# FACTORS BEARING UPON EGG SIZE AND EMBRYONIC PERIOD IN OPISTHOBRANCH MOLLUSCS

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RESUMO - Um conjunto de dados derivados de observações sobre mais de 60 espécies de moluscos opistobrânquios dos oceanos Atlântico e Pacífico, incluindo espécies planctotróficas, le citotróficas e não-pelágicas, foi submetido à análise encontrar uma expressão que ajuste a massa de observações de modo aceitável. A principal finalidade foi quantificar as re lações entre tamanho do ovo, período embrionário e temperatu ra de criação de opistobrânquios A temperatura provou de importância capital na medida que uma mudança de 283 para 296 graus absolutos aumentou a taxa de desenvolvimento um fator de 2.07. O tamanho do ovo foi quase tão importante: um aumento no diâmetro do ovo de 73 para 181 micrômetros aumentou o período embrionário por um fator de 2.02. O de desenvolvimento fez apenas ligeira diferença e diferenças negligenciáveis puderam ser atribuídas ao fato das espécies serem atlânticas ou pacíficas.

ABSTRACT - A data-base derived from observations more than 60 species of opisthobranch molluscs from both Atlantic and Pacific Oceans and including planktotrophic, lecithotrophic, and non-pelagic species was subjected to analysis order to find an expression which fits the mass of data an acceptable way. The principal aim was to quantify the relationship between ovum-size, embryonic period and temperature in opisthobranchs. Temperature proved to be paramount importance to the extent that a change from 283 to 296 degrees absolute increased the development rate а factor of 2.07. Ovum size was almost equally important: an in crease in ovum diameter from 73 to 181 micrometres increased the embryonic period by a factor of 2.02. Development-type made only a slight difference, and negligible differences could be ascribed to whether the species were Atlantic or Pa cific.

### INTRODUCION

Egg development is slowed by factors tending to reduce the rate of penetration of cleavage furrows, while rapid development is encouraged by small size and factors which speed cleavage, such as high temperature.

Embryonic period is a highly characteristic feature of every oviparous species, and has been moulded by natural selection acting upon the evident need for each species make the maximal bestowal of resources for its young without incurring the penalty of slowing down development to hatching. Slowing the rate of early development is dangerous for oviparous species because it prolongs the period of exposure to accidental mechanical damage and to attack by predators at an especially vulnerable stage of the ontogeny. The provi sion of more deutoplasm for each ovum would necessarily slow down early development, because yolk takes the form of inert, heavy material which hinders the penetration of cleavage furrows.

Many viviparous animals have mastered this problem by the expedient of producing small, almost yolk-free (oligo lecithal) ova, which therefore have fewer mechanical constraints governing cleavage rate. The embryo is then nourished hour by hour according to its needs, and protected by the parental body. Oviparous species have perforce evolved other adaptations in order to avoid or mitigate the penalty that should be paid if egg-size is increased. The introduction of meroblastic cleavage by the cephalopod molluscs is a classical example. In these animals, cleavage is initially restricted to a small, relatively yolk-free blastodisc; the great mass of yolk remains undivided until a later stage. This adaptation enables development to move at a brisk pace during a sluggish period of other molluscs lives. It is axiomatic that the inhibiting effect of yolk diminishes with

have avoided the consequences of increasing ovum-size by cy-

cephalopods

time, as it is progressively metabolised. The

tological advances which speed cleavage. Other molluscs have achieved success by introducing mechanisms which diminish the effective ovum-size. Competiti ve aggression between embryonic siblings occurs in some neogastropod molluscs (reviewed by Fretter & Graham, 1962) This may be unfortunate for the individuals which are consumed by their capsule-siblings, but can be viewed as a simple adapta tion to increase the amount of deutoplasm (yolk) available to the fortunate survivors, without slowing down their bryonic development. Another evolutionary approach has invol ved separate packaging of some of the nutrient material either inside the egg-capsule (as extra-zygotic albumen, or or outside it, sometimes taking the form of discrete lozenges, one for each capsule, but occasionally forming amorphous strands in the egg-jelly, having all the visible characteristics of yolk (Boucher 1983) Presumably this material is assembled in the ovary and discharged with oocytes during ovipositon; it has been termed extra-capsular yolk or ECY (Thompson & Salghetti-Drioli, 1984) As yet, there has been no attempt to quantify the effect on developmental rate of either EZA or ECY.

