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Effect of arm regeneration on energy storage and gonad production in *Ophiocoma echinata* (Echinodermata: Ophiuroidea)

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Abstract Two laboratory experiments were conducted on *Ophiocoma echinata* (Lamarck, 1816) collected from Missouri Key, Florida, USA, to ascertain the effects of arm regeneration on energy storage and gonad production. In each experiment individuals were divided into non-regenerating (all arms intact) and regenerating (three arms autotomized) groups and maintained together in a re-circulating seawater system for 2 mo. In Experiment 1, individuals were fed once a week, and in Experiment 2 once every 2 wk. The amount of food energy required for maintenance was estimated to be 0.172 kJ d^{-1}. The lower feeding level (Experiment 2) was below maintenance ration and both groups lost material relative to an initial group. At the higher feeding level (Experiment 1), regeneration of three arms resulted in less storage of organic material, mainly lipid in the stomach, and less gonad production. Thus, regeneration may reduce energy reserves and reproductive output.

Introduction

Regeneration in animals has long been a topic for study, with interest at both the cellular and organismal levels of organization (Morgan 1901; Zeleny 1909; Goss 1969; Dinsmore 1995). Regeneration in animals often follows sublethal disturbance, which is usually caused by partial predation or autotomy in response to a predation attempt (Woodin 1984; Harris 1989). Regeneration ranges from simple wound closure and healing (as in mammals) to complete regeneration of lost parts (as in cnidarians, annelids, molluscs, arthropods, echinoderms and some chordates: Morgan 1901; Goss 1969; McVean 1975; Emson and Wilkie 1980; Skinner 1985; Hay 1986; Arnold 1988; Dinsmore 1995).

Regeneration requires energy beyond that needed for the normal energetic processes of maintenance, growth, and reproduction, as well as time. The cost of regeneration may be direct (the additional energy requirement) or indirect (the loss of functionality due to missing parts). The costs may lead to slower growth, lower reproductive success, and the risk of fatal predation (e.g. Maiorana 1977; Conover and Miller 1978; Woodin 1984; Smith 1992).

Effects of regeneration vary in magnitude and differ across taxa. Smith (1990) suggested that autotomy of a few pereopods in the blue crab *Callinectes sapidus* probably had little impact on its survival or reproduction, but could become important as the number of autotomized pereopods increased. Hill et al. (1982) found regeneration reduced reproduction in one species of the polychaete genus *Capitella*, but not in another. Regeneration is one of the hallmarks of the phylum Echinodermata (Hyman 1955; Emson and Wilkie 1980). Most studies on regeneration in echinoderms have documented the amount or rate of regeneration, but few studies have examined the impact of regeneration on the biology of the individual (Lawrence 1987; Lawrence and Vasquez 1996).

Ophiuroids from a variety of habitats have large percentages of their populations undergoing regeneration throughout the year (Lawrence and Vasquez 1996). Although regeneration has been documented for a number of ophiuroids, especially *Amphiura filiformis* from European waters (e.g. O'Conner et al. 1983), *Microphiopholis gracillima* (*Amphipholis gracillima* in Hendler et al. 1995) is probably the only well-studied ophiuroid in terms of the effects of regeneration (Singletary 1980; Clements et al. 1988, 1993; Dobson et al. 1991; Fielman et al. 1991; Golde 1991; Stancyk et al.

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1994). This species readily undergoes autotomy of its disk (including the stomach and gonads) as well as its arms. These studies have shown that disk regeneration in *M. gracillima* can affect nutrient reserves in the arms and be affected by dissolved organic matter in seawater, and that arm regeneration can increase respiration rates.

Remaining questions about arm regeneration concern energy allocation to various body components in species that do not autotomize the disk, whether arm material is used when the disk is intact, and if the patterns seen in the soft-bottom, burrowing amphiurid *Microphiopholis gracillima* apply to other species in different habitats. Using *Ophiocoma echinata* (Ophiuroidea) as the test organism, this study addresses the following questions: (1) Does regeneration reduce gonad production? (2) Are non-reproductive tissues affected by regeneration? (3) Does the pattern of allocation among non-regenerating and regenerating individuals change with a change in food availability? (4) Does regeneration increase energy demand (measured as increased respiration rate)?

