Adaptive aspects of phenotypic plasticity in echinoderms

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ABSTRACT

Echinoderms show phenotypic plasticity in which variation in environmental conditions elicit graded reaction norms of morphological change. With the sea urchin *Strongylocentrotus purpuratus* under laboratory conditions, decreases in available food caused decreases in dry weights of the gonad and gut coupled with increases in the mass of Aristotle's lantern and length of the demi-pyramids. Spine clipping caused increased spine growth as well as decreases in the gut and gonad masses. Survival rate remained unchanged over a range of feeding and clipping treatments. In the field, at Sunset Bay, Oregon, well-fed sea urchins, with relatively small demi-pyramids, showed survival rates similar to poorly fed sea urchins that had large demi-pyramids. The wide range of morphological change, coupled with the narrow range of change in survival, suggests that morphological plasticity buffers survival and hence would increase fitness.

Phenotypic plasticity shown by other sea urchins includes changes in the relative sizes of Aristotle's lantern in *Diadema antillarum* and *Echinometra mathaei* and seasonal variation in the density of pedicellariae in *Echinus esculentus*. Variation in body size of echinoids and asteroids in different habitats and variation in number of arms in crinoids also may be examples of adaptive plasticity.

Seasonal atrophy of internal organs in the sea cucumber *Parastichopus californicus* has been interpreted as an adaptive response to food limitation but, given the nature of responses in other echinoderms, such an interpretation seems unlikely and the significance of seasonal atrophy of organs in holothurians remains unknown.

RÉSUMÉ

Les aspects adaptatifs de la plasticité phénotypique chez les échinodermes.

Les échinodermes présentent une plasticité phénotypique se traduisant par une succession de modifications normalisées des traits morphologiques sous l'action des variations des facteurs du milieu. Chez l'oursin *Strongylocentrotus purpuratus* en conditions expérimentales, la diminution de l'apport trophique entraîne une baisse de poids sec des gonades et du tube digestif avec, en parallèle, une augmentation du poids de la lanterne d'Aristote et de la longueur des demi-pyramides. Le bris des piquants conduit à l'accroissement de leur taux de croissance et à une baisse de poids des gonades et du tube digestif. Les apports trophiques et le taux de cassure des piquants peuvent varier dans une large mesure sans modifier le taux de survie. En milieu naturel, dans la baie de Sunset (Orégon), des oursins bien nourris, dotés de demi-pyramides relativement petites, présentent des taux de survie similaires à ceux d'oursins défavorisés trophiquement et dotés de hautes demi-pyramides. La gamme étendue des modifications morpholo-

giques, associée aux faibles variations du taux de survie, suggère que la plasticité morphologique régule le taux de survie et accroît les aptitudes.

La plasticité phénotypique d'autres espèces d'oursins inclut les variations de taille relative de la lanterne d'Aristote chez *Diadema antillarum* et *Echinometra mathaei* et les variations saisonnières de la densité des pédicellaires chez *Echinus esculentus*. A titre d'exemples de plasticité adaptative, citons encore les modifications de taille des échinides et des astérides lorsque l'habitat varie, et les variations du nombre de bras chez les crinoïdes.

L'atrophie saisonnière des organes internes chez l'holothurie *Parastichopus californicus* a été interprétée comme une réponse adaptative à la limitation de nourriture mais, étant donnée la nature des réponses chez les autres échinodermes, une telle interprétation semble peu plausible et la signification de cette atrophie saisonnière reste inconnue.

INTRODUCTION

"I speculated whether a species very liable to repeated and great changes of conditions, might not acquire a fluctuating condition ready to be adapted to either conditions." Charles Darwin in a letter to Karl Semper, February 6, 1881 (Darwin and Seward, 1903).

Increased variability of life-history traits decreases fitness (*e.g.* Tuljapurkar, 1982) yet many organisms, including echinoderms, appear to be highly plastic. The current explanation for this apparent contradiction is that, in some manner, variation of a morphological trait actually decreases variability of traits that are nearer to measures of fitness; namely, survival and fecundity. This cybernetic system, proposed by Ashby (1956) is generally invoked in order to explain how plasticity can be adaptive (*e.g.* Caswell, 1983).

A distinction is made between two different types of plasticity that are shown by organisms. The first type of plasticity shows continuous variation as the environment changes and is called a "reaction norm" (Woltereck, 1909 *in* Stearns, 1989), which is the same as "dependent morphogenesis" (Shmal'gauzen, 1949), "modulation" (Smith-Gill, 1983), or "allelic sensitivity" (Schlichting and Pigliucci, 1995). The second type of plasticity shows discontinuous variation and discrete variants are produced when changes in the environment trigger a developmental switch. This type of plasticity is termed "auto-regulative development" (Shmal'gauzen, 1949), "conversion" (Smith-Gill, 1983), or "gene regulation" (Schlichting and Pigliucci, 1995).

