77	(3.1–8.0)	11.6 ± 3.28	(8.5–18.6)
10^5	7	3.4 ± 1.13	(1.7–5.7)	8.3 ± 1.68	(6.1–9.1)
10^4	3	0.9	(0.1–2.1)	0.8	(0.4–1.4)
10^3	3	0.4	(0.1–0.7)	0.2	(0.1–0.3)
0	3	0		0	

In May to June 1979, freshly caught or starved individuals as well as eggs produced by well fed females, were killed and preserved for a few days at most in formalin-seawater. These were rinsed in distilled water, dried to a constant weight for < 1 h at 60 ° to 90 °C in lots totalling > 40 µg dry wt, and weighed on a Cahn Electrobalance, model G.

Results

Influence of Food Concentration

Females kept with males (Fig. 1) produced no eggs after the first day when starved, and almost none at 10^3 and 10^4 cells ml^{-1}. That is, there was a food threshold below which reproduction ceased. At higher food levels, no overall trends were evident in rate of laying during the week. Therefore mean daily rates (Table 1) are representative for this short-term period.

There was no difference (from ANOVA, SNK test; Sokal and Rohlf, 1969; $P<0.05$) between rates at 10^6 and 2 x 10^6 cells ml^{-1}, although rate at 10^6 cells ml^{-1} did exceed ($P\sim0.05$) that at 5 x 10^5 cells ml^{-1}. Thus egg laying was maximal under these conditions when food was at or above 10^6 cells ml^{-1}.

Rates of production of fecal pellets closely paralleled rates for eggs (Table 1). Again, rate at 10^6 cells ml^{-1} exceeded ($P<0.05$) that at 5 x 10^5 cells ml^{-1}, but not that at 2 x 10^6 cells ml^{-1}. Also, rates of egg and fecal pellet production were significantly correlated (Spearman's rank correlations) "within" the two higher food levels (r_s = 1.00 and 0.90 at 10^6 and 2 x 10^6 cells ml^{-1}, respectively), implying that, in this evidently superfluous food supply, individual females that ate more food produced more eggs.

There was no correlation within food levels of rates of egg production and body sizes, within the rather small ranges (maximally 0.73 to 0.81 mm cephalothorax lengths).

Influence of Temperature

Preliminary experiments showed that females without males continued to produce eggs at an undiminished rate (although later ones may have been infertile; see Parrish and Wilson, 1978). Cumulative production of

Table 2. *Acartia clausi hudsonica*. Effect of temperature on production of eggs over a 7 d period, fed 10^6 cells ml^{-1} *Isochrysis galbana*

Temp. °C	No. ♀♀	No. d^{-1}, mean ± S.D. (range)	
		Eggs	Fecal pellets
2.4	9	1.8 ± 0.95 (0.7–3.6)	5.0 ± 1.48 (3.9–8.4)
6.4	6	8.5 ± 2.32 (3.4–10.1)	16.6 ± 3.95 (11.7–23.0)
10.4	15	12.4 ± 2.22 (9.4–16.3)	16.8 ± 4.28 (8.0–25.9)
15.9	12	20.4 ± 3.19 (14.6–23.9)	29.3 ± 9.21 (17.4–46.6)
19.9	8	10.7 ± 1.50 (8.9–12.7)	6.3 ± 1.48 (4.9–9.6)

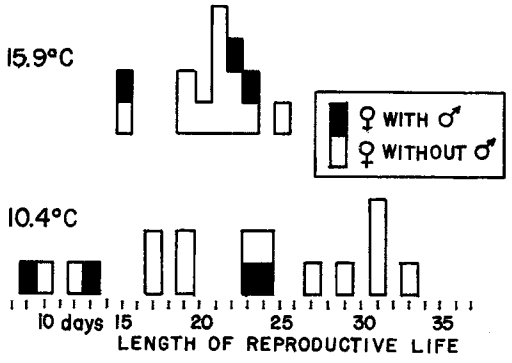

Fig. 3. *Acartia clausi hudsonica*. Frequency distributions of reproductive periods (defined in text) of wild-caught females fed 10^6 cells ml^{-1} *Isochrysis galbana* (changed every 3 d)

eggs through 1 wk by females without males, fed at 10^6 cells ml^{-1}, showed no trends at 6.4 °, 10.4 ° or 15.9 °C, but rates diminished with time at 19.9 °C and increased at 2.4 °C (Fig. 2). The highest temperature has not been observed in Bedford Basin (Krauel, 1969), and presumably had a damaging effect. The lowest temperature is normal seasonally, but may have required acclimation by the females or, alternatively, may have slowed down oogenetic cycles so that more time would be needed to measure an average for full potential rates. It was also noted that only at 2.4 °C did females acquire substantial oil globules.