Materials and methods

Ophiocoma echinata (Lamarck, 1816) ranges throughout the Caribbean, from the southern tip of Florida, USA, to the northern coast of South America (Hendler et al. 1995). It occurs in shallow water (< 5 m depth) and is one of the most abundant brittlestars in reef and rubble habitats (Kissling and Taylor 1977; Sullivan 1988). Its maximum disk diameter is ≃25 mm, with arms 150 mm in length. When disturbed, *O. echinata* typically autotomizes its arms but not its disk. Sexes are separate, with no external dimorphism. *O. echinata* is a broadcast-spawner, with an extended breeding season from spring to early fall (Mladenov 1983).

Ophiocoma echinata was collected from the ocean side of Missouri Key, Florida, USA (24° 40.5′N; 81° 14.9′W). Individuals were close to asymptotic size (disk diameter range = 18 to 24 mm). They were divided into non-regenerating and regenerating groups. Each individual in the non-regenerating group had all five arms intact. Each individual in the regenerating group was induced to autotomize three arms at the disk edge by pinching the arms with a pair of tweezers. Two experiments were conducted using different feeding levels. In Experiment 1, all individuals were fed once a week; the experiment ran from 23 May to 25 July 1993. In Experiment 2, all individuals were fed once every 2 wk; the experiment ran from 3 August to 14 October 1994.

During both experiments, brittlestars were held in eight tubs (18 liters each, with water collected from the field site), with three non-regenerating and three regenerating individuals per tub. Water was maintained at 22 °C and 35‰ S. 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 (with 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. At each feeding, sufficient food (TetraMin fish food at 0.1 g per individual per feeding = 1.89 kJ; average = 0.27 kJ d^{-1} for the group fed once per week, and 0.135 kJ d^{-1} for the group fed once every 2 wk) was given so that some uningested (< 1%) food remained after 24 h. Tubs were cleaned on the day following each feeding.

The respiration rate of nine individuals from each group during Experiment 2 was measured at ten points in time between 5 August and 1 October 1994; the same individuals were used on each date. Each group had approximately the same proportion of males (M) and females (F): 3 M, 6 F non-regenerating; 4 M, 5 F regenerating. At least 3 d separated feeding and any respiration measurement. Brittlestars were placed in small plastic containers (540 ml) that were submerged within a larger aerated water bath, and allowed to adjust for 30 min before the containers were sealed. The containers were then removed from the water bath and placed on a laboratory bench. After 4 h, water was drained from each container into a 50 ml bottle and azide-modified Winkler reagents were added to fix the oxygen (Franson 1992). As a control for changes due to water alone, a container with only water from the water bath was treated in a similar manner. An initial sample was taken for calculating oxygen consumption. Oxygen was measured spectrophotometrically (Oulman and Baumann 1956).

At the start of both experiments, an initial group of individuals were dissected into disk, intact arms, gonads, and stomach (N = 11). Since the initial individuals and those of the experimental treatments were collected at the same time and location, it is assumed that the initial group represented the starting conditions of all individuals. At the end of both experiments individuals were dissected into disk, intact arms, regenerating arms, gonads and stomach. “Disk” refers to the disk with all arms removed at the edge and emptied of the stomach and gonads. “Gonads” refers to the gonad clusters from all ten bursal areas combined and includes the connective tissue that holds the clusters together. “Stomach” refers to the stomach isolated from the rest of the disk. Components were dried in vacuo over sulfuric acid, weighed, and ground in a Wiley mill. The total organic content was determined for all components by ashing samples (10 to 100 mg) in a muffle furnace at 500 °C for 4 h (Paine 1971).

Proximate composition analysis (estimation of kilojoules contained in protein, lipid and carbohydrate) was carried out on the disk, intact arms, and stomach, as well as on ten samples of the food. Proximate analysis was not done on gonads or regenerated arms due to limited amounts of tissue. Samples (5 to 20 mg) for soluble protein analysis were extracted in 1 N sodium hydroxide (5 ml) for 24 h and measured by the method of Lowry et al. (1951). Samples (10 to 300 mg) for lipid analysis were measured by the method of Folch et al. (1957). Samples (5 to 20 mg) for carbohydrate analysis were extracted in tubes containing 5% TCA (5 ml), 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^{-1}, lipid = 9.3 kcal g^{-1}, carbohydrate = 4.2 kcal g^{-1}, kcal or oxygen to kJ = 4.184 kJ $kcal^{-1}$ or 0.0141 kJ mg^{-1} O_2 (Kersting 1972; Brown 1973; Morowitz 1978; Blaxter 1989).

