Optimal growth model for the latitudinal cline of shell morphology in cowries (genus *Cypraea*)

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ABSTRACT

The marine Indo-Pacific cowry, *Cypraea caputserpentis*, shows geographic variation of life history and shell morphology. Adult body size increases with latitude, but shell thickness decreases with latitude. To explain the clinal variations, we study a mathematical model of the optimal growth schedule. The life history of cowries consists of three stages: shell volume increases in the juvenile stage, which is followed by the callus-building stage in which shell thickness increases, and then reproduction starts without further growth in the adult stage. We calculate the lengths of juvenile and callus-building stages that maximize lifetime reproduction. By considering latitudinal change in the mortality and growth-promoting factors, the observed clinal patterns of juvenile traits can be explained by a negative latitudinal gradient of shell-crushing predators. This suggests the importance of a latitudinal gradient of predation pressure for body-size clines in marine ectotherms. On the other hand, latitudinal clines of shell thickness can be explained by a latitudinal gradient of either shell-crushing predation pressure or one of the environmental factors promoting shell thickening, such as seawater temperature.

Keywords: *Cypraea caputserpentis*, latitudinal gradient, optimal growth schedule, phenotypic plasticity, shell thickness.

INTRODUCTION

Many phenetic traits of animals show considerable geographic variation within species. For example, numerous species of the class Gastropoda exhibit geographic variation in shell morphology and other characteristics (Phillips *et al.*, 1973; Seeley, 1986; Reid, 1996; Trussell, 2000), and some show latitudinal clines (Frank, 1975; Kenny, 1983; Tissot, 1984; Trussell, 2000).

The serpent's head cowry, *Cypraea caputserpentis* (Gastropoda: Cypraeidae), displays prominent patterns of geographic variation. Within its broad distribution ranging from southeast Africa to the west Pacific (Tissot, 1984, 1988; Irie, 1997), body size is larger at higher latitudes, whereas the shell is thicker at lower latitudes (Fig. 1). Ecological background causing these gradients of shell morphology has not been studied well. Cowries

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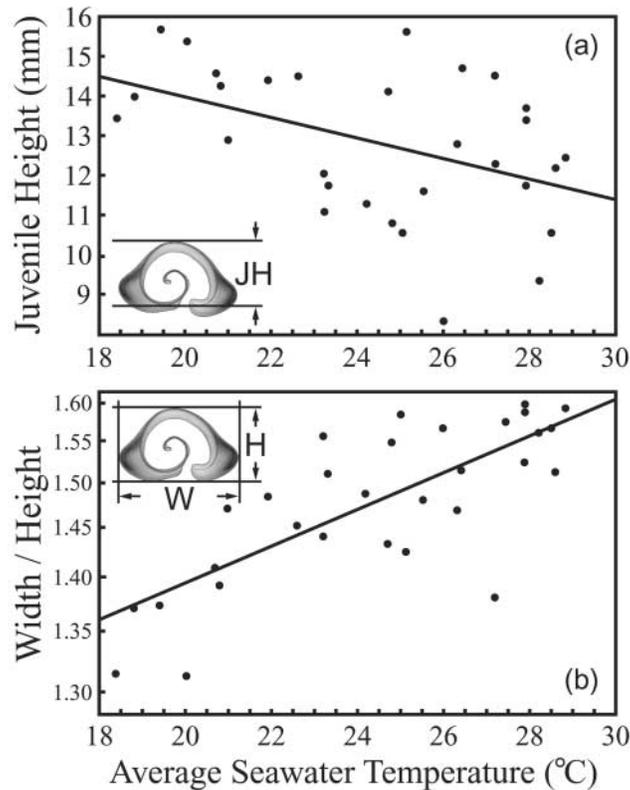
Fig. 1. Latitudinal clines of juvenile shell size and callus thickness in *Cypraea caputserpentis*. Samples were collected from 30 localities covering the whole distribution. Values are means of all individuals at a given locality. (a) The relationship between average seawater temperature and juvenile height (JH). The regression of juvenile height (y) on average seawater temperature (x) is $y = -0.258x + 19.124$ ($r^2 = 0.20$, $P = 0.014$). (b) The relationship between average seawater temperature and width/height (W/H). The regression of arcsin $\sqrt{\text{height/width}}$ (y) on average seawater temperature (x) is $y = -0.579x + 69.536$ ($r^2 = 0.57$, $P < 0.01$). Average surface seawater temperatures were obtained from the National Oceanic and Atmospheric Administration (1984–98) and the Japan Meteorological Agency (1981–93).

are determinate growers. They stop growing when they start reproduction, which is rather exceptional among marine organisms. This simplifies the analysis of their life-history pattern.

