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### DEVELOPMENTAL STRATEGIES IN SPATIALLY VARIABLE ENVIRONMENTS: BARNACLE SHELL DIMORPHISM AND STRATEGIC MODELS OF SELECTION

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## **Abstract**

**Predator-induced defense** in an intertidal **barnacle** (***Chthamalus anisopoma***) is reviewed, and **strategy models** of development are presented in an effort to understand the general conditions under which induced defense is evolutionarily stable. The default developmental form of the barnacle has the conic shape that is characteristic of barnacles, and it is more fecund and faster growing than the induced form. The induced form is more resistant to attack by a specialized gastropod predator, and it is most common near rock crevices that serve as refuges for the predator during high tide. The models suggest that induced defense is evolutionarily stable for a wide range of parameters, even when the cues used for induction are less than perfect predictors of the future environment. These conditions for **evolutionary stability** of induced defense are also very sensitive to the structural and material costs of defense, as well as the cost of plasticity *per se* (i.e., the cost of mechanisms used for sensing the environment). The results also suggest that the conditions for **genetic polymorphism** of canalized morphs are very narrow, and that under some conditions mixtures of canalized and inducible individuals can be evolutionarily stable. This latter result may explain the apparent mixtures of inducible and non-inducible individuals in barnacles, *Daphnia*, and bryozoans.

## **Introduction**

Discrete phenotypic variation in natural populations is of interest because it suggests a trade-off among morphs in their abilities to survive and/or reproduce in the different patches of a heterogeneous environment (Levene 1953; Levins 1962, 1963, 1968; Lloyd 1984). This is true whether the morphs are under strict genetic control, or whether they result from environmentally induced switches between alternative developmental programs. The challenges that such polymorphisms present to ecologists are to determine whether the environment is indeed heterogeneous in a relevant way, whether there are patch-dependent trade-offs among morphs as suggested by theory, and whether the development of individuals is canalized or environmentally induced.

Environmental induction of alternative forms has gained recent theoretical attention as an important evolutionary strategy (Lloyd 1984; Via and Lande 1985; Lively 1986c; Bull 1987; Hazel et al. 1990; Moran 1992; see Travis 1994 for a thorough review), and recent empirical studies suggest that it may be a taxonomically widespread phenomenon in animals (compare Hazel and West 1979; Krueger and Dodson 1981; Grant and Bayly 1981; Yoshioka 1982; Gilbert 1966 1980; Gilbert and Stemberger 1984; Eberhard 1982; Collins and Cheek 1983; Harvell 1984, 1986; Hebert and Grewe 1985; Lively 1986a; Etter 1988; Crespi 1988; Pfennig 1990; reviews in Harvell 1990; Travis 1994; Gotthard and Sören 1995). Most of these later studies have been conducted in the last 15 years, and have uncovered induced adaptive responses that might have been inconceivable in the 1970s. In what follows, I first review predator-induced defense in an intertidal barnacle. Then, using barnacles as a "handle," I present strategy models of selection designed to determine the general conditions under which an induced defense is evolutionarily stable.

## Induced Defense in a Barnacle

The intertidal barnacle *Chthamalus anisopoma* is dimorphic for shell shape in the northern **Gulf of California** (Fig. 14.1), where it overlaps in distribution with the predatory snail, *Acanthina angelica* (Lively 1986a,b). The undefended form of the barnacle has the conic, volcano shape that is characteristic of acorn barnacles (Fig. 14.2), and it is less resistant to attack by *Acanthina*. This snail is a specialized barnacle predator (Paine 1966, Malusa 1985, Perry 1985, Lively 1986a, Dungan 1987), which uses a labial spine to gain access to barnacle prey (See Keen 1971 and Brusca 1980 for photos of *Acanthina*). In a typical attack sequence, the predator first wraps the front margins of its foot around the barnacle's base. The snail then positions the spine over the barnacle's operculum, and rams the spine down. About 45% of the time, the spine is successfully pushed through the operculum of undefended barnacles (Lively 1986a); the spine is then withdrawn and the barnacle is eaten.

The defended morph of the barnacle (Fig. 14.2) is more resistant to attack of this kind, because the aperture is oriented in a plane that is perpendicular to the substratum (Lively 1986a). This 90° shift in the plane of the aperture results from shortening the lateral plates on one side, while lengthening the lateral plates on the other side. Apparently, one side simply stops growing, while the other side continues to grow, pushing the aperture upright. This differential growth makes the barnacle appear bent over, resembling a hood. During the attack sequence, when the predator's spine is rammed down, it usually misses the aperture of the bent morph altogether.