Within each experiment, a one-way ANOVA was used to compare proximate composition and weight data among the initial, non-regenerating and regenerating groups. The proximate composition of intact arms in Experiment 2 was compared using ANCOVA to adjust for size differences. A Bonferroni-adjusted one-way ANOVA was used to compare respiration rates between the non-regenerating and regenerating groups at each of the ten points in time. Regression analysis was used to examine the difference in respiration rates ($\bar{x}$ regenerating minus $\bar{x}$ non-regenerating) over time. 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.

Results

In Experiment 1 (fed weekly), no significant difference was found in disk weight or intact arm weight (per arm) among the three groups (initial, non-regenerating, regenerating) of *Ophiocoma echinata* (Fig. 1). The dry weight of the gonad of the regenerating group was significantly lower than that for the other groups. The dry weight of the stomach of the non-regenerating group was significantly higher than in the initial group, with the mean of the regenerating group between the two.

In Experiment 2 (fed every 2 wk, no significant difference was found in disk weight among the three groups (Fig. 2). A significant difference was found for intact arm weight (per arm). The non-regenerating and regenerating groups had significantly lower dry weights of gonad and stomach than the initial group.

The amount of arm regrowth in regenerating individuals was 25.8 mg (±1.8 SE) in Experiment 1, and 46.8 mg (±2.4 SE) in Experiment 2. The percent dry weight of the organic matter of the regenerating arms (Experiment 1: 38.4% ±1.1 SE; Experiment 2: 31.0% ±1.0 SE) was significantly greater than that of the intact arms (Experiment 1: 22.0% ± 0.5 SE; Experiment 2: 22.0% ± 0.3 SE second) in both experiments.

The proximate composition of the disk, intact arms (per arm) and stomach from Experiment 1 (fed weekly) are presented in Table 1. For the disk, no significant difference was found in organic matter, protein, lipid, or insoluble matter among the groups. The carbohydrate content of the non-regenerating and regenerating groups was significantly lower than that of the initial group. No significant difference was found among the groups for any constituent of the intact arms. For the stomach, no significant difference was found in the protein content among the groups. Organic matter and carbohydrate content of the non-regenerating group were significantly higher than in the initial group, with the regenerating group between the two. The lipid content of the non-regenerating and regenerating groups was significantly higher than in the initial group. The insoluble matter content of all three groups was different, with non-regenerating > regenerating > initial.

The results of the comparisons among groups of the proximate composition of the disk and intact arms from Experiment 2 (fed every 2 wk: Table 2) were similar to those of Experiment 1. The organic matter, protein, lipid, carbohydrate, and insoluble matter contents of the stomach of the non-regenerating and regenerating groups were significantly lower than for the initial group (Table 2).

The respiration rate per unit wet weight was significantly higher for the regenerating group for Time Points 3 to 10 (Fig. 3). Wet weights were: non-regenerating $\bar{x}$ = 11.62 g, and regenerating $\bar{x}$ = 6.07 g. At the first two time points, the respiration rate of the regenerating group was significantly higher when tested by one-way ANOVA ($p < 0.05$), but not when tested by Bonferroni-adjusted one-way ANOVA ($p < 0.005$). The difference between the two groups increased over time after an initial lag period. A regression of the difference in means of the groups against days was not significant (r^2–0.33) when all ten time points were included. It was significant for Time Points 5 to 10 ($r^2 = 0.72$).

Discussion

The difference in respiration rate per unit wet weight between the regenerating group and non-regenerating group increased over time in *Ophiocoma echinata*. The increasing difference between the groups indicates that regeneration began to have an impact on energy demand after 20 d. This is the time necessary for any significant amount of arm to be regenerated in this species. The fluctuating pattern of respiration over time within each group, regardless of cause, points out the need to measure respiration rates in different groups at the same