The proposed relationship for the adaptive significance of reaction norms (Fig. 1) is that as environmental conditions change, morphological features may change substantially but survival may change only slightly. The better the adaptation for resisting environmental change, the smaller the change in survival, which makes the plastic responses in A (Fig. 1) better than in B even though both A and B show major changes in morphology with either positive or negative changes in the sizes of one or more body parts.

Adaptive plasticity of larval morphology has been discussed by Fenaux *et al.* (1988), Boidron-Metairon (1988), Fenaux *et al.* (1994), Hart and Strathmann (1994), and will not be discussed here. Rather, I will focus on plasticity in post-larval stages and, in particular, plasticity of growth

and morphology in response to variation in food and physical aspects of the environment.

Growth plasticity

There is a long history of papers on echinoderms that show that growth in size is highly plastic (reviewed by Lawrence and Lane, 1982). The general factor responsible for causing such variation is considered to be food; however, other possibilities are salinity (*e.g.* Hallam, 1965) as well as unknown factors, as shown by the wide variation in size (1 to 3 cm) of a cohort of *Strongylocentrotus purpuratus* grown under identical conditions for one year (Pearse and Cameron, 1991). There also are reports of shrinkage of the test in sea urchins as well as size decreases in other echinoderms (*e.g.* Ebert, 1967; reviewed by Lane and Lawrence, 1982; Levitan, 1988, 1989).

The usual explanation for the adaptive significance of shrinkage of the test of sea urchins is that, in some manner, it improves survivorship and makes an individual "fit" the environment better. Small individuals require fewer resources and so there would seem to be a clear link between shrinkage and survival; however, there has been no critical test of this contention.
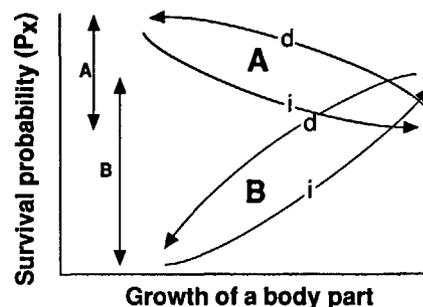

Figure 1

Reaction norms showing changes in survival rate (P$_x$) with changes in growth of an anatomical part such as body size, gonad, etc; for increasing (i) or decreasing (d) changes in growth. A shows a smaller change in survival values than does B.
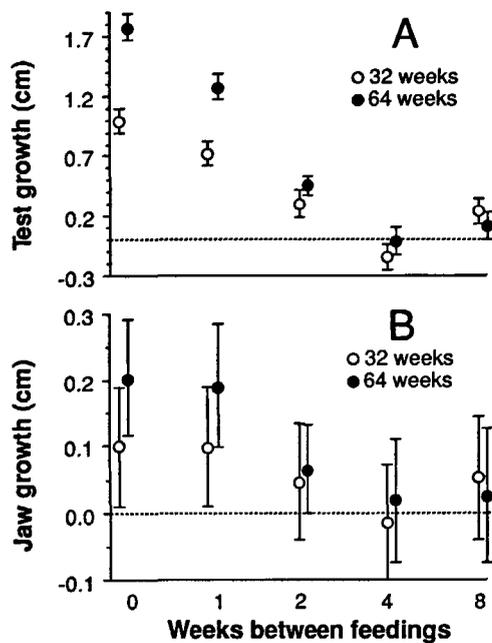
Figure 2

Test growth (A) and jaw growth (B) for Strongylocentrotus purpuratus *maintained at 5 levels of feeding (Fansler, 1983) relative to initial conditions; initial test diameters for feeding levels 0, 1, 2, 4, and 8 weeks respectively were 3.562, 3.449, 3.322, 3.465 and 3.420 cm, all with a standard error of ± 0.027cm and N = 60 for each treatment; The regression of ln (jaw) vs ln (diameter) for an initial sample of 176 was used to estimate initial jaw (J) lengths; ln (J) = [-1.2322 ± 0.0215se] + [0.7871 ± 0.0181se] ln (D); initial jaw lengths were estimated to be 0.793, 0.773, 0.750, 0.776, and 0.768 respectively for the 5 treatments.*

There are associated morphological changes with changes in food. In regular echinoids, the hypothesis that the relative size of Aristotle's lantern changes in response to available food (Ebert, 1980) was tested under laboratory conditions (Fansler, 1983; Edwards, 1986; Levitan, 1989; Edwards and Ebert, 1991) and in the field (Black *et al.*, 1982, 1984; Levitan, 1989). Jaw length, or more correctly, demi-pyramid length, becomes relatively larger when food is scarce and relatively smaller in size when food again becomes abundant. Black *et al.* (1984) showed that *Echinometra mathaei* with large jaws had higher grazing rates than did individuals with smaller jaws both in the field and under laboratory conditions. The reasonable interpretation is that increased jaw size promotes food gathering when food is scarce and so would contribute to buffering survival from environmental variation.