This defense has two direct costs: (1) the bent form grows more slowly, and (2) it is less fecund per unit size (Lively 1986b). Both of these costs result from the structure of the bent form. There is less room for brooding larvae in the bent shell; hence, overall fecundity is reduced. In addition, growth is slower in the bent morph, since it is restricted to one side. Surprisingly, I found no competitive disadvantage of the bent morph (Lively 1986b). The survivorship of bent individuals in competition with conics was not less than that of conics when similarly grown in competition with conics. Hence there is no competitive asymmetry between

morphs that would be analogous to the well-known competitive asymmetries between different species of barnacles that inhabit adjacent zones in the intertidal (Connell 1961, Dungan 1985).

Typically, the snail predators emerge from rock crevices or from under boulders as the tide recedes. They tend to move quickly, while the rocks are still wet, and begin foraging. Once they engage in attack, they move very little, presumably to minimize their water loss while crawling over the rocks, which are sometimes quite hot (Lively and Raimondi 1987). Hence, for the induced defense to be of any value, the bent morph must be able to withstand repeated attack during a low tide. The bent form of the barnacle is sometimes killed during repeated attacks, but generally is much more likely to survive than the typical, conic form of the barnacle (Lively 1986a). When the tide returns and wets the foraging snails, they tend to move back to the rock crevices. This back and forth movement of the predators creates a distinct area where predation intensity is high. In adjacent areas, only a few cm further from crevices, predation intensity is low or absent (Lively 1986a, Lively et al. 1993). Hence there are two discrete patches for predation risk: high-risk and low-risk. (see Menge 1978, Moran 1985, and Garrity and Levings 1981, Fairweather 1988 for similar reports of "crevice effects").

This is the kind of heterogeneous environment that would seem to favor a developmental switch, and indeed the bent form of the barnacle is induced by the presence of Acanthina. The details of this induction are not clear, but juvenile barnacles between the ages of 1 and 5 days old were induced to develop the bent form by placing Acanthina directly on them just prior to inundation by the incoming tide (Lively 1986a). In this experiment, where individuals were followed over time, 37% of the barnacles exposed to the predator developed the bent morphology within 30 days (Lively 1986a). Surprisingly, the rest of the barnacles did not respond to contact with the predator, and they all became the default, conic form. It is not presently known whether the cue is chemical or mechanical, but the addition of herbivorous snails in one experiment did not induce the bent form, suggesting that mechanical stimulation by a snail's foot is not sufficient to induced the defended form (Lively 1986a).

There are two curious twists to these main results that are of theoretical as well as empirical interest. One twist is that some juvenile barnacles exposed to the predator were not induced to develop the attack-resistant form. The second curious twist is that the cue seems to be a poor indicator of the future environment, at least during certain seasons. The reason for this is that the snails aestivate during the summer (Lively 1986a), when most of the barnacle settlement occurs (Raimondi 1990). Hence most barnacles that settle in the high-risk zone during the summer do not receive the cue; they therefore develop as conics and are susceptible to predation when the snails come out of aestivation in the early autumn (Lively et al. 1993). This raises the question: how reliable does the cue have to be in order for selection to favor induced defense over constitutive defense? I have studied this question using strategy models (Lively 1986c), which are extended here in two ways. First, costs of inducibility are added (following Van Tienderen 1991); and second, I assume that there is spatial auto-correlation in the environment, such that inducible individuals make the same developmental choice as their neighbors.

## **Strategy Models of Selection**

### *Selection on Two Canalized Developmental Strategies*

I begin by considering two canalized alternatives, defended and undefended. Along with these pure unconditional strategies, I also consider a stochastic switch between morphs (a mixed strategy) where individuals develop as the undefended morph with an average probability ( $q$ ), which is independent of the patch they settle in. In the context of the barnacles, then, when would we expect to find: (1) unconditional development of the bent form, (2) unconditional development of the conic form, (3) an evolutionarily stable mixed strategy, or (4) an evolutionarily stable state of the population composed of individuals showing either canalized defense or canalized development of the undefended conic form? Further, we want to know which of these three alternatives to expect as the frequency of patch types varies. I use game-theoretic models, which (strictly speaking) assume clonal reproduction. However, sexual

populations will evolve towards the evolutionarily stable (ES) strategy or ES state in population genetic (Maynard Smith 1982) and quantitative genetic models of selection (Taylor 1996).