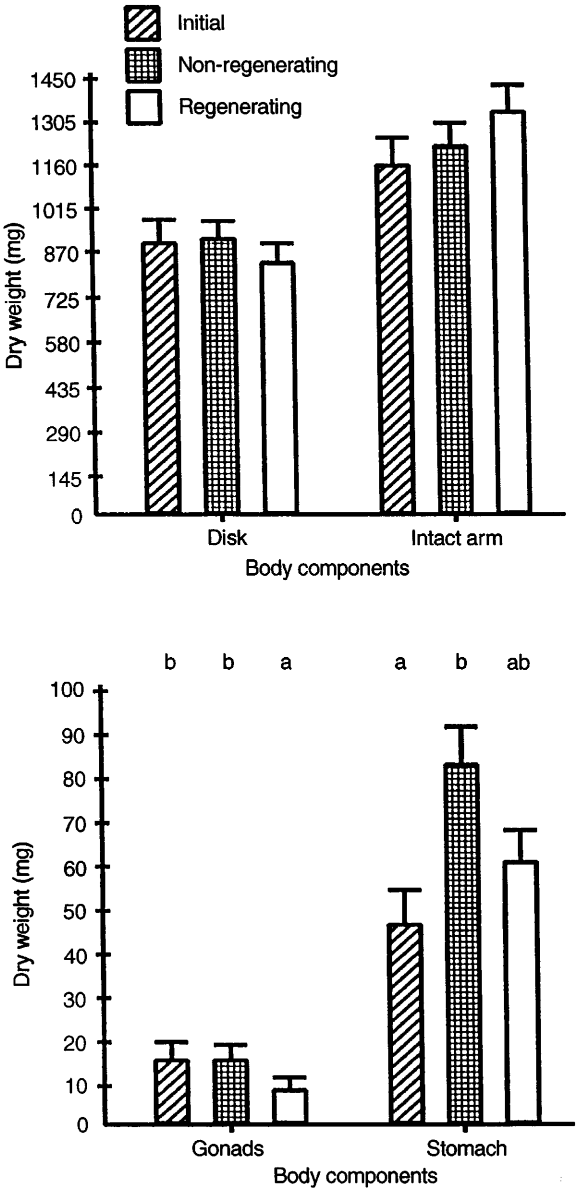

Fig. 1 *Ophiocoma echinata* fed every week (Experiment 1). Dry weight (mg + SE) of disk, intact arms (per arm), gonads, and stomach. Comparison of initial ($N = 11$), non-regenerating ($N = 24$), and regenerating ($N = 24$) individuals (*Different letters above columns* indicate significant difference at $p < 0.05$)

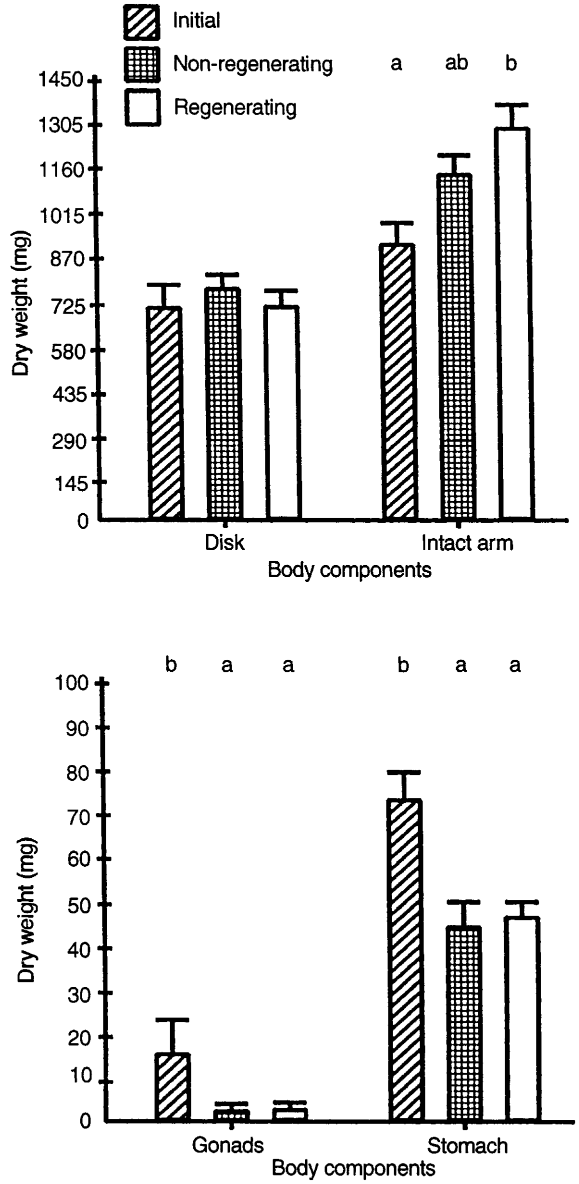

Fig. 2 *Ophiocoma echinata* fed every 2 wk (Experiment 2). Dry weight (mg + SE) of disk, intact arms (per arm), gonads, and stomach. Further details as in legend to Fig. 1