Fansler (1983) studied *Strongylocentrotus purpuratus* and showed the primary pattern of demi-pyramid plasticity that has been repeated for other species (*e.g.* Levitan, 1989). In her study, animals were maintained at several levels of feeding: *ad libitum*, one feeding/week, one feeding every two weeks, one feeding every four weeks, and one feeding every eight weeks. For feedings other than at the *ad libitum* rate, abundant food was supplied for 24 hours and then all remaining food was removed until the next feeding date. Growth was based on original sizes and on samples that were collected at 32 and 64 weeks. The 64 week sample for the two most starved groups of sea

urchins include animals that had died between 32 and 64 weeks; all of the animals fed just once every 8 weeks were dead at 52 weeks.

Well fed animals grew more than starved animals and this pattern held for both the test and demi-pyramids. Growth (Fig. 2) was based on the differences between sizes of the original samples at 32 and 64 weeks (or for the most severely starved animals for all animals that died during the period); accordingly, the base line of zero growth may actually be slightly higher or lower. As it stands, there is no clear evidence for shrinkage of either the test or jaws, which is contrary to results using *Strongylocentrotus purpuratus* in the field that had been tagged with nylon monofilament (Ebert, 1967) as well as results reported by Levitan (1989) who reported substantial shrinkage of *Diadema antillarum* both in the field and in the laboratory. Resorption of calcite certainly is possible (*cf.* David and Néraudeau, 1989) and there may be differences across species with respect to shrinkage. It also remains unclear whether shrinkage would be adaptive in terms of adjusting sea urchins to "fit" local conditions or whether shrinkage would be just a consequence of resorption of tissue used to support survival; the body wall contains a substantial fraction of the organic matter in sea urchins (*e.g.* Giese, 1966) and hence would be expected to be drawn upon during periods of stress.

Relative changes in morphology in response to stress

In Fansler's (1983) work, well fed animals had relatively small jaws (Fig. 3), which was analyzed by an ANCOVA with ln(test diameter) as a covariate so ln(jaw lengths) were all adjusted in the analysis to a common ln (test diameter). Use of ln (test diameter) as a covariate adjusts for the fact that well fed animals grew and poorly fed animals did not. The test diameters of well fed animals grew more rapidly than did jaws (demi-pyramids) whereas in starved individuals, although very little growth took place, jaws grew relatively more than did tests. The most severely starved animals did not appear to change during the course of the experiment. There are two possible
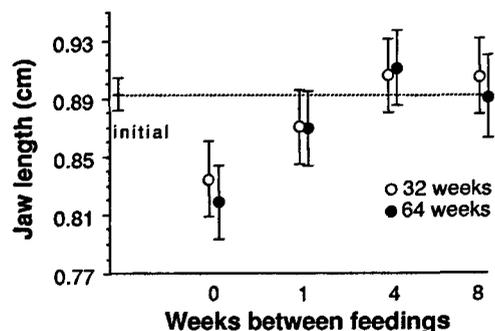

Figure 3

Jaw lengths of Strongylocentrotus purpuratus *adjusted to a common test diameter of 4.142 cm for all groups by ANCOVA with time and feeding treatments as factors and test diameter as a covariate; all measurements ln-transformed before analysis and back-transformed for display above; initial conditions shown for reference but were not included in the ANCOVA (Fansler, 1983).*

explanations for this; one is that each treatment started as a sample of the initial conditions and so some error is expected because initial conditions varied slightly. The second, and I think more reasonable explanation, is that it takes energy to remodel and if there are no resources, then reworking can not take place; there is an energetic cost of plasticity.