Barnacle larvae are planktonic and likely to become widely distributed. They do, however, use cues (such as the presence of conspecifics) for settlement, which increases the likelihood of attachment and metamorphosis in the "right" intertidal zone (Raimondi 1988). Within this zone, I assume that the barnacles settle more or less at random. Let the probability of attachment in the predation-free, low-risk patch be  $p$ ; thus  $(1 - p)$  gives the probability of settling in the high-risk patch where the probability of contact with the predator is high. Similarly, let  $k$  be relative fitness of the defended morph, where  $k < 1$  reflects structural or material costs of investment in defense. Finally, let  $e_{ij}$  be the effect of competition on the  $i^{\text{th}}$  morph when rare in a population of the  $j^{\text{th}}$  morph. For example,  $e_{du}$  gives the relative fitness of a rare, defended individual in a population composed almost entirely of undefended individuals.

In what follows, I assume that the patch frequencies are constant over time, and that the undefended morph cannot survive in the high-risk patch. Now consider a resident, mixed strategy such that all individuals in a large population develop the undefended form with probability  $q$ , and the defended form with probability  $(1 - q)$ . Using standard evolutionary game theory (Maynard Smith 1982; Bulmer 1994), we consider the fate of a rare individual in this population. Let  $q_i$  be the probability of developing as a undefended morph by this rare individual, and let  $(1 - q_i)$  be the probability of developing as the defended form. Assuming that fitness is a linear function of the frequencies of the two morphs in the population, individual fitness is estimated as:

$$W_i = q_i p [q e_{uu} + (1 - q) e_{ud}] + (1 - q_i) (1 - p) [q + (1 - q) e_{dd}] k + (1 - q_i) p [q e_{du} + (1 - q) e_{dd}] k. \quad (1)$$

A mutant strategy can not increase under selection when the resident population is at a local maximum for fitness, which is when:

$$\frac{\partial W_i}{\partial q_i} = q[k(e_{dd} - pe_{du}) + p(e_{uu} - e_{ud}) - k(1-p)] - (ke_{dd} - pe_{ud}) = 0, \quad (2)$$

provided the second derivative is less than or equal to zero, which is indeed the case for eq. (1).

Hence, the evolutionarily stable strategy, represented by the variable  $q^*$ , is

$$q^* = \left[ \frac{ke_{dd} - pe_{ud}}{k(e_{dd} - pe_{du}) + p(e_{uu} - e_{ud}) - k(1-p)} \right]. \quad (3)$$

A mixed strategy at  $q^*$  is also continuously stable (Eshel 1983; Christiansen 1991) when:

$$\left[ \frac{\partial^2 W_i}{\partial q_i^2} + \frac{\partial^2 W_i}{\partial q_i \partial q} \right]_{q_i=q=q^*} < 0, \quad (4)$$

which is satisfied when:

$$\frac{[(e_{uu} - e_{ud}) + k(1 - e_{du})]}{k(1-p)(1 - e_{dd})} < \frac{(1-p)}{p}. \quad (5)$$

Note that the equilibrium attained at  $q^*$  may be achieved by either a (i) mixed strategy, or (ii) a population in which  $q^*$  of the individuals show canalized development of the undefended form (see Maynard Smith 1982). The latter population would represent a genetic polymorphism in a sexual population.

The parameter space for which a mixed strategy or genetic polymorphism might be expected (i.e.,  $0 < q^* < 1$ ) is given graphically in Fig. 14.3. This region of parameter space is



surprisingly narrow (see also Maynard Smith and Hoekstra 1980), and requires that the probability of the low-risk patch ( $p$ ) be on the interval,

$$\left[ \frac{ke_{dd}}{e_{ud}} \right] < p < \left[ \frac{k}{e_{uu} + k(1 - e_{du})} \right]. \quad (6)$$

Canalized development of the defended morph will be favored by selection when  $p < ke_{dd}/e_{ud}$ , and canalized development of the undefended morph will be favored by selection when  $p > k/[e_{uu} + k(1 - e_{du})]$ .

### ***Introduction of a Developmental Switch to the Strategy Set***

I now consider the fate of a rare mutant that responds to cues in the local environment that induce a developmental switch to the defended morph in the high-risk patch. I retain the useful idea of allowing patch frequencies to vary, but also include some probability of making the "wrong" choices in both the low-risk and high risk patches. Biologically this means getting the cue and becoming the defended morph in the low-risk patch (with probability:  $1 - F$ ), or not getting the cue, and becoming the undefended morph in the high risk patch (with probability:  $1 - G$ ).

