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Arm regeneration in the field in *Ophiocoma echinata* (Echinodermata: Ophiuroidea): effects on body composition and its potential role in a reef food web

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Abstract Eighteen percent and 47% of two populations of *Ophiocoma echinata* in the Florida Keys were undergoing regeneration. An individual would take approximately 720 days to completely regenerate three arms. Regeneration of three arms had a greater effect on gonad production in females than in males, and reduced storage material in the stomach of both. Regeneration in *O. echinata* was estimated to be 0.07 kJ m^{-2} day^{-1}, which could provide the equivalent of 0.07% of primary production on a reef to higher trophic levels per day.

Introduction

Disturbance to individual organisms, defined as loss of biomass, may be lethal or sublethal. Sublethal disturbance is caused by physical perturbations (e.g. Ball et al. 1967; Woodley 1980; Tilmant et al. 1994), inter- and intraspecific fighting (e.g. Berzins and Caldwell 1983; Harris 1989; Smith and Hines 1991), and partial predation (e.g. Trevallion 1971; Vlas 1979a; Peterson and Quammen 1982; Turner et al. 1982; Bowmer and Keegan 1983; Clavier 1984; Woodin 1984; Bergman et al. 1988).

In the case of sublethal predation, biomass is transferred to the next trophic level without the death of the prey. The immediate advantage to the prey of being able to regenerate a lost structure is the ability to escape lethal predation, with the long-term advantage of restoring functionality of missing parts and the continued ability to contribute to the reproductive population. The ability to regenerate varies among animals. Examples include regeneration of complete individuals or colonies of protozoans, turbellarians, poriferans, cnidarians and ascidians; body regeneration in annelids and nemerteans; regeneration of siphons, arms or the mantle in mollusks; regeneration of limbs in arthropods; regeneration of arms, spines or internal structures in echinoderms; and regeneration of legs, tails or fins in amphibians, reptiles and fish (Morgan 1901; Swan 1966; Goss 1969; McVean 1975; Emson and Wilkie 1980; Bullière and Bullière 1985; Skinner 1985; Hay 1986; Sugino and Nakauchi 1987; Arnold 1988; Lakes and Mücke 1989; Formanowicz 1990; Wilbur and Semlitsch 1990; Hill et al. 1993; Jokiel and Bigger 1994; Dinsmore 1995; Zajac 1995).

The ability of an organism to recover following injury is essential to its future survival and reproductive success. Recovery requires the allocation of energy to regeneration, which is an addition to the normal energetic processes of maintenance, growth, and reproduction. Regeneration has the potential to affect fitness components by using energy that would otherwise be devoted to them.

Effects of regeneration are not universal across taxa. Smith (1990) suggested autotomy of a few pereopods in the blue crab *Callinectes sapidus* probably had little impact, but as the number increased it could become important. Hill et al. (1982) found regeneration reduced reproduction in one species of the polychaete *Capitella*, but not another. Few studies have demonstrated a reduction in reproduction and the most frequently cited ones are mainly from vertebrates (e.g. Congdon et al. 1974; Maiorana 1977), which have relatively poor regeneration ability. Would a species with high regeneration ability be affected to the same extent?

Regeneration also provides a renewable resource for higher trophic levels, particularly fish (Trevallion 1971;

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Vlas 1979a, b; Clavier 1984; O'Connor et al. 1986). For example, Trevallion (1971) found that siphons of the clam *Tellina tenuis* were nipped by fish, which caused a decrease in growth of the bivalve.

Echinoderms experience sublethal disturbance and are well known for their ability to regenerate (Emson and Wilkie 1980; Lawrence 1990, 1991). Ophiuroids are a major part of both soft and hard bottom communities (Clark 1976; Singletary 1980; Lewis and Bray 1983; O'Connor et al. 1983; Zimmerman et al. 1988; Aronson 1989; Birkeland 1989; Fujita and Ohta 1990). They lose arms or parts of arms, and in some cases the aboral portion of the disk and viscera, to predation by fish and invertebrates, autotomy from physical or chemical perturbations, and in some cases asexual reproduction (Wilkie 1978; Bowmer and Keegan 1983; Mladenov et al. 1983; Dobson 1985; Duineveld and Noort 1986; Aronson 1987, 1988; Blaber et al. 1987; Mladenov and Emson 1988; Packer et al. 1994; Chao and Tsai 1995). From 20% to almost 100% of ophiuroids in a given area may be regenerating lost parts at any one time (Wilkie 1978; Singletary 1980; Bowmer and Keegan 1983; O'Connor et al. 1986; Aronson 1987; Sides 1987; Clements et al. 1988; Sullivan 1988; Stancyk et al. 1994; Soong et al. 1997).

