A wide variety of organisms show morphologically plastic responses to environmental stressors but in general these changes are not reversible. Though less common, reversible morphological structures are shown by a range of species in response to changes in predators, competitors or food. Theoretical analysis indicates that reversible plasticity increases fitness if organisms are long-lived relative to the frequency of changes in the stressor and morphological changes are rapid. Many sea urchin species show differences in the sizes of jaws (demi-pyramids) of the feeding apparatus, Aristotle’s lantern, relative to overall body size, and these differences have been correlated with available food. The question addressed here is whether reversible changes of relative jaw size occur in the field as available food changes with season. Monthly samples of the North American Pacific coast sea urchin *Strongylocentrotus purpuratus* were collected from Gregory Point on the Oregon (USA) coast and showed an annual cycle of relative jaw size together with a linear trend from 2007 to 2009. *Strongylocentrotus purpuratus* is a long-lived species and under field conditions individuals experience multiple episodes of changes in food resources both seasonally and from year to year. Their rapid and reversible jaw plasticity fits well with theoretical expectations.

1. Introduction

Developmental variation of organisms in response to environmental stresses is well known and there are numerous examples of morphological, physiological, behavioural and life-history changes [1–6]. Plastic responses are a part of the norms of reaction of a species and can be continuous or discontinuous and reversible or irreversible [7]. Most morphological responses are not reversible and can occur in both short- and long-lived species, such as rotifers [8] and trees [9]. Less common is reversible plasticity of morphological structures.

Reversible plasticity shows increased fitness if stresses occur many times over the lifespan of individuals. This relationship has been modelled in the context of the mode and breadth of tolerance functions [10] and a plastic response to stress may shift the mode or the variance (breadth) of a tolerance function. There are lags in the plastic response to changing stress both from the non-stressed condition to the stressed and back again as stress is relieved, and the changes may show a hysteresis curve rather than just following a reverse path. Ideally, the response times in both directions should be short to provide maximum fitness.

Examples of reversible morphology include both structures associated with food and feeding as well as defence from predators. The development of a carnivore morph from an omnivore morph in spadefoot toad tadpoles can be shifted back towards a more omnivore morphology by changing diet [11]. Tree frog tadpoles show reversible morphological changes in response to changes in presence of dragon fly nymphs [12]. Some snakes show a rapid increase in intestinal mass following a meal [13] and this is followed by reduction as the meal is digested. Morphological changes have been documented in perch (fish) following shifts in habitat complexity and food type [14]. Galapagos marine iguanas resorb bone and shrink during low food conditions associated with El Niño but recover bone and increase in size when food availability improves [15]. In birds, gizzard size in Japanese quail has shown reversible changes to dietary fibre with a...
hysteresis curve of gizzard length [16] and the bills of marsh sparrows change in size on an annual cycle associated with growth of the keratinized rhamphotheca [17]. The sea urchin Strongylocentrotus purpuratus has shown changes in demi-pyramid (jaw) size in response to changes in available food, and jaws become relatively larger at a low feeding rate; the pattern can be reversed if food is increased [18,19].

Differences in the relative size of jaws (demi-pyramids) of Aristotle’s lantern or the entire lantern have been reported for a large number of sea urchin species in field studies, including S. purpuratus [20], Mesocentrotus (Strongylocentrotus) franciscanus [21,22], Strongylocentrotus droebachiensis [23,24], Echinometra mathaei [25,26], Diadema setosum and Diadema antillarum [25,27], Sterechinus neumayeri [28], Echinochasmus clidonicus [29], Arbacia punctulata [30], Centrostephanus rodgersii [31] and Helicidaris erythrogramma [32]. Changes in jaw and diameter allometry also have been induced under laboratory conditions of food manipulations in S. purpuratus [18,33,34], S. droebachiensis [24,35], M. franciscanus [36,37], D. antillarum [27], Pancentrotus lividus [38] and Lytechinus variegatus [39].

Under laboratory conditions, the change in relative lantern or jaw size can be rapid as reported for S. purpuratus [33], where well-fed sea urchins developed relatively smaller jaws than the original field sample within a month. The time and shape of the reverse course, however, have not been studied in detail [18,19].

Where food is scarce, jaws tend to be large relative to test diameter. Consequently, the relationship between jaw length and test diameter should reflect food conditions in the field and be correlated with growth rates as shown for M. franciscanus [22]. Available food changes seasonally along the Pacific coast of North America [40], and given rapid responses of jaw allometry observed in the laboratory, seasonal changes in relative jaw length would be expected under field conditions. This is the hypothesis we explore for S. purpuratus.