These assumptions are the same as those in a previous model of selection in spatially variable environments (Lively 1986c). The present model also includes some additions and changes that seem warranted. One is that I have included a cost to plasticity per se. By this I mean a fitness cost to developing and maintaining any machinery for sensing the environment and flipping the developmental switch. Let the relative fitness of inducible individuals be  $c$  (where  $0 < c < 1$ ). Note that the cost of plasticity ( $c$ ) is independent of the cost of having the defended structure ( $k$ ). In addition, my previous model allowed mistakes to be made on an individual-by-individual basis, which seems unreasonable given the diffusive nature of most chemical cues. Thus, in the present model, all conditional individuals make the same choice ("right" or "wrong"). So, in a population containing only conditional strategists, defended

individuals only compete for resources with other defended individuals, and undefended individuals only compete with other undefended individuals. The payoff matrix is given in Table 14.1.

To complete the model, we must also know when a conditional strategy can not increase in a population of individuals playing a mixed strategy such that the probability of development as an undefended individual is at the ESS ( $q^*$ ). Setting  $q_i = q$  in eq. (1), and then substituting  $q^*$  from eq. (3) for  $q$ , the fitness of a mixed strategist when the mixed strategy is common is:

$$W_{q^*q^*} = \frac{kp[(1-p)e_{ud} + pe_{du}e_{ud} - e_{dd}e_{uu}]}{k(1 - e_{dd}) + p(e_{ud} - e_{uu}) - kp(1 - e_{du})}. \quad (7)$$

The fitness of a rare conditional mutant in a population of mixed strategists,  $W_{cq^*}$ , is closely approximated by:

$$W_{cq^*} = c\{qp[Fe_{uu} + (1 - F)ke_{du}] + (1 - q)p[Fe_{ud} + (1 - F)ke_{dd}] \\ + q(1 - p)Gk + (1 - q)(1 - p)Gke_{dd}\}. \quad (8)$$

The rare conditional strategy can not increase in a population of mixed strategists when  $W_{q^*q^*} > W_{cq^*}$ . Similarly, the mixed strategy at  $q^*$  cannot increase when rare when  $W_{cc} > W_{q^*c}$ , where  $W_{cc}$  is given in Table 14.1, and

$$W_{q^*c} = p[q(Fe_{uu} + (1 - F)e_{ud}) + (1 - q)k(Fe_{du} + (1 - F)e_{dd}) \\ + (1 - p)(1 - q)k(Ge_{dd} + 1 - G)]. \quad (9)$$

A feeling for the parameter space for which each developmental strategy is evolutionarily stable and can increase when rare can be gained by numerical substitution. I have chosen to examine

this space in terms of the frequency of the low-risk patch ( $p$ ), and the probability of making the wrong choice in the high-risk patch ( $1 - G$ ). This was done by substituting values for the relative fitness of the conditional strategy ( $c$ ), the relative fitness of the defended form ( $k$ ), and the probability of making the wrong choice in the low-risk patch ( $1 - F$ ). To reflect the situation for the barnacles, I have set the interaction coefficients equal to one half (all  $e_{ij} = 0.5$ ), since there was no competitive asymmetry between morphs, but the presence of conspecifics did reduce the size (and hence the fecundity) of both forms. Following these substitutions, I determined the areas of parameter space for which each of the different developmental strategies would resist invasion by rare mutants having any one of the alternative strategies. Induced defense, for example, is evolutionarily stable if an individual having conditional development has a higher expected fitness in a population of conditional individuals than any alternative developmental strategy (defended, undefended, or mixed) when rare. The equations for these calculations are given in Table 14.1 and eqs. (7-9) above.

The results of the numerical substitutions are interesting for several reasons. For example, they show that a mixed developmental strategy is evolutionarily stable for only for a narrow set of parameters (Fig. 14.4); in other words, development of the undefended morph with probability  $q^*$  (such that  $0 < q^* < 1$ ) is subject to invasion by canalized mutants or conditional development over most of the parameter space. When there is no cost to plasticity ( $c = 1$ ), a conditional strategy can increase when rare, and fix, in a population composed of constitutive strategists whenever the average probability of making the right choice is greater than one half (Lively 1986c). This result means that, if the probability of making the right choice is 80% in the low-risk patch (as presented in Fig. 14.4), a conditional strategy can still increase when rare over a narrow region of parameter space when the probability of making the right choice in the high-risk patch is marginally greater than 20%. The region of parameter space for which a conditional strategy can increase when rare increases dramatically as the probability of making the right choice in the high-risk patch increases (Fig. 14.4). The overall result is that a large fraction of the

parameter space contains some frequency of conditional strategists at the ESS, provided there is no cost to the plastic response.