In an attempt to investigate the relationship between ovum-size, embryonic period and temperature in opisthobranch molluscs, we have collected data from various sources. Where the literature is concerned, we have been handicapped in the same way as were Hadfield and Switzer-Dunlap (1984), who noted the deplorably low accuracy of some earlier workers the following terms: "A recurrent problem. is that sizes (and other similar measures) for a species often vary widely among the reports of different authors, or even among the successive publications of a single author" inclined to believe that this denotes scientific inaccuracy rather than a genuine geographical or temporal variation Consequently, we have exercised a form of selection of the data for consideration. We have taken preferentially data published within the last 25 years, when microscopical techni ques for measuring eggs have become well-established worldwi de. We have kept separate those data emanating from Atlantic fauna and the Indo-Pacific fauna. Moreover, we have separated the data derived from the three principal reproduc tive strategies (Thompson, 1967): type 1 (resulting in plank-totrophic larvae), type 2 (lecithotrophic larvae), and type 3 (direct, non-pelagic development) The data are presented in Table 1.

# AIMS

Our aims in scrutinizing these measurements were:

(1) To find an expression which fits the whole mass of data in a mathematically acceptable and biologically understandable way.

(2) To confirm that it is reasonable to assume that, for ova of the same diameter, increase of rearing temperature results in faster development (this is almost axiomatic) and to quantify that rate of increase.

(3) To attempt to show that it is reasonable to assume that, for eggs reared at the same temperature, the larger the egg the longer it takes to develop to hatching.

(4) To see if, within the range of species studied, there is a significant difference in development rate that can be related to whether the species undergo type 1 (planktotrophic), type 2 (lecithotrophic) or type 3 (direct) development.

(5) To see if any significant difference in development rate can be ascribed to whether the species are Atlan - tic or Pacific in habitat.

## **METHODS**

After trying a variety of mathematical relationships and fitting methods, we decided to fit an equation of the type:

$$P = a.D^b e^{\frac{C}{T}}$$

where P is the embryonic period in days, D the ovum diameter in micrometres and T the absolute temperature in Kelvins; a, b and c are constants to be fitted and e is the base of natural logarithms.

The reasons for choosing this particular formula

were:

- (1) In its logarithmic form,  $\ln P = \ln a + b \cdot \ln D + c/T$ , it can be fitted using ordinary multiple-regression methods, which is what we decided to do.
- (2) The fit with the data was as good as the fit of any other three-parameter formula that we tried.
- (3) The temperature term  $e^{\frac{x}{T}}$  is of a form similar to that frequently used in physiological studies, and comparison is therefore easy.

(4) It seems intuitively sensible to use an expression

in which a rate term,  $e^{\overline{T}}$  is divided into a term  $a.D^b$  which represents, in some sense, the 'amount of development to be done'

Against these advantages must be set the need to justify the procedure of fitting the logarithm of the embryonic period by least squares, as opposed to fitting, say. the period itself, the development rate or the logarithm of the rate (all of which would have given different results) Some of the evidence in this paper, for example that relating to normality and homogeneity of residuals, lends support to our choice as being statistically reasonable.

Naturally, more complicated equations could have been used to achieve a closer fit, but some were tried and the improvement in fit did not appear to justify the additional complication.

### RESULTS

The equation which best fitted the selected data was:

4687

$$lnP = -17.4 + 0.775.ln D + 4687/T$$

corresponding to P = 
$$(2.78 \times 10^{-8}).D^{0.775}$$
 e  $\frac{4687}{T}$ 

where P is the embryonic period in days, D the ovum diameter in micrometres and T the absolute temperature in Kelvins.

Inspecting the equation per se, the term  $e^T$  indicates that a 10° C rise in temperature increases the develop ment rate by a factor of about 1.8, which is quite normal

for a physiological process. Also, increase in size incurs a rather small penalty; a doubling of ovum volume multiplies embryonic period by a factor of only 1.2.

embryonic period by a factor of only 1.2.