Although many studies have documented the amount of tissue loss in ophiuroids at a given point in time, relatively few have examined the effects of regeneration in the field over time (Stancyk et al. 1994; Lawrence and Vasquez 1996). As Stancyk et al. (1994) also summarized, ophiuroids have the potential to supply significant amounts of biomass to the next trophic level through regeneration, but have rarely been considered despite being dominant organisms in many marine systems (e.g. Bowmer and Keegan 1983).

The purpose of this study was to answer the following questions using a tropical reef-dwelling ophiuroid as the test subject: (1) Does regeneration reduce reproduction? (2) Are nonreproductive tissues affected by regeneration? (3) Are males affected differently from females during regeneration? (4) What is the rate of regeneration under natural conditions? (5) What is the potential contribution of regeneration to higher trophic levels?

The ophiuroid examined in this study was *Ophiocoma echinata* (Lamarck 1816), which ranges throughout the Caribbean from the southern tip of Florida to the northern coast of South America (Hendler et al. 1995). *O. echinata* is one of the most abundant ophiuroids in the back-reef rubble habitat, and is also found on the reef proper (Lewis and Bray 1983; Sides and Woodley 1985; Sullivan 1988; Hendler et al. 1995).

Materials and methods

The following terms are used throughout this paper. "Regenerating individual" refers to an individual that has any of the five arms undergoing regeneration, as distinguished by a change in the width and color of an arm. "Nonregenerating individual" refers to an individual in which none of the five arms is undergoing regeneration. In the experiments, "disk" refers to the central disk of the ophiuroid with the arms removed at the disk edge, and emptied of the internal contents of the stomach and gonads. "Arms" refer to nonregenerating arms removed from the disk at the disk edge. "Stomach" refers to the stomach isolated from the rest of the disk. "Gonads" refer to the gonads from all ten bursal areas and includes the connective tissue that holds the gonads together. "Regenerating arms" refer to the arm growth following autotomy.

A field census of the number of *Ophiocoma echinata* undergoing regeneration was made at Missouri Key (24° 40.5′N, 81° 14.9′W) and Pigeon Key (24° 42.2′N, 81° 09.3′W), Florida, on 20 February 1994. Both sites consisted of rock rubble scattered among hard-pan (sponges, soft corals and small hard corals on a limestone base) and patches of seagrass in water <2 m deep. Rubble at the two locations was searched haphazardly and the first 100 individuals at both locations were scored as nonregenerating or regenerating.

Two experiments were conducted in the near-shore waters of Pigeon Key, Florida. In experiment 1, rock piles were constructed to mark a location in shallow water (1 m) using rubble surrounding Pigeon Key. Forty nonregenerating *O. echinata* were collected from the same area as the rubble and divided equally into nonregenerating and regenerating experimental groups. Each individual in the nonregenerating group had all five arms intact. Each individual in the regenerating group was induced to autotomize three adjacent arms at the disk edge by pinching the arm with a pair of tweezers. Autotomy of three arms allowed for easy identification of individuals and represented what we considered to be a high, but not unnaturally so, level of disturbance, in an attempt to detect effects of regeneration. All individuals were returned to the field near the rock piles. The experiment ran from 18 February to 5 May 1994. In experiment 2, 60 nonregenerating *O. echinata* were collected from the same area and divided equally into nonregenerating and regenerating experimental groups as in the first experiment. The experiment ran from 5 May to 17 July 1994. The increased sample size in the second experiment allowed for evaluation of male versus female differences.

At the end of both experiments, any nonregenerating individual and those regenerating three arms were collected from the rock piles and transported to the laboratory. Regenerating individuals were identified by the location and number of regenerating arms, disk size, and disk markings. In experiment 1, individuals were transported on ice to allow qualitative examination of stomach contents. This rendered the stomach unavailable for further analysis. In experiment 2, individuals were transported live in separate plastic bags to prevent spawning. All individuals were dissected into body components of disk, arms, gonads, stomach (if available), and regenerating arms.

Body components were dried in vacuo over sulfuric acid, weighed, and ground in a Thomas Wiley intermediate mill. Total organic content was obtained for all components by ashing samples (10–100 mg) in a muffle furnace at 500°C for 4 h (Paine 1971). Samples (5–20 mg) for protein analysis were extracted in 1 N sodium hydroxide (5 ml) for 24 h and measured by the method of Lowry et al. (1951). Bovine serum albumin was used as the standard. Samples (10–300 mg) for lipid analysis were extracted using the method of Folch et al. (1957) and weighed. Samples (5–20 mg) for carbohydrate analysis were extracted in 5% trichloroacetic acid (5 ml) in a hot water bath at 60°C for 2 h and measured by the method of Dubois et al. (1956). Oyster glycogen was used as the standard. Insoluble matter was calculated by subtraction. The energetic conversion factors used were: protein and insoluble matter = 4.2 kcal g^{-1}; carbohydrate = 4.1 kcal g^{-1}; lipid = 9.3 kcal g^{-1} and kJ = 4.184 kJ $kcal^{-1}$ (Kersting 1972; Morowitz 1978; Blaxter 1989).