2. Material and methods

(a) Study species and site

The purple sea urchin S. purpuratus has a reported geographical range from Isla Cerdos, Baja California (28° N) [41] to at least Torch Bay, Alaska (58°33’ N) [42] and is a common and abundant member of both intertidal and subtidal environments. Monthly collections of 20 S. purpuratus were made in the intertidal at Gregory Point, Oregon (43°20’24” N, 124°22’30” W) from January 2007 to July 2009 as part of a study of gonad development related to latitude and ocean conditions [40]. Gregory Point is 0.7 km northwest of Sunset Bay where S. purpuratus has been studied for many years [43,44]. Measurements used for gonad analysis were test diameter and height, total wet weight, and gonad weight. Following dissection, body walls and lanterns were saved and bleached with sodium hypochlorite, soaked in tap water to remove residual bleach and dried. Specimens were saved and subsequently jaws (demi-pyramids) of Aristotle’s lantern were measured with digital callipers. Four of the saved samples were missing lantern parts and so reduced the analysis to 615 individuals. Jaw measurements were from the oral tip of the jaw to the distal shelf that articulates with the epiphysis as used in previous studies [44]. All data have been archived and are available [45].

(b) Methods of analysis

The approach to analysis was to look for an annual cyclical pattern of jaw length, \( J \), relative to test diameter, \( D \), or total wet weight, \( T \). The starting point for analysis was the basic allometric equation

\[
J = a D^b \quad (2.1)
\]

or

\[
\ln J = \ln a + \beta \ln D. \quad (2.2)
\]

Analysis of the annual cyclic change in jaw size started with a modification of a general model used to describe biocycles [46]:

\[
y_i = A + M \cos \left( \frac{2\pi}{\tau} t_i + \phi \right) + \epsilon_i. \quad (2.3)
\]

Two additional parameters were then added to permit \( \beta \) to vary seasonally. Also, year-to-year variation in jaw allometry could occur. To model these additional complications, equation (2.3) was modified [40]:

\[
\ln J_i = A + M \cos \left( \frac{2\pi}{\tau} t_i + \phi \right) + \beta \ln D_i + B_1 t_i + \epsilon_i. \quad (2.4)
\]

where \( \ln D = \ln \)-transformed test diameter, \( D_i \); \( A = \) the mean of \( \ln a \), which in equation (2.4) was seasonally adjusted by \( M \cos(2\pi/\tau + \phi) \); \( M \) is the amplitude of half the predicted change of \( \ln a \); \( \tau \) is duration of one cycle, which was fixed at 1 year; \( t_i \) is time in years when samples were collected starting with \( t = 0 \) at 1 January 2007; \( \phi \) is lag from reference time of the crest of the cycle; \( \beta = \) mean of the allometric exponent adjusted seasonally by \( C \cos(2\pi/\tau + \phi) \); \( C \) is the amplitude of one half predicted change in \( \beta \), and so similar to \( M \); \( B_1 \) is coefficient of linear change with time, \( t_i \) and \( \epsilon_i \) is error.

The inclusion of a coefficient of linear change with time, \( B_1 \), is appropriate in this study but probably would have to be changed for other datasets. For example, a second-order term has been included in analysis [40], but with datasets spanning many years direct inclusion of environmental data probably would be preferable to adding additional higher order terms.

Parameter estimates were made by nonlinear regression [47] using all data, including outliers. Analyses were done with and without the linear term, \( B_1 \), and with and without an annual cycle of allometric change. Comparison of these four models was made using Akaike’s Information Criterion [48] with small sample adjustment, AICc:

\[
\text{AICc} = n \ln(n\sigma^2) + 2K. \quad (2.5)
\]

The number of parameters, \( K \), includes SSE so, for example, in equation (2.4) with both cyclic and linear change with time, \( K = 7 \). AIC differences, \( \Delta_i \), were computed and used to calculate Akaike weight, \( w_i \), which is the weight of evidence of model \( i \) being the best model of the group of models considered.

