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Energy content of *Ophiocoma echinata* (Echinodermata: Ophiuroidea) maintained at different feeding levels during arm regeneration

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Abstract

Individuals of *Ophiocoma echinata* were collected from Missouri Key (FL, USA) in September, 1993 and divided among four feeding levels (fed daily, fed once a week, fed once every 2 weeks, and not fed). Each individual was induced to autotomize three adjacent arms at the disk edge. Energy content of disk, intact arms, gonads, and stomach was examined after 2 months of regeneration. Arm regeneration was inversely related to food level, while stomach and gonad weight was directly related to food level. The four body components were ordered stomach $>$ disk $>$ gonads $>$ intact arms, and the three organic components were ordered lipid $>$ protein $\gg$ carbohydrate with respect to energy differences between feeding treatments. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Disturbance at the organismal level of organization can be defined as loss of biomass (Grime, 1977; Pickett et al., 1989) and may be sublethal. Parts of animals may be lost or damaged due to physical perturbation (e.g. Tilmant et al., 1994), inter- and intraspecific fighting (e.g. Berzins and Caldwell, 1983; Smith and Hines, 1991), and partial predation (e.g. Trevallion, 1971; de Vlas, 1979; Bowmer and Keegan, 1983). The powers of repair range from simple wound closure and healing to complete regeneration of lost parts (Morgan, 1901; Goss, 1969; Hay, 1986; Dinsmore, 1995). The immediate advantage of

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being able to lose a structure is to escape lethal predation or combat, with regeneration restoring functionality in the long term. Recovery from loss requires the allocation of energy and material to regeneration.

Energy allocation has been divided into maintenance of existing somatic tissue, growth of new somatic tissue, reproductive output, and losses due to excretion and is an important characteristic of the life history of organisms (Cole, 1954; Gadgil and Bossert, 1970; Stearns, 1976, 1992; Perrin and Sibly, 1993). Energy allocated for one process cannot be used for any other, so changes in one process may cause subsequent changes in others. Regeneration represents an additional energy expenditure that has rarely been considered for most groups of animals, despite the occurrence of regeneration in most phyla (Goss, 1969).

Echinoderms experience sublethal disturbance and are well known for their ability to regenerate (Emson and Wilkie, 1980; Lawrence and Vasquez, 1996). As examples, regeneration of arms in *Luidia clathrata* (an asteroid found in soft-bottom habitats) is low under low food levels, but high at high food levels (Lawrence et al., 1986; Lawrence and Ellwood, 1991). In contrast, Fielman et al. (1991) suggested that regeneration in *Microphiopholis gracillima* (an ophiuroid found in soft-bottom habitats) (= *Amphipholis gracillima*, Hendler et al., 1995) should take precedence at low food levels to quickly restore functionality. The ophiuroid *Ophiocoma echinata* (Lamarck 1816) is found throughout the Caribbean and inhabits shallow reef/rubble habitats (Hendler et al., 1995). Based on taxonomic affinity, we expect the response of *O. echinata* to arm loss to be more similar to *M. gracillima* than *L. clathrata*. The purpose of this study was to answer the following questions: (1) how are somatic and gonadal tissues affected during regeneration of arms by different food levels? and (2) what is the relationship between food level and the amount of arm regeneration?

2. Materials and methods

Individuals of *O. echinata* were collected from the ocean side of Missouri Key (FL, USA; 24°40.5′N, 81°14.9′W) in September 1993. They were divided among four feeding levels: fed daily, fed once a week, fed once every 2 weeks, and not fed (12 individuals per level). TetraMin fish food was used as the food source. At each feeding enough food was given so that some uningested ($<1\%$) food remained after 24 h (approximately 0.1 g supplied per individual per feeding ≈ 1.89 kJ).

Each individual was induced to autotomize three adjacent arms at the disk edge by squeezing the arms with a pair of tweezers. The ophiuroids were held in eight tubs (18 l each), at a density of six individuals per tub. Water was maintained at 22°C and 35‰ salinity. Each tub contained plastic grating under which the brittlestars could hide. The tubs were connected to a common recirculating filter system. Water leaving each tub passed through a filter (filter floss/charcoal layers) before entering a common water sink (containing an oyster-shell bottom). Water leaving the common water sink passed through a second filter (Magnum 350 canister filter) before entering the delivery system leading to the tubs. Water was not exchanged directly between tubs thus preventing any particulate exchange. All tubs were cleaned daily. Dissolved organic material was not measured. The experiment ran from 2 September to 28 November, 1993.