One-way ANOVA was used to compare groups (Sokal and Rohlf 1995). Since there was a large number of comparisons for the composition data, we considered the five constituents (organic matter, protein, lipid, carbohydrate, and insoluble matter) as a set of comparisons and used $P \leq 0.01$ as the level of significance to adjust for multiplicity. On other tests $P \leq 0.05$ was used as the level of significance. A T^2 test was used to compare four constituents (protein, lipid, carbohydrate, insoluble) of the gonads in the first experiment when a trend was seen in the data, but individual comparisons were not significantly different (Tatsuoka and Lohnes 1988). Normality was checked with an Anderson-Darling test (D'Agostino 1986). Variance homogeneity was checked with Bartlett's test (Sokal and Rohlf 1995). Rank transformation was used on data failing normality or variance homogeneity tests (Conover and Iman 1981).

Results

Forty-seven percent of the individuals at Missouri Key and 18% of the individuals at Pigeon Key were regenerating arms. The stomach contents of the individuals from the first experiment contained fragments of red and green algae, various crustacean parts, foraminiferans, and bottom sediment. The bottom sediment made up the largest part of the stomach contents in every individual.

Experiment 1 composition, winter/spring 1994

No significant difference in dry weights was found between the groups (nonregenerating, regenerating) for the disk, arms on a per arm basis, or gonads (Fig. 1). The dry weight of the three regenerating arms was, collectively, 246 ± 12 mg SE.

No significant difference in the composition of the disk, arms on a per arm basis or gonads was found between groups on either a relative (% dry weight, Table 1) or absolute (kJ, Table 2) basis for any constituent. Although no significant difference was found between groups for the gonads, in each case the regenerating group was lower on an absolute basis for protein, lipid, carbohydrate, and insoluble matter. A T^2 test, which takes all four constituents into consideration simultaneously, found a significant difference ($P = 0.01$) between the groups. The percent dry weight and mass of the organic matter of the three regenerating arms was 20.8 ± 0.3% SE and 52.3 ± 2.8 mg SE, respectively.

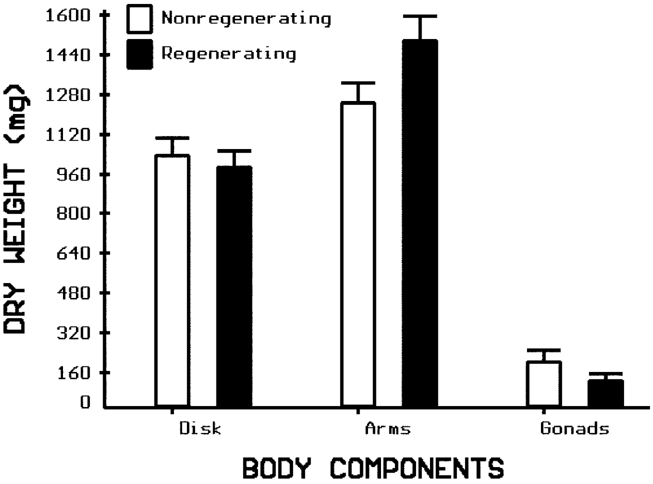

Fig. 1 *Ophiocoma echinata*: a comparison of the dry weights of the disk, arms and gonads (mg ± SE) of nonregenerating and regenerating individuals from the winter season; values for arms are on a per arm basis

Experiment 2 composition, summer 1994

No significant difference in dry weight was found between the groups (nonregenerating, regenerating) within females, males or combined sexes for the disk or arms on a per arm basis (Fig. 2A). The regenerating group had a significantly lower amount of gonad than the nonregenerating group within females and combined sexes; however, no significant difference was found between groups within males (Fig. 2B). Regenerating females had a significantly ($P = 0.0004$) lower amount of gonad than regenerating males. The regenerating group had significantly lower amounts of stomach than the nonregenerating group within females, males and combined sexes (Fig. 2B). The dry weight of the three regenerating arms collectively was 405 ± 37 mg SE for females, 493 ± 56 mg SE for males and 461 ± 39 mg SE for combined sexes.

No significant difference in the composition of the disk or of the arms on a per arm basis was found between groups within females, males or combined sexes on either a relative (% dry weight, Table 3) or absolute (kJ, Table 4) basis for any constituent. The relative composition of the regenerating arms was similar to the whole arms of the regenerating group (Table 3).