It is opportune here to interject that these conclusions are adequately reliable, as may be judged from the standard deviations of the fitted constants, which are tabulated below:

CIOM:		
	value	standard deviation
coefficient of $1/T$ :	4687	+ 628
coefficient of lnD:	0.775	<del>+</del> 0.106
constant term:	-17.4	+ 2.23

Inspection of the residuals (the set of 71 differences between the logarithms of the observed embryonic periods and those predicted by the equation) yields 4 conclusions, of which the first two are of statistical interest and the last two of biological importance (Table 1):

- two of biological importance (Table 1):

  (1) There is no significant correlation (throughout this paper significance is measured at the 5% level) between the numerical size of the residuals and the logarithm of the embryonic period (r = 0.09); in other words, the amount of "scatter" of the points is similar whether the embryonic period is long or short.
- (2) The residuals are normally distributed (judged by d'Agostino's (1971) test)
- (Points (1) and (2) strengthen the case for our choice of method.)
- (3) The mean residuals for species with type 1, type 2 and type 3 development are +0.028, -0.148 and +0.098 res -pectively; these may be compared with the standard deviation of all 71 residuals which is  $\pm$  0.398. Analysis of variance shows the difference between the three means to be not significant.
- (4) The mean residuals for Atlantic and Pacific species are +0.0026 and -0.0052 respectively. The difference is far from significant.

#### CONCLUSIONS

We can now list the four factors that we have considered, in order of their 'importance':

- (1) Temperature is paramount; taking as representative temperatures those corresponding to (mean  $\pm$  standard deviation) of the 1/T values, a change of rearing temperature from 283 to 296 degrees absolute increases the development rate by a factor of 2.07
- (2) Ovum size is almost equally 'important; taking as representative ovum sizes those corresponding to (mean ± standard deviation) of the ln D values, an increase in ovum size from 73 to 181 micrometres increases the embryonic period by a factor of 2.02.
- (3) Development type makes a slight difference; type 2 developers average 20% faster and type 3 developers 7%

period in days. Column 5 contains the natural logarithms of the observed embryonic period. Column 6 gives the predictions of the embryonic periods as made by the empirical equation in the text. The entry in the 'residual' column is the result of subtracting Table 1. Embryonic periods of opisthopranch molluscs. Column 2 lists representative ovum diameters in micrometres, column 3 the absolute temperature and column 4 the embryonic the prediction in column 6 from the observation in column 5.

