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 para 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 ser de importância capital na medida que uma mudança de 283 para 296 graus absolutos aumentou a taxa de desenvolvimento por 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 tempo 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 on 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 in order to find an expression which fits the mass of data in an acceptable way. The principal aim was to quantify the relationship between ovum-size, embryonic period and rearing temperature in opisthobranchs. Temperature proved to be of paramount importance to the extent that a change from 283 to 296 degrees absolute increased the development rate by a 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 redu
ce 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 to
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 an
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 cons -
traints governing cleavage rate. The embryo is then nouri -
shed 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 introduc -
tion 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
time, as it is progressively metabolised. The cephalopods
have avoided the consequences of increasing ovum-size by cy-
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 neo-
gastropod 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 em-
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
EZA) 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 ma-
terial is assembled in the ovary and discharged with the
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 no-
ted the deplorably low accuracy of some earlier workers in
the following terms: "A recurrent problem.   is that   egg
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"   We   are
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   the
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 un-
derstandable way.
        (2) To confirm that it is reasonable to assume that,
for ova of the same diameter, increase of rearing temperatu-
re 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 (plank-
totrophic), type 2 (lecithotrophic) or type 3 (direct) deve-
lopment.
        (5) To see if any significant difference in develop-
ment 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, $\ln P = \ln a + b.\ln D + c/T$, 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 $e^{\frac{c}{T}}$ is of a form similar to that frequently used in physiological studies, and compari - son is therefore easy.

(4) It seems intuitively sensible to use an expression in which a rate term, $e^{\frac{-c}{T}}$ 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:

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

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 $e^{\frac{4687}{T}}$ indicates that a 10° C rise in temperature increases the development 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.
        It is opportune here to interject that these conclu-
sions are adequately reliable, as may be judged from   the
standard deviations of the fitted constants, which are tabu-
lated below:

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

        Inspection of the residuals (the set of 71 differen-
ces 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):
        (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 pe-
riod 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 choi
ce 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 $+$ 0.398. Analysis of   variance
shows the difference between the three means to be not signi
ficant.
        (4) The mean residuals for Atlantic and Pacific spe-
cies are +0.0026 and -0.0052 respectively. The difference is
far from significant.

                        CONCLUSIONS

        We can now list the four factors that we have consi-
dered, in order of their 'importance':
        (1) Temperature is paramount; taking as representati
ve temperatures those corresponding to (mean $+$ standard devia
tion) 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 pe -
riod by a factor of 2.02.
        (3) Development type makes a slight difference; type
2 developers average 20% faster and type 3 developers   7%

Table 1. Embryonic periods of opisthobranch molluscs. Column 2 lists representative ovum diameters in micrometres, column 3 the absolute temperature and column 4 the embryonic 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 the prediction in column 6 from the observation in column 5.

Species	Observations			ln P	Predicted ln P	Residual	Reference
	D	T	P				
Atlantic: type 2							
Adalaria proxima	185	282.5	39	3.664	3.239	+0.425	Thompson, 1958
Tritonia hombergi	200	282.5	37	3.611	3.299	+0.312	Thompson, 1962
Dendronotus frondosus	220	283	32	3.466	3.344	+0.122	Thompson, 1967
Armina tigrina	199	296	8.5	2.140	2.539	-0.399	Eyster, 1981
Eubranchus exiguus	120	296	9.5	2.251	2.147	+0.104	Tardy, 1962
Eubranchus farrani	140	292	8	2.079	2.483	-0.404	Todd, 1981
Eubranchus farrani	137	284	15	2.708	2.918	-0.210	Kress, 1972
Facelina fusca	180	286	9	2.197	3.015	-0.818	Schmekel, 1966
Tenellia pallida	140	290.3	9	2.197	2.577	-0.380	Rasmussen, 1944
Tenellia pallida	72	288	4	1.386	2.191	-0.805	Eyster, 1979
Berthelinia caribbea	100	298.5	15	2.708	1.873	+0.835	Grahame, 1969
Pacific: type 2							
Cuthona adyarensis	180	296	4	1.386	2.461	-1.075	Rao, 1961
Discodoris erythraeensis	140	292	11.5	2.442	2.483	-0.041	Gohar & Abul-Ela, 1959
Rolidina mannarensis	150	303	8	2.079	1.954	-0.125	Rao & Alargaswamy, 1960
Melibe pilosa	128	298	8.5	2.140	2.090	+0.050	Hadfield & Switzer-Dunlap, 1984
Phestilla sibogae	156	298	7	1.946	2.244	-0.298	Hadfield & Switzer-Dunlap, 1984
Berthellina citrina	225	301.5	10	2.303	2.345	-0.042	Gohar & Abul-Ela, 1957
Atlantic: type 3							
Aeolidiella alderi	290	298	13	2.565	2.724	-0.159	Tardy, 1962
Cadlina laevis	380	283	50	3.912	3.767	+0.145	Thompson, 1967
Cuthona nana	160	285	19.5	2.970	2.981	-0.011	Rivest, 1978
Tenellia pallida	103	295	7	1.946	2.082	-0.136	Eyster, 1979
Trinchesia granosa	130	293	18	2.890	2.371	+0.519	Schmekel, 1966
Acteonia cocksi	200	285	24	3.178	3.154	+0.024	Chia, 1971
Philine gibba	379	274.1	120	4.787	4.303	+0.484	Seager, 1979
Retusa obtusa	245	285	28	3.332	3.311	+0.021	Smith, 1967
Pacific: type 3							
Dermatobranchus striatellus	170	297	10	2.303	2.363	-0.060	Hamatani, 1967
Doriopsilla pharpa	203	295	15	2.708	2.608	+0.100	Eyster, 1980
Hypselodoris bennetti	240	295.5	20	**2.996**	2.711	+0.285	Thompson, 1972; Rose, 1981
Okadaia elegans	230	282	18.5	**2.918**	3.437	-0.519	Baba, 1937
Trippa spongiosa	200	300	11	**2.398**	2.332	+0.066	Gohar & Soliman, 1967
Phyllaplysia taylori	150.5	287.5	30	3.401	2.790	+0.611	**Bridges, 1975**