Energy calculations for organic matter, and all calculations for carbohydrate and insoluble matter could not be carried out on gonads for the regenerating group because of the inadequate amounts of tissue. The gonads of the regenerating group were significantly lower than those of the nonregenerating group within females on a relative basis (Table 3) for organic matter and lipid; and on an absolute basis (Table 4) for protein and lipid. No significant difference in the composition of the gonads was found between groups within males on either a relative or absolute basis for any constituent. No significant difference in the composition of the gonads was found between groups within combined sexes on a relative basis for any constituent, nor on an absolute basis for protein. The gonads of the regenerating group were significantly lower than those of the nonregenerating group within combined sexes on an absolute basis for lipid.

No significant difference in the composition of the stomach was found between groups within females, males or combined sexes on a relative basis (Table 3) for any constituent. On an absolute basis (Table 4), the stomach of the regenerating group was significantly lower than that of the nonregenerating group within females, males and combined sexes for organic and insoluble matter; and within combined sexes for protein, lipid and carbohydrate.

Table 1 *Ophiocoma echinata*: a comparison of the relative composition (% dry weight ± SE) of nonregenerating and regenerating individuals from the winter season; *NR* nonregenerating individuals; *R* regenerating individuals

Component (*n*)	Organic matter %	Protein %	Lipid %	Carbohydrate %	Insoluble matter %
Disk					
NR(16)	31.5(±0.6)	9.3(±0.6)	1.38(±0.03)	0.44(±0.02)	20.4(±0.8)
R(10)	31.9(±0.8)	8.8(±0.8)	1.45(±0.06)	0.39(±0.01)	21.3(±1.2)
Arms					
NR(16)	22.9(±0.5)	6.7(±0.3)	0.90(±0.03)	0.25(±0.01)	15.1(±0.6)
R(10)	24.3(±0.5)	7.1(±0.5)	0.98(±0.06)	0.26(±0.01)	15.9(±0.8)
Gonads					
NR(16)	89.7(±0.4)	46.4(±0.5)	15.1(±1.5)	2.3(±0.2)	25.9(±1.5)
R(10)	89.6(±0.5)	49.3(±0.7)	12.9(±1.8)	3.0(±0.3)	24.4(±1.6)

Table 2 *Ophiocoma echinata*: a comparison of the absolute composition (kJ ± SE) of nonregenerating and regenerating individuals from the winter season. Abbreviations as in Table 1; values for arms are on a per arm basis

Component (*n*)	Organic matter kJ	Protein kJ	Lipid kJ	Carbohydrate kJ	Insoluble matter kJ
Disk					
NR(16)	6.42(±0.37)	1.81(±0.15)	0.56(±0.04)	0.08(±0.01)	3.97(±0.26)
R(10)	6.23(±0.44)	1.61(±0.15)	0.55(±0.03)	0.07(±0.01)	4.00(±0.39)
Arms					
NR(16)	5.58(±0.35)	1.59(±0.14)	0.44(±0.03)	0.05(±0.01)	3.50(±0.22)
R(10)	6.14(±0.48)	2.02(±0.20)	0.57(±0.04)	0.07(±0.01)	3.48(±0.36)
Gonads					
NR(16)	3.48(±0.70)	1.28(±0.31)	1.11(±0.25)	0.08(±0.01)	1.01(±0.18)
R(10)	2.43(±0.30)	1.15(±0.13)	0.66(±0.14)	0.06(±0.01)	0.56(±0.06)

Regeneration rate

On a per arm per day basis during winter (experiment 1), 0.95 mg DW (=0.2 mg AFDW=0.004 kJ) was regenerated, or about 0.08% of an intact arm, leading to complete regeneration in 1,158 days. On a per arm per day basis during summer (experiment 2), 2.11 mg DW (=0.47 mg AFDW=0.009 kJ) was regenerated, or about 0.19% of an intact arm, leading to complete regeneration in 521 days. To estimate yearly regeneration, we assume 6 months of summer rates and 6 months of winter rates. In this case on a per arm per day basis, 1.53 mg DW (=0.34 mg AFDW=0.007 kJ) would be regenerated, or about 0.14% of an intact arm, leading to complete regeneration in 720 days.

Discussion and conclusions

Effects of regeneration

The percent of the population of *Ophiocoma echinata* undergoing regeneration in the field is within the range reported for this species from other parts of the Caribbean (Sides 1987; Sullivan 1988), and in the middle to low part of the range reported for other species (Emson and Wilkie 1980; Singletary 1980; Bowmer and Keegan 1983; Duineveld and Noort 1986; Aronson 1987, 1989, 1991; Sides 1987; Clements et al. 1994; Stancyk et al. 1994). A larger number of individuals at the Missouri Key site were undergoing regeneration than at the Pigeon Key site. This was probably a function of cover, as the rubble at the Pigeon Key site was more densely packed, offering better protection from predators.

The first experiment took place during the winter season, whereas the second took place at the start of summer. No significant difference was found between the regenerating and nonregenerating groups for any individual constituent or body component during the winter months. A trend was seen for the gonads that was not significant for any individual constituent, but was significant when the constituents were considered together. The standard error was three to five times higher in winter than in summer, which is why the trends in individual constituents were not significant.