The mean daily rates of egg production (Table 2) increased significantly ($P<0.05$) with each temperature increment between 2.4 ° and 15.9 °C, but the rate at 19.9 °C did not differ from those at 6.4 ° and 10.4 °C (ANOVA, SNK test; Sokal and Rohlf, 1969). The mean daily rate at 10.4 °C exceeded ($t = 2.78$, d.f. 17, $P<0.05$) that at the same temperature and food level in the food-level experiment (cf. Table 1). Possibly the males kept with the females ate some eggs and were not accounted for by the empty egg membranes that occurred occasionally in the food-level experiment.

We conclude that mean daily production rates of eggs (Table 2) are physiologically maximal for the "quality" of food used, between 6.4 ° and 15.9 °C, but are lower than possible at 2.4 °C and not meaningful in nature at 19.9 °C. Again, these rates were correlated with rates of production of fecal pellets between temperature levels (Table 2), and also "within" levels ($r_s = 0.70, 0.26, 0.50$, and 0.65, at 2.4 °, 6.4 °, 10.4 °, and 15.9 °C, respectively; combined $P = 0.017$). As in the food-level experiment, there were no significant correlations of rates of egg production with female lengths within temperature levels.

Longer-Term Egg Production

Females were fed at 10^6 cells ml^{-1}, with and without males at two temperatures, until they died. At 10.4 °C, 14 females without males lived on average (± S.D.) for 28.4 ± 6.8 d and produced 278 ± 91 eggs; 4 females with males averaged 21.0 ± 8.1 d (their males, 14.8 ± 3.8 d) and laid 235 ± 163 eggs. At 15.9 °C, 12 females without males lived 24.3 ± 5.1 d and laid 371 ± 78 eggs; 3 females with males averaged 20.7 d (range 15 to 23 d) of life (their males 14.7 d, range 11 to 18 d) and 323 (range 266 to 384) eggs. Such wide variances tend to mask mean differences.

A sharp drop in rate of egg production generally preceded death of females with or without males. We define a "postreproductive period" as the period when daily egg production by a female persisted until death at a rate < 50% (usually much less) of the mean daily rate of all preceding days. Most females had scattered single days earlier in life when egg output was < 50% of "normal"; 8 females had 2 such days in succession; and one female had a 3 d lapse, then returned to higher rates. One female declined to < 50% output for 5 d beginning on Day 18, recovered for 4 d at a rate only slightly > 50%, then declined further before death. she is considered to have been nominally postreproductive from Day 18.

Postreproductive periods thus defined were quite variable, averaging 4.7 ± 4.1 d (range 1 to 13 d) for 18 females at 10.4 °C, and 3.1 ± 3.4 d (range 0 to 13 d) for 15 females at 15.9 °C. A negative correlation of post-reproductive with reproductive periods might be expected if more-or-less fixed lifespans were occupied to varying degrees by reproductive periods. However, the correlation was weakly positive at 15.9 °C ($r_s = 0.55$, $P<0.05$) and absent at 10.4 °C ($r_s = 0.19$, n.s.). Our mature females from nature had certainly expended different portions of their potential lifespans, so that little understanding of potential reproductive performance can come from the (above) mean reproductive statistics of such females.

Thus, among reproductive periods (Fig. 3), we suggest that only the longer ones – say 27 to 33 d at 10.4 °C and 21 to 25 d at 15.9 °C, mostly without males – are representative of newly moulted females. The total outputs of the 6 such females at 10.4 °C averaged 388 ± 26 eggs, and for the 10 females at 15.9 °C was 404 ± 64 eggs (Student's *t*-test for inhomogeneous variances, mean difference n.s.). If these totals (which include a few eggs from the nominally postreproductive periods) are divided by the

durations of the reproductive periods, rates are 11.5 ± 1.45 eggs d^{-1} at 10.4 °C and 18.8 ± 2.94 eggs d^{-1} at 15.9 °C, very similar to daily rates in short-term experiments (cf. Table 2).

We conclude that a newly moulted female fed in the laboratory on saturating amounts of *Isochrysis galbana* may produce about 400 eggs in her lifetime at a rate that depends on the temperature. The data also suggest that males are not necessary for sustained production of (infertile?) eggs.

Egg and Body Weights

Eight lots of ca 500 eggs gave mean dry weight (S.D. based on total weights) of 0.102 ± 0.018 μg egg^{-1}. Adult females caught for weighing in May to June 1979 differed little in length from those used for egg production in autumn 1978 (0.76 ± 0.04 mm *vs* 0.78 ± 0.02 mm). Four lots of freshly caught females averaged 6.31 ± 0.34 μg, whereas 7 lots of starved (3 to 5 d) females averaged 4.45 ± 0.55 μg. This represents a weight loss equivalent to about 18 eggs, in keeping with the day or two of egg production exhibited by starved females (see above).