time if comparisons are to be made. Golde (1991) found that the respiration rate of *Microphiopholis gracillima* regenerating three arms increased over time. The rate Golde measured in *M. gracillima* is about two times greater than that recorded for *O. echinata*. This may be a result of the faster rate of regeneration in *M. gracillima* (e.g. Stancyk et al. 1994) (which can be several times greater than in *O. echinata*), the low food supply in the present study, and the general phenomenon that smaller species of animals typically have higher per unit mass metabolic rates than larger species.

Sullivan (1988) suggested that the main impact of regeneration on respiration in *Ophiocoma echinata* regenerating one arm occurred in the first 3 d after autotomy, since after 12 d no difference between non-regenerating and regenerating individuals was found. This contradicts the conclusions of the present study, but several points should be noted: (1) Most of Sullivan's measurements were made during the 84 h following autotomy, whereas regeneration takes over 300 d to complete. During the first few hours following autotomy, respiration is not associated with regeneration, but with trauma and wound-healing. (2) Sullivan measured respiration before and after autotomy in the same individuals; thus non-regenerating and regenerating data from different times were compared. Any difference (or lack of difference) could be due to the fluctuating pattern of respiration over time, not from regeneration. (3) Sullivan measured respiration per individual, not per unit weight, possibly masking any difference. The absolute values for respiration from Sullivan's study and the present study are very similar; the differences lie in the time course and how comparisons were made.

As arms regenerate, energy is used for the process of regeneration and the maintenance of new (as well as old) biomass, so that initially the difference in respiration rates per unit weight between non-regenerating and regenerating groups should increase. At some point, the difference in respiration rates between the two groups should decrease as maintenance of existing biomass becomes greater than the amount of new regeneration. Eventually, the respiration rates of the two groups should converge when regeneration stops and the new arm reaches the size of the intact arms. Thus, the cost of regeneration in terms of respiration can be modeled as a curve based on the difference between non-regenerating and regenerating groups after standardizing the non-regenerating rate to zero. The results of the present study represent this difference over the first 2 mo of regeneration (area between the two respiration lines over 58 d = 0.529 mg O_2 g^{-1} h^{-1}). In energy terms, this equals $\simeq$0.18 kJ g^{-1} (0.529 mg O_2 g^{-1} h^{-1} × 24 h d^{-1} × 0.0141 kJ mg^{-1} O_2).

The mass of regenerated arm in Experiment 2 was twice that in Experiment 1. At the lower food level, the amount of arm regenerated increased. This supports the contention of Fielman et al. (1991) that, when in limited supply, energy should be devoted to regeneration in ophiuroids in order to increase resource-capture capabilities. Sköld and Gunnarsson (1996) found that a food pulse increased regeneration in *Amphiura filiformis* from a coastal area, but not in individuals from an offshore area. The relationship between food and regeneration seems to be more complex than a simple "more food equals more growth" paradigm.

The non-regenerating group in Experiment 1 increased storage of organic material in the stomach, mainly in the form of lipid, above that in the initial group. The mass of the disk, intact arms, and gonads, however, did not increase. Based on a change in only one component, the non-regenerating individuals probably received slightly more than the maintenance level ration of food. Increased food has been associated with increased gonad mass in *Amphiura filiformis* and *A. chi-*

Table 1 *Ophiocoma echinata* fed every week (Experiment 1). Proximate composition (kJ ± SE; *N* value in parentheses) of disk, intact arms (per arm), and stomach. Comparison of initial, nonregenerating (*nonregen*), and regenerating (*regen*) individuals. Insoluble matter calculated as protein (*Different superscript letters* indicate differences at $p < 0.05$)