The morphological trends in Figure 3 were reversible. Fansler (1983) switched half of the animals from the most extreme conditions (food supplied *ad libitum* and food supplied once every 8 weeks) at 32 weeks. Results (Fig. 4) showed changes in relative sizes of the jaws: they increased in well fed animals that were subjected to starvation conditions and decreased in starved animals that were switched to feeding

Table 1

Analysis of covariance of ln-transformed dried body parts of Strongylocentrotus purpuratus *based on work by Edwards (1986); factors are 1) time, 2 levels: 16 and 32 weeks; 2) feeding, 2 levels:* ad libitum *and once every 4 weeks; and, 3) clipping, 2 levels: not clipped and clipped every 4 weeks; ln(test diameter) is a covariate; data structure is: A fed and not clipped (N = 20), B fed and clipped (N = 17), C fed once every 4 weeks and not clipped (N = 18), D fed once every 4 weeks and clipped (N = 16).*

| Component	Source	SS	df	MS	F-ratio	P
ln(test)	time T	0.0008	1	0.0008	0.0442	0.8341
$R^2 = 0.960$	feeding F	0.0059	1	0.0059	0.3420	0.5608
	clipping C	0.0017	1	0.0017	0.1010	0.7517
	ln(dia)	7.3411	1	7.3411	427.1996	0.0000
	T × F	0.0319	1	0.0320	1.8591	0.1776
	T × C	0.0685	1	0.068491	3.985676	0.0502
	F × C	0.0055	1	0.0055	0.3185	0.5745
	error	1.0826	63	0.0172		
ln(spines)	time T	0.3575	1	0.3575	9.0126	0.0038
$R^2 = 0.886$	feeding F	0.2049	1	0.2049	5.1668	0.0264
	clipping C	3.0198	1	3.0198	76.1380	0.0000
	ln(dia)	7.0758	1	7.0758	178.4019	0.0000
	T × F	0.1146	1	0.1146	2.8899	0.0941
	T × C	0.3956	1	0.3957	9.9756	0.0024
	F × C	0.3140	1	0.3140	7.9170	0.0065
	error	2.4987	63	0.0397		
ln(lantern)	time T	0.1302	1	0.1302	6.7235	0.0118
$R^2 = 0.816$	feeding F	0.3406	1	0.3406	17.5954	0.0001
	clipping C	0.0349	1	0.0349	1.8045	0.1840
	ln(dia)	4.4530	1	4.4530	230.0195	0.0000
	T × F	0.0055	1	0.0055	0.2828	0.5967
	T × C	0.0093	1	0.0093	0.4813	0.4904
	F × C	0.0064	1	0.0064	0.3309	0.5672
	error	1.2196	63	0.0194		
ln(gut)	time T	7.1508	1	7.1508	85.4572	0.0000
$R^2 = 0.928$	feeding F	11.3231	1	11.3231	135.3187	0.0000
	clipping C	0.6995	1	0.6995	8.3596	0.0053
	ln(dia)	9.9799	1	9.9799	119.2662	0.0000
	T × F	1.3631	1	1.3631	16.2895	0.0001
	T × C	0.1430	1	0.1430	1.7085	0.1959
	F × C	0.5473	1	0.5473	6.5403	0.0130
	error	5.2717	63	0.0837		
ln(gonad)	time T	1.4808	1	1.4808	4.0473	0.0485
$R^2 = 0.946$	feeding F	135.4528	1	135.4528	370.2119	0.0000
	clipping C	1.0980	1	1.0980	3.0009	0.0881
	ln(dia)	24.0812	1	24.0812	65.8174	0.0000
	T × F	3.2370	1	3.2369	8.8471	0.0042
	T × C	0.0770	1	0.0770	0.2104	0.6480
	F × C	0.0055	1	0.0055	0.0149	0.9031
	error	23.0504	63	0.3659		
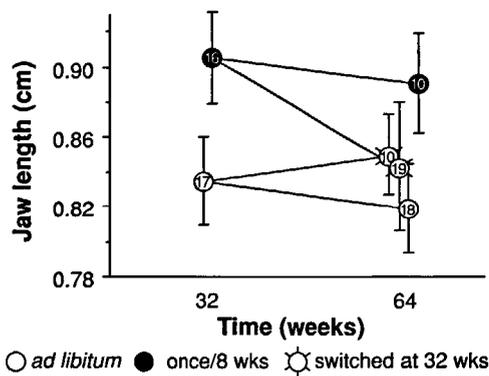
Figure 4

Effect of switching animals from the most extreme treatments, ad libitum food and feeding once/8 weeks; 1/2 of animals were switched after 32 weeks at each treatment and measured after another 32 weeks (Fansler, 1983); ANCOVA following ln-transformation with ln(diameter) as a covariate; error bars are ± 1se with N shown in each dot.

ad libitum. It is of interest that relative jaw sizes matched after 32 weeks of switched feeding. It is as though the animals had no physiological "memory" so that starvation did no damage that could not be reversed by feeding.