Freshly caught stage I copepodites (C-I) weighed 0.55 μg, C-II were 0.87 μg, C-III were 1.27 μg, C-IV were 1.99 μg (2 lots, 1.97 and 2.00 μg), and C-V were 3.36 μg (2 lots, 3.33 and 3.39 μg). The weight increment between these young stages is close to exponential, at an instantaneous rate per stage (± S.E.) of 0.448 ± 0.012. This predicts an adult female weight of 5.07 μg, slightly larger than the mean weight of starved, presumably egg-free females (see above). This might be explained if, in addition to accumulated eggs, starved females also lose some metabolic stores.

Discussion

Although females showed an upper limit of daily egg production on *Isochrysis galbana* as food, there is no direct assurance that different foods or other conditions would not give higher rates. Indeed, Iwasaki *et al.* (1977) concluded that mixed cultures of *I. galbana* and *Monochrysis lutheri* at 15 ° and 20 °C gave higher rates of daily egg production by *Acartia clausi* (probably *A. omorii*) from Japan than did either food by itself. However, they used small numbers of females and found wide variances. The highest rate with mixed food (at 10^6 cells ml^{-1}) at 15 °C was 17.2 ± 3.25 eggs d^{-1} (n = 7) by individuals in darkness, significantly higher than the 10.4 ± 4.06 eggs d^{-1} (n = 4) at 300 lux (their Table 6). Their maximal rate was thus slightly lower ($P<0.05$) than that found by us at 15.9 °C using *I. galbana* alone (Table 2). Similarly, Parrish and Wilson (1978) found that a "standard ration" of *Thalassiosira peseudomonas* (7.15 x 10^3 cells ml^{-1}), *I. galbana* (5.7 x 10^3 cells ml^{-1}), and *Chroomonas salina* (3 x 10^3 cells ml^{-1}) gave much higher ($P<0.01$) laying rates by *A. tonsa* than did a volume equivalent to their "standard ration" of *I. galbana* alone. However, this equivalent volume of *I. galbana* alone is calculated by us from their data as 35 x 10^3 cells ml^{-1}, and is much lower than levels that we found (Table 1) to give maximal rates of laying. Thus we conclude that *I. galbana* may be a very inefficient food for *A. clausi hudsonica*, but there is no evidence that maximal rates found by us were lower than would have been produced by some other foods.

There are many other potential influences on maximal rates of egg production in addition to the possible effect of light mentioned above. Dagg (1977) found that interruptions in "superabundant" food supply for more than 3 h d^{-1} reduced rate of laying in *Acartia tonsa*. Parrish and Wilson (1978) concluded that different "strains" (collected on different dates) of *A. tonsa* had different rates of laying. Reconstruction of variances (from S.E. and n values in their Table 1) indicates that, of the 4 "strains", only 1107At (6 females) had a significantly deviant (higher) mean rate of laying (ANOVA, SNK test; Sokal and Rohlf, 1969; $P<0.05$). They also found, where we did not with more limited experiments, that presence of males increased length of life of females and increased egg production in longer-term experiments.

It is always possible to propose that some other, untried food or conditions would produce higher rates of egg production, perhaps closer to the maximal rate possible in nature. Since *Pseudocalanus* spp. carry their eggs in sacs that can be observed both in nature and the laboratory, the maximal rate of egg production is more readily determined than for species of copepods that lay single eggs (Corkett and Zillioux, 1975). Corkett and McLaren (1978) concluded that the maximal rate of production of egg biomass by female *Pseudocalanus* was equal to the food-satiated specific growth rate (*i.e.*, per unit of weight) of younger stages. This is a reasonable general hypothesis: maximal specific rate of production by adult females is the same as it is in younger stages. We can evaluate this hypothesis as it applies to *Acartia clausi hudsonica*.

We did not measure the growth rate of *Acartia clausi hudsonica* directly, but our estimate of exponential growth between stages can be converted to growth per day from independent estimates of food-satiated durations of these stages, assumed to be *isochronal* (i.e., all stages having the same duration at a given temperature, according to Miller *et al.*, 1977). Data for development of *A. clausi* (= *hudsonica*) from Halifax are given by Corkett and McLaren (1970) only for the period from hatching to C-I at 12.9 °C, but they argue that this period would be the same multiple (ca 4x) of embryonic duration at all temperatures. Using this argument and the temperature (T) function for embryonic duration from McLaren *et al.* (1969), the development time (D) from hatching to C-I (6 nauplius stages) of *A. clausi hudsonica* is given by $D = 4663(T + 8.2)^{-2.05}$. This also gives similar times to the more extensive, but geographically less appropriate, values for *A. clausi* from Washington (see McLaren,