At the end of the experiment individuals were dissected into body components of disk (without the stomach and gonads), intact arms, gonads, stomach, and regenerating arms. The weight of the body components was measured after drying in vacuo over sulfuric acid. The length of the regenerating arms was measured. Total organic concentration was obtained for all body components by ashing samples at 500°C for 4 h (Paine, 1971). Proximate analysis (estimation of kilojoules contained in protein, lipid and carbohydrate) was carried out on the disk, intact arms, gonads, and stomach. Samples for soluble protein analysis were extracted in 1 N sodium hydroxide for 24 h and measured by the method of Lowry et al. (1951). Total lipid was measured by the method of Folch et al. (1957). Samples for soluble carbohydrate analysis were extracted in tubes containing 5% trichloroacetic acid placed in a hot water bath at 60°C for 2 h and measured by the method of Dubois et al. (1956). The energetic conversion factors used were: protein 4.5 kcal/g, lipid 9.3 kcal/g, carbohydrate 4.2 kcal/g and kilojoules 4.184 kJ/kcal (Kersting, 1972; Brown, 1973; Morowitz, 1978; Blaxter, 1989).

One-way analysis of variance (ANOVA) was used to compare feeding levels (Sokal and Rohlf, 1981). Normality was checked with an Anderson–Darling test (D'Agostino, 1986). Variance homogeneity was checked with Bartlett's test (Sokal and Rohlf, 1981). Rank transformation was used on data failing normality or variance homogeneity tests (Conover and Iman, 1981). A Tukey–Krammer test was used to compare groups when ANOVA was significant at $P = 0.05$.

3. Results

No significant difference was found in dry weights of the disk or intact arms among the four feeding levels (daily, weekly, every-2-weeks, not-fed; Fig. 1A). The dry weights of the gonads of all four feeding levels were significantly different (Fig. 1B). As feeding frequency decreased the dry weight of the gonads decreased. The dry weights of the stomach of the two lowest feeding levels were significantly lower than those of the two highest feeding levels (Fig. 1B). The dry weights of the regenerating arms from all four feeding levels were significantly different (Fig. 2). As feeding frequency decreased from daily to weekly to every-2-weeks the dry weight of the regenerating arms increased. However, the dry weight of the not-fed level was between that of the weekly and every-2-weeks levels. A similar trend was found for the length, except the means of the not-fed and every-2-weeks levels were similar (Fig. 2).

To summarize the major trends in the composition results, on a relative basis (percent dry weight) the disk contained less organic matter, protein, and lipid at the lowest feeding level (Table 1). On an absolute basis (kJ), the only difference in the disk was a decrease in lipid at the two lowest feeding levels (Table 2). The relative amount of organic matter in the intact arms decreased at the lowest feeding level, but no single constituent differed (Table 1). No difference was found in the intact arms on an absolute basis for any constituent (Table 2). The relative amount of organic matter in the gonads decreased at the lowest feeding level, while the absolute amount of lipid decreased with