Table 1. (cont.)

Species	Observations			ln P	Predicted ln P	Residual	Reference
	D	T	P				
Atlantic: type 1							
Archidoris pseudoargus	155.5	283	28	3.332	3.072	+0.260	Thompson, 1967
Jorunna tomentosa	79.5	282.5	23	3.135	2.584	+0.551	Thompson, 1967
Acanthodoris pilosa	70	283	10	2.303	2.457	-0.154	Thompson, 1967
Onchidoris bilamellata	90	283	18	2.890	2.651	-0.239	Thompson, 1967
Onchidoris muricata	86.5	282.5	14	2.639	2.650	-0.011	Thompson, 1967
Polycera quadrilineata	80	282	10	2.944	2.619	+0.325	Thompson, 1967
Doto coronata	64	283	16	2.773	2.387	+0.386	Thompson, 1967
Tergipes tergipes	80	293	5	1.609	1.995	-0.386	Tardy, 1964
Tergipes tergipes	75	289	6.5	1.872	2.166	-0.294	Schmekel & Portmann, 1982
Coryphella lineata	67	287.2	7	1.946	2.178	-0.232	Thompson, 1967
Hero formosa	82	283	18	2.890	2.579	+0.311	Thompson, 1967
Tritonia plebia	85	283	10	2.303	2.607	-0.304	Thompson, 1967
Doto fragilis	83	284	18	2.890	2.530	+0.360	Thompson, 1967
Doto pinnatifida	99.5	284	16	2.773	2.671	+0.102	Kress, 1975
Cuthona gymnota	116	289	8.5	2.140	2.504	-0.364	Thompson & Brown, 1984
Eubranchus farrani	90	289	6	1.792	2.307	-0.515	Miller, 1958
Dicata odhneri	80	289	6.5	1.872	2.216	-0.344	Schmekel & Portmann, 1982
Coryphella gracilis	55	285	13.5	2.603	2.154	+0.449	Schmekel & Portmann, 1982
Coryphella pellucida	75	282	13	2.565	2.569	-0.004	Kuzirian, 1979
Coryphella verrucosa	92.5	286	8.5	2.140	2.499	-0.359	Kuzirian, 1979
Coryphella pedata	80	289	6	1.792	2.216	-0.424	Kuzirian, 1979
Alderia modesta	82.5	288	5.2	1.658	2.296	-0.638	Schmekel & Portmann, 1982
Aplysia punctata	98	288	21	3.045	2.430	+0.615	Thompson, 1967
Aplysia depilans	98	298	15	2.708	1.884	+0.824	Thompson & Bebbington, 1969
Aplysia fasciata	102	298	15	2.708	1.915	+0.793	Thompson & Bebbington, 1969
Acteocina canaliculata	91.5	292	5	1.609	2.154	-0.545	Franz, 1971
Doridella obscura	65	298	4	1.386	1.565	-0.179	Perron & Turner, 1977
Pacific: type 1							
Doridella steinbergae	80	286.5	7.8	2.048	2.358	-0.310	Bickell & Chia, 1979
Hermissenda crassicornis	65	287	5.5	1.705	2.168	-0.463	Harrigan & Alkon, 1978
Phestilla melanobranchia	115	295	6.5	1.872	2.167	-0.295	Harris, 1975
Rostanga pulchra	80	285.5	15.5	2.741	2.415	+0.326	Chia & Koss, 1978
Tritonia diomedea	92	284.9	6	1.792	2.558	-0.160	Kempf & Willows, 1977
Elysia chlorotica	76	295	6	1.792	1.847	-0.055	Harrigan & Alkon, 1978
Elysia chlorotica	76	283.5	12	2.485	2.491	-0.006	Harrigan & Alkon, 1978
Aplysia californica	85	295	9	2.197	1.933	+0.264	Kriegstein et al., 1974
Aplysia dactylomela	90	298	8	2.079	1.818	+0.261	Switzer-Dunlap & Harris, 1977
Aplysia juliana	77	298	7	1.946	1.697	+0.249	Switzer-Dunlap & Harris, 1977
Bursatella leachi plei	87	298	7	1.946	1.791	+0.155	Paige, 1979
Dolabella auricularia	92	298	9.5	2.251	1.835	+0.416	Switzer-Dunlap & Harris, 1977
Stylocheilus longicauda	66	298	6.5	1.872	1.577	+0.295	Switzer-Dunlap & Harris, 1977

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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