A female cowry deposits hundreds of thousands of eggs in a single breeding event (Burgess, 1985). Most species of the family Cypraeidae have a pelagic veliger stage, in which the larvae have a minute conical shell (veliconch). At a certain point in their development, the larvae start sinking and settle on the bottom of the sea. After settlement, cowries experience metamorphosis and begin secreting a new shell whorl on their veliconch ('bulla' stage). During this juvenile stage, cowries continue to expand their juvenile shell in oliviform (olive-shape), until the aperture narrows and teeth are moulded on both the columella (the central axis of the shell) and outer lip. In the subsequent pre-adult stage, the

outer surface of the juvenile shell becomes coated with calcareous materials. The shell part thickened in this stage is called the 'callus'. After callus-building is completed, cowries reach maturity and begin reproduction.

Juvenile shell size in *C. caputserpentis* is larger at higher latitudes. This gradient has recently attracted much research effort in the context of the ecology and evolution of body size (Partridge and Harvey, 1988; Pianka, 1995; Willemsen and Hailey, 1999). Controversy regarding the causal mechanisms centres around whether the observed body size gradients are adaptive patterns (David *et al.*, 1977; Coyne and Beecham, 1987; Mousseau, 1997; Partridge and Coyne, 1997; Arnett and Gotelli, 1999) or the outcome of developmental constraints (Cavicchi *et al.*, 1985; Partridge *et al.*, 1994; James *et al.*, 1995; Van Voorhies, 1996; Van Der Have and De Jong, 1996). On the other hand, the clinal variation of callus thickness in *C. caputserpentis* can be regarded as an example of the negative relationship between skeletal calcification and latitude, which is universal among marine gastropods and other invertebrates. Predation by shell-crushing predators is thought to be particularly important in producing this gradient (Vermeij, 1978, 1987), although inorganic properties of seawater that promote precipitation of calcium carbonate are also recognized as potential factors responsible for the cline (Graus, 1974).

Geographical correlation between phenotypic characters and the environment may help reveal the ultimate forces that mould phenotypes (Gould and Johnston, 1972). In many cases, however, selective agents creating the latitudinal clines are not fully understood, because multiple ecological parameters (e.g. temperature, season length, predation pressure, population density) often covary latitudinally.

In this paper, we construct and analyse an optimal life-history model in an attempt to identify the probable factors and underlying mechanisms for the geographic variation in *C. caputserpentis*. We show that a negative latitudinal gradient of mortality is needed to explain the observed patterns – that is, the juvenile shell is smaller, the juvenile stage is shorter and juvenile growth speed is faster at lower latitudes. However, the observed cline of shell thickness can be caused by a latitudinal gradient of shell-crushing predation pressure, by a gradient of the environmental factors promoting calcification, or both. We discuss implications of the model for the factors responsible for the latitudinal pattern of shell morphology of cowries and other ectotherms that have determinate growth.

MODEL

Before the mature stage, cowries grow their shells in the juvenile stage and the subsequent pre-adult stage of callus building (Fig. 2). The callus defends the adult against predators. The living mass of an adult is, however, confined to the part formed during its juvenile stage, and the fecundity of an adult is also controlled by the shell size at the end of the juvenile stage, because the coiling ceases once callus building starts. We call this part of an adult body its 'juvenile shell'. We assume that the volume of the juvenile shell, $V(x)$, increases according to a power function whose parameter, x, is the length of the juvenile stage:

$$V(x) = \alpha x^{\beta} \tag{1}$$

(see Appendix 1 for justification). In exoskeletal animals including cowries, growth rate α depends on the rates of expansion of both living soft-body tissue and skeletal shells. Since the power, β, is related to the allometry between body size and metabolism (see Appendix 1),
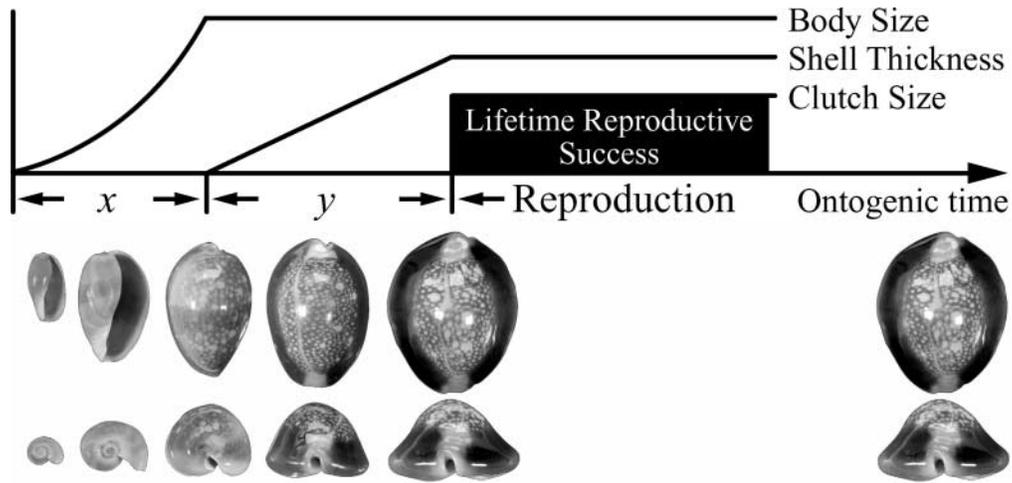
Fig. 2. Framework of growth schedule model and ontogenetic development of *C. caputserpentis* shell (dorsal and anterior views). The ontogeny of cowries after settlement consists of three stages: shell volume increases during the juvenile stage, the callus is thickened during the callus-building stage, then sexual maturation is achieved. The length of the juvenile stage is indicated by *x* and that of the callus-building stage by *y*.

it is independent of latitude. $V(x)$ is concave-up over x, the length of the juvenile stage, because the power β equals 3 (see Appendix 1).