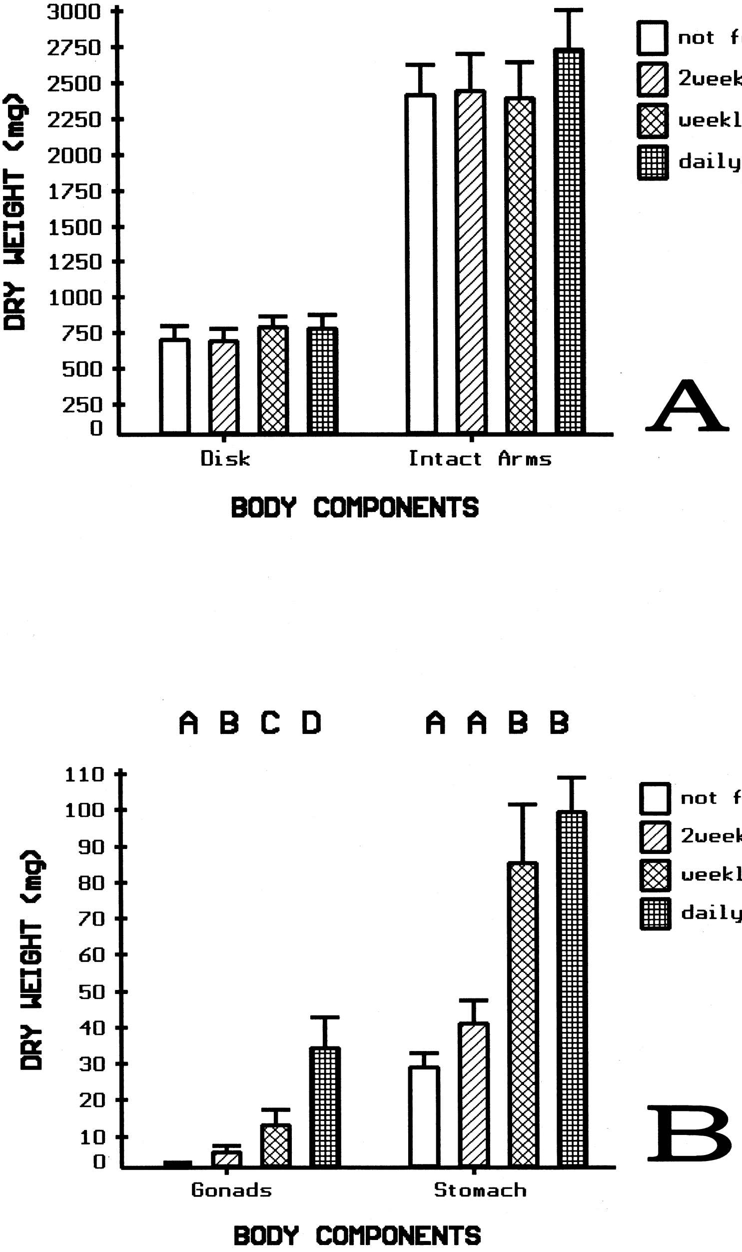

Fig. 1. *Ophiocoma echinata*. Dry weight (±SE) of the (A) disk and intact arms; and (B) gonads and stomach after 2 months' regeneration of three arms for four feeding levels (daily = fed daily; weekly = fed once a week; 2weeks = fed once every 2 weeks; not fed = no particulate food). $N = 12$ for each level. Different letters indicate significant difference at $P \leq 0.05$.

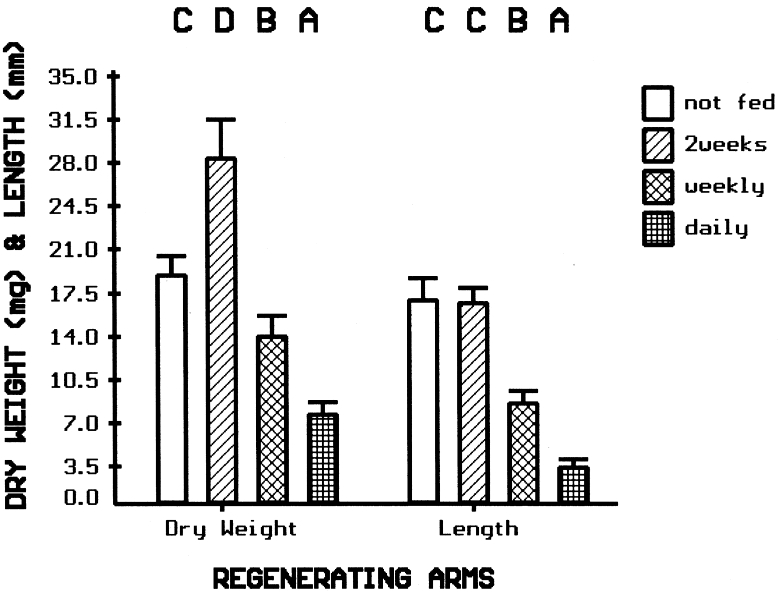

Fig. 2. *Ophiocoma echinata*. Dry weight and average length (±SE) of three regenerating arms after 2 months for four feeding levels (further details as in Fig. 1).

decreased feeding level; however, a complete analysis was not possible due to small amounts of material (Tables 1 and 2). The stomach decreased in protein and lipid on a relative basis and decreased in all constituents on an absolute basis with decreased feeding level (Tables 1 and 2).

4. Discussion

Differences in energy content due to different feeding levels were not evenly distributed across body components or organic constituents. The biggest decrease in all organic constituents took place between individuals in the every-2-weeks and not-fed levels. In several instances, such as with the stomach, a decrease was found between individuals in the weekly and every-2-weeks levels suggesting differential use or storage of energy in body components based on food availability.