Measuring diameter and height of living sea urchins is not easy because spines and associated tubercles can interfere with positioning calliper jaws. Sea urchins are not circular around the ambitus but rather slightly pentagonal and so a measurement of maximum diameter requires positioning callipers running from the centre of an ambulacral area to the centre of the opposite interambulacral. There are also problems with positioning calliper jaws perpendicularly to the sea urchin test. All of these problems can lead to errors or biases in measurement [49]. It is reasonable, however, to assume that unlike linear measurements, weight measurements with a digital balance are mostly free of problems of investigator technique although inconsistency in removing excess water can lead to errors. Comparison of linear and weight measurements over time can address the problem of consistency. There is also a problem that monthly collections might have been made at slightly different microhabitats and so any trends may not indicate the performance of a single site. We approach this problem by asking...
3. Results

Monthly samples collected at Gregory Point always contained a range of sizes (figure 1). Diameter measurements for the 620 dissections had a range of 2.53–9.17 cm with a mean of 6.15 (1.35 s.d.) cm. Total wet weight ranged from 8.26 to 297.7 g with a mean of 119.62 (62.66 s.d.) g. Jaw (demi-pyramid) measurements ranged from 0.53 to 1.64 cm with a mean of 1.35 (0.22 s.d.) cm. Total wet weight ranged from 8.26 to 297.7 g with a mean of 119.62 (62.66 s.d.) g. Jaw (demi-pyramid) measurements ranged from 0.53 to 1.64 cm with a mean of 1.35 (0.22 s.d.) cm (N = 615).

Analysis of ln J as a function of ln D and time (table 1) showed that the model with the most support, largest wᵢ (99.6%), was the one with both a seasonal cycle and a linear trend from 2007 to 2009. Analysis with a trend from 2007 to 2009 but no annual cycle had little support as the best model (wᵢ = 0.37%), which also was the case for an annual cycle but no trend (wᵢ = 0.002%).

The ANCOVA with ln J as the dependent variable, ln D as a covariate and monthly sample date, tᵢ, as a fixed factor (table 2) provides an estimate of ln J for each sample adjusted to an overall mean ln D of 1.78879 (mean D = 5.928 cm). The interaction term of ln D × sample date, tᵢ, was not significant (p = 0.33). A plot of adjusted means of ln J together with the fitted line using the parameters in table 1 both transformed back to J (eᵣ(ln J) = 1) shows both the seasonal and linear trends (figure 2). Jaws were relatively large early in a year and then declined in relative size during the summer with a minimum in October or November. The linear decline could indicate improving food conditions each year from 2007 to 2009. There are, however, other possibilities including problems with measurement or with sampling sea urchins from different microsites during the study.

Wet weights of sea urchins in samples (figure 1) did not change during the study (F₁,618 = 1.747, p = 0.19) but shape might have changed if sea urchins were collected from slightly different microsites. No shape change, however, was detected with the logarithm of height, ln H, as a function of the logarithm of diameter, ln D, and time (table 3). Both the analysis of total weight and analysis of shape indicate that microsite changes during the study were not major contributors to the observed change in jaw : diameter allometry.

Analysis of ln jaw length, ln J, as a function of ln total wet weight, ln T, and time (table 4a) showed a significant linear trend with a negative slope indicating decreasing relative jaw size during the period of study. An ANCOVA with ln J as the dependent variable, ln T, as a fixed factor and sample time, tᵢ, as a fixed factor and sample date, tᵢ, as a fixed factor provided a pattern of monthly ln J adjusted to a common wet weight, ln T (4.58381). This pattern does not differ in any major way from the pattern shown by ln J as a function of ln D (figure 3). There is a cyclical pattern to jaw size relative to diameter or total weight together with a general downward trend from January 2007 to July 2009.

4. Discussion

The suggested significance of relative jaw size related to food is that larger jaws increase the ability to graze and this has been shown for E. mathaei [26] at Rottnest Island, Western Australia. Sea urchins with larger jaws grazed larger areas on rock surfaces. The direct demonstration of increased grazing ability with increased jaw size has not been done for other sea urchin species but the many studies presented in the introduction confirm that there is a relationship between relative jaw size and available food. Our interpretation of results for S. purpuratus at Gregory Point is that relative growth of the jaws and test changes during a year in response to changes in available food, with relatively larger jaws arising in response to decreases in food. The linear trend downward from 2007 to 2009 means that jaws became relatively smaller in addition to the cyclical pattern within a year, suggesting that food availability improved during this time, which is consistent with the maximum annual gonad sizes that were observed from 2007 to 2008 at Gregory Point [40]. Gonads in November 2008 were larger than in November 2007 and the relative size of the jaws was smaller, indicating better food conditions, in 2008 compared with 2007.
Strongylocentrotus purpuratus has shown variation in relative jaw size at a very local scale in Sunset Bay, Oregon, where samples collected approximately 50 m apart were different. The sea urchins with the smallest relative jaw sizes also had the largest test diameters, the largest gonads and the fastest growth rates [43]. Differences in growth related to relative jaw size also have been reported for Mesocentrotus (Strongylocentrotus) franciscanus [22], S. droebachiensis [24], E. chloroticus [30], H. erythrogramma [33], Anthocidaris crassispina [50] and C. rodgersii [32]. The food environment changes around S. purpuratus at Gregory Point on an annual basis [40]. Under laboratory conditions, allometric changes in response to food availability