If there is some cost to plasticity, the region of parameter space for which a conditional strategy is either stable or can increase when rare is greatly reduced (Fig 14.4). Surprisingly, a 10% cost of plasticity (i.e.,  $c = 0.9$ ) reduces this parameter space by about 50% or more, depending on the cost of the defended form ( $k$ ) (see also Van Tienderen 1991, León 1993). Thus it would seem that costs of developing and maintaining the "machinery" for sensing and responding to the environment have the potential to prevent the spread of rare conditional development, especially if the cost of defense is high. Nonetheless, once established, selection would be expected to fix any mutations that reduce the cost of plasticity, thereby increasing the range of conditions that favor induced defense.

The results also show that there are regions of parameter space under which conditional and canalized strategies can both increase when rare ("control polymorphisms," Lively 1986c). These regions reflect earlier results, but add in one striking way: some regions of parameter space support all three strategies. Hence, constitutively defended, constitutively undefended, and conditionally defended strategies can all increase when rare under some conditions. The coexistence of three strategies would seem to be unlikely in the wild, but it is known for male morphs of isopods (Schuster and Wade 1991) and lizards (Sinervo and Lively 1996). Recently, Harvell (in review) has shown the co-occurrence of three developmental types (inducible, constitutive defense, and undefended) in a marine bryozoan.

## **Discussion**

Several points raised by the model seem worth fleshing out. The three most important are: (i) the conditions for a genetically determined polymorphism are very narrow; (ii) the conditions for the existence of conditional development are relatively broad; and (iii) mixtures of conditional and canalized development can be evolutionarily stable for some combinations of parameters.

Regarding the first point, it is of interest to see that the conditions for the evolutionary maintenance of canalized developmental morphs (one defended and one undefended) are very sensitive to patch frequencies and the magnitude of the trade-off between morphs, at least under the assumptions of the present model (Fig. 14.3). Similar results under different assumptions were gained by Maynard Smith and Hoekstra (1980) in their genetic models of selection in spatially variable environments, and thus it seems that multiple niche polymorphism (Levine 1953, Levins 1963) may be expected to be rare in nature. These results have implications for one of the primary hypotheses for the maintenance of sexual reproduction, which relies on soft selection in spatially heterogeneous environments (i.e., the Tangled Bank Hypothesis; see Bell 1982). The idea behind the Tangled Bank hypothesis is that selection for genetic variation might favor the production of sexual offspring over asexual offspring, even if there is a two-fold cost to cross-fertilization. The hypothesis, however, loses some of its force if the conditions for genetic polymorphism are narrow. In any case, the results of the present study suggest that condition developmental strategies, such as induced defense, could increase when rare and fix in a genetically polymorphic population under a wide array of conditions (Fig. 14.4).

The second major point is that induced defense is stable over a wide range of conditions, especially if the cost to plasticity is low, and juveniles make the right choice regarding their future environment in at least one of the patches. These conditions are further increased if the cost of defense is intermediate, such that the fitness of defended individuals is about half that of undefended individuals. These results suggest that when observing multiple discrete morphs in the nature, chances are very good that there is at least partial environmental determination of development. I also found that induced defense can be evolutionarily stable, even when the probability of making a mistake and developing as the "wrong" morph is reasonably high. This may explain one anomaly in the intertidal barnacles reviewed here. A large fraction of the individuals settle in the summer during a period of aestivation by the predator that would otherwise attack them. This results in a decoupling of the high-risk patch with its cue.

Nonetheless, the results suggest that induced defense can be stable to replacement by constitutive defense, even if the inducing cue is a poor predictor of the future.

The third point, and the qualification ("at least partial") in the previous paragraph, stems from the finding that mixtures of canalized and conditional development exist over part of the parameter space (see also Lively 1986c). This result might explain the situation for the barnacles, as well as other similar examples of "control polymorphisms" in Table 14.2. In field experiments, I found that I could only induce about 45% of the barnacles, even though I "inundated" juvenile barnacles with Acanthina. The barnacles in the northern Gulf of California may therefore be a mixture of conditionally defended and constitutively undefended individuals. Alternatively, the mixture of individuals may result from gene flow from the southern Gulf of California, where the predatory snail is absent. In either case, the main point is that mixture of developmental control is a possibility in these barnacles. A plausible quantitative genetic basis to such a mixture is given by Hazel et al. (1990) and Hazel and Smock (1993).