A different set of experiments (Edwards, 1986; Edwards and Ebert, 1991) agreed with the basic aspect of Fansler's experiment with respect to changes in relative size of jaws in response to changes in level of feeding; however, an additional wrinkle was added by Edwards to examine the plastic responses of *S. purpuratus* to spine damage. Feeding levels were *ad libitum* and once every 4 weeks. For the spine damage treatment, spines were clipped with scissors to within 3-4 mm of the milled ring, which is the flange near the base of a spine where muscles are attached. Clipping was done every 4 weeks as one treatment; the other treatment was no clipping.

Results from dissections at 16 and 31 weeks show differences in relative dry weights of body parts. Analysis of covariance was used with ln (body part weights) as dependent variables, time, feeding and clipping as factors and ln (diameter) as a covariate (Tab. 1). Body walls were separated into spines and test for analysis. Spine weights for the clipped treatments were cumulative and so were not only the weights on the day of dissection but included the weights of spines that had been clipped during the course of the study (see Edwards, 1986 and Edwards and Ebert, 1991 for additional details of the methods).

Test weight for a particular test diameter did not change in response to treatments of feeding or clipping (Tab. 1) and the high value of R^2, 0.960, is due to the high correlation between ln (diameter) and ln (test weight). All other body components showed various levels of response to both feeding and clipping treatments. The Type-I error probability values for feeding level are, in general, very low : 0.026 for spines and < 0.0005 for all other body components. The treatment of spine clipping shows higher p-values: 0.184 for the lantern, 0.005 for the gut, 0.088 for the gonad and < 0.0001 for spines. Relationships for feeding x clipping are shown in Figure 5. By using ln (diameter) as a covariate in the analysis, all weights are expressed after adjusting to a common diameter of 4.03 cm. For purposes of plotting, all adjusted means and standard errors were back-transformed to original measurements.

Changes in spine mass due to treatments are remarkable. Spine clipping stimulated calcification so that treatments B and D are not different even though animals in B were fed *ad libitum* and animals in treatment D were fed once every 4 weeks. Resources were reallocated in order to rebuild damaged spines and this repair appears to be an exceedingly important activity. The gut and the gonads, in addition to their primary functions, are storage organs and both decreased in mass in response to spine clipping with p = 0.005 for the gut and 0.088 for the gonads. Lantern
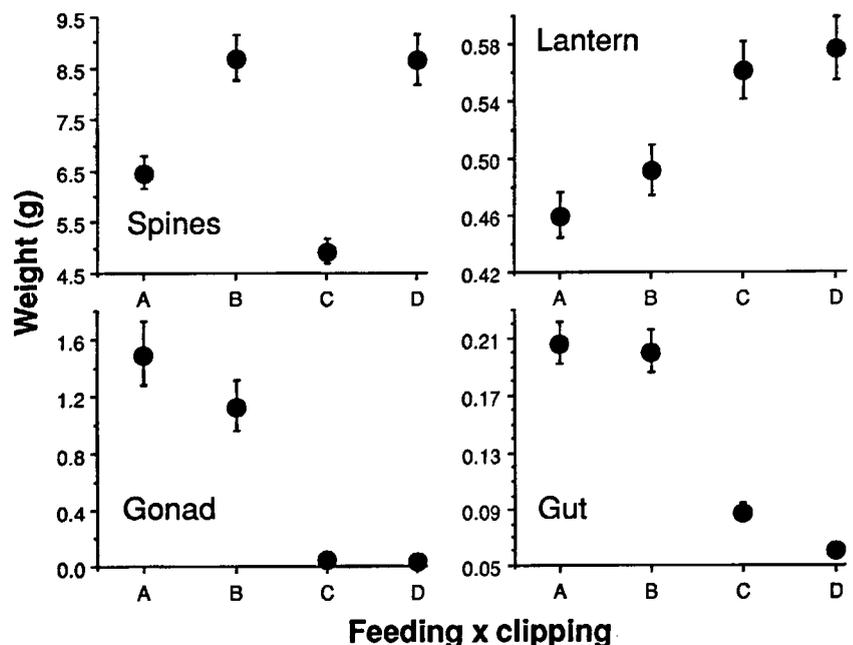

Figure 5

Effect of feeding and spine clipping on relative dry weights of body parts of Strongylocentrotus purpuratus; (Edwards, 1986); 16 and 32 week samples combined; A ad libitum food and no clipping of spines (N = 20); B ad libitum food and spines clipped every 4 weeks (N = 17); C food once every 4 weeks and no spine clipping (N = 18); D food and spine clipping every 4 weeks (N = 16); ANCOVA of ln-transformed data with treatment; error bars are ±1 standard error.

mass increased in response to decreased food (p = 0.012) and although there appears to be an effect of spine clipping (Fig. 5), the response is weak (p = 0.184).