The higher standard error in winter relative to summer indicates that the population was not as synchronized in the timing of gonad development in winter, but the high amount of gonads indicates that at least some were well developed. The pattern of asynchronous gonad development throughout the year with a convergence during summer is the pattern Mladenov (1983a) found for this species in Barbados. Selvakumaraswamy and Byrne (1995) suggested that asynchronous spawning in winter may be a feature of tropical ophiuroids, whereas temperate species are synchronized by more extreme seasonal changes. This points out one of the difficulties in interpreting field results in tropical species, such as *O. echinata*: lack of differences in asynchronous individuals may be due to large variation in the population.

The summer experiment produced the most striking results. Because of the number of individuals recovered and the relatively similar proportions of males to females in each group, analyses based on the sex of the

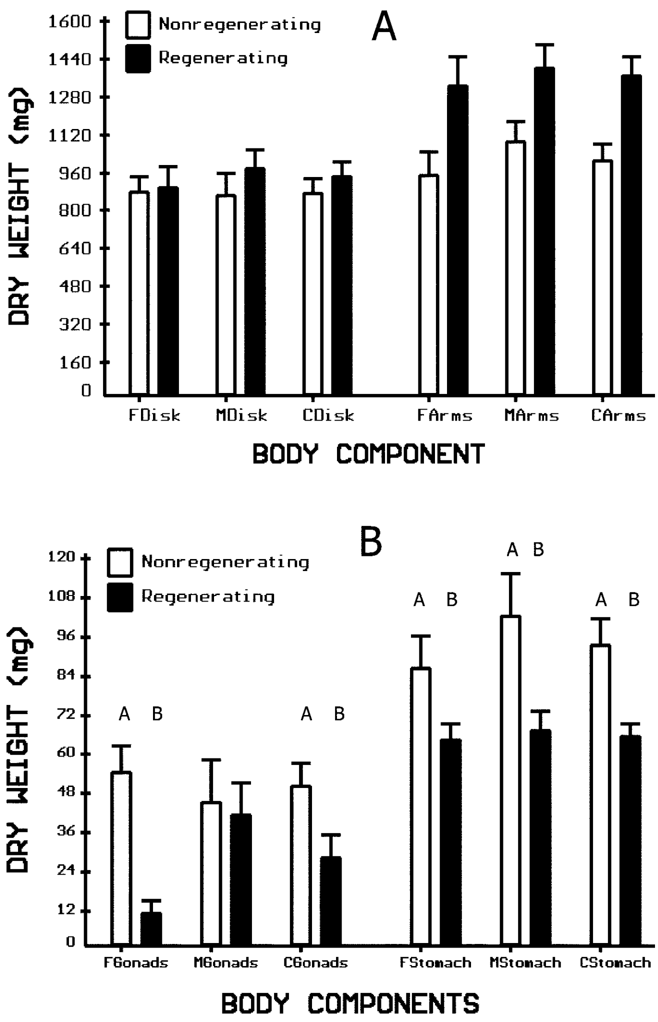

Fig. 2A, B *Ophiocoma echinata*: a comparison of the dry weights (mg ± SE) of nonregenerating and regenerating individuals from the summer season. **A** Disk and arms. Values for arms are on a per arm basis. **B** Gonads and stomach; different letters above bars indicate significant differences; *F* females, *M* males, *C* combined sexes

individuals in each group were carried out. No change occurred in the disk or arms between regenerating and nonregenerating groups for either sex, or when sexes were combined.

The regenerating group contained less stomach, based on absolute amount for the combined sexes, but the percent composition was similar indicating a proportional use of constituents. Males and females both showed similar patterns. The fact that no change occurred in the disk and arms, but did occur in the stomach, indicates the stomach is probably the first source for energy reallocation or storage. A similar pattern of stomach use was found for this species in laboratory experiments (Pomory and Lawrence 1999). During the summer the ophiuroids were more synchronized in their gametogenesis leading to the summer spawning season, and the additional regeneration activity may have been enough to cause a change in the stomach that was not seen in the winter.

Regenerating females showed a significant decrease in the amount of gonad compared with nonregenerating females. No difference was found between the groups for males. Although the absolute amount of gonad in regenerating females decreased four- to fivefold, only a slight change in composition occurred (4–5% for lipid and protein), indicating that the composition of gametes remained fairly constant, with fewer being produced.

In the gonads of females, lipid, protein, and the insoluble fractions contained similar amounts of energy. The contribution to total energy by carbohydrate ranged from two to ten times lower than other constituents. In males, the lipid fraction contained about half the energy of protein, while the other constituents were similar to those in females. The difference between males and females is related to greater lipid stocking of the eggs than sperm (Byrne 1994). Similar patterns are seen in many marine invertebrates (Lawrence 1976).