Finally, the model can be used to consider the effects of gradual changes in the environment over time. For example, consider the effects of changing the frequency of the high-risk patch from close to zero to close to one in Fig 14.4. Intuitively, we would expect an increase in the frequency of the defended, bent morph of the barnacle; and if we were examining the change in the fossil record, we might be inclined to declare saltational evolution of the bent form, because the shell shapes are so different (see Levinton 1988, p. 377). But, depending on the reliability of cues associated with the two patches no such change is expected. An increase in the frequency of the high-risk patch can increase the occurrence of the defended morph in two important ways: (i) replacement of a population composed entirely of constitutively undefended individual by a population composed entirely of constitutively defended individuals; or (ii) a change in a conditional population from mostly undefended phenotypes to mostly defended phenotypes. Hence inferences regarding evolutionary change based on the replacement of one discrete form by another in the fossil record should be made cautiously (Palmer 1985). In addition, changes in the reliability of cues, without necessarily changing the frequency of

patches, can also lead evolutionary change. For example, increasing the probability of making the wrong choice in the high-risk patch can lead to selection for canalization of the defended morph when the high-risk patch dominates the environment. Such selection would lead to genetic assimilation (in the sense of Waddington 1957) of the defended phenotype.

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**Table 14.1.** Payoff matrix for a game between canalized and conditional morphological strategies. "Undefended" represents a strategy for canalized development of an undefended morph. "Defended" represents a strategy for canalized development of a defended morph whose fitness is scaled by a the cost variable,  $\underline{k}$ . "Conditional" represents a strategy for conditional development of a defended morph in a high predation-risk patch, and an undefended morph in a low predation-risk patch. The frequency of the low-risk patch is  $p$ . The probability of making the "wrong" choice in the high-risk patch is  $(1 - \underline{F})$ , and the probability of making the "wrong" choice in the low-risk patch is  $(1 - \underline{G})$ . The variable,  $\underline{c}$ , gives the cost of plasticity; i.e. the cost of maintaining the developmental machinery for sensing and responding to the environment.

<u>Fitness of rare Developmental Strategy</u>	<u>Resident Developmental Strategy</u>		
	<b>Undefended</b> ( $q = 1$ )	<b>Defended</b> ( $q = 0$ )	<b>Conditional</b>
<b>Undefended</b> ( $q_i = 1$ )	$p\underline{e}_{uu}$	$p\underline{e}_{ud}$	$p(\underline{F}e_{uu} + (1 - \underline{F})e_{ud})$
<b>Defended</b> ( $q_i = 0$ )	$\underline{k}[p\underline{e}_{du} + 1 - p]$	$\underline{k}e_{dd}$	$\underline{k}\{p[\underline{F}e_{du} + (1 - \underline{F})e_{dd}] + (1 - p)[\underline{G}e_{dd} + 1 - \underline{G}]\}$
<b>Conditional</b>	$\{p[\underline{F}e_{uu} + (1 - \underline{F})\underline{k}e_{du}] + (1 - p)\underline{G}\underline{k}\}(1 - \underline{c})$	$\{p[\underline{F}e_{ud} + (1 - \underline{F})\underline{k}e_{dd}] + (1 - p)\underline{G}\underline{k}e_{dd}\}(1 - \underline{c})$	$\{p[\underline{F}e_{uu} + (1 - \underline{F})\underline{k}e_{dd}] + (1 - p)(\underline{G}\underline{k}e_{dd})\}(1 - \underline{c})$

**Table 14.2.** Examples of developmental conversion, where less than 100% of the individuals tested could be induced to develop the alternative form. The remaining animals did not develop the alternative form, and may have canalized development.

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Water fleas:	30-79% developed neckteeth when exposed to a predator (Krueger and Dodson 1981)
Rotifer:	13-55% developed spines when exposed to a predator (Stemberger and Gilbert 1984)
Barnacle:	28-46% developed bent form when exposed to predator (Lively 1986a)
Salamander:	7% developed as cannibalistic morph at high density (Collins and Cheek 1981)
Nematode:	6-16% developed as males under high density (Clark 1978)
Bryozoans	80% developed spines when exposed to predator (Harvell, in review)