Group	Organic matter	Protein	Lipid	Carbohydrate	Insoluble matter
Disk					
initial	6.11 ± 0.49 (11)	1.38 ± 0.02 (11)	0.53 ± 0.06 (11)	0.11^{b} ± 0.01 (11)	4.10 ± 0.42 (11)
nonregen	6.38 ± 0.38 (24)	1.50 ± 0.02 (24)	0.46 ± 0.03 (24)	0.08^{a} ± 0.01 (24)	4.34 ± 0.34 (24)
regen	6.27 ± 0.39 (24)	1.42 ± 0.02 (24)	0.44 ± 0.03 (24)	0.08^{a} ± 0.01 (24)	4.34 ± 0.34 (24)
Intact arms					
initial	5.17 ± 0.38 (11)	1.33 ± 0.03 (11)	0.42 ± 0.03 (11)	0.07 ± 0.01 (11)	3.36 ± 0.33 (11)
nonregen	5.24 ± 0.28 (24)	1.33 ± 0.02 (24)	0.34 ± 0.02 (24)	0.07 ± 0.01 (24)	3.49 ± 0.25 (24)
regen	5.79 ± 0.37 (24)	1.38 ± 0.02 (24)	0.39 ± 0.02 (24)	0.08 ± 0.01 (24)	3.99 ± 0.33 (24)
Stomach					
initial	1.04^{a} ± 0.45 (6)	0.30 ± 0.03 (8)	0.35^{a} ± 0.06 (11)	0.04^{a} ± 0.01 (6)	0.33^{a} ± 0.08 (6)
nonregen	2.27^{b} ± 0.20 (16)	0.34 ± 0.03 (23)	0.87^{b} ± 0.12 (23)	0.07^{b} ± 0.01 (16)	0.73^{c} ± 0.04 (6)
regen	1.84^{ab} ± 0.20 (13)	0.24 ± 0.03 (22)	0.67^{b} ± 0.09 (23)	0.06^{ab} ± 0.01 (13)	0.56^{b} ± 0.05 (13)

Table 2 *Ophiocoma echinata* fed every 2 wk (Experiment 2). Proximate composition (kJ ± SE; *N* value in parentheses) of disk, intact arms (per arm), and stomach. Further details as in legend to Table 1

Group	Organic matter	Protein	Lipid	Carbohydrate	Insoluble matter
Disk					
initial	4.79 ± 0.39 (11)	1.27 ± 0.14 (11)	0.53 ± 0.05 (11)	0.06^{b} ± 0.01 (11)	2.92 ± 0.30 (11)
nonregen	4.98 ± 0.22 (24)	1.22 ± 0.09 (24)	0.54 ± 0.05 (24)	0.05^{a} ± 0.01 (24)	3.17 ± 0.20 (24)
regen	4.64 ± 0.22 (24)	1.08 ± 0.10 (24)	0.53 ± 0.04 (24)	0.04^{a} ± 0.01 (24)	2.99 ± 0.18 (24)
Intact arms					
initial	3.80 ± 0.25 (11)	0.86 ± 0.07 (11)	0.39 ± 0.08 (11)	0.09^{b} ± 0.01 (11)	2.47 ± 0.21 (11)
nonregen	4.74 ± 0.22 (24)	0.88 ± 0.07 (24)	0.52 ± 0.04 (24)	0.04^{a} ± 0.01 (24)	3.31 ± 0.18 (24)
regen	5.70 ± 0.11 (24)	1.10 ± 0.08 (24)	0.70 ± 0.07 (24)	0.04^{a} ± 0.01 (24)	3.86 ± 0.20 (24)
Stomach					
initial	1.64^{b} ± 0.12 (11)	0.41^{b} ± 0.05 (11)	0.68^{b} ± 0.05 (11)	0.05^{b} ± 0.01 (11)	0.50^{b} ± 0.04 (11)
nonregen	1.17^{a} ± 0.15 (18)	0.28^{a} ± 0.03 (24)	0.53^{a} ± 0.09 (24)	0.03^{a} ± 0.01 (18)	0.24^{a} ± 0.03 (18)
regen	1.12^{a} ± 0.06 (23)	0.26^{a} ± 0.02 (24)	0.55^{ab} ± 0.04 (24)	0.03^{a} ± 0.01 (23)	0.26^{a} ± 0.03 (23)