Based on total amount of energy, the four body components were ordered intact arms > disk > stomach > gonads. The ordering suggests that the intact arms and disk might be good sources for storage and reallocation of energy for maintenance, reproduction, or regeneration. This, however, is misleading. Most of the energy in the intact arms and disk was contained in the insoluble fraction, followed by protein, which is probably related to the connective tissue and muscle content of the arms and disk (Hyman, 1955; Byrne, 1994). Very little difference was found for the insoluble fraction

Table 1

Ophiocoma echinata; percent dry weight ±SE (ash + organic matter) composition of the disk, intact arms, gonads and stomach after 2 months' regeneration of three arms for four feeding levels[a]

Component and food level	Organic matter	Protein	Lipid	Carbo-hydrate	Insoluble matter
Disk					
Daily	32.8b ±0.8 (12)	9.6b ±0.7 (12)	1.47b ±0.09 (12)	0.63 ±0.02 (12)	21.1 ±0.9 (12)
Weekly	31.2b ±0.7 (12)	8.9b ±0.4 (12)	1.41b ±0.12 (12)	0.62 ±0.02 (12)	20.3 ±0.7 (12)
2 Weeks	31.3b ±1.1 (12)	8.0ab ±0.5 (12)	1.20b ±0.12 (12)	0.64 ±0.02 (12)	21.4 ±1.1 (12)
Not fed	28.2a ±0.8 (12)	7.0a ±0.4 (12)	0.72a ±0.03 (12)	0.62 ±0.01 (12)	19.8 ±0.9 (12)
Intact arms					
Daily	23.2b ±0.7 (12)	5.6 ±0.1 (12)	0.58 ±0.05 (12)	0.33 ±0.01 (12)	16.7 ±0.7 (12)
Weekly	22.5b ±0.5 (12)	5.6 ±0.2 (12)	0.66 ±0.05 (12)	0.34 ±0.01 (12)	15.9 ±0.6 (12)
2 Weeks	21.9ab ±0.6 (12)	5.3 ±0.2 (12)	0.62 ±0.03 (12)	0.33 ±0.01 (12)	15.8 ±0.7 (12)
Not fed	20.5a ±0.7 (12)	5.1 ±0.1 (12)	0.55 ±0.02 (12)	0.33 ±0.01 (12)	14.5 ±0.8 (12)
Gonads					
Daily	92.6b ±1.3 (5)	39.0 ±2.0 (10)	18.8b ±1.0 (12)	N.A.	N.A.
Weekly	89.5b ±0.7 (4)	35.4 ±1.4 (4)	18.8b ±1.2 (8)	N.A	N.A.
2 Weeks	90.0b ±2.8 (3)	N.A.	13.9a ±0.8 (4)	N.A.	N.A.
Not fed	83.4a ±1.3 (4)	N.A.	20.6b ±1.1 (4)	N.A.	N.A.
Stomach					
Daily	93.4 ±0.6 (12)	28.6b ±1.1 (12)	32.1b ±2.0 (12)	3.4 ±0.2 (12)	29.2 ±1.4 (12)
Weekly	92.0 ±0.6 (12)	28.3b ±0.8 (11)	30.8b ±1.3 (11)	3.5 ±0.1 (7)	29.8 ±1.2 (7)
2 Weeks	91.6 ±1.1 (12)	31.8c ±1.0 (12)	20.3a ±1.8 (12)	3.3 ±0.2 (5)	34.4 ±1.9 (5)
Not fed	90.8 ±1.1 (12)	25.8a ±0.8 (12)	23.9a ±2.5 (12)	2.9 ±0.1 (6)	36.7 ±4.1 (6)

[a] Daily = fed daily; weekly = fed once a week; 2weeks = fed once every 2 weeks; not fed = no particulate food). *N* values in parentheses. N.A. = not available due to limited tissue. Different letters indicate significant difference at $P \leqslant = 0.05$.