The potential adaptive significance of plastic adjustment of body parts is shown by comparing survival of animals in the studies of Fansler (1983) and Edwards (1986). Fansler's (1983) experiment was maintained for a longer period of time and the most severe treatment was one feeding every 8 weeks. Survival during the first 32 weeks was high for all treatments (Fig. 6). From 32 to 64 weeks, survival remained high for treatments where animals were fed *ad libitum*, once/week and once every 2 weeks but declined dramatically in treatments where animals were fed once every 4 weeks or 8 weeks.

Edwards study lasted just 31 weeks and the most severe treatment was feeding once every 4 weeks together with spine clipping once each 4 weeks. Following some early mortality during the first 4 weeks, survival was the same in all treatments (Tab. 2) even though changes in the relative sizes of body parts was substantial, which is in agreement with Fansler's results. *Strongylocentrotus purpuratus* is able to maintain high survival rates over a wide range of food availability and spine damage and while it is doing this there are substantial changes in morphology.

Data from the experimental results of Fansler (1983) and Edwards (1986) were combined with field populations at Sunset Bay, Oregon (Ebert, 1980) in a single ANCOVA using ln-transformed data and ln (diameter) as a covariate. Adjusted means show that shifts in relative jaw size that could be induced experimentally were not as extreme as shown by populations in the field (Fig. 7). Animals in the Boulder Field area of Sunset Bay grew rapidly (Ebert, 1968) and attained a large size; the largest individual ever measured in this area exceeded 10.0 cm test diameter. Jaw lengths were relatively small in the Boulder Field (Fig. 7). In the Postelsia Zone, sea urchins were much smaller and grew more slowly. They also had relatively larger jaws. To estimate mortality rates for the field populations (Ebert, unpublish.), size-frequency distributions (Ebert, 1968) were equally weighted, summed, and smoothed using a 5-point moving average. Growth was modeled using the difference equation (Ebert, 1968):

$$S_{t+1} = S_t - K \log_{10}(S_t) + C \qquad (1)$$

and survival rate was assumed to be constant,

Table 2

Mortalities observed by Edwards (1986); all treatments started with 51 animals in each treatment with 10 animals removed for dissection from each treatment at weeks 2,4, and 8; 7 were removed at week 16 so at week 31, 13 animals remained in treatment A, 10 in B, 11 in C and 9 in D; H_0: deaths are independent of treatment; $X^2 = 2.875$, df = 3, p > 0.25 and so fail to reject H_0; results do not indicate an effect of treatment on survival.

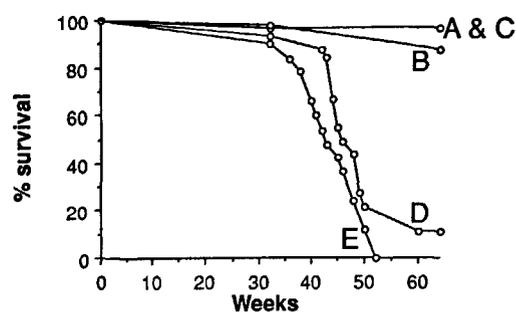|	A	B	C	D	Totals
Deaths due to dissection	50	47	48	46	191
Deaths not due to dissection	1	4	3	5	13
Totals	51	51	51	51	204

Figure 6

Survival of Strongylocentrotus purpuratus *at 5 levels of feeding: A ad lib, B once per week, C once every two weeks, D once every four weeks, E once every 8 weeks (Fansler, 1983).*

$$Nt = N_0 e^{-Zt} \qquad (3)$$

The problem was to find the value of Z that provided the best fit to the observed summed size-frequency distributions, which was done by trial and error. Using this approach, the mortality rates of sea urchins in the Boulder Field and Postelsia Zone were approximately equal: $Z \approx 0.1$ yr^{-1} and Z for the Eelgrass Area was 0.2 yr^{-1}. These are annual survival rates of 0.9 and 0.8 respectively. The significant point is that survival was equally good at the extremes of nutrition and relative jaw size.

Plastic responses of pedicellariae

Plasticity in development of pedicellariae under field conditions has been demonstrated by Ramsay and Campbell (1985). They found that the side of the sea urchin *Echinus esculentus* that bears the madreporite had significantly higher densities of globiferous, tridentate, and trifoliate pedicellariae; that there were more tridentate and trifoliate pedicellariae on the aboral than on the oral surface and highest concentrations of globiferous and ophiocephalous pedicellariae at the ambitus. The most interesting results presented by Ramsay and Campbell (1985) are for pedicellariae densities on *Echinus esculentus* in two collections, one in February and the other in June (Fig. 8). Overall densities were higher in February and density on the aboral surface was about twice the density at the ambitus and three times the density on the oral surface. In June, densities were nearly equal on all surfaces although there still was an apparent trend from oral to aboral. What these results imply is that there are rapid adjustments in production of pedicellariae in response to seasonal changes. Possible adaptive reasons include responses to seasonal changes in sediment loads due to winter storms or seasonal patterns of mero-planktonic larvae that would settle on sea urchins.