Modelling how callus thickness increases with time, we examine two situations in this paper. In the simpler case, 'size-independent calcification', callus thickness increases at a constant speed. Callus thickness, denoted by C, is proportional to the length of the callus-building stage, y, as follows:

$$C(y) = ry \tag{2}$$

where r is the calcification rate and is independent of age. However, r is affected by seawater quality such as temperature and calcium ion concentration (Delbeek and Sprung, 1994). The precipitation of calcium carbonate is limited in cold waters because the solubility of calcium decreases with temperature (Vermeij, 1978). Below, we study the case in which calcification rate also depends on body size.

Mortality of cowries in the field after settlement is caused both by biological factors, including predation, and by physical factors, such as storm damage and temperature stress. Here, we classify them into two categories: the first is the mortality due to durophagous (shell-crushing) predation by molluscivorous crabs or diodontid fishes. A thick callus reduces the risk of shell-crushing predation. The second component of mortality is independent of shell thickness. It comprises both physical factors and non-durophagous predation (by mitrid snails, for example). We write the daily mortality, u, as

$$u = \frac{P}{1 + bC} + m \tag{3}$$

where P (≥ 0) is durophagous predation rate in the absence of a callus, b (> 0) is a constant for defence efficiency, and m (> 0) is the non-durophagous mortality rate (independent of shell thickness). As the callus becomes thicker, daily mortality u decreases and converges to m for an infinitely thick shell. The survivorship until maturation is the product of survivorship in the juvenile stage and that in the callus-building stage. The survivorship until the start of reproduction, denoted by $L_{x,y}$, is

$$L_{x,y} = \exp\left[-(P+m)x - P\int_0^y \frac{\mathrm{d}y'}{1+bC(y')} - my \right] \tag{4}$$

In the juvenile stage, daily mortality is constant ($P+m$), whereas it changes with time during the callus-building stage.

Ectotherms often exhibit an isometric relationship between clutch size and body size (Roff, 1992, 2002). Since living tissue mass is restricted to the volume of juvenile shells, the fecundity, M, is proportional to juvenile shell volume:

$$M = qV \tag{5}$$

where q (> 0) is a positive constant.

The lifetime reproductive success of an individual is

$$\phi = L_{x,y} \int_0^\infty M \mathrm{e}^{-ut}\, \mathrm{d}t \rightarrow \text{maximum} \tag{6}$$

where t denotes the time since the start of the adult stage. The optimal growth schedule of cowries is the one that achieves the maximum lifetime reproductive success given by equation (6).

OPTIMAL GROWTH SCHEDULE

If the speed of callus thickening is constant through time and independent of juvenile shell size (size-independent calcification), we can derive an explicit formula for the optimal life history. Since the fecundity for an individual with zero juvenile stage is zero, the optimal length of the juvenile stage must be positive $x^* > 0$. Hence the derivative of the lifetime reproductive success with respect to x should be zero at the optimal value:

$$\left. \frac{\partial \ln \phi}{\partial x} \right|_{x=x^*} = \frac{\beta}{x^*} - (P+m) = 0 \tag{7}$$

(see Appendix 2 for the calculation of $\ln \phi$). In contrast, the optimal length of the calcification stage (callus-building stage) is either positive or zero. We have the following optimizing conditions:

$$y^* > 0 \text{ and } \left. \frac{\partial \ln \phi}{\partial y} \right|_{y=y^*} = -m + \frac{br-P}{1+bry^*} - \frac{bmr}{P+m(1+bry^*)} = 0 \tag{8a}$$

or

$$y^* = 0 \text{ and } \left. \frac{\partial \ln \phi}{\partial y} \right|_{y=0} = -m + br - P - \frac{bmr}{P+m} < 0 \tag{8b}$$

Optimal length of the juvenile stage

Equation (7) yields the optimal length of the juvenile stage:

$$x^* = \frac{\beta}{(P + m)} \tag{9}$$

From this equation, we see that the optimal length of the juvenile stage x^* decreases with the sum of durophagous predation P and callus-independent mortality m. Moreover, the growth rate of the juvenile shell α has no effect on the optimal juvenile period. From equation (1), we can show that the volume of the juvenile shell produced at the end of the juvenile stage is

$$V(x^*) = \alpha \left(\frac{\beta}{P + m} \right)^{\beta} \tag{10}$$

which is equal to the part of the adult body contributing to reproduction. The size of the juvenile shell $V(x^*)$ decreases with total mortality, converges to zero for infinite mortality (Fig. 3a) and increases with the growth rate α. Both the length of the juvenile stage x^* and the size of the juvenile shell $V(x^*)$ are independent of defence efficiency b and calcification rate r.