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ri 290 298 13 2.565 2.724 -0.159 Tardy, 1962  ri 380 283 50 3.912 3.767 +0.145 Thompson, 1967  160 285 19 2.970 2.987 -0.011 Rivest, 1978  103 295 19 2.990 2.371 -0.013 Rivest, 1979  200 285 18 2.890 2.371 +0.519 Schmedt, 1966  2130 293 18 2.890 2.371 +0.519 Schmedt, 1967  2130 293 28 3.332 3.311 +0.024 Ramatani, 1967  2245 285 28 3.332 3.311 +0.020 Ramatani, 1967  225 295 296 2.708 2.600 Hamatani, 1967  227 2296 2.708 2.600 Hamatani, 1967  228 2.708 2.708 2.708 2.708 2.708 2.708 2.600 Ramatani, 1972  220 2.996 2.711 +0.285 Rhompson, 1972  230 2.95 2.708 2.7	Phestilla siboyae	225	301.5	10	2.303	2.345	-0.042	Gohar & Abul+Ela, 1957
ri 290 298 13 2.565 2.724 -0.159 Tardy, 1962 180 283 50 3.912 3.767 +0.145 Thompson, 1967 1968 180 283 50 3.912 3.767 +0.145 Thompson, 1967 1968 193 295 19.5 2.970 2.981 -0.011 Rivest, 1979 193 295 20.5 289 2.371 +0.021 System, 1978 200 2.371 +0.024 200 2.371 1968 2.087 1979 274.1 120 4.787 4.303 +0.0484 Seager, 1979 245 285 285 2.383 2.363 +0.060 Hamatani, 1967 200 295 15 2.303 2.363 -0.060 Hamatani, 1967 200 295 28 2.303 2.363 -0.060 Hamatani, 1967 200 295 28 2.303 2.303 2.363 -0.060 Hamatani, 1977 200 295 28 2.303	per cherring creams							
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sa 100 285 19.5 2.370 2.381 5.154 10.11 Exteri 1979 2.39 1 2.39 1 2.39 2.371 1.30 2.39 1 2.39 2.371 1.30 2.39 1 2.39 2.371 1.30 2.39 2.37 2.30 2.371 2.30 2.37 2.30 2.30 2.37 2.30 2.30 2.30 2.30 2.30 2.30 2.30 2.30	Cadlina laevis	380	283	000	2.912	000	100	Digeo + 1978
sa 103 295 7 1.946 2.082 -0.130 Sylver, 127, 126 2.082 2.37 40.130 Sylver, 127, 120 2.37 40.184 40.024 Chia, 197 245 285 28 3.37 40.88 40.100 Sweer, 1987 spatiatellus 170 297 10 2.303 2.363 -0.060 Hamatani, 1967 page 2.5 15 2.996 2.711 40.285 Thompson, 1972, 1872 295 20 2.996 2.711 40.285 Thompson, 1972, 1872 20 2.996 2.711 40.285 Shows, 1972 and 150.5 287.5 30 3.491 2.790 40.611 Bridges, 1975	Cuthona nana	160	282	19.0	2.970	106.7	10.0	0.00
sa 130 293 18 2.890 2.371 +0.319 Chia. 1370 283 18 3.178 40.024 Chia. 1370 283 284 1.878 4.303 +0.024 Seager, 1379 274.1 120 4.787 4.303 +0.024 Seager, 1379 245 285 285 3.332 3.311 +0.021 Smith, 1967 285 285 15 2.303 2.363 -0.060 Hamatani, 1967 292 15 2.708 2.303 -0.060 Hamatani, 1967 292 15 2.708 2.303 -0.060 Hamatani, 1967 292 295 15 2.708 2.403 2.403 2.403 2.303 4.010 Express, 1980 293 282 18.5 2.318 3.437 +0.519 Babb, 1937 2.318 2.354 40.066 Gobar & Soliman Lori 150.5 287.5 30 3.401 2.790 4.0.11 Bridges, 1978	Tenellia pallida	103	295		1.946	7.087	00.1.00	Eyster, 1979
200 285 24 3.178 4.154 40.024 Chish 19/1 379 245 28 3.178 4.313 40.484 Seager, 1379 245 285 28 3.332 3.311 40.021 Smith, 1967 striatellus 170 297 10 2.303 2.363 -0.060 Hamatani, 1967 pa 120 295 15 2.908 2.608 +0.100 Eyser, 1967 netti 240 295.5 20 2.996 2.711 +0.285 Thompson, 1972, 240 295.5 20 3.918 3.437 +0.519 Babb, 1937 Lori 150.5 287.5 30 3.401 2.790 +0.611 Bridges, 1975	Princhesia granosa	130	293	18	2.890	2.371	40.519	Schmekel, 1950