Plastic responses in other echinoderms

Morphological plasticity in other echinoderm groups also has been explored although adaptive significance is, in some cases, uncertain. Possible candidates are visceral resorption in holothurians (Fankboner and Cameron, 1985) and variation in arm number in asteroids or crinoids (*cf.* Lawrence, 1986).

Arm number in crinoids may be variable within a species. For example, Liddell (1982) found that *Nemaster rubiginosa* had a mean of 17.2 arms in Jamaica (N = 50), 22 in Curaçao N = 13), and 23.5 in Barbados (N = 15). There also were geographic differences in other morphological features of *N. rubiginosa* associated with feeding (Liddell and Lohlhorst, 1982). What is unclear from these studies is whether the differences represent plastic responses to food differences either as a "reaction norm" (Stearns, 1989) or "conversion/gene regulation" (Smith-Gill, 1983; Schlichting and Pigliucci, 1995). It is unknown whether crinoids could be induced to change the number of arms in response to environmental changes and, if so, whether changes would be adaptive in the sense of buffering survival rates.

Certainly one of the strangest seasonal cycles in echinoderms is evisceration or atrophy of internal organs in holothurians (*e.g.* Bertolini, 1930; Swan, 1961; Jespersen and Lutzen, 1971; Fankboner and Cameron, 1985). In *Parastichopus californicus* (Fankboner and Cameron, 1985) organs degenerate each year during the fall and regenerate over a very short period in winter (Fig. 9). The proposed explanation is that it is energetically cheaper to get rid of organs during periods of low food and then build new ones when food is again abundant. The short period between the onset of degeneration and the beginning of regeneration is only 1-2 months, which seems too short a period for response to food changes given the response rates of echinoids (Fansler, 1983; Edwards, 1986). This certainly does not appear to be the same sort of plastic resource allocation that one sees in adjustment of Aristotle's lantern in sea urchins or even the use of gonads as storage organs because structures needed for processing food are resorbed or eviscerated – unless sea cucumber nutrition is greatly misunderstood and the digestive tract really is primarily a storage organ, which seems unlikely (*cf.* Jangoux and Lawrence, 1982). I find it more likely that the annual loss of
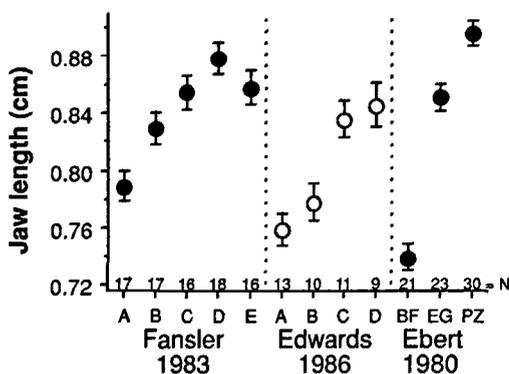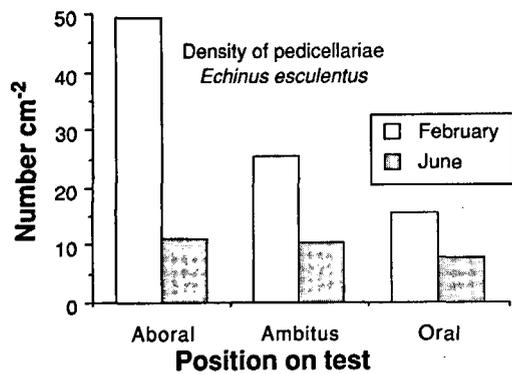

Figure 8

Total numbers of pedicellariae per cm² at three positions on tests of Echinus esculentus *collected at the University Marine Biological Station, Millport, Isle of Cumbrae (from Ramsay and Campbell, 1985).*

the digestive tract has an explanation that does not hinge on an adaptive response to food stress.