Optimal length of the callus-building stage

From equation (8a), we have

$$y^* = \frac{\sqrt{bPr} - (P + m)}{bmr} \tag{11}$$

which is equal to the optimal length of the callus-building stage providing it is positive. But, if equation (11) is negative, the optimal strategy is to have no callus ($y^* = 0$). The optimal thickness of callus at the adult stage $C(y^*)$ is simply proportional to y^*, as given by equation (2).

Durophagous predation pressure P and calcification rate r strongly affect the optimal values of the length of the callus-building stage y^* and final callus thickness $C(y^*)$. Both y^* and $C(y^*)$ are zero either if P is very small or if P is very large with any given r, as illustrated in the shaded regions in Figs 3b and 3c. It is obvious that no callus should be produced in the absence of predators. However, foregoing callus-building under highly intensive predation pressure is quite interesting.

When $r > (m + P)^2/bP$ holds, y^* and $C(y^*)$ are positive, implying that the optimal strategy is to have some callus. The dependence of these parameters is as follows:

1. *Durophagous predation P-dependence*. If we change predation pressure P with the other parameters remaining fixed, both the callus-building period and final callus thickness attain their maxima at an intermediate value of predation pressure P. Specifically, they attain their maxima at $P = br/4$, which is indicated by the broken lines in Figs 3b and 3c. For a very high predation pressure, it is no longer worthwhile to invest in defence; instead, the optimal strategy is to invest more in juvenile growth.
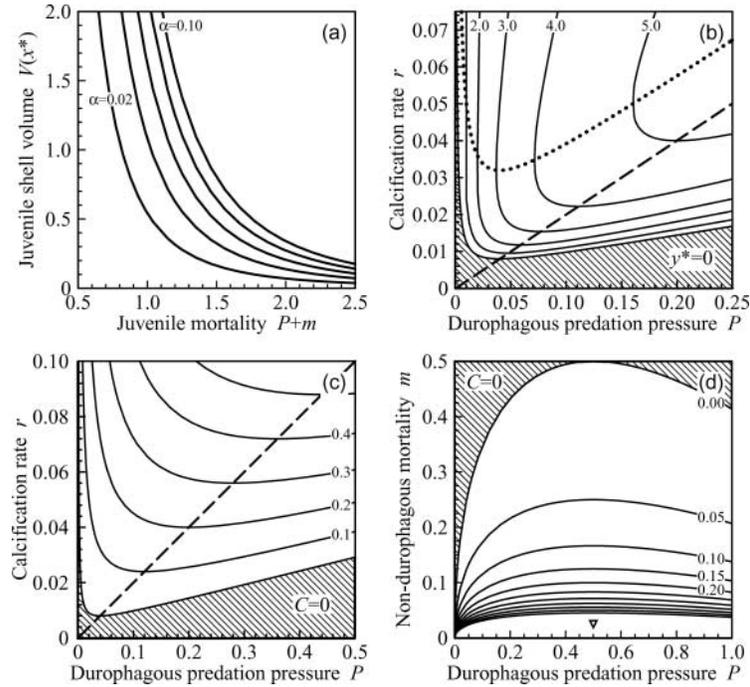
Fig. 3. Optimal values in the size-independent calcification case. (a) Juvenile shell volume, $V(x^*)$, as five functions of mortality with different growth rate values. $\beta = 3$. (b) The length of the callus-building stage, y^*, as a function of durophagous predation pressure and calcification rate. The optimal callus-building period is zero in the shaded area. In the area where $y^* > 0$, the callus-building period increases with P above the dashed line and decreases with r above the dotted line. $m = 0.04$. (c) Callus thickness, $C(y^*)$, as a function of durophagous predation pressure and calcification rate. No callus is built in the shaded area. In the area where $C(y^*) > 0$, optimal callus thickness increases with P above the dashed line. $m = 0.04$. (d) Callus thickness as a function of durophagous predation pressure and non-durophagous mortality. No callus is built in the shaded area. The small triangle indicates very large values for callus thickness. $r = 0.1$. Common parameter value: $b = 20.0$.

2. *Calcification rate r-dependence*. If we change calcification rate r with predation pressure P remaining fixed, the optimal callus-building period y^* attains a maximum value at an intermediate value of r given by

$$r = \frac{4(m^2 + 2Pm + P^2)}{bP} \tag{12}$$

which is indicated by the dotted curve in Fig. 3b. However, there is no intermediate r that produces the maximum adult callus thickness $C(y^*)$ (see Fig. 3c). The optimal callus thickness always increases with calcification rate. A very fast rate of calcification makes it possible to produce a thick callus within a short period.