The gonads of nonregenerating females were similar to those of nonregenerating males in total energy content, indicating that the effect of regeneration was not due to differences in energy of the final product. Production of gametes requires energy for two purposes: one is the amount contained in the gonad, and the other is the amount used in the metabolic process of creating the gonad. Since the final energy content was similar, the process of making gonads appears to be energetically more expensive in females than males. Another factor that may play a role is composition of the gonads, specifically the higher lipid content of eggs. Lipid may be harder to acquire from natural sources of detritus. The decrease in the stomach, which was 25% lipid, would supply not only energy, but also raw material for building eggs.

The difference in gonads could have been from resorption of material rather than lower production, but this is not the case in this particular instance. The two experiments ran back to back, so that the nonregenerating individuals at the end of the first experiment served as an initial sample for the second experiment. After accounting for a slight difference in disk size between the experiments, the gonads of the nonregenerating group in the second experiment were about one-third the size of the nonregenerating initial group. This suggests that a spawning event took place near the start of the second experiment, which would mean the individuals were in a state of building the gonads. This also raises the possibility that *O. echinata* can spawn more than once in a year.

The amount of arm regeneration was affected by season. Regeneration in winter was about half that of summer, probably due to temperature differences, which were about 12–15°C. The composition of regenerating arms was similar to intact arms indicating that differences in composition in the early stages of regeneration found in laboratory experiments (Pomory and Lawrence 1999) do not last as regeneration continues. A nonsignificant tendency for heavier arms on a per arm basis in

Table 3 *Ophiocoma echinata*: a comparison of the relative composition (% dry weight ± SE) of nonregenerating and regenerating individuals from the summer season. *FNR* female, nonregenerating individuals; *FR* female, regenerating individuals; *MNR* male, nonregenerating individuals; *MR* male, regenerating individuals; *CNR* combined sexes, nonregenerating individuals; *CR* combined sexes, regenerating individuals. Groups with different letters indicate significant differences at $P \le 0.01$

Component (*n*)	Organic matter %	Protein %	Lipid %	Carbohydrate %	Insoluble matter %
Disk					
FNR(14)	33.1(±1.1)	10.0(±0.7)	1.53(±0.04)	0.51(±0.02)	21.1(±1.6)
FR(9)	30.3(±1.2)	7.5(±0.6)	1.41(±0.05)	0.44(±0.02)	20.9(±1.4)
MNR(11)	31.5(±1.1)	8.6(±0.6)	1.46(±0.05)	0.44(±0.02)	21.6(±0.8)
MR(12)	30.9(±1.1)	9.3(±0.7)	1.35(±0.06)	0.47(±0.02)	19.8(±1.3)
CNR(25)	32.7(±0.8)	9.4(±0.5)	1.50(±0.03)	0.48(±0.02)	21.3(±0.9)
CR(21)	30.6(±0.8)	8.5(±0.5)	1.37(±0.04)	0.46(±0.02)	20.3(±0.9)
Arms					
FNR(14)	22.5(±0.7)	6.2(±0.4)	1.04(±0.03)	0.30(±0.04)	15.0(±0.6)
FR(9)	22.0(±0.8)	5.4(±0.5)	0.98(±0.07)	0.22(±0.03)	15.4(±0.7)
MNR(11)	22.5(±0.5)	5.5(±0.6)	0.99(±0.04)	0.27(±0.03)	15.8(±0.7)
MR(12)	22.9(±0.5)	5.7(±0.6)	1.07(±0.11)	0.28(±0.04)	15.8(±0.5)
CNR(25)	22.6(±0.5)	5.9(±0.3)	1.02(±0.02)	0.28(±0.02)	15.4(±0.5)
CR(21)	22.5(±0.4)	5.6(±0.4)	1.03(±0.07)	0.25(±0.03)	15.6(±0.6)
Regenerating arms					
FR(7)	22.9(±0.4)	5.6(±0.4)	1.5(±0.1)	0.39(±0.05)	15.4(±0.6)
MR(12)	22.3(±0.4)	5.9(±0.3)	2.1(±0.3)	0.33(±0.03)	13.9(±0.6)
CR(19)	22.5(±0.3)	5.8(±0.2)	1.9(±0.2)	0.35(±0.02)	14.5(±0.5)
Gonads					
FNR(14)	92.2(±0.3)**B**	42.4(±1.0)	20.3(±0.8)**B**	2.5(±0.1)	27.0(±1.4)
FR(6)	87.3(±1.4)**A**	37.1(±1.7)	15.8(±0.9)**A**	–	–
MNR(10)	87.8(±0.5)	36.1(±1.5)	10.2(±0.7)	3.1(±0.2)	38.4(±2.4)
MR(12)	88.5(±0.5)	38.8(±0.8)	11.0(±1.0)	–	–
CNR(24)	89.6(±0.5)	39.8(±1.1)	16.1(±1.2)	2.8(±0.1)	30.9(±1.7)
CR(18)	88.1(±0.6)	38.2(±0.8)	12.6(±0.9)	–	–
Stomach					
FNR(14)	94.2(±0.3)	27.3(±1.2)	25.0(±1.6)	3.7(±0.2)	38.2(±1.7)
FR(9)	93.7(±0.3)	29.1(±1.6)	25.2(±1.8)	3.9(±0.3)	35.5(±1.6)
MNR(11)	93.3(±0.2)	25.6(±1.6)	27.1(±2.1)	3.3(±0.2)	37.3(±1.7)
MR(12)	92.8(±0.4)	27.5(±1.1)	25.7(±2.4)	3.7(±0.3)	35.9(±2.8)
CNR(25)	93.9(±0.2)	26.6(±0.9)	25.9(±1.3)	3.6(±0.1)	37.8(±1.2)
CR(21)	93.2(±0.3)	28.2(±0.9)	25.5(±1.5)	3.8(±0.2)	35.7(±1.6)