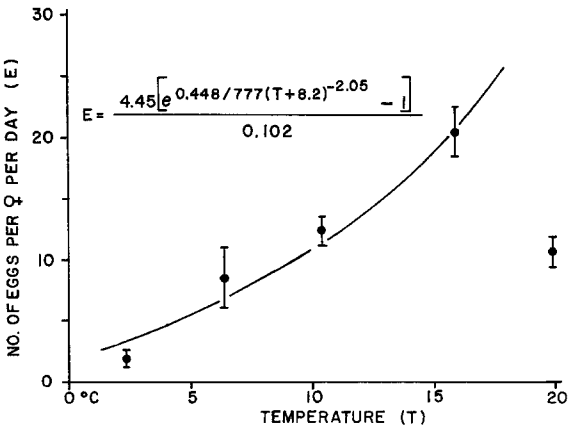

Fig. 4. *Acartia clausi hudsonica*. Observed mean rates (with 95% confidence limits of mean, from Table 2) of egg production by females compared with a predictive curve based on the growth rate of younger stages.

1978). From this equation (i.e. 4663/6 = 777), the duration of any isochronal stage is $777(T + 8.2)^{-2.05}$, and growth in $\mu g \cdot \mu g^{-1} \cdot d^{-1}$ (from our observed growth coefficient of 0.448 per stage) is:

$$\exp\left[0.448/777(T + 8.2)^{-2.05}\right] - 1$$

This can be used to predict potential production rate at any temperature of egg biomass by an egg-free female (starved weight 4.45 μg), which can then be expressed as egg number by using our estimate of egg weight (0.102 μg). The agreement with observation is excellent (Fig. 4), low rates at 2.4° and 19.9 °C having been explained earlier. Use of the estimate from regression of the weight of an egg-free female (5.04 μg, see Results) gives slightly higher, but adequate, predictions. Since development rate and body size (hence growth rate) of some copepods (including *A. clausi*) may be temperature dependent and unaffected by food levels for extensive periods in coastal marine waters (McLaren, 1978), we suggest that Fig. 4 may often describe the situation in nature.

Data from copepods other than *Pseudocalanus* (Corkett and McLaren, 1978) are inadequate for the wider testing of this hypothesis. The work by Parrish and Wilson (1978) is perhaps the most thorough study of egg production, but they did not estimate this in terms of biomass. The maximal rates found by them in *Acartia tonsa* were in two experiments with "mated" females at 18 °C fed on "standard ration" (see above). These females produced on average 59.9 ± 6.62 (n = 5) and 65.3 ± 3.76 (n = 5) eggs d^{-1}, respectively, between Day 1 and Day 14. Miller *et al.* (1977) state that food-satiated copepodites of *A. tonsa* grow at an instantaneous rate of 0.58 $\mu g \cdot \mu g^{-1}$ to a final, "unripe" female dry wt of about 4.7 μg (from their Fig. 5). It can also be estimated (interpolating from their Fig. 7) that *A. tonsa* develops rapidly at ca 1.22 stages·d^{-1} at 18 °C. Thus, instantaneous growth rate is about 0.708 $\mu g \cdot \mu g \cdot d^{-1}$ at this temperature, and a female of 4.7 μg should produce egg biomass at a maximal rate of ca 4.8 $\mu g \cdot d^{-1}$. This is more than the 2.66 $\mu g \cdot d^{-1}$ that would be produced by *A. clausi hudsonica* at 18 °C, if they were able to produce maximally at this high temperature (cf. Fig. 4). Unfortunately, there are no reliable data on egg weights of *A. tonsa*, although Miller *et al.* (1977, their Fig. 7) extrapolate weights of older stages to an estimated egg weight of ca 0.07 μg. This gives a predicted egg number (from 4.8 μg 0.07 μg^{-1}) of ca 69 d^{-1}, similar to that observed by Parrish and Wilson (1978, see above). However, in view of the approximations involved, it may be best to conclude only that high rates of production found in *A. tonsa*, compared with our findings for *A. clausi hudsonica*, are reasonable in view of the high experimental temperature, the high specific growth rate of *A. tonsa* and, possibly, its smaller egg weight.

Our data on length of reproductive periods and total egg production may be less reliable than our estimates of short-term rates of egg production, if long residence in the laboratory is inimical. Possibly these parameters could be predictable from comparative studies. For example, total number of eggs produced could be determined by a more-or-less fixed complement of primary oocytes among copepod species, or by a fixed capacity among species for total biomass production. *Pseudocalanus* from Halifax (Corkett and McLaren, 1969) produce maximally about half as many eggs as did *A. clausi hudsonica*, but their eggs may be about 3x as heavy (Corkett and McLaren, 1978). Parrish and Wilson (1978, their Fig. 2) show that, with males present, *A. tonsa* produced about 3x as many eggs as did our *A. clausi hudsonica*, but their eggs are presumably not one-third as heavy (see above). No rules seem manifest in these comparisons, and it may be that the length of the reproductive period of females varies widely among species as a demographic adaptation.

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