Table 2

Ophiocoma echinata; kilojoule±SE composition of the disk, intact arms, gonads and stomach after 2 months' regeneration of three arms for four feeding levels; insoluble matter calculated as protein (further details as in Table 1)

Component and food level	Organic matter	Protein	Lipid	Carbo-hydrate	Insoluble matter
Disk					
Daily	4.94 ±0.42 (12)	1.38 ±0.16 (12)	0.43c ±0.04 (12)	0.09 ±0.01 (12)	3.04 ±0.29 (12)
Weekly	4.81 ±0.35 (12)	1.31 ±0.10 (12)	0.42c ±0.04 (12)	0.08 ±0.01 (12)	3.00 ±0.25 (12)
2 Weeks	4.07 ±0.27 (12)	1.03 ±0.11 (12)	0.31b ±0.03 (12)	0.08 ±0.01 (12)	2.66 ±0.18 (12)
Not fed	3.71 ±0.31 (12)	0.95 ±0.13 (12)	0.19a ±0.02 (12)	0.08 ±0.01 (12)	2.50 ±0.18 (12)
Intact Arms					
Daily	12.05 ±1.05 (12)	2.93 ±0.15 (12)	0.61 ±0.06 (12)	0.16 ±0.02 (12)	8.35 ±0.87 (12)
Weekly	10.43 ±0.98 (12)	2.54 ±0.14 (12)	0.62 ±0.09 (12)	0.14 ±0.01 (12)	7.13 ±0.82 (12)
2 Weeks	10.27 ±0.98 (12)	2.44 ±0.12 (12)	0.57 ±0.05 (12)	0.14 ±0.02 (12)	7.14 ±0.84 (12)
Not fed	9.71 ±0.99 (12)	2.23 ±0.06 (12)	0.66 ±0.07 (12)	0.14 ±0.01 (12)	6.84 ±0.92 (12)
Gonads					
Daily	N.A.	0.30 ±0.07 (10)	0.25c ±0.06 (12)	N.A.	N.A.
Weekly	N.A.	0.19 ±0.04 (4)	0.13bc ±0.03 (8)	N.A.	N.A.
2 Weeks	N.A.	N.A.	0.08b ±0.02 (4)	N.A.	N.A.
Not fed	N.A.	N.A.	0.03a ±0.01 (4)	N.A.	N.A.
Stomach					
Daily	2.38b ±0.22 (12)	0.53c ±0.04 (12)	1.25b ±0.15 (12)	0.06c ±0.01 (12)	0.54b ±0.06 (12)
Weekly	2.63b ±0.46 (7)	0.45c ±0.07 (11)	1.05b ±0.24 (11)	0.07c ±0.01 (7)	0.60b ±0.07 (7)
2 Weeks	1.20a ±0.20 (5)	0.24b ±0.03 (12)	0.36a ±0.08 (12)	0.03b ±0.01 (5)	0.34a ±0.04 (5)
Not fed	0.75a ±0.09 (6)	0.14a ±0.01 (12)	0.27a ±0.04 (12)	0.02a ±0.01 (6)	0.24a ±0.04 (6)

for any body component; and very little or no difference was found for any constituent in the intact arms.

At extremes of food availability the overall quantity of the gonad differs, but the organic content seems to remain constant. This might have the advantage of producing at least some viable gametes, rather than a lot of inferior ones. No evidence exists for storage of nongametic nutritive tissue in the gonads of ophiuroids (Mladenov, 1983; Byrne, 1994) in the way that takes place in echinoids (Lawrence, 1987a). The gonads have the potential to contribute energy to other activities through the resorption of gametes, although the total amount is probably small unless a fully mature gonad is completely resorbed.

The constituent that differed the most between feeding levels on both a relative and, more importantly, absolute basis for all body components was the lipid fraction, followed by protein. The stomach had similar or greater absolute amounts of energy for these fractions than the arms despite being 10- to 20-times smaller in size. For example, the difference in energy in lipid was 1 kJ for the stomach, 0.3 kJ for the disk, 0.2 kJ for the gonads, and none for the arms.

The stomach of ophiuroids has been ignored as a major energetic component, probably because of its small size (Lawrence, 1976, 1987a; Lawrence and Lane, 1982). The enterocytes of the ophiuroid stomach contain lipid droplets (Jangoux, 1982; Byrne, 1994), which suggests a storage function, but this has never been linked to the overall energetics of the animal (Lawrence, 1987b). We suggest the stomach plays a key role in energy storage and reallocation to maintenance, reproduction, and regeneration in *O. echinata*. Bourgoin and Guillou (1990) found the size of the stomach inversely related to gonad production in *Acrocnida brachiata* in the field. The disk and intact arms may play a larger role during longer term energy deprivation, and certainly play a role in species that autotomize the aboral portion of the disk including the stomach and gonads (e.g. Dobson et al. 1991).