3. *General mortality m-dependence*. Both the length of the callus-building stage y^* and adult callus thickness $C(y^*)$ decrease with non-durophagous mortality (m), as illustrated in

Fig. 3d. The optimal strategy is to have no callus ($y^* = C(y^*) = 0$) if the following inequality holds:

$$m > \sqrt{bPr} - P \qquad (13)$$

The adaptive benefit of having a costly callus decreases with the ratio of non-durophagous mortality m relative to durophagous predation pressure P. If non-durophagous mortality is sufficiently high, the time needed to make callus is better used for growth (juvenile stage) and reproduction (adult stage) than callus building.

Expected life span

We also examined the expected life span of cowries with the optimal growth schedule. As explained in Appendix 3, the relative life span, or the life expectancy at the time of settlement, can be calculated as the time-integral of survivorship. Expected life span increases with calcification rate (Fig. 4a) and decreases with mortality (Figs 4b and 4c). A short life span tends to be found in the parameter ranges where the optimal callus thickness is zero except for very small P (see Discussion).
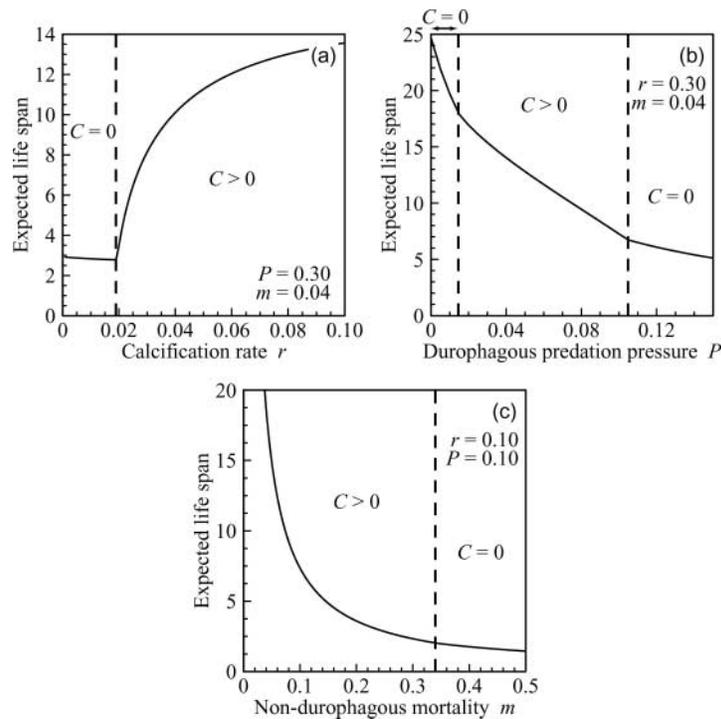

Fig. 4. Expected life span of individuals with optimal lengths of juvenile and callus-building stages as functions of (a) calcification rate, (b) durophagous predation pressure and (c) non-durophagous mortality in the size-independent calcification case. Optimal callus thickness shifts between zero and a positive value over the vertical dashed lines.

SIZE-DEPENDENT CALCIFICATION

Here we consider the case in which the growth rate of callus thickness is proportional to the volume of juvenile shell (i.e. living soft body mass) and is inversely proportional to the surface, which is an assumption more realistic than equation (2). We approximate the shape of juvenile shells by a sphere. The result is

$$\frac{\mathrm{d}C}{\mathrm{d}y} = r\frac{V}{S} = r\left(\frac{V}{36\pi}\right)^{1/3} \tag{14}$$

where V and S are the volume and surface area of a sphere, respectively, and r (> 0) is a constant (as in equation 2). Combining equations (14) and (1), we have

$$C = r\left(\frac{\alpha x^{\beta}}{36\pi}\right)^{1/3} y \tag{15}$$

In this case, the callus thickness increases in proportion to the length of the callus-building stage y, but it also increases with the length of the juvenile stage x.

When the speed of callus growth depends on body size, the equation for the optimal x^* and y^* that maximize the lifetime reproductive success can be solved only numerically. The parameter dependence of the optimal values in the size-dependent calcification case differs from the size-independent callus-building studied in the previous sections, in two ways: (1) calcification rate r affects both x^* and $V(x^*)$, and (2) growth rate α and the power β affect both y^* and $C(y^*)$.

Figure 5a illustrates the contours of optimal x^* with the two axes of predation pressure P and calcification rate r. In the region below the dotted curve, no callus is the optimal solution. Above the curve, some callus is produced, in which x^* depends on r, and takes the maximum values for an intermediate r-value (Fig. 5a). Optimal $V(x^*)$ shows very similar dynamics on the same plot (graph not shown). These contrast sharply with the size-independent calcification case, in which both x^* and $V(x^*)$ are independent of r. The r-dependence of both y^* and $C(y^*)$ for size-dependent calcification is very similar to that for size-independent calcification (graphs not shown).