regenerating individuals can be seen in the data. Structural enhancement of the remaining arms may be a response to arm loss.

Most information from the field on the effects of regeneration in ophiuroids is for soft-bottom, burrowing ophiuroids in the family Amphiuridae, which can autotomize arms and disk (Bourgoin and Guillou 1994; Clements et al. 1994; Stancyk et al. 1994). *O. echinata* is relatively slow at regenerating arms, compared with maximum rates for amphiurids. During the summer, *Microphiopholis gracillima* regenerates five times faster (Stancyk et al. 1994) than *O. echinata*. This probably results from the greater size and structural robustness of *O. echinata*.

Regeneration stopped completely in winter in *M. gracillima* (Stancyk et al. 1994), while it slowed down in *O. echinata*. Seasonality seems to play a role in energy allocation even in a tropical species, which typically encounters low seasonal fluctuations compared with temperate species. Based on estimates of the longevity, the time it takes to reach asymptotic size, and regeneration rates (Turner 1974; O'Connor et al. 1983, 1986; Munday and Keegan 1992; Dahm 1993; Munday 1993; Sköld et al. 1994; Stancyk et al. 1994; Josefson 1995; present study), ophiuroids have the ability to regenerate their total asymptotic size biomass multiple times in their lifetime.

Sullivan (1988) calculated that *O. echinata* regenerating one arm would take 315 days to regenerate completely. Although the conditions of Sullivan's experiments were different from ours in several ways, it appears that, as the number of arms lost increases, the rate of tissue regeneration per arm decreases, but the total amount of tissue regenerated for all arms increases. This pattern has been found for a number of species (Salzwedel 1974; Mladenov 1983b; Fielman et al. 1991; Clements et al. 1994). The importance of the pattern is the change in the rate of regeneration. Increasing the number of arms lost from one (Sullivan 1988) to three (present study) approximately doubled, not tripled, the estimated amount of time to completely regenerate arms. This is evidence that the physiology is changing to accommodate varying levels of tissue loss so that different magnitudes of arm loss could have nonlinear effects on fitness.

Trophic transfers

An organism that regenerates may contribute energy to the next trophic level multiple times, without dying, which would not necessarily be measured by single point estimates of production. Net primary production on coral reefs is about 100 kJ m^{-2} day^{-1} (1,800–2,200 g m^{-2}

Table 4 *Ophiocoma echinata*: a comparison of the absolute composition (kJ ± SE) of non-regenerating and regenerating individuals from the summer season. Abbreviations as in Table 3. Values for arms and regenerating arms are on a per arm basis. Groups with different letters indicate significant differences at $P \le 0.01$