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## Figure Legends

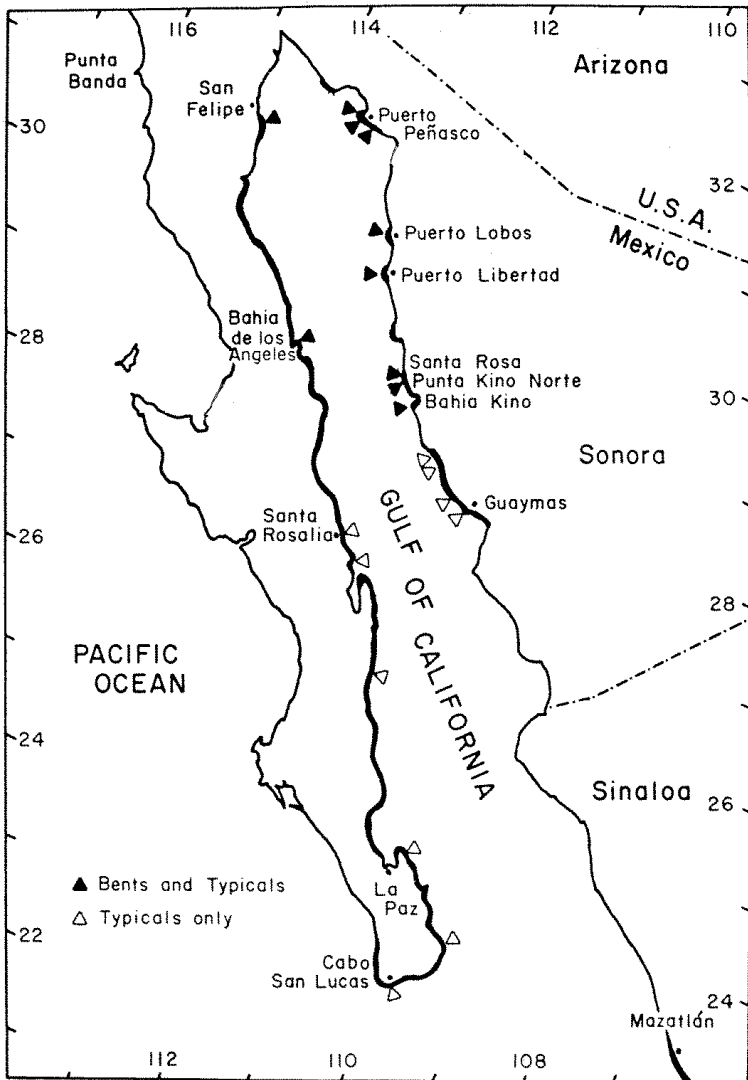
**Fig. 14.1.** Map of the Gulf of California, showing the known distributions of the bent form of the barnacle, Chthamalus anisopoma and the predatory snail, Acanthina angelica (closed triangles). The conic form of the barnacle is distributed throughout the Gulf of California (open and closed triangles).

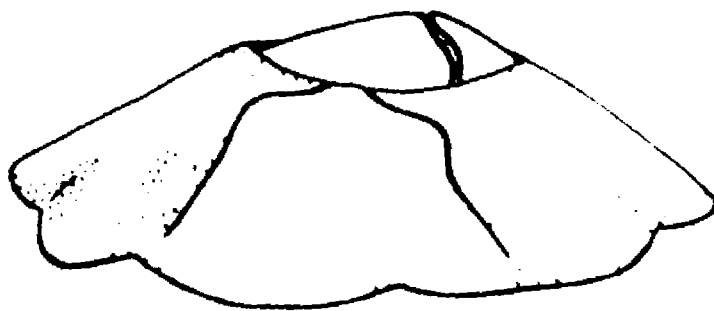
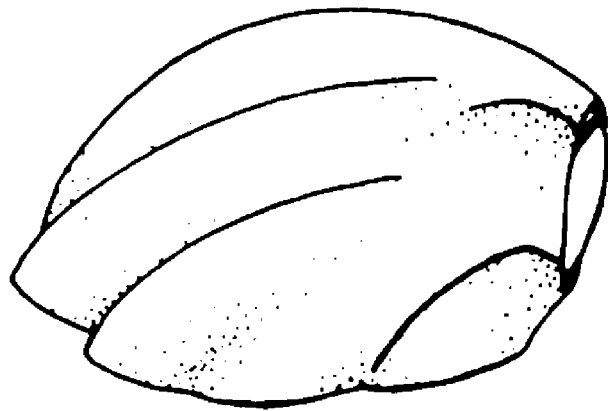
**Fig. 14.2.** Line drawings of the "conic" and "bent" morphs of the intertidal barnacle, Chthamalus anisopoma. The bent form (top) of the barnacle is induced by presence of the gastropod snail, Acanthina angelica, and it is more resistant to attack by this predator. The conic form (bottom) grows faster and is more fecund per unit size. The basal diameter of adult C. anisopoma ranges from 2-7 mm (Brusca 1980, Lively 1986b).