Figures 5c and 5d show the callus-building period y^* and the final callus thickness $C(y^*)$ in the optimal strategy. Note that y^* and $C(y^*)$ increase with the growth rate α when some callus is to be produced ($C(y^*) > 0$). Again this contrasts with size-independent calcification, in which y^* and $C(y^*)$ are independent of α. The dependence of x^* and $V(x^*)$ on the growth rate α differ slightly between size-dependent and size-independent calcification. In Fig. 5b, for example, the increasing rate of $V(x^*)$ changes over the boundary between $C(x^*) = 0$ and $C(x^*) > 0$ (shown as a dotted line). The corresponding graph for the juvenile period x^* is similar to Fig. 5a, except that the vertical axis is growth rate α, instead of calcification rate r.

DISCUSSION

Clines in body size

Adult body size of *C. caputserpentis* increases with latitude. A similar trend is found in snails (Frank, 1975; Trussell, 2000), including some cypraeid species (Kay, 1961; Tissot, 1984), insects (Alpatov, 1929; Bryant, 1977; Arnett and Gotelli, 1999; Robinson and
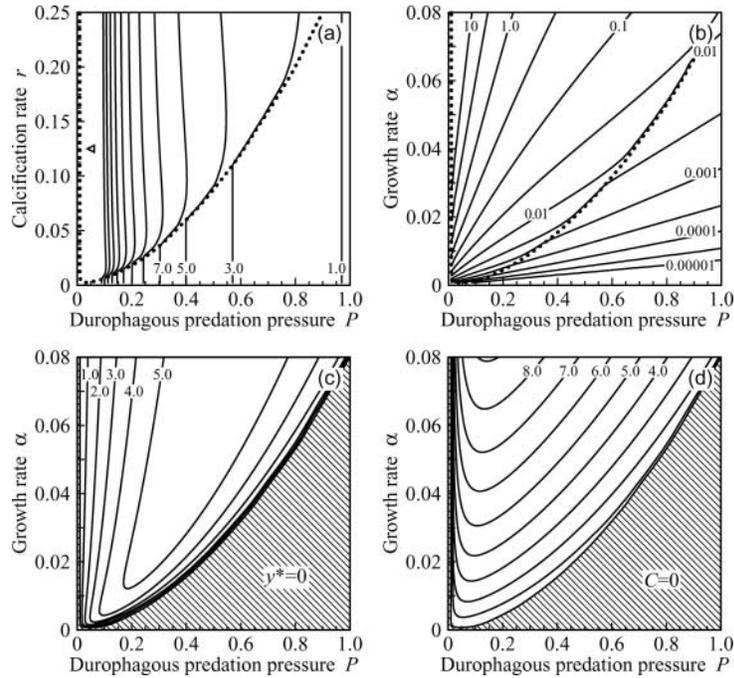
Fig. 5. Optimal values in the size-dependent calcification case. (a) Juvenile stage, x^*, as a function of durophagous predation pressure and calcification rate. No callus is built below the dotted line. The small triangle indicates very large values for the juvenile period. $\alpha = 0.8$. (b) Juvenile shell volume, $V(x^*)$, as functions of durophagous predation pressure and growth rate. No callus is built below the dotted line. The small triangle indicates very large values for juvenile shell volume. $r = 1.0$. (c) The length of the callus-building stage, y^*, and (d) callus thickness, $C(y^*)$, as functions of durophagous predation pressure and growth rate. No callus is built in the shaded areas. $r = 1.0$. Common parameter values: $b = 20.0$, $m = 0.04$, $q = 1.0$, $\beta = 3$.

Partridge 2001), amphibians (Ashton, 2002), reptiles (Ashton, 2001), birds (James, 1970) and mammals (Ashton *et al.*, 2000). Greater growth efficiency and shorter development time at lower latitudes are often associated with a smaller body size in many ectotherms. In cowries, individuals raised in an aquarium with a higher water temperature tend to have a faster growth rate and a shorter juvenile period (T. Irie, unpublished data).

   Our calculations revealed that higher juvenile mortality results in a shorter juvenile period and a smaller juvenile shell size. Our model assumes that juvenile mortality is the sum of durophagous predation pressure and non-durophagous mortality. A higher pressure of durophagous predation at lower latitudes is supported by the positive correlation between the average seawater temperature and the frequency of fragmented shells (Fig. 6). The decrease in the incidence of repaired shell injuries with latitude has been documented in many gastropod species (Vermeij, 1978, 1982, 1987; Vermeij *et al.*, 1980). On the other hand, a latitudinal cline of non-durophagous mortality (*m*), which includes other biological causes and the physical causes of mortality, has not been reported for cowries. In the absence of clear evidence of systematic latitudinal dependence of *m*, we may argue that the total juvenile mortality ($P + m$) is likely to decrease with latitude.
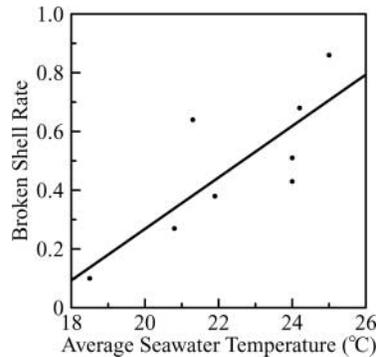
Fig. 6. The relationship between average seawater temperature and broken shell rate (defined as the number of broken shells divided by the total number of all beach-drifted shells) for *C. caputserpentis* collected from eight Japanese localities. The regression of broken shell rate (y) on average seawater temperature (x) is $y = 0.088x - 1.484$ ($r^2 = 0.64$, $P = 0.017$). Average surface seawater temperatures were obtained from the Japan Meteorological Agency (1981–93).