Component (*n*)	Organic matter kJ	Protein kJ	Lipid kJ	Carbohydrate kJ	Insoluble matter kJ
Disk					
FNR(14)	5.73(±0.46)	1.65(±0.14)	0.51(±0.03)	0.08(±0.01)	3.49(±0.35)
FR(9)	5.24(±0.34)	1.27(±0.17)	0.49(±0.05)	0.07(±0.01)	3.41(±0.24)
MNR(11)	5.48(±0.59)	1.39(±0.15)	0.49(±0.05)	0.07(±0.01)	3.53(±0.41)
MR(12)	5.81(±0.30)	1.72(±0.18)	0.51(±0.03)	0.08(±0.01)	3.50(±0.20)
CNR(25)	5.62(±0.36)	1.54(±0.10)	0.50(±0.03)	0.07(±0.01)	3.51(±0.26)
CR(21)	5.56(±0.23)	1.53(±0.13)	0.50(±0.03)	0.07(±0.01)	3.46(±0.15)
Arms					
FNR(14)	4.18(±0.38)	1.13(±0.13)	0.38(±0.04)	0.05(±0.01)	2.62(±0.24)
FR(9)	5.67(±0.39)	1.32(±0.16)	0.49(±0.04)	0.05(±0.01)	3.81(±0.32)
MNR(11)	4.85(±0.37)	1.15(±0.17)	0.42(±0.03)	0.05(±0.01)	3.23(±0.24)
MR(12)	6.13(±0.35)	1.47(±0.18)	0.57(±0.04)	0.07(±0.01)	4.02(±0.32)
CNR(25)	4.48(±0.27)	1.14(±0.10)	0.40(±0.02)	0.05(±0.01)	2.89(±0.18)
CR(21)	5.93(±0.26)	1.41(±0.10)	0.54(±0.03)	0.06(±0.01)	3.92(±0.23)
Regenerating arms					
FR(7)	0.62(±0.05)	0.14(±0.02)	0.08(±0.01)	0.010(±0.003)	0.39(±0.03)
MR(12)	0.75(±0.08)	0.18(±0.02)	0.13(±0.02)	0.010(±0.003)	0.44(±0.06)
CR(19)	0.71(±0.05)	0.17(±0.6)	0.11(±0.01)	0.010(±0.003)	0.42(±0.04)
Gonads					
FNR(14)	1.17(±0.16)	0.43(±0.06)**B**	0.42(±0.06)**B**	0.03(±0.01)	0.29(±0.04)
FR(6)	–	0.10(±0.03)**A**	0.08(±0.02)**A**	–	–
MNR(10)	1.03(±0.25)	0.33(±0.08)	0.19(±0.05)	0.04(±0.01)	0.47(±0.10)
MR(12)	–	0.32(±0.07)	0.17(±0.03)	–	–
CNR(24)	1.09(±0.13)	0.39(±0.05)	0.32(±0.05)**B**	0.03(±0.01)	0.35(±0.05)
CR(18)	–	0.25(±0.05)	0.14(±0.02)**A**	–	–
Stomach					
FNR(14)	1.96(±0.12)**B**	0.45(±0.05)	0.84(±0.11)	0.06(±0.01)	0.61(±0.06)**B**
FR(9)	1.44(±0.11)**A**	0.34(±0.02)	0.64(±0.08)	0.04(±0.01)	0.42(±0.03)**A**
MNR(11)	2.38(±0.31)**B**	0.48(±0.05)	1.14(±0.20)	0.06(±0.01)	0.70(±0.07)**B**
MR(12)	1.54(±0.15)**A**	0.37(±0.04)	0.70(±0.09)	0.05(±0.01)	0.42(±0.04)**A**
CNR(25)	2.14(±0.19)**B**	0.46(±0.03)**B**	0.97(±0.11)**B**	0.06(±0.01)**B**	0.65(±0.04)**B**
CR(21)	1.49(±0.09)**A**	0.36(±0.02)**A**	0.67(±0.06)**A**	0.04(±0.01)**A**	0.42(±0.03)**A**

year^{-1} × 4.7 kcal g^{-1} × 4.184 kJ kcal^{-1}/365 days year^{-1}; Whittaker 1975; Odum 1983; Longhurst and Pauly 1987). *O. echinata* regenerating three arms produced 0.021 kJ ind^{-1} day^{-1} (6-month-summer:6-month-winter average).

Using a medium density of 10 ind m^{-2} and 33% for the level of regeneration in the population (Sides 1987; Sullivan 1988; present study), this is equivalent to 0.07 kJ m^{-2} day^{-1}. Taking Sullivan's (1988) growth rate and our energetic values for the arms, *O. echinata* regenerating one arm would produce 0.05 kJ m^{-2} day^{-1}. Therefore, regeneration could contribute the equivalent of 0.05–0.07% of net primary production on a reef to higher trophic levels on a renewable basis from just this species.

The two main pathways for energy flow in a reef system are the primary production pathway and the detritus pathway (Newell and Field 1983; Wetzel 1984). Regeneration in *O. echinata* forms a link between the two. Material entering the detritus pathway is turned back into material used by secondary and tertiary consumers without eliminating the linking organism. The regenerated material–predator link resembles the herbivore–plant link more closely than the traditional predator–prey paradigm of complete consumption. Other examples from the coral-reef habitat include partial predation by fish, gastropods or asteroids followed by regeneration in hard corals (Sammarco 1996; Cumming 1999), soft corals (Harvell and Suchanek 1987), sponges (Hoppe 1988; Dunlap and Pawlik 1998), bryozoans (Palumbi and Jackson 1982; Todd and Havenhand 1989) and crinoids (Meyer 1985). Given the number of species of ophiuroids, crinoids, holothuroids, asteroids, poriferans, bryozoans, cnidarians, polychaetes and crustaceans that are common on coral reefs and that have the ability to regenerate, regeneration could represent a significant amount of energy flow through the coral reef system.

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