### Table 1. Analysis of monthly jaw length, J, and test diameter, D, measurements of S. purpuratus collected at Gregory Point, OR, USA, from January 2007 to July 2009; data were first transformed using natural logarithms; \( \ln J = A + M \cos(2\pi t_1/30 + \phi) + \beta \ln D + C \cos(2\pi t_1/30 + \phi) \ln D + B_1 t_1 + e_i; \) definition of parameters given in text.

<table>
<thead>
<tr>
<th>model</th>
<th>parameter</th>
<th>estimate</th>
<th>s.e.</th>
<th>-95%</th>
<th>+95%</th>
<th>parameter</th>
<th>no.</th>
<th>SSE</th>
<th>AICc</th>
<th>( w_i ) %</th>
</tr>
</thead>
<tbody>
<tr>
<td>cycle and trend</td>
<td>( A )</td>
<td>-1.3212</td>
<td>0.0163</td>
<td>-1.3532</td>
<td>-1.2891</td>
<td>7</td>
<td>1.7783</td>
<td>-3581.10</td>
<td>99.632</td>
<td></td>
</tr>
<tr>
<td></td>
<td>( M )</td>
<td>0.0580</td>
<td>0.0233</td>
<td>0.0122</td>
<td>0.1037</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>( \phi )</td>
<td>-1.4254</td>
<td>0.2365</td>
<td>-1.8898</td>
<td>-0.9610</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( \beta )</td>
<td>0.8220</td>
<td>0.0090</td>
<td>0.8043</td>
<td>0.8397</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( C )</td>
<td>-0.0260</td>
<td>0.0129</td>
<td>-0.0513</td>
<td>-0.0007</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( B_1 )</td>
<td>-0.0144</td>
<td>0.0029</td>
<td>-0.0202</td>
<td>-0.0086</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 2. Strongylocentrotus purpuratus at Gregory Point, OR, USA; ANCOVA of \( \ln J \), as a function of \( \ln D \), with sample time, \( t_i \), as a fixed factor; \( N = 615; \ R^2 = 0.94. \)

<table>
<thead>
<tr>
<th>source</th>
<th>SS</th>
<th>d.f.</th>
<th>MS</th>
<th>F-ratio</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \ln D )</td>
<td>24.8431</td>
<td>1</td>
<td>24.8431</td>
<td>8460.2572</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>sample, ( t_i )</td>
<td>0.1965</td>
<td>30</td>
<td>0.0066</td>
<td>2.2305</td>
<td>0.002</td>
</tr>
<tr>
<td>error</td>
<td>1.7120</td>
<td>583</td>
<td>0.0029</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 3. Strongylocentrotus purpuratus at Gregory Point, OR, USA; the natural logarithm of test height, \( \ln H \), as a function of the logarithm of diameter, \( \ln D \), and time in years; 20 individuals dissected each month; \( N = 620, \ R^2 = 0.93. \)

<table>
<thead>
<tr>
<th>effect</th>
<th>coefficient</th>
<th>s.e.</th>
<th>( t )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>constant</td>
<td>-1.0626</td>
<td>0.0242</td>
<td>-43.9000</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>( \ln ) diameter</td>
<td>1.2396</td>
<td>0.0133</td>
<td>92.9184</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>time (year)</td>
<td>-0.0046</td>
<td>0.0044</td>
<td>-1.0339</td>
<td>0.302</td>
</tr>
</tbody>
</table>

Figure 2. Change in \( \ln J \) length adjusted to a mean \( \ln D \) test diameter of 1.78879 (5.982 cm) of S. purpuratus at Gregory Point, OR, USA, by ANCOVA; sample date as fixed factor; \( \ln \) values back transformed for plotting; fitted line based on parameters in table 1.