379 274.1 120 4.787 4.303 +0.484 Seager, 1979 245 285 2.88 3.332 3.311 +0.021 Smith, 1967 striatellus 170 297 10 2.303 2.363 -0.060 Hamatani, 1967 pa pa etti 2.30 2.95 15 2.708 2.408 40.100 Eyeser, 1980 pa etti 2.30 2.95 18.5 2.318 3.437 +0.285 Exp. 1980 pa 10.21 2.30 3.00 11 2.396 2.312 +0.066 Gobar & Soliman pari 150.5 2.87.5 30 3.401 2.790 +0.611 Bridges, 1975	Acteonia cocksi	200	285	24	3.178	3,154	+0.024	Chia, 19/1
striatellus 170 297 10 2.303 2.353 -0.060 Hamatani, 1967 pa 203 295 15 2.396 2.701 +0.285 Thompson, 1967 netti 230 295, 2.0 2.996 2.711 +0.285 Thompson, 1972; 2.0 2.996 2.711 +0.285 Thompson, 1972; 2.0 30 30 11 2.399 3.437 +0.519 Babi, 1937 and 10.5 2.91 3.437 +0.519 Babi, 1937 and 10.5 2.790 40.611 Bridges, 1975	philips gibbs	379	274.1	120	4.787	4.303	+0.484	Seager, 1979
striatellus 170 297 10 2.303 2.363 -0.060 Hamatani, 1967 pa 27 10 2.303 2.363 -0.060 Hamatani, 1967 pa 2.303 2.363 -0.060 Hamatani, 1967 pa 2.303 2.303 -0.060 Hamatani, 1967 pa 2.303 2.304 2.304 2.304 2.304 10.285 Thompson, 1972 pa 2.30 2.30 2.30 10.285 pa 2.304 2.305 40.066 Gobar & Goliman Loris 150.5 287.5 30 30 31 2.396 2.332 40.066 Gobar & Goliman Loris 150.5 287.5 30 30 31 2.390 40.611 Bridges, 1975	FILLIANCE GLODE	275	285	28	3 332	3.311	+0.021	Smith, 1967
striatellus 170 297 10 2.303 2.363 -0.060 Hamatani, 1967 pa 2.303 2.96 2.608 +0.100 Eyster, 1980 netti 240 295.5 20 2.996 2.711 +0.285 Thompson, 1972; 230 282 18.5 2.918 3.437 +0.519 Babi, 1937 and 200 300 310 2.996 2.332 +0.066 Gohar & Soliman lors 150.5 287.5 31 3.491 2.790 +0.611 Bridges, 1975	Ketusa obtusa	Ç	1	2				
striatellus 170 297 10 2.303 2.363 -0.060 Hammatani, 1967 pa 203 295 15 2.306 2.608 +0.100 Eyster, 1980 netti 240 295.5 20 2.996 2.711 +0.285 Thompson, 1972; netti 230 282 18.5 2.918 3.437 -0.519 Baba, 1937 and 10.00 11 2.32 +0.066 Gobar Soliman lori 150.5 287.5 30 3.411 2.790 +0.611 Bridges, 1975	Pacific: type 3							
State Land 20 25 15 2.706 2.608 +0.100 Eyeter, 1980 metti 240 295. 50 2.996 2.131 +0.285 Thompson, 1972 metti 230 295. 5 2 2.996 2.337 +0.285 Thompson, 1973 230 3.00 310 2.396 2.332 +0.066 Gohar & Soliman Lori 150.5 287.5 30 3.401 2.790 +0.611 Bridges, 1975	and later attended the	0.2.1	207	10	2.303	2.363	-0.060	Hamatani, 1967
pu 240 295.5 20 2.996 2.711 +0.285 Thompson, 1972; 130 282 18.5 2.918 3.437 -0.519 Baba, 1937 200 300 18.5 2.918 2.332 +0.066 Gohar & Soliman 10x1 150.5 287.5 31 3.401 2.790 +0.611 Bridges, 1975	Dermarobranchus striaterius	2 0	200	· ·	2 708	2.608	+0.100	
Netta 240 295. 2 2 2 3 4 3 7 -0.519 Babb, 1937 2 3 0 1 2 2 9 0 2 1 2 2 0 2 1 2 1 2 1 2 1 2 1 2 1 2 1	Doriopsilla pharpa	200	200	10	2 006	2 711	+0.285	Thompson, 1972; Rose, 1981
230 202 11 2.398 2.332 +0.066 100ri 150.5 287.5 30 3.401 2.790 +0.611	Hypselodoris bennetti	240	0.000	100	2.0.2	3.437	-0.519	Baba, 1937
lori 150,5 287,5 30 3.401 2.790 +0.611	Okadaia elegans	730	707		300	2 3 3 3	+0.046	Gobar & Soliman, 1967
150.5 287.5 30 3.401	Trippa spongiosa	200	000	11			100.01	Bridges 1975
	Phyllaplysia taylori	150.5	287	30	704.0		110.01	