On the basis of the negative latitudinal gradient of juvenile mortality, our model explains the observed patterns that the final body size is smaller and the juvenile stage is shorter at lower latitudes. This suggests the importance of juvenile mortality as an ultimate factor in the body-size clines of the other organisms with determinate growth. Note that our models can hold also for species without a callus if the callus-building stage is skipped ($y^* = 0$). The general conclusion that increased juvenile mortality favours earlier maturation at a smaller size agrees with this prediction made by previous models without a callus-building stage (e.g. Roff, 1992; Stearns, 1992; Sibly and Atkinson, 1994; Abrams and Rowe, 1996).

Mortality is not the only environmental parameter that changes latitudinally. The latitudinal gradient of growth rate might also be important. In shell-bearing animals, the maximum rate of shell construction is likely to limit the growth rate during the juvenile stage (Palmer, 1981). Seawater temperature is particularly important in relation to calcification; the precipitation of calcium carbonate in shell surfaces is limited in cold waters because the solubility product of calcium carbonate increases with decreasing temperature (Graus, 1974; Clarke, 1983; Vermeij, 1987). The growth rate α can reflect this effect in our model.

However, according to our analysis in the size-independent calcification case, the optimal length of the juvenile stage, given by equation (9), is independent of growth rate α. In the size-dependent calcification case, there is a parameter range in which the optimal length of the juvenile stage decreases with growth rate, but the optimal volume of the juvenile shell increases. These results indicate that the negative latitudinal gradient of the growth rate does not explain the observed pattern of a shorter juvenile period at lower latitudes. In conclusion, no growth-related environmental parameter by itself can explain the body-size clines in cowries.

In the above argument, we tacitly assumed that the life history of each cowrie population is adapted to each local environment. This can be realized by genetic adaptation, but it may also be realized by phenotypic plasticity, in which the same genotype can develop different phenotypes that are adapted to local environments. Perhaps temperature during development is used as a cue to distinguish different environments. In black abalones, seawater

temperature determines not only the growth rate but also the time required to mature via the 'effective accumulative temperature', which is defined as the sum of the difference between the biological zero point and the seawater temperature over the stage (Uki and Kikuchi, 1984; Hahn, 1994). The same plasticity might work for cowries, in which case their growth rate, juvenile period and final body size would be the result of a reaction norm, with temperature used as an environmental cue. Such a reaction norm might have evolved on the basis of a reliable positive correlation between average temperature and predation pressure. However, in a freshwater snail, *Physella virgata*, the body size at maturity and the age of maturity are influenced by water-borne chemical cues from predatory crayfish (Crowl and Covich, 1990).

Clines in shell thickness

According to our model, if durophagous predation pressure (P) increases with all the other parameters fixed, the optimal callus thickness increases for small P, then reaches a plateau, and finally decreases at a very strong predation pressure (Figs 3c and 5d). Since both callus thickness and predation pressure are higher at lower latitudes, the observed gradients of the predation pressure should be within the range in which callus thickness increases with P.

   We studied in detail the case in which the speed of callus thickening depends only on calcification rate (r), which is affected by the precipitation rate of calcium carbonate, but is independent of body size. The case in which the callus thickening rate depends on body size is more realistic but less tractable than the case of size-independent calcification. In both cases, optimal callus thickness increases with calcification rate r *given* any positive P. Because the precipitation of calcium carbonate is higher at lower latitudes as discussed above, not only durophagous predation pressure but also the environmental parameter promoting calcification can be an ultimate factor of the negative latitudinal cline of callus thickness in cowries.

   In other molluscan species, the latitudinal clines of calcification are found both as intraspecific (Trussell, 2000) and interspecific patterns (Graus, 1974). Studies on several molluscan species have reported that a thicker callus is induced by water-borne cues from predatory crabs and damaged conspecifics (Palmer, 1985; Appleton and Palmer, 1988; Trussell, 1996, 2000; Leonard *et al.*, 1999).

Short life span in molluscs without an external shell

The model demonstrated that having no callus is advantageous only for limited ranges of the parameters (Figs 3d and 3e). Such a situation arises in the four cases shown in Table 1. These conditions may correspond to the environments in which molluscan species without an external shell (e.g. slugs and sea slugs) and those with vulnerable, semi-transparent shells (e.g. cavoliniids and succineids) live. Heller (1990) demonstrated that a short-lived mode of life is often correlated with the lack of an external shell and with having semi-transparent shells in both marine and terrestrial molluscs. Our model shows that a shorter expected life often arises when the optimal callus thickness is zero (Fig. 4, Table 1).