**Fig. 14.3.** Conditions for genetic polymorphism. Both figures give the equilibrium values of a constitutively undefended morph,  $q^*$ , as a function of (1) the relative fitness of the defended morph, and (2) the frequency of the low-risk patch where predation is a rare event. In the top figure, there are no competitive asymmetries, thus the interaction coefficients are all set to one half (i.e., all  $e_{ij} = 0.5$ ). Note the step-like transition between selection for fixation of the defended form and selection for fixation of the undefended form as the frequency of the low-risk patch increases. In the bottom figure, the interaction coefficients are set to reflect the most extreme type of competitive asymmetry, where the undefended morph excludes the defended morph ( $e_{du} = 0$ ), while the defended morph has no effect on the fitness of the undefended morph ( $e_{ud} = 1$ ). Both morphs decrease the fitness of an individual of the same kind by 50% ( $e_{uu} = 0.5$ ;  $e_{dd} = 0.5$ ). Note that the transition between fixed states is less steep than in the top figure, but the transition is nonetheless quite abrupt. In both figures, the equilibrium at  $q^*$  meets the conditions of eqs. (4 & 5) and is continuously stable.

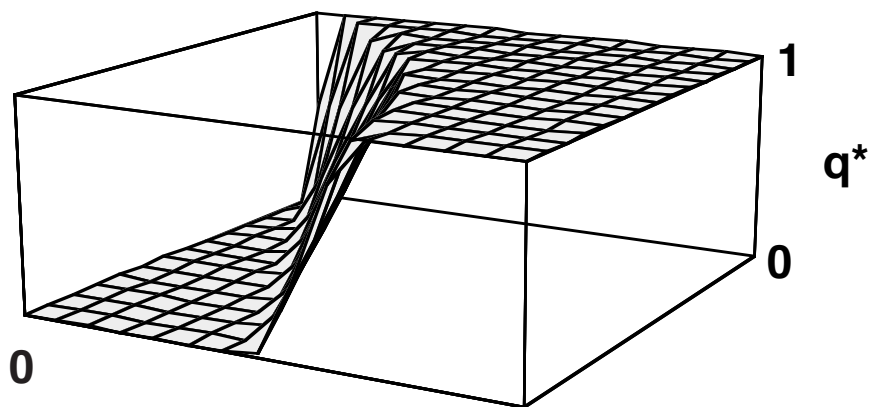
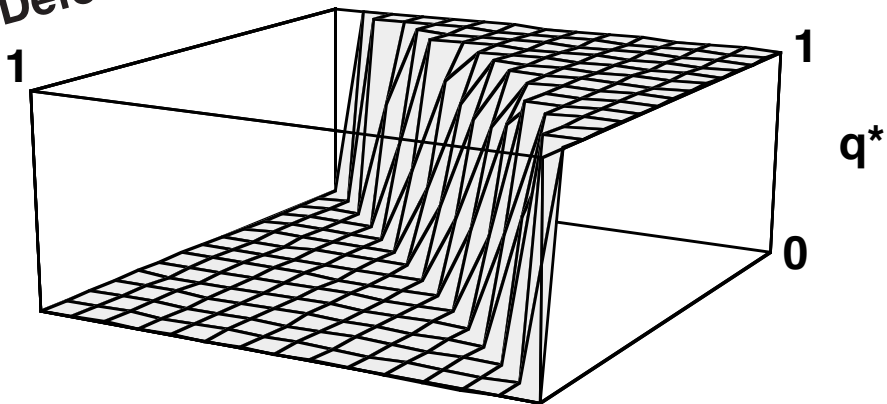


**Fig. 14.4.** Conditions for evolutionary stability of three developmental strategies and mixtures of these same strategies. The "torso" is the parameter space where constitutively defended and constitutively undefended developmental strategies can both increase when rare and reach a continuously stable equilibrium. The right "leg" is the region where constitutively undefended development and conditional defense can both increase when rare; and the left "leg" is where constitutively defended development and conditional defense can increase when rare (conditions for continuous stability were not analyzed for either leg). In the region marked "Z," all three strategies have a rare advantage. For the calculation of these figures, the probability of making the right choice in the low-risk patch was set at 80% ( $\underline{F} = 0.80$ ), and the interaction coefficients were all set at one half (i.e., all  $\underline{e}_{ij} = 0.50$ ). The left-hand figures assume that the defended morph (however produced) has only 25% of the reproductive output as the undefended morph; the right-hand figures assume that the defended morph has a relative fitness of 75%. Similarly, In the top two figures, there is no cost to plasticity per se ( $\underline{c} = 1$ ), but in the bottom two figures, plastic individuals have a relative fitness of 90% ( $\underline{c} = 0.90$ ). Note that the parameter space under which the conditional strategy is an ESS is sharply reduced by a small cost to plasticity. Note also that changes in patch frequency or the probability of mistakes will lead to changes in the frequencies of the two morphs, which may or may not be genetically based.





Relative Fitness of  
the Defended Morph



Frequency of  
Low-Risk Patch