Carbohydrate represented the smallest energy constituent, ranging from less than one to three percent of total energy. Even significant changes in carbohydrate content probably have little impact on the overall energetics of an individual because of its small contribution to the total amount of energy.

O. echinata switches allocation of energy between regeneration and storage/reproduction during the initial stages of regeneration based on the level of available energy. At low levels of available energy regeneration takes place, while at higher levels regeneration is minimized and storage/gonad development increases. This implies that the constraint on the various uses of energy is not necessarily related to limiting resources of the environment, but may entail physiological bottlenecks or switches of the organism.

The pattern of allocation is opposite to that found by Lawrence et al. (1986) and Lawrence and Ellwood (1991) for the asteroid *L. clathrata* in which high levels of available energy enhanced all processes relative to low levels. The pattern in *O. echinata* is similar to the predictions made by Fielman et al. (1991) based on work with the ophiuroid *M. gracillima*. The contrasting results may be related to anatomical differences. Asteroids have gonads and pyloric caeca extending into the arms, while most ophiuroids do not. Therefore the regrowth of arms in asteroids allows for a large increase in storage and reproduction that does not occur in ophiuroids. The studies on *L. clathrata* lasted longer and may also reflect changing patterns of allocation over time.

Regenerating arms of not-fed individuals were similar in length to those of individuals fed every-2-weeks, but their mass was less. This suggests that increases in length come first in regenerating arms. Other ophiuroids have produced similar results (Salzwedel, 1974; Fielman et al., 1991; Stancyk et al., 1994). The arms of ophiuroids are used for resource capture (Warner, 1982). Increasing regeneration under low food conditions may quickly increase resource capture capabilities, thus affording higher resource acquisition in the long run.

The inverse relationship between regeneration and food supply is probably a short-term phenomenon. Since stored resources would have to be used for maintenance as well as regeneration it is unlikely that individuals with low food levels could continue to regenerate more than those with high food levels over the time necessary to regenerate a complete set of arms. Presumably a limit exists to the amount of energy that can be stored or allocated to gonad production under high food levels, after which it could be directed toward regeneration.

Why does *O. echinata* not maximize all processes (storage, reproduction, and regeneration) when food availability is high? We suggest several possible reasons that are not mutually exclusive. Absorption efficiencies of the stomach might be low, so that not enough energy is taken in to cover all processes even though food is abundant. Based on absorption efficiencies of other echinoderms (Lawrence, 1987b) this seems unlikely.

Dynamic models of energy allocation predict switching of resources away from growth to reproduction when the benefits of reproduction outweigh those of growth (Perrin and Sibly, 1993). The models failed to consider regeneration, but the same idea may apply. If energy intake meets energy needs the importance of regenerating other feeding structures in an individual with two intact arms may be minimized and resources can be devoted to reproduction or storage.

In this study, both gonad and storage content (but not regeneration) were high at high food levels, so that *O. echinata* is intermediate between maximizing all processes and switching between only one process at a time. Energy storage has been viewed in two ways: as a result of excess energy, or as a consequence of timing, such as when resources can be acquired outside the reproductive season and reallocated to reproduction at the appropriate time (Perrin and Sibly, 1993). We suggest if energy can be stored easier or faster than it can be used for gonad production, storage would be beneficial even during the reproductive season, especially if the reproductive season is long.

The results pose a problem for the interpretation of allocation pattern as a life-history characteristic. In the present study, at low food levels regeneration took precedence over reproduction and storage. At high food levels reproduction and storage took precedence over regeneration, at least during the initial stages of regeneration. Life history implies that patterns arise over evolutionary time and are characteristic of a species. In the present case, multiple patterns were seen at the same time in the same species. Therefore the patterns are not life-history characteristics, but phenotypic responses to current resource availability. Similar responses have been observed in several disparate taxa such as asteroids (Lawrence and Ellwood, 1991), guppies (Reznick and Yung, 1993), and butterflies (Boggs and Ross, 1993). In cases where multiple patterns are seen within a species based on the current environmental conditions we suggest that the variation in pattern represents the life-history characteristic. The plasticity is evolving separately from the specific trait (Stearns, 1989; Thompson, 1991).

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