Strongylocentrotus purpuratus has shown variation in relative jaw size at a very local scale in Sunset Bay, Oregon, where samples collected approximately 50 m apart were
**Table 4. Strongylocentrotus purpuratus at Gregory Point, OR, USA; N = 615.**

(a) In jaw as a function of ln wet weight and sample time, $t_i$; time = 0 at 1 January 2007; $r^2 = 0.94$; interaction term $p = 0.09$ and analysis redone without interaction

<table>
<thead>
<tr>
<th>effect</th>
<th>coefficient</th>
<th>s.e.</th>
<th>$t$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>constant</td>
<td>-1.1451</td>
<td>0.0134</td>
<td>-85.5000</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>lnF</td>
<td>0.2823</td>
<td>0.0029</td>
<td>98.6934</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>sample, $t_i$</td>
<td>-0.0131</td>
<td>0.0028</td>
<td>-4.7352</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

(b) In jaw length, lnJ, as a function of ln total wet weight, lnF, and sample (time), $t_i$ as a fixed factor; $r^2 = 0.94$; interaction term, lnF x $t_i$, $p = 0.74$ and so not included in analysis

<table>
<thead>
<tr>
<th>source</th>
<th>SS</th>
<th>d.f.</th>
<th>MS</th>
<th>F-ratio</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>lnF</td>
<td>25.06936</td>
<td>1</td>
<td>25.0694</td>
<td>9837.7112</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>sample, $t_i$</td>
<td>0.17304</td>
<td>30</td>
<td>0.0058</td>
<td>2.2634</td>
<td>0.0002</td>
</tr>
<tr>
<td>error</td>
<td>1.48565</td>
<td>583</td>
<td>0.0026</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Figure 3.** Comparison of ln jaw length adjusted to a mean ln test diameter of 1.78879 (5.982 cm) (open circles as in figure 1) and ln total wet weight adjusted to a mean total wet weight of 4.58381 (97.868 g) (filled circles) showing similar patterns of a cycle and a downward trend; ln values back transformed for plotting. (Online version in colour.)

Table 4 shows patterns of change in relative jaw size seen in both field and laboratory experiments [58] indicated resorption of test plates. No statistically significant decrease in test diameter, however, was found in S. purpuratus fed only one day every eight weeks in the laboratory [18,19]. There always is some food in the field and so it is unlikely sea urchins would shrink while those starved in the laboratory did not. In general, changes in jaw allometry are probably best thought of as due to changes in resource allocation to body parts rather than resorption and rebuilding and so would be energetically very inexpensive. In this regard, jaw allometry differs from the changes in gut structures of snakes or birds [13,16] or bones in iguanas [15], which require energy first to breakdown test plates [56,57] without resorption of skeletal elements, although the very large changes shown for *D. antillarum* in both field and laboratory experiments [58] indicated resorption of test plates. No statistically significant decrease in test diameter, however, was found in *S. purpuratus* fed only one day every eight weeks in the laboratory [18,19]. There always is some food in the field and so it is unlikely sea urchins would shrink while those starved in the laboratory did not. In general, changes in jaw allometry are probably best thought of as due to changes in resource allocation to body parts rather than resorption and rebuilding and so would be energetically very inexpensive. In this regard, jaw allometry differs from the changes in gut structures of snakes or birds [13,16] or bones in iguanas [15], which require energy first to breakdown and then rebuild. *Diadema antillarum*, however, may be an exception [58] and deserves additional study.

Allometric adjustments of jaws of sea urchins indicate changes in available food. Adjustments are reversible and rapid and so fit well with the model presented by Gabriel [10], but additional work is needed that focuses on how the reversible changes explicitly contribute to fitness. If, as suggested, reversible plasticity is very inexpensive in terms of both energy and materials, small changes in survival of large individuals of long-lived species can be very important, as shown for the long-lived sea urchin *M. franciscanus* [59].
Fitness measured as population growth rate was most sensitive to changes in survival of large M. franciscanus and the same would be true for long-lived S. purpuratus. Changes in jaw allometry would have small benefits in improving survival but because of low cost nevertheless would be adaptive.

There is growing interest in the genomics, transcriptomics and proteomics in studies of plasticity [60–65]. The genome of S. purpuratus has been sequenced [66] and so provides the basis for understanding the design of gene regulatory networks involved in translating environmental cues into changes in relative growth. Various aspects of biomineralization in sea urchins have used molecular techniques [65–69] and regulatory systems would be involved [70,71]. Details of linking the changes in stress associated with available food will involve cell-signalling systems. The changes of relative jaw size we have shown for S. purpuratus may provide a model system for exploring the details of regulatory networks involved in reversible plasticity.

Acknowledgements. Monthly collections and dissections were done by Bruce Miller, Oregon Department of Fish and Wildlife, Charleston, Oregon. Miller also froze body walls and lanterns and sent them to Villanova University for further processing. Collection was done under a permit from the Oregon Department of Fish and Wildlife.

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