DISCUSSION

The plasticity shown in echinoderms can be described as "norms of reaction", following current usage (*e.g.* Gomulkiewicz and Kirkpatrick, 1992; Schlichting and Pigliucci, 1995), in the sense that a graded environmental change elicits a graded morphological response. I could not find examples of developmental switches in echinoderms although such may occur. For example, color morphs of many echinoderms are puzzles. The brittle star *Ophiothrix spiculata*, ranges from yellow, orange and red to blue and purple (personal observation) and the ground color of the doral surface of *Ophiothrix angulata* can be blue, violet, pink, rose, crimson, brown, gray or green (Hendler *et al.*, 1995). It is uncertain whether the color morphs are a genetic polymorphism or due to develop-
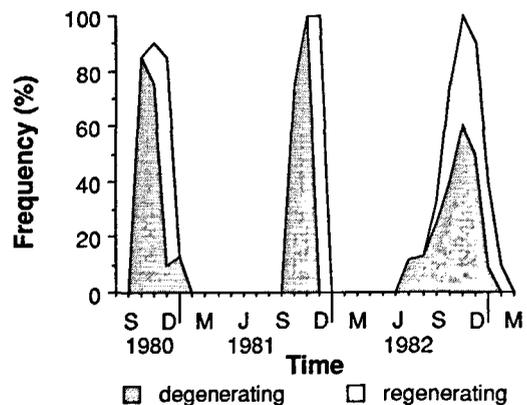

Figure 7

ANCOVA of jaw lengths (dependent variable) of Strongylocentrotus purpuratus *in two laboratory experiments (Fansler, 1983; Edwards, 1986) and field samples from Sunset Bay, Oregon (Ebert, 1980); time = 32 weeks for laboratory dissections; test diameter was a covariate and treatments or sites were factors; all data were ln-transformed; treatment symbols for Fansler (1983) and Edwards (1986) as given in previous figures; for Sunset Bay, Oregon, Ebert (1980) BF = Boulder Field, EG = Eel Grass Area, PZ = Postelsia Zone; adjusted means and error bars(± 1se) were back-transformed for plotting; N in each sample is shown above x-axis.*

Figure 9

Periodic degeneration and regeneration of internal organs of the sea cucumber Parastichopus californicus; *frequency is the percent of individuals in samples; data replotted from Fankboner and Cameron (1985).*

mental conversion. Similarly, in Hawaii, the sea urchin *Heterocentrotus mammillatus* shows great variation in colors of primary and secondary body spines so some individuals have brown primary spines and white secondary spines; others have red primary and secondary spines, etc. Whether due to developmental conversion or genetic polymorphism, there are no reasonable suggestions concerning possible adaptive significance of the different color morphs.

Wide norms of reaction would be expected in species that live in fluctuating environments, that show limited movement to adjust behaviorally for fluctuations, or are saddled with both of these conditions. In a sense, many echinoderms are secondarily sessile (*cf.* Frank, 1981) or sufficiently slow moving that behavior may be insufficient to avoid environmental stresses. Under these constraints, substantial plasticity would be expected.

The experimental studies of *Strongylocentrotus purpuratus* by Fansler (1983) and Edwards (1986) both showed morphological shifts in response to environmental stresses but, at the same time, only small shifts in survival for over half a year. It is unlikely that *S. purpuratus* ever is confronted in the field with natural conditions as severe as treatments D and E by Fansler or treatments C and D by Edwards that also are sustained for over six months. The reaction norms are sufficiently broad that *S. purpuratus* probably never starves to death in the field as shown by the similarity of survival rates for sea urchins at Sunset Bay, Oregon, that live with different levels of food and show relative jaw sizes more extreme than those that could be induced by experimental conditions. The laboratory and field results both indicate wide reaction norms for morphological features coupled with a narrow range of survival probabilities, which suggests an adaptive role for morphological plasticity at least in *Strongylocentrotus purpura-*

tus and, by extension, to other echinoids (*e.g.* Black *et al.*, 1982, 1984; Levitan, 1988, 1989).

Studies with other echinoderms can be interpreted in the context of adaptive plasticity that buffers survival rates. Size variation and reported shrinkage in asteroids (*e.g.* Vevers, 1949) or holothuroids (reviewed by Lawrence and Lane, 1982) all may indicate buffering of survival although no survival estimates are available in these studies. Similarly, the observed differences in crinoid arm number (*e.g.* Liddell, 1982) or changes in distribution and abundances of pedicellariae on *Echinus esculentus* (Ramsay and Campbell, 1985) make sense in terms of possibly modifying survival probabilities. Seasonal atrophy of internal organs of *Parastichopus californicus* (Fankboner and Cameron, 1985), however, does not make sense in this context because rather than adjusting the relative size of structures associated with food processing, the structures are thrown away. In echinoids, this would be the equivalent of shrinking the size of Aristotle's lantern when food was in short supply rather than increasing lantern size, as is observed. Throwing away the gut to spite the gonads seems unlikely, which is not to say it isn't the case. Echinoderms are crafty in their adaptations and do not share their wisdom with us easily.

Acknowledgments

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