Table 1. (cont.)

Atlantic: type 1 Archidoris pseudoargus Jorunna tomentosa Acanthodoris pilosa Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata	Δ	d L	Д,	ln P	In P	Residual	Reference	
Atlantic: type 1 Archidoris pseudoargus Jorunna tomentosa Acanthodoris pilosa Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata								
Archidoris pseudoargus Jorunna tomentosa Acanthodoris pilosa Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata								
Archidoris pseudoargus Jorunna tomentosa Acanthodoris pilosa Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata			0		0		1001	
Jorunna tomentosa Acanthodoris pilosa Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata	155	283	87	3.332	3.072	+0.200	Tuosdwout	
Acanthodoris pilosa Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata	79.5	282.5	23	3.135	2.584	+0.551		
Onchidoris bilamellata Onchidoris muricata Polycera quadrilineata	70	283	10	2.303	2.457	-0.154	Thompson, 1967	
Onchidoris muricata Polycera quadrilineata	06	283	18	2.890	2.651	+0.239	Thompson, 1967	
Polycera quadrilineata	86.5	282.5	14	2.639	2,650	-0.011	Thompson, 1967	
	80	282	10	2.944	2.619	+0,325	Thompson, 1967	
Doto coronata	4	283	16	2.773	2.387	+0.386	Thompson, 1967	
Borginos torginos	* C	500	ı ır	509	1 995	-0.386	Tardy, 1964	
Teldibes celdibes	0 1	000	יי		27.0	200	Cohmobol & Dortmann 1982	1982
rergipes rergipes	0 :	700	0.0	7,07	7. TOO	200	Thompson 1967	1001
Coryphella lineata	/ 9	7.187		1.946	2.1.2	20.0-	THOMPSON, 1967	
Hero formosa	82	283	80	2.890	2.579	+0.311	Luosdwour	
Tritonia plebia	82	283	10	2,303	2.607	-0.304	Thompson, 1967	
Doto fragilis	83	284	18	2.890	2.530	+0.360	Kress, 1975	
Doto pipnatifida	99.5	284	16	2.773	2.671	+0.102	Thompson & Brown, 1984	, 1984
Cuthona gymnota	116	289	8,5	2.140	2.504	-0.364	Miller, 1958	
Enbranchus farrani	06	289		1.792	2.307	-0.515	Schmekel & Portmann, 1982	ann, 1982
Dicata odbneri	0 80	289	6.5	1.872	2.216	-0.344	Schmekel & Portmann,	ann, 1982
Corvohella gracilis	20.00	285	13.5	2.603	2.154	+0.449	Kuzirian, 1979	
Corvohella pellucida	75	282	13	2.565	2.569	-0.004	Kuzirian, 1979	
Corvohella verrucosa	92.5	286	8.5	2.140	2.499	-0.359	Kuzirian, 1979	
Corvohella pedata	80	289	9	1.792	2,216	-0.424	Schmekel & Portmann, 1982	ann, 1982
Alderia modesta	82.5	288	5.2	1,658	2.296	-0.638	Thompson, 1967	
Anlysia minctata	86	288	21	3.045	2.430	+0.615	Thompson & Bebbington,	
Aplysia depilans	86	298	15	2,708	1.884	+0.824	Thompson & Bebbington,	
Aplysia fasciata	102	298	15	2.708	1,915	+0.793	Thompson & Bebbington,	ngton, 1969
Acteocina canaliculata	91.5	292	2	1.609	2.154	-0.545	Franz, 1971	
Doridella obscura	65	298	4	1,386	1.565	-0.179	Perron & Turner, 1977	1977
Pacific: type 1								
Doridolla etcinbergae	C	286 5	7 8	2 048	2.358	-0.310	Bickell & Chia. 1979	1979
DOLLIGHTIS SCETTISCE Gae	2 4			100	0 2 1 0	-0.463	Harrigan & Alkon 1978	1978
nermissenda crassicornis	נפר	207	יי	1 872	2 167	-0.295	Harris 1975	2111
Prestilla meranopranchia	C T T	1000		10.	201.0		Orize C Want 107	0
Rostanga pulchra	08	285.5	15.5	7.74T	7.410	+0.326	Chia & NOSS, 1970	7,701
Tritonia diomedea	7.6	784.9	17	2.398	2.228	00T.0-	Velipt & Willows, 1977	7767
Elysia chlorotica	9/	295	9	1.792	1.847	-0.055	Harrigan & Alkon, 1978	1978
Elysia chlorotica	92	283.5	12	2.485	2.491	900.0-	Harrigan & Alkon, 1978	, 1978
Aplysia californica	85	295	6	2.197	1.933	+0.264	Kriegstein et al., 1974	
Aplysia dactylomela	06	298	80	2.079	1.818	+0.261	Switzer-Dunlap & Harris,	
Anlysia inliana	7.7	298	7	1.946	1.697	+0.249	Switzer-Dunlap &	Harris, 1977
Burgatella leachi plei	87	298	7	1.946	1.791	+0.155	Paige, 1979	
Dolaholla anriomaria	65	298	9.5	2,251	1,835	+0.416	Switzer-Dunlap &	
DOIGNETTA AULICUIALIA	20	000		1 872	1 577	10 0t	Switzer-Dunlan & Harrie	

slower development to hatching than type 1 species, but these differences are not statistically significant.

(4) Negligible differences can be ascribed to whe - ther the species are Atlantic or Pacific.

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