   Land snails that have no shells or thin ones live in environments in which calcium availability is very low (r is very small). In addition, some of their natural enemies, such as birds, should be capable of crushing shells (P is very large). Our model predicts that 'lacking a callus' is likely to evolve in such an environment. On the other hand, tropical sea slugs have

Table 1. Comparison of expected life span between with and without callus

Condition to skip callus-building:	Relative life span of individuals without callus is:
r is small	shorter than that with callus
P is zero or very small	longer than that with callus
P is large	shorter than that with callus
m is large	shorter than that with callus

no protecting shells but they co-exist with calcified shells in the same habitats. In such an environment, shell-crushing predation is potentially strong (P is very large) but calcification occurs quickly (r is large). This may be an example in which two or more strategies can co-exist in the same environments. These shell-less marine molluscs are often protected by camouflage or noxious chemicals rather than defensive armour.

In this paper, we have investigated a model restricted to the life history of cowries. It assumes that body growth is determinate and that a juvenile shell does not affect growth rate or defence. The present model can be applied to indeterminate growers if it is altered to allow individuals to choose between growth and reproduction at all points in their lives. It will be interesting to see whether such a model with indeterminate growth makes different predictions to those presented here.

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APPENDIX 1: POWER FUNCTION GROWTH

Although von Bertalanffy's growth equation (von Bertalanffy, 1938) is often a good descriptor of animal growth, it has been pointed out that it should not be used in models of age and size at maturity

(Day and Taylor, 1997; Czarnole'ski and Kozlowski, 1998). Instead, we assume power function growth in juvenile growth. Denoting the shell volume at time x by $V(x)$, growth occurs according to a differential equation of the form

$$\frac{dV}{dx} = aV^k \tag{A1}$$

Solving the differential equation for V and approximating the initial volume V_0 to zero gives

$$V(x) = \sqrt[1-k]{a(1-k)x} \tag{A2}$$

We redefine $\alpha \equiv a(1-k)$ and $\beta \equiv 1/(1-k)$, leading to equation (1). The power k often takes two-thirds (e.g. Day and Taylor, 1997) and hence $\beta = 3$.

APPENDIX 2: LIFETIME REPRODUCTIVE SUCCESS

Lifetime reproductive success, ϕ, is calculated as $L_{x,y} \times M \times E_r$, where E_r represents the integral of the probability of survival from the start of reproduction to infinity. In the size-independent calcification case, this measure can be written from equation (6):

$$\phi = \frac{e^{-(P+m)x-my}qV_0x^\alpha(1+bry)}{(1+bry)^{P/br}[P+m(1+bry)]} \tag{A3}$$

Taking the logarithm leads to

$$\ln\phi = -(P+m)x - my + \ln(qV_0x^\alpha) + \ln(1+bry)^{1-\frac{P}{br}} - \ln[P+m(1+bry)] \tag{A4}$$

which gives equations (7) and (8). When $\beta = 3$, the lifetime reproductive success in the size-dependent calcification case is

$$\phi = \frac{q\alpha x^3(1+bKy)^{1-\frac{P}{br}}}{\exp[(P+m)x+my][P+m(1+bKy)]} \tag{A5}$$

where $K = r\left(\dfrac{\alpha}{36\pi}\right)^{1/3}xy$

APPENDIX 3: RELATIVE LIFE SPAN

If the survivorship from age 0 to age x is denoted as $l(x)$, the integral of $l(x)$ over time from 0 to infinity gives the life expectancy at age 0. In our model, the relative life span, or the life expectancy at the time of settlement (the start of the juvenile stage), equals the sum of the integrals of survivorship curve for three ontogenic stages.

   Using the common daily mortality (equation 3), the integral for the juvenile stage, E_x, is

$$E_x = \int_0^x e^{-(P+m)t}dt = \frac{1-e^{-(P+m)x}}{P+m} \tag{A6}$$

The integral for the callus-building stage, E_y, is the product of the survival rate at the end of the previous stage and the integral of the survival function for this stage:

$$E_y = e^{-(P+m)x} \int_0^y \exp\left(-P \int_0^t \frac{dy'}{1 + bC(y')} - my\right) dt$$

$$= e^{-(P+m)x} \int_0^y \frac{e^{-mt}}{(1 + brt)^{P/br}} \, dt$$

(A7)

The integration can be done numerically. Finally, the integral for the adult stage is:

$$E_r = L_{x,y} \int_0^\infty \exp\left[-\left(\frac{P}{1 + bry} + m\right)t\right] dt$$

(A8)

The life expectancy of a newly settled individual, $E(x,y)$, is

$$E(x,y) = E_x + E_y + E_r$$

(A9)