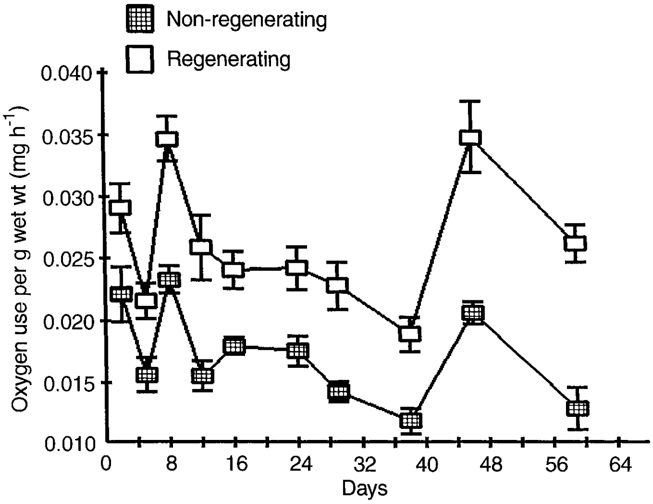

Fig. 3 *Ophiocoma echinata* fed every 2 wk (Experiment 2). Respiration rates per gram wet weight (mg h^{-1} ± SE). Comparison of non-regenerating and regenerating individuals ($N = 9$)

ajei (Sköld and Gunnarsson 1996) and *Ophiocoma echinata* (Pomory 1997). Since this did not occur in *O. echinata* in Experiment 1 of the present study, which took place during the time of the extended breeding season for this species (Mladenov 1983), storage must have been taking precedence over gonad production.

The regenerating group from Experiment 1 showed a decrease in gonad material, which may have been resorbed and transferred to regeneration or maintenance. This implies that the regeneration of three arms was enough to cause an increase in energy demand slightly exceeding the maintenance ration provided by the weekly feeding. It also demonstrates that at low food levels regeneration has priority over gonad maintenance This may be beneficial strategy if increased food-gathering ability leads to increased gonad production or survival in the long run, even though there is a short-term loss.

In Experiment 2, both non-regenerating and regenerating groups showed a decrease in gonad and stomach compared to initial individuals, while the mass of the disk and intact arms stayed the same. Feeding every 2 wk obviously resulted in a food level below the maintenance ration.

Based on the relative changes in the non-regenerating group compared to the initial group within the two experiments (gaining organic material in Experiment 1 on a ration of 0.27 kJ d^{-1}, and losing organic material in Experiment 2 on a ration of 0.135 kJ d^{-1}), the maintenance ration is estimated to be 0.172 kJ d^{-1}. On the maintenance ration, an organism should not gain or lose organic material relative to starting conditions.

Although the two experiments were not run at the same time, we believe the estimate of the maintenance ration is valid for the following reasons: (1) The time span of each experiment was within the extended reproductive season. This is supported by the fact that the gonad mass of the initial groups (which correlates with ripeness: Mladenov 1983), was similar (Figs. 1 and 2). (2) The experiments were conducted under laboratory conditions, so temperature and salinity were constant and similar for both experiments during the time any changes were taking place. Other differences in energy content between the initial groups were mainly an artifact of size. For example, based on kJ g^{-1}, the organic content of the stomach was 20.3 ± 0.7 (Experiment 1) and 22.4 ± 0.5 (Experiment 2). Slight differences in the initial groups would not dramatically affect the estimate because it is derived from the relative change within each experiment not the absolute difference between the two experiments (i.e. if one starts with X units of stored energy and receives a maintenance level diet, one should finish with X units of stored energy).

Absorption efficiency in echinoderms varies greatly among species and with food type, but using an estimate of 50% based on other echinoderms that feed on detritus (Lawrence 1987), the energy available for maintenance would be 0.09 kJ d^{-1}. The amount of energy used by the non-regenerating group, estimated from respiration rates, was 0.07 kJ d^{-1}. The estimate of the maintenance ration represents a lower limit as temperature, activity level and food level were all relatively low during the experiments.

Ophiocoma echinata relies on reserves in the stomach rather than in the arms. Amphiurids (such as *Microphiopholis gracillima*) often autotomize the disk, thereby completely losing the gonads and stomach and necessitating the use of reserves in the arms. Amphiurid populations typically have higher frequencies and faster rates of arm regeneration in (e.g. Bowmer and Keegan 1983; Stancyk et al. 1994), and a greater propensity to regenerate the disk (e.g. Dobson et al. 1991; Stancyk et al. 1994) compared to *O. echinata* (Sullivan 1988; Pomory 1997). This suggests that amphiurids may be better adapted for regeneration. Aronson (1987, 1991) argued that ophiuroids have become more cryptic over evolutionary time in response to increased predation. Even within the class Ophiuroidea, known for its powers of regeneration (Wilkie 1978; Emson and Wilkie 1980), differences exist in the process among groups. We suggest the habitat/predator environments of the groups may not only influence behavioral or habitat changes, as Aronson proposed but physiological processes as well.

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